

Systematics of the *Bufo Valliceps*  
Group (Anura: Bufonidae) of  
Middle America

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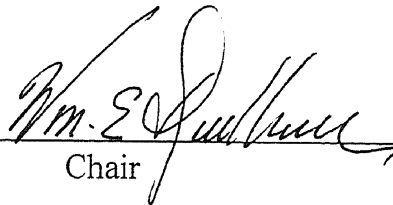
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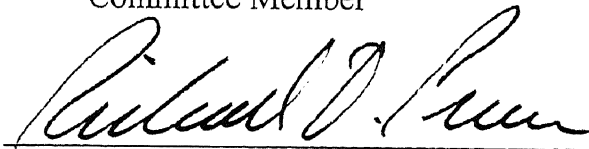
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## ABSTRACT

A phylogenetic analysis of morphological characters revealed that the species content of the *Bufo valliceps* group is limited to eight species (two of them new) occurring between the southern United States and Costa Rica. Several Middle American species usually associated with this group are shown to be closely related, but outside of the *Bufo valliceps* group. The monotypic genus *Crepidophryne* is placed in the synonymy of *Bufo*. The taxon *Bufo valliceps macrocristatus* is recognized as a species distinct from *Bufo valliceps*. Seven species in the *Bufo valliceps* group appear to be allopatric with respect to one another and are restricted to humid primary forest habitat on the lower slopes of the major mountain ranges of southern Mexico, Guatemala, Honduras, and Costa Rica. The species *Bufo valliceps* is widespread in humid lowland habitats from the southern United States to Costa Rica that are either naturally more open (e.g., savanna) or disturbed secondary growth. There are great differences in size, shape, skin texture, and color pattern between northern and southern populations of this species; however, these differences do not vary along a smooth cline among populations from intermediate areas. Nor is there a discrete break among these continuous variables that separate the northern and southern morphs. Variation in *Bufo valliceps* is characterized by a high degree of inter- and intrapopulational variation that cannot be attributed to simple trends associated with latitude, altitude, or climate. *Bufo ibarraii*, long assumed to be in the *Bufo valliceps* group but here shown to lie outside of the group, is reviewed and rediagnosed with respect to other similar Central American toads. The taxon *Bufo valliceps microtis* is placed in the synonymy of *Bufo coccifer*. Diagnostic accounts for all species in the *Bufo valliceps* group and a key to the species are provided.

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## TABLE OF CONTENTS

Abstract.....	ii
Prologue.....	iii
Acknowledgments.....	iv
Table of Contents.....	vi
List of Tables.....	vii
List of Figures.....	viii
Introduction.....	1
Materials and Methods.....	4
I. A new species of toad (Anura: Bufonidae) from the Pacific Highlands of Guatemala and southern Mexico, with comments on the status of <i>Bufo valliceps macrocristatus</i> .....	6
II. A new species of toad (Anura: Bufonidae) from Oaxaca, Mexico, with comments on the status of <i>Bufo cavifrons</i> and <i>Bufo cristatus</i> .....	27
III. Geographic variation in <i>Bufo valliceps</i> (Anura: Bufonidae), a widespread lowland Mesoamerican toad.....	51
IV. A review of the Guatemalan toad <i>Bufo ibarraii</i> (Anura: Bufonidae), with distributional and taxonomic notes on <i>Bufo valliceps</i> and <i>Bufo coccifer</i> .....	68
V. A phylogenetic analysis of the toads (Anura: Bufonidae) of Middle America, with special reference to the <i>Bufo valliceps</i> group.....	85
VI. Diagnoses and a key to the <i>Bufo valliceps</i> group of Middle America.....	109

Literature Cited.....	136
Appendix I: Specimens examined for alpha taxonomic work.....	157
Appendix II: Specimens examined for phylogenetic work.....	168
Appendix III: Tables.....	171
Appendix IV: Figures.....	192



## LIST OF TABLES

1.1	Morphometric variation in <i>Bufo tutelarius</i> .....	171
1.2	Morphometric variation in <i>Bufo macrocristatus</i> .....	173
2.1	Comparison of the major diagnostic features of several toads from the lower montane forests of southern Mexico.....	175
2.2	Morphometric variation in <i>Bufo spiculatus</i> , <i>B. cavifrons</i> , and <i>B. cristatus</i> .....	178
3.1	Results of the first four principal components in a PCA of male <i>Bufo valliceps</i> from throughout their range.....	179
3.2	Results of the first four principal components in a PCA of male <i>Bufo valliceps</i> from the Yucatan Peninsula.....	180
3.3	Standardized coefficients from the canonical variables of the first two canonical axes.....	181
3.4	Jackknifed classification matrix generated by the DFA of <i>Bufo valliceps</i> .....	182
4.1	Morphometric variation in <i>Bufo ibarraii</i> .....	184
5.1	Summary of species content of the <i>Bufo valliceps</i> Group.....	185
5.2	The data matrix for the phylogenetic analysis.....	186
5.3	The species of the <i>Bufo valliceps</i> Group.....	191

## LIST OF FIGURES

Fig. 1.1.— <i>Bufo tutelarius</i> in life.....	193
Fig. 1.2.—Dorsal and lateral aspect of the head of <i>Bufo tutelarius</i> .....	195
Fig. 1.3.—Adult male and female specimens of <i>Bufo tutelarius</i> .....	197
Fig. 1.4.— Distribution of locality records for <i>Bufo tutelarius</i> and <i>Bufo</i> <i>macrocristatus</i> .....	199
Fig. 1.5.—Dorsal and lateral aspect of the head of <i>Bufo macrocristatus</i> .....	201
Fig. 1.6.—Adult male and female specimens of <i>Bufo macrocristatus</i> .....	203
Fig. 2.1—Dorsal and lateral aspect of the head of <i>Bufo spiculatus</i> .....	205
Fig. 2.2.—Color pattern variation among adult <i>Bufo spiculatus</i> .....	207
Fig. 2.3.—Skin texture <i>Bufo spiculatus</i> .....	209
Fig. 2.4.—Relative size and shape of the cranial crests and parotoid glands of six similar species of crested toads in southern Mexico.....	211
Fig. 2.5.—Map showing the distribution of <i>Bufo spiculatus</i> , <i>B. cavifrons</i> , and <i>B.</i> <i>cristatus</i> .....	213
Fig. 2.6.— <i>Bufo cristatus</i> in life.....	215
Fig. 3.1.—Geographic distribution of <i>Bufo valliceps</i> .....	217
Fig. 3.2.—Map showing the location of the 19 samples of <i>Bufo valliceps</i> studied in the range-wide morphometric analyses:.....	219
Fig. 3.3.—Mean scores with 95% confidence intervals on Principal Component I for each sample population of <i>Bufo valliceps</i> .....	221
Fig. 3.4.—Map of the Yucatan Peninsula showing location of nine samples of <i>Bufo</i> <i>valliceps</i> used in the morphometric analysis along the Yucatán precipitation gradient.....	223

Fig. 3.5.—Plot of mean canonical discriminant scores for 19 samples of <i>Bufo</i> <i>valliceps</i> .....	225
Fig. 3.6.—A precise representation of Porter’s (1962) Figure 26 showing the relationship between crest height and elevation at collection site.....	227
Fig. 3.7.—Comparison of typical adult males from Izabal, Guatemala and Coahuila, Mexico.....	229
Fig. 4.1.— <i>Bufo ibarra</i> i in life.....	231
Fig. 4.2.—Adult female and male specimens of <i>Bufo ibarra</i> i.....	233
Fig. 4.3.—Comparison of dorsal skin texture of adult male and female <i>Bufo</i> <i>ibarra</i> i.....	235
Fig. 4.4.—Comparison of adult male <i>Bufo ibarra</i> i and <i>Bufo coccifer</i> collected in southeastern Guatemala.....	237
Fig. 4.5.—Generalized map of Guatemala showing locality records for <i>Bufo coccifer</i> , <i>B. ibarra</i> i, and <i>B. valliceps</i> .....	239
Fig. 4.6.—The holotype of <i>Bufo valliceps</i> var. <i>microtis</i> Werner.....	241
Fig. 5.1—Nomenclature of the dorsal cranial crests used for species in the <i>Bufo</i> <i>valliceps</i> Group.....	243
Fig. 5.2—Nomenclature of the lateral cranial crests used for species in the <i>Bufo</i> <i>valliceps</i> Group.....	245
Fig. 5.3—Dorsal view of the skulls of two species of <i>Bufo</i> illustrating conditions of the frontoparietal-nasal relationship.....	247
Fig. 5.4—Lateral view of the maxilla-quadratojugal articulation in three species of <i>Bufo</i> .....	249
Fig. 5.5—Lateral view of the skulls of two species of <i>Bufo</i> illustrating relationship of the ventral and zygomatic rami of the squamosal.....	251

Fig. 5.6—Shape of the nasal bones in two species of <i>Bufo</i> .....	253
Fig. 5.7—Strict consensus tree of the 70 fundamental trees produced by the analysis.....	255
Fig. 5.8—Strict consensus of trees in Island 1.....	257
Fig. 5.9—Strict consensus of trees in Island 2.....	259
Fig. 5.10—Strict consensus of trees in Island 3.....	261
Fig. 5.11—Strict consensus of trees in Island 4.....	263
Fig. 5.12—Fundamental Tree 70, the only tree in Island 5.....	265

## INTRODUCTION

In 1988 I first travelled to Texas where, with little effort, I discovered my first individual of *Bufo valliceps*. Within a year of this discovery I had the opportunity to conduct field work in eastern Guatemala where, with little effort, I also found *Bufo valliceps*. I left Guatemala with the strong impression that the toads I found there were different from those so common in Texas. Following this hunch, I initiated research into the systematics of the distinctive, and sometimes beautiful, toads of the *Bufo valliceps* group; the results of this research form the present dissertation.

Although many of the relevant species were described in the 19<sup>th</sup> Century, it was not until 1950 when Firschein first attempted to organize the Middle American *Bufo* into species groups. Firschein (1950) proposed a *Bufo valliceps* group (content: *Bufo cristatus* and *B. valliceps*) and a *Bufo cristatus* Group (content: *Bufo cavifrons* and *B. cristatus*); Firschein's efforts did not address the affinities of several other crested toads and are somewhat unclear in that he placed *B. cristatus* simultaneously in two different groups. Subsequent to Firschein's initial efforts, Blair (1956, 1959, 1961) alluded to a *B. valliceps* Group, but did not indicate the full content of the group. Tihen (1962) provided the an explicit proposal of the content of the *B. valliceps* group, broken into "South American" and "Mexican" sections. Blair (1966), took great exception to Tihen's (1962) action and claimed, citing Blair (1959, 1963) to have already proposed the content of the group; Blair (1959, 1963) mentioned the group, but did not provide a full list on included species. Blair (1966) provided a summary of the group whose content somewhat matches that of Tihen's (1962) "Mexican Section." Porter (1962, 1964a) provided a thorough review of the species in Mexico. Table 5.1 summarizes the species proposed to be

members of the *B. valliceps* group in major works on these toads since Firschein's (1950) initial efforts with the group.

These various proposals of the content of the *B. valliceps* group are phenetic assemblages (e.g., Duellman and Schulte, 1992) based on overall similarity and (apparently) geographic proximity of the included species. The historical reality of the majority of species groups within the large genus *Bufo* have never been tested in a phylogenetic context. However, Morrison (1994), in an explicitly phylogenetic analysis, found no evidence to support the monophyly of the *Bufo spinulosus* group of South America and Graybeal (1997) provided evidence support for the monophyly of the *Bufo boreas* group of western North America.

Thus, the membership of the *B. valliceps* group of most authors (Table 5.1; and summarized by Frost, pers. comm.) included some, most, or all of the Middle American toads bearing a conspicuous array of cranial crests. Porter (1962, 1964a) reviewed the Mexican and U.S. populations of the widespread species *B. valliceps* and concluded that the proposed subspecies (*B. valliceps microtis*, *B. valliceps macrocristatus*, and *B. valliceps wilsoni*) were insufficiently distinct to deserve recognition and; he also expanded Firschein's (1950) concept of *B. cavifrons* to encompass three allopatric populations. Nevertheless, Taylor and Smith (1945), Stuart (1954), and Blair (1972) all commented on the extraordinary morphological variation among populations of *B. valliceps*. Against this background of research, and taking advantage of a wealth of material collected recently from remote areas of Middle America, I have reviewed several apparent alpha-level problems among these toads and have assessed the historical reality of the *B. valliceps* group.

The systematics of the species generally referred to the *B. valliceps* group (Frost, pers. comm.) have received little attention since Porter (1962, 1964a) reviewed the Mexican species and speculated about their evolution. Blair (1966) reported the results of hybridization experiments involving members of the group and Blair (1972) reviewed previously published opinions regarding the group. Porter (1970) reviewed the literature pertinent to *B. valliceps* and presented a complete distribution map; Savage, (in Frost, 1985:52) pointed out that some of Porter's (1970) records from Guatemala, El Salvador, Nicaragua, and Costa Rica are based on misidentified specimens of *Bufo luetkeni*. In two studies of the evolution of *Bufo* based on immunological similarities, Maxson et al. (1981) and Maxson (1984) used a few species to represent an assumedly monophyletic *B. valliceps* group.

Although there are certainly several taxonomic problems among the species of *Bufo* in Middle America, I have chosen to address those that seem relevant and critical to the larger task of defining a monophyletic *B. valliceps* group. These were chosen based on my own experiences trying to identify material that I have collected and also material that I so frequently have found misidentified in museum collections. It was also necessary to review geographic variation in the widespread species *B. valliceps* in order to verify Porter's (1970) claim that none of the proposed subspecies of this taxon deserve recognition. As such, I have reviewed in detail the status and distribution of the following species: *B. cavifrons*, *B. cristatus*, *B. ibarrae*, and *B. valliceps*; these reviews have produced the description of four new species and several other taxonomic rearrangements (Mendelson, 1994; Chapters I–IV). A phylogenetic analysis of Middle American bufonids appears in Chapter V and, based on the results of this analysis,

species accounts including diagnoses and a key to the species in the *Bufo valliceps* group are presented in chapter VI.

## MATERIALS AND METHODS

Each chapter in this dissertation has its own section describing the materials and methods relevant to that body of work. However, all of the work in this dissertation was based on observations taken from museum specimens. Acronyms used to represent museums are those suggested by Leviton, et al. (1985) with the addition of MZFC for the Museo de Zoología, Universidad Autónoma de México. Altogether, thousands of specimens were examined during the course of this work; however, only those most carefully studied have been included in the lists of specimens examined. For example, while visiting a museum I would sometimes sort through hundreds of specimens of the abundant and widespread species *Bufo valliceps* in order to find those specimens that appeared to represent other species—these latter specimens, regardless of their final taxonomic referral, were examined closely and are included in the lists of specimens examined.

A major portion of this project involved a revision of the alpha-level systematics of several Middle American toads. It is, therefore, germane to state the species concept that was employed in this work. I have taxonomically identified (as species) populations (or presumed groups of populations) that have the properties of the Evolutionary Species of Wiley (1978, 1981), Frost and Hillis (1990), and Kizirian (1994). Such populations are inferred to be on separate phylogenetic trajectories based on observations of discontinuities of morphological characters. In some cases, such as *Bufo valliceps* (Chapter III) where variation was apparent, such discontinuities were not apparent and no



taxonomic action has been proposed. In other cases (e.g., Chapter I) clearly diagnosable, and allopatric, populations were discovered and recognized as species.

The phylogenetic analysis (Chapter V) included in this work is based on the principals of parsimony analysis (e.g., Hennig, 1966; Kluge and Farris, 1969; Wiley, 1981) and is founded, to a large extent, on Hennig's (1966) Auxiliary Principle stating that similarities apparent among taxa are homologous; morphological convergences are then discovered a posteriori in the context of a phylogenetic analysis including all characters. Although only morphological characters were used in this study, these characters were combined in a single analysis following the Total Evidence approach of Kluge (1989).

**CHAPTER I**  
**A NEW SPECIES OF TOAD (ANURA: BUFONIDAE) FROM**  
**THE PACIFIC HIGHLANDS OF GUATEMALA AND SOUTHERN**  
**MEXICO, WITH COMMENTS ON THE STATUS OF**  
***BUFO VALLICEPS MACROCRISTATUS***

**INTRODUCTION**

The Pacific Highlands of Guatemala and southern Mexico comprise three relatively distinct adjacent mountain ranges: the Chimalapas, the Sierra Madre de Chiapas, and Volcanic Cordillera of Guatemala. The latter two ranges form an effectively unbroken high ridge, with peaks of over 4000 m (Volcán Tacaná), that parallels the Pacific Coast from the Oaxaca/Chiapas, Mexico, border southeastward to the Department of Escuintla, Guatemala—a distance of about 400 km. Volcán Tacaná, at the Mexico/Guatemala border, demarcates the end of the non-volcanic Sierra Madre de Chiapas and the beginning of the Volcanic Cordillera of Guatemala (the Fuegan Area of Campbell and Vannini, 1989). The Chimalapas are isolated to the northwest of the Sierra Madre de Chiapas by a low pass near the Oaxaca/Chiapas border; this area has been referred to as the "Chima Wilderness" by MacDougall (1971), the "Southeastern Oaxacan Highlands" by Campbell (1984), the "Chimalapas" region by the local inhabitants, and printed as the "Sierra de Niltepec" and "Sierra Atravesada" on many maps.

Herpetological collections from the Pacific Highlands are few, especially from the extremely steep slopes on the Pacific versant. Eizi Matuda assembled collections from several areas of the Sierra Madre de Chiapas in the 1940's; these formed the basis for the descriptions of several new species (e.g., *Anolis matudai* Smith). The slopes of Volcán

Tacaná have been relatively well explored (Landy et al., 1966) and collections from there have served as the basis for the description of new species (e.g., *Bufo tacanensis* Smith). The herpetofauna of the Pacific versant of the Volcanic Cordillera of Guatemala has been poorly sampled (reviewed by Campbell and Vannini, 1988). Herpetological collections were made in the western extreme of the Chimalapas (near Zanatepec and La Gloria) by the botanist and explorer T. MacDougall (MacDougall, 1971). These collections were reported upon by Firschein and Smith (1957, wherein *Bufo valliceps macrocristatus* was described) and by Lynch and Smith (1965, 1966). More recent field work in the Chimalapas, most notably by J. A. Campbell and J. D. Johnson, has been concentrated on the slopes of Cerro Baúl. By virtue of these series of specimens from Cerro Baúl, I became aware of the existence of the undescribed species of *Bufo* from the cloud forests of the region that is described herein.

#### MATERIALS AND METHODS

Terminology, measurements, and general format follow that of Mendelson (1994); the format of the diagnoses are slightly modified in order to present additional information. I considered specimens bearing nuptial excrescences and vocal slits to be males and determined sex of other specimens by direct observation of the gonads. I made all measurements with digital calipers and rounded to the nearest 0.1 mm. Foot-webbing formulae follow that of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Snout–vent length is abbreviated as SVL throughout. Museum acronyms are those proposed by Leviton et al. (1985), with the addition of MZFC for the Museo de Zoología, Facultad de Ciencias, Universidad Autónoma de México.

*Bufo tutelarius* sp. nov.

Figs. 1.1–1.3

*Bufo valliceps*—Porter, 1963:fig. 8 [in part; for records plotted in the Pacific highlands of Guatemala and southern Mexico]; Porter, 1970:94.1 [in part; for records plotted on map from the Pacific highlands of Guatemala and southern Mexico]; Johnson, 1989:60 [in part; records from the Sierra Madre de Chiapas, specifically those from the Sierra Madre de Chiapas, Chiapas, Mexico]; Campbell and Vannini, 1989:table 2 [in part; for records indicated from Cuchumatan Subarea of the Huehuetenangan Area; likely based on the UMMZ specimens from Aldea Paraiso, Huehuetenango, Guatemala]; Flores-Villela, 1993:16 [in part; for records representing "Tropical Highlands" of Chiapas, Mexico, and Guatemala].

*Bufo cavifrons*—Johnson, 1989:42,60 [in part; for records from the Sierra Madre de Chiapas, specifically those from near Cerro Baúl, Oaxaca, Mexico].

**Holotype**.—UTA A-13135, an adult male from Colonia Rodolfo Figueroa, 19.0 km NW Rizo de Oro, Oaxaca, Mexico, 1370 m (16° 32'N, 94° 08'W), obtained by J. A. Campbell, D. M. Hillis, and W. W. Lamar on 2 August 1983.

**Paratopotypes**.—Males: KU 200883–84, UTA A-4180, 4181, 13085–87, 13089, 13091–94, 13134, 13137, 13138, 13142–43, 13145; UTEP 4968, 4971. Females: UTA A-4177–4179, 4185, 4889, 13088, 13090, 13132–33, 13136, 13139–41, 13144; UTEP 4969–70, 4972; MZFC 5276–78; CAS 163713. All specimens are from the slopes of Cerro Baúl or the vicinity of the village of Colonia Rodolfo Figueroa (situated on the south slope of Cerro Baúl), Oaxaca, Mexico.

**Paratypes**.—Males: AMNH 70016–18; UMMZ 88344 (five specimens), 94545, 126797, 126801–02. Females: AMNH 70015; UMMZ 88344, 94542–44, 102253, 102256, 107791 (two specimens), 126796, 126798, 126799, 126800 (two specimens), 126803–05; MVZ 113616, 165511, 180391. See Appendix I for specific localities.

*Referred specimens.*—see Appendix I.

*Diagnosis.*—A large species of *Bufo* (males to 76.2 mm SVL; females to 103.6 mm SVL) having the following combination of characters: (1) tympanum small, about 36% diameter of orbit in males, about 39% in females; (2) preorbital crest present, pretympanic crest absent, or weakly developed in large individuals; (3) tibia short, robust, about 41% SVL in males, about 38% SVL in females; (4) feet short, about 41% SVL; (5) skin rugose in both sexes with diffuse keratin medially, smoother, with scattered conical keratinized tubercles, laterally; (6) lateral row of tubercles in both sexes as a distinct series of small pointed tubercles; (7) vocal slits small, located posteriorly in mouth, absent or unilateral in some specimens; (8) *m. interhyoideus* poorly differentiated from the *m. intermandibularis*, not forming a pigmented vocal sac, vocal slits (when present) lead into small pouches that, when bilateral, are separated medially; (9) snout acutely pointed in dorsal view, rounded in profile; (10) cranial crests in both sexes moderately thick, not hypertrophied or dorsally protuberant; (11) parotoid glands large, ovoid, not protuberant; and (12) color on distal areas of digits similar to that on proximal areas.

This species is most similar to the widespread lowland species *Bufo valliceps*, from which it may be distinguished by having smaller tympana, larger parotoid glands, and by lacking an *m. interhyoideus* that forms a bilobed, pigmented vocal sac. *Bufo bocourti* and *B. tacanensis* differ by lacking tympana. *Bufo cavifrons* (sensu stricto) and *Bufo cristatus* differ by having greatly hypertrophied cranial crests. *Bufo canaliferus* differs by being smaller and by lacking parietal crests. *Bufo macrocristatus* (see below), with which *B. tutelarius* may be sympatric, differs by having a head that is about as wide as long (wider than long in *B. tutelarius*), smoother skin on the venter, cranial crests that

are thin and produced vertically above the level of the eyelid in females, and thickened to form a small knob in males, and by having a generally more gracile habitus.

*Description of holotype.*—Body robust; head slightly wider than long, width 38.6% SVL, length 37.3% SVL; snout sharply pointed in dorsal view, acutely rounded in profile, rostral keel distinct; canthal, preorbital, supraorbital, postorbital, supratympanic, and parietal crests present, moderately thickened with dorsal margins bearing darkened keratinized surfaces; pretympenic crest barely evident, short; skin on top of head co-ossified with underlying cranial bones; nostril protuberant, directed dorsally; canthus rostralis forming distinct canthal crest; loreal region slightly concave; lip slightly rounded, with distinct supralabial crest extending from level of anterior margin of orbit to corner of jaw; distinct V-shaped notch at symphysis of upper jaw; eye-nostril distance 50.0% diameter of orbit; tympanum distinct, ovoid, width 86.4% of height, width 36.0% width of orbit, with raised annulus, upper margin contacting supratympanic crest. Forelimb short, slender; hand broad with long, slender fingers; relative lengths of fingers II < IV < I < III, webbing absent, lateral fringe on fingers formed by rows of spinose tubercles; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, round, low, flat; pollical tubercle smaller than palmar tubercle, distinct, ovoid, low, flat; subarticular tubercles distinct, elevated, triangular in profile, single, except distal tubercles on Fingers III and IV bifid; supernumerary tubercles of unequal size, distinct, elevated, round, scattered evenly on palm and fingers; Finger I with thickened pad dorsally, bearing patch of dark brown, granular, nuptial excrescences. Hind limbs short, slender, tibia length 43.4% SVL; foot length 43.2% SVL; tarsal fold absent, replaced by row of distinctly enlarged, sharply conical, tubercles; outer metatarsal tubercle small, low, ovoid; inner metatarsal tubercle

about same size as outer metatarsal tubercle, raised, ovoid, slightly spade-shaped; toes short, slender; relative lengths of toes I < II < V < III < IV; lateral fringe present on each side of all toes, distinct; webbing thin, webbing formula I1-2<sup>1/2</sup>II1-3+III2-3IV3<sup>1/2</sup>-2V; tips of digits not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles distinct, raised, triangular in profile, all single; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surface of foot and toes, except small cluster of larger, diffuse, flat tubercles over ventral surface of heel.

Skin on dorsum of body covered with many conical tubercles, most lateral bearing single keratinized apices, most medial bearing diffuse patches of dark brown keratin; parotoid glands larger than eyelids, distinctly raised, dextral gland ovoid, sinistral gland slightly triangular; lateral row of tubercles on body distinctly enlarged, pointed, most bearing single keratinized apices; venter, throat, flanks, and ventrolateral surfaces covered with tiny, evenly distributed, conical tubercles, each with single keratinized apex; dorsal surfaces of limbs, hands, and feet covered with sharply conical keratinized tubercles, those on hind limbs slightly larger than those on forelimbs.

Choanae small, subcircular, widely spaced; teeth absent; tongue long, ovoid, about three times as long as wide, free posteriorly for about one-half its length; vocal slits small, about one-fourth length of tongue, situated posteriorly; vocal sac not well developed, invaginations associated with vocal slits separated by a thin medial septum; skin of throat not differentiated.

**Coloration of holotype:** In preservative, dorsum of body and head uniform dull brown with broken linear series of small dark brown spots across midline of head at level of posterior margin of eyelids; indistinct dark brown markings at dorsal base of thighs;

one distinct dark brown marking on dorsum of forearms, tibia, tarsi, and feet; lateral row of tubercles bordered inferiorly by a diffuse dark brown stripe extending onto flanks; loreal and supralabial areas dull brown; tympanum and surrounding area darker brown; venter and throat cream; ventral surfaces of hands, tibia, and feet dull gray, largest tubercles on hands and feet cream.

*Measurements of holotype (in mm):* SVL 68.1, tibia length 29.6, foot length 29.4, head length 25.4, head width 26.3, orbit diameter 10.0, tympanum diameter 3.6, supratympanic crest length 5.1, parotoid gland length 9.9, parotoid gland width 6.4, Finger I length 10.2, Finger III length 11.7.

*Coloration in life.*—(Fig. 1.1: UTA A-13088, female, paratype; from UTA Color Transparency 94) Dorsum of body dark gray with pale cream middorsal stripe; scattered small spots on top of head and dorsal margins of cranial crests black; dorsolateral surface of body, top of head, loreal area, and dorsal surfaces of limbs dull rust-brown; stripe inferior to lateral row of tubercles dark gray; tympanum and surrounding area and markings on limbs dark brown bordered by thin black lines; supralabial area pale brown; eye bronze with black reticulations.

*Variation.*—Morphometric variation is given in Table 1.1. Few specimens (e.g., KU 20884, UTA A-4178) have a nearly uniform dull brown dorsal coloration, as does the holotype (Fig. 1.3). The more common dorsal pattern consists of a dull brown dorsum with scattered, small, dark brown or black markings (e.g., UTA A-13141, UTA A-4889). The dark stripe bordering the inferior edge of the lateral series of tubercles is distinctly darker than other surfaces in some specimens (e.g., UTA A-4177, UTEP 4968) and may be broken so as to create a bold, marbled pattern (e.g., UTA A-13134). The middorsum is darker brown than the area bordering the superior edge of the lateral series of tubercles



in some specimens (e.g., MZFC 5278, UTA A-4180). A cream middorsal stripe is evident in some individuals (e.g., MZFC 5277 [Fig. 1.3], CAS 163713). The ventral pattern varies from uniform dull cream (the more common condition in adult specimens) to diffusely mottled with dark gray (e.g., UTEP 4968, UTA A-13142). Porter (1962:fig. 8) suggested that ventral mottling indicates sexual immaturity in species of the *Bufo valliceps* group (sensu Porter, 1962). However, among the specimens of *B. tutelarius*, several individuals with ventral mottling (UTEP 4968, 4971, UTA A-4177) are mature (i.e. nuptial excrescences or oviductal eggs present).

The texture of the skin on the dorsum varies along a continuum from rough (condition of the holotype) to relatively smooth with few, scattered, larger tubercles that may not bear keratinized apices (e.g., UTA A-13134). Texture of the dorsal skin on most specimens may be characterized as: medial surface bearing evenly distributed low, nonpointed tubercles, each bearing a patch of granular keratin; most lateral tubercles larger, pointed and bearing single keratinized apices, and less evenly distributed than those over medial surface. The size, shape, and degree of coalescence of the tubercles comprising the lateral series varies greatly, but they are always distinct and easily discernible from the texture of the skin of proximal areas. No consistent sexual dimorphism in color pattern or skin texture is evident other than that no females examined have the unpatterned dorsum that is present in a few males.

Nuptial excrescences are present on the first finger only (condition of the holotype), or they may be evident on the first, second, and third fingers (e.g., AMNH 70016–18).

**Reproductive biology.**—The eggs, tadpoles, and breeding behavior of *B. tutelarius* are unknown. The vocal slits and sac are poorly developed; this species may

have a weak advertisement call, if any. Because the breeding season of this species is unknown, the degree of seasonal development and regression of the vocal apparatus is unknown (see Discussion). Most, if not all, of the surface water in the cloud forests of the Pacific Highlands is in the form of streams; *B. tutelarius* may be a stream breeding species. Adult females collected in June (UTA A-4177), July (MZFC 5276–78), and August (UTA A-13132) have well-developed ova. However, an adult female collected in March (UTA A-4889) and another collected in August (UTA A-13133) have immature, unpigmented ova; perhaps these individuals had recently deposited mature eggs.

**Distribution and ecology.**—Of the three principal areas of the Pacific Highlands, *Bufo tutelarius* is known from two—the Chimalapas and the Sierra Madre de Chiapas, including Volcán Tacaná (1.4), from elevations between 1050–2000 m. Most of the specimens from the Chimalapas are from the slopes of Cerro Baúl, mostly from the immediate vicinity of the small village of Colonia Rodolfo Figueroa, which is situated at the headwaters of the Río Mono Blanco (a tributary of the Río Negro, Atlantic drainage). The specimens collected by T. MacDougall from above Zanatepec (AMNH 70015–18) are from the same general area of the Chimalapas—Zanatepec is a town on the lowlands of the Isthmus of Tehuantepec, but is only about 20 air km SW of Cerro Baúl. In the Sierra Madre de Chiapas, this species is known from several localities from throughout the Pacific versant. In Guatemala, this species is known from the slopes of Volcán Tacaná (see Appendix) and from the series collected by L. C. Stuart in the Montañas de Cuilco at Aldea Paraiso, Huehuetenango; these latter mountains are a small and somewhat isolated range which lies between the Sierra de los Cuchumatanes and the Volcanic Cordillera of Guatemala. There are no specimens from the Volcanic Cordillera

of Guatemala. The most thorough collection from this range (Campbell and Vannini, 1988) contains *Bufo canaliferus*, *Bufo bocourti*, and *Bufo marinus*.

On the slopes of Cerro Baúl, individuals of *B. tutelarius* have been found active by day and night on the forest floor, and by night along the road just outside Colonia Rodolfo Figueroa; this stretch of road passes through undisturbed cloud forest (as of August 1992). The valley through which the Río Mono Blanco flows, below the western slope of Cerro Baúl, is relatively low (approximately 1000 m) and has been converted to pasture for cattle. Extant vegetation along tributaries draining the slopes on the western side of this valley appear to be remnant gallery rainforest; the slopes to the west are relatively dry pine-oak forest with a sparse understory of bunch grasses. No individuals of *B. tutelarius* are known from this valley, or the adjacent dry slopes. However, *Bufo marinus* is common in the pastures of the valley (Field Notes of J. R. Mendelson, 13 July 1992). At the time that he collected the series from the Montañas del Cuilco, L. C. Stuart described the area thusly: "Oak and pine is the predominant vegetation to about 1400 m and they give the country a dry aspect even in the rainy season. Above that [whence the toads were collected], where undisturbed, a broadleaf forest with some pine takes over. Coffee is raised throughout the valley up to about 1800 m in what valley bottom exists, but not on the slopes....Corn is grown above the coffee....and a bit of fine virgin forest [lies] above the corn on very steep slopes...." (Field Notes of L. C. Stuart, 2 July 1966). All specimens of *B. tutelarius* obtained by Stuart were collected by natives, usually in the coffee groves (apparently shaded) at elevations between 1650–2000 m.

**Etymology.**—The specific epithet, *tutelarius*, is a Latin noun used in apposition meaning custodian, or guardian, and is applied in reference to the likelihood that this species is the largest anuran in the cloud forests of the Pacific Highlands. By virtue of its

size and deliberate demeanor, this species may be envisaged as the guardian of the still poorly known anuran fauna of these still relatively intact forests.

**Remarks.**—Three specimens (MVZ 138938–39, 146487) from the slopes of Volcán Tacaná are here tentatively referred to *B. tutelarius*. These specimens are adult males that differ from typical *B. tutelarius* by appearing to have narrower heads, small bilateral vocal slits, smoother skin texture, and by generally being more gracile in habitus. In fact, they appear much more similar to those few males of *B. macrocristatus* (see below) which have thin cranial crests.

#### THE STATUS OF *BUFO VALLICEPS MACROCRISTATUS*

Firschein and Smith (1957) based their description of *Bufo valliceps macrocristatus* on collections resulting from early biological explorations into the Chimalapas area of Oaxaca by T. MacDougall. The holotype and some of the paratypes are from the Chimalapas, whereas other paratypes are from the Ruins of Palenque, Chiapas (see below). This taxon was diagnosed from other similar *Bufo* (viz., *Bufo v. valliceps*) by having more spinose skin, greater hypertrophy of the cranial crests (but not so great as in *Bufo cavifrons*), usual absence of the pretympanic, preocular, and subocular crests, a smaller tympanum, and greater pigmentation on the belly.

Baylor and Stuart (1961) described *Bufo valliceps wilsoni*, and commented on the status of *B. v. macrocristatus*. They suggested that the hypertrophy of the cranial crests in the latter taxon was an artifact of preservation (specimens in the type series are desiccated and poorly preserved) and stated that the diagnostic characters of *B. v. macrocristatus* are within the range of variation of *B. valliceps*. Baylor and Stuart (1961) doubted the validity of *B. v. macrocristatus*, but deferred any taxonomic action until more, and better preserved, material was available. Since this publication, *B. v.*

*macrocristatus* has remained an unrecognized taxon inasmuch as Porter (1970) and Flores-Villela (1993) recognized no subspecies of *B. valliceps* (but see Liner, 1994, and Tihen, 1962). Examination of the type series has revealed that the holotype and some of the paratypes, in fact, represent a distinct species.

*Bufo macrocristatus* Firschein and Smith

Fig. 1.5—1.6

*Bufo valliceps macrocristatus* Firschein and Smith, 1957:219–221.

*Bufo valliceps*—Baylor and Stuart, 1961:198; Porter, 1963:242–243 [in part; for specimens from the "mountains of Oaxaca and the Gulf lowlands of Chiapas"]; Porter, 1970:94.1 [did not recognize *Bufo valliceps macrocristatus*]; Flores-Villela, 1993:16 [in part, for records representing "Tropical Highlands" of Chiapas, Mexico, and Guatemala]; Wilson and McCranie, 1993:2 [in part; for reference to tadpoles from Soluschiapa, Chiapas].

*Bufo cavifrons*—Porter, 1963:232 [in part; for specimens from "near Rayón, Chiapas"]; Johnson, 1989:42,60 [in part; for specimens from the "Northern Highlands," Chiapas]; Korky and Webb, 1973.

*Bufo macrocristatus*—Tihen, 1962:168 [listed as a member of the Mexican Section of the *Bufo valliceps* group; no localities or specimens given].

**Holotype**.—UIMNH 35583, a subadult female, from between La Gloria and Cerro Azul (presumably nearer Cerro Azul), Oaxaca, Mexico, obtained by T. MacDougall between 24–26 March, 1950 (see Remarks).

**Diagnosis**.—A moderate-sized species of *Bufo* (males to 68.7 mm SVL; females to 76.8 mm SVL) having the following combination of characters: (1) tympanum small, about 41% diameter of orbit in males, about 44% in females; (2) preorbital crest absent,

or very weak, except in large females, where it is present and thin, pretympanic crest short (not reaching level of inferior margin of tympanum), thin, or absent; (3) tibia relatively long, about 43% SVL, slender; (4) feet relatively long, about 47% SVL; (5) dorsal skin in females relatively smooth, with well-spaced, discrete, conical tubercles, dorsum of males covered with low, round tubercles, some conical tubercles may be present on legs; (6) lateral row of tubercles in males present as a series of low, discrete round tubercles, in females present as a series of widely spaced sharply pointed tubercles; (7) vocal slits small, located posteriorly in mouth, bilateral; (8) *m. interhyoideus* poorly differentiated from the *m. intermandibularis* and undifferentiated posteriorly, forming a small, unilobed unpigmented sac; (9) snout acutely pointed in dorsal view, rounded, or slightly protruding in profile; (10) cranial crests low and thick in most males, junction of parietal and supraorbital crests often hypertrophied to form a small knob, crests in females high (well above level of dorsal margin of eyelid), thin, often with vertically striated texture on medial surfaces; (11) parotoid glands moderately large, conspicuously protuberant, usually ovoid; and (12) color on distal areas of digits distinctly paler than that on proximal regions, orange in life.

*Bufo macrocristatus* is most similar to *Bufo cavifrons* (sensu stricto) from the Sierra de los Tuxtlas, but differs by having more tuberculate skin, larger and more ovoid parotoid glands, larger tympana relative to the eyes, longer tibia, smaller vocal slits, and the cranial crests of females are vertically produced and thin, rather than greatly thickened and knoblike. *Bufo macrocristatus* is similar to *Bufo campbelli*. *Bufo campbelli* is known from rainforest habitat in lower montane areas (below 1000m) of eastern Guatemala (Mendelson, 1994), Honduras, southern Mexico (see Appendix I for records from Mexico and Honduras), and the Maya Mountains of Belize, but *Bufo*

*macrocristatus* differs by having larger, more protuberant and ovoid parotoid glands and cranial crests that are thickened in males and vertically produced and thin in females. *Bufo canaliferus* differs by being smaller and by lacking parietal crests. *Bufo bocourti* and *Bufo tacanensis* differ by lacking tympana. *Bufo valliceps* differs by having shorter legs, larger tympana, and by having the *m. interhyoideus* forming a large, bilobed, pigmented sac.

**Variation.**—Morphometric variation is given in Table 1.2. Variation in the extent of hypertrophication of the cranial crests is evident. In males, a small, but distinct, rounded knob usually is present at the junction of the supraorbital, postorbital, and parietal crests (e.g., UIMNH 11309, KU 75201); a few specimens lack this feature (e.g., UIMNH 35584, CAS 170161). Dorsal coloration (in alcohol) is usually pale, or dark, brown without markings and with some degree of darker coloration that follows the ventral border of the descending series of lateral tubercles (e.g., UMMZ 123994, KU 75201); a few specimens are similarly patterned, but with a few (sometimes paired) small black markings (e.g., CAS 170161, KU 41576). The venter is usually dull cream with some degree of distinct black markings. The extent of these markings varies greatly among individuals from finely reticulate (e.g., KU 138932) to nearly entirely black (e.g., CAS 163845); in most specimens the black markings are more distinct and concentrated on the posterior half of the venter. One specimen (UIMNH 11309) has become very dark in preservative, but appears to lack black markings on the venter and, in another similarly preserved specimen (UIMNH 35584), they are barely visible. Porter (1962:fig. 8, as *B. cavifrons*) provided a photograph of a series of specimens that illustrates the ontogenetic decrease in the degree of black pattern on the venter. Although this often may be the case, some adult males (e.g., KU 41576, CAS 163845) retain extensive black

pigmentation on the venter. Most specimens bear a single transverse brown bar on the forelimb and each segment of the hind limb; in a few specimens these bars are not evident (e.g., CAS 163845), perhaps due to preservation technique. In life, MZFC-LCM 281 (an adult female) had the tips of the fingers distinctly orange (A. Nieto, personal communication); in preservative the tips are pale cream and are much lighter than proximal areas of the fingers. The texture of the skin on the dorsum is usually finely granular (almost smooth) with low, rounded tubercles which are usually few and scattered (e.g., UMMZ 123994 [Fig. 1.6]), but may be relatively evenly distributed over the dorsum (e.g., CAS 170161). The venter is finely granular.

The few extant female specimens have hypertrophied crests which may be knob-like, as in males (e.g., UTA A-13014), but most have crests that are thinner and vertically expanded (e.g., UIMNH 35583, CAS 163782). Females are highly variable in color pattern: UTA A-13014 has a pale brown dorsum with few, small, black markings and a dull cream venter with scattered black markings, similar to that of most male specimens; CAS 163782 and UMMZ 123994 (Fig. 1.6) have dark brown dorsal color with 5–7 large black markings and dull cream venters with conspicuous bold black marbled pattern; UIMNH 35583 (holotype) is poorly preserved but has three moderate-sized distinct black markings on the dorsum (2 are paired in the nuchal area, the other is dextral over the sacrum); and UIMNH 35586 (paratype) also is poorly preserved but appears to have had a pale dorsal stripe bordered on each side by bold darker stripes. The texture of the skin varies from nearly smooth with scattered low tubercles (e.g., UIMNH 35583, 35586, UTA A-13014) to granular with scattered sharply conical tubercles; the tubercles that form the lateral series and those on the limbs are usually especially sharply conical (e.g., CAS 163782, UMMZ 123994 [Fig. 1.6]).



*Reproductive biology.*—The tadpole of *Bufo macrocristatus* (as *Bufo cavifrons*) was described by Korky and Webb (1973) from a lot collected near Soluschiapa, Chiapas. Because these tadpoles were associated with metamorphs and adults that they referred to *Bufo cavifrons*, they allocated them to that species. I have examined these postmetamorphic individuals (UTEP 5879–84) and refer them to *B. macrocristatus*. I examined another series (UTA A-27857–59) of tadpoles of *B. macrocristatus*, and they closely match those described by Korky and Webb (1973). The present series differs from their description only by having a distinct fine reticulate pattern of melanophores on the dorsal tail fin rather than being sparsely flecked with melanophores; in both cases, the ventral tail fin lacks melanophores. Nevertheless, the tadpole of *B. valliceps* has a more bold, non-reticulate pattern of melanophores on the dorsal tail fin (Korky and Webb, 1973; KU 157685). Korky and Webb (1973) correctly stated that the tadpole of *B. macrocristatus* (=their *B. cavifrons*) may be distinguished from that of *B. valliceps* by having a different pattern on the dorsal tail fin and by having a smaller median gap in tooth row A-2. I have found also that whereas tadpoles of *B. valliceps* are nearly uniformly black, those of *B. macrocristatus* are brown; under magnification the color appears as evenly distributed discrete brown melanophores. Furthermore, the tadpole of *B. valliceps* has a much larger nostril (about 40% diameter of eye vs. about 10%) and a short, simple, medial vent tube, whereas the vent tube of *B. macrocristatus* is longer with the ventral and medial margins extended to produce the appearance of a long, dextral vent tube.

Wilson and McCranie (1993:2) briefly describe tadpoles from Honduras that they refer to *B. valliceps* and stated that they are identical to those described by Korky and Webb (1973). Wilson and McCranie (1993:2) criticized Korky and Webb (1973) for the

criteria by which they allocated the tadpoles to species and suggested that they described a geographic variant of the tadpole of *B. valliceps*; I do not concur with Wilson and McCranie (1993) on this matter. Geographic variation in the morphology of tadpoles is known to occur (Savage, 1960) but this has never been studied in *B. valliceps*. It is not clear what species is represented by the tadpoles from Honduras that were discussed by Wilson and McCranie (1993).

Breeding behavior in *Bufo macrocristatus* is unknown. The presence of vocal slits and a small undifferentiated vocal sac suggests that this species may have only a weak advertisement call, if any at all (see Discussion). The only female that appears to be mature (UTA A-13014) was collected on 13 June and has well-developed ova. Males collected between 14 June (KU 75201) and 11 January (UIMNH 35584) have well-developed nuptial excrescences. The tadpoles reported by Korky and Webb (1973) were found in a slow-moving roadside rivulet, and the others reported herein (UTA A-27857–59) were found in a shallow depression in a slow-flowing seep in a grassy field on the edge of a recently felled cloud forest (J. A. Campbell, personal communication).

***Distribution and ecology.***—The type locality of *Bufo macrocristatus* is in the western area of the Chimalapas, and other records are from the Atlantic versants of the Northern Highlands and the Eastern Highlands (sensu Breedlove, 1973) of Chiapas, Mexico, and their geographic extension into Guatemala on the wet Caribbean slopes of the Sierra de los Cuchumatanes, as well as the northern slopes of the Sierra Madre de Chiapas (Fig. 1.4). This distribution matches closely the distribution of Montane Rainforest in the area (Breedlove, 1973). The Atlantic versants of the Northern Highlands and the Eastern Highlands correspond to the "Crescent Area" of Wendt (1993), who discussed its unique flora. This area receives more than 3000 mm of precipitation

annually, making it one of the wettest areas of Middle America (Wendt, 1993). Most of the specimens do not have elevational data associated with them, but apparently they were found at elevations of about 1400–1600 m. The verified maximum elevational extreme is 1767 m (MVZ 138932–37), and the minimum must be near 300 m at Palenque, Chiapas, where several of the paratypes were collected. Thus, this species seems primarily to occur in pine-oak-*Liquidambar* cloud forest; the record from 868 m in the Selva Lacandona (KU 41576) could have been taken in Montane Rainforest, or Lower Montane Rainforest (sensu Breedlove, 1973), because either may occur at this elevation in this area, depending on local conditions (Breedlove, 1973). Just as is the case with *Bufo campbelli* and *B. cavifrons*, *B. macrocristatus* seems to be associated with streams and may breed there; KU 58294–98, 58300–303 were collected along streams in cloud forest (Field Notes of W. E. Duellman, 16 June, 5 August 1960).

**Etymology.**—The specific epithet is derived from the Greek *makros*, meaning long (perhaps mistakenly intended to mean large; see Brown, 1956:502), and the Latin *crista*, meaning crest; the name *macrocristatus* is in reference to the enlarged cranial crests evident especially in females.

**Remarks.**—Perusal of T. MacDougall's field notes that are now archived in the AMNH library indicates that the holotype was collected by MacDougall on 25 March 1950 (reported as 24–26 March in the UIMNH catalog and in the original description). The holotype is described by MacDougall as "a medium size frog, dark with small tubercles along sides and on back." At the time, MacDougall at the base of a divide, from the crest of which he noted "...Cerro Atravesado in view to SE and Cerro Azul to E or slightly S of E..." and he goes on to describe thickets of tree ferns, many *Synacantha*

palms, and the collection of a male Quetzal; these notes strongly suggest that the holotype was found in primary cloud forest habitat.

Baylor and Stuart (1961) stated that UIMNH 11309 (a paratype from Palenque, Chiapas, not a paratopotype as was stated by them) is actually a typical specimen of *Bufo valliceps*. This specimen clearly represents *Bufo macrocristatus*. However, UIMNH 11308 (a paratype, also from Palenque, Chiapas) is a small mature female of *B. valliceps*, with the diagnostic large tympana and short legs; it is possible that Baylor and Stuart (1961) intended to refer to this specimen in their discussion. The presence of *Bufo valliceps* in the environs of Palenque is not surprising; in fact Firschein and Smith (1957:220) mentioned that this species is present in "the nearby village of Palenque." *Bufo valliceps* occurs in many types of disturbed habitats throughout southern Mexico and actually may be ecologically separated from other species of *Bufo* that occur in proximal undisturbed habitat; such is the case in eastern Guatemala where *B. valliceps* and *B. campbelli* occur, respectively, in disturbed and undisturbed habitats about coffee plantations (Mendelson, 1994). Specimens of *B. macrocristatus* (KU 58294–98, 58300–303) were taken along a cascading mountain stream in a remnant of cloud forest at elevation of 1680–90 m, near Rayón Mescalapa, Chiapas, but nearby *B. valliceps* (KU 58361–66, 58367–70) were found in muddy pools and ditches in disturbed areas at 1675 and 1700 m (Field Notes of W. E. Duellman, 14–16 June 1960, 5 August 1960). *Bufo valliceps* typically occurs below 1000 m but may invade disturbed habitats over a wide range of elevations.

## DISCUSSION

Liu (1935) surveyed the diversity of vocal sac structure among frogs and proposed a standardized terminology for these structures. Tyler (1971a, 1971b)

described the morphology of vocal sacs in hylid frogs. Using their terminology, *Bufo valliceps* (KU 195052, MZFC 5204, adult males with nuptial excrescences) possesses an *m. interhyoideus* that is poorly differentiated from the *m. intermandibularis*. The *m. interhyoideus* becomes thinner posteriorly and forms a large, darkly pigmented sac that forms two lobes: a larger, anterior lobe, and a smaller, posterior lobe; the posterior lobe is visible only when the overlying anterior lobe is deflected anteriorly. The free margin of the anterior lobe is continuous with the post mandibular septum, which is also pigmented. The submandibular skin is entirely free from the underlying musculature in the area between the margins of the mandibles and the integumental insertion of the post mandibular septum and is not differentiated to form an external vocal sac (sensu Liu, 1935). Nevertheless, while calling, males of *B. valliceps* do achieve considerable distension of the gular area. In *Bufo tutelarius* (UTEP 4971, adult male with nuptial excrescences), the *m. interhyoideus* is poorly differentiated from the *m. intermandibularis*, but it is not differentiated posteriorly to form a sac and it is unpigmented. The post mandibular septum is thin, transparent, and short, so that the overlying skin is closely associated with the underlying musculature. The vocal slits lead into small pouches that are separated medially by a septum; the vocal sac does not appear to be distensible. In *Bufo macrocristatus* (KU 58302, adult male with nuptial excrescences), the *m. interhyoideus* is poorly differentiated from the *m. intermandibularis* and is undifferentiated posteriorly but forms a small unilobed and unpigmented sac which lacks a medial septum; the vocal slits in this species are very small.

Inger (1958) described the vocal sac of *Bufo alvarius* and remarked that any frog with vocal slits has a vocal sac (or sacs). As such, *B. tutelarius* has a vocal sac (or bilateral sacs). Because the tone of an anuran advertisement call is generated by the

laryngeal cartilages, the absence of a vocal sac and slits does not preclude such calls in many species (e.g., *Hyla crassa*, Caldwell, 1974; Inger and Greenberg, 1956).

Inger and Greenberg (1956) described the seasonal development of secondary sexual characteristics of the males of two African species of *Bufo* (viz., vocal slits, sac, nuptial excrescences, and skin texture). Such a study has never been conducted on any of the species discussed in this paper. However, I have observed well-developed vocal sacs in specimens of *B. valliceps* that were collected between 24 February (KU 55878 from Campeche) and 18 October (KU 24364 from Veracruz). A single adult male (KU 25846 from Veracruz) collected on 30 December lacks keratin on the nuptial excrescence and has a smaller, less pigmented vocal sac than I have otherwise seen in this species. In Louisiana, USA, *B. valliceps* has been heard calling between 5 April and 15 September (Dundee and Rossman, 1989). Thus *Bufo valliceps* seems to have a long breeding season, but it is unclear to what extent the vocal apparatus develops or regresses seasonally. In light of these observations it is difficult to determine whether the lack of a differentiated vocal sac in the available specimens of *B. tutelarius* represent a seasonal collecting bias or a typical, and thus diagnostic, characteristic of the species. The diagnostic value of the condition of the vocal sac in different species will not become apparent until seasonal development associated with breeding has been studied adequately; at this time sufficient samples of many species in Middle America do not exist.

**CHAPTER II**  
**A NEW SPECIES OF TOAD (ANURA: BUFONIDAE) FROM**  
**OAXACA, MEXICO, WITH COMMENTS ON THE STATUS OF**  
***BUFO CAVIFRONS* AND *BUFO CRISTATUS***

**INTRODUCTION**

There has been considerable confusion associated with the identity of the quite distinctive, but poorly known, toads of the forests of the lower montane areas of southern Mexico. Firschein (1950) described *Bufo cavifrons* from the isolated Sierra de los Tuxtlas in Veracruz, Mexico, and resolved over 100 years of confusion associated with the name *Bufo cristatus* Wiegmann. Porter (1963) reviewed the taxonomic status and distribution of these toads and several others including the rather ubiquitous *Bufo valliceps* Wiegmann. Since these classic works, new material has been collected that now allows further clarification of the species-level diversity of these crested toads of the wet forested slopes of southern Mexico.

According to Porter's (1963) taxonomy, the name *B. cristatus* is applicable to a few specimens with massive cranial crests from the southern Sierra Madre Oriental and the name *B. cavifrons* is applicable to the populations with variably hypertrophied cranial crests from three distinct cloud forest areas: the Sierra de los Tuxtlas, the Selva Negra area on the Atlantic versant of the Chiapas highlands, and the Sierra de Juárez of Oaxaca, Mexico. Mendelson (1997) demonstrated that the population of the Selva Negra and many other populations along the Atlantic slopes of Oaxaca and Chiapas, Mexico, and Guatemala are referable to *Bufo macrocristatus* Firschein and Smith. The recognition of *B. macrocristatus* as distinct from the other two populations of *B. cavifrons* (Sierra de

Juárez, Sierra de los Tuxtlas; sensu Porter, 1963) suggests that a review of the status of these two populations is warranted. Herein I review these populations and also rediagnose *Bufo cristatus* with respect to morphological characteristics of other superficially similar toads in Mexico.

#### MATERIALS AND METHODS

General terminology and measurements follow that of Mendelson (1994). The format of the diagnoses and the specific terminology of the morphology of the vocal sac follows those used in the description of *Bufo tutelarius* (Mendelson, 1997). Males were identified by the presence of nuptial excrescences and vocal slits; sex of specimens lacking these features was determined by observation of the gonads. I made all measurements with digital calipers and rounded to the nearest 0.1 mm. Foot-webbing formulae follow that of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Snout–vent length is abbreviated as SVL. Museum acronyms are those proposed by Leviton et al. (1985), with the addition of MZFC for the Museo de Zoología, Facultad de Ciencias, Universidad Autónoma de México. Individual specimens from UMMZ lots are indicated by their catalog (= lot) number in association with the individual collector's catalog number [e.g., UMMZ 118195 (WED 11706)]. I compared specimens of the three species considered in this paper with all species of the *Bufo* in Mexico and Central America, however I present diagnoses that only consider those species with which they are likely to be confused based on overall appearance and geographic occurrence—viz., some species of the *Bufo valliceps* group (sensu Blair, 1972).

#### *Bufo spiculatus* sp. nov.

*Bufo cristatus*—Shannon, 1951:470 [in part, for referral of USNM 123691, from San Lucas Camotlán, Oaxaca].



*Bufo cavifrons*—Porter, 1963:232 [in part, for referral of AMNH 60435, from San Pedro Sochiapan, Oaxaca].

*Bufo valliceps*—Porter, 1963:236 [in part, for referral of USNM 123691, from San Lucas Camotlán, Oaxaca].

**Holotype.**—KU 137523, an adult female from 2.8 km S Vista Hermosa, Oaxaca, Mexico, 1570 m (17°43'N, 96°22'W), obtained by J. P. Caldwell on 14 June 1970.

**Paratypes.**—From the Sierra de Juárez, Oaxaca, Mexico—Females: UTA A-13013, from Metates; UTA A-6585, from near Campamento Vista Hermosa; KU 86670, from 3 km S Vista Hermosa, 1600 m; KU 137522, from 2 km S Vista Hermosa, 1520 m; MZFC 4608-09, from Santiago Comaltepec; MZFC 5317, from 1–2 km SW Metates, ca. 800 m; UTEP 5878, from 10 mi [16.1 km] S Valle Nacional, 4200 ft [1280 m]; TCWC 58009, from Villa [sic] Hermosa, 1000 m; UCM 39764, 52515, from Comaltepec Ixtlan, Vista Hermosa; MVZ 14682, from Mexico Hwy 175, 7.7 mi [12.4 km] S La Esperanza. Males: KU 86669, from Vista Hermosa, 1600 m; AMNH 71397 and 71433, from Yelagago, Boone Hallberg's Ranch, 4500 ft [1371 m]. From the Sierra Mixe, Oaxaca, Mexico—Female: USNM 123691, from San Lucas Camotlán.

**Referred specimens.**—All juveniles from the Sierra de Juárez, Oaxaca: UTEP 5877, from 10 mi [16.1 km] S Valle Nacional, 4200 ft [1280 m]; AMNH 60435, from San Pedro Sochiapan; AMNH 71122–23, from Yexicobe, on trail to Yelagago, 5600 ft [1706 m]; KU 86671, from 0.5 km E Vista Hermosa, 1550 m; LSU 37811 and 37825, from 2.4 mi [3.9 km] N Vista Hermosa.

**Diagnosis.**—A large species of *Bufo* (males to 71.4 mm SVL; females to 103.0 mm SVL) having the following combination of characters: (1) tympanum small, 30–36% diameter of orbit in males, 33–41% in females; (2) preorbital crest present, thin, in

females, absent in males, pretympenic crest absent, or weakly developed in large individuals; (3) tibia short, 38–44% SVL; (4) feet relatively short, 40–45% SVL; (5) skin smooth, with distinct spiculate tubercles concentrated posteriorly and on limbs, evident especially on females; (6) lateral row of tubercles present as a series of conical or high, rounded tubercles in males, in females as a series of sharply pointed tubercles; (7) vocal slits absent; (8) *m. interhyoideus* not forming a pigmented vocal sac; (9) snout sharply pointed in dorsal view, rounded in profile; (10) cranial crests low and thick in males, crests in females low, moderately thick, usually with crenulate texture on vertical surfaces; (11) parotoid glands large, conspicuously protuberant, usually triangular; (12) tips of digits of fingers distinctly paler than rest of digit.

*Bufo spiculatus* (Fig. 2.1, 2.2) is similar to *B. cavifrons* (*sensu stricto*) but differs by lacking vocal slits and sac, females having distinctive spiculate tubercles concentrated on the posterior portion of the dorsum and on the limbs (Fig. 2.3), and cranial crests relatively low and thick with a crenulate texture; *B. cavifrons* has smooth skin and cranial crests that are smooth, thick, and greatly elevated vertically. *Bufo macrocristatus* is quite variable (Mendelson, 1997), but in most cases specimens may be distinguished from *B. spiculatus* by having vocal slits and a small vocal sac, fewer or less sharply pointed tubercles on the dorsal skin, larger tympana, and more ovoid parotoids. *Bufo valliceps*, with which *B. spiculatus* may be sympatric, has shorter legs, larger tympana, distinct preorbital and pretympenic crests, and large vocal slits associated with a large pigmented vocal sac. Some male specimens of *Bufo tutelarius* Mendelson, from the Sierra Madre de Chiapas and associated highlands, lack vocal slits; however, this species differs by having uniformly rugose dorsal skin texture, low and nonhypertrophied cranial crests, and ovoid parotoid glands. Table 2.1 summarizes the major diagnostic features of *B.*

*spiculatus* and other similar species; relative size and shape of the cranial crests and parotoid glands of *B. spiculatus* and similar species are compared in Fig. 2.4.

**Description of the holotype.**—Body robust; head slightly wider than long, width 38.6% SVL, length 36.9% SVL; snout sharply pointed in dorsal view, acutely rounded in profile, rostral keel distinct; canthal, preorbital, supraorbital, postorbital, supratympanic, and parietal crests present; medial surfaces of canthal, supraorbital, posterior surface of postorbital, lateral surface of parietal, lateral and medial surface of parietal crests with distinct crenulate texture; pretympanic crest present merely as a small knob, less than one-eighth height of tympanum; skin on top of head coossified with underlying cranial bones; nostril protuberant, directed dorsally; canthus rostralis forming distinct, raised, canthal crest; loreal region concave; lip distinct, rounded; supralabial crest indistinct, extending length of upper jaw; distinct V-shaped notch at symphysis of upper jaw; eye–nostril distance 62.9% diameter of orbit; tympanum distinct, ovoid, width 90.0% height, width 52.2% width of orbit, with raised annulus, upper margin contacting supratympanic crest, posterior margin of annulus obscured by overlying flesh. Forelimb short, slender; hand broad, with long slender fingers; relative lengths of fingers  $II < IV < III < I$ , webbing absent, lateral fringe on fingers slight, intermittent, formed by rows of closely associated tubercles; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, polygonal, low, flat; pollical tubercle smaller than palmar tubercle, distinct, ovoid, low, flat; subarticular tubercles distinct, elevated, triangular in profile, single except distal tubercle on Finger III bifid; supernumerary tubercles of unequal size, large, distinct, elevated, round, scattered evenly over palm and ventral surfaces of fingers. Hind limbs short, slender, tibia length 39.8% SVL; foot length 44.0% SVL; tarsal fold absent, replaced by a row of distinctly enlarged,

sharply conical tubercles; outer metatarsal tubercle small, low, ovoid; inner metatarsal tubercle larger than outer metatarsal tubercle, raised, ovoid; toes long, slender, relative lengths of toes  $I < II < V < III < IV$ ; lateral fringe present on both sides of all toes, distinct; webbing thin, webbing formula  $II - 2^{1/2} III 1 - 2^{1/2} III 2 - 3^{1/2} IV 3^{1/2} - 1^{1/2} V$ ; tips of digits not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles single, distinct, raised, rounded in profile; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surface of foot and toes.

Skin on dorsum of body smooth with scattered, sharply conical tubercles becoming larger and more concentrated laterally and posteriorly; parotoid glands larger than eyelids, distinctly raised, subtriangular, smooth; lateral row of tubercles on body present as an intermittent series of sharply pointed, conical tubercles, smaller than the larger tubercles on dorsum and legs; sacral area and dorsal surfaces of arms and legs covered with large, sharply pointed, conical tubercles, tubercles on arms smaller than those of legs; skin on throat and all ventral surfaces rough, covered with small conical tubercles.

Choanae large, ovoid, widely spaced; teeth absent; tongue long, ovoid, about four times as long as wide, free posteriorly for about one-half its length.

**Coloration of holotype:** In preservative, dorsum of body red-brown medially, becoming gray-brown laterally; top of head gray-brown; flanks slightly paler than lateral dorsal area; lateral row of tubercles coincides with boundary between dorsolateral coloration and dark brown lateral coloration; dorsal markings consist of an intermittent, thin, gray middorsal stripe, widest over the urostyle, a charcoal-black chevron, the apex of which lies just posterior to the termini of the parietal crests, two unequal bilateral ovoid charcoal-black markings just posterior to the level of the scapulae, each edged

laterally by a diffuse cream area, and a distinct black bar, bordered by thin cream bands, extending across the head between the junctions of the parietal and supraorbital crests; the dorsal surfaces of the arms and legs are dark gray, a few of the many tubercles thereupon with pale gray or dull cream apices; forearms, tarsi, shanks, feet each bearing an indistinct, wide, transverse bar, slightly darker than adjacent areas; dark brown lateral coloration extends anteriorly over the tympanic area, ending dextrally as a thin, distinct, black bar extending obliquely from ventroposterior margin of eye to lip, ending sinistrally at the same level, but no oblique black bar present; loreal and suborbital regions gray-brown with single bilateral diffuse brown suborbital markings; lateral surface of parotoid glands dark brown, sharply separated from dorsal coloration of glands; dorsal surfaces of Fingers III and IV dark brown dorsally with dull cream tips; Fingers I and II dull cream throughout; dorsal surfaces of toes dull cream, Toes IV and V with indistinct dark brown transverse markings; throat dull brown with diffuse cream markings; venter dull cream with scattered diffuse dull brown markings, becoming more concentrated and contiguous over pectoral area, grading into throat coloration; ventral surfaces of hands dark brown with most tubercles dull yellow; ventral surfaces of forearms dark gray-brown, ventral surfaces of humeral areas dull cream; ventral surfaces of legs dull cream with scattered, small, diffuse dull brown markings.

*Measurements of holotype (in mm):* SVL 97.2, tibia length 38.7, foot length 42.8, head length 35.9, head width 37.5, orbit diameter 11.6, tympanum diameter 4.7, supratympanic crest length 7.3, parotoid gland length 14.2, parotoid gland width 7.4, Finger I length 16.1, Finger III length 17.3.

*Coloration in life:* Janalee P. Caldwell (Field Notes, 14 June 1970) provided the following notes on the holotype: "Dorsum brown, changing to gray dorsolaterally. Dark

brown on sides. Limbs striped gray and dark brown. 3 dark brown spots on dorsum and interorbital stripe dark brown. Venter tan with brown spots. tan line on upper lip. Eye gold with black reticulation and dark stripe through center."

**Variation.**—Morphometric variation among the few available specimens is summarized in Table 2.2. Coloration of an adult female (KU 137522) was described as follows (Field Notes of J. P. Caldwell, 16 July 1970): "Top of dorsum brown; gray middorsal stripe, outlined by tiny amount of dull yellow, and very dark brown. Dorsolateral areas of dorsum dull yellow, becoming gray far down on sides. Dark gray stripe on sides extending forward to tympanum. Sides of head brown; light brown stripe on upper lip; dark brown stripe lower lip. Yellow-brown between crests on top of head, bordered behind by thin lines of dull yellow and dark brown. Small spot of same colors just posterior to this area, and anterior to the middorsal stripe of the same colors. Dorsal surfaces of limbs gray and brown striped. Soles of feet gray with reddish tubercles. Venter mottled gray and tan. Eye mostly black, with gold reticulations. Variation in color pattern among preserved specimens is reviewed below.

**Females:** Most specimens bear dorsal patterns similar to that of the holotype, varying only in the size, number, and location of black dorsal markings; four subadult specimens (MZFC 4608–09, 5317; KU 86671) each bear single, bilateral, small black spots in the concavity formed in the space between the parietal, postorbital, and supratympanic crests; among the adults, only KU 137522 bears any trace of these markings. The dorsal stripe is conspicuous and broad in some specimens (e.g., KU 137522, UTA A-13013). One specimen (KU 86670) lacks conspicuous dorsal markings and interorbital bar and another (TCWC 58009) is similar except that it has a poorly defined, but complete, middorsal stripe; the ground color of these specimens is similar to

that of the holotype—red-brown middorsally, becoming gray-brown laterally. The ventral surfaces of the adult female paratypes are all less boldly marked with diffuse dark markings than is that of the holotype; the venter of most specimens is overall dull cream with few, indistinct, dark markings. All females bear the distinctly spiculate dorsal skin texture that characterizes the holotype; UTA A-13013 is slightly less spiculate than are the others. The parotoid glands of most females are more distinctly triangular than are those of the holotype. The cranial crests of USNM 123691 are somewhat thicker than are those on the other specimens; a photograph of this specimen (as *Bufo valliceps*) was presented by Porter (1964a:fig. 6).

**Males:** Among the three specimens, AMNH 71397 is dark brown laterally and pale brown dorsally with four bilateral small black markings, a distinct interorbital bar, and a poorly defined dorsal stripe. The remaining specimens (AMNH 71433, KU 86669) are similar in being dark brown laterally, but AMNH 71433 is pale brown dorsally with several very small black markings, poorly defined brown interorbital bar, and no middorsal stripe, while KU 86669 is nearly uniform dark brown (perhaps as a result of preservation) with a barely visible middorsal stripe, and no dorsal markings or interorbital bar. The venters of all specimens are dull yellow with bold dark brown mottling. The skin texture is similar to that of the females, however, the tubercles over the sacral area and legs are neither as large, nor as sharply pointed, as in the females. The specimens from AMNH each show signs of physical injury and, apparently, subsequent infection (i.e., missing digits and swollen areas). The dorsal tubercles of AMNH 71433 are more numerous and more globose than are those on all other specimens; a swollen and misshapen dextral eyelid on this specimen suggests the possibility that this skin texture may be abnormal. The cranial crests are moderately thick, but only AMNH

71397 shows some vertical development of the crests; the area at the junction of the parietal, supraorbital, and postorbital crests is raised to form a small knob, similar to that characteristic of males of *Bufo macrocristatus* (Mendelson, 1997). The cranial crests of KU 86669 are thinner than are those of the other males. The parotoid glands are large (approximately three times length of eyelid), smooth, well defined, and protuberant (AMNH 71397, 71433) or somewhat smaller and less protuberant (KU 86669). All specimens lack vocal slits. Each specimen bears a small thickened area on the dorsomedial surface of Finger I (least developed in AMNH 71397) and KU 86669 bears a trace of keratinous nuptial excrescence thereupon; no thickened area is apparent on Finger II.

**Reproductive biology.**—The tadpole of *B. spiculatus* is unknown, as is the breeding behavior. This is somewhat surprising because J. P. Caldwell (1973) conducted an intensive survey (1969–1970) of anuran breeding biology in lentic and lotic habitats along a transect that included the northern slope of the Sierra de Juárez. Although her research was concentrated on hylid and centrolenid frogs, it is clear from her notes that her collections are comprehensive and represent all taxa that she encountered; her collections do not include any eggs or larvae possibly referable to *B. spiculatus*. The adult females collected between January (date unknown) and 14 June (TCWC 58009, UTA A-13013, KU 137523) have well developed oviducal eggs and the remaining two specimens (KU 86670, KU 137522), collected on 20 June and 16 July, respectively, have minute, unpigmented ovarian eggs; these meager data suggest that *B. spiculatus* may breed during the rainy season (July–January; Caldwell, 1973).

**Distribution and ecology.**—*Bufo spiculatus* is known from few specimens that all were found on the northern (Gulf of Mexico) slopes of the Sierra de Juárez and the



adjacent Sierra Mixe, Oaxaca, Mexico (Fig. 2.5). In the Sierra de Juárez this steep slope grades from lowland rainforest at the base up to cold, elfin pine-fir forest atop Cerro Pelón at 3200 m (see Bogert, 1968, for a review of the vegetation of the slopes of Cerro Pelón). Cloud forest conditions and characteristic vegetation (viz., tree ferns, *Liquidambar*) prevail to unusually high elevations along the northern slope of the Sierra de Juárez, from about 1000 m to almost 3000 m, presumably because of the moist trade winds rising from the humid gulf lowlands. *Bufo spiculatus* has been collected at 800–1689 m, an elevational range that on this slope corresponds almost entirely to cloud forest habitat; perusal of the available notes indicates that all specimens apparently were collected in primary forest. The holotype was "on hillside about 10 m from stream at night" (Field Notes of J.P. Caldwell, 14 June 1970) and another (KU 137522) was active on the forest floor, at about 1300 h, following a night of rain (Field Notes of J. P. Caldwell, 16 July 1970). Notes associated with other specimens (AMNH 71397, 71433) describe the habitat as "rain forest." I found MZFC 5317 sequestered in deep leaf litter by day near the settlement of Metates, at about 800 m, in a patch primary rainforest just below the level of cloud forest.

**Etymology.**—The specific epithet is derived from the Latin *spica*, and is used as an adjective in reference to the distinctive spiculate skin texture evident especially on females of this species.

**Remarks.**—Shannon (1951), citing the notes of collector and linguist W. S. Miller, provided the local Mixe name "*nooch*" for this species; evidently this name is applied to all toads. Porter (1963) referred the population of toads from the cloud forest of the Sierra de Juárez to *B. cavifrons* evidently based on his examination of AMNH 60435 (a juvenile), inasmuch as this is the only specimen that he cited. In fact, it does

seem that virtually all other specimens of this species have been collected after Porter completed his project. However, Porter (1963:236) also referred the single specimen from the Sierra Mixe (USNM 123691) "on the basis of cranial morphology and general appearance..." to *Bufo valliceps*.

Although there are many species of amphibian currently known only from the Sierra de Juárez (e.g., *Hyla calvicollina*, *Hyla cyanomma*, *Hyla echinata*, *Eleutherodactylus polymniae*, *Pseudoeurycea juarezi*, and several species of *Thorius*), the high cloud forests of the Sierra de Juárez do share a number of species with the Sierra Mixe to the east (Campbell and Frost, 1993), such as *Hyla sabrina* and *Hyla celata* (Toal and Mendelson, 1995), as well as *Bufo spiculatus*. Additional field work in the Sierra Mixe is likely to demonstrate that the montane herpetofaunas of these two ranges are quite similar. The cloud forests of the Sierra de Juárez and the Sierra de los Tuxtlas (where *B. cavifrons* occurs) are separated by some 150 km of lowland habitat. A few species (e.g., *Anotheca spinosa*,) are known to have disjunct populations in each of these forests but several others are currently being reviewed, and it is likely that several taxa currently considered to occur in both areas actually represent different species (A. Nieto, personal communication; D. B. Wake, personal communication).

#### **THE STATUS OF *BUFO CAVIFRONS* AND *BUFO CRISTATUS***

The amount of confusion that has been associated with the taxonomy of the montane crested toads of southern Mexico (see Firschein, 1950, and Porter, 1963, for review), the high percentage of misidentified specimens in museum collections, and the recent taxonomic changes among these toads (Mendelson, 1997, this paper), necessitate rediagnoses of *B. cavifrons* and *B. cristatus*. I have also taken this opportunity to review briefly the natural history of these poorly known species.

*Bufo cavifrons* Firschein

*Bufo cavifrons* Firschein (1950:84–85, pl. I) [Holotype: UIMNH 8741 from 500 feet [152.4 m] below peak of Volcán San Martín, San Andrés Tuxtla, Veracruz, Mexico].

**Diagnosis.**—A large species of *Bufo* (males to 79.9 mm SVL; females to 99.8 mm SVL) having the following combination of characters: (1) tympanum small, 31–44% diameter of orbit in males, 39–46% in females; (2) preorbital crest absent, or present as a thin strip of raised bone in large females, pretympanic crest absent; (3) tibia relatively short, 36–47% SVL, robust; (4) feet relatively short in females, about 37–46% SVL; (5) skin smooth, with few scattered conical tubercles laterally and posteriorly in some females, scattered clusters of keratin over all dorsal surfaces in breeding individuals; (6) lateral row of tubercles usually present only as a continuous raised welt in males, in females present as a series of widely spaced, non-pointed, low tubercles; (7) vocal slits large, bilateral; (8) *m. interhyoideus* forms a small, unilobed unpigmented sac; (9) snout acutely pointed in dorsal and lateral view; (10) cranial crests high and thick, parietal crests produced vertically to form rounded knobs in both sexes, sometimes larger in females; (11) parotoid glands relatively small, non-protuberant, usually conspicuously triangular; (12) color of tips of fingers distinctly paler than rest of digit.

*Bufo cavifrons* is most similar to *B. macrocristatus*; however *B. cavifrons* differs by having smoother skin, smaller and more triangular parotoid glands, smaller tympana relative to the eye, shorter tibia, and larger vocal slits. In some cases, it may be difficult, beyond geography, to distinguish some individuals of *B. cavifrons* from some of *B. macrocristatus*. In such cases the nature of the hypertrophy of the cranial crests is helpful; some female *B. macrocristatus* have raised crests, but they are never so thickened as are those of female *B. cavifrons*, and in male *B. macrocristatus* the only

thickened part of the crests appears as a small knob at the junction of the parietal, supraorbital, and postorbital crests. *Bufo campbelli* is a smaller, more gracile, toad with low and thin cranial crests. *Bufo valliceps*, with which *B. cavifrons* may be sympatric near disturbed habitats, has low, non-hypertrophied crests, shorter legs, distinct preorbital and pretympanic crests, a larger tympanum, and the *m. interhyoideus* forming a large, bilobed, pigmented sac. Table 2.1 summarizes the major diagnostic features of *B. cavifrons* and other similar species; relative size and shape of the cranial crests and parotoid glands of *B. cavifrons* and similar species are compared in Fig. 2.4.

**Coloration in life.**—Firschein (1950: 84–85, his figs. 3, 4) adequately described and illustrated the color of the female holotype. A male specimen (KU color transparency 963, from Volcán San Martín; probably an individual from the lot UMMZ 118195, W. E. Duellman, personal communication) appears nearly uniform yellow-brown with a dark brown scapular chevron, thin interorbital bar, and thin line following the inferior border of the lateral row of tubercles; femur, tibia, shank, and foot each with a single wide pale brown transverse bar; many apparently keratinized, low, flat tubercles on all dorsal surfaces appear black. Shannon and Werler (1955:367) observed a large breeding aggregation and noted considerable variation of color pattern: "The vertebral light stripe [of females] is only occasionally distinct. A variable number of black spots may be scattered over the dorsal surface [presumably patches of keratin that are typical on breeding individuals]. The interorbital black bar is usually present. The coloration of the males was variable but in most specimens it consisted of a copper to brownish-yellow ground color. Some showed large black markings arranged in pairs along the middorsal line. Each pair of spots might be likened to the arms of a chevron, in which the arms fail

to meet at the apex." The iris is deep bronze (Field Notes of W. E. Duellman, 22 January 1958; KU color transparency 963).

**Variation.**—Morphometric variation is summarized in Table 2.2.

**Females:** Most specimens bear a dorsal pattern that includes a partial or complete pale dorsal stripe that may be relatively wide (e.g., UTA A-6322) or narrow (e.g., TNHC 30966), and an array of dark markings, usually arranged bilaterally that may form a partial (e.g., LSU 11762) or complete scapular chevron (e.g., TNHC 21282). Other dark markings may be scattered over the dorsum (e.g., UTA A-6321), but are usually in a somewhat paired bilateral arrangement. In some individuals a pair of bilateral dark wavy lines demarcate the lateral margins of the dorsal stripe (e.g., UMMZ 118195 [WED 11757]). A few individuals have virtually no dorsal pattern, except for a thin dorsal stripe (e.g., UMMZ 118195 [WED 11711]). Usually there are broad paravertebral areas of reddish brown (in alcohol) that become paler laterally as they approach the row of lateral tubercles. In all specimens these tubercles are pointed and lie along a distinct band of pale gray or brown (in alcohol) coloration and are bordered ventrally by a broad dark stripe that covers the lateral surface of the animal. All specimens have a dark transverse bar that extends across the head between the junctions of the parietal and supraorbital crests. A series of females collected from a breeding aggregation (UMMZ 118195; Field Notes of W. E. Duellman, 22 January 1958) all have scattered discrete clusters of granular keratin over all dorsal surfaces that appear as dark markings.

**Males:** Variation in dorsal pattern in males corresponds closely to that observed in females. Males are nearly uniform dull brown dorsally with only a thin dorsal stripe (e.g., UMMZ 118195 [WED 11742]); others have dark markings that are scattered (e.g.,

UTA A-2347), somewhat paired and bilateral (e.g., TNHC 21284), or forming both complete and partial dorsal chevrons (e.g., UMMZ 118195 [WED 11713]). The transverse bar across the head is usually present, but may be absent (e.g., UMMZ 118195 [WED 11742]). The paravertebral reddish-brown areas are usually present, but usually less distinct than in females. The row of lateral tubercles are usually low and indistinct, appearing as a continuous low fleshy ridge; they lie along a usually indistinct pale brown area and are bordered ventrally by a distinct thin dark lateral stripe. The lateral coloration ventral to this stripe is much paler than is that of females, where this dark stripe is broad and covers most of the lateral surfaces. In a few individuals the lateral tubercles are nearly absent (e.g., TNHC 19086). As in breeding females (see above), all dorsal surfaces of breeding males are covered with scattered discrete clusters of granular keratin.

**Reproductive biology.**—Breeding aggregations have been observed on 20–25 January (Shannon and Werler, 1955; Field Notes of W. E. Duellman, 1958). Both observations indicate that *B. cavifrons* breeds in and near springs at the head of streams on the side of the volcano. Shannon and Werler (1955) observed a series of heavy rains to cause scouring of the volcanic rock stream bed that effectively destroyed an entire cohort of egg clutches; one of these clutches was about 46 ft [14 m] in length and contained about 2000 eggs. Males have an advertisement call that was described as a "low, soft, trill" (Field Notes of W. E. Duellman, 22 January 1958). Shannon and Werler (1958) give a brief description of the tadpole that does not adequately distinguish the tadpole of *B. cavifrons* from that of *B. valliceps* (see key by Altig, 1987:80). If Shannon and Werler did collect these tadpoles, they most likely would have been deposited in the UIMNH with the remainder of F. A. Shannon's personal collection (H. M. Smith,

personal communication); however, I could not locate any record of them (in 1995) in the collections of UIMNH and I know of no other preserved tadpoles of *B. cavifrons*.

**Distribution and ecology.**—*Bufo cavifrons* is known only from the Sierra de los Tuxtlas, Veracruz, Mexico. Within this relatively small and isolated range, most specimens have been collected from the slopes of Volcán San Martín. However, specimens exist that were collected on the lower slopes of Volcán Santa Marta and several lower elevation localities such as Zapoapan and Tebanca (Fig. 2.5; Appendix I). It seems that *B. cavifrons* is similar to *B. campbelli* and *B. macrocristatus* in that it is found in primary forest whereas nearby disturbed areas harbor the ubiquitous species *B. marinus* and *B. valliceps*. In 1992, I spent three days on the lower slopes (up to 1000 m) of Volcán San Martín with A. Nieto and found no *B. cavifrons*; however, we did encounter many *B. valliceps* and *B. marinus* in disturbed areas below 900 m. This may be attributable to the fact that, with the exception of the lands held by Los Tuxtlas Biological Station (UNAM), all areas of this volcano below about 900 m have been cleared for agriculture; we encountered several logging teams traveling to higher elevations in search of specific hardwood trees.

**Etymology.**—The specific epithet is derived from the Latin *cavus*, meaning hollow, and *frons*, meaning brow; the name *cavifrons* is in reference to the distinctive hollowed appearance of the top of the head produced by the extreme hypertrophy of the cranial crests.

**Remarks.**—Porter (1962, 1963) and other authors (e.g., Johnson, 1989) referred many, but not all, specimens of *Bufo* from the Atlantic slopes of highlands in Chiapas and Oaxaca, Mexico, to *B. cavifrons* (see synonymies in Mendelson, 1997). Herein, the name is considered to apply only to the high-crested population that apparently occurs

throughout the Sierra de los Tuxtlas, Veracruz. Restriction of *B. cavifrons* to apply only to the population in the Sierra de los Tuxtlas serves to increase the relative endemism of this area. The herpetofauna of the Sierra de los Tuxtlas is among the most unique assemblages in Mexico (Shannon and Werler, 1955; Firschein and Smith, 1956; Campbell, 1984; Perez-Higadera, et al., 1987; Flores-Villela, 1993), and this relative endemism will certainly rise as the systematics of other groups are reviewed (see comments in Remarks for the account of *B. spiculatus*).

*Bufo cristatus* Wiegmann

*Bufo cristatus* Wiegmann, 1833:660–661 [Cotypes: ZMB 3523–3524, from Jalapa, Veracruz, Mexico; ZMB 3523 apparently lost sometime subsequent to Kellogg's (1932) examination of the specimen; ZMB 3524 designated lectotype by Firschein, 1950:83, although Porter (1963:233) claims this designation].

*Bufo occipitalis* Camerano, 1879:889–90 [Holotype: Museo Regionale di Scienze Naturali Torino An464, from Mexico]; Gunther, 1885–1902:250, Pl. 69. Synonymy fide Kellogg (1932).

*Bufo valliceps*—Brocchi, 1882:79; Günther, 1885–1902:252.

*Bufo cavifrons*—Webb and Fugler, 1957:33–34.

**Diagnosis.**—A medium-sized species of *Bufo* (males to 54.8 mm SVL; females to 87.3 mm SVL) having the following combination of characters: (1) tympanum small, 35–36% diameter of orbit in females, 30–31% diameter of orbit in males; (2) preorbital crest present, thin in largest females, absent in males, pretympanic crest absent; (3) tibia short, 37–42% SVL; (4) feet 42–45% SVL in females, 41–42% SVL in males; (5) dorsal skin texture smooth with few scattered, distinct, conical tubercles that become more



concentrated on the legs; (6) lateral row of tubercles present as an intermittent series of indistinct, small, pointed or rounded tubercles; (7) vocal slits absent in the two largest males (see Remarks); (8) vocal sac presumably absent (see Remarks); (9) snout shape acutely pointed in dorsal view, sloping and pointed in lateral view; (10) cranial crests large and distinctly thickened, parietal crests produced vertically and laterally to form large raised ovoid masses, lateral expansion fills space between parietal, postorbital, and supratympanic crests; (11) parotoid glands very large, protuberant, ovoid; (12) color of tips of fingers apparently similar to rest of digit (see below).

*Bufo cristatus* may not easily be mistaken for any other toad in Middle America. *Bufo cavifrons* has hypertrophied cranial crests, but *B. cristatus* differs by having the parietal crest as a swollen ovoid mass that fills the space between the parietal, postorbital, and supratympanic crests, much larger parotoid glands, smaller tympana, and (perhaps) by lacking vocal slits and sac. Table 2.1 summarizes the major diagnostic features of *B. cristatus* and other similar species; relative size and shape of the cranial crests and parotoid glands of *B. cristatus* and similar species are compared in Fig. 2.4.

**Coloration in life.**—A color transparency of a live male has been reproduced in Fig. 2.6. This specimen was sent to W. F. Blair and apparently was never deposited in a museum (R. Altig, personal communication). A color print from this transparency indicates that the dorsal surface of the head and middorsum are dark brown. The middorsal color on the body fades gradually to pale brown laterally as it approaches the level of the row of lateral tubercles. The stripe ventral to the lateral tubercles is black. The hind limbs are gray with dark brown transverse bars. The visible forelimb is gray-brown with a dark brown transverse bar that has a paler brown center. The tips of the digits are distinctly orange-yellow. The iris is bronze with black reticulations.

**Variation.**—Morphometric variation among the few adult specimens is summarized in Table 2.2. Photographs of the lectotype (ZMB 3424) appear in Firschein (1950:figs. 3, 4) and Porter (1963:fig. 4). This specimen has become almost totally white in preservative and no pattern or colors may be discerned; the photograph of the holotype of *B. occipitalis* (not examined) in Gavetti and Andreone (1993:Pl. VII.3) indicates that it is similarly faded. The colors and patterns of the remaining specimens that I have examined are also somewhat faded, but are summarized below. The skin texture of all specimens is mostly smooth dorsally with scattered, isolated, pointed tubercles that are larger and more numerous laterally and on the limbs.

**Females:** The three adult females (KU 39586, 39588, MCZ 35764) are nearly uniform dark brown over all dorsal surfaces and each has a pale brown thin, intermittent, dorsal stripe. One (KU 39588) has a faint transverse bar across the head, similar to that of *B. cavifrons*, and this bar is distinct, but incomplete, in another specimen (MCZ 35764). No transverse bars are evident on the limbs. The tips of the digits are mostly pale cream (only slightly paler than the rest of the digit) with some dark brown evident on the dorsomedial surface of each digit tip. A dark brown stripe is barely evident just ventral to the descending row of lateral tubercles. The lateral surface of the parotoid glands are distinctly darker brown than are the dorsal surfaces. The ventral surfaces of these two specimens are dull cream with some dull brown diffuse mottling concentrated over the pectoral area.

**Males:** A single male (KU 39587) is small, but may be mature (see below). This specimen is nearly uniform pale brown dorsally, becoming slightly gray-brown laterally at the level of the row of lateral tubercles. A thin pale dorsal stripe is present over the urostyle. The hind limbs show no trace of transverse markings, but each forelimb bears a

single, barely visible, transverse bar. A distinct black stripe extends posteroventrally, ventral to the lateral tubercles, from the level of the posterior margin of the supratympanic crest to the flank, becoming thinner posteriorly. The tips of the digits are as described above in females. The venter is dull cream with scattered irregular diffuse dark brown markings.

**Juveniles:** Two well preserved specimens (UIMNH 57141, UMMZ 115427) have reddish brown paravertebral areas that become pale gray-brown laterally at the level of the descending row of lateral tubercles. Both specimens have scattered distinct black dorsal markings; some are paired and bilateral, forming broken chevrons over the scapular area. Both specimens have interorbital black bars extending laterally over the cranial crests and onto the eyelids. The middorsal stripe over the urostyle is present, but extends anteriorly, becoming thinner and disappearing at the level of the scapulae on UIMNH 57141. The lateral black stripe described above is present on both specimens, but is very thin on UMMZ 115427; both have the lateral surfaces covered by a wide dark reddish brown stripe. The parotoid glands are distinctly more pale than are the surrounding areas on UMMZ 115427 and the rostral region is covered with distinct black vermiculations on UIMNH 57141. Transverse bars are present on each segment of the hind limb and on the radioulnar segment of the forelimb. The tips of the digits are as described in the adult specimens. The ventral surfaces are dull cream with extensive areas of diffuse dark pigment.

**Reproductive biology.**—As with other aspects of the natural history of this species, its reproductive biology is virtually unknown. The diagnostic characteristics of the tadpole were presented in a key (Altig, 1987). Tadpoles were collected on 26 December 1969 (UMMZ 151887; not examined) and 22 December 1970 (KU 144722) in

fast moving streams about 1 m in depth where the tadpoles clustered on the lee sides of boulders; the tadpoles were attached to rock surfaces by their oral discs and swayed in the current (R. Altig, personal communication). A single small male (KU 39587; SVL 54.8 mm) may be mature, despite its small size. This specimen has well developed testes and traces of keratinous nuptial excrescences on small thickened thumb pads, but vocal slits are not present. Males of *B. cristatus* may lack vocal slits, and perhaps an advertisement call.

***Distribution and ecology.***—Adults and juveniles of *B. cristatus* are known from few localities in the central part of the Sierra Madre Oriental (Fig. 2.5); these localities are the environs of Jalapa, Huatusco, and Coscomatepec, Veracruz, and Tezuitlan, Puebla. Ronald Altig collected tadpoles that he referred to *B. cristatus*, probably correctly, from near Atzalan, Veracruz (UMMZ 151571, 151887; not examined by me). These localities are within a narrow band of cloud forest on the Atlantic versant of the Sierra Madre Oriental. Pelcastre-Villafuerte and Flores-Villela (1992:fig. 1) showed this to be a narrow, but continuous, band of cloud forest (listed as *Bosque mesofilo de montana*), but Campbell (1982) clearly stated that the cloud forests near Tezuitlan, Puebla, and Jalapa, Veracruz, are disjunct. This is because the intervening highlands are not oriented quite perpendicular to the moisture-rich gulf trade winds and the local rain-shadow effects of Cofre de Perote. My observations on distribution of forest in the area in 1992 revealed extensive clearing; I saw virtually no forest between Huatusco and Jalapa, Veracruz, nor between Jalapa, Veracruz, and Tezuitlan, Puebla, below about 2500 m (Field Notes of J. R. Mendelson, 1–3 July, 1992). Near Tezuitlan, most remaining forest is above 2000 m—too high, perhaps, for *B. cristatus* to occur.

**Etymology.**—The specific epithet is derived from the Latin *crista*, meaning crest, and is used as an adjective; the name *cristatus* is in reference to the distinctive hypertrophied crests of this species.

**Remarks.**—Firschein (1950) redescribed *B. cristatus* and greatly clarified the confused taxonomic history of this species, especially with respect to *B. valliceps*. Also he was the first to designate ZMB 3524 as the lectotype of *Bufo cristatus*, although Porter (1963:233) claimed to have done so. When R. Kellogg visited the Turin Museum in 1930, the holotype of *Bufo occipitalis* could not be located (Kellogg, 1932:49). This specimen evidently has been located because a photograph appears in Gavetti and Andreone (1993:Pl. VII.3) with the catalog number An464; however, a catalog number for this specimen was not provided in the original description.

While examining specimens in many collections in the U.S., I found a large number of specimens of *B. valliceps* from the Sierra Madre Oriental, particularly from the area near Orizaba and Cuautlapan, Veracruz, that were misidentified as *B. cristatus*. Typically, these specimens represent older material that was likely identified based on the accounts given by Taylor and Smith (1945) and Smith and Taylor (1948), wherein they referred their specimens of *B. valliceps* from Cuautlapan and Potrero Viejo, Veracruz, to *B. cristatus*; these misidentifications have remained as such, despite Firschein's (1950) clear resolution of this problem.

If the records from the Jalapa, Veracruz, region and those from the Tezuitlan, Puebla, region represent disjunct populations that correspond to Campbell's (1982) distribution of cloud forests in this region, then *B. cristatus* seems to have a distribution similar to that of the poorly differentiated species-pairs *Anolis scheidii*–*Anolis naufragus* (Nieto, 1994) and *Rhadinaea forbesi*–*Rhadinaea marcellae* (Nieto and Mendelson,

1997). However, insufficient material exists to determine whether this pattern of differentiation is found among specimens of *B. cristatus* from these two areas.

## CHAPTER III

### GEOGRAPHIC VARIATION IN *BUFO VALLICEPS* (ANURA: BUFONIDAE), A WIDESPREAD LOWLAND MESOAMERICAN TOAD

#### INTRODUCTION

Savage (1982) recognized four general biogeographic assemblages in Mesoamerica: (1) Widespread Tropical; (2) South American; (3) Tropical Middle American; (4) Extratropical North American. Species in the Widespread Tropical component are distributed primarily in the lowlands; the distributions of these species (e.g., the snake colubrid *Lampropeltis triangulum*) sometimes also include substantial parts of North and South America. A common lowland distributional pattern encompasses the Atlantic Coastal Plain of Mexico and Central America, from extreme southern Texas southward along the Atlantic versant to Costa Rica or Panama. The distributions of some of these species extend across the low Isthmus of Tehuantepec in southern Mexico and continue northward and/or southward along the Pacific versant of Mesoamerica. This pattern is shared by many vertebrates, including birds such as the Red-billed Pigeon (*Columba flavirostris*) and Chachalacas (*Ortalis* spp.), and mammals such as the ocelot (*Felis pardalis*) and armadillo (*Dasypus novemcinctus*). Few of these species extends much further north than the lower Rio Grande River Valley at the USA-Mexico boundary, and the freshwater fish faunas of North and Mesoamerica apparently are sharply separated at a latitude near Río Soto la Marina, Tamaulipas (Espinosa-Pérez, et al., 1993). Although many anurans (e.g., *Smilisca baudinii*, *Phrynohyas venulosa*, *Hypopachus variolosus*) have the general tropical lowland distribution described above, the ranges of only two species (*Bufo valliceps* and *Rana berlandieri*) include areas both north of the lower Rio Grande River Valley and also as far south as southern Veracruz. Among anurans with predominantly tropical distributions, *B. valliceps* is notable because it occurs well north

of the zero-degree (Celsius) isotherm—located at a latitude near Río Soto la Marina, Tamaulipas (Rzedowski, 1994).

*Bufo valliceps* is a ubiquitous species that occurs in virtually all open habitats from extreme southwestern Mississippi, across Texas to the Big Bend region, southward along the Atlantic coast to extreme northeastern Costa Rica, and across the Isthmus of Tehuantepec and southeastward along the Pacific coasts of Chiapas and Guatemala, at elevations from sea level to 1700 m (Fig. 3.1). This distribution includes an enormous variety of habitats and climatic regimes—e.g., relatively aseasonal rainforests of eastern Nicaragua; dry and seasonally cold Chihuahuan desert of Val Verde County, Texas; wet and seasonally cool swamps of southern Louisiana; cool and perpetually wet Atlantic slopes of the Chiapas Highlands in Mexico; and hot and seasonally dry thorn forest in the upper Grijalva River Basin of Huehuetenango, Guatemala. However, *B. valliceps* seems to be ubiquitous open habitats, whether the grasslands are natural (e.g., the Texas Gulf Coast) or the secondary growth and pastures resulting from human activities in areas of former rainforest in eastern Guatemala (Mendelson, 1994). The habitat preference of *B. valliceps* resembles that of the well-known human commensal *Bufo marinus* (Zug and Zug, 1979) in that the toad is often abundant in villages and agricultural areas.

Studies of geographic variation of wide-ranging tropical anurans are relatively few, and many are now outdated because of collection of new material (e.g., the present study) or taxonomic rearrangements (e.g., *Rana pipien*; Hillis, 1988). Lee (1993) presented an insightful analysis of small-scale geographic variation in the hylid frog *Smilisca baudinii* along a drastic precipitation gradient on the Yucatan Peninsula, and addressed specifically the relationship between body size and local climatic regimes. Duellman (1970) provided succinct accounts of variation in Mesoamerican hylid frogs. Zug and



Zug (1979) briefly mentioned geographic size-variation in *B. marinus*, and Savage (1960) reported geographic variation in the tadpole of this species. Many authors (Stuart, 1954; Duellman, 1960; Porter, 1965; Lynch and Smith, 1966; McDiarmid and Foster, 1981; Mendelson, 1997a) have commented on geographic variation in *Bufo coccifer*, but the taxonomic problems associated with variation in this taxon have not been addressed adequately. The present study is an attempt to summarize geographic variation in *B. valliceps* across its enormous and varied range. This study complements that of K. R. Porter, but differs by considering the entire range of the species, excluding several populations that represent different species (Mendelson, 1997b, c), and by being based on more specimens than were available to Porter.

Porter (1962, 1963, 1964a, 1970) reviewed the taxonomic status, distribution, and geographic variation of *Bufo valliceps*, with special reference to Mexican populations. He acknowledged a great amount of morphological variation across its geographic range, especially with respect to overall size, skin texture, and development of cranial crests. Nevertheless, Porter (1970) chose not to recognize any of the subspecies that had been proposed—viz., *B. valliceps macrocristatus* Firschein and Smith from the Atlantic rainforests of Oaxaca; *B. valliceps wilsoni* Baylor and Stuart from the Grijalva Valley of Chiapas and adjacent Guatemala; and *B. valliceps microtis* Werner from Honduras. Subsequent to Porter's papers, more specimens from remote regions of southern Mexico have been collected; these specimens allowed for resolution of taxonomic problems pertaining to certain populations that were referred by Porter and others variously as *B. cavifrons*, *B. cristatus*, and *B. valliceps*. Mendelson (1994, 1997a,b) reviewed much of this newer material and recognized or described *B. macrocristatus*, *B. campbelli*, *B. spiculatus*, *B. tutelarius*, all of which had previously been confused, at least partially,

with *B. valliceps*. Mendelson (1997c) referred the taxon *B. valliceps microtis* to the synonymy of *B. coccifer*. Although it is clear that some of the morphological variation observed by Porter is attributable to species-level variation that occurs among these newly recognized species, the fact remains that *B. valliceps* has a large geographic distribution and exhibits remarkable morphological variation.

In the northern areas of its range, *B. valliceps* are larger than are conspecifics in southern Mexico and Central America (Porter, 1970). Blair (1963, 1972) commented generally on differences in dorsal color, throat color in males, and size among populations from northern and southern extremes of the range. Porter (1964a) summarized geographic variation in snout-vent length (SVL) and characteristics of the advertisement calls of males for populations from Texas through southern Mexico, and Porter (1962) summarized other morphological variation in these same populations. The remarkable level of variation in color patterns among individuals of *B. valliceps* from Nicaragua and the Yucatan Peninsula were discussed by Villa (1972) and Lee (1996), respectively. Finally, several authors (Porter, 1963, 1964a; Blair, 1966, 1972; Branson, 1995) have reported that the height of the cranial crests is directly correlated with the elevation at which a particular population occurs; this claim warrants specific attention and is discussed in more detail.

Herein, I summarize geographic variation in *Bufo valliceps*, and replicate part of Lee's (1993) analysis of variation in anuran body size along the precipitation gradient on the Yucatan Peninsula. I also address other apparent trends in morphological variation among populations of *B. valliceps*, and I discuss the remaining taxonomic issues of the status of *B. valliceps wilsoni* and *Bufo nebulifer* Girard.

#### MATERIALS AND METHODS

I surveyed specimens of *Bufo valliceps* from all areas of its range between Louisiana and Estelí, Nicaragua; I have not seen specimens from Mississippi, Arkansas, or Costa Rica, but rely on reports by others (Conant and Collins, 1991; J. M. Savage, pers. comm.) for the accuracy of these records. Note that for localities from the USA or Mexico only state or county designations are provided. The morphometric survey included only adult males from 19 populations (Fig. 3.2); sexual maturity was assessed by presence of nuptial excrescences and vocal slits. The following morphometric features were measured in a manner following that of Duellman (1970:fig. 2): snout-vent length (SVL); tibia length (TIB); foot length (FTL); head length (HL); head width (HW); tympanum width (TYMP). The following features were measured in a manner following that of Mendelson (1994): orbit diameter (ORB); eye–nostril distance (END); length of supratympanic crest (SPTYMP); length of parotoid gland (PARL); width of parotoid gland (PARL). The following features were measured in a manner following that of Lee and Crump (1981): femur length (FML); metatarsal length (ML); radioulna length (RUL); hand length (HDL). All measurements were taken with digital calipers, rounded to the nearest 0.1 mm, and log-transformed. Principal components analysis (PCA; covariance matrix), One-Way ANOVA, and Tukey's Method for Unplanned Comparisons were performed using MINITAB (Macintosh ver. 10.5; Minitab Statistical Software, 1995). Stepwise discriminant function analysis (DFA) was performed using the BMDP computer program.

## RESULTS

### *Geographic Variation in Size*

*Bufo valliceps* from the northern part of the range are substantially larger than most individuals of the species from southern Mexico and Central America. Differences in

mean SVL among the 19 populations are shown in Figure 3.2; ANOVA indicated significant differences among these populations ( $F = 42.29$ ;  $df = 18$ ;  $P < 0.0001$ ).

**Range-wide comparisons.**—The loadings resulting from a PCA of the 15 morphometric variables measured on adult males representing these 19 populations are displayed in Table 3.1. The first four principal components (PC) accounted for 89.4% of the variation. All of the loadings on the first PC were of the same sign and of similar magnitude and, therefore, seem to represent overall size and size-correlated variation among all variables. The remaining PCs represented nonsize-correlated variation within the sample. The PC II has a strong positive loading for SPTYMP and high negative loadings for PARL and PARW. The PC III also had similar high loadings for SPTYMP (negative loading) and PARL (positive loading), as well as relatively high negative loadings for PARW, FML, and TIB. The PC IV had a high negative loading for TIB and high positive loadings for END, and TYMP. Despite these strong loadings, plots of individual scores on PC I–IV showed little dispersion among the representatives of the populations. Therefore, I directed my efforts toward comparison of overall size using PC I as an indicator.

An ANOVA of scores on PC I revealed significant differences in overall size among the 19 populations between Texas and Estelí, Nicaragua ( $F = 37.95$ ;  $df = 18$ ;  $P < 0.0001$ ). Tukey's Method identified homogenous sets of these populations based on overall size (Fig. 3.3) and demonstrated a general trend of size-increase with increased latitude. However, this trend is not entirely consistent. For example, the sample from Brazoria County, on the Gulf Coast of Texas, is contained within sets that include samples from Guatemala and Nicaragua; likewise, the sample from Louisiana is contained within sets including populations from southern Mexico and Guatemala. The largest toads in this

analysis form a small set of two samples from central and western Texas. The sets containing the next overall largest toads included samples from most of the northern populations (excluding Louisiana and Brazoria County, Texas), as well as samples from Huejutla, Hidalgo (south of the Tropic of Cancer) and from Pueblo Nuevo X-Can, Quintana Roo, at the northeastern tip of the Yucatan Peninsula. A mid-sized group of sets includes a variety of disjunct localities including Louisiana, southern Texas, Cuautlapam (Veracruz), and two samples from near the base of the Yucatan Peninsula. The sets containing the smallest toads included samples from northern (Brazoria County, Texas), intermediate (Acayucan, Veracruz, and the Grijalva Valley of Chiapas and adjacent Guatemala), and southern localities (Nicaragua and the Pacific Coast of Guatemala). These results suggest that in the northern area of their range, *B. valliceps* are larger than those in the southern areas, but there is no smooth north–south cline in overall size.

These results provide conflicting evidence with respect to the hypothesis that anurans from more xeric environments are larger than those from more mesic areas. For example, the largest toads are from areas that receive little mean annual rainfall: 855 mm (Dallas, Texas; 1961–1990), 810 mm (Austin, Travis County, Texas; 1961–1990), and 472 mm (Del Rio, Val Verde County, Texas; 1961–1990). However, toads from areas receiving similarly scant amounts of rainfall were much smaller (Figs. 3.2, 3.3)—e.g., for example: 675 mm, Brownsville, southern Texas; 832 mm, Cintalapa, Chiapas (= Grijalva Valley; rainfall data from Johnson, 1990). The smallest toads did come from rather wet areas: 1220 mm (San Pedro Sula, Depto. Cortes, Honduras; 1944–1982); 2500 mm (Tapachula, Chiapas, [near Champerico, Guatemala]; Shelford, 1963); and 1740 mm (Veracruz, Veracruz [near Acayucan]; 1971–1980). However, Chinijá, Alta Verapaz, Guatemala,

receives about 4000 mm of rain each year (Duellman, 1963), and the sample of toads from this locality was not among the smallest in this study (Figs. 3.2, 3.3).

*Size variation along a precipitation gradient.*—The loadings resulting from PCA of the 15 morphometric variables from nine populations over the length of the Yucatan Peninsula are displayed in Table 3.2. The first four PCs accounted for 81.3% of the variation among the specimens included in the analysis. As with the overall analysis, all of the loadings on PC I are of the same sign and of similar magnitude and, therefore, seem to represent overall size and size-correlated variation among all variables. The remaining PCs represent nonsize-correlated variation within the sample. The second PC has a high positive loading for FML, PC III has high negative loadings for ORB and END, and PC IV has a high positive loading for HW. Despite these strong loadings, plots of individual scores on PC I–IV showed little dispersion among the representatives of the nine populations. However, there are significant differences in overall size among the samples of *B. valliceps*, as indicated by the results of an ANOVA on PC1 scores ( $F = 6.07$ ;  $df = 8$ ;  $P < 0.0001$ ). The mean score for PC I and standard deviation for each population, and the homogeneous subsets of populations identified by Tukey's Method are shown in Fig. 3.4. Toads from the more xeric northwestern portion of the peninsula (e.g., Mérida, Chichén Itza) are not significantly larger than those from the rainforests of Chinija, Guatemala (Fig. 3.4). In fact, the two populations that compose a distinct subset in this analysis are from opposite ends of the peninsula— La Libertad, El Petén, Guatemala, and Pueblo Nuevo X-Can, Quintana Roo. La Libertad lies in a savanna habitat having a relatively high, but seasonal, rainfall, whereas Pueblo Nuevo X-Can lies in a region that has unusually high rainfall compared to the rest of the northern peninsula (Lee, 1980).

**Discriminant Function Analysis.**—I performed an initial stepwise DFA of the 15 morphometric variables from the 19 sample populations of (Fig. 3.2). All variables except TIB varied significantly among groups ( $F < 0.05$ ) in the initial analysis; a second analysis that specified the 14-variable model for the canonical discriminant analysis was performed. Group means were different ( $F < 0.001$ ) at each step in the 14-variable model and 100 % of the variation was displayed on five canonical axes; the first two axes displayed 99 % of the variation (CAN I, CAN II; Fig. 3.5). Review of the standardized (pooled within-group variances) coefficients for the canonical variables (Table 3.3) reveals that dispersion on CAN I is primarily because of variance among groups in the following variables: snout-vent length; foot length; head width; orbit diameter; and eye-nostril distance. Dispersion on CAN II also was caused by variance in snout-vent length, foot length, and head width, but this axis also displayed dispersion caused by variance among groups in head length and parotoid width.

None of the 19 sample populations had 100 % correct classifications in the jackknifed classification matrix of the 14-variable model (Table 3.4). The samples with the highest percentage of correct classifications were Sample 11 (92.3%), Sample 5 (91.7%), Sample 1 (87.5%), and Sample 12 (82.1%). The samples with the lowest percentage of correct classifications were Sample 2 (13.3%); Samples 7 and 8 (25.0%), and Sample 3 (35.7%). The pattern of misclassifications (Table 3.4) indicates a slight geographic trend among the samples. Northern toads (Samples 1–8) tended to be misclassified as members of other northern samples. Toads from more southerly samples (Samples 6, 9) were primarily misclassified as members of either more northern or more southern samples, and southern toads (Samples 10–19) tended to be misclassified usually as members of

other southern populations, but also as members of any but the largest northern samples (Samples 3, 4, 7, 8).

### *Qualitative Comparisons*

There is considerable variation in external features of *Bufo valliceps*. As with the morphometric variation described above, there are some geographic trends, but inter-individual variation in dorsal pattern and skin texture obfuscate discrete characterizations of the different populations.

Toads from northern localities (e.g., USA, northern Mexico) are remarkably consistent in having a sharply granular dorsal skin texture, granular ventral skin, relatively small, ovoid or subtriangular parotoid glands, an indistinct lateral descending row of tubercles, and a relatively wide, distinct, middorsal pale stripe (Fig. 3.7). The dorsal pattern lateral to the middorsal stripe may be strongly marbled, with either dark brown or tan-yellow shades predominating, mostly pallid, or nearly uniform dull brown; usually, there is a distinct dorsolateral pale area, along the dorsal border of the lateral descending row of tubercles. The venter is always immaculate and may appear (in preservative) pale yellow, whitish, or dull tan. The lateral descending row of tubercles is bordered ventrally by a dark brown stripe that becomes thin or broken on the flanks.

The tubercles on all dorsal surfaces of the body are large, densely distributed, sharply pointed, and keratinized. Usually, there is a single keratinized apex surrounded by a granular patch of keratin and often these are coalesced into a keratinous blotch from which a pointed center arises. These tubercles give the toad a rough, granular texture. The ventral skin texture is granular with many tiny, pointed tubercles, each bearing a single keratinized apex. Males and females also have heavy layers of keratin on the peripheral surfaces of all cranial and facial crests. The parotoid glands may be relatively



large and ovoid, as in individuals from the Grijalva Valley, in Chiapas and adjacent areas of Huehuetenango, Guatemala (discussed below under *B. valliceps wilsoni*), or relatively small and distinctly triangular, as in some individuals from the Yucatan Peninsula. Most individuals, regardless of origin, have ovoid or subtriangular parotoid glands.

The color patterns among *Bufo valliceps* from southern Mexico and Central America are extraordinarily variable, even among individuals from a single locality. In some, the dorsal pattern is uniformly dark brown, or nearly so, with or without a thin, middorsal pale stripe, whereas in others, it is nearly uniformly tan and lacks dorsal markings. Other individuals are pale brown with distinct black or dark brown, paired markings, with or without a distinct interorbital bar, or pale brown with a complex marbled pattern of small dark brown blotches. Nearly every intermediate pattern and combination of the above extremes may be found among *B. valliceps* from Veracruz to Nicaragua. Laterally, all individuals have a dark area below the lateral descending row of tubercles. This dark area is wide, dark brown or pale gray, and extends from the tympanic area, or the level of the insertion of the arm, onto the flank; in some individuals, the dark area becomes diffuse and disappears anterior to the flank. The ventral pattern usually is dull cream with any number of diffuse or distinct dark markings that sometimes are expressed as a uniform dull gray area on the throat and pectoral area; few individuals have immaculate venters.

Southern toads have a smoother skin texture than do those from the northern areas. The tubercles on the dorsum of the body of southern toads are less numerous, low, round and bear a small patch of granular keratin; few individual tubercles are pointed, and some specimens have little keratin atop the dorsal tubercles. The ventral skin texture is smoother than in the northern toads, with many low, round tubercles; some southern

individuals have pointed and unkeratinized tubercles on the venter and, therefore, have a relatively granular ventral texture similar to that of the northern toads. The tubercles forming the lateral descending row may be indistinct or distinct, and low and round, or high and pointed. Few adults of either sex have keratin on the peripheral margins of the cranial crests; when present, the keratin is thin and brown, rather than black.

Northern and southern *Bufo valliceps* differ in overall size, color pattern, and skin texture. However, I have not identified a clear disjunction in the distribution that corresponds with these characteristic differences. Samples from northern Veracruz and southern Tamaulipas are intermediate in size (Figs. 3.2, 3.3; Sample 9) and have a mixture of color patterns and skin textures (among and within individuals) typical of both more northern and southern samples.

#### DISCUSSION

It is clear that there is considerable morphological variation in *B. valliceps* across its extensive range, and that there are few apparent trends that correspond with geographical parameters. These toads vary extremely in size, color pattern, parotoid gland shape, and skin texture. The inconsistent variation has caused many specimens to be misidentified and resulted in general taxonomic confusion with respect to several populations of crested toads in Mexico and Central America (Mendelson, 1994, 1997 *a,b,c*). The range of *B. valliceps*, as considered here (Fig. 3.1), includes both Central America and a substantial area of North America. Across this range, and indeed east-to-west from Louisiana to western Texas, populations of *B. valliceps* are subject to diverse environmental regimes of seasonal rainfall and freezing temperatures. Moreover, this toad occurs from sea level to at least 1700 m, and these populations are subject to

different local conditions of rainfall and cloud cover. Few clear morphological trends seem to be associated with these environmental variables.

### ***Body Size and Aridity***

Lee (1993) reviewed the theoretical literature that predicts that amphibians, because of their high rates of cutaneous evaporative water loss, presumably *should* adapt to arid environments by evolving larger body size in order to achieve a favorable surface-to-volume ratio. He also pointed out that no rigorous test of this prediction had been carried out prior to his work with the ubiquitous tropical treefrog *Smilisca baudinii*. Lee (1993) compared morphometric variables among samples of *S. baudinii* along a sharp precipitation gradient that exists on the Yucatan Peninsula. He found, contrary to the theoretical predictions, that there was no direct correlation between body size and aridity in this species and that, in fact, frogs from the more mesic base of the peninsula were larger than those from the more arid coastal tip. However, Lee (1993) did find that frogs from the drier, more seasonal areas have slightly smaller appendages—a finding consistent with the surface-volume desiccation argument. My analysis of overall size among samples of *B. valliceps* across the same precipitation gradient on the Yucatan Peninsula revealed that although there are differences in overall size among populations of *B. valliceps* in this area, these differences do not seem to be correlated with the precipitation gradient. Similarly, among samples from throughout the range of *B. valliceps*, there is considerable variation in overall size, and the largest toads were from relatively arid areas in Texas, Coahuila, and Nuevo Leon. However, toads from other arid areas, such as the Grijalva Valley in Chiapas, were quite small. Conversely, although the smallest toads did come from relatively wet areas, not all samples from wet areas were particularly small.

Lee (1993) discussed the inherent difficulty in adequately testing a seemingly simple hypothesis such as correlation between body size and aridity. The elegance of his study lies in the fact that he identified the Yucatan Peninsula as a perfect testing ground for such a study; it is a relatively small area and is nearly uniform with respect to elevation and temperature profile. The environments from which my samples across Mesoamerica originated differ substantially in nearly every environmental aspect—not the least of which includes relatively severe winters (with snowfall) at the northern periphery of the range. These climates are so different that I deem them incomparable. The great amount of morphological variation in *B. valliceps*, and the lack of obvious trends with respect to geography and climate, lead me to concur with Lee (1993) that simple predictions of correlation between morphology and climate are easier to generate than to demonstrate, and that such correlations simply are not relevant to Mesoamerican anurans.

#### ***Crest Height and Elevation***

A series of papers (Porter, 1963, 1964a; Blair, 1966, 1972; Branson, 1995) reported that there is a direct correlation between the height of the cranial crests and elevation, and use the population near Cuautlapam, Veracruz (near 1000 m in the Sierra Madre Oriental) as an example. These claims, presented without supporting data, seem to have their only basis in a figure presented in Porter's (1962:fig. 26) dissertation. Because the original data used to support this apparent correlation are not widely available, and because such a correlation between morphology and elevation would be interesting if true, I review Porter's (1962) treatment of the matter.

Porter's original figure (1962:fig. 26) is represented in Fig. 3.7; several points require attention. First, Porter's concept of *Bufo valliceps* included all specimens referable to *B. macrocristatus* (Mendelson, 1997a); this is a sexually dimorphic, montane species in

which females have dramatically enlarged crests. Other specimens that Porter referred to *B. valliceps* subsequently have been referred to other species such as *Bufo spiculatus*, which have larger cranial crests than *B. valliceps* (Mendelson, 1997b). Because Porter did not provide a list of the specimens included in his analysis, it is impossible to determine which, if any, of these other crested toads were mixed in with his samples of *B. valliceps*. Second, Porter apparently did not separate the sexes for his morphometric summaries; this is particularly unsettling because females are larger than males in overall size and may differ somewhat in certain proportions, especially in the case of specimens now referred to *B. macrocristatus*. Third, Porter (1962:5) did not describe adequately how he measured crest height; I abandoned my own attempts to measure this feature because I could not develop a repeatable measurement based on homologous landmarks. In summary, Porter's analysis of correlation between crest height and elevation is suspect because it seems likely that he included among his samples individuals referable to other species, including upland species with greatly enlarged crests; moreover, he did not account for sexual dimorphism in size, and he did not describe adequately his measurement techniques.

Pursuant to my concerns with Porter's methodology, it is interesting to note that, despite how the results have been presented in subsequent literature, there seems to be no actual direct correlation between crest height and elevation (Fig. 3.6). Comparison of the mean crest height/SVL ratios from below 200 m and near 1400 m indicates less than 1% difference, and the line between these two points probably does not have a slope near 1.0; Porter did not perform a regression analysis on these data. What is evident from this plot is a remarkable amount of variation in specimens from an elevation of about 1000 m;

most specimens of *B. macrocristatus* have been collected from near 1000 m of elevation (Mendelson, 1997b).

### *Taxonomic issues*

In a series of papers (Mendelson, 1994; 1997a,b,c), I have resolved much of the taxonomic confusion surrounding populations of crested toads that previously (and inconsistently) were referred to *B. cavifrons*, *B. cristatus*, and *B. valliceps*. I removed the taxon *B. valliceps macrocristatus* Firschein and Smith from the synonymy of *B. valliceps*, recognizing it as a full species, and transferred the taxon *B. valliceps microtis* Werner to the synonymy of *Bufo coccifer*. Two taxa remain to be considered—*B. valliceps wilsoni* Baylor and Stuart and *Bufo nebulifer* Girard.

Baylor and Stuart (1961) described the subspecies *B. valliceps wilsoni* based on a series of specimens collected by L. C. Stuart at Jacaltenango, Huehuetenango, Guatemala. This locality is in the upper Grijalva Valley, at the base of the Sierra de los Cuchumatanes. The region is quite dry and thorn scrub forest prevails. The key diagnostic features of this taxon are the presence of relatively large parotoid glands and short supratympanic crests. The authors were careful to compare their specimens with *B. valliceps* from many other areas, and chose a comparative specimen from El Petén, Guatemala to illustrate the distinctive nature of *B. valliceps wilsoni* (Baylor and Stuart, 1961:figs. 1, 2); they also cautiously pointed out that recognition of this new taxon was not meant to imply that all other populations referred to *B. valliceps* were conspecific. Their choice of a comparative specimen from El Petén exaggerates the distinctness of *B. valliceps wilsoni*, because some specimens from the base of the Yucatan Peninsula have unusually small and triangular parotoid glands, as does the specimen in their figure. When specimens from the Grijalva Valley are compared with specimens from other areas

of Mexico, the differences in the size and shape of the parotoid glands and the length of the supratympanic crests are less apparent. Nonetheless, L. C. Stuart's careful eye, particularly with respect to the stout nature of the supratympanic crests, prevails in this case. Individuals from the Grijalva Valley are consistently different from *B. valliceps* from other areas. However, I do not recommend recognition of the taxon *B. wilsoni* at this time.

Baird and Girard (1852) described *Bufo granulosis* based on a specimen collected "between Indianola and San Antonio," Texas, during the U.S.-Mexico boundary survey. Inasmuch as this name was preoccupied by *Bufo granulosis* Spix 1824, the replacement name *Bufo nebulifer* Girard 1854 was proposed. Peters (1863) placed *B. nebulifer* in the synonymy of *B. valliceps* Wiegmann 1833. The northern *B. valliceps* are larger and have a distinctive pattern and skin texture compared to *B. valliceps* from Central America; these differences perhaps warrant recognition of *B. nebulifer*. However, in light of the general variation in these continuous characters among and within populations of *B. valliceps*, and the lack of a discrete character by which to diagnose the northern and southern populations, I do not propose recognition of *B. nebulifer* at this time.

## CHAPTER IV

### A REVIEW OF THE GUATEMALAN TOAD *BUFO IBARRAI* (ANURA: BUFONIDAE), WITH DISTRIBUTIONAL AND TAXONOMIC NOTES ON *BUFO VALLICEPS* AND *BUFO COCCIFER*

#### INTRODUCTION

Stuart (1954a), in his description of *Bufo ibarraii*, focused his diagnosis primarily on differentiating this species from the widespread and similar species *Bufo coccifer* Cope. Since then relatively few additional specimens, all from Guatemala, have been collected; often these have been cataloged in museums as either *B. coccifer* or *Bufo valliceps* Wiegmann. Otherwise, attention to the status and biology of *B. ibarraii* has been limited mostly to its inclusion in checklists (e.g., Stuart, 1963; Frost, 1985; Campbell and Vannini, 1989). Porter (1966) described the advertisement call. Porter and Porter (1967) inferred placement of *B. ibarraii* in the *B. coccifer* group but Blair (1972), based on hybridization data published by Blair (1966), specifically disagreed with their argument and placed *B. ibarraii* in the *B. valliceps* group. Martin (1972) also placed *B. ibarraii* in the *B. valliceps* group based on the overall osteological similarity of these species. The *B. valliceps* group, regardless of the placement of *B. ibarraii*, is an assemblage of Central American toads that have conspicuous cranial crests (see Blair, 1972, for review).

Despite the paucity of attention to *B. ibarraii*, it has been an unacknowledged participant in a larger problem that has received considerable comment over the past 30 years—the taxonomic status of different populations of *B. coccifer* in Middle America.



This problem perhaps is complicated further by the fact that a long-ignored subspecific taxon of *B. valliceps* is herein shown to be a synonym of *B. coccifer*.

## MATERIALS AND METHODS

I examined external characteristics and the condition of the vocal slits of most of the specimens identified as *B. coccifer*, *B. ibarraii*, or *B. valliceps* from Guatemala in several major collections, including the types of the latter two species. Because of taxonomic problems associated with the name *B. coccifer* (see below), I have restricted my survey of comparative material of this species to specimens from Guatemala. Nevertheless, I have seen material from elsewhere and I am quite sure that *B. ibarraii* is not conspecific with any toad found elsewhere in Mexico or Central America. I considered specimens bearing nuptial excrescences and vocal slits to be males and determined the sex of other specimens by direct observation of the gonads. I took all measurements with digital calipers and rounded to the nearest 0.1 mm. General format and terminology follow that of Mendelson (1994, 1997). Terminology relating to the morphology of the vocal sac and related structures follows that of Tyler (1971*a, b*) and Carter (1979). Format and terminology of the tadpole description follows that of McDiarmid and Foster (1981). Names used for the faunal areas of Guatemala (e.g., Fuegan area) are those proposed by Campbell and Vannini (1989). Snout–vent length is abbreviated as SVL throughout. Museum acronyms are those proposed by Leviton et al. (1985).

## RESULTS

### A Review of *Bufo ibarraii*

*Bufo ibarraii* Stuart

Figs. 4.1–4.4

*Bufo coccifer*—Cope, 1887:11 (in part; for specimens from Guatemala City); Lynch and Smith, 1966:fig. 2 (in part; for records plotted in the Southeastern Highlands of Guatemala, but see comments below).

*Bufo microtis*—Schmidt and Stuart, 1941:238 (in part; UMMZ 84083 = *B. ibarra*).

*Bufo ibarra* Stuart, 1954a:162 (Holotype: UMMZ 108000, from Aserradero San Lorenzo [about 12 air line km slightly East of North of Jalapa], Jalapa, Guatemala, 1725 m).

The original description by Stuart (1954a) is thorough and adequately demonstrates this species to be distinct from other similar species, regardless of the taxonomic confusion surrounding *B. coccifer*. I will not duplicate his descriptive efforts herein, but I do present a rediagnosis that is somewhat more comprehensive than the original.

**Diagnosis.**—A large species of *Bufo* (males to 77.0 mm SVL; females to 94.4 mm SVL) having the following combination of characters: 1) tympanum evident externally, about 45% diameter of orbit in males, about 40% in females; 2) canthal, supraorbital, supratympanic, postorbital, parietal, preorbital, pretympanic, supralabial crests present, distinct; parietal crests low, thin, sharply angled medially; 3) tibia short, about 40% SVL; 4) feet short, about 40% SVL; 5) dorsal skin texture sexually dimorphic, females with scattered sharply pointed tubercles more concentrated laterally and on hind limbs, and males with dorsal tubercles round, nonpointed; 6) lateral descending row of enlarged tubercles indistinct, or absent; 7) vocal slit unilateral (sinistral or dextral); 8) *m. interhyoideus* poorly differentiated from *m. intermandibularis*, but differentiated posteriorly forming a large unilobed vocal sac with little or no pigmentation, lacking a medial septum; 9) snout shape rounded in lateral view, weakly pointed in dorsal view; 10) cranial crests distinct, thick, with globular texture on large individuals, except parietal

crests, which are thin, low, weak, especially in males; 11) parotoid glands large, ovoid, length about twice that of eyelid, protuberant; 12) skin on top of head between cranial crests usually smooth, lacking tubercles.

The presence of a unilateral vocal slit in males distinguishes *B. ibarraii* from most other species of *Bufo* in Mexico and northern Central America. *Bufo coccifer* is similar to *B. ibarraii* and has a unilateral vocal slit, but is a smaller species (males to about 60 mm SVL, females to about 70 mm SVL; Fig. 4.4) in which there is no sexual dimorphism in skin texture. Both sexes in *B. coccifer* have dorsal skin texture similar to that of female *B. ibarraii* (Fig. 4.3), with numerous dorsal tubercles that are rounded and protuberant middorsally, becoming more concentrated and more pointed laterally. Furthermore, *B. coccifer* differs by usually having few or many tubercles on the skin between the cranial crests on the top of the head (this area usually smooth in *B. ibarraii*), and always having smaller, round parotoid glands, and a darkly pigmented vocal sac. *Bufo bocourti* is a superficially similar species from the highlands of Guatemala and Chiapas; however, it may be distinguished easily from *B. ibarraii* by lacking external tympana and vocal slits. *Bufo luetkeni* has a unilateral vocal slit and a lateral row of enlarged tubercles, but these tubercles may be indistinct in some individuals; however, *B. luetkeni* differs from *B. ibarraii* by having small, usually round, parotoid glands that are about 50% size of the eyelid, or smaller, and by having a relatively long, straight, and thin supratympanic crest rather than a short thick, somewhat globose condition as in *B. ibarraii*. *Bufo valliceps* has bilateral vocal slits, thinner cranial crests, a distinct lateral row of enlarged tubercles, and less protuberant, usually triangular, parotoid glands.

**Variation.**—Morphometric variation is summarized in Table 4.1. All specimens examined have a pale middorsal stripe that may be narrow with straight margins (e.g.,

CAS 70753) or wide with wavering margins (e.g., CAS 70727). All specimens have a pale interorbital mark that is bordered anteriorly and posteriorly by associated less distinct dark markings; usually the pale interorbital markings are distinct, but in few individuals (e.g., MVZ 143357) they are indistinct. Some individuals (e.g., MVZ 143351 [male], KU 190067 [female]) of either sex have a dorsal pattern that includes a pair of wide pale stripes that extend posterolaterally along the dorsal margin of the lateral row of tubercles (if present) from the posterior margin of the parotoid gland and become indistinct on the flank. Typically, females have a dorsal pattern that consists of a contrasting array of irregular black, brown, gray, and cream markings arranged in a somewhat bilateral fashion on either side of the middorsal stripe. These markings become less distinct laterally and grade into the ventral coloration which is uniform dull cream with few irregular and indistinct gray markings. Males are generally more pallid, with an indistinct array of brown and dark gray, somewhat bilateral, markings over a dorsal ground color of dull gray or pale brown.

Most specimens have no tubercles on the skin between the cranial crests, but a few specimens do have a small number of these tubercles (e.g., KU 190069). Despite this low level of variation, these tubercles are a rather useful diagnostic character for distinguishing this species from *B. coccifer*. Sexual dimorphism in dorsal skin texture (females with spinose tubercles, males with rounded tubercles; Fig. 4.3) is consistent among all individuals examined. The texture of the skin on the venter of females is uniform with small granular tubercles bearing tiny keratinized apices; however, males may have smooth venters with an areolate texture (e.g., MVZ 143343) composed of tubercles lacking keratinous apices, or a ventral skin texture similar to that of females (e.g., MVZ 143357). Perhaps ventral skin texture in males varies depending on the

reproductive state of the individual, as described for some species of *Bufo* from Africa (Inger and Greenberg, 1956). However, contrary to the condition described by Inger and Greenberg (1956), dorsal skin texture in males appears always to be nonspinose, regardless of reproductive state. For example, the males in a series (KU 97595–609) of *B. ibarraii* were calling when they were collected (Porter, 1966:62) and all have dorsal tubercles that lack keratinous apices.

All adult males have a unilateral vocal slit. Among 54 males from a large series (CAS 70719–825) from Volcán Agua, Guatemala, the vocal slits were dextral in 22 specimens, and sinistral in 32 specimens.

**Reproductive biology.**—Stuart (1954b:44) tentatively referred a lot (UMMZ 139516; G. Schneider, personal communication) of tadpoles collected at Finca Bucaral, Depto. Progreso, on the south slope of the Sierra de las Minas, to *B. ibarraii*; he collected no other species of *Bufo* at this locality. He commented that they were similar to the tadpoles of other species of *Bufo* in Guatemala, except *B. bocourti*, but that they were somewhat paler in color and had a "...much shorter outer tooth row than I have observed in tadpoles of other species of the genus." I have examined these tadpoles and, although they are not well preserved, I concur with Stuart that these are the tadpoles of *B. ibarraii*. With the assistance of J. A. Campbell I have referred several other lots (see below and Appendix I) of tadpoles to this species. In no case was it possible to associate directly metamorphosing individuals to an adult morphology; however, in each case the tadpoles have a consistent morphology distinct from that of any other *Bufo* tadpole in the local area and, in a few cases, *B. ibarraii* is the only toad known from the area.

**Description of tadpole:** The following description is based on three tadpoles at Gosner (1960) Stages 35–38 chosen at random from a lot (UTA A-39114). Body ovoid in dorsal

view, widest anterior of midlength; snout hemispherical in dorsal profile, rounded in lateral profile; eyes dorsal, directed laterally, separated by a distance about 2 times eye width in dorsal view; nostrils large, almost 50% diameter of eye in lateral view, directed dorsally, slightly closer to eye than to tip of snout. Spiracle sinistral at about level of longitudinal axis, short, angled posterodorsally, outer wall shorter than inner wall. Vent tube short, right and left walls attaching at same site, ventral wall slightly longer than other walls, attached to ventral fin medially, tube lays to dextral side despite medial attachment. Caudal musculature widest at base, gradually tapering to pointed tip, tip ending before posterior margin of caudal fin, not raised distally. Caudal fin moderately developed, extending to base of caudal musculature, tip rounded; dorsal fin slightly higher than ventral fin, highest just anterior to midlength of tail; ventral fin nearly uniform height throughout its length.

Mouth small, anteroventral, emarginate laterally with wide dorsal and ventral gaps in uniserial marginal papillae. Tooth row formula  $2(2)/3$ ,  $A-1 = A-2 > P-1 = P-2 > P-3$ ;  $A-2$  gap wide, equal to one-fourth length  $A-1$ . Upper jaw moderately wide, finely serrate, medial part shallowly convex, lateral processes taper abruptly posterolaterally; length of lower jaw about equal to length of upper jaw, finely serrate, shallowly V-shaped.

In preservative (10% buffered formalin), body uniform pale brown dorsally, melanophores becoming large, discrete, ventrolaterally; lateral areas of venter with distinct pigmentation, covering outer 2–5 coils of intestine, other ventral surfaces unpigmented except for few, isolated small clusters of large melanophores. Caudal musculature nearly uniform pale brown, with slight tendency towards mottling ventrally. Dorsal fin transparent with pale brown pigmentation forming an indistinct mottled

pattern, becoming more concentrated dorsally; pattern on ventral fin similar to that of dorsal fin, but pattern restricted to posterior half of fin.

The tadpole of *B. ibarra* is nearly identical to that of *B. coccifer* from Costa Rica, as described by McDiarmid and Foster (1981). The former seems to differ by having larger nostrils, uniform (rather than saddled) coloration on the caudal musculature, more extensive ventral pigmentation, and perhaps by having a functionally dextral (rather than strictly medial) vent tube. However, judgment of the condition of the vent tube is somewhat subjective and can be difficult to determine on some specimens; I have not examined positively identified tadpoles of *B. coccifer*.

**Breeding behavior:** Porter (1966) collected a series of *Bufo ibarra* from breeding congregations on 29 June and 22 July; he observed males calling from the banks of ponds. Most of the many specimens collected near Purulhá, Baja Verapaz, have been collected near a large marsh that existed there until about 1990, at which time the marsh was channeled and treated with chemicals to control mosquitoes (J. A. Campbell, personal communication); no individuals have been observed in this area since 1990. Stuart (1954*b*) mentioned breeding activity by this species in water holes and wet meadows in early June; tadpoles (UTA A-39114) were collected from a small pond near Jalapa, Jalapa, on 27 July.

**Distribution.**—*Bufo ibarra* is known from scattered localities at moderate elevations (1360–1980 m) in the pine-oak zone of southern and central Guatemala (Fig. 4.5). It is known in the Southeastern Highlands (*sensu* Stuart, 1954*b*) from the vicinity of Guatemala City and eastward to the area around Jalapa, Depto. Jalapa. There are no records from the region east of Jalapa, in the Departments of Santa Rosa, Jutiapa, and Chiquimula, where the Southeastern Highlands become progressively lower and more

xeric (Stuart, 1954*b*; Campbell and Vannini, 1989). It seems that *B. ibarra*i is replaced by *B. coccifer* in these lower dry forests and grasslands (Stuart, 1954*a, b*; Fig. 4.5). There are many records from the western end of the Sierra de las Minas, near Purulhá (see Appendix I) and two records (KU 186305; UMMZ 126307) from the western area of the Sierra de Chuacús. These records suggest a continuous distribution, in appropriate habitat, north of the Río Motagua along the Chuacús-Minas highland formation. There are a few records from moderate elevations along the southeastern flank of the Sierra de los Cuchumatanes. These records are from along the northern drainages of the upper Río Negro system, near Aguacatan and San Pedro Necta, Depto. Huehuetenango, and southwest of Huehuetenango (see Appendix I). Stuart (1954*c*) described pine-oak habitat at moderate elevations along this drainage. There is a series of specimens (MVZ 143343–57) from La Libertad—just west of these latter records, but in the upper Río Selagua drainage of the Montañas del Cuilco. Finally, I have examined the single specimen (UMMZ 84083, 1 km S San Gerónimo, Depto. Progreso) purportedly from the arid Salamá basin that Schmidt and Stuart (1941) originally referred to *Bufo microtis* and that Stuart (1954*a*) later referred to *B. ibarra*i. I concur with Stuart's final identification, however I suspect that this specimen came from pine-oak habitat (perhaps slightly more distant than 1 km S of San Gerónimo) rather than the actual floor of the basin itself, where Schmidt and Stuart (1941) described arid conditions that are quite unlike the pine-oak habitat from which all other specimens of *B. ibarra*i seem to have been collected. Indeed, in a photograph taken from just south of San Gerónimo (Schmidt and Stuart, 1941:fig 21) it is clear that sparse pine-oak habitat does occur on the slopes that surround the Salamá basin; Schmidt and Stuart (1941:236) briefly described pine-oak conditions in this area; no other specimens of *B. ibarra*i have been collected from this region.



Many areas of Guatemala require much more fieldwork before the distributions of the native herpetofauna can be considered to be "known" (Campbell and Vannini, 1989). Therefore, care must be taken when considering apparent absences of certain species from particular areas. Nevertheless, it is interesting that there are no records of *B. ibarra* from what seems to be suitable habitat in the southwestern highlands (= the Chimaltenangan area), the Fuegan area, and the Quecchian area. The highlands of Alta Verapaz comprise the Quecchian area and are contiguous with the Sierra de las Minas along the divide that separates the Río Polochic and Río Chixoy drainages. *Bufo ibarra* is not known from the relatively well documented Quecchian area (see Stuart, 1948, 1950, for review), whereas it is known from the western end of the Sierra de las Minas. It seems likely that this species actually does not occur in the Quecchian area. This same distributional pattern obtains for the snake *Rhadinaea godmani*; however, *Rhadinaea hempsteadae* does occur in both areas (Mendelson and Kizirian, 1995).

**Etymology.**—The specific epithet is a patronym for Sr. Jorge A. Ibarra, Director of the Museo Nacional de Historia Natural de Guatemala, and a friend of L. C. Stuart. Stuart's choice of name seems particularly appropriate because this species seems to be endemic to Guatemala.

**Remarks.**—Specimens referred to *B. nebulifer* (= *B. valliceps*) by Salvin (1860:460) from Dueñas, Guatemala, may represent *B. ibarra*; presumably these specimens are deposited in the BMNH, but I have not examined them. According to J. A. Campbell (personal communication), it is likely that *B. ibarra* is the common toad around Dueñas, and I have seen specimens (TNHC 31344, 31378–80) from this locality.

Stuart (1954a:163) described the condition of the vocal slits in *B. ibarra* as "Vocal slits conspicuous." Inasmuch as this statement appears in the description of the holotype

section of his paper (i.e., Stuart was not referring to the condition of the slits in the species in general), I must assume that Stuart did not notice that there was only one vocal slit. Apparently, Lynch and Smith (1966:21) committed the same error when they referred to multiple vocal slits in the description of *B. cycladen*; the holotype (UIMNH 57142) has a unilateral (dextral) vocal slit. Liu (1935) listed *B. coccifer* as having both unilateral and bilateral vocal slits, without mentioning specific specimens. Although my survey of *B. coccifer* is incomplete, I have observed only unilateral slits in the various specimens I have examined from throughout its range. In specimens of *Bufo* with unilateral vocal slits, I have noticed that there usually is a corresponding shallow groove on the side lacking a slit. Perhaps it is possible to mistake this groove for a fully developed vocal slit.

The vocal sac of *B. ibarra* (KU 97617, adult male with nuptial excrescences) is large and overlies the pectoral musculature in the space between the post-mandibular and pectoral septa. There is no medial septum in the sac, and therefore the single vocal slit communicates with the entire sac. This morphology is similar to that described and illustrated by Inger and Greenberg (1956) for *Bufo regularis*. The large size of the vocal sacs of the specimens of *B. ibarra* that I examined suggests that the sac is capable of considerable expansion when inflated; however, I have not observed calling males of this species. McDiarmid and Foster (1981) reported that the vocal sac of calling male *B. coccifer* in Costa Rica becomes greatly inflated; my observations indicate that the morphology of the vocal sac of this species is similar to that of *B. ibarra*. The vocal sac of *B. ibarra* may be unpigmented (KU 97613, 97616), or may have scattered patches of pigmentation. The vocal sac of *B. coccifer* is uniformly and heavily pigmented such that

the sac appears as a dark patch through the submandibular skin; the vocal sac of *B. ibarra* is not visible through the skin.

#### THE PROBLEM OF *BUFO COCCIFER* AND *BUFO VALLICEPS MICROTIS*

*Taxonomic confusion surrounding Bufo coccifer.*—A sporadic debate, mainly in the form of brief comments, has developed in the literature (e.g., Stuart, 1954a, 1963; Duellman, 1960; Porter, 1965; Zweifel, 1965; McDiarmid and Foster, 1981) concerning the taxonomic status of populations of *B. coccifer* throughout its extensive range. Lynch and Smith (1966) described the Mexican population as *Bufo cycladen*, and Porter (1967) subsequently suggested that this taxon is a *nomen dubium*. Nevertheless, *B. cycladen* is in the recent checklist of Mexican species by Liner (1994), but not in that by Flores-Villela (1993). Clearly, the problem of the taxonomy of *B. coccifer* requires further attention that is beyond the scope of this paper. However, the confusion regarding *B. coccifer* is relevant to the present review of *B. ibarra*.

In the original description, Stuart (1954a) was careful to adequately diagnose *B. ibarra* from the similar and nearly sympatric population of *B. coccifer* in the Department of Jalapa, Guatemala. However, previous to the description of *B. ibarra*, Schmidt and Stuart (1941) referred a single specimen (UMMZ 84083) to *Bufo microtus* [sic] Werner; Stuart (1954a:162) later referred this same specimen to *B. ibarra*. Werner (1896) proposed the trinomial *Bufo valliceps* var. *microtis* based on a single specimen from "Honduras." Kellogg (1932:70) provided additional descriptions and measurements from the holotype (ZMB 13200, an adult female) and listed the trinomial in the synonymy of *B. valliceps*. Stuart (1954a:162) commented on the vague nature of the original description and suggested that, "Reexamination of the type may reveal that Werner was naming the Honduranian and Guatemala populations of '*coccifer*';" however,

Stuart did not examine the type specimen. This possibility apparently was not considered by Lynch and Smith (1966) or Porter (1965, 1967). Indeed, in his reviews of Mexican *Bufo* and *B. valliceps*, Porter (1963, 1970) declined to recognize any of the proposed subspecies of *B. valliceps*, including *B. v. microtis*. Porter (1970:94.2) placed *B. v. microtis* in the synonymy of *B. valliceps* because the "type-locality of *microtis* is not well defined and specimens from Honduras will key to *valliceps* ..." Evidently, Porter did not examine the holotype of *B. v. microtis* because, as Stuart (1954a) predicted, it is referable to *B. coccifer* based on the characteristic nature of the cranial crests, parotoid glands, and texture of the skin (Fig. 4.6). Therefore, this trinomial should be removed from the synonymy of *B. valliceps* and added to that of *B. coccifer*. Determination of whether *B. coccifer* has precedence over *B. cycladen* for the Mexican, and perhaps the Guatemalan, populations is unclear and must await a long overdue review of *B. coccifer*.

Lynch and Smith (1966) were careful to compare specimens from the population they named as *B. cycladen* with arguably topotypic specimens of *B. coccifer* (for which the type locality is unclear; see Dunn and Stuart, 1951, for review) from Costa Rica. However, Porter (1967) listed several apparent inconsistencies in their review of geographic variation in *B. coccifer*. Based on the localities indicated in the Southeastern Highlands of Guatemala on the map presented by Lynch and Smith (1966:fig. 2), it is possible that they included some misidentified specimens of *B. ibarraei* among their comparative samples of *B. coccifer* (*sensu lato*) and that this is partly responsible for the problematic (*fide* Porter, 1967) diagnosis of *B. cycladen*. However, Porter (1967) did not suggest this possibility and, because Lynch and Smith (1966) did not list the specimens they examined, I cannot verify this suspicion. Nevertheless, given the great

number of misidentified specimens of *B. ibarrae* that I have encountered in collections, it does not seem an unreasonable possibility.

***Distributional notes on Bufo coccifer and Bufo valliceps in Guatemala.***—The most recent distributional information on *B. coccifer* in Guatemala is that provided by Campbell and Vannini (1989), who listed this species as occurring in the Sierra de Chuacús-Sierra de las Minas formation, the Jalapan area (= the Southeastern Highlands), and along the Pacific coastal plain. My survey corroborates this distribution except that I have referred all *B. coccifer*-like specimens that I have seen from the Sierra de Chuacús and Sierra de las Minas to *B. ibarrae*. Thus, *B. coccifer* is known in Guatemala from relatively few localities in two areas: in the Southeastern Highlands from the lower, more xeric areas between the towns of Jutiapa, Jalapa, Esquipulas, and Concepción las Minas, and from near Champerico, Depto. Retalhuleu, and Escuintla, Depto. Escuintla, on the Pacific coastal plain (Fig. 4.5). The southeastern Pacific coastal plain is covered with dry forest habitat contiguous with that of the Southeastern Highlands, and this species may occur along the extreme southeastern coast of Guatemala. However, the coastal plain becomes progressively more mesic to the northwest—toward Champerico and the Mexican border (Campbell and Vannini, 1989). *Bufo coccifer* often is considered an inhabitant of scrub forest (Porter, 1963), and Stuart (1954*b*) commented on the apparent variety of habitats in which this species has been collected—if indeed, they all represent the same species. Porter (1963:fig.3) showed no records of *B. coccifer* along the Pacific coastal plain of Guatemala, and only one from the adjacent plain of Chiapas, Mexico; Johnson (1989) listed this species as occurring in this area of Chiapas, but I have examined no specimens from there.

The biogeography of the herpetofauna inhabiting the subhumid areas of Guatemala was thoroughly reviewed by Stuart (1954c) and Campbell and Vannini (1988a). Stuart (1954c) described a relatively continuous subhumid corridor that connects similar xeric habitats in the Southeastern Highlands, the Motagua Valley, the Salamá Basin, and the upper Grijalva Valley in Guatemala. He cited the distributions of several species (e.g., *Sceloporus variabilis*) as indicators of the biogeographic continuity of these areas. As evidence of biogeographic continuity over the few upland pine-oak habitats that separate the major subhumid areas in Guatemala, Stuart (1954c:20) cited the distribution of "a chain of *Bufo coccifer*-like toads," specifically referring to the as yet undescribed *B. ibarraí*. However, *B. coccifer* has never been found in either the Motagua Valley or the Salamá Basin. I am unaware of specimens of *B. coccifer* from the Grijalva Valley, and Johnson (1990) was unclear regarding the presence and distribution of this species in this valley; Porter (1963:fig. 3) did not record specimens from the Grijalva Valley. In another biogeographic scenario, Campbell and Vannini (1988a) reviewed evidence supporting the previous existence of a Pacific coastal subhumid corridor—presently interrupted by mesic conditions that occur from central coastal Chiapas, Mexico, to central coastal Guatemala—and proposed that this hypothesis best explains the present distribution and differentiation of *Heloderma* in the region. The present information on the distribution of *B. coccifer* corroborates the hypothesized Pacific Subhumid Corridor.

The distribution of *B. valliceps* in eastern Guatemala includes the entire Petén area (Campbell and Vannini, 1989) and extends up the Polochic Valley past the town of Tukurú, Alta Verapaz (see Appendix I). However, in the Motagua Valley this species occurs only in the mesic area generally east of the Zacapa/Izabal departmental border (see Appendix I). Schmidt and Stuart (1941) and Stuart (1948, 1950) noted that this

species does not occur in even slightly arid areas in eastern Guatemala, such as the Río Cahabón and upper Río Motagua valleys; my observations corroborate this distributional pattern. In areas such as the lower Polochic Valley of eastern Guatemala, *B. valliceps* is present in every variety of habitat in the region, but is especially abundant in disturbed areas associated with coffee production, *milpas*, pastures, and human settlements (Mendelson, 1990, 1994). *Bufo valliceps* does not occur in the highland areas of central Guatemala, and its distribution on the Pacific versant of Guatemala cannot be explained easily (see below). Many other records of this species have been reported (e.g., Porter, 1970), but I have found that usually these records are based on specimens that have been misidentified (often they actually are *B. ibarraí*), or that I have elsewhere (Mendelson, 1994, 1997) determined to represent undescribed or unrecognized species (e.g., *Bufo campbelli*, *Bufo macrocristatus*).

I have examined specimens of *B. valliceps* from relatively few localities along the Pacific Coast of Guatemala, two records from the Southeastern Highlands, and a single record from the southern base of the Montañas del Cuilco (see Appendix I; Fig. 4.5). The records of *B. valliceps* from the Pacific Coast of Guatemala suggest that it occurs along the entire coastal plain and well up onto the piedmont of the Volcanic Cordillera. However, this area is relatively well known (Campbell and Vannini, 1988a), and there are far fewer records from the coastal plain than one would expect for a toad that is usually conspicuous and ubiquitous wherever it occurs. Furthermore, it seems to be absent in areas apparently similar to those on the Atlantic versant where it is abundant. For example, Campbell and Vannini (1988b) reported on a comprehensive survey of the herpetofauna of a coffee *finca* on the Pacific slope of Volcán Santa María; *B. valliceps* was not found at this locality. Whereas in a less comprehensive survey (Mendelson,

1990) of similar habitats in the Polochic Valley, this species was found to be abundant. I can offer no geographical or ecological explanations for the paucity of records and scattered nature of the apparent distribution of *B. valliceps* on the Pacific versant of Guatemala.



## CHAPTER V

### A PHYLOGENETIC ANALYSIS OF MIDDLE AMERICAN TOADS (ANURA: BUFONIDAE), WITH SPECIAL REFERENCE TO THE *BUFO VALLICEPS* GROUP

#### INTRODUCTION

Many of the relevant species of *Bufo* were described in the 19<sup>th</sup> Century; however, it was not until 1950 that an attempt was made to organize the Middle American taxa into species groups. Firschein (1950) proposed the *Bufo valliceps* Group (content: *Bufo cristatus* and *B. valliceps*) and the *Bufo cristatus* Group (content: *Bufo cavifrons* and *B. cristatus*). Firschein did not consider the relationships of several other crested toads (e.g., *B. mazatlanensis*) and his taxonomic arrangement is unclear because he placed *B. cristatus* simultaneously in two different groups. Subsequently Blair (1959, 1961) alluded to a *B. valliceps* Group, but did not define it. Based on osteology, Tihen (1962) provided an explicit proposal of the content of the *B. valliceps* Group and divided it into "South American" and "Mexican" sections. Blair (1966) disagreed with Tihen claiming that he (Blair, 1959, 1963) already had proposed the content of a *B. valliceps* Group—a claim that is not justified in Blair's earlier papers. Blair (1966) provided a summary of the group whose content somewhat matches that of Tihen's (1962) "Mexican Section." Porter (1962, 1963) provided a thorough review of the species in Mexico. In major works on the *Bufo valliceps* Group since 1950, 19 species have been assigned to the group by one or more authors (Table 5.1). These various discussions and proposals for the *B. valliceps* Group are phenetic assemblages (e.g., Duellman and Schulte, 1992) based on overall similarity and (apparently) geographic proximity of the included species.

The historical reality of the most species groups within the large genus *Bufo* never have been tested in a phylogenetic context. Recently, Graybeal (1997) provided evidence to support the monophyly of the *Bufo boreas* Group of western North America. However, Morrison (1994) found no evidence to support the monophyly of the *Bufo spinulosus* Group of South America,

Most authors (Table 5.1; and summarized by Frost, 1985, pers. comm.) have included some, most, or all of the Middle American toads bearing a conspicuous array of cranial crests (Figs. 5.1,5.2) in the *B. valliceps* Group. Porter (1962, 1964) reviewed some of the populations of the widespread species *B. valliceps* and concluded that the proposed subspecies (*B. valliceps microtis*, *B. valliceps macrocristatus*, and *B. valliceps wilsoni*) were insufficiently distinct to deserve recognition and he expanded Firschein's (1950) concept of *B. cavifrons* to include three allopatric populations. Nevertheless, Taylor and Smith (1945), Stuart (1954), and Blair (1972) all commented on the extraordinary morphological variation among populations of *B. valliceps*. Against this background of research, and taking advantage of a wealth of recently collected material from remote areas of Middle America, I have reviewed several apparent taxonomic problems among these toads and described several new species (Mendelson, 1994, 1997a-c).

The systematics of the species generally referred to the *Bufo valliceps* Group (Frost, 1985, pers. comm.) have received little attention since Porter (1962, 1964) reviewed the Mexican species and speculated about their evolution. Blair (1966) reported the results of hybridization experiments involving members of the Group and reviewed (Blair, 1972) previously published opinions regarding the group. Porter (1970) reviewed the literature pertinent to *B. valliceps* and presented a complete distribution map; Savage, (*in* Frost, 1985:52) pointed out that some of Porter's (1970) records from Guatemala, El Salvador,

Nicaragua, and Costa Rica are based on misidentified specimens of *Bufo luetkeni*. In two studies of the evolution of *Bufo* based on immunological distances, Maxson et al. (1981) and Maxson (1984) used a few species to represent the *B. valliceps* Group (sensu Blair, 1972, and Cei, 1972).

The taxonomic history of Bufonidae is fraught with paraphyletic and monotypic genera (Graybeal and Cannatella, 1995). The definition and membership of the phenetic species groups within *Bufo* have never been agreed upon by any two authors. Graybeal's (1997) recent molecular analysis of the phylogeny of Bufonidae was successful in identifying several major lineages within the family, but this analysis was necessarily at such a scale that tests of the monophyly of all species groups within *Bufo* were not possible. Nevertheless, the results of Graybeal's (1997) analysis do support a monophyletic *Bufo boreas* Group and do not support recognition of others (e.g., *B. cognatus* Group) as they are usually considered (Frost, pers. comm.). Herein, I present evidence from a phylogenetic analysis of morphological characters to support recognition of a monophyletic *B. valliceps* Group. Although the content of this group has never been agreed upon, the total list includes 19 species and, as such, includes most of the species of *Bufo* in Middle America. Certainly, the systematics of these species is crucial toward understanding the history of anuran evolution in Middle America.

#### MATERIALS AND METHODS

I identified and scored 45 morphological characters (described below) from 36 bufonid and four leptodactylid species. Of the species of *Bufo* included, 15 have been included in the *B. valliceps* Group (Table 5.1). Most of these transformation series were identified during my own surveys of skeletal and preserved specimens; however, a few characters were modified from those analyzed by Morrison (1994). All character states

in this analysis were scored directly from specimens; no data were taken from the literature except for information regarding the inguinal fat bodies and the sternum, which were taken from da Silva and Mendelson (*in press*). Some character states could not be coded because the bone was absent in a particular species (e. g., the nature of the medial head of the neopalatine in species that lack neopalatines). In these cases of logical inconsistency, the relevant characters were coded as unknown (?). When possible, multiple specimens were examined in order to assess individual variation. In the few cases in which multiple character states were observed among individuals, the character was coded as polymorphic to account for all observed conditions. All characters were treated as unordered and equally weighted. The complete data matrix appears in Table 5.2.

There are many unresolved taxonomic problems among the species of Bufonidae. For example, the myriad of forms presently referred to the species *Bufo typhonius* clearly represent several distinct species (Hoogmoed, 1986, 1990; Duellman and Mendelson, 1995); Santos-Barrera (1995) suggested that *Bufo occidentalis* also represents a complex of species. In these cases, I limited my examination of specimens (whole and skeletal) to apparently similar specimens from a limited area, in an attempt to insure that I have not confounded my analysis with unacknowledged species-level variation.

Many genera and species groups in Bufonidae lack evidence of monophyly (Graybeal and Cannatella, 1995). This analysis was designed only to test the monophyly of the *Bufo valliceps* Group. The general analysis was designed following the outgroup selection criteria of Nixon and Carpenter (1993). The designation of the ingroup (Bufonidae) was based on evidence of its monophyly provided by Graybeal and Cannatella (1995). Trees resulting from the parsimony analysis (below) were rooted

using an outgroup vector based on observations of character transformation series from four leptodactylid species (*Ceratophrys ornata*, *Leptodactylus pentadactylus*, *Odontophrynus americanus*, and *Telmatobius hintoni*). When unequivocal polarities could not be argued (i.e., character states differed among the four outgroup species), the outgroup vector was coded as unknown (?) for that character transformation series. I used leptodactylids as outgroup species based on the results of analyses by Ford (1989) and the summary by Ford and Cannatella (1993) that indicate that Leptodactylidae is paraphyletic with respect to Bufonidae. Because there is no evidence to suggest which “leptodactylid” taxa are closest relatives to Bufonidae, so I chose four species that differ in overall morphology and for which skeletal material was available. In order to test the monophyly of the *Bufo valliceps* Group (sensu Blair, 1972) with respect to other bufonids, I included species from Middle America as well as species from North America, South America, Europe, Asia, and Africa; I have not assumed that the species of the *B. valliceps* Group would be restricted to Middle America.

The phylogenetic analysis using all characters was performed using PAUP ver. 3.1.1 (Swofford, 1993) on a Power Macintosh 9500/120. A heuristic search was performed using Tree-bisection-reconnection (TBR) branch swapping, with 1000 random addition sequences (starting seed = 754773; randomly chosen) and saving all minimum length trees at each replicate. All character transformation series were assumed to be unordered. MacClade (Maddison and Maddison, 1992) was used to enter, edit, and manipulate the data matrix and also to trace characters on resulting trees. Branch support for each node in the strict consensus tree of all most parsimonious trees was determined by calculation of decay indices (Bremer, 1988, 1994) using the program Autodecay ver. 2.9.6 (Eriksson, 1996). Decay indices are quantified as the extra length needed to lose a branch in the

consensus of near-most-parsimonious trees (Bremer, 1994) and are simply the number of steps (tree length) between the most parsimonious trees and longer trees that do not support that node; thus, a high decay index indicates stronger support for a particular node than does a low index. Autodecay (Eriksson, 1996), given the strict consensus of the most parsimonious trees, generates a Nexus file and instructs PAUP to search for longer trees while keeping track of the persistence of each node among longer trees. Islands of most parsimonious trees (sensu Maddison, 1991) were identified by examining the output from the random addition replicate searches and identifying the replicates that discovered novel most parsimonious trees. These trees were saved into separate files and, whenever multiple trees formed an island, strict consensuses of these trees were produced for each island.

Specimens used in this study were primarily dried skeletons and whole, preserved specimens in the University of Kansas Herpetological Collections (KU); in a few cases, double or single cleared-and-stained specimens were available. Other specimens were made available by the Texas Natural History Collection, Texas Memorial Museum, at University of Texas (TNHC); Collection of Vertebrates, University of Texas at Arlington (UTA); Museum of Zoology, University of Michigan (UMMZ). Osteological terminology it that of Trueb (1993).

## CHARACTERS

### *Frontoparietals*

These paired dermal bones overlie the dorsolateral area of the braincase, overlapping the posterior area of the sphenethmoid. They may be slender (the plesiomorphic condition in anurans; Trueb, 1993), or laterally expanded to form a dorsal roof over the

medial part of the orbit. In some anurans, the frontoparietals bear additional superficial bone (exostosis) that may be elaborated into a variety of textures or crests.

1. *Supraorbital flange on frontoparietals*.—I considered the frontoparietal to have a supraorbital flange if this bone extended laterally beyond the lateral margin of the posterior limit of the sphenethmoid. Some species also have a postorbital flange on the frontoparietals (e.g., *Bufo marmoratus*) that may be in contact with the squamosal (Character 33). The posteromedial margin of the orbit, between the supraorbital and postorbital flanges, is a smooth curve whose shape and extent varies continuously among species. Character states: 0: absent (frontoparietal does not enter orbit); 1: present (frontoparietal enters orbit).

2. *Frontoparietal-nasal contact*.—In some taxa, the anterior margins of the frontoparietals diverge laterally to form an embayment in which the underlying sphenethmoid is visible. I did not include this condition as a separate character state because it is possible that the extent of anteromedial ossification of the frontoparietals may vary with ontogeny. Nevertheless, specimens having this medial embayment were coded as having full contact with the nasals (State 2) unless contact between the two bones was limited to their extreme lateral margins (State 1). This character is illustrated in Fig. 5.3. Character states: 0: no contact; 1: lateral contact only; 2: full contact.

3. *Contact between frontoparietals*.—The paired frontoparietals sometimes are synostotically fused in highly ossified anurans. However, lacking histological preparations, my observations were limited to “contact” or “non-contact.” A taxon was scored as State 1 if the frontoparietals were clearly separate over about half of their length. Character states: 0: medial contact through entire length; 1: frontoparietals divergent anteriorly.

4. *Occipital artery pathway*.—The pathway of the occipital artery over the prootic may be partially or entirely enclosed in a bony canal formed by the frontoparietal. The parietal crest (Character 8), if present, develops directly over the path of the occipital canal. Although all species with parietal crests (e.g., *Bufoluetkeni*) have fully covered occipital canals, some species have fully covered occipital canals but lack parietal crests (e.g., *B. alvarius*). Character states: 0: open (entirely); 1: fully covered; 2: partially covered (open posteriorly); 3: partially covered (open anteriorly).

#### *Cranial Crests*

Terminology used for cranial crests follows Mendelson (1994); these are illustrated in Figs. 5.1 and 5.2. Cranial crests are elaborations that develop through the addition of superficial bone to the frontoparietals, nasals, etc. through ontogeny.

5. *Canthal crest (on nasal)*.—The canthal crest is formed by a distinct raised ridge of bone that lies along the anterolateral margin of the nasal. When present, this crest is apparent externally in preserved specimens. Character States: 0: absent; 1: present.

6. *Preorbital crest (on maxillary process of nasal)*.—The preorbital crest is formed by a vertical ridge of bone that lies along the length of the maxillary process of the nasal. In some species (e.g., *Bufo campbelli*, *B. macrocristatus*), this crest may be indistinct in both preserved and skeletal specimens. It seems that in these species, development of this crest is associated with size (Mendelson, 1994, 1997). I have coded the crest as present in all species in which it appears in any specimen, regardless of sexual or size-related variation. Character States: 0: absent; 1: present.

7. *Supraorbital crest (on frontoparietal)*.—The presence of a supraorbital crest is contingent upon lateral development of the frontoparietal; in this sense, this character is closely associated (but not necessarily linked) to Character 1. However, I identified



species with a supraorbital flange (Character 1: State 1) and no supraorbital crest (e.g., *Bufo haematiticus*) as well as species that lack a supraorbital flange (Character 1: State 0), and have a supraorbital crest (e.g., *B. americanus*). Thus, I considered these two features as separate transformation series. However, most of the species examined that have a supraorbital flange also have a supraorbital crest (and vice versa).

The degree of development of the supraorbital crest varies along a continuum that I did not choose to characterize arbitrarily. Thus, species such as *Bufo marinus* and *B. valliceps* were scored identically as State 1. I chose to score the more extreme cases of development separately. The supraorbital crest was coded as hypertrophied (State 2) if it appeared as a distinctly raised mass of bone (e.g., *B. cavifrons*). The supraorbital crest of *B. typhonius* is distinctly, and uniquely, expanded vertically to form a conspicuous blade-shaped crest (State 3). Character States: 0: absent; 1: present; 2: present, hypertrophied, thick; 3: present, flared vertically, thin.

8. *Parietal crest (on frontoparietal)*.—The parietal crest was coded as hypertrophied (State 2) if it was a distinctly raised mass of bone (e.g., *Bufo cavifrons*). Presence of a parietal crest invariably is associated with a covered occipital canal. (See discussion in account of Character 4.) Character States: 0: absent; 1: present; 2: present, hypertrophied.

9. *Postorbital crest (on frontoparietal and squamosal)*.—The postorbital crest is a complex character in the sense that, although coded as a single transformation series, it is actually formed by the coincident cresting of both the posterolateral margin of the frontoparietal and the medial portion of the otic ramus of the squamosal. All species having this crest also have the frontoparietal in contact with the squamosal (Character 33: State 1); however, in some species these bones are in contact, but they lack a postorbital crest (e.g., *Bufo maculatus*). Character states: 0: absent; 1: present.

10. *Supratympanic crest (on otic ramus of squamosal)*.—The supratympanic crest is formed by a ridge of bone along the lateral margin of the otic ramus of the squamosal. When present, this crest usually is conspicuous, and lies just dorsal to the tympanum. Character states: 0: absent; 1: present; 2: present, flared.

11. *Pretympanic crest (on zygomatic ramus of squamosal)*.—Degree of development of the pretympanic crest varies in the same manner as the preorbital crest (Character 6). I coded its presence in a similar manner. Character states: 0: absent; 1: present.

12. *Suborbital crest (on pars facialis of maxilla)*.—The suborbital crest is an elongate ridge of bone projecting laterally from the pars facialis of the maxilla; the crest is oriented parallel to the upper lip, and is visible on preserved specimens. In at least some species (e.g., *Bufo valliceps*), the degree of development of this crest seems to be associated with size. I coded the crest as present in a species if I observed it on any whole or skeletal specimen. Character States: 0: absent; 1: present.

#### *Sphenethmoid and Neopalatines*

The sphenethmoid is two bones fused together that form the anterior wall of the neurocranium. In *Bufo*, the sphenethmoid is synchondrotically fused laterally to the planum anorbitale, forming the anterior margin of the orbit, and anteriorly to the solum nasi (forming the anterior plate of the sphenethmoid. The anterior extent of ossification of the solum nasi varies among taxa. In dried skeletons, the cartilaginous (anteriormost) portion of the solum nasi is commonly missing as a result of the labors of dermestid beetle larvae. The neopalatines (sensu Trueb, 1993) are a pair of bones on the ventral surface of the planum antorbitale that invest the maxillae laterally and sphenethmoid medially. The neopalatines vary in size among bufonids, and are absent in a few taxa (e.g., *Melanophryniscus*). In cases in which the neopalatines are absent (Character 18:

State 1), characters relating to these bones (e.g., Character 14) were coded as unknown (?).

13. *Extent of anterior ossification of sphenethmoid.*—Determination of the anterior extent of the sphenethmoid in dried skeletal specimens is difficult because the degree of ossification may vary among individuals and species, and may be affected by preparation techniques (e.g., dermestid beetle larvae). Furthermore, the use of the vomers as landmarks assumes that the size and position of these bones is invariant among species. Because of these possible confounding factors, I strived to be conservative and consistent in coding this transformation series; doubtless more phylogenetic signal can be gained from examination of cleared and double-stained specimens. Character states: 0: not extending, or extending only slightly beyond level of neopalatines; 1: extending anteriorly beyond posterior margin of vomers; 2: very long, reaching premaxilla.

14. *Extent of medial separation between neopalatines.*—Character states: 0: widely separated; contact sphenethmoid only marginally; 1: nearly in contact at midline of sphenethmoid.

15. *Ventral ridge on neopalatine.*—The nature of the ventral ridge on the neopalatine seems to vary along a continuum from smooth to serrate. I observed intra-element and bilateral variation in this character, so I did not score the nature of this ridge as different states. However, clearly distinct odontoids (State 2) seem to be unique to *Bufo alvarius*. Character states: 0: ridge absent; 1: ridge present; 2: odontoids present.

16. *Width of medial head of neopalatine.*—Character states: 0: same width as at midlength; 1: broader than width at midlength.

17. *Width of lateral head of neopalatine.*—Character states: 0: same width as at midlength; 1: broader than width at midlength.

18. *Neopalatine*.—Character states: 0: present; 1: absent.

19. *Relationship of neopalatine and maxilla*.—Character states: 0: in contact with maxilla; 1: not in contact with maxilla.

#### *Parasphenoid*

The parasphenoid is a relatively simple T-shaped bone. The anterior margin of the cultriform process invests the ventral surface of the sphenethmoid, and the posterolateral alae invest the prootic and underly the otic capsule.

20. *Shape of cultriform process*.—In taxa with a short, terminally rounded cultriform process (State 2), the process does not reach the level of the planum antorbitale (Character 21, State 1). Although it is possible these states are not independent, the intent of Character 20 is to describe observed differences in the shape of the cultriform process. Character states: 0: margins nearly parallel through length of process; 1: process becoming distinctly narrower anteriorly; 2: broad, rounded.

21. *Anterior extent of cultriform process*.—Character states: 0: reaches level of antorbitale; 1: does not reach level of planum antorbitale.

22. *Ventral crest on alae*.—Distinct ventral crests are present along the lengths of the alae in a few species (e.g., *Bufo luetkeni*). Character states: 0: absent; 1: present.

#### *Premaxilla, Maxilla, and Quadratojugal*

The premaxillae are paired bones that form the anterior margin of the maxillary arcade. They bear simple, dorsal alary processes that contact the superior pre-nasal cartilages. The maxilla forms most of the maxillary arcade and bears a dorsal pars facialis and a lingual pars palatina. In bufonids, both the premaxilla and the maxilla lack teeth. The quadratojugal completes the maxillary arcade in bufonids. This is small element articulates with both the posterior end of the maxilla and the pars articularis of

the palatoquadrate cartilage; the posterior end of the palatoquadrate is ossified to form the quadrate bone in many species that have robust quadratojugals.

23. *Angle of alary process of premaxilla.*—The angle of the alary processes often are distorted in dry skeletal specimens. Although cleared-and-stained specimens would be preferable, I think it is quite possible to distinguish the three states in this transformation series and to discount minor deflections attributable to the drying process. Character states: 0: vertical; 1: angled anteriorly; 2: angled posteriorly.

24. *Pterygoid process on pars palatina of maxilla.*—In all species examined, the anterior process of the pterygoid is in broad contact with the pars palatina of the maxilla. In some species (e.g., *Bufo perplexus*), this region of the pars palatina extends medially, forming a pterygoid process. I coded this process as present if the anterior margin of the pterygoid fossa was formed by the maxilla, rather than the more usual condition in which the anterior margin of the fossa is formed by the junction of the pterygoid and the pars palatina of the maxilla. Character states: 0: absent; 1: present.

25. *Teeth.*—The absence of teeth has been posited as a synapomorphy for Bufonidae (Graybeal and Cannatella, 1995), although other neobatrachians (e.g., brachycephalids) also lack teeth. Character states: 0: absent; 1: present.

26. *Quadratojugal.*—The three conditions identified are illustrated in Fig. 5.4. Character states: 0: slender; 1: robust; 2: absent.

27. *Nature of maxilla-quadratojugal overlap.*—This character is illustrated in Fig. 5.4. Character states: 0: maxilla lateral to quadratojugal; 1: maxilla ventral to quadratojugal; 2: maxilla dorsal to quadratojugal.

#### *Pterygoid and Squamosal*

These bones form the basis for the suspensorium supporting the maxillary arcade; both bones typically are triradiate in anurans. Laterally, the ventral ramus of the squamosal invests the palatoquadrate, the zygomatic ramus usually is short and projects anteroventrally from the dorsal region of the squamosal. In a few taxa (e.g., *Bufo granulosis*), the zygomatic ramus is long and in contact with the maxilla. Dorsally, the squamosal bears an otic ramus that extends medially to invest the crista parotica and, in some cases, is in contact with the frontoparietal. The anterior ramus of the pterygoid invests the pterygoid process of the palatoquadrate, and extends anteriorly to the level of the neoplatine and the maxillary process of the nasal. The medial ramus of the pterygoid invests the basal process of the palatoquadrate and the ventral portion of the otic capsule; this process may be in contact with the ala of the parasphenoid. The ventral ramus of the pterygoid invests the articular process of the palatoquadrate and braces medially the ventral ramus of the squamosal and the posterior end of the maxillary arcade.

28. *Anterior extent of anterior ramus of pterygoid.*—Character states: 0: in contact with neoplatine; 1: not in contact with neoplatine.

29. *Medial ramus of pterygoid.*—Character states: 0: abuts parasphenoid ala; 1: broad contact with parasphenoid ala, along shared lateral margins; 2: overlaps parasphenoid ala ventrally.

30. *Dorsal flange on medial ramus of pterygoid.*—In a few species (e.g., *B. spinulosus*), a thin flange of bone projects dorsally from the medial ramus of the pterygoid that, in a well-prepared, dried skeleton, may be viewed from either anterior or posterior perspective. Character states: 0: absent; 1: present.

31. *Length of zygomatic ramus of squamosal.*—Character states: 0: absent; 1: short; 2: long, nearly in contact with maxilla; 3: long, in contact with maxilla.

32. *Relationship between zygomatic and ventral rami of squamosal.*—The space between the angle of zygomatic and ventral rami of the squamosal may be filled with bone to such an extent that these rami are no longer discrete (State 0); this is possible whether the ventral ramus is short (Character 32, State 1; e.g., *Bufo crucifer*) or long (Character 32, State 2; e.g., *B. coccifer*). This character is illustrated in Fig. 5.5. Character states: 0: space between zygomatic and ventral rami filled with bone; 1: space between zygomatic and ventral rami not filled with bone.

33. *Relationship between squamosal and frontoparietal.*—In many bufonids, these two elements are in contact dorsal to the crista parotica as the result of both a posterolateral extension of the frontoparietal and a medial extension of the otic ramus of the squamosal. The contact may be slight, as in *Bufo funereus*, or extensive and forming a bony shelf over the crista parotica, as in *B. marinus*. Character states: 0: not in contact; 1: in contact.

#### *Nasals*

The nasals are paired dermal bones that overlie the nasal capsule. A lateral maxillary process may extend posteriorly and be in contact with the pars facialis of the maxilla. The anterior shape and extent of the nasals is variable among taxa and, in an extreme form, may project forward well beyond the level of the maxilla (e.g., *Rhamphophryne*).

34. *Shape of anterior tip of nasals.*—Three general conditions of the nasals were identified and are illustrated in Fig. 5.6. Character states: 0: short, broad; 1: elongate, narrow; 2: elongate, broad.

35. *Angle of profile of nasals.*—In lateral view, the nasals may have a distinct straight profile, or they may be slightly curved ventrally. This character is illustrated in Fig. 5.6. Character states: 0: straight, sloped; 1: curved ventrally.

36. *Midline contact of nasals*.—In *Rhamphophryne macrorhina* the nasals are in contact posteriorly, but diverge laterally about the unusually extended and ossified sphenethmoid (state = 2). Trueb (1973:fig. 2-2c) illustrated a similar condition in the skull of *R. acrolopha*. Character states: 0: in contact; 1: separate; 2: in contact posteriorly, divergent anteriorly.

37. *Ossification around nares*.—In a few species (e.g., *Bufo granulosis*) the nasal and the pars facialis of the maxilla are hyperossified such that thin layer of dermal bone covers the space between these proximal elements; this condition leaves only a small opening to accommodate the naris. Character states: 0: narial area not ossified; 1: narial area entirely ossified.

#### *Stapes*

The stapes is a bony shaft that, when present, transmits vibrations from the external tympanum to the operculum and associated inner ear elements.

38. *Condition of stapes*.—The stapes of most anurans, when present, is a simple rod-shaped bone. In some of the bufonids examined (e.g., *Bufo canaliferus*) and in *Leptodactylus pentadactylus*, the stapes is distinctly compressed anteroposteriorly, in the shape of a blade-shaped element (State 2). Character states: 0: stapes absent; 1: rod-shaped; 2: blade-shaped.

#### *Postcranial and Soft Anatomy*

39. *Xiphisternum*.—A free sternum (not covered by the *vagina recti*) is unique to most bufonids; however, the relative size of the exposed xiphisternum varies discontinuously between a small exposed portion (State 1; e.g., *Bufo boreas*) and a distinct large transparent disc that overlies the anterior region of the *m. rectus abdominis* (State 2; e.g.,



*B. valliceps*). Descriptions and illustrations of these conditions were presented by da Silva and Mendelson (*in press*). Character states: 0: covered; 1: free, small; 2: free, large.

40. *Omosternum*.—The omosternum is a prezonal (= anterior to the glenoid fossae) element of the pectoral girdle. It may be cartilaginous or partially mineralized. This element is homoplastic among frogs and is present in few species of *Bufo* (e.g., *Bufo valliceps*). Character states: 0: absent; 1: present.

41. *Relationship of epicoracoid cartilages*.—The epicoracoid cartilages of the pectoral girdle may be free and overlapping at the midline (the classic “arciferal” condition) or they may be fused to one another at the midline (the classic “firmisternal” condition). Character states: 0: free; 1: fused.

42. *Vocal slits*.—The vocal slits of male anurans are simple openings on the floor of the mouth that allow air to enter the vocal sac during the cycling of air associated with production of the advertisement call (described in Duellman and Trueb, 1986); taxa that lack vocal slits also lack a vocal sac. Although rarely reported, many species of *Bufo* (e.g., *B. ibarraii*) have unilateral vocal slits (State 1) that may be either dextral or sinistral in position among individual males from the same populations (Mendelson, 1997c). Character states: 0: absent; 1: unilateral; 2: bilateral.

43. *Parotoid glands*.—Although apparently absent in some bufonids, parotoid glands seem to be a synapomorphy for the Bufonidae; however, they never have been characterized thoroughly (Graybeal and Cannatella, 1995). Character states: 0: absent; 1: present, parallel to midline, oblong or ovoid; 2: present, divergent, ovoid or triangular; 3: present, small, round; 4: present, tiny cluster of pores at corner of cranial crests.

44. *Lateral descending row of tubercles on skin*.—Several species of bufonids (e.g., *Bufo typhonius*) have a distinct series of tubercles that are enlarged with respect to other

lateral tubercles. These tubercles form a distinct series that begins near the posterolateral margin of the parotoid gland and form a ventrally descending series onto the flank, where they become indistinct. Character states: 0: absent; 1: present.

45. *Inguinal fat bodies*.—A description and illustration of these organs, unique to bufonids, were presented in da Silva and Mendelson (*in press*). Character states: 0: absent; 1: present.

## RESULTS

Maximum parsimony analysis of the data matrix required approximately 6 hr of computation time and yielded 70 most parsimonious trees ( $2.4 \times 10^{51}$  trees are possible with this data matrix; Felsenstein, 1978) having a length of 213 steps (68–496 steps possible), with a retention index (Farris, 1989) of 0.66 and a consistency index (Kluge and Farris, 1969) of 0.319. A strict consensus of these trees is presented in Fig. 5.7; 11 clades support several monophyletic groups within Bufonidae; clades are numbered as they appear in Fig. 5.7

With respect to the Middle American species included in this analysis, the clade ((*B. haematiticus* (*B. typhoni*us, *Rhamphrophryne macrorhina*)) is the sister group to all other species in the analysis (Clade 2) except those in the most basal clade (*Atelopus ignescens*, *Melanophryniscus moreirae*). *Bufo periglenes* is the sister species to a large clade containing all other Middle American species, as well as several species from Africa, Asia, Europe, and North and South America (Clade 7). All other Middle American species are included, along with the Asian species *B. asper* and *B. melanostictus* in a large clade (Clade 5) containing three smaller clades (Clades 9–11), all of which are in a basal polytomy with many single species. However, Clade 9 (*B. americanus*, *B. occidentalis*) suggests that the latter Mexican species has its relationships with North

American toads. Clade 10 supports a resolved group of small-to-medium-sized Middle American species, including the monotypic genus *Crepidophryne*, and Clade 11 supports recognition of a monophyletic *B. valliceps* Group.

Of the species included in this analysis, *Bufo valliceps*, *B. campbelli*, *B. cavifrons*, *B. melanochlorus*, and *B. macrocristatus* are included in the *Bufo valliceps* Group. Because assessment of synapomorphies to support any clade is dependent upon the topology and because I have no a priori justification for choosing a single tree from among the 70 shortest trees, I cannot provide a list of synapomorphies for the group. Nevertheless, all species in the *B. valliceps* Group have an omosternum (Character 41: 1). This structure is uncommon in bufonids and, in the total absence of evidence to suggest a close relationship with *B. haematiticus* (and, presumably, the entire *B. guttatus* Group), which also have omosterna, this feature may be posited as a synapomorphy for the *B. valliceps* Group.

Branch support for all nodes in the strict consensus tree (Fig. 5.7) were low. The species pairs (*B. macrocristatus*, *B. cavifrons*) and (*B. typhoni*, *R. macrorhina*) have decay indices = 2, all other nodes have decay indices = 1.

The 70 most parsimonious trees were partitioned among five islands (sensu Maddison, 1991) containing 3, 61, 3, 2, and 1 tree, respectively. Strict consensus trees for each island of trees appear in Figs. 5.8 and 5.9. Examination of the consensus trees representing each island reduces the number of possible topologies that must be considered. (All possibilities must be considered in the case of a large polytomy appearing in a strict consensus of all most parsimonious trees.) Thus the issue of the sister clade to the *Bufo valliceps* Group may be addressed. In Island 1 (Fig. 5.8), *B. crucifer* and *B. marinus* are the sister clade to the *B. valliceps* Group. Among the 61 trees in Island 2

(Fig. 5.9), neither of these species are the sister to the *B. valliceps* Group; in this island the sister is among the species *B. mazatlanensis*, *B. coccifer*, *B. ibarraii*, *B. coniferus*, *B. luetkeni*, and *B. granulosus* (hereafter referred to as “the other crested Central American toads”) that have previously been referred to the *B. valliceps* Group (Table 5.1). Among the three trees that form Island 3 (Fig. 5.10), the sister to the *B. valliceps* Group is again among the other crested Central American toads, however in two of these trees *B. marinus* and *B. crucifer* form a clade nested within these other crested species. In both trees in Island 4 (Fig. 5.11) *B. marinus* and *B. crucifer*, once again, form the sister clade to the *B. valliceps* Group. Finally, the single tree forming Island 5 (Fig. 5.12) shows a monophyletic clade comprising the other crested Central American toads as the sister to the *B. valliceps* Group.

#### DISCUSSION

The results of this analysis have identified the existence of support for a monophyletic *Bufo valliceps* Group. The content of this group (Table 5.3) differs greatly from all previous concepts of the group (Table 5.1); nearly half of the species in the group have been described or recognized only recently (Mendelson, 1994; 1997*a,b*). The level of discordance between the previous concepts of the *B. valliceps* Group (Table 5.1) and the group discovered in this analysis reinforces the inherent danger of assuming the monophyly of phenetic groups in higher level analyses in which only single species are used to represent groups of presumably closely related species. To date, the only other species group within *Bufo* that has been similarly tested in a phylogenetic analysis is the *B. boreas* Group (Graybeal, 1997); clearly, much systematic work remains to be done before an explicitly historical classification of Bufonidae will be available.

Although some areas of the tree produced by this analysis (Fig. 5.7) are poorly resolved and all nodes have weak branch support (decay indices), the monophyly of the *Bufo valliceps* Group is unequivocal. The shared presence of an omosternum (nearly unique within Bufonidae) limits the membership to eight species (Table 5.3). Because of lack of material, I was unable to include *B. cristatus*, *B. spiculatus*, and *B. tutelarius* in this study but I include them in the *B. valliceps* Group based on my examination of all characters that can be scored externally (e.g., cranial crests, parotoid glands) and verification (via dissection) of presence of an omosternum. In the present analysis, presence of bilateral vocal slits is a synapomorphy for the *B. valliceps* Group. However, *B. cristatus*, *B. spiculatus*, and *B. tutelarius* lack vocal slits. (But see Mendelson, 1997a, regarding variation in *B. tutelarius*.) Shared absence of vocal slits may support a close relationship among these three allopatric montane species. Resolution of relationships among species of the *B. valliceps* Group will not be possible until more material (i.e., specimens for skeletal preparation and/or tissues for molecular analyses) is available

The remaining Middle American *Bufo* that have been proposed to be in the *B. valliceps* Group (Table 5.1), but that are outside the group as it is delimited here, are scattered about the tree (Fig. 5.7). *Bufo occidentalis* is the sister to *B. americanus* (Clade 9) and, therefore, appears to have its closest relatives among the North American species; the broad distribution of *B. occidentalis* on the Mexican Plateau and Sierra Madre Occidental, is contiguous with the Great Plains, Chihuahuan Desert, and Rocky Mountains of the United States and Canada. *Bufo perplexus* and *B. canaliferus* are the most basal member of a clade (Clade 10) containing the small, distinctive species *B. fastidiosus*, *B. holdridgei*, and *Crepidophryne epiotica* from the cloud forests of Costa Rica and Panama. The placement of *B. perplexus* in a resolved clade that does not

include *B. marmoreus* (placed in the unresolved polytomy [Clade 8]) does not support recognition of a monophyletic *B. marmoreus* Group (present in the summary by Frost, pers. comm.). In the strict consensus tree (Fig. 5.7), *B. luetkeni*, *B. mazatlanensis*, *B. coccifer*, *B. ibarraii*, and *B. coniferus* are in a large polytomy (Clade 8) that includes the *B. valliceps* Group and the two resolved clades (Clades 9, 10) just discussed; all of these species lack omosterna and have unilateral vocal slits. Comparisons of the trees from the five islands of most parsimonious trees indicates that the sister clade to the *B. valliceps* Group lies either among these species (plus *B. granulatus*) or among the species presently referred to the *B. marinus* Group (e.g., *B. marinus*, *B. crucifer*).

Graybeal conducted a phylogenetic analysis of Bufonidae using data from mitochondrial and nuclear DNA sequences and morphology (Graybeal, 1997:figs. 5, 13; hereafter referred to as “Graybeal's analysis”). Although Graybeal analyzed different species than I did, there are sufficient species common to both analyses to allow comparisons. In both studies, a basal split separates the clade containing *Atelopus* and *Melanophryniscus* from a larger clade containing all species of *Bufo* and several other genera. Both analyses reveal that *Bufo* is demonstrably paraphyletic with respect to several smaller, or monotypic, genera such as *Crepidophryne*; Graybeal and Cannatella (1995) reviewed the status of supraspecific taxa in Bufonidae, and commented on this and other apparent problems with the taxonomy of Bufonidae. Both Graybeal's molecular analysis (her fig. 5) and combined molecular and morphological analysis (her fig. 13) indicate that the *B. valliceps* Group is more closely related to the other crested Central American toads than to *B. marinus*—as was discovered in several of the islands of most parsimonious trees in this study.

In my analysis, *Crepidophryne* is in a monophyletic group with four species of *Bufo* (Node 10), and this clade is nested well inside a much larger group of species of *Bufo*. Graybeal's analysis also indicated that recognition of *Crepidophryne* contributes to the paraphyletic nature of *Bufo*. *Crepidophryne epiotica* is a relatively autapomorphic species characterized by phalangeal reduction, webbing on the hands, coccygeal flanges, and other unique features (Savage and Kluge, 1961); however, the evidence from two independent analyses (Graybeal, 1997; present study) indicates that these autapomorphies have evolved in the single species *epiotica*, from ancestors nested within *Bufo*—as, in fact, Savage and Kluge (1961), specifically proposed. Therefore, in an effort to contribute toward recognition of a monophyletic *Bufo*, I hereby designate *Crepidophryne* Cope a junior synonym of *Bufo* Laurenti.

My analysis differs from Graybeal's analysis with respect to the species of *Bufo* with which *Bufo epioticus* is most closely related. In Graybeal's analysis, *B. epioticus* is in a polytomy including a species of *Rhamphophryne*, *B. coniferus*, *B. fastidiosus*, and *B. periglenes*. Although all of these species were included in my analysis, only the placement of *B. fastidiosus* as a close relative of *B. epioticus* is in agreement with Graybeal's analysis. In my analysis, *Rhamphophryne* is in a basal clade including *B. typhoni* and *B. haematiticus* that is the sister to all other *Bufo*; this relationship is not evident in Graybeal's analysis. If I am correct, this clade of distinctive species, and their presumed close relatives among the *B. guttatus* Group (sensu Duellman and Schulte, 1992)—viz., the *B. typhoni* complex (Hoogmoed, 1986, 1990) and the genus *Rhamphophryne* (Trueb, 1971), should be referred to the genus *Rhaebo* Cope. However, pending a more robust analysis that includes more species from these species groups and also *Rhamphophryne*, I do not propose this action at this time.

This analysis suggests that, for the most part, the *Bufo* of Middle America form a monophyletic assemblage. The Middle American radiation also has a complex relationship with the putative, and predominantly South American, *B. granulosis* and *B. marinus* Groups (here represented by 1 and 2 species, respectively). Few species of *Bufo* occur extensively in both South and Middle America and, of these, several (e.g., *B. typhoniis*, *B. granulosis*) are widely considered to be unresolved complexes of species (summarized by Frost, pers. comm.). This analysis places both of the Asian species included in the matrix (*B. melanostictus*, *B. asper*) amongst the Mesoamerican species. The recovered history of other groups (e.g. eublepahrid geckoes [Grismer, 1988]; xenosaurid lizards [Estes et al., 1988; Harvey, 1993]) also suggests shared histories of the Mesoamerican and Asian faunas, but it is possible that the few Asian species included in this analysis simply are convergent with the Mesoamerican radiation.



## CHAPTER VI

### ACCOUNTS AND KEY TO THE SPECIES OF THE BUFO VALLICEPS GROUP

#### *Bufo campbelli* Mendelson

*Bufo campbelli* Mendelson, 1994:4–12.

*Bufo valliceps*—Stuart, 1943:14; Stuart, 1963 [in part; for records indicated in low montane areas of eastern Guatemala]; Porter, 1970:94.1 [in part; for records plotted along Caribbean versant of southern Mexico, Belize, Guatemala, and Honduras]; Lee, 1980:pl. 3 [in part; for records plotted in lower montane areas of Belize and eastern Guatemala; Campbell and Vannini, 1989:table 2 [in part; for records indicated from the Petén, Sierran, and Quecchian Faunal Areas]; Lee, 1996 [in part; for specimens cited from lower montane areas of Belize and eastern Guatemala].

*Bufo valliceps valliceps*—Duellman, 1963:221 [in part; for specimens collected near Chinajá, Alta Verapaz, Guatemala].

**Holotype.**—KU 186320, from Las Escobas, 5.1 km W Puerto Santo Tomás, Montañas del Mico, Departamento de Izabal, Guatemala, 104 m; J. A. Campbell collector.

**Diagnosis.**—A moderate-sized species of *Bufo* (males to 68.0 mm SVL; females to 89.1 mm SVL) having the following combination of characters: (1) tympanum small, about 40% diameter of orbit; (2) preorbital and pretympanic crests absent or weakly developed in large individuals; (3) tibia long, about 48% SVL; (4) foot long, about 46% SVL; (5) skin relatively smooth, especially in males, with few scattered sharply conical tubercles; (6) lateral row of tubercles present usually as a low, smooth series of welts in males and as discrete sharply pointed tubercles in females; (7) vocal slits present, bilateral; (8) *m. interhyoideus* forming a small, unilobed, unpigmented sac; (9) snout

sharply pointed in dorsal view, acutely rounded in profile; (10) cranial crests low, thin; (11) parotoid glands small, distinctly triangular; (12) color of tips of digits distinctly paler than rest of digit, yellow or orange in life.

*Bufo campbelli* is most similar to *B. melanochlorus*, a species known only from Costa Rica, but differs by having larger parotoid glands that with the anterior breadth of the gland about equal to the width of the eyelid, a patterned venter with indistinct dark smudge on the throat and sternal area, distinct dark flecks concentrated especially on the pelvic and femoral areas and the throat, and digital tips paler than the rest of the digit.

*Bufo campbelli* occurs sympatrically with *B. valliceps* but may be easily distinguished by having longer legs, smaller tympanum, preorbital and pretympanic crests absent or poorly developed in larger individuals, smoother skin, longer head, and snout acutely rounded in lateral view and pointed in dorsal view, and *m. interhyoideus* not forming a large, bilobed, pigmented vocal sac. *Bufo campbelli* may be sympatric with *B. macrocristatus* in some lower montane areas along the Atlantic base of the Sierra de los Cuchumatanes and the Chiapas Highlands; it may be distinguished from *B. macrocristatus* by having smaller, more triangular, parotoid glands and low, thin cranial crests that are never thickened (as in males of *B. macrocristatus*) or distinctly vertically prominent and thin (as in females of *B. macrocristatus*). Although *B. campbelli* bears an overall similarity to *B. cavifrons*, both sexes of the latter species have distinctly thickened cranial crests that form large bony knobs at the junction of the postorbital, supraorbital, and parietal crests.

**Color pattern.**—Mendelson (1994) provided a complete description and illustration of the color pattern in this species. Females have a pale or dark brown dorsal color with a distinct pattern of dark brown and black markings commonly arranged in bilateral pairs, a black interorbital bar, and usually black or dark brown lateral areas

ventral to the lateral row of tubercles. Males are usually unicolored pale tan, some individuals have a few small black dorsal markings and an interorbital bar. A narrow black stripe ventral to the lateral row of tubercles may be present. Individuals of both sexes have pale digital tips and a ventral pattern consisting of a variety of dark spots, concentrated especially posteriorly and on the underside of the limbs, or as a dark diffuse gray smudge over the pectoral area and throat.

**Reproductive biology.**—The tadpoles and breeding behavior of *B. campbelli* are unknown. Calling males have been observed near streams in primary rainforest in January.

**Distribution and ecology.**—This species occurs along the Caribbean versant of southern Mexico and northern Nuclear Central America from southern Veracruz, Mexico, to Atlantida, Honduras. Most specimens have been found in primary rainforest in lower montane areas (below 1000 m) of ranges such as the Maya Mountains, Montañas del Mico, Sierra de Santa Cruz, and Sierra de las Minas; many individuals have been found in the vicinity of streams or small rivers.

**Etymology.**—This species was named in honor of Jonathan A. Campbell, who collected the holotype and has contributed greatly to our knowledge of the Guatemalan herpetofauna.

**Remarks.**—Specimens representing this species invariably have been misidentified as *B. valliceps* in museum collections. Indeed, large collections of toads from lower montane areas (i.e., coffee *fincas*) along the Caribbean versant of northern nuclear Central America often contain specimens of both *B. campbelli* and *B. valliceps*. Field notes associated with specimens (when available) usually indicate that *B. campbelli* were collected in primary forest and *B. valliceps* were collected in villages, agricultural

areas, or some form of secondary growth. Interestingly, among all of the material collected by L. C. Stuart in Alta Verapaz and other areas of Guatemala, I am aware of only two small series (UMMZ 89170, 124385) of *B. campbelli* collected by him.

*Bufo cavifrons* Firschein

*Bufo cavifrons* Firschein, 1950:84–85.

**Holotype.**—UIMNH 8741, from 500 feet [152.4 m] below peak of Volcán San Martín, San Andrés Tuxtla, Veracruz, Mexico; I. L. Firschein collector.

**Diagnosis.**—A large species of *Bufo* (males to 79.9 mm SVL; females to 99.8 mm SVL) having the following combination of characters: (1) tympanum small, about 45% diameter of orbit; (2) preorbital crest absent, or present as a thin strip of raised bone in large females, pretympanic crest absent; (3) tibia relatively short, about 40% SVL, robust; (4) foot relatively short, about 40% SVL; (5) skin smooth, with few scattered conical tubercles laterally and posteriorly in some females, scattered clusters of keratin over all dorsal surfaces in breeding individuals; (6) lateral row of tubercles usually present only as a continuous raised welt in males, in females present as a series of widely spaced, non-pointed, low tubercles; (7) vocal slits large, bilateral; (8) *m. interhyoideus* forming a small, unilobed unpigmented sac; (9) snout acutely pointed in dorsal and lateral view; (10) cranial crests high and thick, parietal crests vertically prominent to form rounded knobs in both sexes, sometimes larger in females; (11) parotoid glands relatively small, not protuberant, usually conspicuously triangular; (12) color of tips of digits paler than rest of digit.

*Bufo cavifrons* is most similar to *B. macrocristatus*; however, *B. cavifrons* differs by having smoother skin, smaller and more triangular parotoid gland, smaller tympanum

relative to eye, shorter tibia, and larger vocal slits. In some cases, it may be difficult, beyond geography, to distinguish some individuals of *B. cavifrons* from some of *B. macrocristatus*. In such cases the nature of the hypertrophy of the cranial crests is helpful. Some female *B. macrocristatus* have raised crests, but they are never so thickened as are those of female *B. cavifrons*; in male *B. macrocristatus*, the only thickened part of the crests appears as a small knob at the junction of the parietal, supraorbital, and postorbital crests. *Bufo campbelli* is a smaller, more gracile, toad with low and thin cranial crests. *Bufo valliceps*, with which *B. cavifrons* may be sympatric near disturbed habitats, has low, nonhypertrophied crests, shorter legs, distinct preorbital and pretympenic crests, larger tympana, and *m. interhyoideus* forming a large, bilobed, pigmented sac.

**Color pattern.**—Firschein (1950) described and illustrated the color of the female holotype. Mendelson (1997b) reviewed variation in color pattern. In preservative, most specimens have a distinct middorsal pale area that may be wide or narrow, a dark interorbital bar, and paired dark markings that may include a partial or complete scapular chevron; some individuals lack most dorsal markings and are nearly uniform dark or medium brown.

**Reproductive biology.**—Shannon and Werler (1958) gave a brief description of the tadpole that does not adequately distinguish the tadpole of *B. cavifrons* from that of *B. valliceps* (See key by Altig, 1987.) Breeding aggregations have been observed in January around springs at the heads of streams on the side of the Volcán San Martín. Males have a soft advertisement call.

**Distribution and ecology.**—*Bufo cavifrons* is known only from the Sierra de los Tuxtles, Veracruz, Mexico, where it has been collected on the slopes of Volcán San

Martín and Volcán Santa Marta, as well as several localities at lower elevations, such as Zapoapan and Tebanca. Most specimens seem to have been found in primary forest, whereas nearby disturbed areas harbor the ubiquitous species *B. marinus* and *B. valliceps*.

**Etymology.**—The specific epithet is derived from the Latin *cavus*, meaning hollow, and *frons*, meaning brow; the name *cavifrons* is in reference to the distinctive hollowed appearance of the top of the head produced by the extreme hypertrophy of the cranial crests.

**Remarks.**—Porter (1964a) referred three allopatric montane populations in southern Mexico to *Bufo cavifrons*. Mendelson (1997a,b) restricted the name *B. cavifrons* to apply only the population occurring in the Sierra de los Tuxtlas, Veracruz, Mexico; the other populations being referred to *Bufo macrocristatus* Firschein and Smith, and *Bufo spiculatus* Mendelson. Nevertheless, I have found specimens in museums representing *B. cavifrons* (sensu stricto) from the Sierra de los Tuxtlas invariably to have been correctly identified—no doubt because of their distinctive appearance. Porter's (1967) report of *B. cavifrons* from Nicaragua is based on a specimen referable to *B. valliceps*.

*Bufo cristatus* Wiegmann

*Bufo cristatus* Wiegmann, 1833:660–661.

*Bufo occipitalis* Camerano, 1879:889–90 [Holotype: Museo Regionale di Scienze Naturali Torino An464, from Mexico]; Günther, 1885–1902:250, pl. 69. Synonymy fide Kellogg (1932).

*Bufo valliceps*—Brocchi, 1882:79; Günther, 1885–1902:252.

*Bufo cavifrons*—Webb and Fugler, 1957:33–34.

*Lectotype*.—ZMB 3524, from Jalapa, Veracruz; designated lectotype by Firschein, 1950:83; F. Deppe collector.

*Diagnosis*.—A medium-sized species of *Bufo* (males to 54.8 mm SVL; females to 87.3 mm SVL) having the following combination of characters: (1) tympanum small, about 33% diameter of orbit; (2) preorbital crest present, thin in largest females, absent in males, pretympanic crest absent; (3) tibia relatively short, about 40% SVL; (4) foot about 42% SVL SVL in males; (5) dorsal skin texture smooth with few scattered, distinct, conical tubercles that become more concentrated on the legs; (6) lateral row of tubercles present as an intermittent series of indistinct, small, pointed or rounded tubercles; (7) vocal slits absent; (8) vocal sac absent; (9) snout acutely pointed in dorsal view, sloping and pointed in lateral view; (10) cranial crests large and distinctly thickened, parietal crests vertically prominent and laterally forming large, raised, ovoid masses; lateral expansion fills space between parietal, postorbital, and supratympanic crests; (11) parotoid glands very large, protuberant, ovoid; (12) color of tips of digits similar to rest of digit.

*Bufo cristatus* may not be mistaken easily for any other toad in Middle America. *Bufo cavifrons* has hypertrophied cranial crests, but *B. cristatus* differs by having the parietal crest as a swollen ovoid mass that fills the space between the parietal, postorbital, and supratympanic crests, much larger parotoid glands, smaller tympana, and by lacking vocal slits and sac.

*Color pattern*.—A photograph of a live individual appears in Mendelson (1997b). Most specimens are nearly uniform dark brown dorsally, with a pale brown thin, broken middorsal stripe.

**Reproductive biology.**—The diagnostic characteristics of the tadpole were presented in a key (Altig, 1987). Tadpoles have been collected in the month of December in fast moving mountain streams. Males of *B. cristatus* lack vocal sacs, and also perhaps an advertisement call.

**Distribution and ecology.**—The few records for this species are all from the central part of the Sierra Madre Oriental, between the towns of Jalapa, Veracruz, and Tezuitlan, Puebla. These localities are within a narrow band of cloud forest on the Atlantic versant of the Sierra Madre Oriental between elevations of about 1200–2000 m.

**Etymology.**—The specific epithet is derived from the Latin *crista*, meaning crest, and is used as an adjective; the name *cristatus* is in reference to the distinctive hypertrophied crests of this species.

**Remarks.**—Despite its very distinctive appearance and the thorough efforts of Firschein (1950) and Porter (1963), *B. cristatus* has had a relatively tortuous taxonomic history; most specimens catalogued in museums under this name are *B. valliceps*. This confusion seems largely attributable to the fact that there are so few actual specimens of *B. cristatus* that most people have never seen the species. *Bufo cristatus* is perhaps known from no more than 12 specimens (11 of which I have examined). Of these few specimens several lack detailed locality data, most are poorly preserved, several are juveniles, and only one is an adult male. I am unaware of any specimens collected after 1970.

*Bufo macrocristatus* Firschein and Smith

*Bufo valliceps macrocristatus* Firschein and Smith, 1957:219–221.



*Bufo valliceps*—Baylor and Stuart, 1961:198; Porter, 1963:242–243 [in part; for specimens from the “mountains of Oaxaca and the Gulf lowlands of Chiapas”]; Porter, 1970:94.1 [did not recognize *Bufo valliceps macrocristatus*]; Flores-Villela, 1993:16 [in part, for records representing “Tropical Highlands” of Chiapas, Mexico, and Guatemala]; Wilson and McCranie, 1993:2 [in part; for reference to tadpoles from Soluschiapa, Chiapas].

*Bufo cavifrons*—Porter, 1963:232 [in part; for specimens from “near Rayón, Chiapas”]; Johnson, 1989:42,60 [in part; for specimens from the “Northern Highlands,” Chiapas]; Korky and Webb, 1973.

*Bufo macrocristatus*—Tihen, 1962:168 [listed as a member of the Mexican Section of the *Bufo valliceps* group; no localities or specimens given].

**Holotype.**—UIMNH 35583, from between La Gloria and Cerro Azul (presumably nearer Cerro Azul), Oaxaca, Mexico; T. MacDougall collector.

**Diagnosis.**—A moderate-sized species of *Bufo* (males to 68.7 mm SVL; females to 76.8 mm SVL) having the following combination of characters: (1) tympanum small, about 42% diameter of orbit; (2) preorbital crest absent or very weak, except in large females, in which it is present and thin, pretympanic crest short (not reaching level of inferior margin of tympanum), thin, or absent; (3) tibia relatively long, about 43% SVL; (4) foot relatively long, about 47% SVL; (5) dorsal skin in females relatively smooth, with well-spaced, discrete, conical tubercles, dorsum of males covered with low, round tubercles, some conical tubercles may be present on legs; (6) lateral row of tubercles in males present as a series of low, discrete round tubercles, in females present as a series of widely spaced sharply pointed tubercles; (7) vocal slits small, located posteriorly in mouth, bilateral; (8) *m. interhyoideus* poorly differentiated from *m. intermandibularis*

and undifferentiated posteriorly, forming small, unilobed, unpigmented sac; (9) snout acutely pointed in dorsal view, rounded, or slightly protruding in profile; (10) cranial crests low and thick in most males, junction of parietal and supraorbital crests often hypertrophied to form a small knob, crests in females high (well above level of dorsal margin of eyelid), thin, commonly with vertically striated texture on medial surfaces; (11) parotoid glands moderately large, conspicuously protuberant, usually ovoid; and (12) color of digital tips paler than on rest of digit, orange in life.

*Bufo macrocristatus* is most similar to *Bufo cavifrons*, but differs by having more tuberculate skin, larger and more ovoid parotoid glands, larger tympanum relative to the eye, longer tibia, smaller vocal slits, and cranial crests of females are vertically prominent and thin, rather than greatly thickened and knoblike. *Bufo macrocristatus* differs from *B. campbelli* by having larger, more protuberant and ovoid parotoid glands and cranial crests that are thickened in males and vertically prominent and thin in females. *Bufo canaliferus* differs by being smaller and by lacking parietal crests. *Bufo bocourti* and *Bufo tacanensis* differ by lacking tympana. *Bufo valliceps* differs by having shorter legs, larger tympana, and by having the *m. interhyoideus* forming a large, bilobed, pigmented sac.

**Color pattern.**—Mendelson (1997a) described the color patterns of males and females of this species. Females are highly variable in color pattern and may have a pale brown dorsum with few, small, black markings (similar to most males), or have dark brown dorsal color with five to seven large black markings, or any combination of the above with or without a pale middorsal stripe. In males, dorsal coloration is usually pale, or dark, brown without markings and with some degree of darker coloration that follows the ventral border of the row of lateral tubercles; a few specimens have a few (sometimes

paired) small black dorsal markings. In both sexes, the digital tips may be distinctly orange; in preservative the tips are pale cream and much paler than proximal areas of the fingers.

**Reproductive biology.**—The tadpole of *Bufo macrocristatus* was described (as *Bufo cavifrons*) by Korky and Webb (1973) from a lot collected near Soluschiapa, Chiapas; Mendelson (1997a) provided additional diagnostic information regarding this tadpole. Breeding behavior in *B. macrocristatus* is unknown. The presence of vocal slits and a small undifferentiated vocal sac suggests that this species may have an advertisement call. A female collected in June has well-developed ova. Males collected between June and January have well-developed nuptial excrescences. The tadpoles reported by Korky and Webb (1973) were found in a slow-moving roadside rivulet, and others (see Mendelson, 1997b) have been found in a slow-flowing seep.

**Distribution and ecology.**—*Bufo macrocristatus* is known from the very wet rain and cloud forests along the Atlantic versant from the Chimalapas in eastern Oaxaca, Mexico, to the Sierra de los Cuchumatanes, Huehuetenango, Guatemala. Apparently, most specimens were collected in primary forest, usually along streams, at elevations of about 300–1800 m.

**Etymology.**—The specific epithet is derived from the Greek *makros*, meaning long—but perhaps intended to mean large—and the Latin *crista*, meaning crest; the name *macrocristatus* is in reference to the enlarged cranial crests evident especially in females.

**Remarks.**—The taxon *macrocristatus* was originally described as a subspecies of the widespread and variable species *B. valliceps*. This taxon was never widely accepted, and Porter (1963, 1970) relegated it to the synonymy of *Bufo valliceps*. However, Porter (1963) also referred specimens that represent *B. macrocristatus* to *B. cavifrons*. Based on

this taxonomic confusion, specimens of *B. macrocristatus* have been referred to inconsistently in the literature and museum catalogs as either *B. cavifrons* or *B. valliceps*.

*Bufo melanochlorus* Cope

*Bufo melanochlorus* Cope, 1877:85.

*Bufo melanochloris* Taylor, 1952; incorrect subsequent spelling.

**Holotype.**—USNM 30592, from Eastern Costa Rica; W. M. Gabb collector.

**Diagnosis.**—A moderate-sized species of *Bufo* (males to 65 mm SVL; females to 103 mm SVL) having the following combination of characters: (1) tympanum small, about 36% diameter of orbit; (2) preorbital crest present, thin, in females, absent in males, pretympenic crest absent, or weakly developed in large individuals; (3) tibia long, about 48% SVL; (4) foot relatively short, about 42% SVL; (5) skin smooth, with few scattered distinct, pointed tubercles concentrated posteriorly and on limbs, evident especially on females; (6) lateral row of tubercles present as a series of low rounded tubercles in males, in females as a series of sharply pointed tubercles; (7) vocal slits small, located posteriorly in mouth, bilateral; (8) *m. interhyoideus* forming small, unpigmented vocal sac; (9) snout sharply pointed in dorsal and lateral view in males, females with snout pointed in dorsal view, bluntly rounded rounded in profile; (10) cranial crests low, thin; (11) parotoid glands small, triangular; (12) digital tips same color as rest of digit.

*Bufo melanochlorus* is most similar to *Bufo campbelli*, a species known to occur in Mexico, Belize, Guatemala, and Honduras, but differs by having smaller parotoid glands with the anterior breadth of the gland less than the width of the eyelid, an unpatterned venter, and digital tips that are the same color as the rest of the digit. *Bufo melanochlorus* differs from *B. valliceps* by having smoother skin, smaller and more

triangular parotoid glands, smaller tympanum that is well separated from the pretympanic crest, lower and thinner cranial crests, and weakly developed preorbital and pretympanic crests. *Bufo coniferus*, also known from Costa Rica, differs by having a unilateral vocal slit, small round parotoid glands, green dorsal coloration, and numerous dark, sharply pointed, dorsal tubercles.

**Color pattern.**—Males have a uniform rusty-tan to brown dorsal color with a light middorsal, usually a pair of light dorsolateral stripes, and a dark lateral stripe extending from the parotoid gland to the flank that is bordered above by a white line. Juveniles and females commonly have the same pattern, but with dark dorsal spots. The venter in both sexes is dull yellow in life (dull cream in preservative).

**Reproductive biology.**—This species breeds in large rocky-bottomed streams at times of low water levels during the dry season (January and February). The tadpole has not been described (Lips and Savage, 1996).

**Distribution and ecology.**—*Bufo melanochlorus* is known from lowland and lower montane forests on the Atlantic versant of Costa Rica, as well as from the lowland forests in the southwestern Pacific versant; elevational range is 20–1080 m. This species is usually found in leaf litter in primary forest, or along streams when breeding.

**Etymology.**—The specific epithet is derived from the Greek *melanos*, meaning black, and *chloros*, meaning green.

**Remarks.**—Jay Savage (pers. comm.) provided much of the information in this species account. The original spelling for this taxon is “*melanochlorus*.” Taylor (1952) was the first to publish the spelling “*melanochloris*” and, presumably because of its completeness, information in Taylor's (1952) influential work quickly became established in the subsequent literature.

*Bufo spiculatus* Mendelson

*Bufo spiculatus* Mendelson, 1997:60–66.

*Bufo cristatus*—Shannon, 1951:470 [in part, for referral of USNM 123691, from San Lucas Camotlán, Oaxaca].

*Bufo cavifrons*—Porter, 1963:232 [in part, for referral of AMNH 60435, from San Pedro Sochiapan, Oaxaca].

*Bufo valliceps*—Porter, 1963:236 [in part, for referral of USNM 123691, from San Lucas Camotlán, Oaxaca].

**Holotype.**—KU 137523, an adult female from 2.8 km S Vista Hermosa, Oaxaca, Mexico, 1570 m; J. P. Caldwell collector.

**Diagnosis.**—A large species of *Bufo* (males to 71.4 mm SVL; females to 103.0 mm SVL) having the following combination of characters: (1) tympanum small, about 36% diameter of orbit; (2) preorbital crest present, thin, in females, absent in males, pretympanic crest absent, or weakly developed in large individuals; (3) tibia short, about 40% SVL; (4) foot relatively short, about 42% SVL; (5) skin smooth, with distinct spiculate tubercles concentrated posteriorly and on limbs, evident especially on females; (6) lateral row of tubercles present as a series of conical or high, rounded tubercles in males, in females as a series of sharply pointed tubercles; (7) vocal slits absent; (8) *m. interhyoideus* not forming pigmented vocal sac; (9) snout sharply pointed in dorsal view, rounded in profile; (10) cranial crests low and thick in males, crests in females low, moderately thick, usually with crenulate texture on vertical surfaces; (11) parotoid glands large, conspicuously protuberant, usually triangular; (12) digital tips distinctly paler than rest of digit.

*Bufo spiculatus* is similar to *B. cavifrons* but differs by lacking vocal slits and sac, females having distinctive spiculate tubercles concentrated on the posterior portion of the dorsum and on the limbs, and cranial crests relatively low and thick with a crenulate texture; *B. cavifrons* has smooth skin and cranial crests that are smooth, thick, and greatly elevated vertically. *Bufo macrocristatus* is quite variable, but in most cases specimens may be distinguished from *B. spiculatus* by having vocal slits and a small vocal sac, smoother skin, larger tympana, and more ovoid parotoid glands. *Bufo valliceps*, with which *B. spiculatus* may be sympatric, has shorter legs, larger tympana, distinct preorbital and pretympanic crests, and large vocal slits associated with a large pigmented vocal sac. Some male specimens of *B. tutelarius* lack vocal slits; however, this species differs by having uniformly rugose dorsal skin texture, low and nonhypertrophied cranial crests, and ovoid parotoid glands.

**Color pattern.**—Mendelson (1997b) provided a complete description and illustration of the color pattern of this species. Females are red-brown or gray dorsally and may be unmarked or may have few small black markings and/or a pale middorsal stripe. Males are brown dorsally with few black markings and with or without a middorsal stripe. The ventral pattern in both sexes is dull cream or yellow with scattered brown markings or mottling. In both sexes the tips of digits are distinctly paler than rest of digit.

**Reproductive biology.**—The tadpole of *Bufo spiculatus* is unknown, as is the breeding behavior; meager data suggests that this species breeds during the July–January rainy season.

**Distribution and ecology.**—*Bufo spiculatus* is known from few specimens that all were found on the northern slopes of the Sierra de Juárez and the adjacent Sierra Mixe,

Oaxaca, Mexico. All specimens were collected in primary cloud forest between 800–1689 m.

**Etymology.**—The specific epithet is derived from the Latin *spica*, and is used as an adjective in reference to the distinctive spiculate skin texture evident especially on females of this species.

**Remarks.**—It is surprising that so few specimens of this toad have been collected despite the fact that Mexican Highway 75 now allows relatively easy access to the still-forested (as of 1992) northern slope of the Sierra de Juárez, and the fact that many herpetological collections have been made in the vicinity of the village of Vista Hermosa. Porter (1963) referred the population of toads from the the Sierra de Juárez to *B. cavifrons* and a single specimen from the Sierra Mixe to *Bufo valliceps*.

*Bufo tutelarius* Mendelson

*Bufo tutelarius*—Mendelson, 1997:15–21.

*Bufo valliceps*—Porter, 1964a:fig. 8 [in part; for records plotted in the Pacific highlands of Guatemala and southern Mexico]; Porter, 1970:94.1 [in part; for records plotted on map from the Pacific highlands of Guatemala and southern Mexico]; Johnson, 1989:60 [in part; records from the Sierra Madre de Chiapas, specifically those from the Sierra Madre de Chiapas, Chiapas, Mexico]; Campbell and Vannini, 1989:table 2 [in part; for records indicated from Cuchumatan Subarea of the Huehuetenangan Area; likely based on the UMMZ specimens from Aldea Paraiso, Huehuetenango, Guatemala]; Flores-Villela, 1993:16 [in part; for records representing "Tropical Highlands" of Chiapas, Mexico, and Guatemala].



*Bufo cavifrons*—Johnson, 1989:42,60 [in part; for records from the Sierra Madre de Chiapas, specifically those from near Cerro Baúl, Oaxaca, Mexico].

**Holotype.**—UTA A-13135, an adult male from Colonia Rodolfo Figueroa, 19.0 km NW Rizo de Oro, Oaxaca, Mexico, 1370 m; J. A. Campbell, D. M. Hillis, and W. W. Lamar collectors.

**Diagnosis.**—A large species of *Bufo* (males to 76.2 mm SVL; females to 103.6 mm SVL) having the following combination of characters: (1) tympanum small, about 37% diameter of orbit; (2) preorbital crest present, pretympanic crest absent, or weakly developed in large individuals; (3) tibia short, robust, about 40% SVL; (4) foot short, about 41% SVL; (5) skin rugose in both sexes with diffuse keratin medially, smoother, with scattered conical keratinized tubercles, laterally; (6) lateral row of tubercles in both sexes as a distinct series of small pointed tubercles; (7) vocal slits small, located posteriorly in mouth, absent or unilateral in some specimens; (8) *m. interhyoideus* poorly differentiated from the *m. intermandibularis*, not forming a pigmented vocal sac, vocal slits (when present) lead into small pouches that, when bilateral, are separated medially; (9) snout acutely pointed in dorsal view, rounded in profile; (10) cranial crests in both sexes moderately thick, not hypertrophied or dorsally protuberant; (11) parotoid glands large, ovoid, not protuberant; and (12) digital tips same color as rest of digit.

This species is most similar to the widespread lowland species *Bufo valliceps*, from which it may be distinguished by having smaller tympana, and by lacking an *m. interhyoideus* that forms a bilobed, pigmented vocal sac. *Bufo bocourti* and *B. tacanensis* differ by lacking tympana. *Bufo cavifrons* and *Bufo cristatus* differ by having greatly hypertrophied cranial crests. *Bufo canaliferus* differs by being smaller and by lacking parietal crests. *Bufo macrocristatus*, with which *B. tutelarius* may be sympatric, differs

by having a head that is about as wide as long (wider than long in *B. tutelarius*), smoother skin on the venter, cranial crests that are thin and vertically prominent above the level of the eyelid in females, or thickened to form a small knob in males.

**Color pattern.**—Mendelson (1997a) provided a complete description and illustration of the color pattern in this species. Males and females have a dull brown dorsum with scattered, small, dark brown or black markings with or without a pale brown or cream middorsal stripe. The venter is usually dull cream with few or no darker markings. The tips of the digits are not distinctly paler than the rest of the digit.

**Reproductive biology.**—The eggs, tadpoles, and breeding behavior of *B. tutelarius* are unknown. The vocal slits and sac are poorly developed; this species may have a weak advertisement call, if any. Adult females collected June–August have well-developed ova.

**Distribution and ecology.**—*Bufo tutelarius* is known from the Pacific and Atlantic versants of the Chimalapas, Sierra Madre de Chiapas, Volcán Tacaná, and the Montañas de Cuilco, between extreme southeastern Oaxaca, Mexico, and extreme southwestern Guatemala. Specimens have been taken from elevations between 1050–2000 m; this species inhabits higher elevations than any other species in the *B. valliceps* group. All specimens appear to have been found in primary cloud forest or pine-oak forest.

**Etymology.**—The specific epithet, *tutelarius*, is a Latin noun used in apposition meaning custodian, or guardian, and is in reference to the large size of this species.

**Remarks.**—Despite the apparent physical continuity of the Pacific Highlands of southern Mexico and Guatemala, no specimens of *B. tutelarius* have been collected in the Volcanic Cordillera of Guatemala southeast of Volcán Tacaná. The Pacific slopes of this

cordillera have been reasonably well explored; apparently this species does not occur there. Also, all specimens of this species from the Sierra de Chimalapas in Oaxaca, Mexico, have been collected on, or near, the slopes of Cerro Baúl; *Bufo macrocristatus* has not been collected on this mountain. As such, it is possible that *B. tutelarius* and *B. macrocristatus* are parapatric in the eastern and western areas, respectively, of the Sierra de Chimalapas.

*Bufo valliceps*

*Bufo valliceps* Wiegmann, 1833:657–659.

*Bufo trachypus* Wiegmann, 1833:657. *Nomen nudum*.

*Bufo granulosus* Baird and Girard, 1852:173. [Holotype: USNM 2595, from between Indianola and San Antonio, Texas, USA]; name preoccupied by *Bufo granulosus* Spix, 1824.

*Bufo nebulifer* Girard, 1854:47. Replacement name for *Bufo granulosus* Baird and Girard.

*Bufo sternosignatus* [part] Günther, 1958:68–69. Name restricted to Venezuelan population.

*Chilophryne nebulifera* Cope, 1862:346–359.

*Incilius nebulifera* Cope, 1863:43–54.

*Bufo cristatus*—Taylor and Smith, 1945:559, pl. 23, figs. 5, 6.

*Bufo valliceps wilsoni* Baylor and Stuart, 1961:195–202. [Holotype: UMMZ 119391, from Jacaltenango (ca. 50 air-line km northwest of Huehuetenango), Huehuetenango, Guatemala].

*Bufo cavifons*—Porter, 1967:66.

**Syntypes.**—ZMB 3525–27, 3532 (five specimens), from Mexico and Veracruz, Mexico; F. Deppe collector.

**Diagnosis.**—A large species of *Bufo* (males to 88 mm SVL, females to 121 mm SVL) having the following combination of characters: (1) tympanum large, about 50% diameter of orbit; (2) preorbital and pretympanic crests present, distinct; (3) tibia short, about 38% SVL; (4) foot short, about 39% SVL; (5) skin rough, with many evenly distributed rounded tubercles over all dorsal surfaces, some specimens with relatively smooth skin, or evenly distributed sharply pointed tubercles; (6) lateral row of tubercles present as series of distinct rounded, or pointed, tubercles; (7) vocal slits large, bilateral; (8) *m. interhyoideus* forming large, bilobed (anteroposteriorly), pigmented vocal sac; (9) snout usually pointed in dorsal view, rounded in profile; (10) cranial crests low, robust; (11) parotoid glands variable, usually subtriangular or ovoid; (12) digital tips same color as rest of digit.

*Bufo valliceps* may be distinguished from all other species in the *B. valliceps* Group by having a relatively larger tympanum (about 50% diameter of eye) that is in contact with, or nearly so, the pretympanic crest, by having both the preorbital and pretympanic crests present and distinct, bilateral vocal slits and a darkly pigmented bilobed (anteroposteriorly) vocal sac, and by having the cranial crests unhypercrophied, low, and robust.

**Color pattern.**—Photographs of this species appear in Blair (1972), Villa (1974), Conant and Collins (1991), and Lee (1996). The dorsal color pattern of this species is quite variable. Individuals may be dull brown with bold black and yellowish marbling, or have a nearly uniform dorsal color of brown, from tan to almost black including gray-brown or reddish brown. Most specimens have pale brown or cream middorsal stripe and

a lateral stripe (below the lateral series of tubercles) that is darker than the dorsal color. The venter is usually dull cream or gray, with few or no darker markings.

**Reproductive biology.**—Breeding takes place in ponds, puddles, marshes, or still pools in ditches. Breeding season is prolonged throughout the summer season so long as sufficient warmth and rainfall are present (Dundee and Rossman, 1989; Lee, 1996). The tadpole was illustrated and described by Limbaugh and Volpe (1957) and Lee (1996). Lee (1996) described the advertisement call and Porter (1964*b*) summarized geographic variation in the call. Sullivan and Wagner (1988) described social behavior of calling males and analyzed variation in call characteristics among males. Ryan and Sullivan (1989) analyzed temporal and spatial aspects of advertisement call transmission. Natural hybridization between *B. valliceps* and *B. woodhousei* has been studied by Brown and Brownell (1971) and Brown (1971*a*) and hybridization with *B. houstonensis* was studied by (Brown, 1971*b*).

**Distribution and ecology.**—*Bufo valliceps* is known from southern Arkansas, Louisiana, and Alabama, USA, southward along the Atlantic coast to extreme northeastern Costa Rica, and along the Pacific coast from the Isthmus of Tehuantepec to Guatemala/El Salvador border from elevations between 0–1700 m (Porter, 1970; Villa, 1974; Conant and Collins, 1991; Mendelson, 1997*a*). This species seems to occur primarily in open habitats, such as savanna, and may be abundant in disturbed habitats such as villages, pastures, agricultural areas, or secondary growth (Mendelson, 1994; Lee, 1996). Parmley (1988) reported Pleistocene fossils from western Texas that lie outside the present range of the species. McAllister et al. (1989) described the endoparasites from a population northern Texas.

**Etymology.**—The specific epithet is derived from the Latin *vallis*, meaning valley, and the Greek *cephalon*, meaning head; the name *valliceps* is in reference to the hollow, valley-shape produced by the cranial crests on top of the head.

**Remarks.**—*Bufo valliceps* is the most widespread member of the *Bufo valliceps* Group and, because of its proclivity to inhabit disturbed areas, is the most likely species of the group to be encountered in most areas of Middle America. Porter (1970) reviewed the pertinent literature prior to 1970. This common toad has been the subject of popular articles (e.g, Branson, 1995) and numerous research articles (e.g, Porter, 1964*a, b*). Presumably because it is easy to obtain, *Bufo valliceps* is commonly represented in higher level analyses of relationships among bufonids (e.g, Graybeal, 1997) or amphibians in general (Hay, et al., 1995). Firschein (1950) resolved confusion surrounding the identification and status of *Bufo cristatus* with respect to *B. vallieps*. Porter (1964*a*,1970) reviewed distribution, variation, and taxonomic issues up to that point in time. Savage (in Frost, 1985:52) remarked that Porter's (1970) records from El Salvador and parts of Guatemala, Nicaragua, and Costa Rica were in error. Mendelson (1994, 1997*a*) further clarified the taxonomic status of this species by describing or recognizing *B. campbelli*, *B. tutelarius*, and *B. macrocristatus*, all of which had been confused to some extent with *B. valliceps*. Mendelson (1997*c*) reviewed the distribution of *B. valliceps* in Guatemala, demonstrated that *B. ibarraii* Stuart is distinct from *B. valliceps*, and that the taxon *Bufo valliceps microtis* Werner is referable to the synonymy of *Bufo coccifer*.

## A Key to the Species of the *Bufo valliceps* Group

The *Bufo valliceps* group (sensu lato) is diagnosed by having a complete array of cranial crests, a lateral series of enlarged tubercles, an omosternum, and vocal slits in males present and bilateral, or absent (never unilateral). Species of this group occur from the southern United States (Louisiana, Texas) to Costa Rica, usually in humid habitats between 0–2000 m elevation. Some species (e.g., *B. valliceps*) may be abundant and conspicuous in disturbed habitats such as villages and corn fields, whereas other species (e.g., *B. spiculatus*) seem to be secretive and inconspicuous in primary forest.

Terminology for cranial crests appears in Figs. 5.1 and 5.2; sketches of general morphology of cranial crest of different species appear in Figs. 1.2, 1.5, 2.1, and 2.4.

1. Parietal crests conspicuously hypertrophied and bulbous..... 2  
Parietal crests straight, low or high and blade like, thin or with small knob at junction with supraorbital, postorbital and parietal crests..... 3
  
2. Parietal crests expanded laterally, filling space between parietal, postorbital, and supratympanic crests; parotoid glands large (length 2–2.5 times width of eyelid), ovoid; vocal slits absent, known only from central Sierra Madre Oriental, Mexico..... *B. cristatus*
  
- Parietal crests not expanded laterally; space between parietal, postorbital, and supratympanic crests present; parotoid glands small (length 1–1.5 times width of eyelid), triangular; vocal slits present, bilateral; known only from Sierra de los Tuxtlas, Mexico..... *B. cavifrons*

3. Cranial crests low, robust, with or without small bony knob at junction of supraorbital, postorbital, and parietal crests; medial and lateral surfaces smooth, or with slight striated texture; dorsal skin texture usually evenly granular..... 4

Cranial crests low, thin and smooth, or moderate to high, with or without lateral texture; dorsal skin texture relatively smooth with scattered, discrete, sharply pointed tubercles..... 6

4. Cranial crests low, robust, smooth; diameter of tympanum about 50% diameter of eye, usually in contact with, or barely separated from pretympanic crest; preorbital and pretympanic crests present, robust; vocal slits bilateral, large ( $\frac{1}{3}$ – $\frac{1}{2}$ ) length of tongue; vocal sac large, black; digital tips usually same color as rest of digit; parotoid glands, skin texture, and color pattern variable; known from southern USA to Costa Rica below 1700 m..... *B. valliceps*

Cranial crests low, robust, smooth, with or without small bony knob at junction of supraorbital, postorbital, and parietal crests; diameter of tympanum less than 45% diameter of eye, well separated from pretympanic crest (if present); pretympanic and preorbital crests present or absent; vocal slits absent, or present, small ( $\leq \frac{1}{3}$  length of tongue), bilateral; vocal sac absent, or small, unpigmented; digital tips paler or same color as rest of digit; parotoid glands ovoid; skin texture and color pattern variable..... 5



5. Cranial crests low robust, without any hypertrophied areas; diameter of tympanum about 37% diameter of eye, well separated from pretympenic crest; pretympenic crest short, indistinct in all but largest females; preorbital crest present; vocal slits small ( $\leq 1/4$  length of tongue), bilateral, unilateral, or absent; vocal sac absent; digital tips same color as rest of digit; parotoid glands moderately sized, length about 1.5 times eyelid, ovoid; dorsal skin texture relatively evenly granular; dorsal color brown with few or no darker markings, with or without middorsal stripe; ventrum usually uniform dull cream, or with diffuse gray coloration in some areas; known from Cerro Baúl, Oaxaca, Mexico, Sierra Madre de Chiapas, and Volcán Tacaná and Montañas de Cuilco of Guatemala..... *B. tutelarius*

Cranial crests robust, usually with an small bony knob at junction of supraorbital, postorbital, and parietal crests, sometimes extending posteriorly to produce a hypertrophied parietal crest; diameter of tympanum about 40% diameter of eye, well separated from pretympenic crest; pretympenic crest absent, or present, short; preorbital absent, or present, thin; vocal slits present, small ( $\leq 1/3$  length of tongue), bilateral; vocal sac small, unpigmented; digital tips distinctly paler than rest of digit, orange or yellow in life; parotoid glands large, length about  $1\frac{1}{2}$ –2 times eyelid, ovoid; dorsal skin texture usually evenly granular, but may be relatively smooth with scattered discrete tubercles; dorsal color usually dull brown with no, or few, darker markings and with or without a thin middorsal stripe; ventrum dull cream with distinctive black markings that may cover most ventral surfaces, becoming diffuse or marbled at all margins; known from rain and cloud forests of eastern Oaxaca, Mexico (Chimalapas) and along the Atlantic slope of the

Chiapan Highlands, and the wet Atlantic slope of the Sierra de los Cuchumatanes of Guatemala..... *B. macrocristatus* (male)

6. Cranial crests low, thin, smooth; dorsal skin texture relatively smooth..... 7

Cranial crests moderate to high, robust or blade-like, usually with distinct striated or crenulate texture on lateral surfaces; skin relatively smooth with scattered discrete sharply pointed tubercles, sometimes becoming highly concentrated posteriorly and on hind limbs..... 8

7. Venter patterned with indistinct dark smudge on the throat and sternal area and distinct speckling concentrated especially on the throat, pelvic, and femoral areas; digital tips paler than rest of digit; anterior breadth of parotoid glands about equal to the width of eyelid; vocal slits present, bilateral; vocal sac small, unpigmented; known from Atlantic slope rain forests from southern Veracruz, Mexico, to Atlantida, Honduras..... *B. campbelli*

Venter relatively immaculate; digital tips same color as rest of digit; anterior breadth of parotoid glands less than width of eyelid; vocal slits present, bilateral; vocal sac small, unpigmented; known from lowlands and lower montane forests on Atlantic versant of Costa Rica and lowlands of southwestern Pacific versant..... *B. melanochlorus*

8. Region at junction of supraorbital, postorbital, and parietal crests usually distinctly raised, thin and blade-like, with distinct striated texture; dorsal texture relatively smooth

with few scattered sharply pointed tubercles; known from rain and cloud forests of eastern Oaxaca, Mexico (Chimalapas) and along the Atlantic slope of the Chiapan Highlands, and the wet Atlantic slope of the Sierra de los Cuchumatanes of Guatemala..... *B. macrocristatus* (female)

Cranial crests robust, without distinctly raised areas, usually with distinct crenulate texture on lateral surfaces; dorsal texture relatively smooth with many scattered sharply pointed tubercles, becoming highly concentrated posteriorly and on legs to produce a distinctly rough texture; vocal slits and sac absent; known only from the forested northern slopes of the Sierra de Juárez and the adjacent Sierra Mixe, Oaxaca, Mexico..... *B. spiculatus*

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## APPENDIX I

### SPECIMENS EXAMINED FOR ALPHA-LEVEL STUDIES

#### *Bufo campbelli*

BELIZE: TOLEDO: Maya Mountains, SW end Little Quartz Ridge, UTA A-8984, 85

GUATEMALA: ALTA VERAPAZ: N slope Sierra de las Minas, Finca Pueblo Viejo, along Río Chiquito, above Sechiquito village, 100 m, UTA A-28866, 67; N slope Sierra de las Minas, Finca Pueblo Viejo, Río Tinajas/Río Pueblo Viejo divide, 4.5 air km SSE Pueblo Viejo, 335 m, UTA A-28893; N slope Sierra de las Minas, Finca Pueblo Viejo, E slope Río Chiquito/Quebrada Cancoy divide, 7–7.5 air km SSW Pueblo Viejo, 731 m, UTA A-28897; vicinity of Pueblo Viejo, UTA A-33012; Chinajá, 140 m, KU 55901, 55909. EL PETÉN: 8 km NNW Chinajá, 120 m, KU 55875–77, 55882–86; 10 km NNW Chinajá, 120 m, KU 55888–90; 11 km NNW Chinajá, 120 m, KU 55898; 15 km NW Chinajá, 120 m, KU 55917. IZABAL: Montañas del Mico, 7.8 km WSW Puerto Santo Tomás, UTA A-18196, 97; Montañas del Mico, Las Escobas, 5.1 km WSW Puerto Santo Tomás, 122 m, UTA A-18200, 21672, 33043–45, 33574, 75 KU 190089, 92, 94, 190103–106, 190108–112, 190116–131; Montañas del Mico, 6.0 km WSW Puerto Santo Tomás, UTA A-21674, 75; Montañas del Mico, 5.5 km WSW Puerto Santo Tomás, near Las Escobas, UTA A-24721; 0.8 km W Aldea Vista Hermosa, Los Amates, 500–950 m, KU 190086, 87, 190134–136, 190138, 190140, 190143, 190148, 190150, 190151; Sierra de Santa Cruz, 10.0 km W Finca Semuc headquarters, Semococh, UTA A-24934, 24941, 26417; Sierra de Santa Cruz, ca. 4.5 km S Finca Semuc headquarters, UTA A-24937, 38; Sierra de Santa Cruz, Finca Semuc, UTA A-24940, 24944; Seshan, UTA A-26420–22; Sierra de Santa Cruz, Finca Semuc, 4 km W Finca Semuc headquarters, Seyamch, UTA A-26415; El Estor, Sierra de Santa Cruz, Finca Semuc, Cerro Sechoc, UTA A-33055, 58;

Sierra de Santa Cruz, 6.0 km S Franco, UTA A-33059–63; Sierra de Santa Cruz, Finca Semuc, 3 road km S headquarters, UTA A-33577, 79–83. HONDURAS: W of San Pedro, Hacienda Santa Ana (FMNH 4627, 4630). ATLANTIDA: Cordillera Nombre de Dios, S slope Cerro Bufalo, 800 m (KU 194206–07); Quebrada del Oro, 880 m (KU 209267); Lancetilla (AMNH 54788). COLON: Belfate (AMNH 45721). COPAN: Laguna del Cerro, 810 m (KU 209265); Montaña del Cerro Azul, 1080 (KU 209266). YORO: Montaña la Ruidosa, above Calpules, 1500 m (KU 209268); Montaña la Ruidosa, above Calpules, 1600 m (KU 209269); Subirana Valley (FMNH 21792). MEXICO: CHIAPAS: 11 mi [17.7 km] W Mal Paso, 400 ft [122 m] (TCWC 21483–84); 10 mi [16.1 km] W Mal Paso, 400 ft [122 m] (TCWC 21485). VERACRUZ: 25 km SE Jesús Carranza, 250 ft [76 m] (KU 27466).

*Bufo cavifrons*

MEXICO: VERACRUZ: Lake Catemaco (TNHC 30967, 31094); 500 ft [152.4 m] below peak of Volcán San Martín, San Andres Tuxtla (UIMNH 8741, holotype); S slope Volcán San Martín, 3800 ft [1158 m] (UMMZ 118195, 55 specimens); S slope Volcán San Martín (UTA A-2347); 7.7 mi [12.4 km] NW Sontecomapan (UTA A-6320, 7923–24); 7.5 mi [12.1 km] NW Sontecomapan (UTA A-6321–22); Volcán San Martín (TNHC 26588, 26591, 27109–10, 27137 27141, 27145, 27147); ; 4 mi [6.4 km] ENE Tapalapan, 1600 ft [488 m] (LSU 7829); 3 mi [4.8 km] NNW Ocotal Chico, 4300 ft [1311 m] (LSU 11762); Río Quezalapam, 2 mi [3.2 km] E Lago Catemaco (TCWC 21270–72); Volcán San Martín, 1164 m (TCWC 23907, 30966); Colonia de Bastonal, above Quezalpam (TCWC 19086–87); Dos Arroyos, 5 mi [8.0 km] E Zapoapan, Los Tuxtlas (TCWC 21278, 21282–85, 21287, 21289); 4 mi [6.4 km] SE Tebanca, Los Tuxtlas (TCWC

21274–76); lower falls of Río Quezalpam, Quezalpam (TCWC 19084–85); Bastonal, E of Cuetzalapa, E of Lago Catemaco (CM 52749, 3 specimens); Bastonal, 8 mi [12.9 km] E Cuetzalapa, Lago Catemaco (CM 41596); Los Tuxtlas, Santa Marta (MZFC 4660, 4693).

*Bufo cristatus*

MEXICO: PUEBLA: Tezuitlán (KU 39586–89). VERACRUZ: Jalapa (ZMB 3524, lectotype), MCZ 8362; 4 mi [6.4 km] SE Atzalan (KU 144722, larvae); 3.6 mi [5.8 km] S Coscomatepec, Rio Chocaman, 4300 ft [1310 m] (UMMZ 115427); 7.2 mi [11.6 km] SW Huatusco (UMMZ 123278); S side Orizaba, below village of Chilapa (MCZ 35764); 7 mi [11.2 km] E Tezuitlan (Puebla) (UIMNH 57141).

*Bufo ibarraí*

GUATEMALA: BAJA VERAPAZ: Chilasco (UTA A-47567–69); circa 5 km S Chilasco, 1800 m (MVZ 143379); 8 km ESE Chilasco, Finca Miranda, 6500 ft [1981 m] (MVZ 150931); 50.2 km NW El Rancho (UTA A-5016); CA-14, 29.0 mi [46.7 km] NW El Rancho (UTA A-5049); CA-14, 50.2 km NW El Rancho (UTA A-5015); 4.8 mi [7.7 km] SSE Purulhá, Plantación Santa Teresa (UTA A-7417); 9.1 mi [14.6 km] W Salamá (by road to Purulhá) (UTA A-7432); 2.4 mi [3.9 km] W Purulhá (UTA A-8502–07); 3.5 mi [5.6 km] W Purulhá (UTA A-30495 larvae); 3.2 km WNW Purulhá (UTA A-17117–18); 3.5 km W western Purulhá turnoff (UTA A-17242–17244); 2.7 km W western Purulhá turnoff (UTA A-17245); 3.8 km W Purulhá, 1536 m (KU 186288–303); 7.7 km SE Purulhá, 1615 m (KU 186304); 3.8 km W Purulhá, 1524 m (KU 190067); 4.2 km W Purulhá, 1524 m (KU 190068–70); 3.4 km W Purulhá, 1524 m (KU 190071); 2.0 km W

Purulhá (UTA A-38145–49); Hwy CA-17 between El Rancho and Cobán, km 126 (UTA A-43977–78); 1 km S San Gerónimo (UMMZ 84083). EL QUICHE: Joyabaj (KU 186305); La Primavera, between Sacapulas and Santa Cruz Quiche, 6600 ft [2012 m] (UMMZ 126307). GUATEMALA: Amatitlan (UTA A-38144); 11.2 km SW Guatemala City, 4600 ft [1402 m] (KU 97595–609); 21 km SW Guatemala City, 4480 ft [1366 m] (KU 97610–19); Guatemala City, zone 10, 4820 ft [1469 m] (TNHC 31384, 31387, 31390, 31392, 31395, 31399, 31401–02, 31405, 31408, 31416–20, 31422, 31426, 31430–33); Guatemala City, between zone 5 and zone 15, km 2.5 (UTA A-25824); E side Guatemala City, zone 16, 1 km N Vista Hermosa III on road to Santa Rosita (UTA A-25825–32); Santa Catarina Pinula, San Miguel Buena Vista, 1700 m (UTA A-43951, UTA A-47570–74); Guatemala City, zone 15, Vista Hermosa III, 1510 m (UTA A-28959–60); Parque San Jorge Muxbal, 1850 m (UTA A-32993). HUEHUETENANGO: Aguacatan (UMMZ 120046); 2 km NE Aguacatan, 1640 m (UMMZ 120047–48); 2.8 km E Aguacatan, 1600 m (KU 58412–13); Huehuetenango, patio of Casa Maryknoll (UMMZ 124382); 22 km SSW Huehuetenango (KU 116959); 3 km W Huehuetenango, 6100 ft [1859 m] (TNHC 29452–57); at La Libertad, 1700 m (MVZ 143343–57); San Pedro Necta (UMMZ 130059; larvae); circa 1 km E San Pedro Necta, 1615 m (UMMZ 119352). JALAPA: Jalapa (TNHC 33666–72); 8.5 km NW Jalapa (TNHC 31442); 7.5 km WSW Jalapa, on road to Miramundo (UTA A-39114 larvae); Jalapa–Miramundo rd, at km 101 (UTA A-38118); Falda Oeste Volcán Jumay (UTA A-47565); 1.6 mi [2.5 km] NE El Mojón (UTA A-38127–40); 0.7 mi [1.1 km] NE El Mojón (UTA A-38141); Aserradero San Lorenzo (circa 12 air km NNE Jalapa), 1725 m (UMMZ 108000, 106806 [10 specimens], 106807 [3 specimens]). PROGRESO: Finca Bucaral (UMMZ 106808, 139516 larvae). SACATEPEQUEZ: 3 km W Dueñas (TNHC 31378); 1.3 mi [4.4 km] W

Finca San Rafael Urias at Dueñas (TNHC 31344, 31379–80); San Antonio (CAS 70826–27); Volcán Agua (CAS 70719–825).

*Bufo macrocristatus*

GUATEMALA: HUEHUETENANGO: on ridge about 2 km NW Barillas, 5900 ft [1798 m] (MVZ 143380). MEXICO: CHIAPAS: 5.6 km S Rayón Mescalapa, 1680 m (KU 58294–99); 6.2 km S Rayón Mescalapa, 1690 m (KU 58300-03); 6.8 km E Rayón Mezcala (UTA A-27857–59 larvae); 6 mi [9.7 km] S Soluschiapa, 1300 ft [396 m] (UTEP 5879–84); 4 mi [6.4 km] S Rayón, 5500 ft [1676 m] (UTEP 5885); 1.1 mi [1.8 km] N Ixtahuacan, 1100 ft [336 m] (UTEP 9523); 3.5 mi [5.6 km] S Rayón (UMMZ 126248); 11.3 mi [18.2 km] NW Pueblo Nuevo Solistahuacan, 5000 ft [1524 m] (KU 75201); 2 mi [3.2 km] W Agua Escondida, 2850 ft [869 m] (KU 41576); 16.1 km NW Pueblo Nuevo Solistahuacan (UTA A-13014); 18.6 road km N Pueblo Nuevo, 1560 m (UMMZ 123994, 4 specimens); 19.0–20.8 mi [30.2–33.5 km] N by MX Hwy 195 of Jitotol, 5500 ft [1676 m] (MVZ 138932–37, CAS 142614); Mahosik, Tenejapa, 20 mi [32.2 km] NE San Cristobal (MVZ 99521); Mahosik, Tenejapa, 18 mi [29.0 km] NE San Cristobal (MVZ 99522); Municipio Tenejapa, Paraje Mahosik (CAS 163314–15); 9 km E Lago de Montebello, on road to Santa Elena (CAS 139870–71); Dos Lagos, 4 km E Laguna Tziskao, in Lagos de Montebello National Park, 4500 ft [1372 m] (CAS 163844–45); ridge between Pantepec and Tapalapa, 5800 ft [1768] (CAS 163936); Municipio Villacorzo, between Agrónimos Mexicanos and Cerro Tres Picos, about 4000 ft [1219 m] (CAS 170161); 3 mi [4.8 km] E Lago Tsikoa, Montebello National Park (CAS 163782–89); 10–12 km below Lago Tziskao, 4000 ft [1219 m] (CAS 16390); El Mercadito, Cintalapa (CAS 10076–77); Ruins of Palenque (UIMNH 11309, 11311). OAXACA:

between La Gloria and Cerro Azul (UIMNH 35583); mountains between La Gloria and Juchitán (UIMNH 33584–86); La Gloria (UIMNH 40995); San Isidro La Gringa, Santa María Chimalapa (MZFC-EPR 37, MZFC-LCM 258); Chalchijapa, Santa María Chimalapa (MZFC-EPR 67, 70, 107, MZFC-LCM 281).

*Bufo spiculatus*

MEXICO: OAXACA: Vista Hermosa, 1600 m (KU 86669); 2.8 km S Vista Hermosa, 1570 m (KU 137523); 2.4 mi [3.9 km] N Vista Hermosa (LSU 37811, 37825); 0.5 km E Vista Hermosa, 1550 m (KU 86671); Campamento Vista Hermosa (UTA A-6585); 3 km S Vista Hermosa, 1600 m (KU 137522); 10 mi [16.1 km] S Valle Nacional, 4200 ft [1280 m] (UTEP 5877); 2 km S Vista Hermosa, 1520 m (KU 86670); Santiago Comaltepec (MZFC 4608–09; 1–2 km SW Metates, ca. 800 m (MZFC 5317); Metates (UTA A-13013); 10 mi [16.1 km] S Valle Nacional, 4200 ft [1280 m] (UTEP 5878); Villa [sic] Hermosa, 1000 m (TCWC 58009); Comaltepec Ixtlan, Vista Hermosa (UCM 39764, 52515); Mexico Hwy 175, 7.7 mi [12.4 km] S La Esperanza (MVZ 14682); Yelagago, Boone Hallberg's Ranch, 4500 ft [1371 m] (AMNH 71397, 71433); San Pedro Sochiapan (AMNH 60435); Yexicobe, on trail to Yelagago, 5600 ft [1706 m] (AMNH 7112223); San Lucas Camotlán (USNM 123691);

*Bufo tutelarius*

GUATEMALA: HUEHUETENANGO: Sierra del Cuilco, Finca El Injerto, 5500 ft [1676 m] (UMMZ 126305); Aldea Paraiso, 1625–75 m (UMMZ 126799–03); Aldea Paraiso, 1650 m (UMMZ 126796–97, 126804); Aldea Paraiso, 1750 m (UMMZ 126805); near Hoja Blanca Cumbre, 2000 m (UMMZ 126798). SAN MARCOS: 1 km [by air] SE San Rafael Pie de la Cuesta, Finca Santa Julia, 1050 m (MVZ 109302); 1.25 km E and 0.75

km S San Rafael Pie de la Cuesta, Finca Santa Julia, 1100 m (MVZ 138938–40, 159523, 165511–13, 180391); 1.5 km [air] SE San Rafael Pie de la Cuesta, Finca Santa Julia, 1075 m (MVZ 113616, 146487–88, 146490). MEXICO: CHIAPAS: Porvenir (UMMZ 94545); Monte Cristo, Dept. San Bartolome (UMMZ 88344–45); Chicomuselo (UMMZ 94542); Mazapa (UMMZ 94543–44); El Phenix, 45 mi [72.4 km] NW Arriaga (UMMZ 102253, 102255–56); 5 mi [8.0 km] NW Monserrate El Fenix (UMMZ 107791); Region Soconusco (UIMNH 33528); Mt. Male (UMMZ 94554); Chiapas-Oaxaca border, 10 mi [16.1 km] NW Rizo de Oro, 5500 ft [1676 m] (CAS 16397); E side Cerro Baúl, just E Tres Picos, 6000 ft [1829 m] (CAS 163715–21); Cerro Tres Picos, Tonalá, 5000 ft [1524 m] (UIMNH 37405–06). OAXACA: Juchitán and Zanatepec (AMNH 70015–18); Cerro Baúl, 10.5 road mi [16.9 km] NW Rizo de Oro, Chiapas (UTEP 4968–72); Colonia Rodolfo Figueroa, S of Cerro Baúl, 20 km W Rizo de Oro (UTA A-4177–85); W slope Cerro Baúl, 1 mi [1.6 km] N Colonia Rodolfo Figueroa (UTA A-4889); Cerro Baúl, 19.0 km NW Rizo de Oro (UTA A-13085–94, 13096); Colonia Rodolfo Figueroa, 19.0 km NW Rizo de Oro, Chiapas (UTA A-13132–36); S slope Cerro Baúl (UTA A-13137–45); about 20 air km NW Rizo de Oro, Chiapas, NW slope Cerro Baúl, about 1600 m (MZFC 5262); along Rizo de Oro–Colonia Rodolfo Figueroa road, 3–4 road km SE Colonia Rodolfo Figueroa, 1350–1400m (MZFC 5276–79); Cerro Baúl, 19 km NW Rizo de Oro, 1525–1980 m (KU 200883–84); 12 mi [19.3 km] W of Rizo de Oro along ridge S of Cerro Baúl, 5000 ft [1524 m] (CAS 163713); Sierra Madre, above Zanatepec (UIMNH 56830); Rancho Carlos Minne, about 40 km Rizo de Oro (Chiapas), 3800 ft [1158 m] (AMNH 78561).

*Bufo valliceps*

GUATEMALA: ALTA VERAPAZ: 16.4 km W Tucurú (UTA A-7418-19, 7421-28).  
CHIQUIMULA: Esquipulas (UMMZ 106794). EL PETÉN: 8 km NNW Chinijá (KU 55873-74, 58376, 55878-81); 10 km NNW Chinijá (KU 55887); 11 km NNW Chinijá (KU 55891-92, 55894-96); 16 km NNW Chinijá, Río San Roman (KU 55900, 55911-12, 55913 -16); 15 km NNW Chinijá (KU 55918); 8.6 mi W El Cruce (KU 156414-15); 1.9 mi S La Libertad (KU 156409-13); ca 4 mi N Poptun (KU 156396-403); 3 mi S Tikal (156416-20); Tikal (LSUMZ 28138-39); Toocog, 15 km S La Libertad (KU 55920); Uaxactun (KU 156390-95). HUEHUETENANGO: Cuilco, Carretera Cuilco-Canibal, 1105 m (UTA A-47564); Jacaltenango (UMMZ 119371-74, 119380, 126298).  
IZABAL: Quirigua, Puebla Ranch, United Fruit Company (CAS 70828-35, 70837-38); 1.8 km km SW Morales turnoff on Hwy CA-9, 85 m (KU 190101); 4 km ENE Morales turnoff on Hwy CA-9, 85 m (KU 190102); Río Blanco, 120 m (KU 190098), 99; 3.2 km SW Puerto Santo Tomás, 12 m (KU 190132); Aldea Vista Hermosa, Los Amates, 700 m (KU 190141-42); Aldea Vista Hermosa, Los Amates, 135 m (KU 190146-47); El Estor, Club Sechoc (UTA A-34048); Puerto Libre Hotel, at road fork between Puerto Santo Tomás and Puerto Barrios (UTA A-21677-78); N slope Sierra de las Minas, Finca Pueblo Viejo (UTA A-28869-71, 28874, 28876, 28878-79, 28885, 28894, 28898); Nickel Mine Airstrip at El Estor (KU 7429); 1.7 mi W El Estor, Las Dantas (UTA A-7430-31); Montañas del Mico, 1.4 km WSW Puerto Santo Tomás, near Las Escobas (UTA A-24738-39); Sierra de Santa Cruz, 10.0 km W Finca Semuc headquarters, Semococh (UTA A-24932-33, 24942); Montañas del Mico, 5.1 rd km WSW Puerto Santo Tomás, Las Escobas (UTA A-33046). ESCUINTLA: circa 26 air km SE Escuintla, Finca El Caobanal, 100m (UTA A-28957-58, 28961); 7.7 km SSW Santa Lucía Cotzumalguapa, on road to Las Playas (UTA A-29009-20); [Finca] El Salto, near water



tank by the falls (MVZ 88352); Finca El Salto, ca 2 km E Escuintla, 1000 ft [304 m] (MVZ 104375); Río Guacalate, near Masagua (USNM 125240–45). JALAPA: 6.9 km SE Jalapa on Rn 19 (TNHC 31345, 31500–08). JUTIAPA: Finca La Trinidad, near Casa Grande (UMMZ 107818). RETALHULEU: Hacienda Casa Blanca, 1–3 km N and NW Casa Grande (UMMZ 107820); 3.2 km N Champerico (UTA A-25849–64). SACATEPEQUEZ: 1.4 km SSE San Antonio (TNHC 31492–96). SAN MARCOS: road between La Blanca and Tilapa, 3 m (UTA A-47538). SANTA ROSA: 11.9 km W Chiquimulilla, 49 m (KU 97704–12). SUCHITEPEQUEZ: Mazatenango, Finca El Horizonte (LSU 9323, 9328); Río Nahualate, 9 mi NNW Tiquasate (Depto. Escuintla) (USNM 125307). HONDURAS: ATLÁNTIDA: Corozal, ca. 15 km E La Ceiba (LSUMZ 21611, 21614). CHOLUTECA: 28.8 mi S Sabana Grande (LSUMZ 33625). COLÓN: Puerto Casilla (LSUMZ 22473); Río Grande (LSUMZ 33626); Trujillo (LSUMZ 22491, 27743). COPAN: 4.3 mi SW Santa Rosa de Copán (LSUMZ 22457); 9 km S La Entrada (LSUMZ 22588–89, 22591–92, 22597). CORTES: W of San Pedro, Hacienda Santa Ana (FMNH 4617–20, 4624, 4626, 4629–30); 12 km E San Pedro, Lake Ticamaya (FMNH 4632); Copán (FMNH 28513); 3.2 km NE San Pedro Sula (KU 97713–22); Cerro Cusuco, 1520 m (KU 209270); Quebrada de Colorado, ca Buenos Aires (KU 194223). GRACIAS A DIOS: Tancin, 15 km NW Puerto Lempira (LSUMZ 21600). OLANCHO: 0.5 km WNW Catamacas (LSUMZ 21590, 21592–94); Escuela Nacional de Agricultura, 4.5 km SE Catamacas (LSUMZ 21597); 3.4 km N San Esteban, 510 m (KU 209271); 15.7 km S San Esteban, 480 m (KU 209272); 5.6 km S San Esteban, 450 m (KU 209273); 4.6 km S San Esteban, 440 m (KU 209274–75). SANTA BARBARA: W side Lago de Yojoa, 775 m (KU 65544); San Jose de los Andes, 1610 m (KU 209279–80). YORO: 2 km S Coyoles on Río Aguan, 120 m (KU 101179); Rancho San Lorenzo, 25 km WSW Coyoles (LSUMZ 21606); 0.5 km N

Coyoles (LSUMZ 21607); Santa Rita (KU 192295); Subirana Valley (FMNH 21789–21792). MEXICO: CAMPECHE: 5 km S Champotón (KU 70991–71003); 3 km N Hopelchen (KU 75231–33); Dzibalchén (KU 75234–37); 7.5 km W Escárcega (KU 71004–71021); 1 km W Escárcega (KU 71022–33). CHIAPAS: 26 km N Ocozocoautla (UTEP 5817–19, 5823); 1 km N Ocozocoautla (UTEP 5821, 5824, 5831); 20 km N Ocozocoautla (UTEP 5822); 23–24 km N Ocozocoautla (UTEP 5825–27); 2.4–5.3 km W Ciudad Cauhuatemoc (KU 97723–26); 1 km N Tuxtla Gutiérrez (UTEP 5828–29, 5833); 54.5 km S Pueblo Nuevo Solistahuacan (TNHC 27029–32); 41 km S Pueblo Nuevo Solistahuacan (TNHC 27046, 27048, 27052); San Fernando (TNHC 25233–34, 25237, 25239–40); 38 mi W Cintalapa (TNHC 27057–59); 3 mi E Cintalapa (TNHC 27054–55, 27358); 10 mi E Cintalapa (TNHC 27359). COAHUILA: spillway canal below Don Martin dam (KU 128778–86); 2–6 mi W Sacramento (KU 47010–13); Río Salado de los Nadadores, El Cariño (KU 80310–15). HIDALGO: 12.5–38.5 km SW Huejutla (UTA A-13110, 13113–19, 13121–31). NUEVO LEÓN: La Huasteca Cañon (KU 192507–19). OAXACA: 6 km N Palomares (KU 58333–60). QUINTANA ROO: Pueblo Nuevo X-Can, 10 m (KU 71036–50). VERACRUZ: 12.8 km N Acayucan (KU 97672–85); Cautlapan (KU 97686, 105521–26); 16 km NE Fortín de las Flores (KU 97687–96); Portrero Viejo (KU 25836–45, 25847–51, 26720–24); Cautlapan (TNHC 27014–19, 17, 27123–28). YUCATÁN: Chichen Itzá (KU 71059–61; FMNH 26956–58); 12 km E Chichen Itzá (KU 71062); 17 km N Piste on rd to Tzitsin (KU 751950); Xocchel (KU 156435–37); 12.3–16.8 mi E Izamal (KU 156439–41); Mérida (FMNH 40653–58, TNHC 33224). NICARAGUA: ESTELÍ: 7 km N, 16 km E Condega, 1200 m, (KU 85253–57); 5 km N, 14 km E Condega, 40 m (KU 85251). MATAGALPA: 10.5 km N, 9 km E Matagalpa, 960 m (KU 85258–62). NUEVO SEGOVIA: 5 km N, 2.5 km E Jalapa, 680 m (KU 112722–26); 1.5

km N, 1 km E Jalapa, 660 m (KU 112727–39). ZELAYA: Bonanza (KU 85263–67, 101178); El Recreo, S side Río Mico, 25 m (KU 112708–21); 11 mi W Muelle de los Bueyes, Hwy 7 (KU 136410). USA: LOUISIANA: EAST BATON ROUGE PAR.: 4 mi S Baton Rouge (KU 22519–26; 22527) 1.6 mi E jct River Road and Brightside Dr. (KU 145509); ca 2 mi S LSU campus on River Road (KU 145510); 0.9 mi S East Feliciana (KU 145511–16). LIVINGSTON PAR.: ca. jct rtes 16 and 1026 (KU 145507). ST. CHARLES PAR.: 3.6 mi N Norco (KU 145508). TEXAS: ATASCOSA CO.: Benton (KU 11997). BEXAR CO.: Somerset (KU 20045–46); Helotes (KU 11590). BRAZORIA CO.: 5 mi E Liverpool (KU 44884–908); 1 mi S Freeport (KU 44909–15). CAMERON CO.: Brownsville (KU 11591–608, 14100–01, 14309–32). DALLAS CO.: Dallas (KU 33556); South Cockrell Hill Road (UTA A-581–83); Oak Cliff (UTA A-1861). PARKER CO.: 2.0 mi NW Wheatland (UTA A-7228). STARR CO.: Rio Grande (KU 11998–99). TARRANT CO.: 8.0 mi W Fort Worth (UTA A-486); Arlington (UTA A-384, 9144, 17450–52, 41964); Benbrook–Aledo Road (UTA A-1223); E of US Hwy 377, jct of Mary's Creek and Vickery Blvd (UTA A-7390). UVALDE CO.: FM 1022, 2.6 mi S Rte 90 (UTA A-37382). TRAVIS CO.: Austin (TNHC 15643–47, 15649–53, 15654–57). VAL VERDE CO.: Moose Canyon at jct Pecos River (KU 195052); Route 90, 1.4 mi E loop 25 (UTA A-37378–37380); State Hwy 163, 67.6 km S jct Interstate Hwy 10 (UTA A-17453); 18 mi NE Comstock (TNHC 32355–57). WALKER CO.: Park Road 40 at entrance Huntsville State Park (UTA A-37279–80); 0.25 mi down Fish Hatchery Rd (UTA A-41586); New Waverly (UTA A-40957); Texas Dept. of Corrections, Ellis Unit (UTA A-41696–98); Pritchett Field (UTA A-42327–48). WEBB CO.: 4 mi N Laredo (KU 23383).

## APPENDIX II

### SPECIMENS EXAMINED FOR PHYLOGENETIC ANALYSIS

(all are dry skeletons, except those labelled: C&S = cleared and stained; Alc = alcoholic specimens)

**BUFONIDAE:** *Atelopus igenescens*: ECUADOR: COTOPAXI: Mulaló, 2990 m (KU 146764); Chimborazo: 15 km SE Pungalá, Hacienda Alao, 3100 m (KU 132107 [C&S]).  
*Bufo alvarius*: USA: ARIZONA: Pima: 16 mi S Tucson (KU 14082); Santa Cruz: 5 mi N Tucumcari (KU 14081). *B. americanus*: USA: KANSAS: Douglas Co.: Lawrence (KU 16467, 18211). *B. asper*: MALAYSIA: PANANG: Gunnong Benom (KU 147208). *B. bocourti*: GUATEMALA: HUEHUETENANGO: Laguna de Vecha (KU 117369, 117371). *B. boreas*: USA: COLORADO: Gunnison Co.: Gothic, 10,000 ft. (KU 135222–23). *B. calamita*: PORTUGAL: northern Portugal (KU 148621). *B. campbelli*: GUATEMALA: EL PETEN: 11 km NNW Chinajá (KU 55898 [C&S]). *B. canaliferus*: GUATEMALA: SUCHITEPEQUEZ: Volcán Zuníl (CAS 70560, 70619 [C&S]). *B. cavifrons*: MEXICO: VERACRUZ: Volcán San Martín (UMMZ 152822–23). *B. coccifer*: COSTA RICA: PUNTARENAS: 4 km WNW Esparta (KU 68147–49). *B. coniferus*: COSTA RICA: CARTAGO: Moravia de Turriabla, 1200 m (KU 68150–51); Tapanti, 1200 m (KU 91814–15). *B. crucifer*: BRASIL: ESPIRITO SANTO: Sooretama, Linhares (KU 93112); SÃO PAULO: Campo Grande, Santo Andre (KU 93093–94). *B. epioticus*: PANAMA: BOCAS DEL TORO: N slope Cerro Pando, 1450 m (KU 117383, 107394 [C&S]). *B. fastidiosus*: PANAMA: BOCAS DEL TORO: N slope Cerro Pando, 1810 m (KU 117372–73). *B. funereus*: RWANDA: KIBUNGU TERRITORY: Rwasburo, 1600 m (KU 155084–85). *B.*

*holdridgei*: COSTA RICA: HEREDIA: Rama Sur Río Las Vueltas, 2100 m (KU 117377–78). *B. granulatus*: BRAZIL: RIO DE JANEIRO: Barra de São João (KU 93125); COLOMBIA: MAGDALENA: El Rodadero de Gaira, 5 m (KU 170090); PANAMA: VERAGUAS: 3.4 km N Montijo, 40 m (KU 104322 [C&S]). *B. haematiticus*: PANAMA: DARIEN: Cerro Quia, 740 m (KU 96160, 96162); Tacaruna, 550 m (KU 77659). *B. holdridgei*: COSTA RICA: HEREDIA: Rama Sur Río Las Vueltas, 2100 m (KU 117379). *B. ibarraei*: GUATEMALA: JALAPA: Jalapa (TNHC 54532). *B. luetkeni*: COSTA RICA: PUNTARENAS: 2.4–3.0 km NW Esparta (KU 68153); NICARAGUA: MANAGUA: Tipitapa (KU 84928–29); RIVAS: 1.5 km N Moyogalpa (KU 84926). *B. occidentalis*: MEXICO: PUEBLA: 14.4 km W Huachinango (KU 59871). *B. macrocristatus*: MEXICO: CHIAPAS: 6.2 km S Rayón Mescalapa, 1690 m (KU 58302 [C&S]). *B. marmoreus*: MEXICO: GUERRERO: 5.6 km S San Andreas de la Cruz, 420 m (KU 84893–94); OAXACA: 4.5 km W Tehuantepec (KU 59865). *B. melanochlorus*: COSTA RICA: PUNTARENAS: 2 km NW Dominical, 10 m (KU 91667 [C&S]). *B. marinus*: NICARAGUA: MANAGUA: 3 mi SW Managua (KU 42566); RIVAS: Lago de Nicaragua, Isla de Ometepe (KU 84938). *B. maculatus*: ZAIRE: KISANGANI TERRITORY: Yafolo (KU 155100). *B. mazatlanensis*: MEXICO: SINALOA: 6 km NE El Fuerte, 150 m (KU 78985); SONORA: between Alamos and Minas Nuevas, 427 m (KU 186792). *B. melanostictus*: INDONESIA: CENTRAL JAVA: Bojolali, 450 m (KU 153940); SINGAPORE: 3.5 mi W, 1.5 mi N mouth Singapore River (KU 129017). *B. perplexus*: MEXICO: GUERRERO: 20 km S Iguala (KU 186795); MORELOS: 3.5 km W Cuautlixco, 1300 m (KU 84896, 84898). *B. periglenes*: COSTA RICA: PUNTARENAS: 2 mi ENE Monteverde, 1590 m (KU 107916). *B. spinulosus*: BOLIVIA: POTOSÍ: Río Tupiza, 12.5 km SSE Tupiza, 2920 m (KU 160270–72). *B. typhoni*: ECUADOR: NAPO: Santa Cecilia, 340 m (KU 152909). *B. valliceps*:

MEXICO: CHIAPAS: 14.4 km SW Las Cruces, 700 m (KU 68155–56); OAXACA: 6 km N Palomares (KU 59874–76); USA:TEXAS: Bexar Co.,: Somerset (KU 20422).

*Melanophryniscus moreirae*: BRAZIL: RIO DE JANEIRO: Itatiaia (KU 93179 [C&S]).

*Rhamphophryne macrorhina*: COLOMBIA: ANTIOQUIA: Santa Rita, 1930 m (KU 124947).

**LEPTODACTYLIDAE:** *Ceratophrys cornuta*: PERU: MADRE DE DIOS: Cuzco Amazónico, 15 km E Puerto Maldonado, 200 m (KU 205884). *Leptodactylus pentadactylus*: PANAMA: CANAL ZONE: Madden Forest Reserve, 160 m (KU 117367–68). *Odontophrynus americanus*: BRASIL: SÃO PAULO: Campos do Jordão (KU 92968, 100437). *Telmatobius hintoni*: BOLIVIA: POTOSÍ: 6 km W Betanzos, 3330 m (KU 160190–91).

## APPENDIX III

### TABLES

Table 1.1. Morphometric variation in *Bufo tutelarius*. Note that many of the extant specimens of this species seem to be subadults. The extent to which the morphometry of this species changes through ontogeny is not known. Mean  $\pm$  1 SD above range, in parentheses; all measurements in mm.

Variable	Males <i>n</i> = 32	Females <i>n</i> = 34
Snout–vent length	62.8 $\pm$ 7.1 (49.2–76.2)	80.0 $\pm$ 13.2 (56.5–103.6)
Tibia length	25.8 $\pm$ 3.0 (20.6–31.4)	30.7 $\pm$ 4.8 (22.7–39.9)
Foot length	27.2 $\pm$ 3.2 (21.2–32.5)	31.4 $\pm$ 4.6 (24.2–39.2)
Head length	23.3 $\pm$ 2.2 (19.8–27.5)	29.3 $\pm$ 4.1 (22.6–37.8)

Table 1.1 (cont'd).

Head width	$25.2 \pm 2.4$ (21.2–29.9)	$32.3 \pm 5.0$ (24.6–41.2)
Orbit diameter	$9.1 \pm 0.7$ (8.0–10.3)	$10.9 \pm 1.3$ (8.6–13.7)
Tympanum diameter	$3.3 \pm 0.4$ (2.4–4.0)	$4.2 \pm 0.7$ (2.9–5.7)
Supratympanic crest	$3.9 \pm 0.7$ (2.8–5.2)	$5.3 \pm 1.1$ (2.8–7.9)
Finger I length	$10.2 \pm 1.1$ (7.9–12.8)	$13.4 \pm 2.3$ (9.3–18.9)
Parotoid length	$10.2 \pm 1.3$ (8.0–12.6)	$12.1 \pm 2.3$ (8.4–16.9)
Parotoid width	$5.9 \pm 0.6$ (4.7–7.1)	$7.0 \pm 1.2$ (5.3–9.6)



Table 1.2. Morphometric variation in *Bufo macrocristatus*. Mean  $\pm$  1 SD above range, in parentheses; all measurements in mm.

Variable	Males <i>n</i> = 21	Females <i>n</i> = 9
Snout–vent length	59.4 $\pm$ 3.6 (51.9–68.7)	69.0 $\pm$ 8.4 (50.1–81.8)
Tibia length	25.8 $\pm$ 1.8 (21.6–30.1)	28.8 $\pm$ 3.1 (23.7–33.8)
Foot length	26.9 $\pm$ 1.5 (25.0–29.9)	28.5 $\pm$ 3.4 (21.0 + 33.2)
Head length	20.9 $\pm$ 1.5 (18.9–25.8)	25.2 $\pm$ 3.0 (19.9–30.4)
Head width	22.1 $\pm$ 1.7 (19.7–27.0)	26.9 $\pm$ 3.0 (20.8–32.5)
Orbit diameter	7.8 $\pm$ 0.5 (6.5–8.8)	9.1 $\pm$ 1.0 (7.2–11.1)

Table 1.2 (cont'd)

Tympanum diameter	$3.2 \pm 0.3$ (2.6–3.7)	$4.0 \pm 0.5$ (2.8–4.7)
Supratympanic crest	$4.4 \pm 0.5$ (3.6–5.8)	$6.2 \pm 0.6$ (5.2–7.4)
Finger I length	$9.3 \pm 0.9$ (8.1–11.5)	$11.4 \pm 1.4$ (8.3–13.7)
Parotoid length	$9.1 \pm 0.6$ (7.8–10.1)	$10.2 \pm 1.3$ (7.9–12.2)
Parotoid width	$5.2 \pm 0.5$ (4.6–6.0)	$5.2 \pm 0.7$ (4.0–6.5)

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Table 2.1. Comparison of the major diagnostic features of several toads from the lower montane forests of southern Mexico. Descriptions pertain to both sexes unless otherwise indicated. Measurements and observations taken from specimens reported herein, except those for *Bufo valliceps* which were taken from an unpublished data set representing specimens from throughout its range in USA and Mexico.

Feature	<i>Bufo caviifrons</i>	<i>Bufo cristatus</i>	<i>Bufo macrocristatus</i>
Tympanum/orbit	male: 31–44% female: 39–46%	male: 30–31% female: 35–36%	male: 35–47% female: 39–47%
Tibia length/SVL	36–47%	37–42%	38–47%
Vocal slits mm	present, long, bilateral	absent?	present, short, bilateral
Vocal sac mm	small, unpigmented, unilobed	absent?	small, unpigmented, unilobed
Cranial crests	high, thick, smooth; parietal crests expanded vertically, forming high rounded knob	high, thick, smooth; parietal crests expanded vertically and laterally, forming large bony mass	male: low, thick; small rounded knob at junction parietal X supraorbital crests female: high, thin, bladelike; often with striated texture

Table 2.1 (cont'd)

Feature	<i>Bufo cavifrons</i>	<i>Bufo cristatus</i>	<i>Bufo macrocristatus</i>
Pretympanic crest	absent	absent	present, short
Dorsal skin texture	female: smooth, sometimes with scattered conical tubercles male: smooth	smooth with few scattered conical tubercles	female: smooth with few scattered conical tubercles male: uniformly covered with low round tubercles
Lateral tubercle row	male: low continuous welt of coalesced tubercles female: widely spaced, non-pointed, low tubercles	intermittent series, indistinct, pointed or round tubercles	male: low, discrete round tubercles female: widely spaced sharply pointed tubercles
Tips of digits	paler than digit	same color as digit?	paler than digit
Distribution	Sierra de los Tuxtlas; 400–1600m	Sierra Madre Oriental; approx. 1200–2000m	Caribbean slope Chiapas Highlands; Chimalapas; 300–1800m

Table 2.1 (cont'd)

Feature	<i>Bufo spiculatus</i>	<i>Bufo valliceps</i>
Tympanum/orbit	male: 30–36% female: 33–41%	male: 32–56% female: 43–53%
Tibia length/SVL	38–44%	34–44%
Vocal slits mm	absent	present, long, bilateral
Vocal sac mm	absent	large, pigmented, bilobed
Cranial crests	low, thick, highly textured	low, smooth, not hypertrophied
Preorbital crest	absent (thin in large female)	present
Pretympanic crest	absent (short in large individuals)	present
Dorsal skin texture	smooth with distinct scattered spiculate tubercles	uniformly covered with low round tubercles
Lateral tubercle row	male: high, pointed or rounded tubercles female: sharply pointed tubercles	very variable; usually an even series of small pointed or rounded tubercles
Tips of digits	paler than digit	same color as digit
Distribution	Sierra de Juárez; 800–1600m	Widespread, 0–1700m

Table 2.2. Morphometric variation in *Bufo spiculatus*, *B. cavifrons*, and *B. cristatus*.

Mean  $\pm$  1 SD above range (in parentheses); all measurements in mm.

Variable	<i>Bufo spiculatus</i>		<i>Bufo cavifrons</i>		<i>Bufo cristatus</i>	
	Males <i>n</i> = 3	Females <i>n</i> = 10	Males <i>n</i> = 37	Females <i>n</i> = 21	Males <i>n</i> = 2	Females <i>n</i> = 4
Snout-vent length	67.8 $\pm$ 2.53 (65.8–71.4)	87.1 $\pm$ 13.9 (63.2–102.7)	70.0 $\pm$ 5.4 (54.8–79.9)	81.9 $\pm$ 9.4 (64.9–92.9)	52.9 $\pm$ 2.8 (50.9–54.8)	78.4 $\pm$ 9.9 (69.1–87.3)
Tibia length	27.4 $\pm$ 0.7 (26.5–28.3)	34.8 $\pm$ 5.3 (26.5–42.3)	28.2 $\pm$ 1.2 (24.6–29.9)	31.2 $\pm$ 3.2 (24.9–35.5)	20.1 $\pm$ 1.6 (19.0–21.2)	32.4 $\pm$ 4.5 (28.3–36.9)
Foot length	29.5 $\pm$ 2.0 (27.3–32.1)	36.9 $\pm$ 6.2 (26.3–44.2)	30.8 $\pm$ 1.5 (26.1–35.1)	32.6 $\pm$ 3.6 (24.8–36.3)	22.3 $\pm$ 0.8 (21.7–22.9)	34.8 $\pm$ 5.0 (29.3–39.2)
Head length	24.9 $\pm$ 0.9 (24.2–26.1)	32.3 $\pm$ 5.2 (23.7–38.3)	24.1 $\pm$ 1.3 (20.6–26.0)	29.3 $\pm$ 2.8 (22.6–32.9)	18.6 $\pm$ 1.3 (17.6–19.5)	30.1 $\pm$ 4.2 (26.2–234.2)
Head width	25.6 $\pm$ 0.9 (24.5–26.6)	34.9 $\pm$ 5.8 (25.1–43.4)	24.8 $\pm$ 1.6 (19.9–27.8)	31.7 $\pm$ 3.1 (24.1–36.4)	19.3 $\pm$ 1.5 (18.2–20.3)	33.3 $\pm$ 4.7 (28.3–37.8)
Orbit diameter	9.1 $\pm$ 0.5 (8.4–9.7)	10.9 $\pm$ 1.2 (8.8–12.6)	9.0 $\pm$ 0.5 (7.5–9.8)	10.4 $\pm$ 0.7 (8.8–11.3)	6.9 $\pm$ 0.1 (6.8–6.9)	10.0 $\pm$ 1.8 (8.4–12.4)
Tympanum diameter	3.0 $\pm$ 0.1 (2.9–3.0)	4.0 $\pm$ 0.6 (2.9–4.7)	3.4 $\pm$ 0.3 (2.7–4.0)	4.4 $\pm$ 0.4 (3.5–5.2)	2.1 $\pm$ 0.0	3.6 $\pm$ 0.6 (3.0–4.4)
Supratympanic crest	4.6 $\pm$ 0.1 (4.5–4.8)	6.4 $\pm$ 1.4 (4.3–9.0)	5.0 $\pm$ 0.4 (4.2–5.6)	6.3 $\pm$ 0.9 (4.7–7.6)	3.0 $\pm$ 0.4 (2.7–3.3)	5.3 $\pm$ 0.9 (4.3–6.4)
Finger I length	10.8 $\pm$ 0.7 (10.3–11.8)	14.6 $\pm$ 2.8 (10.5–18.7)	10.5 $\pm$ 0.9 (8.3–12.0)	13.2 $\pm$ 1.4 (10.3–15.7)	8.3 $\pm$ 0.9 (7.6–8.9)	13.5 $\pm$ 2.3 (11.2–15.5)
Parotoid length	11.4 $\pm$ 1.3 (9.7–12.7)	12.7 $\pm$ 2.6 (8.9–14.7)	9.6 $\pm$ 1.0 (7.1–11.3)	11.1 $\pm$ 1.8 (8.1–14.3)	9.9 $\pm$ 0.8 (9.3–10.5)	14.9 $\pm$ 2.2 (12.7–17.5)
Parotoid width	6.0 $\pm$ 1.3 (5.0–7.8)	6.6 $\pm$ 0.9 (5.1–7.6)	5.2 $\pm$ 0.6 (3.6–6.2)	5.4 $\pm$ 0.7 (4.6–6.9)	5.6 $\pm$ 0.1 (5.5–5.7)	8.4 $\pm$ 0.7 (7.4–9.0)

Table 3.1. Results of the first four principal components explaining 89% of the variation in a PCA (covariance matrix) performed on 15 log-transformed morphometric variables measured on male *Bufo valliceps* representing 19 populations from throughout the range of the species. Loadings of each variable are also shown.

Variable	PC 1	PC 2	PC 3	PC 4
Eigenvector	0.057243	0.003921	0.002469	0.001992
Proportion of variance	0.780	0.053	0.034	0.027
Cumulative proportion	0.780	0.833	0.867	0.894
Snout-vent length	-0.258	0.023	0.078	0.113
Femur length	-0.292	-0.066	0.248	0.042
Metatarsal length	-0.252	0.081	0.058	-0.074
Radioulna length	-0.234	0.134	0.177	-0.016
Hand length	-0.246	0.032	0.102	-0.042
Tibia length	-0.252	0.102	0.389	-0.569
Foot length	-0.246	0.017	0.147	-0.128
Head length	-0.258	0.026	0.120	0.072
Head width	-0.284	0.089	0.106	0.055
Orbit diameter	-0.188	0.041	0.091	0.088
Eye–nostril distance	-0.234	0.085	-0.122	0.462
Tympanum diameter	-0.263	-0.135	0.083	0.577
Supratympanic crest length	-0.270	0.660	-0.608	-0.109
Parotoid length	-0.308	-0.418	0.460	-0.279
Parotoid width	-0.267	-0.560	-0.277	-0.091

Table 3.2. Results of the first four principal components explaining 81% of the variation in a PCA (covariance matrix) performed on 15 log-transformed morphometric variables measured on male *Bufo valliceps* representing nine populations from across the length of the Yucatan Peninsula. Loadings of each variable are also shown.

Variable	PC 1	PC 2	PC 3	PC 4
Eigenvector	0.017310	0.003854	0.002758	0.002265
Proportion of variance	0.537	0.120	0.086	0.070
Cumulative proportion	0.537	0.657	0.742	0.813
Snout-vent length	-0.237	-0.089	0.017	0.034
Femur length	-0.308	0.931	0.151	0.053
Metatarsal length	-0.247	-0.048	-0.010	-0.070
Radioulna length	-0.215	-0.095	-0.025	0.071
Hand length	-0.257	-0.118	0.027	0.110
Tibia length	-0.182	-0.079	0.006	0.025
Foot length	-0.193	-0.146	-0.014	0.010
Head length	-0.235	-0.122	0.099	-0.071
Head width	-0.300	-0.121	-0.083	0.756
Orbit diameter	-0.317	0.043	-0.767	-0.435
Eye–nostril distance	-0.315	-0.171	0.608	-0.451
Tympanum diameter	-0.261	-0.079	0.017	0.003
Supratympanic crest length	-0.276	-0.050	0.004	0.059
Parotoid length	-0.243	-0.043	-0.007	0.012
Parotoid width	-0.239	-0.040	0.007	-0.031



Table 3.3. Standardized (pooled within-group variances) coefficients for the canonical variables on the first two canonical axes; cumulative proportion of dispersion (variance) displayed on each axis shown in parentheses.

Variable	Canonical Axis I (0.987)	Canonical Axis II (0.995)
Snout–vent length	-0.79626	0.65282
Femur length	0.29343	-0.01370
Metatarsal length	0.36157	0.04695
Radioulna length	0.36908	-0.29779
Hand length	0.04474	-0.25055
Foot length	-0.85926	0.80126
Head length	0.40648	1.133394
Head width	-0.61490	-1.64387
Orbit diameter	0.72146	-0.20203
Eye–nostril distance	0.61903	-0.22798
Tympanum diameter	0.20178	0.30574
Supratympanic crest length	-0.33749	0.31473
Parotoid length	0.34510	0.20732
Parotoid width	-0.48930	-0.76280

Table 3.4. Jackknifed classification matrix from the 14-variable model generated by the stepwise DFA of 19 sample populations of *Bufo variegatus*. The bold figures indicate the number of specimens correctly classified; the number in parentheses indicates the number of specimens in that sample.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	<b>7 (8)</b>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	<b>2 (15)</b>	2	2	2	0	4	2	0	0	0	1	0	0	0	0	0	0	0
3	0	2	<b>5 (14)</b>	4	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
4	0	0	2	<b>8 (13)</b>	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
5	0	0	0	0	<b>11 (12)</b>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6	2	2	1	0	0	<b>9 (18)</b>	0	0	0	0	0	2	0	0	0	0	1	1	0
7	0	2	1	2	0	0	<b>2 (8)</b>	0	0	0	0	0	0	0	1	0	0	0	0
8	0	1	0	2	0	0	1	<b>2 (8)</b>	1	0	0	0	0	0	0	0	0	0	0
9	0	1	0	0	0	0	0	1	<b>11 (19)</b>	2	0	2	1	0	0	0	0	0	0
10	0	0	0	0	0	0	0	1	0	<b>6 (15)</b>	2	1	1	0	0	0	2	0	1
11	0	0	0	0	0	0	0	0	0	0	<b>12 (13)</b>	0	0	0	0	1	0	0	0
12	1	0	0	0	0	0	0	0	1	0	0	<b>23 (28)</b>	2	0	0	0	0	0	1
13	1	0	0	0	0	0	0	0	0	0	0	2	<b>11 (19)</b>	0	0	0	1	1	0
14	0	1	0	0	0	0	2	0	0	0	1	0	0	<b>14 (19)</b>	1	0	0	0	0
15	0	0	0	0	0	0	0	0	0	1	0	0	0	3	<b>6 (12)</b>	0	0	0	0
16	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	<b>7 (11)</b>	1	1	0
17	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	4	<b>1 (22)</b>	1	0
18	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	9	<b>9 (15)</b>	2
19	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	2	1	1	<b>6 (14)</b>

Table 4.1. Morphometric variation in *Bufo ibarraei*.

Mean  $\pm$  1 SD above range (in parentheses);

all measurements in mm.

Variable	Males $\underline{n=33}$	Females $\underline{n=36}$
Snout-vent length	70.2 $\pm$ 5.6 (59.7-77.0)	81.8 $\pm$ 5.0 (72.2-94.4)
Tibia length	27.0 $\pm$ 1.7 (22.3-29.7)	29.9 $\pm$ 1.5 (27.3-34.1)
Foot length	27.7 $\pm$ 1.7 (24.5-30.4)	31.0 $\pm$ 1.5 (28.0-34.1)
Head length	23.2 $\pm$ 1.7 (20.2-26.5)	26.3 $\pm$ 1.3 (24.0-33.3)
Head width	26.9 $\pm$ 1.7 (23.4-30.8)	30.9 $\pm$ 1.5 (28.2-33.3)
Orbit diameter	9.7 $\pm$ 0.6 (7.9-10.7)	10.8 $\pm$ 0.5 (9.7-11.9)
Tympanum diameter	4.4 $\pm$ 1.2 (3.4-9.9)	4.3 $\pm$ 0.3 (3.4-11.2)
Supratympanic crest length	3.6 $\pm$ 0.3 (2.9-4.2)	4.4 $\pm$ 0.5 (3.4-11.2)
Parotoid length	8.3 $\pm$ 0.9 (6.6-10.6)	8.7 $\pm$ 1.3 (6.5-11.2)
Parotoid width	6.1 $\pm$ 0.6 (4.4-7.4)	6.5 $\pm$ 0.6 (5.1-7.9)

Table 5.1. Summary of species content of the *Bufo valliceps* group by authors of major systematics reviews since 1950.

Species	Firschei n, 1950	Tihen, 1962	Porter, 1962	Blair, 1966	Blair, 1972	Martin, 1972	Frost, pers. comm.
<i>B. alvarius</i>	–	+	–	–	–	–	–
<i>B. campbelli</i>	na	na	x	na	na	na	+
<i>B. canaliferus</i>	–	+	–	–	–	–	+
<i>B. cavifrons</i>	–	+	+	+	+	+	+
<i>B. coccifer</i>	–	+	–	–	–	–	–
<i>B. coniferus</i>	–	–	x	x	+	+	+
<i>B. cristatus</i>	+	x	+	+	+	x	+
<i>B. gemmifer</i>	–	+	+	+	+	+	+
<i>B. ibarraii</i>	na	–	–	+	+	+	+
<i>B. luetkenii</i>	–	–	x	+	+	+	+
<i>B. macrocristatus</i>	na	+ <sup>1</sup>	+ <sup>2,4</sup>	x	+ <sup>2</sup>	x	+ <sup>2</sup>
<i>B. marmoreus</i>	–	+	–	–	–	–	–
<i>B. mazatlanensis</i>	–	+	+	+	+	+	+
<i>B. melanochlorus</i>	–	–	x	x	+	x	+
<i>B. occidentalis</i>	–	–	–	x	–	–	+
<i>B. perplexus</i>	–	+	–	–	–	–	–
<i>B. tutelarius</i>	na	na	+ <sup>3</sup>	na	na	na	na
<i>B. spiculatus</i>	–	na	+ <sup>4</sup>	na	na	na	na
<i>B. valliceps</i>	+	+	+	+	+	+	+

Codes: + = included in *Bufo valliceps* group

– = not included in *Bufo valliceps* group

x = not mentioned in work, or beyond scope of work

na = species not described at time of study

1 = combination used without justification or precedent

2 = taxon considered, but purposely included in synonymy of *Bufo valliceps*.

3 = population(s) referable to this taxon considered, but purposely included in synonymy of *Bufo valliceps*.

4 = population(s) referable to this taxon considered, but purposely included in synonymy of *Bufo cavifrons*.

Table 5.2. The data matrix used for phylogenetic analysis. Characters described in text.

Taxon	Characters									
	1	2	3	4	5	6	7	8	9	10
<i>Ceratophrys</i>	0	2	0	1	0	0	0	0	0	0
<i>Telmatobius</i>	0	0	1	0	0	0	0	0	0	0
<i>Leptodactylus</i>	0	0	0	0	0	0	0	0	0	0
<i>Odontophrynus</i>	0	0	1	1	0	0	0	0	0	0
vector	0	?	?	?	0	0	0	0	0	0
<i>Atelopus ignescens</i>	0	0	1	3	0	0	0	0	0	0
<i>Bufo alvarius</i>	1	2	0	1	0	1	1	0	1	0
<i>B. americanus</i>	0	2	1	0	0	0	1	0	1	0
<i>B. bocourti</i>	1	2	0	2	0	1	1	1	1	0
<i>B. boreas</i>	0	0	1	0	0	0	0	0	0	0
<i>B. calamita</i>	0	1	1	0	0	0	0	0	0	0
<i>B. canaliferus</i>	0	1	0	1	0	0	1	0	1	0
<i>B. cavifrons</i>	1	0/1/2	0	1	1	0	2	2	1	1
<i>B. coccifer</i>	1	2	0	1	1	1	1	1	1	1
<i>B. coniferus</i>	1	2	0	1	1	1	1	1	1	1
<i>B. crucifer</i>	1	2	0	1	0	1	1	0	1	1
<i>B. fastidiosus</i>	0	2	0	1	0	0	0	0	1	1
<i>B. funereus</i>	0	2	0	1	0	0	0	0	0	0
<i>B. granulatus</i>	1	2	0	1	0	1	1	0	1	1
<i>B. haematiticus</i>	1	0	0	1	0	0	0	0	0	0
<i>B. ibarra</i>	1	2	0	1	1	1	1	1	1	1
<i>B. luetkeni</i>	1	2	0	1	1	1	1	1	1	1
<i>B. maculatus</i>	0	2	0	1	0	0	0	0	0	0
<i>B. marinus</i>	1	2	0	1	1	1	1	0	1	1
<i>B. marmoreus</i>	0	1	0	1	0	1	0	0	1	1
<i>B. mazatlanensis</i>	1	2	0	1	1	1	1	1	1	1
<i>B. melanostictus</i>	1	2	0	0	1	1	1	0	1	1
<i>B. occidentalis</i>	0	2	0	0	0	0	1	0	1	0
<i>B. perplexus</i>	0	2	0	2	0	0	0	0	1	0
<i>B. typhonius</i>	1	1	0	1	0	0	3	0	0	2
<i>B. valliceps</i>	1	2	0	1	1	1	1	1	1	1
<i>Crepidophryne</i>	1	2	0	1	1	0	1	0	1	1
<i>R. macrorhina</i>	1	2	0	1	0	0	1	0	0	0
<i>B. spinulosus</i>	0	0	0	0	0	1	0	0	0	0
<i>B. holdridgei</i>	0	2	0	1	0	0	0	0	1	1
<i>B. asper</i>	1	2	0	1	0	0	1	0	1	1
<i>B. periglenes</i>	0	2	0	1	0	0	0	0	0	0
<i>Melanophryniscus</i>	0	0	1	1	0	0	0	0	0	0
<i>B. campbelli</i>	1	1	1	1	1	1	1	1	1	1
<i>B. melanochlorus</i>	1	1	0	1	1	1	1	1	1	1
<i>B. macrocristatus</i>	1	2	0	1	1	1	2	2	1	1

	11	12	13	14	15	16	17	18	19	20
<i>Ceratophrys</i>	0	0	2	1	2	1	1	0	0	0
<i>Telmatobius</i>	0	0	0	0	0	0	0	0	0	1
<i>Leptodactylus</i>	0	0	0	1	1	0	1	0	0	1
<i>Odontophrynus</i>	0	0	1	1	1	0	1	0	0	1
vector	0	0	?	?	?	?	?	0	0	?
<i>Atelopus ignescens</i>	0	0	2	0	0	0	0	0	1	2
<i>B. alvarius</i>	0	0	0	0	2	0	1	0	0	1
<i>B. americanus</i>	0	0	0	1	1	1	1	0	0	1
<i>B. bocourti</i>	0	0	0	1	1	0	1	0	0	1
<i>B. boreas</i>	0	0	0	0	1	0	0	0	0	1
<i>B. calamita</i>	0	0	0	1	1	0	1	0	0	1
<i>B. canaliferus</i>	0	0	1	0	0	0	1	0	0	1
<i>B. cavifrons</i>	1	1	1	1	1	0	1	0	0	1
<i>B. coccifer</i>	1	1	1	1	1	0	1	0	0	1
<i>B. coniferus</i>	1	1	1	0	1	0	1	0	0	1
<i>B. crucifer</i>	0	0	0	1	1	0	1	0	0	1
<i>B. fastidiosus</i>	0	0	0	0	0	0	1	0	0	2
<i>B. funereus</i>	0	0	0	0	0	0	0	0	0	1
<i>B. granulatus</i>	1	1	1	1	1	0	1	0	0	1
<i>B. haematiticus</i>	0	0	1	0	0	0	0	0	0	1
<i>B. ibarra</i>	1	1	1	1	1	0	1	0	0	1
<i>B. luetkeni</i>	1	1	1	1	1	0	1	0	0	1
<i>B. maculatus</i>	0	0	0	1	1	0	0	0	0	1
<i>B. marinus</i>	1	1	1	1	1	0	1	0	0	1
<i>B. marmoreus</i>	0	0	1	1	1	0	1	0	0	1
<i>B. mazatlanensis</i>	1	1	1	1	1	0	1	0	0	1
<i>B. melanostictus</i>	1	0	0	1	1	0	1	0	0	1
<i>B. occidentalis</i>	0	0	0	1	1	1	1	0	0	0
<i>B. perplexus</i>	0	0	1	1	1	0	1	0	0	1
<i>B. typhoni</i>	0	0	2	0	0	0	0	0	0	0
<i>B. valliceps</i>	1	1	1	1	1	0/1/2	1	0	0	1
<i>Crepidophryne</i>	1	0	1	?	?	?	?	1	?	2
<i>R. macrorrhina</i>	0	0	2	0	0	0	0	0	0	2
<i>B. spinulosus</i>	0	0	0	1	1	0	1	0	0	1
<i>B. holdridgei</i>	0	0	1	0	0	0	1	0	0	1
<i>B. asper</i>	0	0	0	0	1	0	0	0	0	1
<i>B. periglenes</i>	0	0	0	0	0	0	0	0	0	1
<i>Melanophryniscus</i>	0	0	2	?	?	?	?	1	?	2
<i>B. campbelli</i>	1	1	1	0	1	0	1	0	0	1
<i>B. melanochlorus</i>	1	1	1	0	1	0	1	0	0	1
<i>B. macrocristatus</i>	1	1	1	1	1	0	1	0	0	1

	21	22	23	24	25	26	27	28	29	30
<i>Ceratophrys</i>	0	0	2	1	1	1	0	0	1	1
<i>Telmatobius</i>	0	0	2	0	1	0	0	0	0	1
<i>Leptodactylus</i>	0	0	2	0	1	1	1	1	0	0
<i>Odontophrynus</i>	0	0	2	1	1	0	0	0	0	0
vector	0	0	2	?	1	?	?	?	?	?
<i>Atelopus ignescens</i>	1	0	0	0	0	1	?	1	0	1
<i>B. alvarius</i>	1	0	0	1	0	1	2	0	0	0
<i>B. americanus</i>	0	0	0	1	0	0	1	0	0	0
<i>B. bocourti</i>	0	0	2	1	0	0	0	0	1	0
<i>B. boreas</i>	1	0	2	0	0	0	1	0	0	0
<i>B. calamita</i>	1	0	0	0	0	0	1	0	0	0
<i>B. canaliferus</i>	0	0	0	1	0	1	0	0	1	0
<i>B. cavifrons</i>	1	0	0	1	0	0	0	0	1	0
<i>B. coccifer</i>	0	0	0	1	0	1	0	0	1	0
<i>B. coniferus</i>	1	0	0	0	0	1	0	0	1	0
<i>B. crucifer</i>	1	0	0	0	0	1	1	0	2	1
<i>B. fastidiosus</i>	1	0	0	0	0	1	0	1	0	0
<i>B. funereus</i>	1	1	0	0	0	0	1	0	0	1
<i>B. granulatus</i>	0	1	0	1	0	1	0	0	1	1
<i>B. haematiticus</i>	1	0	1	0	0	0	0	1	0	1
<i>B. ibarraii</i>	0	1	0	0	0	1	0	0	1	0
<i>B. luetkeni</i>	0	1	0	1	0	1	0	0	1	0
<i>B. maculatus</i>	0	0	0	0	0	0	1	0	1	0
<i>B. marinus</i>	1	1	0	0	0	1	1	0	2	1
<i>B. marmoreus</i>	0	0	0	0	0	0	0	0	1	0
<i>B. mazatlanensis</i>	0	0	0	1	0	1	0	0	1	0
<i>B. melanostictus</i>	0	0	0	0	0	0	0	0	0	0
<i>B. occidentalis</i>	0	0	0	0	0	0	0	0	0	0
<i>B. perplexus</i>	0	0	0	0	0	1	0	0	0	0
<i>B. typhonius</i>	1	0	1	1	0	1	1	0	2	1
<i>B. valliceps</i>	1	0	0	1	0	0	0	0	1	0
<i>Crepidophryne</i>	1	0	0	1	0	1	0	?	0	0
<i>R. macrorrhina</i>	1	0	1	1	0	1	0	1	2	1
<i>B. spinulosus</i>	1	0	0	0	0	0	1	0	0	1
<i>B. holdridgei</i>	0	0	0	0	0	1	0	0	0	0
<i>B. asper</i>	1	0	1	0	0	0	0	1	0	0
<i>B. periglenes</i>	1	0	2	0	0	0	0	0	0	1
<i>Melanophryniscus</i>	1	0	0	0	0	0	?	?	0	0
<i>B. campbelli</i>	1	0	0	1	0	0	0	0	1	0
<i>B. melanochlorus</i>	1	0	0	0	0	0	0	0	1	0
<i>B. macrocristatus</i>	1	0	0	1	0	0	0	0	1	0

	31	32	33	34	35	36	37	38	45	39
<i>Ceratophrys</i>	3	1	1	0	0	0	1	1	0	0
<i>Telmatobius</i>	1	0	0	0	1	1	0	1	0	0
<i>Leptodactylus</i>	1	1	0	0	1	0	0	2	0	0
<i>Odontophrynus</i>	1	1	0	0	0	0	0	1	0	0
vector	?	?	?	0	?	?	?	?	0	0
<i>Atelopus ignescens</i>	1	?	0	0	1	1	0	0	0	0
<i>B. alvarius</i>	1	1	1	0	1	0	0	1	1	2
<i>B. americanus</i>	1	1	1	0	1	0	0	2	1	1
<i>B. bocourti</i>	1	0	1	1	1	0	0	0	1	1
<i>B. boreas</i>	1	1	1	0	1	0	0	2	1	1
<i>B. calamita</i>	1	1	0	0	1	0	0	2	?	1
<i>B. canaliferus</i>	1	1	1	2	1	0	0	2	0	2
<i>B. cavifrons</i>	1	0	1	1	0	0	0	2	0	2
<i>B. coccifer</i>	2	0	1	1	1	0	1	2	1	2
<i>B. coniferus</i>	2	1	1	1	1	0	0	1	0	2
<i>B. crucifer</i>	1	0	1	1	1	0	0	2	0	2
<i>B. fastidiosus</i>	2	0	1	2	1	0	0	0	0	1
<i>B. funereus</i>	1	0	1	0	1	0	0	2	1	2
<i>B. granulatus</i>	3	1	1	1	0	0	1	2	1	1
<i>B. haematiticus</i>	1	0	1	0	1	0	0	1	0	1
<i>B. ibarraii</i>	2	1	1	1	1	0	0	2	1	2
<i>B. luetkeni</i>	2	1	1	1	1	0	0	1	1	2
<i>B. maculatus</i>	1	1	1	0	1	0	0	1	1	1
<i>B. marinus</i>	1	1	1	1	1	0	0	1	1	2
<i>B. marmoreus</i>	1	1	1	1	1	0	0	2	1	1
<i>B. mazatlanensis</i>	1	1	1	1	1	0	0	2	1	2
<i>B. melanostictus</i>	1	1	1	1	0	0	0	2	1	2
<i>B. occidentalis</i>	1	1	1	0	1	0	0	2	1	2
<i>B. perplexus</i>	1	1	1	1	1	0	0	2	1	1
<i>B. typhoni</i>	1	0	1	1	0	0	0	2	0	2
<i>B. valliceps</i>	2	1	1	1	0	0	0	2	1	2
<i>Crepidophryne</i>	2	0	1	2	1	0	0	0	0	2
<i>R. macrorhina</i>	1	0	1	2	1	2	0	0	0	2
<i>B. spinulosus</i>	1	1	0	0	1	0	0	1	1	1
<i>B. holdridgei</i>	2	0	1	2	1	0	0	0	0	1
<i>B. asper</i>	1	1	1	0	1	0	0	1	0	1
<i>B. periglenes</i>	1	0	1	1	1	0	0	0	0	1
<i>Melanophryniscus</i>	0	?	0	0	1	1	0	0	0	0
<i>B. campbelli</i>	1	1	1	1	0	0	0	2	0	2
<i>B. melanochlorus</i>	1	1	1	1	0	0	0	2	0	2
<i>B. macrocristatus</i>	1	1	1	1	0	0	0	2	0	2



	40	41	42	43	44
<i>Ceratophrys</i>	1	0	2	0	0
<i>Telmatobius</i>	1	0	0	0	0
<i>Leptodactylus</i>	1	0	2	0	0
<i>Odontophrynus</i>	0	0	2	0	0
vector	?	0	?	0	0
<i>Atelopus ignescens</i>	0	1	0	0	0
<i>B. alvarius</i>	0	0	2	2	0
<i>B. americanus</i>	0	0	2	1	0
<i>B. bocourti</i>	0	0	0	1	0
<i>B. boreas</i>	0	0	0	1	0
<i>B. calamita</i>	0	0	1	1	0
<i>B. canaliferus</i>	0	0	1	2	1
<i>B. cavifrons</i>	1	0	2	2	1
<i>B. coccifer</i>	0	0	1	3	0
<i>B. coniferus</i>	0	0	1	3	1
<i>B. crucifer</i>	0	0	2	2	1
<i>B. fastidiosus</i>	0	0	0	4	1
<i>B. funereus</i>	0	0	0	1	0
<i>B. granulatus</i>	0	0	1	2	0
<i>B. haematiticus</i>	1	0	1	2	1
<i>B. ibarrae</i>	0	0	1	2	0
<i>B. luetkeni</i>	0	0	1	3	0
<i>B. maculatus</i>	0	0	1	1	0
<i>B. marinus</i>	0	0	2	2	1
<i>B. marmoreus</i>	0	0	1	2	0
<i>B. mazatlanensis</i>	0	0	1	2	0
<i>B. melanostictus</i>	0	0	1	1	0
<i>B. occidentalis</i>	0	0	2	1	0
<i>B. perplexus</i>	0	0	1	2	1
<i>B. typhonus</i>	0	0	2	2	1
<i>B. valliceps</i>	1	0	2	2	0
<i>Crepidophryne</i>	0	0	0	4	1
<i>R. macrorhina</i>	0	0	0	2	1
<i>B. spinulosus</i>	0	0	0	3	0
<i>B. holdridgei</i>	0	0	0	4	0
<i>B. asper</i>	0	0	2	2	0
<i>B. periglenes</i>	0	0	0	2	0
<i>Melanophryniscus</i>	0	1	0	0	0
<i>B. campbelli</i>	1	0	2	2	1
<i>B. melanochlorus</i>	1	0	2	2	1
<i>B. macrocristatus</i>	1	0	2	2	1

Table 5.3. The species of the *Bufo valliceps* group.

Species	Distribution
<i>Bufo campbelli</i> Mendelson	Atlantic versant Mexico, Guatemala, Honduras
<i>Bufo cavifrons</i> Firschein	Sierra de los Tuxtlas, Veracruz, Mexico
<i>Bufo cristatus</i> Weigmann	Sierra Madre Oriental, Mexico
<i>Bufo melanochlorus</i> Cope	Atlantic lowlands Costa Rica
<i>Bufo macrocristatus</i> Firschein and Smith	Atlantic versant southern Mexico, Guatemala
<i>Bufo spiculatus</i> Mendelson	Sierra de Juárez, Sierra Mixe, Oaxaca, Mexico
<i>Bufo tutelarius</i> Mendelson	Pacific versant southern Mexico, Guatemala
<i>Bufo valliceps</i> Weigmann	Widespread, lowlands southern USA–Costa Rica

**APPENDIX IV**  
**FIGURES**

Fig. 1.1—*Bufo tutelarius* in life (UTA A-13088). Adult female from the type locality.  
Reproduced from UTA Color Transparency 94, photographed by W. W. Lamar.



Fig. 1.2—Dorsal (right) and lateral (left) aspect of the head of *Bufo tutelarius* (UTA A-131135, holotype). Scale bar = 5 mm.

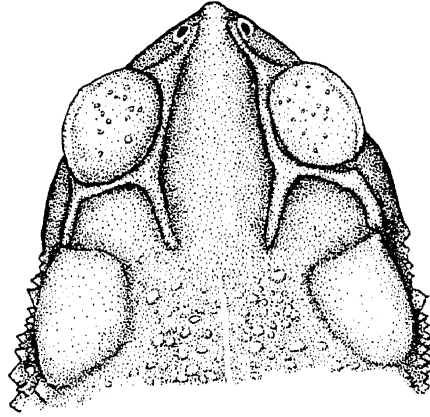
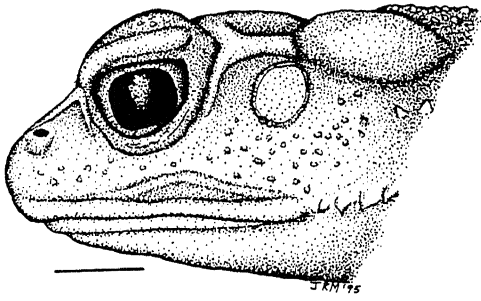


Fig. 1.3—Adult male (right; UTA A-13135 holotype) and female (left; MZFC 5277) specimens of *Bufo tutelarius* from Cerro Baúl, Oaxaca, Mexico, showing some of the variation in dorsal pattern in this species. Note the similar development of the cranial crests evident in both sexes.





Fig. 1.4—Generalized map of the highlands of Guatemala and Chiapas, Mexico, showing locality records for *Bufo tutelarius* (circles) and *Bufo macrocristatus* (triangles). The stippled pattern represents elevations 800–2000 m, and the striped pattern represents elevations >2000 m. Some symbols represent more than one specific locality.

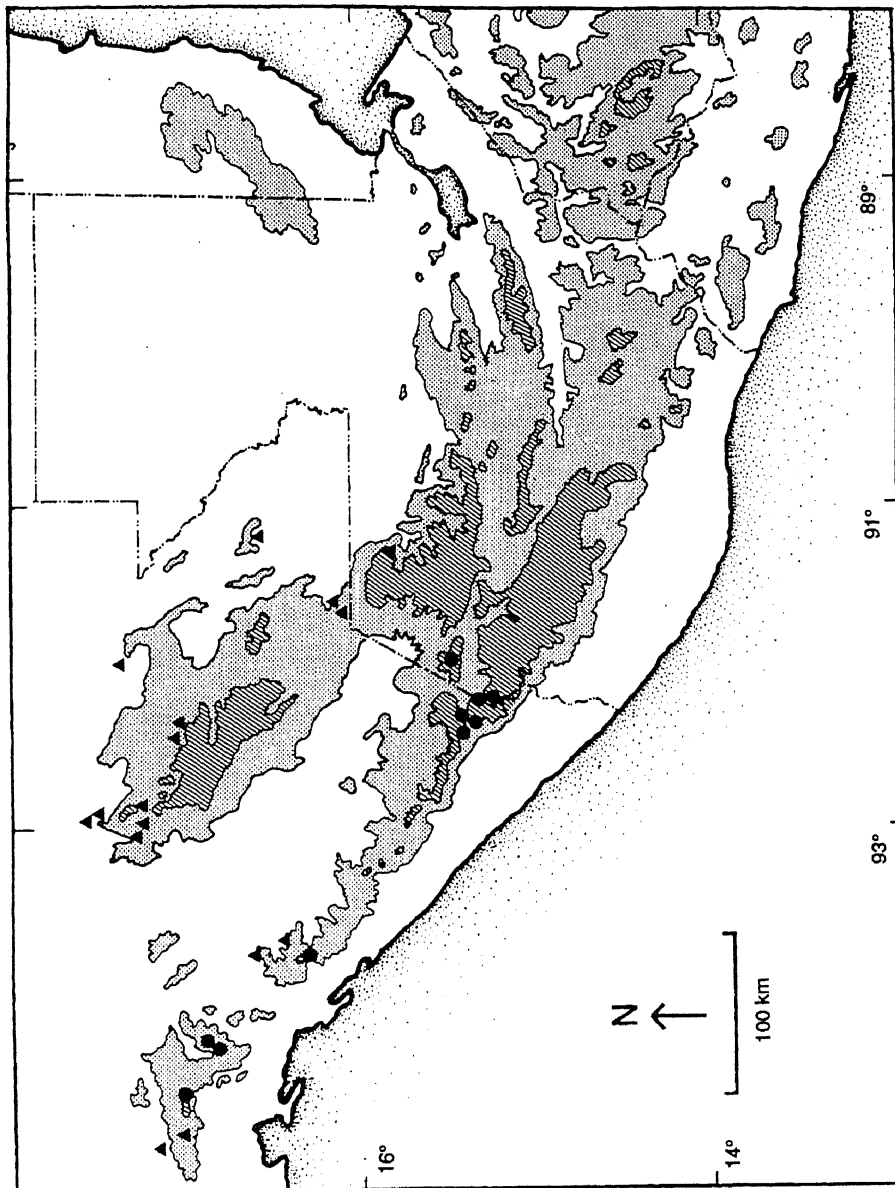


Fig. 1.5—Dorsal (right) and lateral (left) aspect of the head of *Bufo macrocristatus* (MZFC LCM 281, adult female from near the type locality).

Scale bar = 5 mm.

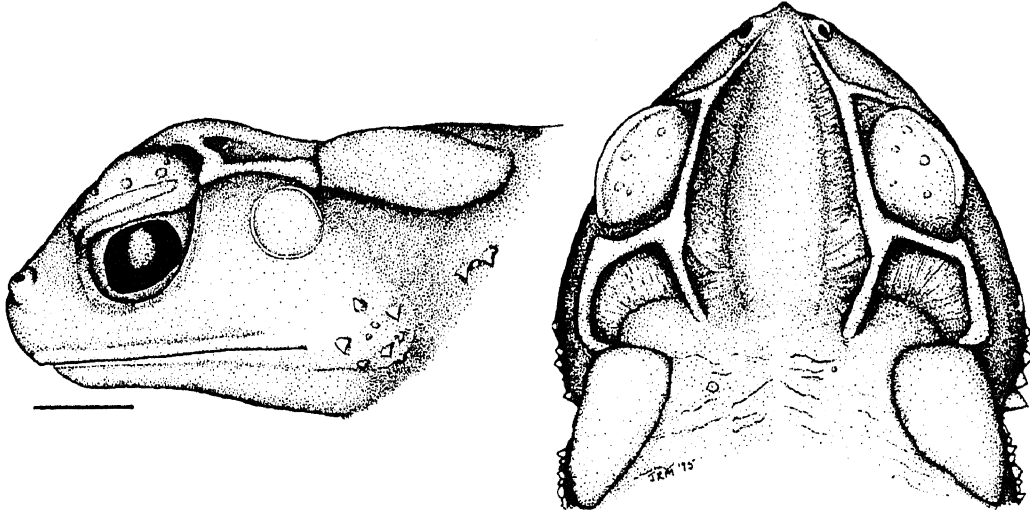


Fig. 1.6—Adult male (right) and female (left) specimens of *Bufo macrocristatus*, both from series UMMZ 123994, from the Selva Negra region of Chiapas, Mexico. Note the sexual dimorphism in the development of the cranial crests, and the texture and pattern of the dorsal skin.

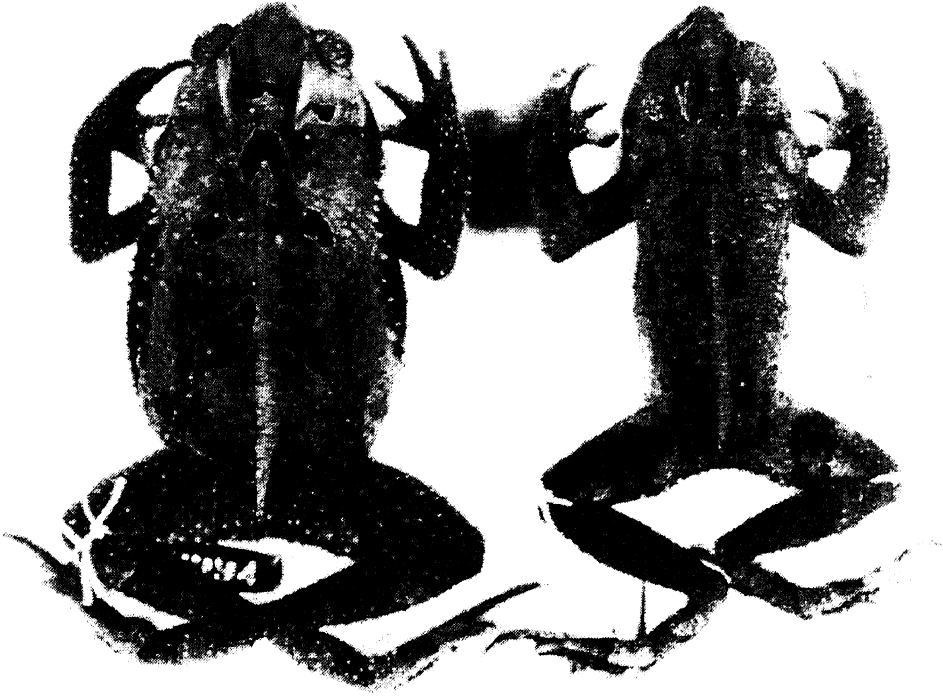
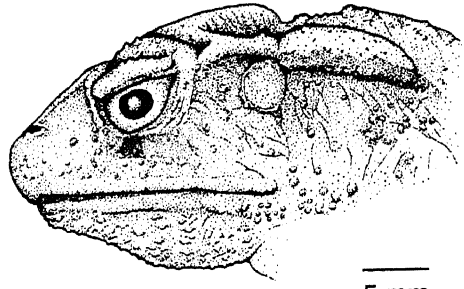


Fig. 2.1—Dorsal (right) and lateral (left) aspect of the head of *Bufo spiculatus* (KU 137523, adult female holotype). Note texture of cranial crests. Original figure by Christopher A. Sheil.





5 mm

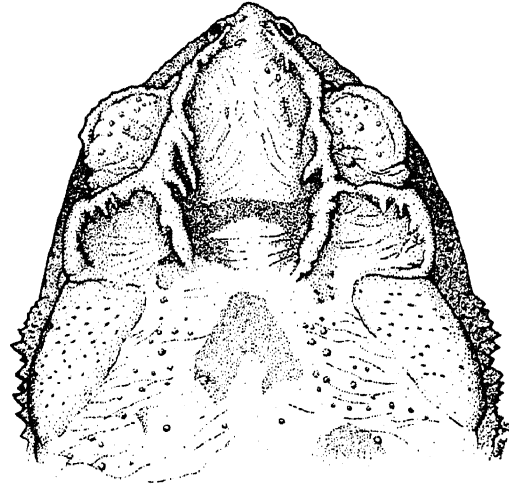


Fig. 2.2.—Color pattern variation among adult *Bufo spiculatus*. Specimens shown are, from left: KU 137523 adult female, holotype; KU 137522 adult female, paratype; and AMNH 71397 adult male, paratype. Note spiculate texture of skin on the females, especially on the limbs and posterior portion of the dorsum.

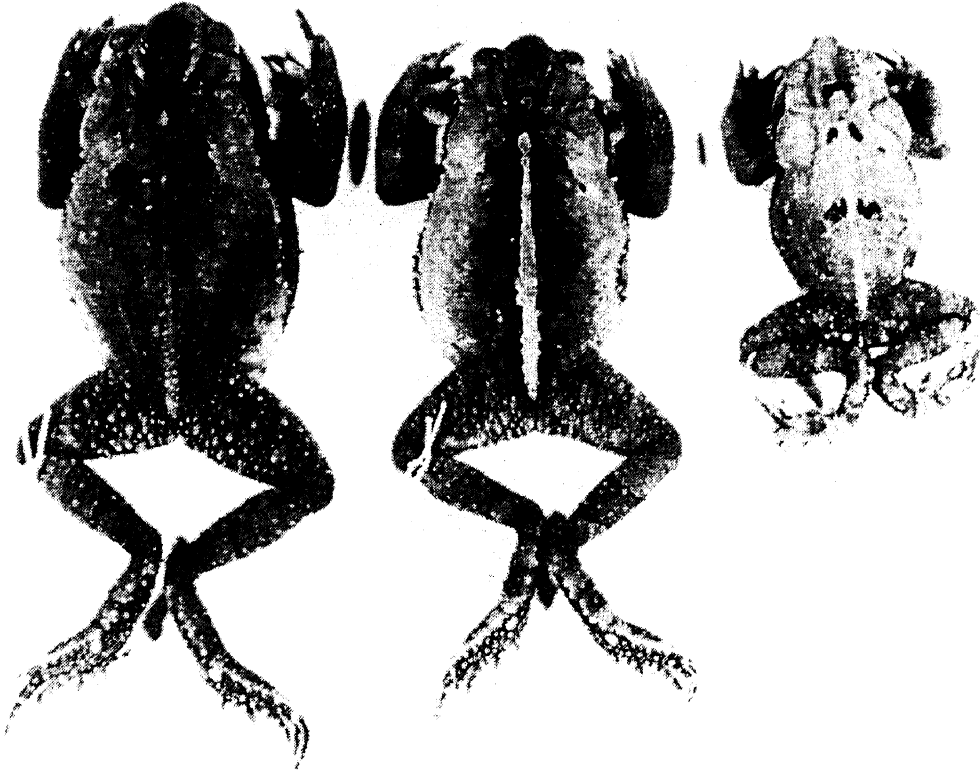
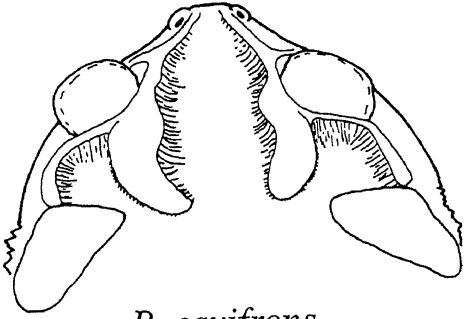


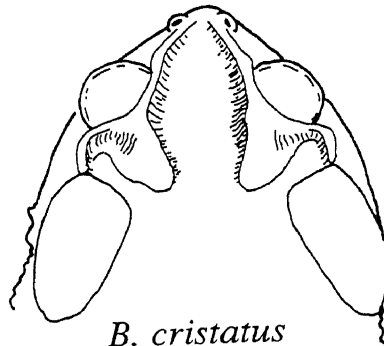
Fig. 2.3.—Skin texture of the dorsal surface of the left femoral area of *Bufo spiculatus* (KU 86670, adult female) showing distinctive spiculate tubercles.



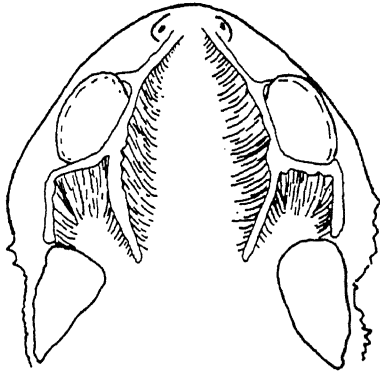
Fig. 2.4.—Diagrammatic representation of the relative size and shape of the cranial crests and parotoid glands of adult females of six similar species of crested toads in southern Mexico.



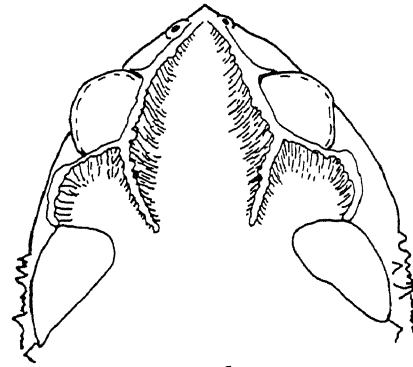
*B. cavifrons*



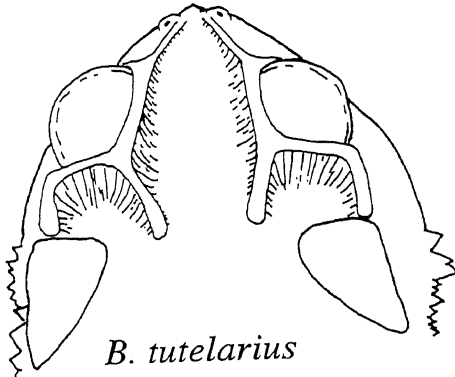
*B. cristatus*



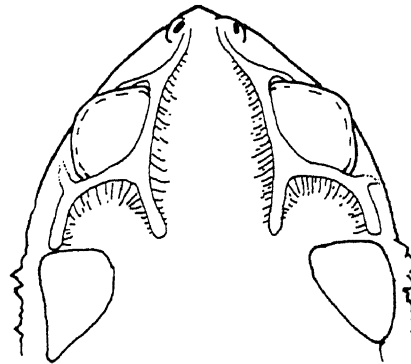
*B. macrocristatus*



*B. spiculatus*



*B. tutelarius*



*B. valliceps*

Fig. 2.5.—A generalized map showing the distribution of the toads discussed in this paper. The shaded area represents elevations above 1000 m. Triangles represent localities for *Bufo spiculatus*, circles represent *B. cavifrons*, and squares represent *B. cristatus*. Some symbols represent more than one specific locality. A single locality for *B. spiculatus* is not shown: San Lucas Camotlán, Oaxaca ( $16^{\circ} 57'$ ,  $95^{\circ} 44'$ ; 1689 m); this locality is on the northern slope of the Sierra Mixe, SE of the Sierra de Juárez.



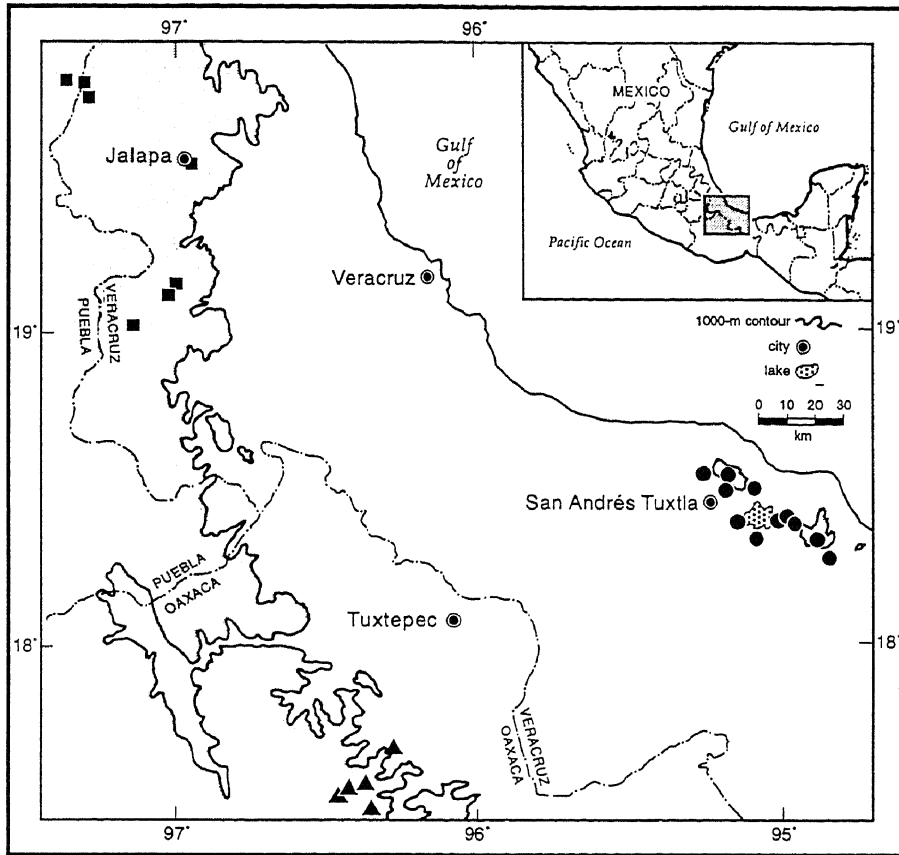


Fig. 2.6.—*Bufo cristatus* in life. An adult male from 7 mi [11.3 km] E Tezuitlan, Puebla, Mexico; specimen not extant. Photograph by R. Altig.



Fig. 3.1.—Geographic distribution of *Bufo valliceps*, modified from Porter (1970) and excluding erroneous records from El Salvador and western Nicaragua (Frost, 1985:52, 63). *Bufo valliceps* is absent in all areas above 1700 m of elevation.

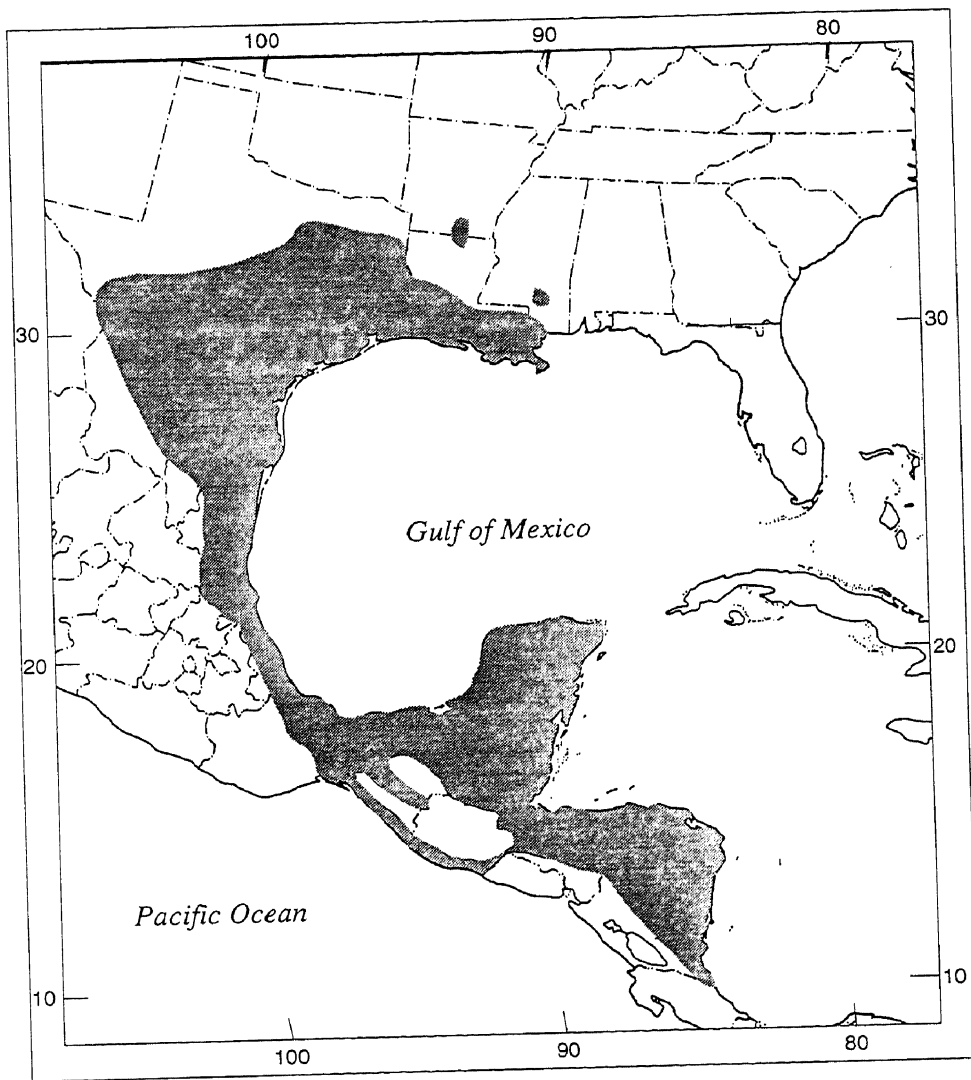


Fig. 3.2.—Map showing the location of the 19 samples of *Bufo valliceps* studied in the range-wide morphometric analyses: (1) Baton Rouge, East Baton Rouge Parish, Louisiana; (2) Walker County, Texas; (3) Tarrant and Dallas counties, Texas; (4) Austin, Travis County, Texas; (5) Liverpool, Brazoria County, Texas; (6) Brownsville, Cameron County, Texas; (7) Val Verde County, Texas; (8) Don Martin Dam, Coahuila; (9) Huejutla, Hidalgo; (10) Cuautlapam, Veracruz; (11) Acayucan, Veracruz; (12) Tuxtla Guitiérrez, Chiapas; (13) Chinijá, Alta Verapaz, Guatemala; (14) Escárcega, Campeche; (15) Pueblo Nuevo X-Can, Quintana Roo; (16) Tucuru, Alta Verapaz, Guatemala; (17) Champerico, Retalhuleu, Guatemala; (18) San Pedro Sula, Cortés, Honduras; (19) Condega, Estelí, Nicaragua. Inset shows the mean snout-vent length and 95% confidence intervals for populations.

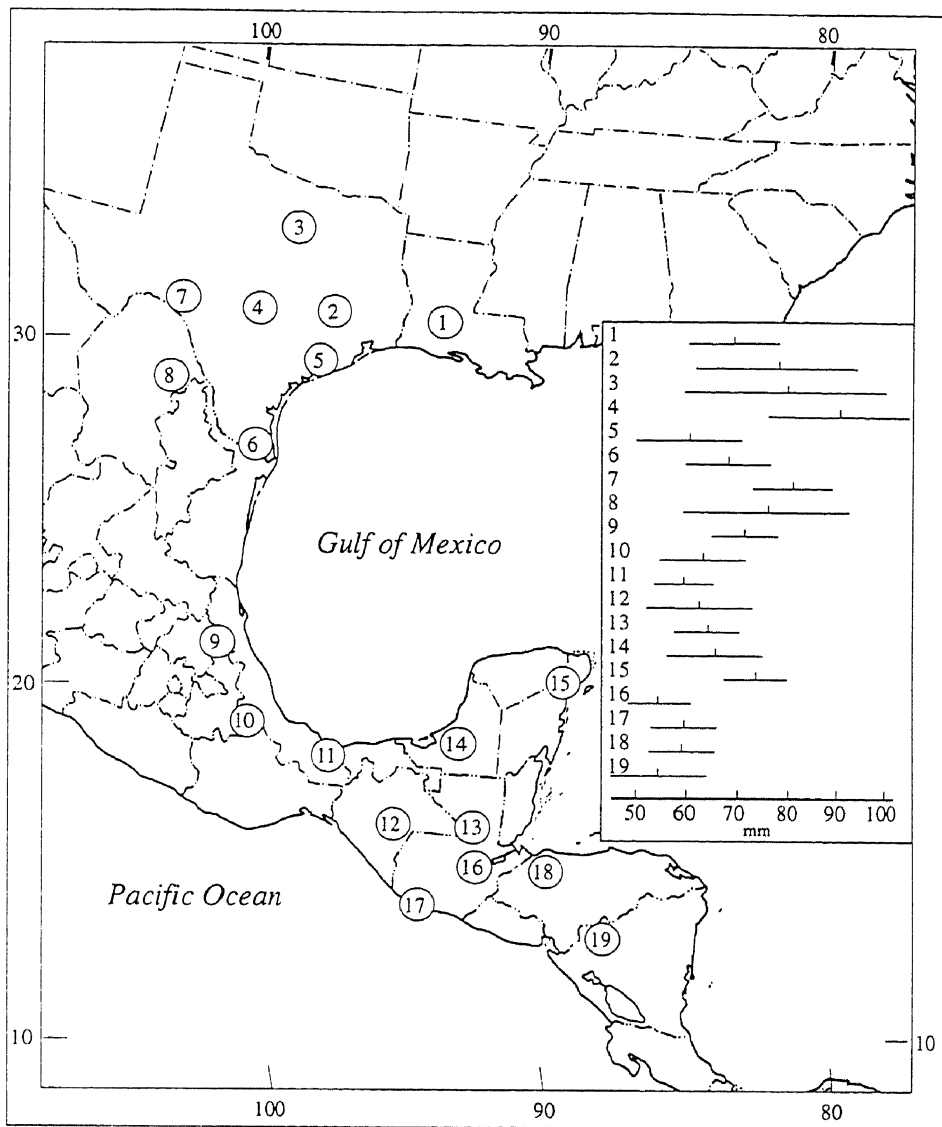


Fig. 3.3.—Mean scores with 95% confidence intervals on Principal Component I for each sample population of *Bufo valliceps* (Fig. 2), ranked by magnitude. The vertical bars to the right indicate homogeneous subsets of samples identified by Tukey's Method.



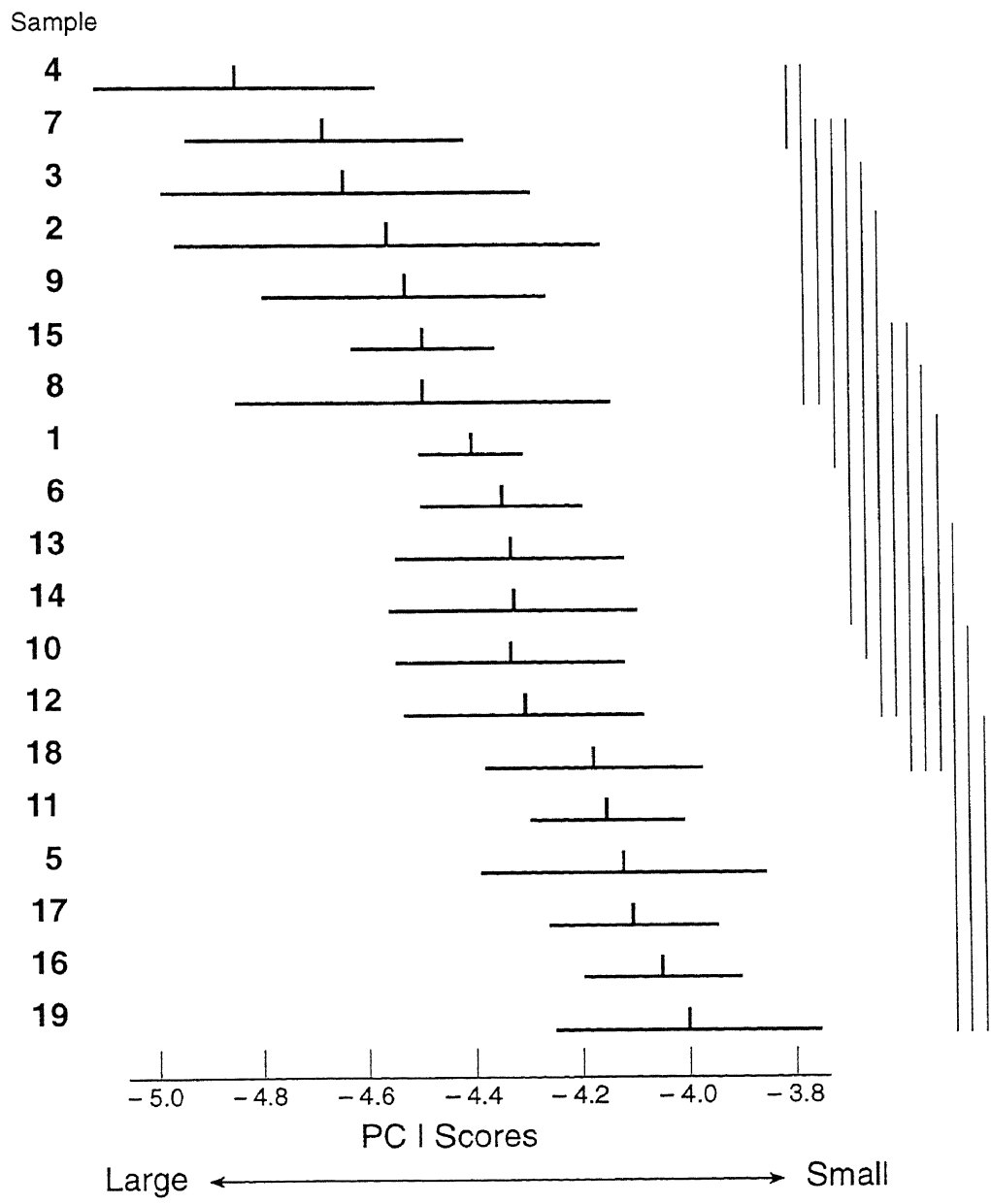


Fig. 3.4.—Map of the Yucatan Peninsula showing location of nine samples of *Bufo valliceps* used in the morphometric analysis along the Yucatán precipitation gradient: (1) Chinajá, Alta Verapaz, Guatemala; (2) La Libertad, El Petén, Guatemala; (3) Tikal, El Petén, Guatemala; (4) Escárcega, Campeche; (5) Champotón, Campeche; (6) Dzibalchen, Campeche; (7) Mérida, Yucatán; (8) Chichen Itzá, Yucatán; (9) Pueblo Nuevo X-Can, Quintana Roo. Inset shows mean scores and 95% confidence intervals for each sample on Principal Component I, ranked by magnitude. The vertical bars to the right indicate homogeneous subsets of samples identified by Tukey's Method.

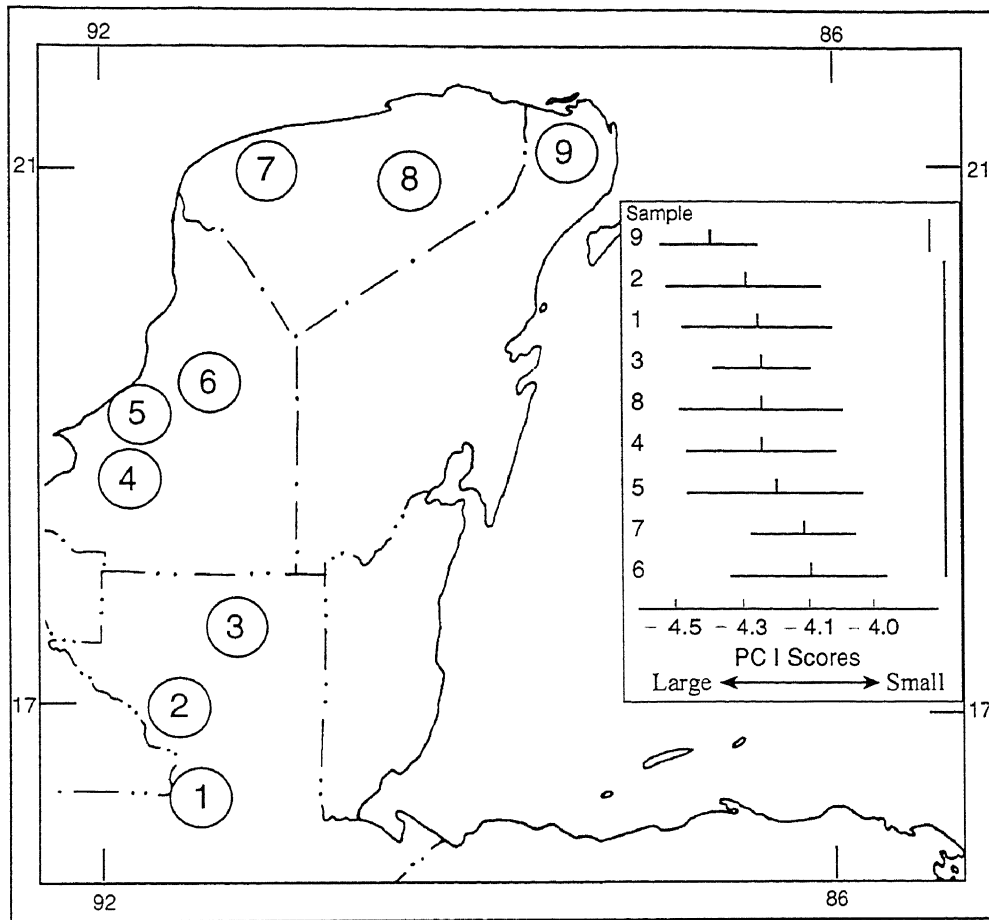


Fig. 3.5.—Plot of mean canonical discriminant scores for 19 samples of *Bufo valliceps*. Circles represent approximate 95% confidence intervals around each mean score. For purposes of clarity, prediction intervals are not shown, but these have a diameter of 2.45 units on each axis and, therefore, would indicate substantial overlap among many groups.

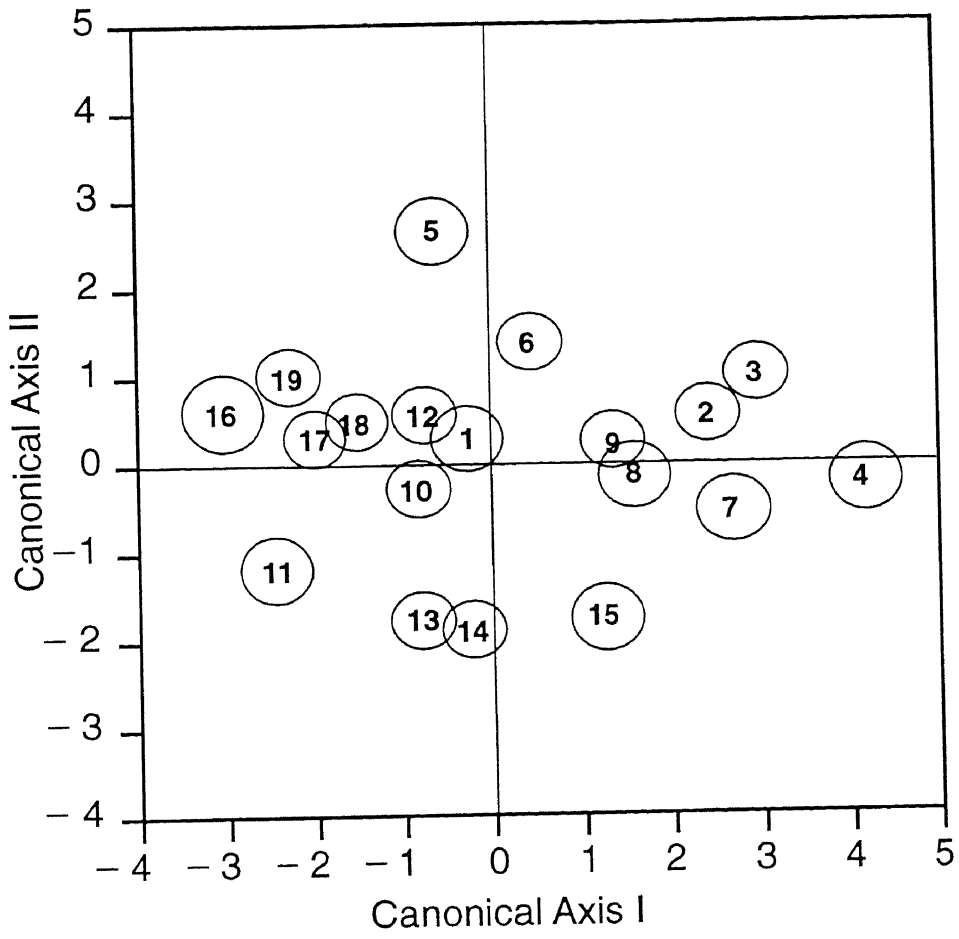


Fig. 3.6.—A precise representation of Porter's (1962) Figure 26 showing the relationship between crest height and elevation at collection site. Porter's original caption: "The relationship between maximum crest height and the elevation of the collecting site for *B. valliceps*. The black line indicates the mean cranial crest height, the [light] gray area one standard deviation either side of the mean, the [dark gray] area two standard errors either side of the mean. All collecting site elevations were rounded-off to the nearest 100 meters."

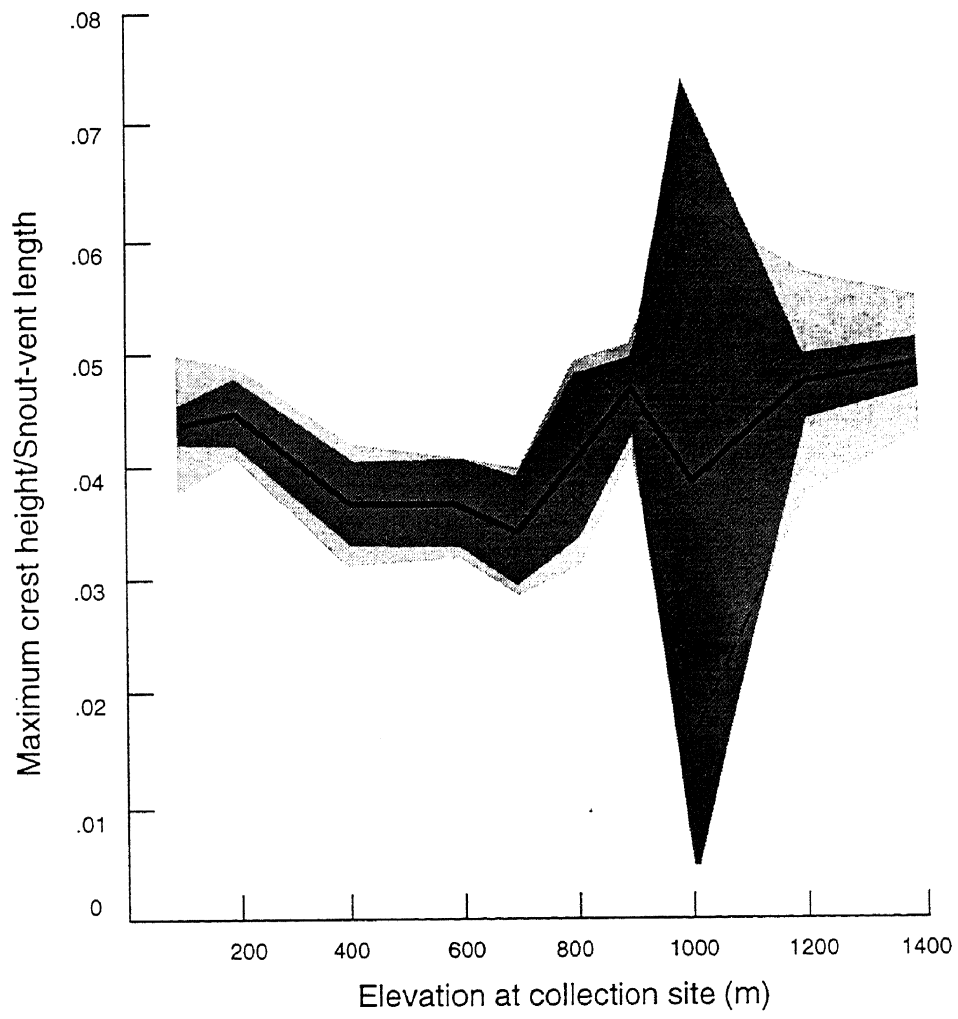


Fig. 3.7.— Comparison of typical adult male *Bufo valliceps* from Izabal, Guatemala (left; KU 19011) and Coahuila, Mexico (right; KU 47011). Note differences in overall size and the distinctive middorsal stripe of the male from Coahuila.



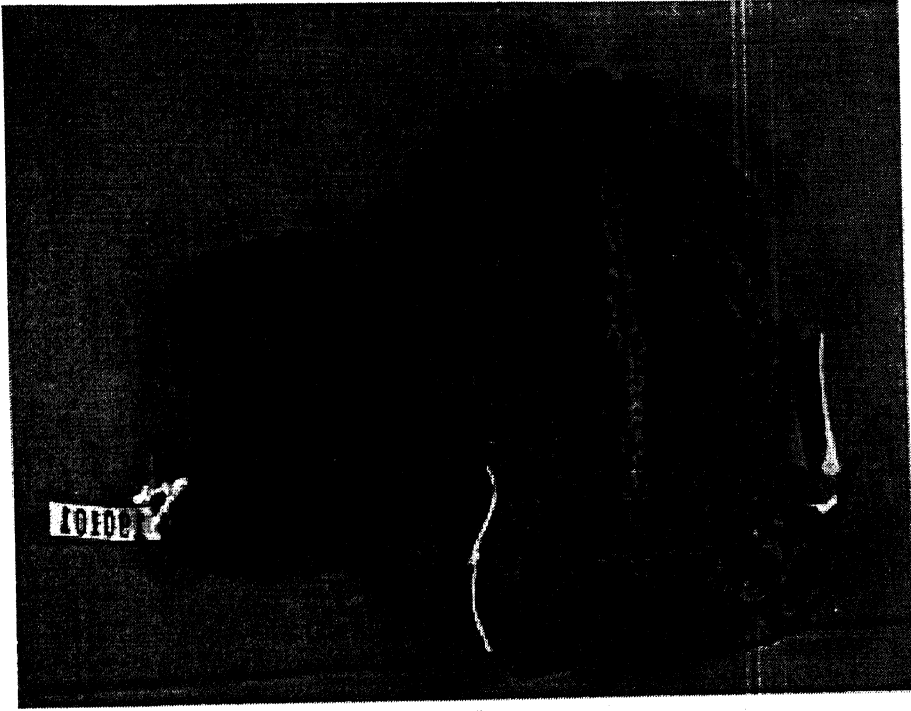


Fig. 4.1.—*Bufo ibarraii* in life (KU 186302). Adult male from near Purulhá, Baja Verapaz, Guatemala. Reproduced from KU Color Transparency 6651; photographed by J. A. Campbell.

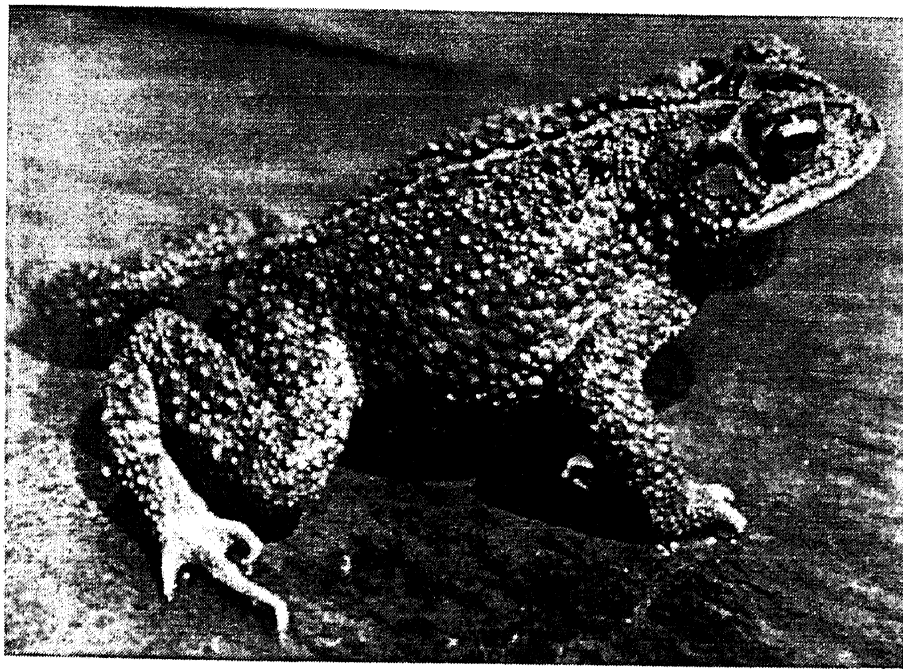


Fig. 4.2.—Adult female (left; KU 190067) and male (right; KU 186299) specimens of *Bufo ibarraei* from near Purulhá, Baja Verapaz, Guatemala.

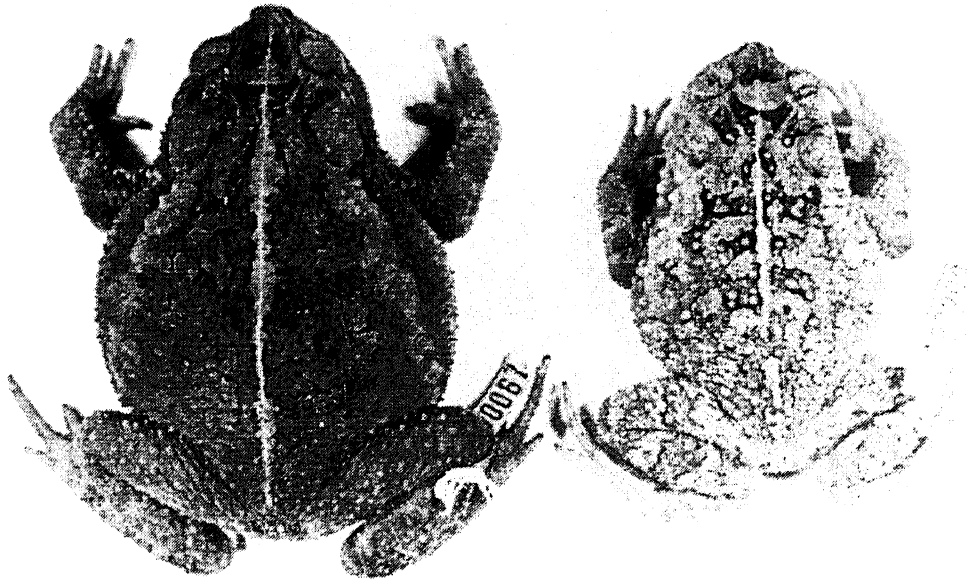


Fig. 4.3.—Comparison of dorsal skin texture of adult male (upper; KU 186299) and female (lower; KU 190067) *Bufo ibarraei*. Note the more spiculate nature of the tubercles on the female.

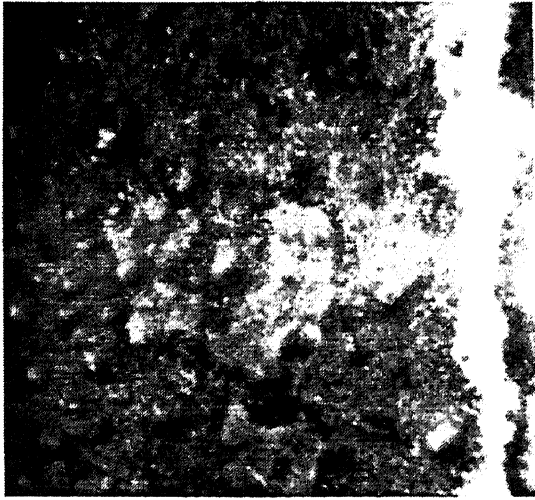
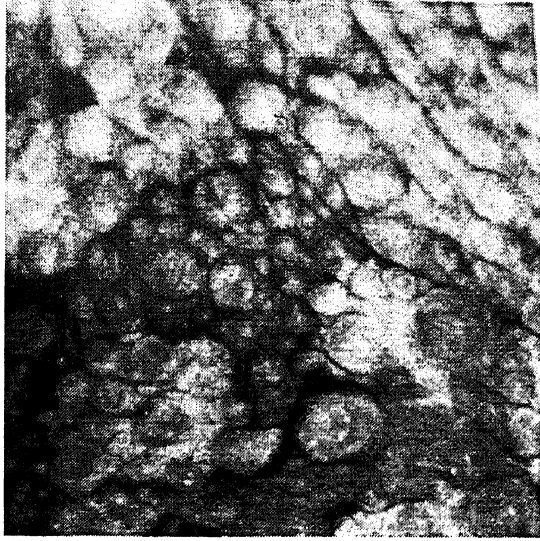


Fig. 4.4.—Comparison of adult male *Bufo ibarra* (left; UTA A-38130) and *Bufo coccifer* (right; UTA A-38124) collected in southeastern Guatemala. Note the differences in size, skin texture, shape of the parotoid glands, and development of the cranial crests.



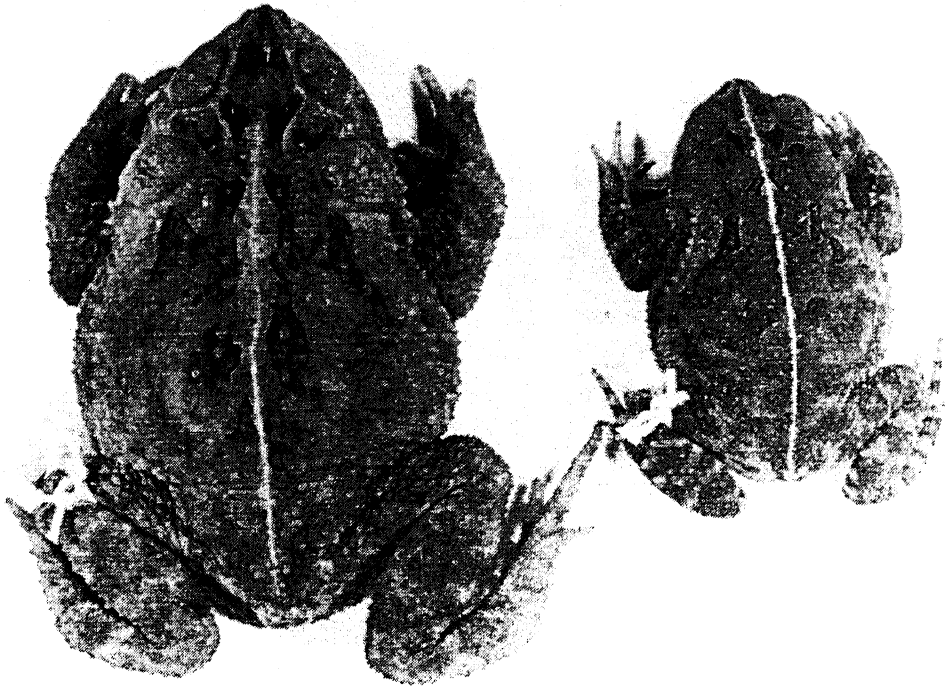


Fig. 4.5.—Generalized map of Guatemala. The light gray areas represent elevations 800–2000 m, the dark gray areas represent elevations >2000 m. Circles represent localities for *B. coccifer*, squares represent *B. ibarraii*, and triangles represent *B. valliceps*. Records for *B. valliceps* from the eastern lowlands of the Atlantic versant, where this species is widespread and abundant, are not shown. Some symbols represent more than one specific locality.

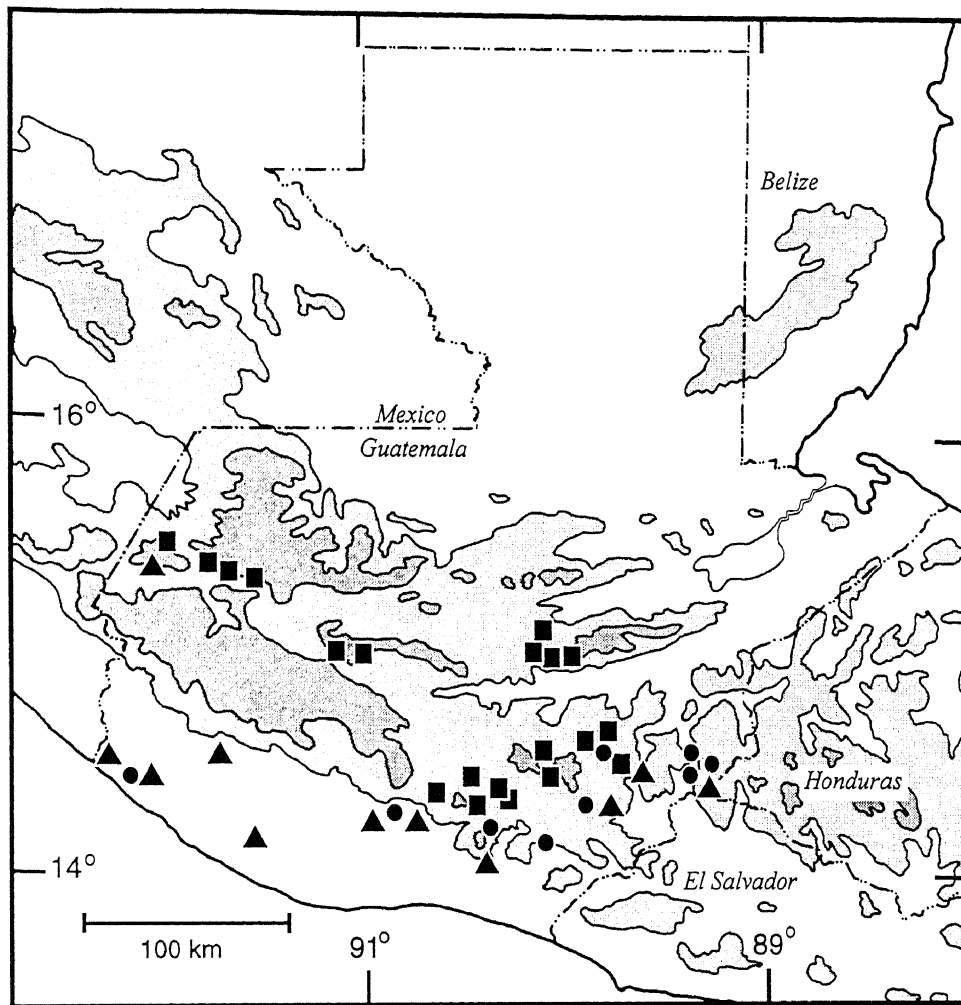


Fig. 4.6.—The holotype (ZMB 13200) of *Bufo valliceps* var. *microtis* Werner, an adult female from "Honduras." This taxon is herein referred to the synonymy of *Bufo coccifer*.



Fig. 5.1—Nomenclature of the dorsal cranial crests used for species in the *Bufo valliceps* Group. Drawing modified from Mendelson (1994); original drawing of *Bufo campbelli* by Greg Willis.

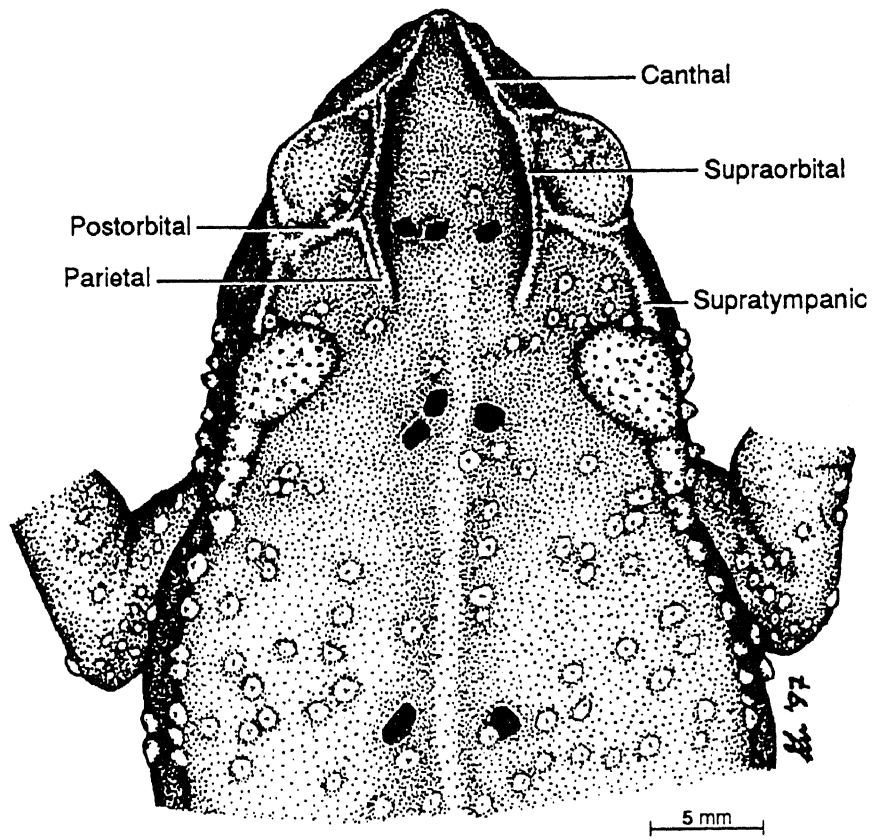


Fig. 5.2—Nomenclature of the lateral cranial crests used for species in the *Bufo valliceps* Group. Original drawing of *Bufo valliceps* (KU 92599; Mexico: Nuevo León) prepared by Jenny B. Pramuk.



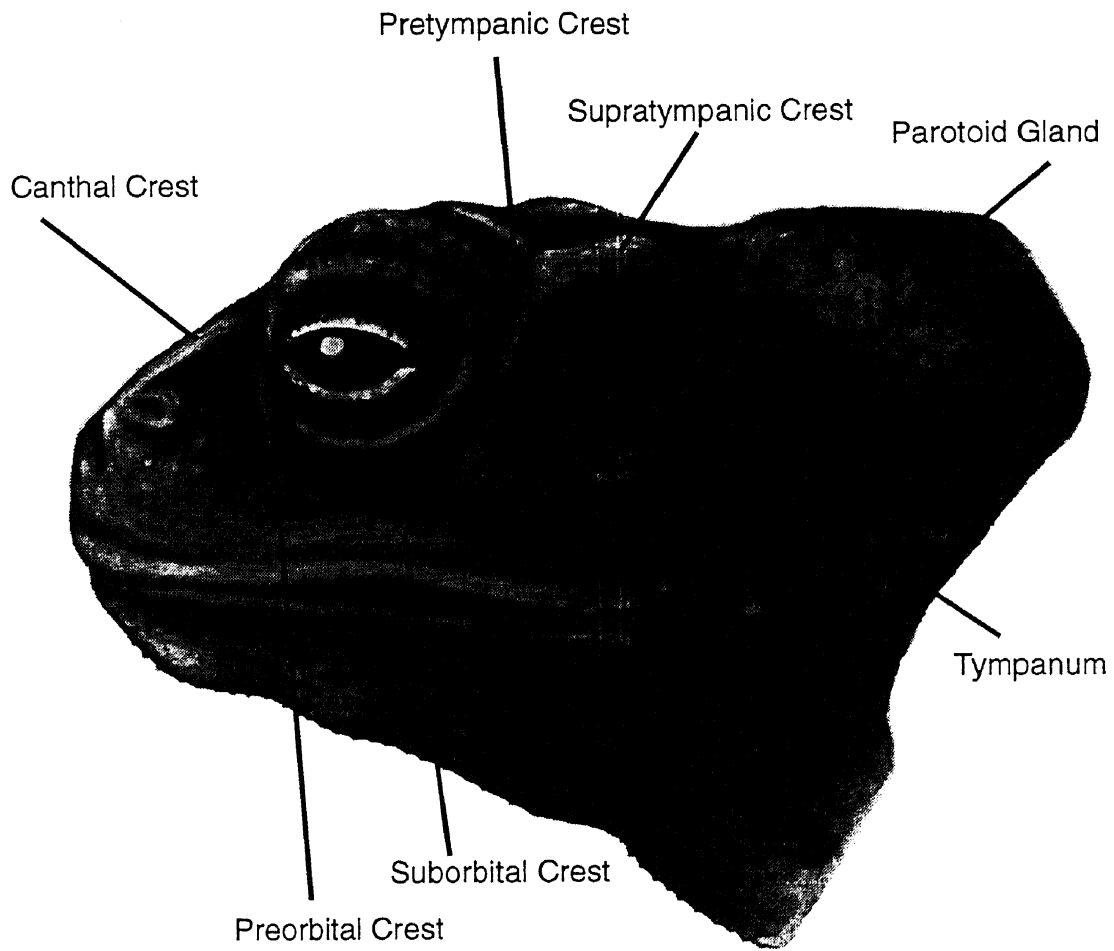


Fig. 5.3—Dorsal view of the skulls of two species of *Bufo* illustrating conditions of the frontoparietal-nasal relationship. Upper figure (*B. calamita*; KU 148621) showing lateral contact only (Character 2: 1) and lower figure (*B. luetkeni*; KU 84926) showing full contact (Character 2: 2). Scale bar represents 5 mm.

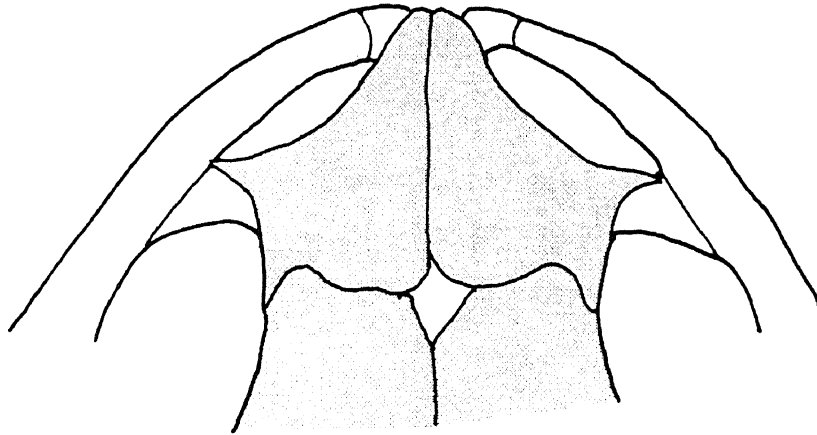
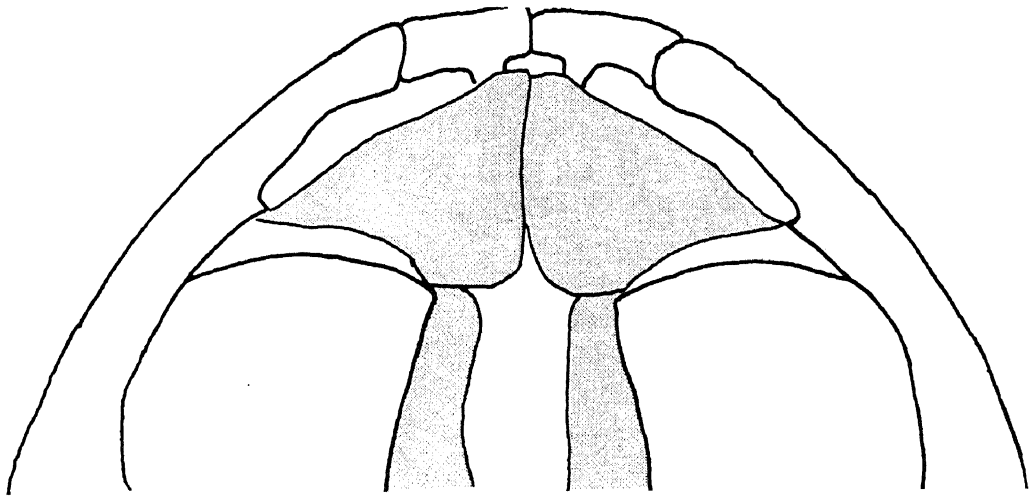
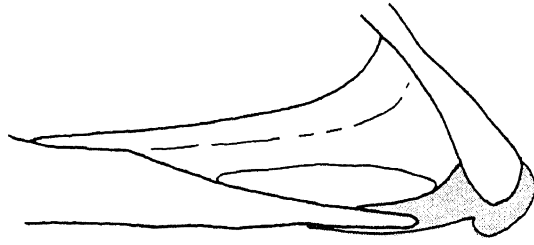
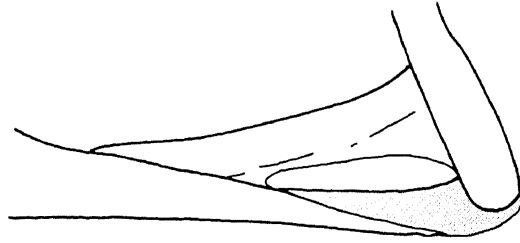


Fig. 5.4—Lateral view of the maxilla-quadratojugal articulation in three species of *Bufo*: (A) *B. cavifrons* (UMMZ 152822) showing slender quadratojugal (Character 26: 0) and maxilla lateral to quadratojugal (Character 27: 0); (B) *B. crucifer* (KU 93093) showing maxilla ventral to quadratojugal (Character 27: 1); (C) *B. alvarius* (KU 14082) showing robust maxilla (Character 26: 1) and maxilla dorsal to quadratojugal (Character 27: 2).

A



B



C

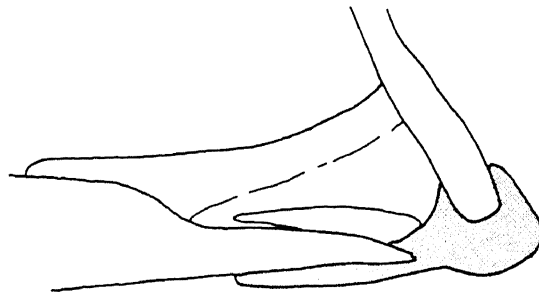


Fig. 5.5—Lateral view of the skulls of two species of *Bufo* illustrating relationship of the ventral and zygomatic rami of the squamosal; rami are indicated by arrows. Upper figure (*B. valliceps*; KU 59875) showing space between rami not filled with bone (Character 32: 1) and lower figure (*B. coccifer*; KU 68148) showing space between rami filled with bone (Character 32: 0).



5 mm

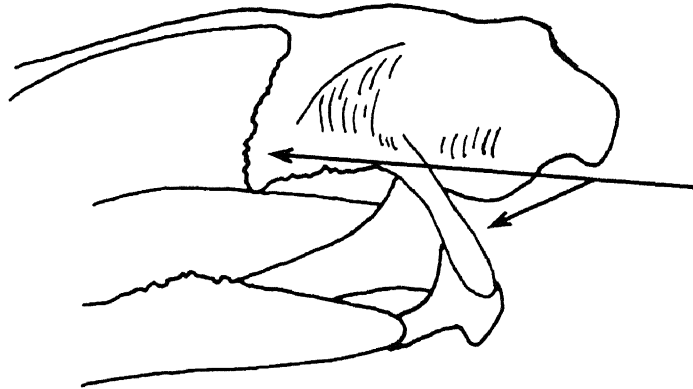
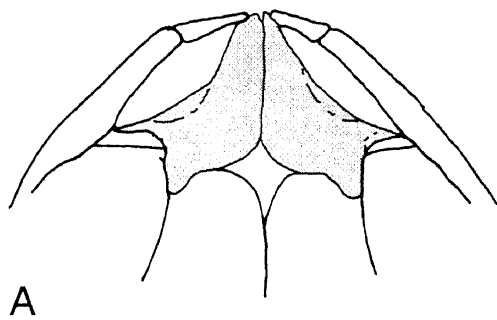
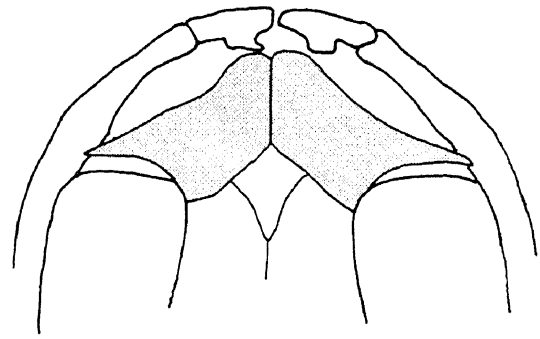


Fig. 5.6—Shape of the nasal bones in two species of *Bufo*. Sketches A and B (*B. valliceps*; KU 59874) show elongate, narrow anterior tip (Character 34: 1) and straight, sloped profile (Character 35: 0), respectively. Sketches C and D (*B. occidentalis*; KU 59871) show short, broad anterior tip (Character 34: 0) and ventrally curved profile (Character 35: 1).



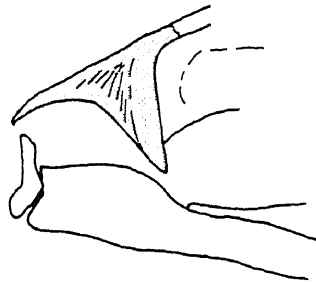


A

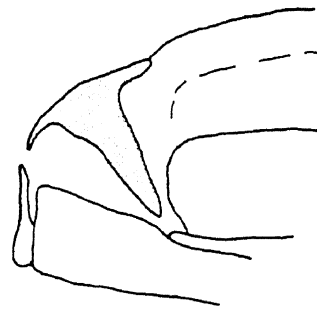


C

5 mm



B



D

Fig. 5.7—Strict consensus tree of the 70 fundamental trees produced by the analysis. Clades are numbered as referred to in text.

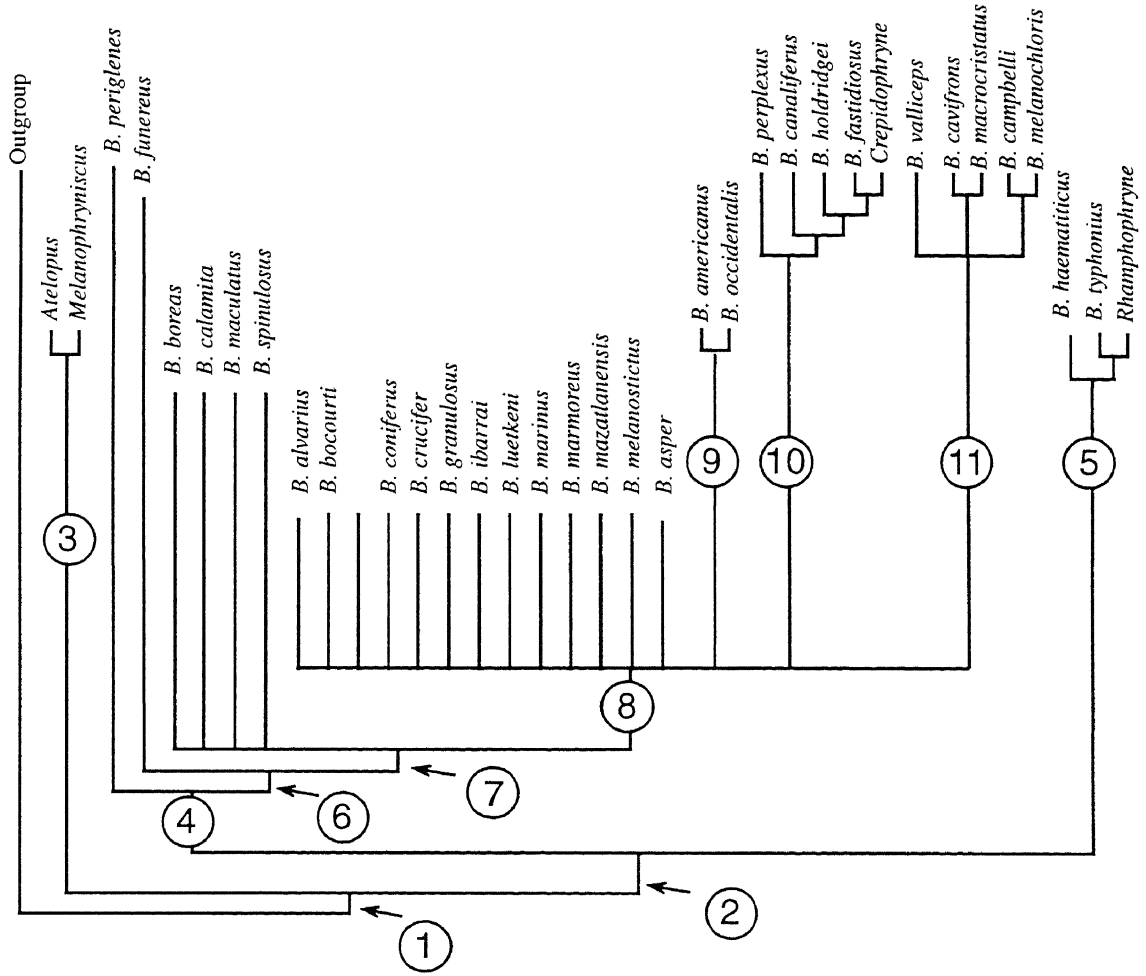


Fig. 5.8—Strict consensus of three fundamental trees in Island 1.

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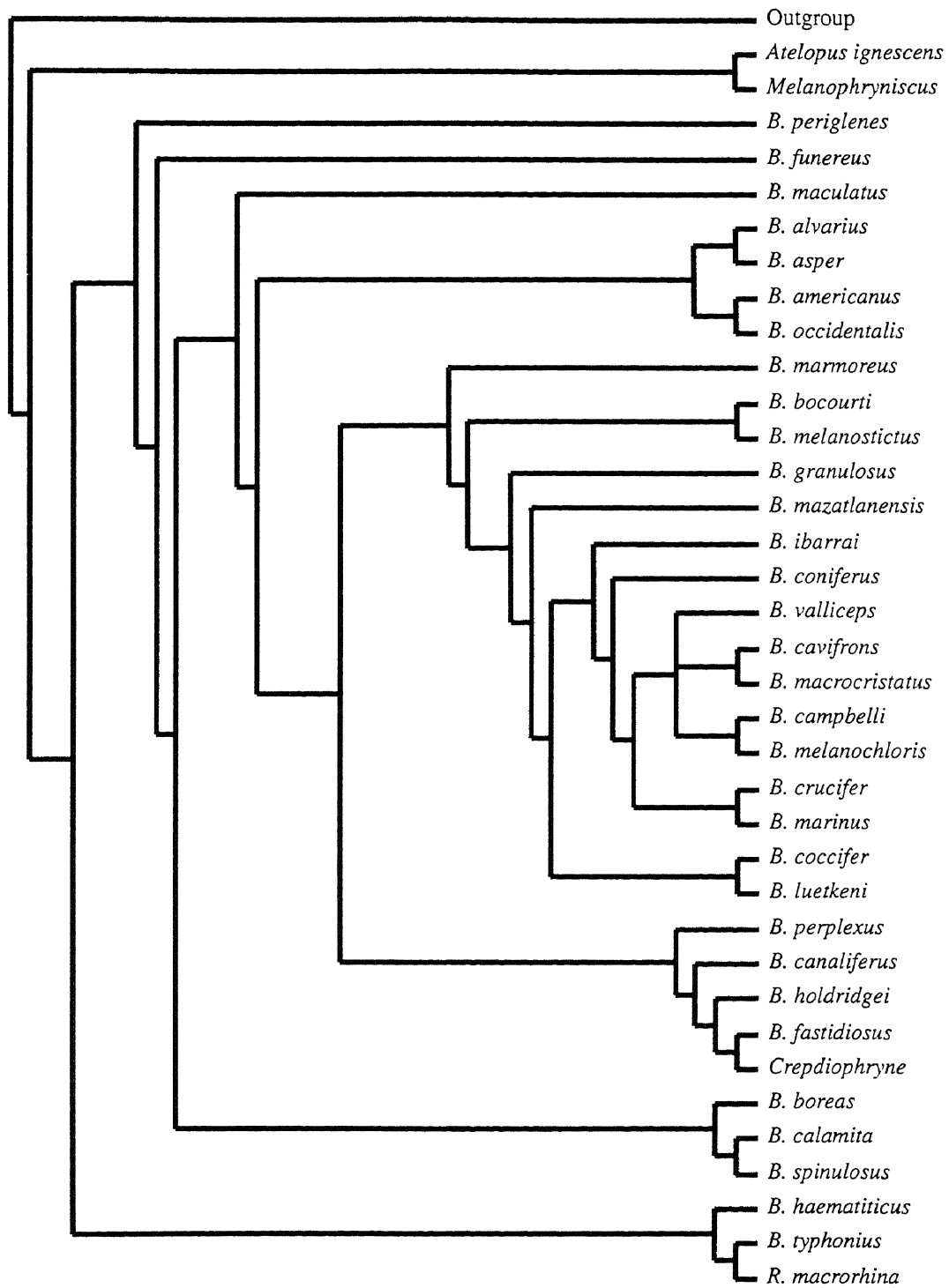


Fig. 5.9—Strict consensus of 61 fundamental trees in Island 2.

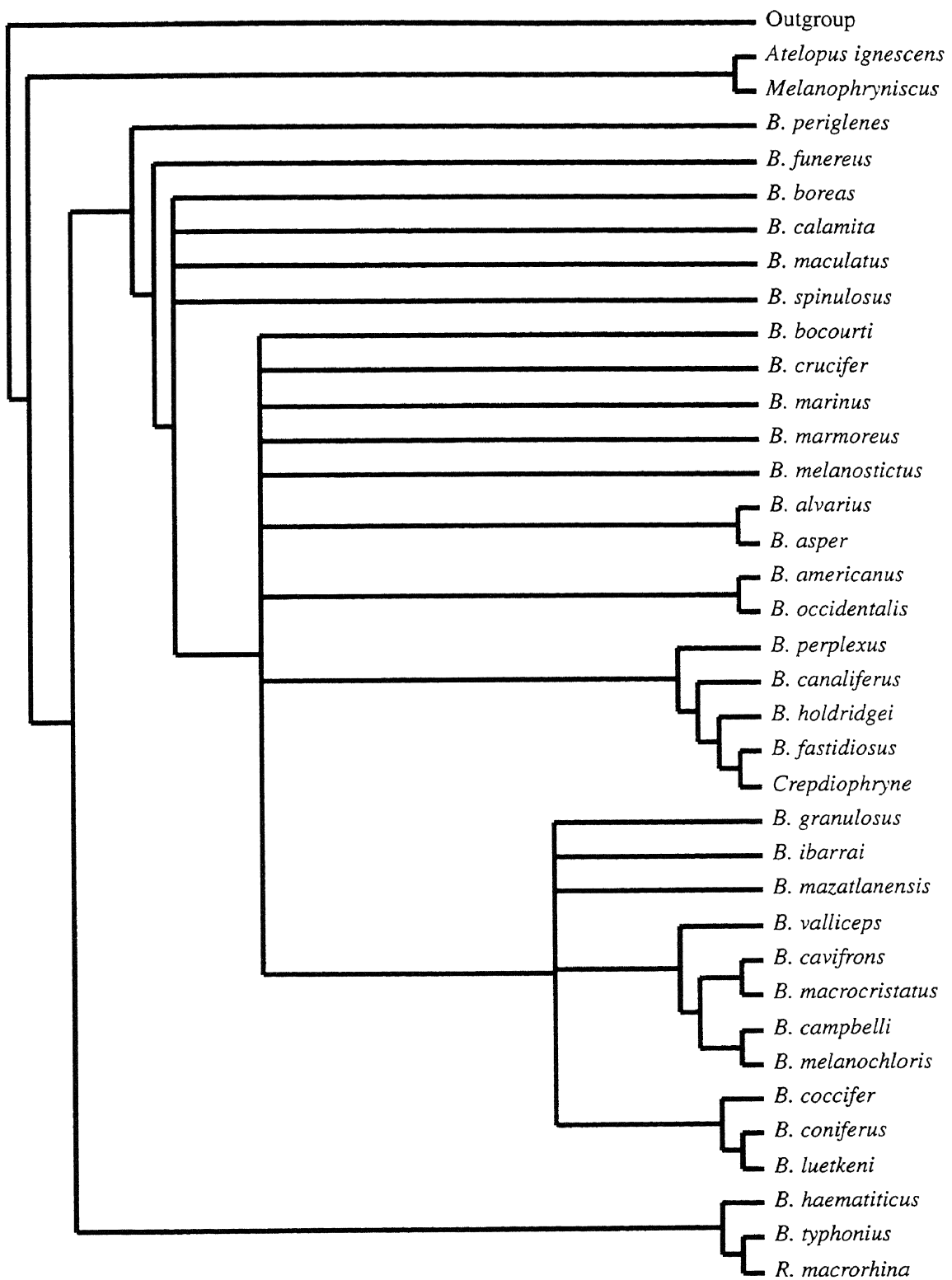




Fig. 5.10—Strict consensus of three fundamental trees in Island 3.

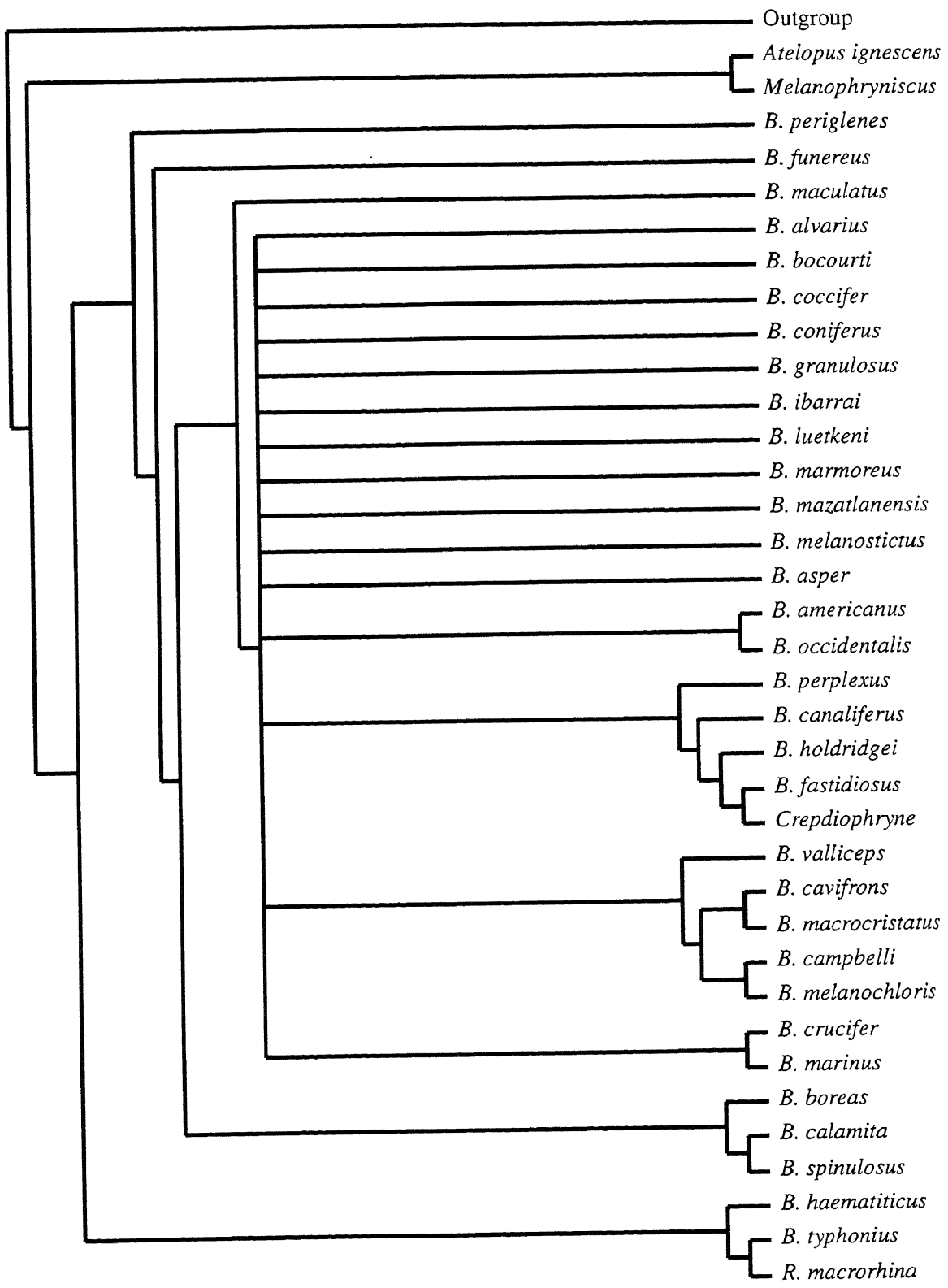


Fig. 5.11—Strict consensus of two fundamental trees in Island 4.

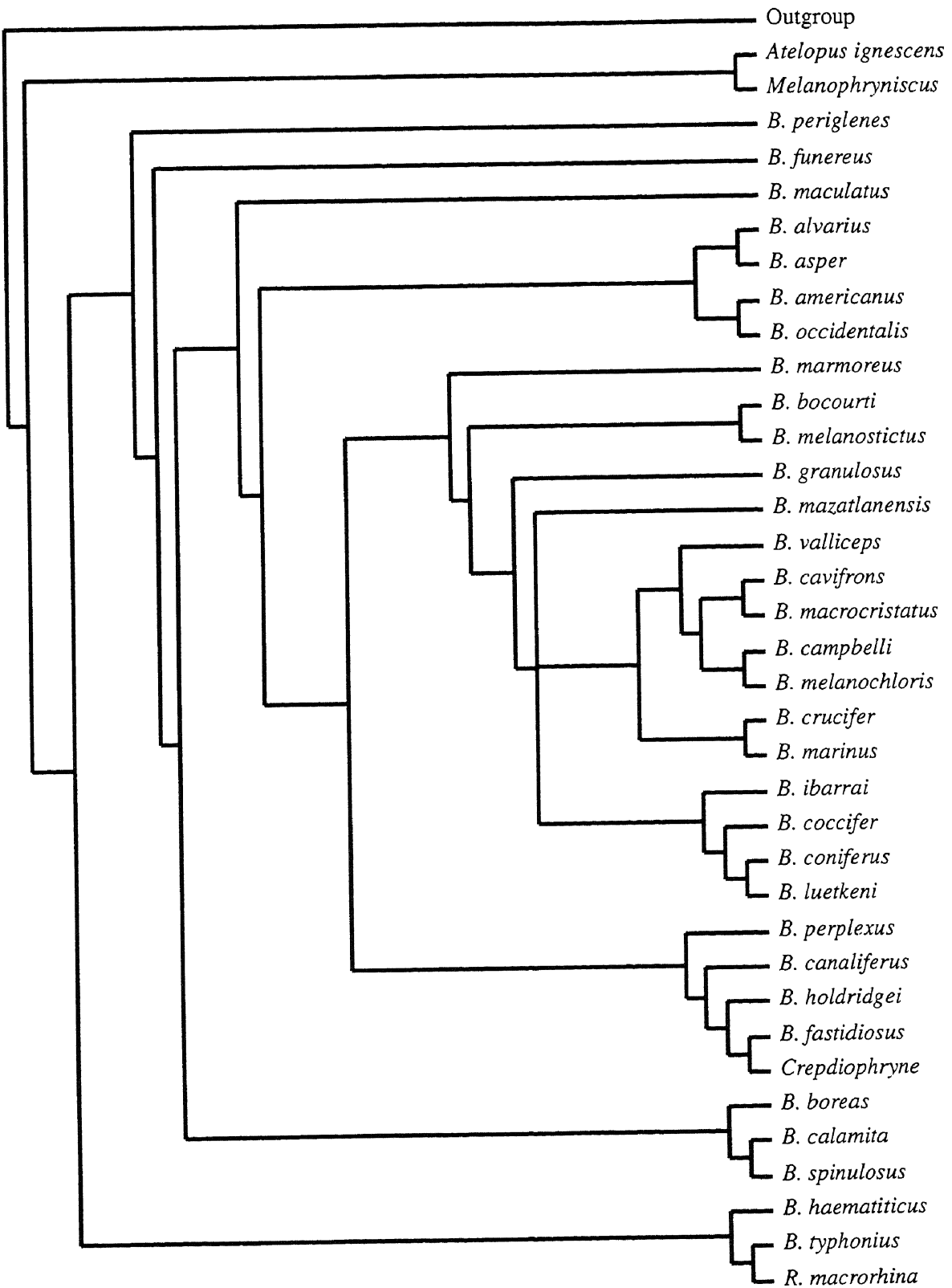


Fig. 5.12—Fundamental Tree 70, the only tree in Island 5.

