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Description of a New Species of *Bufo* from Northern Peru with Comments on Phenetic Groups of South American Toads (Anura: Bufonidae)

WILLIAM E. DUELLMAN AND RAINER SCHULTE

A new species of arboreal toad, *Bufo arborescandens*, is from the forested slopes of the Cordillera Central in northern Peru. It lacks cranial crests, tympana, and tarsal folds; an adult male has a cluster of keratinous spines on the thumb. This small toad is placed in the *Bufo veraguensis* group, for which a key to the species and summary of distributions are provided. Of the 51 species of *Bufo* recognized in South America, 45 are allocated to eight phenetically defined groups.

Se describe una nueva especie de sapo arbóreo, *Bufo arborescandens*, de las laderas boscosas de la Cordillera Central en el norte peruano. Esta especie carece de crestas craneales, tímpano, y pliegues tarsales. Un macho adulto tiene un grupo de espinas queratinizadas en el pulgar. Este pequeño sapo se incluye en el grupo *Bufo veraguensis*, para el cual se provee una clave de identificación y un resumen de las distribuciones de las especies. De las 51 especies de *Bufo* reconocidas de Suramérica, 45 especies se asignan a ocho grupos que se los define fenéticamente.

THE genus *Bufo* is nearly cosmopolitan and contains more than 200 species (Duellman and Trueb, 1986). Fifty-one species are recognized currently in South America, as updated from Frost (1985) by Duellman and Ochoa (1991) and Hoogmoed (1985, 1989, 1990). However, this number will increase substantially with the taxonomic recognition of many populations now recognized as "*Bufo typhonius*" (Hoogmoed, 1986, 1990).

The discovery of a distinctive new species of toad in northern Peru necessitated comparison of the new species with many taxa which have been associated with various phenetic groups of *Bufo*. The purposes of this paper are (1) to describe a new species of *Bufo*, (2) to assign the new species to a species group of *Bufo*, (3) to define phenetically the groups of *Bufo* in South America, and (4) to comment on, and provide a key to, the species in the *B. veraguensis* group.

MATERIALS AND METHODS

For the characteristics of the members of the species groups, we have relied on the literature plus examination of specimens in the Museum of Natural History, University of Kansas (KU). The osteological terminology follows Martin (1972), and the terminology for the cranial crests follows Cei (1980). The scheme for webbing

formulae is that of Savage and Heyer (1967) as modified by Myers and Duellman (1982).

DESCRIPTION OF NEW SPECIES

Toads of the genus *Bufo* generally are terrestrial or fossorial, but one of us (WED) has observed *B. coniferus* Cope at heights to 1.5 m above the ground on trees and vines in Costa Rica and Panama. Also, at least one of the diurnal species of "*B. typhonius*" (Linnaeus) commonly perches on low vegetation at night; another species of "*B. typhonius*" calls from pond fronds up to 2 m above the ground (Hoogmoed, 1986). Therefore, it came as a surprise to discover toads in large bromeliads 5-6 m above the ground in the Andes. Comparisons of specimens of this toad with samples of named species indicate that these arboreal toads are undescribed. We propose the name

Bufo arborescandens n. sp.

Fig. 1

Holotype.—KU 209395, an adult male, from a pass approx. 5 km (by road) NE of Mendoza (06°18'S, 77°27'W, elev. approx. 2400 m), Provincia Rodriguez de Mendoza, Departamento de Amazonas, Peru, obtained on 23 July 1981 by Rainer Schulte.

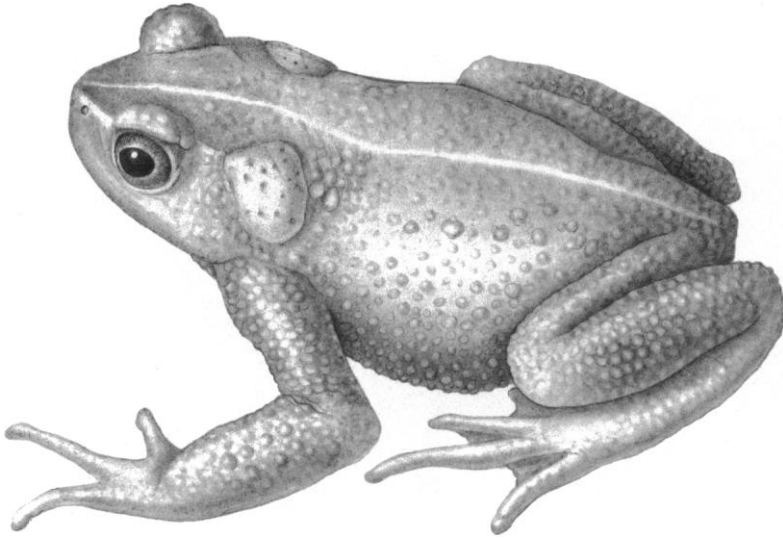


Fig. 1. Holotype of *Bufo arborescendens*, KU 209395, 35.3 mm SVL.

Paratype.—KU 209394, a gravid female, collected with the holotype.

Diagnosis.—A small *Bufo* attaining a snout-vent length (SVL) of 38.0 mm and having the following characters: (1) cranial crests absent; (2) tympanum and plectral apparatus absent; (3) parotoid glands ovoid, nearly as wide as long; (4) lateral row of inconspicuously enlarged tubercles on body; (5) ventral granules not enlarged or elevated; (6) tarsal fold absent; (7) fingers less than one-third and toes about one-half webbed; (8) no sexual dimorphism in dorsal tubercles; (9) thumb in breeding male bearing cluster of keratinous spines.

Bufo arborescendens is placed in the *B. veraguensis* group (see following section). It differs from all species in that group, except *B. fissipes* and *B. nesiotes*, in lacking cranial crests, and from all except *B. fissipes*, *B. quechua*, and *B. veraguensis* in lacking tympana. The parotoid glands are subtriangular in *B. arborescendens*, *B. leptoscelis*, and *B. veraguensis*, whereas they are ovoid in *B. nesiotes* and elongate in the other species. *Bufo arborescendens* is like *B. leptoscelis*, *B. nesiotes*, *B. quechua*, and *B. veraguensis* in having the fourth toe at least one-half webbed, whereas in *B. fissipes* the webbing is rudimentary, and in *B. inca* the webbing does not extend to the midlength of the fourth toe (Gallardo, 1961). The cluster of spines on the thumb in the breeding male of *B. arborescendens* immediately separates this spe-

cies from all other South American *Bufo*, except *B. corynetes*, which has large, elevated glands on the dorsum of the body and only basal webbing on the feet (Duellman and Ochoa, 1991).

Description.—For characters in which the two specimens differ, the condition in the male holotype is followed by that of the female paratype (in parentheses). Body robust; head slightly wider than long, width 33.1% (34.2%) of SVL, length 29.5% (31.6%) of SVL; snout subacuminate in dorsal view, truncate in profile; top of head flat; cranial crests absent; skin not coossified with underlying cranial bones; upper eyelid 61.7% (56.6%) of interorbital distance; internarial area flat; nostril not protuberant, directed laterally; canthus rostralis rounded; loreal region barely concave; lip rounded; shallow V-shaped notch at symphysis of upper jaw; eye-nostril distance 70.3% (71.1%) of eye length; tympanum absent (Fig. 1). Forelimb moderately long, robust; hand broad with short fingers; relative lengths of fingers 1 < 2 < 4 < 3; webbing fleshy, extending as fringe on lateral edges of fingers; webbing formula I1-2II2-3III3-2IV; tips of digits slightly expanded; palmar tubercle low, nearly round; pollical tubercle elongate, elevated; subarticular tubercles low, diffuse; thumb in male bearing 32 (right) and 33 (left) pointed, keratinous spines (Fig. 2). Hind limbs short with large feet; tibia length 34.0% (35.0%) of SVL; foot length 36.8% (43.4%) of SVL; tar-

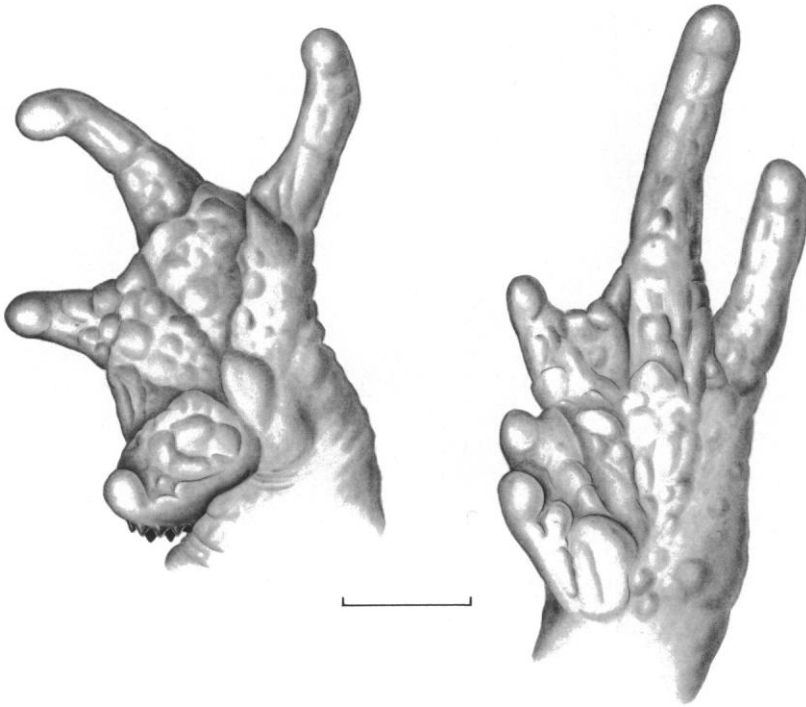


Fig. 2. Hand and foot of *Bufo arborescandens*, KU 209395. Line = 5 mm.

sal fold absent; outer metatarsal tubercle round, flat, barely elevated, much smaller than large, elevated, ovoid inner metatarsal tubercle; toes moderately long; relative lengths of toes $1 < 2 < 3 < 5 < 4$; webbing fleshy, extending as fringe on lateral edges of toes; webbing formula I1–I1I1–2III1½–3IV3–2V; tips of toes slightly expanded; subarticular tubercles low, round.

Skin on dorsum of head, body, and limbs bearing evenly distributed, small, round non-spinous tubercles; paratoid gland broadly ovoid, widest posteriorly, width about four-fifths length, descending onto side of head, with anterior edge broadly separated from eye; row of six slightly enlarged tubercles dorsolaterally on body extending from point above axilla to groin; enlarged glands absent on limbs; row of small conical tubercles on margins of upper and lower jaws. Skin on throat smooth with scattered small tubercles; skin on other ventral surfaces granular. Anal opening not protuberant, directed posteriorly at upper level of thighs.

Choanae small, ovoid; vomerine odontophores, maxillary, premaxillary, and vomerine teeth absent; tongue elongately ovoid, twice as

long as wide, widest posteriorly, free behind for about one-half its length. In male, vocal slit extending from posterolateral base of tongue toward angle of jaw; vocal sac single, median, subgular.

Color in preservative: In male holotype, dorsum reddish brown with narrow, cream, middorsal line; venter pale tan; cream stripe on midventral surface of tarsus; irregular small brown blotches on ventrolateral surface of forearm. In female paratype, dorsum uniform pale reddish tan (middorsal line absent); sides of head and flanks brown; narrow cream stripe extending from posterior corner of eyelid to groin; venter cream with brown spots on posterior part of belly and ventral surfaces of hind limbs; margins of lower jaw with small brown spots; anterior surfaces of the forelimbs brown.

Color in life: Dorsum reddish brown; pale yellow middorsal stripe in holotype.

Measurements (in mm): Measurements of male holotype are followed by those of female paratype. SVL 35.3, 38.0; tibia length 12.0, 13.3; foot length 13.0, 16.5; head length 10.4, 12.0; head width, 11.7, 13.0; interorbital distance 4.7,

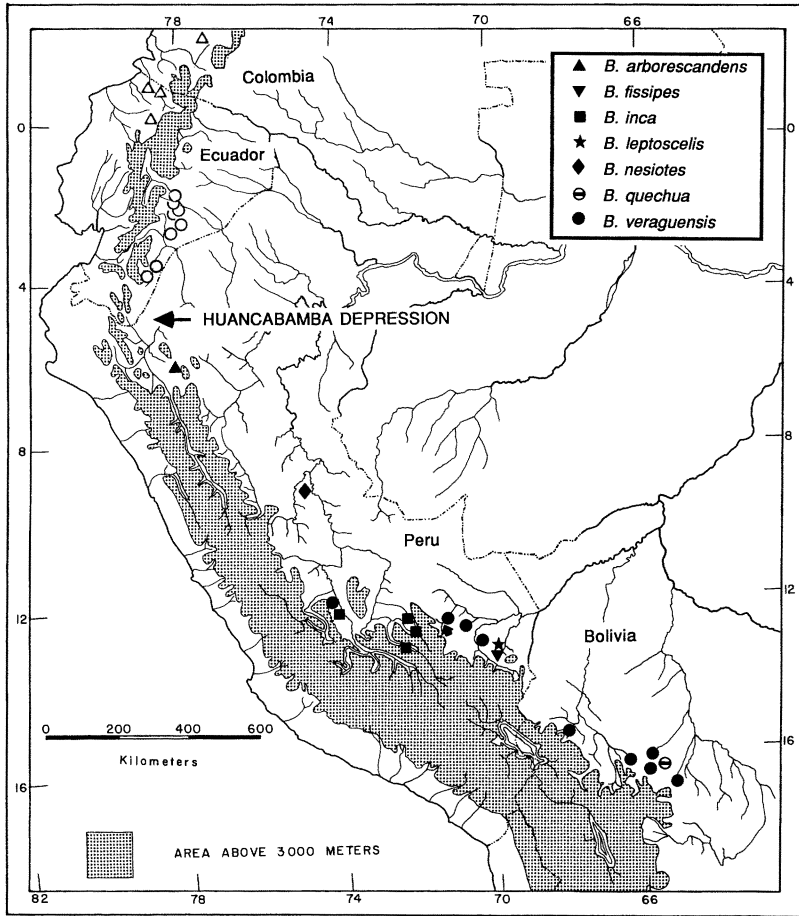


Fig. 3. Western South America showing distribution of species in the *Bufo veraguensis* group, based on localities listed in the literature (principally Gallardo, 1961, and Savage, 1969) and specimens in the Museum of Natural History, University of Kansas, Lawrence, Kansas. The arrow in southern Peru indicates the locality where *B. inca* and *B. veraguensis* occur sympatrically. Open triangles in western Ecuador indicate known localities for *Andinophryne* (Hoogmoed, 1985, 1989). Circles in eastern Ecuador are localities for *Rhampophryne festae* (updated from Trueb, 1971). Other species of *Rhampophryne* occur in northern Colombia.

5.3; upper eyelid width 2.9, 3.0; eye-nostril distance 2.6, 2.7; eye length 3.7, 3.8; paratoid gland length 4.9, 4.8; paratoid gland width 4.0, 4.4.

Distribution and ecology.—*Bufo arborescandens* is known only from the type locality in the northern part of the Cordillera Central (Fig. 3). Three principal Andean cordilleras exist farther south in Peru. The western Cordillera Occidental is separated from the Cordillera Central by the Río Marañón, and the Cordillera Central is separated from the eastern Cordillera Oriental by the Río Huallaga. At the latitude of the type

locality, the Cordillera Central is the principal eastern-most cordillera, because the northern extent of the Cordillera Oriental lies farther south.

The type locality is a ridge overlooking the cultivated valley of Mendoza and is on the south side of the road from Chachapoyas to Mendoza. The toads were found by day after slender, smooth-barked trees having diameters of 10–20 cm were felled. Large, arboreal bromeliads having diameters of 50–80 cm were in the crowns of the trees 5–6 m above the ground. Both individuals of *B. arborescandens* were found

in one large bromeliad. Specimens of *Eleutherodactylus schultzei* were found in the same bromeliad and in other bromeliads on the ridge (Duellman, 1990).

Etymology.—The specific name is derived from the Latin *arbor* meaning tree and the Latin *scando* meaning climb. The name alludes to the arboreal habits of the species.

Remarks.—Savage (1969, 1972) noted that two species of *Bufo* described by Schmidt (1857) purportedly from Panama probably had incorrect locality data. Savage (1969) referred *B. veraguensis* to toads previously called *B. ockendeni* Boulenger and known only from southern Peru and Bolivia. Savage (1972) suggested that *B. simus* probably is from Peru or Bolivia. Considering the possibility that *B. simus* might apply to the new species described here, we compared our specimens with the description of two syntypes of *B. simus* (both juveniles) provided by Savage (1972). The syntypes of *B. simus* differ from *B. arborescendens* (characters in parentheses) by having (1) small spicules and scattered round tubercles that tend to form longitudinal series on the dorsum (uniform nonspinous tubercles); (2) a lateral row of enlarged tubercles (dorsolateral row of inconspicuously enlarged tubercles); (3) first and second fingers equal in length (first finger shorter than second); and (4) a low tarsal fold (tarsal fold absent).

PHENETIC GROUPS OF SOUTH AMERICAN *BUFO*

Tihen's (1962) initial attempt to characterize species groups of New World *Bufo* based on osteological features was expanded by Martin (1972). External characters were used by Gallardo (1962, 1965) and Cei (1968, 1972) in defining groups of *Bufo* in South America. Based on data provided by these authors, Hoogmoed (1990), and our own observations, eight phenetic groups of *Bufo* can be recognized in South America. In the following accounts of the species groups, the characters are listed numerically for easy comparison. Most species are assigned to groups by a combination of osteological and external characters. However, when the osteological features are not known, only external characters are used. The distributions of most groups were mapped by Cei (1968).

The eight groups contain 45 of the 51 recognized species. The other six species are poor-

ly known or not associated with known populations:

Bufo diptychus Cope, 1862, has no known type specimen, and the name is not associated with any known populations, although Frost (1985) listed the distribution as "Peru and Paraguay."

Bufo gnustae Gallardo, 1967, is known from a single specimen from Río Santiago, Provincia Jujuy, Argentina. Although Gallardo (1967) assigned it to the *B. ockendeni* (= *veraguensis*) group, it differs notably from other members of that group by having large, rectangular parotoid glands, large tubercles on the dorsum, and an orbitotympanic crest.

Bufo hypomelas Boulenger, 1913, is known only from juveniles from the Pacific versant of Colombia and Ecuador. According to Hoogmoed (1989), the dorsum is smooth, lateral enlarged tubercles are absent, the parotoid glands are narrow and elongate, the tympanum is visible but indistinct, the snout is truncate and projecting beyond the mouth, and the first finger is shorter than the second. Unlike all other neotropical *Bufo*, the dorsum is boldly patterned with white circles and vermiculations.

Bufo ocellatus Günther, 1859 [1858], was placed in the synonymy of *B. typhonius* by Boulenger (1882). Cochran (1955) resurrected the name and assigned to it two specimens from Minas Gerais, Brazil, the only specimens other than the holotype, which is a stuffed skin. Cei (1968) provided no reasons for his allocation of *B. ocellatus* to the *B. guttatus* group. Cochran's (1955) description and illustrations of the specimens from Minas Gerais do not fit the definition of that group.

Bufo schneideri Werner, 1894, named from "Paraguay," may be an older name for *B. paracnemis* Lutz, 1925 (Gallardo, 1962).

Bufo simus Schmidt, 1857, was based on juveniles purportedly from western Panama. Savage (1972) studied two of the syntypes and concluded that the name is not applicable to any known species in Costa Rica or Panama. He suggested that the specimens may have been collected in Peru or Bolivia, as was the case of *B. veraguensis* Schmidt, 1857; the latter name is applicable to toads in southern Peru formerly known as *B. ockendeni* Boulenger, 1902 (Savage, 1969).

Another nominal species has been reported from South America. *Bufo intermedius* Günther, 1859 [1858], is known only from four syntypes purportedly from the Andes of Ecuador (type

description) or from Guayaquil (label in jar), but it is not included in the South American fauna. Hoogmoed (1989) studied the types and concluded that the specimens probably originated from Mexico or Central America and are representatives of the *B. valliceps* group.

Bufo crucifer Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal partially roofed; (3) exostosing of dermal roofing bones moderate; (4) all cranial crests present, elevated slightly, smooth; parietal, preocular, and post-orbital crests weak; (5) skin on dorsum smooth with scattered low tubercles; (6) lateral row of enlarged tubercles present or absent; (7) parotoid glands moderate, elongate; (8) tympanum visible; (9) snout subtriangular in dorsal view, truncate in profile; (10) first finger longer than second.

Content.—One species: *B. crucifer* Wied-Neuwied, 1821.

Distribution.—Bahia, Brazil, to Misiones, Argentina, and eastern Paraguay.

Comment.—Osteologically, *B. crucifer* is most like members of the *B. marinus* group, from which it differs by having relatively low cranial crests, comparatively smooth dorsal skin, and smaller parotoid glands.

Bufo granulosus Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely roofed; (3) exostosing of dermal roofing bones moderate; (4) all cranial crests present, varying from low and granular to moderately elevated; (5) skin on dorsum with many small, keratinous-tipped tubercles; (6) lateral row of enlarged tubercles absent; (7) parotoid glands small to moderately large, round to subtriangular, granular; (8) tympanum visible; (9) snout round to subtriangular in dorsal view, round and protruding slightly in profile; (10) first finger shorter than second.

Content.—Four species: *B. dorbignyi* Duméril and Bibron, 1841, *B. fernandesi* Gallardo, 1957, *B. granulosus* Spix, 1824, *B. pygmaeus* Myers and Carvalho, 1952.

Distribution.—Discontinuous from central Panama through much of South America to Provincia Buenos Aires in northeastern Argentina; absent from much of the Amazon Basin.

Comment.—All of the species listed were recognized as subspecies of *B. granulosus* by Gallardo (1965). Evidence exists that several other nominal subspecies deserve specific recognition (Frost, 1985).

Bufo guttatus Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely roofed; (3) exostosing of dermal roofing bones weak; (4) supraorbital, canthal, and parietal crests present, low, smooth; (5) skin on dorsum smooth or with scattered low warts; (6) lateral row of enlarged tubercles absent (present in *B. caeruleostictus*); (7) parotoid glands moderate in size, smooth, ovoid to elongate; (8) tympanum visible; (9) snout round in dorsal view, truncate in profile; (10) first finger longer than second.

Content.—Six species: *B. anderssoni* Melin, 1941, *B. blombergi* Myers and Funkhouser, 1951, *B. caeruleostictus* Günther, 1859, *B. glaberrimus* Günther, 1868, *B. guttatus* Schneider, 1799, *B. haematiticus* Cope, 1862.

Distribution.—Nicaragua to Ecuador west of the Andes; Guianan region to upper Amazon Basin.

Comment.—The species in this group are unique among neotropical *Bufo* in having an omosternum. Cei (1968) included *B. manicorensis* Gallardo, 1961, and *B. ocellatus* Günther 1859 [1858] in the *B. guttatus* group. The former is now considered to be a synonym of *B. granulosus* (Hoogmoed, 1990), and the position of the latter is questionable. Hoogmoed (1989) added *B. caeruleostictus* to the group.

Bufo marinus Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely roofed; (3) exostosing of dermal roofing bones pronounced; (4) all cranial crests present, elevated, keratinized or not; (5) skin on dorsum with large and small tubercles; (6) lateral row of enlarged tubercles absent; (7) parotoid glands large, ovoid or elongate; (8) tympanum distinct;

(9) snout round in dorsal view, truncate in profile; (10) first finger longer than second.

Content.—Six species: *B. arenarum* Hensel, 1867, *B. ictericus* Spix, 1824, *B. marinus* (Linnaeus, 1758), *B. paracnemis* Lutz, 1925, *B. poeppigii* Tschudi, 1845, *B. rufus* Garman, 1877.

Distribution.—Mexico and Central America to northern Peru on the Pacific lowlands and throughout northern South America and the Amazon Basin east of the Andes (*B. marinus*). The other species occur on the eastern slopes of the Andes from Peru to Bolivia and in the lowlands of Bolivia and eastern Brazil to central Argentina.

Comment.—Cei (1980) recognized *B. arenarum* and *B. rufus* in a group separate from the *B. marinus* group. Henley (1985) examined a limited number of specimens identified as *B. marinus* and *B. poeppigii* and concluded that the latter was a subspecies of the former. Numerous specimens at the University of Kansas from the Andean slopes of Peru and Bolivia are quite distinctive and are allocated to *B. poeppigii*, a species distinct from *B. marinus* in the adjacent lowlands.

Bufo spinulosus Group

Characteristics.—(1) Frontoparietals narrow, fused with prootics; (2) occipital canal not roofed; (3) exostosing of dermal roofing elements weak; (4) cranial crests low or absent; (5) texture of skin on dorsum sexually dimorphic, nearly smooth in females, spinous in males; (6) lateral row of enlarged tubercles absent; (7) parotoid glands small, round to ovoid; (8) tympanum distinct or absent (*B. cophotis*, *B. corynetes*, and *B. variegatus*); (9) snout round in dorsal view, truncate or round in profile; (10) first finger longer than second.

Content.—Thirteen species: *B. achalensis* Cei, 1972, *B. arequipensis* Vellard, 1959, *B. arunco* Molina, 1782, *B. atacamensis* Cei, 1961, *B. cophotis* Boulenger, 1900, *B. corynetes* Duellman and Ochoa, 1991, *B. flavolineatus* Vellard, 1959, *B. limensis* Werner, 1901, *B. rubropunctatus* Guichenot, 1843, *B. spinulosus* Wiegmann, 1834, *B. trifolium* (Tschudi, 1845), *B. variegatus* (Günther, 1870), *B. vellardi* Leviton and Duellman, 1978.

Distribution.—Andes from southern Ecuador to central Chile and Argentina, mesic habitats on Pacific lowlands from northern Peru to central Chile, and austral forests of southern Argentina and Chile.

Comments.—Cei (1968, 1972) placed *B. chilensis* (= *B. arunco*; Ortiz and Lescure, 1989) in this group. Although this species possesses the external characters of the group, it differs osteologically. The frontoparietals are narrow; the occipital canal is partly or completely roofed, and cranial crests are present. Martin (1972) suggested that the addition of dermal bone is secondary in *B. arunco*. The position of this species remains to be resolved. *Bufo corynetes* and *B. variegatus* are tentatively placed in the *B. spinulosus* group (Duellman and Ochoa, 1991); both have the cranial characters of the group, but these two species differ from all other South American *Bufo* by having longitudinal series of enlarged glands on the dorsum. The taxonomic status of several subspecies of *B. spinulosus* recognized by Vellard (1959) is questionable (Cei, 1972).

Bufo typhonius Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely roofed; (3) exostosing of dermal roofing bones weak; (4) supraorbital, parietal, postorbital, and canthal crests prominent; supratympanic crest commonly expanded dorsolaterally; (5) skin on dorsum smooth or with small, scattered tubercles; (6) lateral row of enlarged tubercles present; (7) parotoid glands moderate in size, elongate; (8) tympanum distinct; (9) snout pointed in dorsal view, acuminate and protruding anteriorly in profile; (10) first finger equal to, or longer than, second.

Content.—Seven species: *B. ceratophrys* Boulenger, 1882, *B. dapsilis* Myers and Carvalho, 1945, *B. iserni* (Jiménez de la Espada, 1875), *B. nasicus* Werner, 1903, *B. roqueanus* Melin, 1941, *B. sternosignatus* Günther, 1859 [1858], *B. typhonius* (Linnaeus, 1758).

Distribution.—Central Panama to Ecuador on Pacific versant; northern South America (exclusive of llanos of Colombia and Venezuela), Amazon Basin, and southeastern Brazil.

Comment.—Hoogmoed (1986, 1990) noted that “*B. typhonius*” was a complex of many species and indicated that populations now referred to that species may not be closely related.

Bufo valliceps Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely roofed; (3) exostosing of dermal roofing bones pronounced; (4) all cranial crests present; (5) skin on dorsum bearing many tubercles; (6) lateral row of enlarged tubercles present; (7) parotoid glands small, round to ovoid; (8) tympanum distinct; (9) snout round in dorsal view, truncate in profile; (10) first finger longer than second.

Content.—One species in South America: *B. confiferus* Cope, 1862.

Distribution.—Costa Rica and Panama and the Pacific versant of South America to northern Ecuador.

Comment.—Eleven other species are widely distributed from south-central United States through Mexico and Central America.

Bufo veraguensis Group

Characteristics.—(1) Frontoparietals broad, fused with prootics; (2) occipital canal completely closed; (3) exostosing of dermal roofing bones weak; (4) supraorbital and parietal crests weak in some species; all crests absent in others; (5) skin on dorsum bearing small tubercles; (6) lateral row of enlarged tubercles present in some species; (7) parotoid glands moderately small, ovoid, subtriangular, or elongate; (8) tympanum distinct or absent; (9) snout subacuminate or round in dorsal view, truncate or round in profile; (10) first finger shorter than (*B. arborescandens* and *B. nesiotus*) or longer than second (other species).

Content.—Seven species: *B. arborescandens* n. sp., *B. fissipes* Boulenger, 1903, *B. inca* Stejneger, 1913, *B. leptoscelis* Boulenger, 1912, *B. nesiotus* Duellman and Toft, 1979, *B. quechua* Gallardo, 1961, *B. veraguensis* Schmidt, 1857. Hoogmoed (1990) suggested that *B. inca* and *B. leptoscelis* are synonyms of *B. veraguensis*; however, spec-

imens referable to *B. inca* and *B. veraguensis* occur sympatrically in southern Peru.

Distribution.—Amazonian slopes of Andes in Peru and Bolivia.

Comment.—This group was recognized as the *B. ockendeni* group by Gallardo (1961). Cei (1968, 1972) and Frost (1985) included many of these species in the *B. typhonius* group. The tadpole of only one species, *B. veraguensis*, is known (Cadle and Altig, 1991). The large, ventral mouth and oral sucker of this lotic tadpole distinguish it from the tadpoles of all other *Bufo*.

SYNOPSIS OF THE *BUFO VERAGUENSIS* GROUP

The small species of toads assigned to the *B. veraguensis* group can be identified by the following key:

1. Cranial crests absent 2
 Cranial crests present 4
2. Row of enlarged dorsolateral tubercles present *B. arborescandens*
 Row of enlarged dorsolateral tubercles absent 3
3. Tympanum not visible; webbing on foot rudimentary *B. fissipes*
 Tympanum visible; webbing on foot extending to midlength of fourth toe *B. nesiotus*
4. Tympanum not visible 5
 Tympanum visible 6
5. Supraorbital crest absent; tarsal fold absent; parotoid gland elongate *B. quechua*
 Supraorbital crest present; tarsal fold consisting of single row of granules; parotoid gland subtriangular *B. veraguensis*
6. Supraorbital crest present; tarsal fold consisting of single row of granules *B. inca*
 Supraorbital crest absent; tarsal fold absent *B. leptoscelis*

Members of the *B. veraguensis* group occur in the Andes from northern Peru (*B. arborescandens* in Departamento de Amazonas) to central Bolivia (Fig. 3). Most species (*B. fissipes*, *B. inca*, *B. leptoscelis*, *B. quechua*, *B. veraguensis*) occur on the forested Amazonian slopes of the Andes in southern Peru and adjacent Bolivia. *Bufo nesiotus* is known only from the isolated Serranía de Sira, east of the principal chain of the Andes in central Peru (Duellman and Toft, 1979). The type locality of *B. arborescandens* is about 600 km northwest of the next northernmost record

for a member of the group, the Serranía de Sira. The forested slopes of the Andes in the intervening area have been poorly collected, and additional populations of named species or new species are expected there.

The distribution of the group probably does not extend much farther north than the area in which *B. arborescandens* is known, because the Andean chain is interrupted by the Huanca-bamba Depression, a major barrier to north-south distributions in the Andes (Duellman, 1979). Furthermore, to the north of the depression the *B. veraguensis* group seems to be replaced ecologically by *Rhampophryne* (Trueb, 1971) and *Andinophryne* (Hoogmoed, 1985) (Fig. 3).

Most specimens of the *B. veraguensis* group have been collected in cloud forests at elevations of 1280–2600 m. Only at one locality in the Cosñipata Valley in southern Peru have two species been found sympatrically—*B. inca* and *B. veraguensis*. Possibly *B. fissipes* and *B. leptoscelis* also are sympatric; the type locality of the former is “Santa Domingo, Carabaya, S. E. Peru, 6000 feet” (Boulenger, 1903), and that of the latter is “Santo Domingo, Carabaya, S. E. Peru, 6500 feet” (Boulenger, 1912).

In addition to specimens and localities listed by Duellman and Toft (1979), Gallardo (1961), and Savage (1969), the following specimens are in the Museum of Natural History, the University of Kansas:

Bufo inca: Peru: Cuzco: Machu Picchu, 2000 m, KU 136035–41; 4 km WSW Santa Isabel, 1700 m, KU 139050–52, 139431 (young).

Bufo veraguensis Bolivia: La Paz: Sacramento Alto, 8 km N Chuspipata, 2575 m, KU 197082. Peru: Ayacucho: Tutumbaro, Río Piene, 1840 m, KU 163092. Cuzco: 2 km WSW Santa Isabel, 1580 m, KU 139132; 4 km WSW Santa Isabel, 1700 m, KU 139115–31, 139437 (young), 163082–92, 164084 (skeleton).

DISCUSSION

The foregoing grouping of South American *Bufo* is strictly phenetic. The great similarities among species within some groups (e.g., the *B. guttatus* and *B. spinulosus* groups) suggest that these may be monophyletic.

Cannatella (1986) hypothesized phylogenetic relationships of the neotropical genera of bufonids. Three genera were not included in his analysis—*Peltophryne* Fitzinger, 1843, from the Antilles; *Andinophryne* Hoogmoed, 1985, from

Ecuador and Colombia; and *Atelophryniscus* McCranie, Wilson, and Williams, 1989, from Honduras. Cannatella (1986) suggested that the presence of cranial crests and parotoid glands is derived, and therefore he concluded that the so-called bufonines—*Bufo*, *Crepidophryne*, *Peltophryne*, and *Rhampophryne* (all of which have these characters)—are more closely related to one another than any is to other neotropical bufonids. These are the so-called atelopodines (*Atelopus*, *Dendrophryniscus*, *Frostius*, *Melanophryniscus*, *Oreophrynella*, and *Osornophryne*), all of which have partial or full fusion of the epicoracoid cartilages in the pectoral girdle. The bufonines have arciferal pectoral girdles, but in *Rhampophryne* the epicoracoids barely overlap (Trueb, 1971). Combinations of characters found in *Andinophryne*, *Atelophryniscus*, and some species in the *B. veraguensis* group indicate that more homoplasy exists than has been recognized previously.

According to Hoogmoed (1985), *Andinophryne* has parotoid glands (a bufonine character) but has partially fused epicoracoids and lacks cranial crests (atelopodine characters). *Andinophryne* is like most *Bufo* in having a distinct tympanum, and it shares the presence of a lateral row of enlarged tubercles with all members of the *B. typhonius* and *B. valliceps* groups and some members of the *B. veraguensis* group.

McCranie et al. (1989) noted that *Atelophryniscus* has an arciferal pectoral girdle, cranial crests, parotoid glands, and a lateral row of enlarged tubercles (all bufonine characters) but that the absence of a tympanum (the columella is present) and the gastromyzophorous type of tadpole are shared only with *Atelopus*. Subsequently, Cadle and Altig (1991) described a gastromyzophorous type of tadpole of *B. veraguensis*.

The monophyly of the *B. veraguensis* group is highly suspect. Four species lack tympana, a condition found in only three other species in South America (*B. cophotis*, *B. corynetes*, and *B. variegatus*) and six montane species in Middle America (*B. bocourti*, *B. fastidiosus*, *B. holdridgei*, *B. periglenes*, *B. peripatetes*, and *B. tacanaensis*). The cranial crests are reduced (four species) or absent (three species); the absence of cranial crests is shared with *Andinophryne* and the atelopodine genera. The presence of a lateral row of enlarged tubercles in five of the seven species is shared with species in the *B. typhonius*, *B. crucifer*, and *B. valliceps* groups and the species of *Andinophryne* and *Atelophryniscus*. The tadpole

of *B. veraguensis* shares oral disc characters and a ventral sucker with tadpoles of *Atelophryniscus* and *Atelopus*.

Until adequate material is available for skeletal preparations of the species in the *B. veraguensis* group, the osteological characters cannot be assessed. A thorough phylogenetic study of neotropical *Bufo* is needed before the generic relationships can be analyzed.

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Systematics of the *Acanthophtalmus kuhlii* Complex (Teleostei: Cobitidae), with the Description of a New Species from Sarawak and Brunei

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The *Acanthophtalmus kuhlii* complex from southeast Asia is found to contain three species. A description of meristic, morphometric, and color characters as well as sexual dimorphism is given for the genus and for each of the three species. In the past, lack of such descriptions has resulted in the recognition of several questionable nominal taxa. From the 21 characters examined, 14 were subjected to principal component and discriminant function analyses. Of the nine nominal species and subspecies associated with *A. kuhlii*, only two remain valid, *A. kuhlii* and *A. cuneovirgatus*. The third species of the complex, *A. agmus* n. sp., is described from northern Sarawak and Brunei. *Acanthophtalmus cuneovirgatus* has a disjunct distribution, occurring in southern Thailand, West Malaysia, and Java, and is easily distinguished from other species of the complex by the presence of nasal barbels. *Acanthophtalmus kuhlii* and *A. agmus* are most similar, but the latter is recognized using a combination of vertebral counts and morphometric features. *Acanthophtalmus agmus* has a very irregular color pattern in adults, unlike either of the other two species. A key to the species of the *A. kuhlii* complex is presented, and the origins of the new species *A. agmus* are hypothesized.

THE *Acanthophtalmus kuhlii* complex, including what are commonly known as the banded kuhli loaches, has been studied by various ichthyologists (Fraser-Brunner, 1940; Hora, 1941; Tweedie, 1956), but a thorough examination of specimens from their entire geograph-

ic range has never been achieved. This has led to the recognition of several questionable nominal taxa at the species and subspecies levels. New taxa were described from very few specimens, and comparative studies with type specimens of other species were rarely conducted.