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TAXONOMY OF THE *ATELOPUS IGNESCENS* COMPLEX (ANURA: BUFONIDAE): DESIGNATION OF A NEOTYPE OF *ATELOPUS IGNESCENS* AND RECOGNITION OF *ATELOPUS EXIGUUS*

LUIS A. COLOMA[1], STEFAN LÖTTERS[2], AND ANTONIO W. SALAS[3]

[1]*Pontificia Universidad Católica del Ecuador, Museo de Zoología, Av. 12 de Octubre y Roca, Apdo. 17-01-2184, Quito, Ecuador*
[2] *Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany*
[3]*Asociación de Ecología y Conservación (ECCO), Apdo. 0359, Lima 18, Perú*

ABSTRACT: We review several populations of *Atelopus* from high altitudes of Ecuador formerly allocated to *Atelopus ignescens*. For *A. ignescens*,we designate a neotype and provide data on variation and distribution. *Atelopus ignescens* is a species restricted to the northern Andes, and it is characterized by the unique presence of a patch of brown spiculae and coni on the gular and pectoral regions of females. We also recognize *A. exiguus* as a valid species from the Andean highlands of southern Ecuador and describe the lectotype, call, and tadpole. *Atelopus exiguus* is diagnosed by characters of external morphology and coloration in life. Some specimens of *A. exiguus* lack Toe I, an unusual feature that deserves further research.

Key words: Amphibia; Bufonidae; *Atelopus ignescens; Atelopus exiguus;* Taxonomy; Distribution; Tadpole; Vocalization; Ecuador

ACCORDING to Rivero (1963) and Peters (1973), one of the most common and widespread amphibians at high elevations in Ecuador is *Atelopus ignescens* (Cornalia, 1849). Peters (1973) concluded that *A. ignescens* ranges from Tulcán (Provincia Carchi) south to the region of southern Cuenca (Provincia Azuay). Several authors have suggested that *A. ignescens* may actually be a complex of species (Gray, 1983; Lötters, 1996*a*,*b*). Thus, this complex comprises several populations from the inter-Andean valleys and higher parts of the major Andean Cordilleras in Ecuador and southern Colombia (Frost, 1985). According to Gray (1983), this remarkable geographical range of about 500 km (maximum airline distance) for a high-altitude species is the result of unsolved taxonomic problems. These problems include (1) the type material of *A. ignescens* is lost (Conci, 1967; Frost, 1985; Lötters, 1996*b*), (2) status of *Phryniscus laevis* var. *exigua* Boettger, 1892 (usually considered a synonym of *A. ignescens* Peters, 1973) is in need of resolution, (3) additional collections and data have revealed the presence of undescribed species (Coloma, 1997), and (4) phylogenetic relationships among putative species have not been analyzed. The purpose of this paper is to address the two former problems.

MATERIALS AND METHODS

Specimens examined in addition to the type material of *Atelopus exiguus* (see below) are listed in Appendix I. Museum acronyms follow Leviton et al. (1985), Frost (1985), and Duellman (1993).

Other abbreviations used throughout the text are: SVL (snout–vent length), TIBL (tibia length), FOOT (foot length), HLSQ (head length from the squamosal), HLEX (head length from the exoccipital), IOD (interorbital distance), HDWD (head width), EYDM (eye diameter), EYNO (eye to nostril distance), ITNA (internarial distance), RDUL (length of flexed forearm), HAND (hand length), THBL (thumb length) and SW (sacrum width). Measurements of frogs were taken following Gray and Cannatella (1985). When comparing SVL of *Atelopus exiguus* and *A. ignescens*, data were log transformed and a Student's unpaired *t*-test was used to assess the significance of differences between means.

We determined sexual maturity by the

presence of eggs or convoluted oviducts in females and by the presence of nuptial excrescenses covering the dorsum of Finger I in males.

Following Duellman and Trueb (1986), we use spiculae to refer to pustular warts and coni to refer to spiculae with pointed projections. Measurements of frogs and tadpoles were taken (to the nearest 0.1 mm) with MAX-CAL® digital calipers; when necessary, measurements were made under a dissecting microscope. Webbing formulae are indicated in the manner described by Savage and Heyer (1969), with modifications suggested by Myers and Duellman (1982) and Savage and Heyer (1997). The webbing formula is a subjective approximation, because in some cases the distinction between webbing and lateral fringes is ambiguous. In such cases, a range is indicated when a single specimen is described (e.g., a neotype). Within the diagnoses, a range also indicates the intraspecific variation recorded. Drawings were made using a camera lucida attached to a Wild M3B microscope.

Tadpoles of *Atelopus exiguus* were referred provisionally to this species because they were collected near the type locality—where this is the only species of *Atelopus* known to occur. Ecological distributions of each species follow the Ecuadorian life zones defined by Cañadas-Cruz (1983). Climatological data for the life zones are also taken from Cañadas-Cruz (1983).

Recordings were made with a Sony TCD5M tape recorder and a Sony ECM 959 microphone. Two calls were analyzed from a copy (deposited in the tape archive of QCAZ) of the original recording. Calls were edited and analyzed using Canary 1.1. (Charif et al., 1993) and were input in a frequency range of 44.1 kHz. Acoustic terminology follows Heyer et al. (1990).

RESULTS

Designation of a Neotype of Atelopus ignescens *(Cornalia, 1849)*

Gray (1983) recognized an "*Atelopus ignescens* complex" for populations from the Andes of southern Colombia and northern Ecuador. Within this complex, he distinguished a population, he called "Core", from the type locality of *A. ignescens* (in the environs of Latacunga, Provincia de Cotopaxi) and its vicinity. Because the type material of *A. ignescens* is lost (Conci, 1967; Frost, 1985; Lötters, 1996*b*), and in order to facilitate comparisons among similar species and populations, a neotype is essential. We designate a neotype for *A. ignescens* as a first step to resolve the systematics of the *A. ignescens* complex. We follow guidelines of article 75 of the International Code of Zoological Nomenclature (1985) and present data on variation. The locality for the neotype (20 km airline SE of Latacunga) is chosen because it is located near the original type locality, there is a well preserved series of specimens from this locality, and these specimens fit well with Cornalia's (1849) description. A neotype from Latacunga cannot be designated because the type locality is now degraded ecologically and that population is now extinct.

Atelopus ignescens (Cornalia, 1849)

Phryniscus ignescens Cornalia, 1849:316. Types lost (originally at MSNM). From "in locis humidus circa Latacunga prope Quito;" restated as Latacunga (2771 m), Provincia de Cotopaxi, Ecuador, by Peters (1955).

Phryniscus laevis Günther, 1859:43. Five syntypes: BM 55.6.26.7–8 from "Panama," BM 47.12.28.45 from "Quito," BM 44.6.3.16 from "Chili." Synonymy fide Jiménez de la Espada (1875).

Phrynidium laeve Cope, 1867:196.

Atelopus laevis Cope, 1868:117.

Atelopus ignescens Jiménez de la Espada, 1875:139.

Atelopus carinatus Andersson, 1945:15. Holotype: NHRM 1909 from "Eastern Ecuador." Synonymy fide Rivero (1963).

Atelopus ignescens ignescens Rivero, 1965: 137.

Neotype.—QCAZ 702, adult female, from approximately 20 km (airline) southeast of Latacunga, on road from San Miguel de Salcedo to Lagunas de Anteojos and toward the east, 01° 01′ S, 78° 25′ W,

approximately between 3200–3800 m, at the border between Provincias de Cotopaxi and Napo, Ecuador; obtained on 29 November 1987 by Giovanni Onore and Luis A. Coloma.

Diagnosis.—(1) A large *Atelopus* (SVL in males 34.2–41.4, $\bar{x}$ = 37.8, n = 15; females 35.6–48.2, $\bar{x}$ = 42.5, n = 15); (2) limbs short (tibia length/SVL = 0.309–0.399, n = 30); (3) phalangeal formula for hand 2-2-3-3; (4) foot webbing formula **I**(1/2–1)—(0–2)**II**(1/2–1)—(1–3)**III**(1–3)—(2–3)**IV**(2–3)—1**V**; (5) snout nearly truncate, slightly protruding beyond lower jaw; (6) tympanic membrane, tympanic annulus, and stapes absent; (7) dorsal surfaces bearing few warts, (8) black coni (gray in preservative) on forelimbs, flanks, and dorsal surfaces of thighs; (9) vertebral neural processes inconspicuous; (10) dorsum uniform black; (11) venter yellow to bright orange and red in life (cream, pale yellow to uniformly brown in preservative); (12) gular-pectoral region bearing spiculae and coni.

Atelopus ignescens may be readily distinguished from all known species in the genus (based on specimens examined and listed in Coloma, 1997) by having a patch of brown spiculae and coni on gular and pectoral region. This patch is more prominent in females than in males. The only other *Atelopus* that possess nearly uniform black dorsums and that can be confused with *A. ignescens* are *A. boulengeri* Peracca, 1904, *A. carrikeri* Ruthven, 1916 (senior synonym of *A. leoperezii* Ruíz-Carranza, Ardila-Robayo and Hernández-Camacho, 1994 fide Coloma, 1997), *A. ebenoides*, and *A. eusebianus*. However, *A. ignescens* is smaller (SVL of females 35.6–48.2, $\bar{x}$ = 42.5 mm, n = 15; SVL of males 34.2–41.4, $\bar{x}$ = 37.8 mm, n = 15) than *A. carrikeri* [SVL of females 52.4–62.1, $\bar{x}$ = 57.0 mm, n = 4; SVL of males (taken from the original description of *A. leoperezii*) 41.1–46.7, $\bar{x}$ = 43.5, n = 3)] and *A. boulengeri* (SVL of females 62.6–73.1, $\bar{x}$ = 65.9 mm, n = 4; SVL of males 50.4–52.5, $\bar{x}$ = 51.7 mm, n = 3). *Atelopus ignescens* differs from *A. ebenoides* and *A. eusebianus* by having a uniformly cream venter, or a translucent belly suffused with poorly defined black marks (solid black with cream marks in *A. ebenoides* and *A. eusebianus*) in preservative.

Description of neotype.—(Figs. 1A, 2) Adult female; body robust; head about as long as wide; head length and head width less than one-third SVL (HLSQ/SVL 0.261, HDWD/SVL 0.257); snout truncate, protruding beyond lower jaw in dorsal and lateral views; nostrils oval, slightly protuberant, directed laterally, situated at level of mandibular symphysis; canthus rostralis distinct, flared, weakly concave from eye to nostril; EYNO about three fourths of EYDM (EYNO/EYDM 0.756); loreal region concave; lips not flared; interorbital region and occiput flat; palpebrum flared; postorbital crest prominent and glandular (two glandular areas defined); pretympanic and tympanic area spiculate, tympanic membrane and tympanic annulus absent; choanae small, rounded, widely separated; tongue twice as long as wide, broadest anteriorly, free for half its length posteriorly; ostia pharyngea absent.

Forearm relatively short (RDUL/SVL 0.263); inner metacarpal tubercle indistinct, outer metacarpal tubercle round; subarticular tubercles at base of fingers distinct; supernumerary palmar tubercles distinct; tips of digits with round pads, on which a circummarginal groove is absent; thumb apparently with two phalanges, (THBL/HAND 0.795); webbing on hands absent, fingers lacking lateral fringes; relative lengths of fingers III > IV > II > I (Fig. 2). Tibia relatively short (TIBL/SVL 0.328); tarsal fold absent; inner metatarsal tubercle elevated, oval; outer metatarsal tubercle round, elevated, conical, about half size of inner metatarsal tubercle; supernumerary plantar tubercles absent, subarticular tubercles present, but not clearly visible; digital pads conspicuous, round, distinct; plantar surfaces wrinkled with minute black spiculae; webbing formula **I**0—2**II**1—(2–3)**III**1—3**IV**3—1**V**; relative length of toes IV > V = III > II > I (Fig. 2).

Dorsal surfaces smooth except for round warts on sacral region and spiculae anterior to cloacal region; numerous spiculae and coni on flanks, anterior and proximal upper surface of forelimb, and dorsal surfaces of

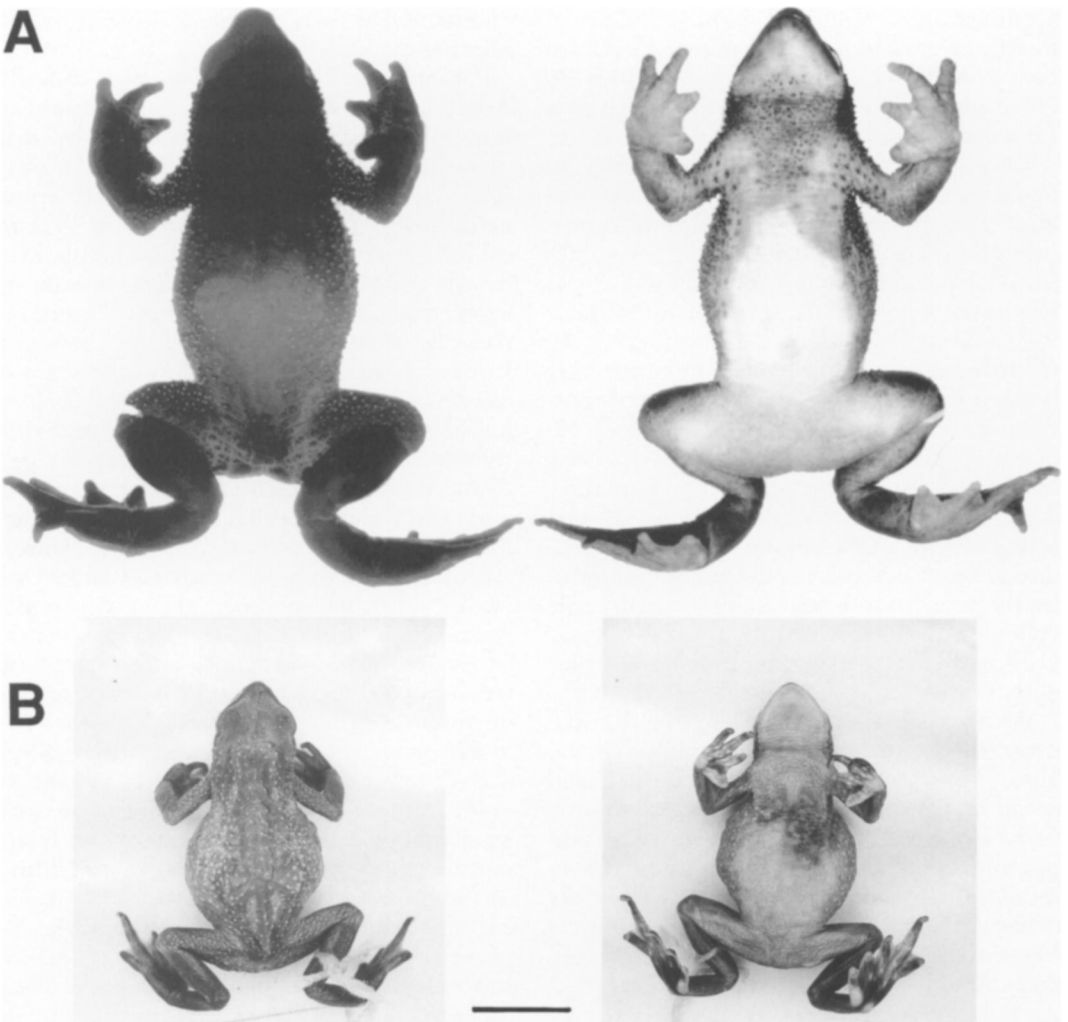

FIG. 1.—Dorsal and ventral views of (A) neotype QCAZ 702 of *Atelopus ignescens* and (B) lectotype SMF 4046 of *A. exiguus*. Scale bar = 1.0 cm.

hind limbs; ventral surfaces of body wrinkled; mental region with minute spiculae; gular and pectoral with dark coni and spiculae arranged in the shape of an inverted triangle; belly lacking warts, spiculae, and coni; undersides of thighs wrinkled, but lacking warts; cloacal sheath with rugose borders, opening at midlevel of thighs, directed posteriorly; one pair of low, elevated warts ventrolateral to cloacal opening.

Measurements (in mm).—SVL 49.4, TIBL 16.2, FOOT 19.5, HLSQ 12.9, HDWD 12.7, ITNR 4.1, EYDM 4.1, IOD 3.3, EYNO 3.1, RDUL 13.0, HAND 11.2, THBL 8.9, SW 14.6.

Coloration in preservative (70% ethanol): entire dorsum black, slightly paler laterally; flanks dark brown with gray coni; throat and chest cream, suffused with brown, with gray spiculae and coni; belly cream with two small, brown marks posteriorly, one of them round and the other irregular; palmar and plantar surfaces gray; undersides of limbs dark to pale brown; black line on upper border of nictitating membrane.

Variation.—Mensural variation of specimens from the neotype locality (15 females and two males, QCAZ 702–16, 1857–58) is presented in Table 1. These specimens resemble the neotype in coloration of the dorsum and flanks. In the two males, the venter, throat, abdomen, and undersides of the thighs are almost entirely yellowish cream except for a brown suffusion in the mental and gular regions. A brown cloacal patch is present in one male. Ventral coloration in females varies from almost entirely cream to uniformly brown. Morphological variation among specimens from the neotype locality is related to sexual dimorphism and ontogenetic change. Males have spiculae and coni, but coni are scattered and mostly concentrated in the postocular area in the temporal region. Females have spiculae and coni on the entire flanks and on the fore- and hind limbs. In males, there are a few, scattered spiculae on the gular and pectoral regions, whereas females have a patch of spiculae and coni in the gular and pectoral regions. A large female (QCAZ 704; SVL = 48.9 mm) has numerous coni covering the throat and chest and scattered coni on the belly. A small female (QCAZ 709; SVL = 41.7 mm) has spiculae on the gular and pectoral regions but lacks coni, and some of the spiculae are gray. Males possess nuptial excrescences covering the entire dorsum of Finger I and three quarters of the proximal dorsum of Finger II.

Populations from Oyacachi, Mojanda, Páramo de Guamaní, Zumbagua, Limpiopungo, and near Chimborazo (localities indicated in detail in Appendix I, Fig. 7) are herein considered as conspecific with *A. ignescens*. Specimens from these populations are similar to those described above. In some specimens, a cream mark is present on the inner surfaces of the tibiae; two specimens (out of five) from Lagunas de Mojanda have a cream inner metatarsal tubercle, sharply contrasting with the otherwise gray, plantar coloration.

Our description agrees with Cornalia's (1849) original description and that of Peters (1973) who provided data of color in life for specimens from Quito and 5 km W of Papallacta. Peters (1973) also presented mensural variation based on 26 males and eight females, but he did not explicitly state from where his sample was taken. He examined more than 500 individuals in a range from Tulcán to southern Cuenca; thus, he might have mixed several samples including populations regarded by others as different species (e.g., *Atelopus exiguus*). To account for geographic variation, we present variation based on a sample from Páramo de Guamaní, along with mensural variation in specimens from the locality of the neotype (Table 1).

Color in life.—Color in life of individuals from the neotype locality is lacking. Color transparencies of living individuals from the Páramo de Guamaní indicate that the dorsum and flanks, including warts, spiculae, and coni, are uniform black. The venter is orange–red, darker in the gular region than on the belly and slightly suffused with yellow on the belly. A black anal patch covers the proximal ventral surfaces of thighs. Ventral surfaces of limbs are black except on arms, which are orange red. Orange–red marks are present on the ventral surfaces of forearms, thighs and shanks. The iris is black. Specimens from near Limpiopungo, Quito, and near Chimborazo resemble the Guamaní individuals in coloration of the dorsum and flanks. A specimen from Quito (specimen without a museum number) and a specimen from Chimborazo (QCAZ 641) have the belly suffused with poorly defined black marks and the rest of the belly translucent; yellow eggs are visible through the ventral skin. Heselhaus and Schmidt (1988, 1994), Patzelt (1989:figs. 470, 475, 476), and Lötters (1996*a,b*) provided color photographs of *Atelopus ignescens*.

Distribution.—This species is known only from Imbabura, Pichincha, Cotopaxi, Napo, Chimborazo, and Bolívar provinces in the northern Andes of Ecuador between elevations of 2800–4200 m (Fig. 7). The distribution encompasses inter-Andean valleys, as well as higher parts of subparamo and paramo habitats between the western and eastern cordilleras of the Andes. This distribution lies mainly within Low Montane Humid Forest, Humid

TABLE 1.—Measurements (in mm) of adults of *Atelopus exiguus*, of *A. bomolochos* (females from specimens of original description), and of two populations of *A. ignescens*. Mean (±SD) are listed below range. Some data are lacking because of difficulties associated with taking the measurement.

	A. exiguus		*A. bomolochos*		*A. ignescens*			
	Males (n = 13)	Females (n = 6)	10 km S Cutchil Males (n = 5)	Females (n = 5)	Guamani Males (n = 15)	Guamani Females (n = 15)	20 km SE Salcedo Males (n = 2)	20 km SE Salcedo Females (n = 12)
SVL	21.1–27.1 23.4 ± 1.5	28.7–35.4 31.7 ± 2.5	32.1–42.1 36.8 ± 3.8	40.3–48.4 45.4 ± 3.2	34.2–41.4 37.8 ± 1.9	35.6–48.2 42.5 ± 3.3	35.9–36.3 36.1 ± 0.3	37.5–51.1 45.7 ± 3.7 (n = 15)
TIBL	8.1–9.7 8.6 ± 0.5	8.8–12.3 10.2 ± 1.3	12.3–15.4 14.4 ± 1.4	15.2–17.2 16.1 ± 0.9	11.5–14.6 13.4 ± 0.9	12.7–15.5 14.5 ± 0.8	14.1–14.7 14.4 ± 0.4	14.6–17.8 15.9 ± 0.9
FOOT	8.4–10.9 9.3 ± 1.0	10.1–14.0 11.9 ± 1.4	12.6–17.4 15.5 ± 2.2	— —	11.7–16.3 14.0 ± 1.3	13.8–16.3 15.2 ± 0.8 (n = 14)	13.9–15.4 14.6 ± 1.1	15.6–19.5 18.1 ± 1.2
HLSQ	7.2–7.7 7.2 ± 0.3	8.1–10.1 8.8 ± 0.7	10.5–13.0 11.8 ± 1.0	11.7–12.8 12.4 ± 0.5	9.4–11.5 10.9 ± 0.5	10.2–12.7 11.7 ± 0.7	10.5–11.2 10.9 ± 0.5	12.1–13.8 12.8 ± 0.5
HDWD	7.1–8.4 7.8 ± 0.5	7.3–9.1 8.4 ± 0.7	9.7–12.1 10.8 ± 1.0	12.8–13.6 13.0 ± 0.4	9.8–12.1 11.3 ± 0.7	10.3–12.8 12.0 ± 0.7	10.2–11.5 10.9 ± 0.9	11.8–13.7 12.6 ± 0.6
EYDM	2.7–3.6 3.0 ± 0.3	3.0–3.6 3.4 ± 0.3	3.2–4.0 3.7 ± 0.3	4.7–5.4 5.1 ± 0.3	3.2–4.0 3.4 ± 0.3 (n = 14)	3.3–4.5 3.8 ± 0.4 (n = 14)	3.3 ± 3.8 3.6 ± 0.4	3.3–4.3 3.8 ± 0.4
EYNO	1.4–2.0 1.7 ± 0.2	1.9–2.3 2.0 ± 0.2	2.7–3.3 2.9 ± 0.3	2.2–3.2 2.8 ± 0.4	2.0–2.8 2.5 ± 0.2	2.3–3.3 2.8 ± 0.3	2.8 2.8 ± 0.0	2.7–3.5 3.1 ± 0.2
ITNA	2.2–3.1 2.6 ± 0.3	2.1–3.4 2.9 ± 0.5	3.5–4.2 3.9 ± 0.3	— —	3.4–4.5 4.0 ± 0.3	3.8–4.7 4.3 ± 0.3	4.4 4.4 ± 0.0	3.9–5.1 4.7 ± 0.4
RDUL	6.1–7.1 6.6 ± 0.3	7.8–10.4 8.7 ± 1.0	10.0–13.1 11.4 ± 1.3	— —	9.1–11.5 10.8 ± 0.7	10.6–13.3 12.0 ± 0.7	10.9–11.3 11.1 ± 0.3	11.9–13.8 13.0 ± 0.6
HAND	5.4–6.6 5.9 ± 0.4 (n = 9)	6.3–7.9 7.3 ± 0.7	8.1–10.5 9.6 ± 1.1	— —	7.3–9.7 8.4 ± 0.6	7.9 ± 10.2 9.4 ± 0.7 (n = 14)	8.0–9.1 8.6 ± 0.8	9.1–11.4 10.5 ± 0.7
THBL	3.2–4.2 3.7 ± 0.3 (n = 12)	4.1–5.6 4.7 ± 0.6	4.9–6.4 5.8 ± 0.7	— —	5.8–7.9 6.8 ± 0.5	5.2–8.8 7.8 ± 1.0 (n = 11)	6.4–6.5 6.5 ± 0.1	7.7–9.3 8.5 ± 0.6

Montane Forest (Humid Subparamo), Very Humid Montane Forest (Very Humid Subparamo), and Humid Subalpine Forest. Annual mean precipitation varies from 250–500 mm in Humid Subalpine Forest to 1000–2000 mm in Low Montane Humid Forest; annual mean temperature varies from 3–6 C in Humid Subalpine Forest to 7–12 C in Humid and Very Humid Montane Forest, and 12–18 C in Low Montane Humid Forest.

Etymology.—The specific name *ignescens* is the present participle of the Latin *ignescere* meaning to catch fire. Presumably the name alludes to the orange ventral color.

Remarks.—Lötters (1996*b*) provided summarized information and literature references about *A. ignescens.* Several populations from the Andes of southeastern Colombia (from Laguna La Cocha, Departamento Nariño), southwestern Colombia (from paramo of Guachucal, Departamento Nariño), and northern Ecuador (from paramo El Angel, Provincia Carchi) resemble *Atelopus ignescens,* as described herein. An unpublished phylogenetic analysis (Coloma, 1997) does not support the hypothesis that populations from Guachucal and El Angel ("Guachucal" populations of Gray, 1983) are sister taxa of *A. ignescens;* thus, they may not be conspecific. In contrast, the "Cocha" population, recognized by Gray (1983), is placed as sister taxa of *A. ignescens* and they may be conspecific. The "Guachucal" populations can be diagnosed from *A. ignescens* by lacking a patch of brown spiculae on the gular and pectoral regions in females and by the presence of white color on the inner and outer metatarsal tubercles (absent in most populations of *A. ignescens,* variable in specimens from Lagunas de Mojanda). The "Cocha" population and *A. ignescens* share the unique presence of a patch of brown spiculae on the gular and pectoral regions in females. However the "Cocha" specimens are larger (SVL of adult females 40.3–50.1, $\bar{x}$ = 44.6 mm, n = 8; SVL of adult males 36.7–37.3, $\bar{x}$ = 36.9 mm, n = 3) than our samples referred to *A. ignescens* and differ by having dorsi and flanks entirely orange-red to entirely black (our samples of *A. ignescens* have entirely black dorsi and flanks). We consider that the "Cocha" population requires further analysis prior to confidently assign it to *A. ignescens.*

The neotopotype and associated specimens (QCAZ 702–16, 1857–58) are one of the last series of specimens of *Atelopus ignescens* collected alive. They were found active during the day, in paramo habitat, on 29 November 1987. Three females (QCAZ 703, 705–706) (out of 17 specimens collected) were found dead. Judging by the size (SVL 41.3, 43.8, and 42.2 respectively) of dead individuals collected with the neotype, presumably they were not old females. No specimens of *A. ignescens* have been encountered since March 1988, when two specimens (QCAZ 275–276) were found in the surroundings of Oyacachi, Napo Province. Repeated efforts to find *A. ignescens* at the neotopotypic and other localities of its range have been in vain. No studies have attempted to identify possible causes of the disappearance of *A. ignescens* from the Ecuadorian highlands. Considering that some of the areas of the distribution of *A. ignescens* appeared pristine, the species possible extinction remains puzzling, and it is reminiscent of catastrophic declines of *Atelopus* reported elsewhere (La Marca and Reinthaler, 1991; Pounds and Crump, 1994; Stebbins and Cohen, 1995; Lötters, 1996*b*; La Marca and Lötters, 1997; Lips, 1998).

Status of Atelopus exiguus *(Boettger, 1892)*

Atelopus exiguus originally was described as *Phryniscus laevis* var. *exigua. Atelopus laevis* Günther, 1859 (including var. *exigua*) was considered to be a synonym of *A. ignescens* by Nieden (1926). Rivero (1963) and Peters (1973) followed Nieden (1926) in considering *A. laevis* as a synonym of *A. ignescens.* However, Rivero (1963) along with Gray and Cannatella (1985) recognized *exigua* as a subspecies of *A. ignescens,* whereas Peters (1973) placed *A. exiguus* in the synonymy of *A. ignescens.* McDiarmid (1971) treated this taxon as *A. exigua.* Lötters (1996*b*) treated *A. exiguus* as a valid species and provided some morphological data and a color photograph. Taxonomic confusion surrounding this species is not

surprising, because the original description is merely four lines in a footnote, and the type series of *A. exiguus* was not examined by any of the preceding authors. In his catalogue of type specimens in the Senckenberg Natur-Museum, Mertens (1967) gave this taxon specific status, used the name *Atelopus exiguus* for the first time, and designated a lectotype. Our study of the types confirms Mertens' recognition of the specific status of *A. exiguus*. Also, recent field work has provided additional material that helps to clarify the taxonomic status of *A. exiguus*. In the following section, we redescribe *A. exiguus* based on the type material and additional specimens using external morphological characters (including color in life) and some osteological data. Moreover, descriptions of the call and tadpole are provided.

Atelopus exiguus (Boettger, 1892)

Phryniscus laevis var. *exigua* Boettger, 1892:22 (footnote). 10 syntypes: SMF 4046–51, 3170–71, 3916, and one lost, from "Zurucuchu, W-Anden von Cuenca, 3250 m, Ecuador."
Atelopus ignescens (part.) Nieden, 1926: 83.
A[telopus]. ignescens exigua Rivero, 1963: 108.
Atelopus exiguus Mertens, 1967:43.
A[telopus]. exigua McDiarmid, 1971:6.
Atelopus ignescens (part.) Peters, 1973:24.
A[telopus]. ignescens exigua Gray and Cannatella, 1985:912.
Atelopus exiguus Lötters, 1996*b*:26.

Lectotype.—SMF 4046 (= Cat. Boettger 1151f.), adult female, from Ecuador, Provincia Azuay, Zurucuchu (= Laguna Llaviuco), W of Cuenca, 3250 m above sea level, collected by F. C. Lehmann in 1890.

Paralectotypes.—SMF 4047–51, 3170–71, 3916; same data as lectotype.

Comments on type series.—Nine types are currently deposited at SMF. Boettger (1892:22) originally listed eight specimens, plus a male and female in copula (n = 10 specimens). The types have been preserved for more than 100 yr; except for inflexible or damaged phalanges, they are in relatively good condition. The series contains six adult males (for sexual identification in the genus see Peters, 1973: 8)—SMF 4048–5, 3171, and 3916. There are two adult females (with eggs visible through the skin of the venter)—SMF 4046 (lectotype) and 3170 (still in amplectant position with SMF 3171). SMF 4047 is considered to be a female because the forelimbs do not show typical male characters.

Diagnosis.—(1) A relatively small *Atelopus* (SVL in males 21.1–27.1 mm, $\bar{x}$ = 23.4, n = 13; females 28.7–35.4 mm, $\bar{x}$ = 31.7, n = 6); (2) limbs short (tibia length/SVL = 0.305–0.347, n = 4); (3) phalangeal formula for hand 2-2-3-3; (4) foot webbing formula **I**0—(1/2–1)**II**(1/2–1)—(1–3)**III**(1/2–2)—(1–3)**IV**(1–3)—(1/2–2)**V**; (5) snout acuminate protruding beyond lower jaw; (6) tympanic membrane, tympanic annulus, and stapes absent; (7) dorsal surfaces bearing few warts, (8) flat, yellow spiculae (cream in preservative) on forelimbs, dorsum, flanks, and dorsal surfaces of thighs; (9) vertebral neural processes inconspicuous; (10) dorsum and flanks bright yellowish-green to blackish-green; (11) venter yellow to orange (cream in preservative); palmar and thenar tubercles white; (12) gular and pectoral region lacking spiculae and coni.

The only species of other *Atelopus* that possess uniform green dorsums and that can be confused with *A. exiguus* are *A. angelito* Ardila-Robayo and Ruiz-Carranza, 1998, *A. bomolochos* Peters, 1973, *A. eusebianus* Rivero and Granados-Díaz, 1993, *A. muisca* Rueda-Almonacid and Hoyos, 1991, and *A. peruensis* Gray and Cannatella, 1985. All are larger than *A. exiguus*. For measurements of original material of *A. bomolochos* see Table 1; SVL's from the original descriptions of the following species are as follows: *A. angelito* males 33–34.8, $\bar{x}$ = 33.8 mm, n = 6; female = 41 mm; of *A. eusebianus* males 32.5–36.1, $\bar{x}$ = 34.2 mm, n = 6; females 30.0–45.4, $\bar{x}$ = 39.8 mm, n = 12; of *A. muisca* males 28.1–32.6, $\bar{x}$ = 30.7 mm, n = 12; females 35.2–42.4, $\bar{x}$ = 38.6 mm, n = 14; of *A. peruensis* males 32.8–38.5, $\bar{x}$ = 35.6 mm, n = 15; females 38.4–45.2, $\bar{x}$ = 43.5 mm, n = 14.

Atelopus exiguus may be further distin-

guished from *A. bomolochos* by (1) lacking dark irregular spots on the dorsum or dorsolateral lines on the head [according to Peters (1973), both patterns are present in the holotype and usually in the paratypes of *A. bomolochos*]; (2) the presence of a well-defined conical inner metatarsal tubercle [not conical in *A. bomolochos* (Peters, 1973)]; (3) having white metatarsal tubercles which contrast with adjacent palmar and thenar gray surfaces [unicolor soles in *A. bomolochos* Peters, (1973); although this character is variable in a population from 10–19.3 km S of Cutchil, see Remarks below]; and (4) coloration in life as follows: there is no color description of living topotypic material of *A. bomolochos*, but individuals assigned to this species from 3 to 19.3 km S of Sigsig, Provincia Azuay (QCAZ 1861–69, 1893–94, KU 217335–46) varied from dorsum and flanks entirely yellowish orange to yellowish brown, with a pale green suffusion to others with dark green dorsum (in *A. exiguus* the dorsum and flanks are dark to bright green, but never orange or yellow); the iris is black with a bright green ring around the pupil (in *A. exiguus* the iris is almost entirely black and there is no green ring around the pupil).

Atelopus exiguus differs from *A. angelito*, *A. eusebianus*, and *A. muisca* by lacking black (in preservative gray or brown) marks on the gular, chest, belly and undersides of thighs regions and from *A. peruensis* by lacking black flanks (although some *A. peruensis* have dull green flanks; Gray and Cannatella, 1985), by lacking contrasting yellow tips of digits (in life), and by having vocal slits in males. *Atelopus peruensis* also possess well-developed posterolateral processes on the hyoid (Gray and Cannatella, 1985; their Fig. 6); these are absent or poorly developed in *A. exiguus* (Fig. 4A,B).

Atelopus exiguus differs from *A. ignescens* by having: (1) significantly smaller size (Table 1): SVL of males is significantly different (*t*-test, $t = 18.5$, df = 20, $P < 0.0001$); SVL of females is significantly different (*t*-test, $t = 6.03$, df = 17, $P < 0.0001$); (2) dorsum and flanks bright yellowish-green to blackish-green (dark brown to black dorsum in *A. ignescens*); it also possesses yellow spiculae (black in *A. ignescens*); (3) white (in preservative cream) plantar tubercles (brown in *A. ignescens*, variable in specimens from Lagunas de Mojanda); (4) poorly developed palmar tubercles (Fig. 3) (numerous distinct palmar tubercles in *A. ignescens*; Fig. 2); (5) coni lacking (present in *A. ignescens*); females lack gray spiculae and coni in the gular and pectoral region (present in *A. ignescens*); (6) the posterolateral processes of the hyoid apparatus poorly developed, or absent (Fig. 4A,B) [distinct in *A. ignescens* (Fig. 4C); see also Gray and Cannatella, 1985: Fig. 6].

Description of lectotype.—(Fig 1B). Adult female with eggs visible through skin on venter; body robust; head as long as wide; head length and width less than one-third SVL (HLSQ/SVL 0.278, HDWD/SVL 0.268); snout pointed from above, dorsum of snout weakly depressed; snout projecting in lateral view; nostril lateral, visible from above; canthus distinct, straight from nostril to tip of snout, concave from eye to nostril; EYNO about three-fourths of EYDM (EYNO/EYDM 0.769); loreal region concave; lips slightly flared; interorbital region and occiput flat; temporal area slightly convex; supratympanic area with distinct gland, tympanic membrane and tympanic annulus absent; choanae small, rounded, widely separated; tongue twice as long as wide, broadest anteriorly, free for half its length posteriorly; ostia pharyngea absent.

Forearm relatively short (RDUL/SVL 0.278); outer metacarpal tubercle distinct, inner weak; palmar surface relatively smooth with only few poor developed tubercles; thumb apparently with two phalanges, (THBL/HAND 0.625); fingers lacking lateral fringes; webbing formula **I**1—2**II**1 1/2—2 1/2**III**3—3**IV**; relative lengths of fingers III > IV > II > I. Tibia relatively short (TIBL/SVL 0.346); inner and outer metatarsal tubercles well developed, outer more prominent, round; plantar surfaces relatively smooth with only few poor developed tubercles; subarticular tubercles restricted to proximal joints of phalanges; fingers lacking lateral fringes;

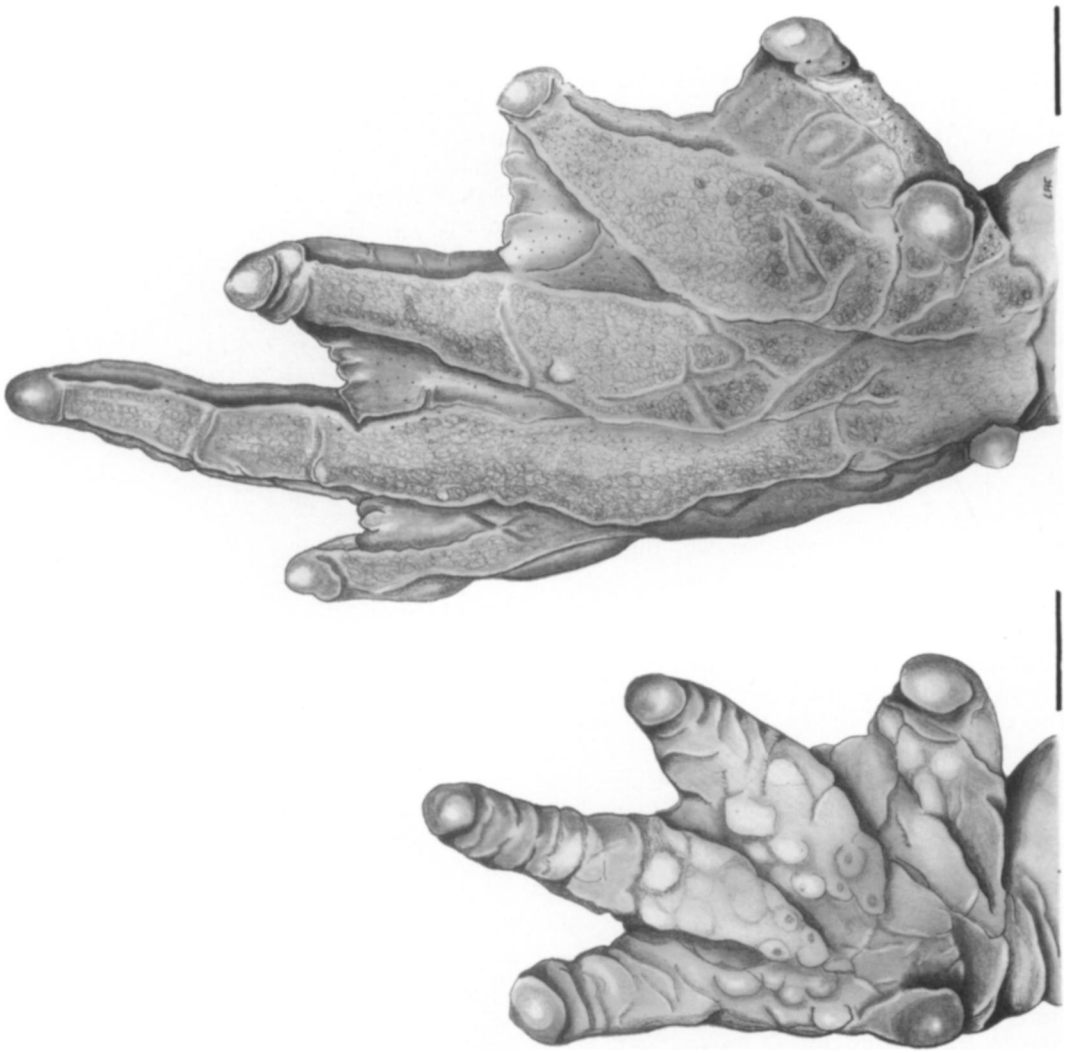

FIG. 2.—Ventral views of right hand and right foot of neotype of *A. ignescens*. Scale bar = 2.0 mm.

webbing formula **I**0—1**II**1—1**III**1—2**IV**2—1**V**; relative lengths of toes IV > V > III > II > I. Dorsum with spiculae, few on proximal part of head and on middorsum, concentrated laterally and ventrolaterally, continuing onto temporal region, forelimbs, and hind limbs; rest of extremities and distal snout relatively smooth; belly smooth with skin on chest wrinkled.

Measurements (in mm).—SVL 30.6, TIBL 10.0, FOOT 12.5, HLSQ 8.7, HLEX 12.5, IOD 3.3, HDWD 8.2, EYDM 3.5, EYNO 1.9, ITNA 8.1, RDUL 8.5, HAND 7.9, THBL 4.7.

Coloration in preservative (70% ethanol): ground color of dorsum yellowish brown, olive-green middorsally and on head, with white spiculae; pale yellow on

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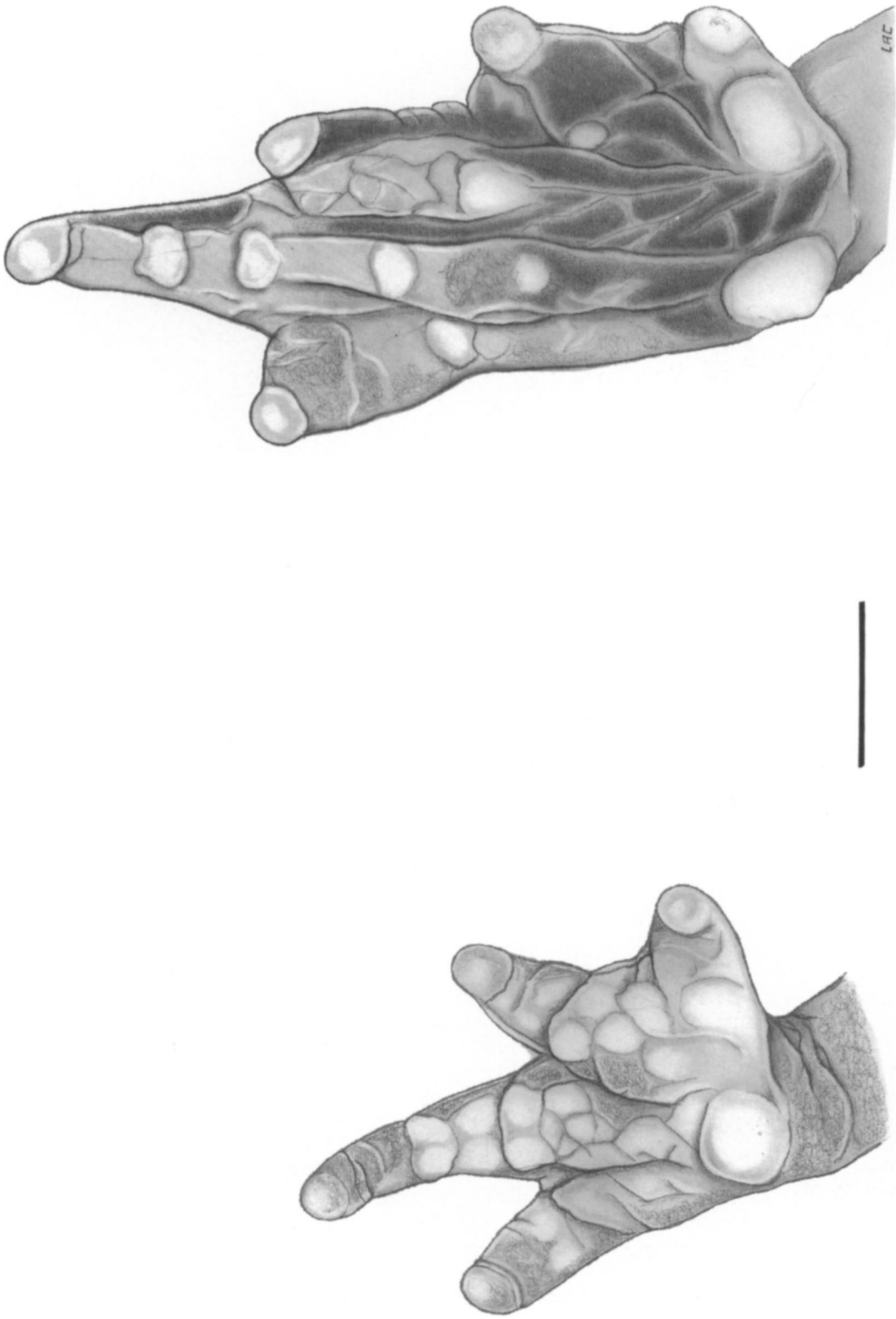
FIG. 3.—Ventral views of right hand and right foot of *Atelopus exiguus* (MHNG 2258.41). Scale bar = 2.0 mm.



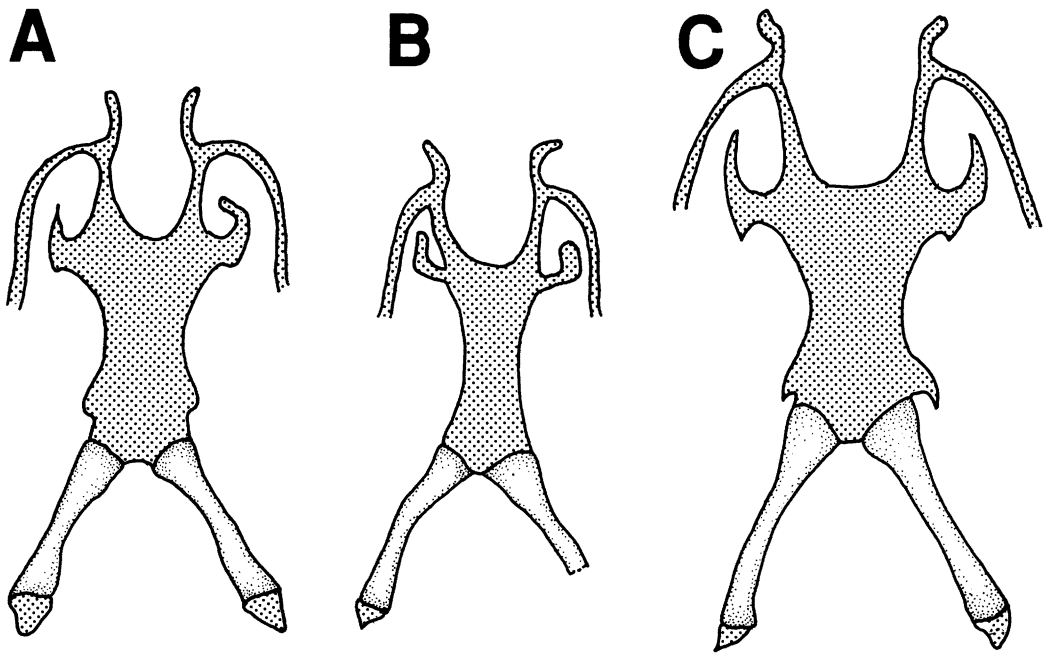


FIG. 4.—Ventral view of hyoids of cleared-and-stained (A) female *Atelopus exiguus* (KU 120381), (B) male *A. exiguus* (KU 120385) and (C) *A. ignescens* (QCAZ 266). Dotted pattern indicate cartilage. Scale bar = 2 mm.

throat, belly, forelimb, and hind limb; rest of extremities olive-green; plantar and palmar surfaces brownish yellow with pale yellow tubercles.

Variation.—The following is based on the paratopolectotypes and recently collected specimens (n = 24). Coloration in preservative varies from reddish brown to pale yellow. Some individuals have reddish-brown or brown spots in the cloacal area. Plantar and palmar surfaces vary from dark brown, with pale yellowish tips of toes and fingers, to uniform pale yellow without contrasting tubercles. Some specimens possess foot webbing like the lectotype, whereas others have a wide fringe on Toe IV that is continuous with webbing among the toes (see diagnosis).

Morphometric variation is indicated in Table 1. Sexual dimorphism is evident; females are larger than males (Table 1); males have keratinized nuptial pads on the dorsal and inner surfaces of the thumb and proximal phalange of Finger II; forelimbs of females are long and slender, but short and robust in males; spiculae are well developed in females, but they may be reduced to only a few spiculae in males, males have vocal slits. One adult female (QCAZ 1666) has more numerous and clumped spiculae on the flanks and dorsum than subadult females (e.g., MHNG 2499.75, 2499.79 and QCAZ 3744).

It is noteworthy that four of 23 specimens (QCAZ 3744, MHNG 2258.42, 2499.76 and 2499.78, one juvenile and three males respectively) lack Toe I. The skeletal components of Toe I are lacking (Fig. 5).

Color in life.—John D. Lynch (field notes, 19 June 1968, KU 120381–87; n = 7) described topotypic material: "Dorsum dark to bright green with yellow spinules; flanks same; venter yellow anteriorly, pale orange posteriorly; undersides of hands white, thenar tubercles white, sole black; posterior surfaces of thighs yellow green; groin pale orange." Color transparencies of QCAZ 3744 from the type locality and QCAZ 8835 from a nearby locality (Quimsacocha) agree with this description in

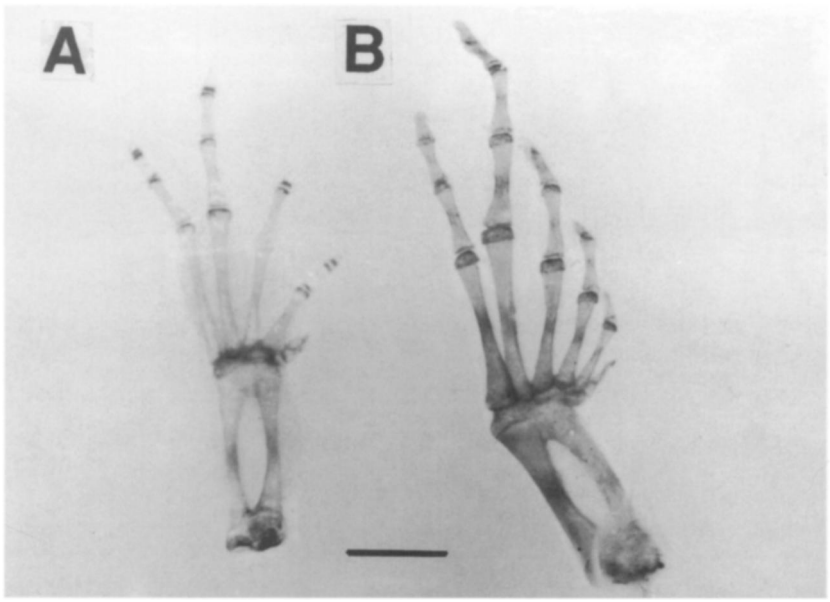


FIG. 5.—Dorsal view of right foot of cleared-and-stained *Atelopus exiguus:* (A) MHNG 2499.76 (note absence of Toe I) and (B) QCAZ 4957. Scale bar = 2.0 mm.

general; the iris was almost entirely black with only weak traces of a golden ring around the pupil. Lötters (1996*b*:Figs. 8, 12) provided color photographs of individuals of *Atelopus exiguus* from Bosque de Mazán and the type locality.

Tadpoles.—Measurements (in mm) of developmental stages of tadpoles (sensu Gosner, 1960) from a series of 13 larvae (QCAZ 3668–3669) are given in Table 2. The tadpole belong to Type-IV of Orton (1953) and to the gastromyzophorous ecomorphological guild defined by Altig and Johnston (1989). Series QCAZ 3668 was collected in the Río Quinuas, about 15 km W of Cuenca, 3150 m, Provincia Azuay, Ecuador, on 28 July 1989, by Stella de la Torre, Felipe Campos Y., and Luis A. Coloma; QCAZ 3669 has the same data as QCAZ 3668, but was collected at 3540 m.

TABLE 2.—Measurements (in mm) of developmental stages sensu Gosner (1960) of 13 tadpoles of *Atelopus exiguus* (QCAZ 3668–69).

Stage	*n*	Body length	Total length
25	1	3.9	10.3
26	4	$\bar{x}$ = 4.7 (4.0–5.3)	$\bar{x}$ = 11.8 (10.2–13.4)
27	1	5.3	12.1
28	2	$\bar{x}$ = 4.7 (4.5–4.9)	$\bar{x}$ = 12.4 (12.2–12.6)
29	1	5.1	13.6
31	1	6.7	16.9
34	1	6.3	16.8
35	1	6.7	17.8
36	1	7.5	21.0

The following description is based on an individual in Stage 31 (from series QCAZ 3668) (Fig. 6). Total length 16.9 mm; body elongately ovoid, depressed dorsally, about two-thirds as high as wide; greatest width at posterior part of body; snout bluntly rounded in dorsal view and sloping in profile; body constricted slightly at levels of eyes and spiracle; nostrils small, about one-third distance from eyes to tip of snout; eyes dorsal, directed dorsolaterally, diameter 1.0 mm; interocular distance 1.5 mm; spiracle sinistral, elongate, ventral to horizontal body axis, directed posterodorsally, originating at midpoint of body; diameter of spiracular opening about one-half length of free tube; vent tube short, medial. Caudal musculature robust anteriorly, narrowing abruptly at point just posterior to midlength, terminating anterior to end of tail; dorsal fin slightly highest

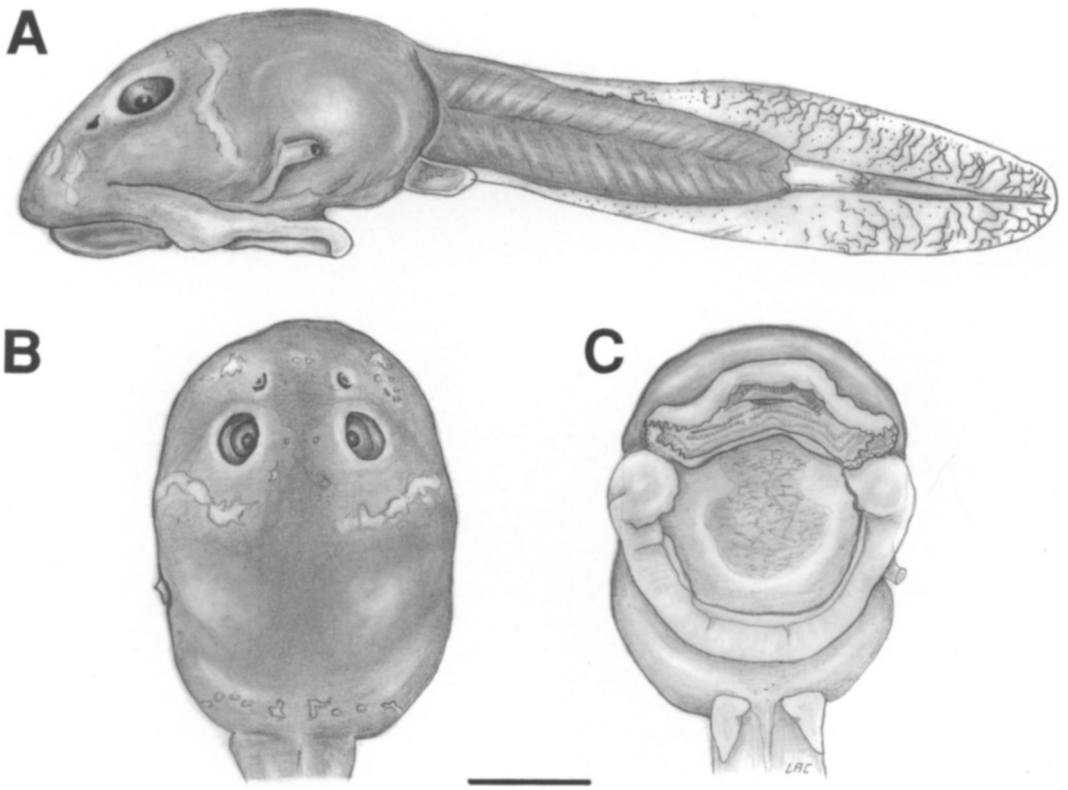


FIG. 6.—Tadpole of *Atelopus exiguus* (QCAZ 3668): lateral, dorsal, and ventral views. Scale bar = 2.0 mm.

posterior to midlength of tail; fins subequal in height; tail length 60.5% of total length; tail height 2.6 mm at midlength of tail, dorsal fin not extending onto body; tip of fin rounded.

Mouth ventral, surrounded by labia forming complete oral disc, 4.4 mm wide; one row of marginal papillae anteriorly, two rows at corners of mouth, no papillae posteriorly; tooth row formula 2/3, complete rows angulate anteriorly; jaw sheaths slender, serrate; upper sheath narrow, but slightly wider medially; lower sheath slightly curved; suctorial disc extending from posterior labium posteriorly for three-fourths length of body, forming complete disc with raised edge that is broadened at its juncture with labium.

Coloration in preservative: dorsum and sides of body dark brown; two translucent symmetrical marks posterior to eyes; scattered small translucent dots on distal part of body, forming line across body; translucent mark on midsnout and one symmetrical translucent mark on snout; spiracle with scattered brown pigments; anterior half of caudal musculature dark brown, unpigmented posteriorly except for scattered brown stippling at midregion of unpigmented area; fins with brown flecks forming reticulate patterns on distal part of tail; oral disc brown; edge of suctorial disc translucent, venter brown.

In life (based on color transparencies), body entirely black with bluish-white marks on rostrum, across midbody and on distal part of body; caudal musculature black until midlength, followed by a white area and black at distal end; fins translucent with black reticulations.

Distribution and natural history.—Atelopus exiguus is known from elevations of approximately 3150–3850 m in Parque Nacional Cajas, Bosque Protector Mazán and surrounding areas in Provincia Azuay, southern Ecuador (Fig. 7). It occurs in

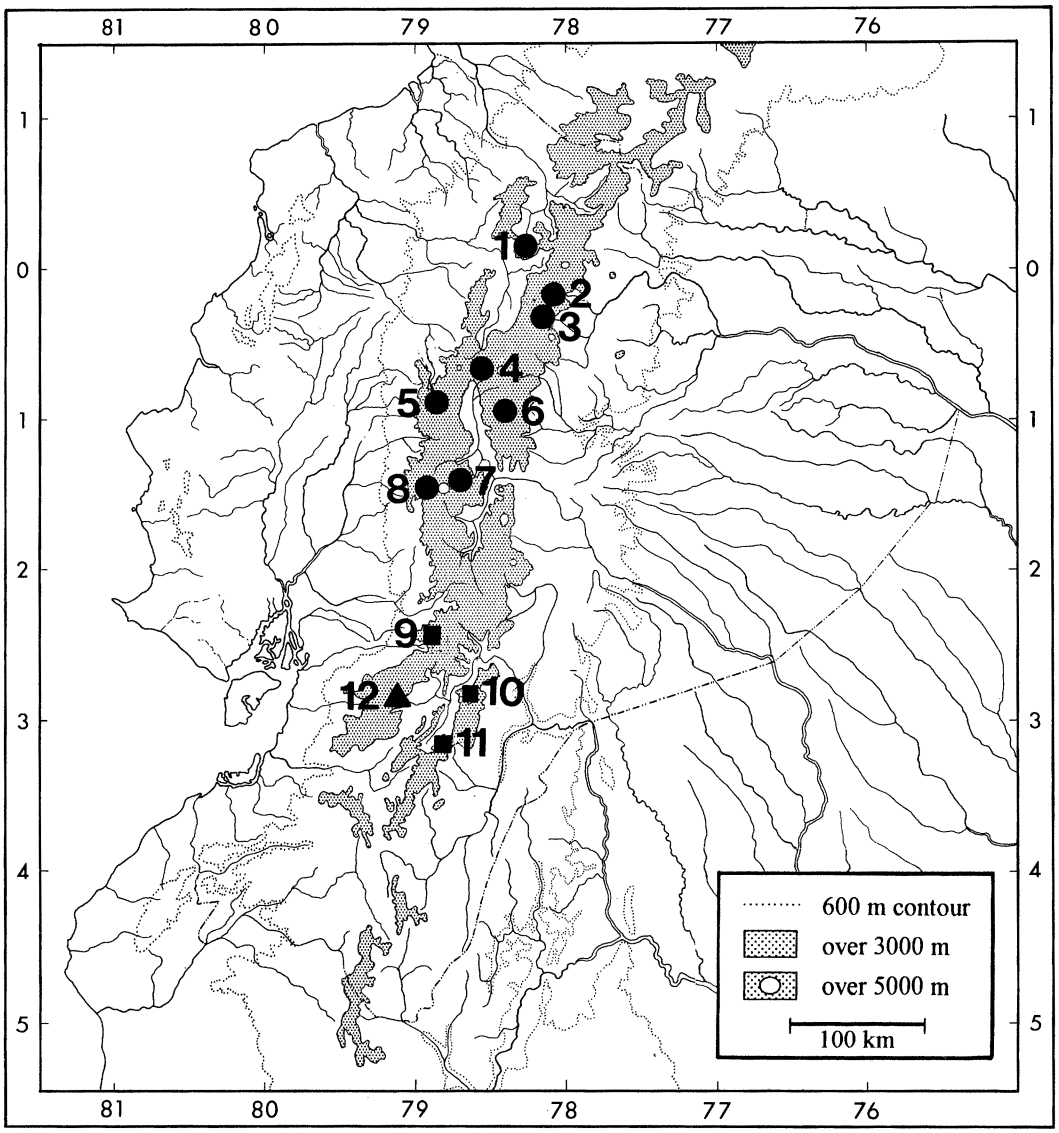


FIG. 7.—Map of Ecuador showing localities of *Atelopus ignescens* (circles), *A. bomolochos* (squares), and *A. exiguus* (triangle). 1 = *Provincia Imbabura:* Lagunas de Mojanda; 2 = *Provincia Napo:* Oyacachi; 3 = *Provincia Pichincha:* Páramo de Guamaní, La Virgen, 3800–4200 m; 4 = *Provincia Cotopaxi:* Laguna de Limpiopungo, 4000 m; 5 = Zumbagua; 6 = *Provincias Cotopaxi-Napo:* ca. 20 km (airline) southeast of Latacunga; 7 = *Provincia Chimborazo:* 20 km N Riobamba; 8 = *Provincia Bolívar:* ca. Chimborazo (Ambato-Guaranda road); 9 = *Provincia Cañar:* between Juncal and General Morales, app. 2500 m; 10 = *Provincia Azuay:* Sevilla de Oro; 11 = 3 km E Sigsig, 10–19.3 km E Cutchil; 12 = *Provincia Azuay:* Zurucuchu and nearby localities.

subparamo and paramo in the Very Humid Montane Forest Life Zone, where annual mean precipitation is 1000–2000 mm, and annual mean temperature is 7–12 C.

QCAZ 1666 was collected close to a river (F. Toral, field notes, no date). QCAZ 3744 was found after a rain in a pasture area at the surroundings of Laguna Llaviuco (S. Lötters and A. Widmer field notes, February 1993); QCAZ 8835 was found active during the day in cushion vegetation in paramo habitat (D. Tirira, field notes,

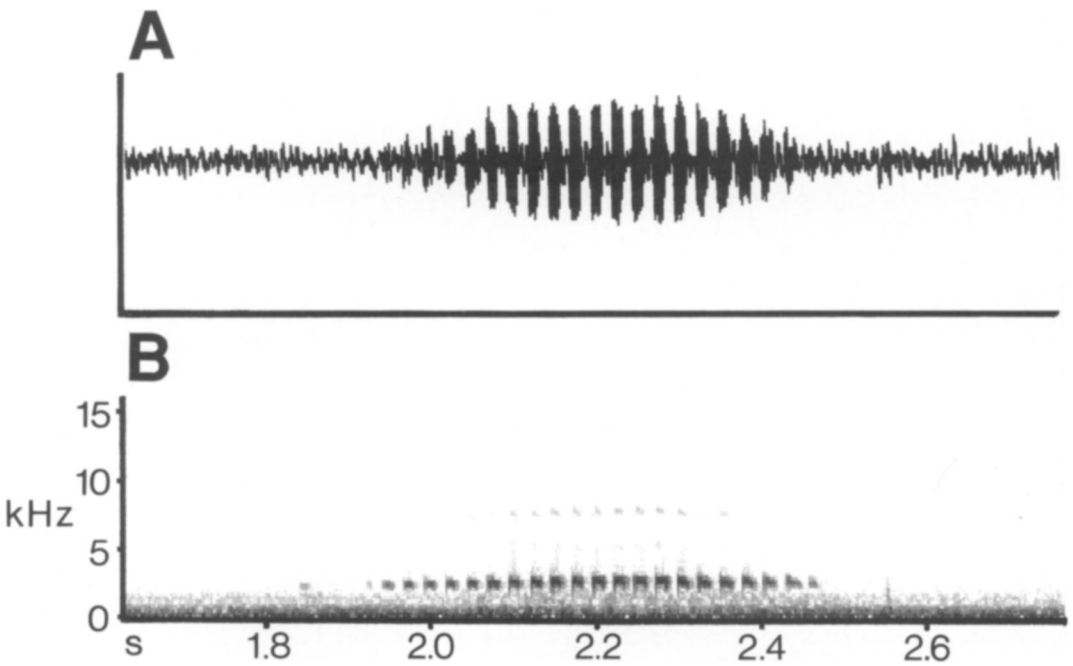


FIG. 8.—(A) Oscillogram and (B) audiospectrogram of pulsed call of *Atelopus exiguus*.

20 May 1995). Read (1986) provided the only known data on the natural history of *Atelopus exiguus*. He treated *A. exiguus* under the name *A. ignescens* and reported the species to be a very common diurnal frog in the Río Mazán Valley (Provincia Azuay). Specimens were found under stones or walking on trails. Calling occurred chiefly in the mornings, particularly on warm days following some heavy rains. Some males called from crevices beside small seepages of running water. Amplectant pairs were encountered quite frequently during July–September 1986, particularly after heavy rains; though spent females seemed more common from the middle of September. Five amplectant pairs were collected in mid-September and they were still amplexing one month later under captive conditions. A clutch was found attached to the bottom of a stone in a slowly flowing tributary of the Mazán River. Tadpoles were found in considerable numbers in the many small streams descending from the paramo as well as in the Mazán River at about 3400 m. During September, large concentrations of juveniles and newly metamorphosed specimens were found in piles of loose stones and under vegetation bordering a trail close to the Mazán River.

A recording of the call (National Sound Archive [BM] 16517; original tape 862A 10.00–16.17) was made by Morley Read during the day on 5 August 1986; it contains two vocalizations of the same individual. The animal was calling from inside a hole beside a small stream beside the main path. Both are pulsed calls (Fig. 8) consisting of 19–21 notes (= pulses sensu Cocroft et al., 1990). Calls last 0.48–0.52 s. The interval between calls is 11.6 s. Each note has a mean duration of 0.012 s (n = 40); mean internote interval is 0.0138 s (n = 38). The dominant frequency is at about 2150–2700 Hz (Fig. 8). It increases gradually through the call. The call begins quietly, gradually increases in intensity to a peak near the end of the call, then decreases to the end of the call. Note rate remains constant through the call.

Etymology.—The specific name *exiguus* is the Latin adjective for small.

Remarks.—Some specimens of a popu-

lation of *Atelopus* from 10–19.3 km S of Cutchil, Provincia Azuay, (QCAZ 1861–69, KU 217335–40, 217441–46) resemble *A. exiguus* as described herein. However, we tentatively assign this population to *A. bomolochos* based on the size of individuals. Size of individuals of this population (SVL of females 42.7–45.6, $\bar{x}$ = 43.8 mm, n = 4; SVL of males 32.1–42.1, $\bar{x}$ = 36.9 mm, n = 5) approximates that of *A. bomolochos,* in contrast to the smaller *A. exiguus* (Table 1). Variation in this population includes entirely yellowish-orange individuals (KU 217442, QCAZ 1861–68) and others which have a dark green dorsum with flat, yellow spiculae on flanks, and contrasting white, conical, inner metatarsal tubercles (KU 217444–45); these characters of the two latter specimens are typical of *A. exiguus.* However, one of the latter individuals (KU 217444) also has black spots on the dorsum, which is characteristic of *A. bomolochos.* If these patterns represent clinal variation, *A. bomolochos* and *A. exiguus* are conspecific (but see discussion below). Nevertheless, even if *A. exiguus* represents only geographic variation within *A. bomolochos,* it is clearly not a population of *A. ignescens* as suggested by previous authors (Gray and Cannatella, 1985; Peters, 1973; Rivero, 1963).

DISCUSSION

The systematics of the populations included within *Atelopus ignescens* have been difficult to assess, because of the lack of detailed alpha taxonomic work and unknown phylogenetic relationships. Gray (1983) informally proposed two phenetic complexes of populations (*A. ignescens* complex and *A. exigua-bomolochos* complex). Peters (1973:16) considered *A. bomolochos* to be closely related to *A. ignescens.* In contrast, Gray (1983) postulated that *A. bomolochos* is more similar to *A. exiguus.* At present there is no compelling evidence of a close relationship between *A. bomolochos* and *A. ignescens.* However, the similarity between *A. exiguus* and *A. bomolochos* deserves more detailed analyses. Recognition of *A. bomolochos* and *A. exiguus* as distinct species draws attention to the differences between these putative taxa. Perhaps, more important, an unpublished phylogenetic analysis does not place these two species as sister taxa (Coloma, 1997). However, this analysis is not strongly supported because of poor knowledge of outgroups, character polymorphism, and continuous variation of most characters among species.

Lynch (1993) postulated that species lacking a terminal phalange of the thumb compose an hypothetical monophyletic group that he called the *flavescens* group, whereas the species which retain the terminal phalange comprise the *ignescens* group for which there is no evidence of its monophyly. Gluesenkamp (1995) suggested that reduced phalangeal formulae is not phylogenetically informative in *Osornophryne* (a genus related to *Atelopus:* see Cannatella, 1986; Graybeal, 1997) because of the plasticity of this character within this genus. Similar plasticity seems to be present in species of *Atelopus.* Ruíz-Carranza and Osorno-Muñoz (1994) reported species having intraindividual variation in that character. Additionally, Vélez-Rodríguez and Ruiz-Carranza (1997) doubted the informativeness of the phalangeal character because of much character conflict. Until this character and others are analyzed in further detail, the monophyly of the *flavescens* group sensu Lynch (1993) has to be regarded as questionable.

The digital reduction (four toes in 17% specimens, n = 23) of *Atelopus exiguus* is an intriguing feature which requires further research. Digital reduction in this species may be related to its small size (maximum SVL = 35.4 mm) as has been documented in other anurans (Alberch and Gale, 1985). Previously, complete loss of one toe has only been reported for *Psyllophryne didactyla* (Brachycephalidae) and *Didynamipus sjoestedti* (Bufonidae) (Alberch and Gale, 1985). We report herein the first recorded instance of intraspecific variation in this character.

In spite of the morphological homogeneity of larvae of *Atelopus,* several morphological features, as well as coloration, are useful in distinguishing among the larvae of 29 species (according to our records) for which information is available.

Among the 29 species, only brief notes on larvae of 16 species are provided by Ruíz-Carranza and Osorno-Muñoz (1994), Ruíz-Carranza et al. (1994), and Vélez-Rodríguez and Ruiz-Carranza (1997), and few comparisons are possible. The tadpole of *A. exiguus* is rather similar to that of other high altitude species such as *A. ignescens* (Duellman and Lynch, 1969), *A. peruensis* (Gray and Cannatella, 1985), and *A. subornatus* (Lynch, 1986), and it shares with them black color in life and a shallow tail. It is distinguished from *A. ignescens* and *A. peruensis* by having white marks on the body and tail and from *A. subornatus* by lacking white bands on the tail. The position of marks (white, metallic gold, yellowish brown, or yellow in live specimens, and white, light gray, or translucent in preserved specimens) on the rostrum, behind the eyes and at distal part of the dorsal body of *A. exiguus* larvae is similar to *A. balios* (Coloma and Lötters, 1996), *A. certus* (Duellman and Lynch, 1969), *A. tricolor* (Lavilla et al., 1997), *A. elegans, A. eusebianus, A. famelicus, A. farci, A. pictiventris, A. sonsonensis* (Vélez-Rodríguez and Ruiz-Carranza, 1997), *A. simulatus* (Ruíz-Carranza and Osorno-Muñoz, 1994), *A. varius* (Lötters 1996*b*; Starrett, 1967), *A. spumarius* (Duellman and Lynch, 1969; Haas, 1995) (including *A. pulcher* described by Gascon, 1989), and *A. zeteki* (Lindquist and Hetherington, 1998). Larvae of *Atelopus exiguus* are distinguished from those of *A. balios, A. certus, A. tricolor, A. varius, A. spumarius,* and *A. zeteki* by having a more long tail (tail length 60.5% versus 52%, 51.5%, 56%, 57.6%, 49.6% and 52.5%, respectively; data taken or calculated from the tadpole descriptions). *Atelopus exiguus* larvae are distinguished from those of *A. sonsonensis* by having white marks in life instead of yellow marks. The black body and uniform black caudal musculature of the tadpole of *A. exiguus* distinguishes it from larvae of *A. flavescens* (Lescure, 1981) and *A.* sp. (Mebs, 1980, under the name *A. cruciger*). *Atelopus exiguus* larvae are distinguished from those of *A. carrikeri* (senior synonym of *A. leoperezii* fide Coloma, 1997), *A. ebenoides* (*A. e. marinkellei* sensu Vélez-Rodríguez and Ruiz-Carranza, 1997), *A. laetissimus, A. muisca, A. nahumae, A. quimbaya, A sernai, A. minutulus,* and *A. nicefori* by having conspicuous white marks on the rostrum, posterior to the eyes and at distal part of the dorsal body. *Atelopus sernai* has rostral marks but lacks the other marks.

The relevance of tadpole characters to the systematics of *Atelopus* was discussed by Duellman and Lynch (1969), Coloma and Lötters (1996), Lavilla et al. (1997), and Vélez-Rodríguez and Ruiz-Carranza (1997). Lavilla et al. (1997) stated that larvae of *A. tricolor* were unique in possessing a single submarginal papilla on each side of the oral disc; however they failed to compare them to the larvae of *A. balios* which possess submarginal papillae at the same position. Vélez-Rodríguez and Ruiz-Carranza (1997) suggested that the absence of conspicuous white or yellow marks on dorsum and flanks of body and tail may be plesiomorphic for *Atelopus,* based on a comparison with larvae of *Bufo marinus* and *B. margaritifer* (= *B. typhonius*) which have a uniform black or brown coloration.

The call of *Atelopus exiguus* is similar in overall structure to the pulsed calls of 10 other species of *Atelopus* for which descriptions are available (Cocroft et al., 1990). This is the first call of a species of *Atelopus* from paramo habitat to be described, and its structural similarity to calls of lowland and midelevation species suggests that environmental selection pressures played a minor role in call evolution in *Atelopus.* In contrast, some studies have found evidence of selection for different calls in different habitats; for example in populations of *Acris crepitans* (Ryan et al., 1990; Ryan and Wilczynski, 1991). Physical and spectral parameters such as call length, notes per call, notes per second, and dominant frequency fall within the range of variation described for other species of *Atelopus* (ranges of call length 227–1240 ms, notes per call 14–99, notes per second 39.3–146, and dominant frequency 1620–3380 Hz; Cocroft et al., 1990). The note rate, which remains constant through the call, is similar to *A. cruciger* and *A.*

varius. This is in contrast to eight other species in which note rate increases from the beginning to the end of the call. The structure of the pulsed call of *A. exiguus* is similar to that described for other *Atelopus* by Cocroft et al. (1990). These authors argued that lack of divergence in calls of *Atelopus* is due to the rarity of sympatry among species and to the relatively minor importance of acoustic communication in their intraspecific social interactions, and the former hypothesis is supported by us in that *A. exiguus* is not sympatric with any other *Atelopus*.

Larval and call features may or may not be important in assessing phylogenetic relationships in groups of anurans. For example, larval characters have added phylogenetic information to the anlysis of relationships of New World microhylid genera (Wild, 1995). On the other hand, when examining the phylogeny of frogs of the *Physalaemus pustulosus* species group, Cannatella et al. (1998) proposed that the incongruence between call data and other data partitions is consistent with the idea that the advertisement calls of this group are under strong sexual selection and of limited phylogenetic utility. The phylogenetic importance and evolutionary history of larval and call characters in *Atelopus* should be tested as more comparative data across taxa become available.

Resumen

Se revisa la taxonomía de algunas poblaciones de *Atelopus* de zonas altas de Ecuador, las cuales previamente fueron incluidas en *Atelopus ignescens*. Se designa un neotipo para *Atelopus ignescens* y se presenta datos de variación y distribución. *Atelopus ignescens* es una especie restringida a los Andes del norte de Ecuador, y se caracteriza por la presencia única de una zona de espículas y conos en las regiones gular y pectoral de las hembras. Se reconoce a *Atelopus exiguus* de los altos Andes del sur de Ecuador como una especie válida; además se describe su lectotipo, canto y renacuajo. Se la diagnostica por caracteres de morfología externa y coloración en vivo. Algunos especímenes de *Atelopus exiguus* carecen del Dedo I del pie; esta característica es inusual y requiere ser más investigada.

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APPENDIX I

Specimens Examined

Atelopus bomolochos.—ECUADOR: *Provincia Azuay:* vic. E. of Cuenca, 2535 m, CAS 85139–41; Sevilla de Oro (2800 m), 82 km E of Cuenca, CAS 85341, 93912 (paratopotypes); 3 km E of Sigsig, 2460 m, QCAZ 1893–94; 10 km S Cutchil, QCAZ 1861–69, KU 217335–36, 217441–44; 19.3 km S Cutchil, KU 217445; *Provincia Cañar:* between Juncal and General Morales, app. 2500 m, CAS 93906 (paratype).

Atelopus boulengeri.—ECUADOR: *Provincia Mo-*

*rona Santiago:*Río Piuntza, 1830 m, KU 147071–72, 147074, 147076–77, 147079.

Atelopus carrikeri.—COLOMBIA: *Departamento Magdalena:* Sierra Nevada de Santa Marta, Cuchilla Cebolleta, ICN 32429 (C&S); *Departamento Guajira:* Santa Marta mountains, Páramo de Macotama (2430–4570 m elevation), UMMZ 48273 (paratype); *Departamento del César:* Río Guatapurí, Sierra Nevada de Santa Marta, USNM 123561–62.

Atelopus exiguus.—ECUADOR: *Provincia Azuay:* Zurucuchu, W of Cuenca, 3250 m, SMF 4046 (lectotype), 4047–51, 3170–71, 3916 (paralectotypes); Laguna de Zurucuchu (= Laguna Llaviuco), 3200 m, KU 120381 (cleared and stained), 120385 (cleared and stained), 120387, QCAZ 3744; 10 km W Cuenca, QCAZ 4957 (cleared and stained); Río Quinuas, 15 km W Cuenca, 3150 m, QCAZ 3668 (12 tadpoles), QCAZ 3669 (1 tadpole); Parque Nacional Cajas, 15–20 km W Cuenca, 3200 m, MHNG 2499.72–75, 2499.76 (cleared and stained), 2499.77–79; Bosque de Mazán, QCAZ 1666; Lagunas de Cajas, 3850 m, MHNG 2258.41–42; Girón, Quimsacocha (páramo sur del Cajas), 3700 m, QCAZ 8835.

Atelopus ignescens.—ECUADOR: *Provincia Imbabura:* Lagunas de Mojanda, QCAZ 1852–56; *Provincia Napo:* Oyacachi, QCAZ 275–76; *Provincia Pichincha:* Páramo de Guamaní, La Virgen, 3800–4200 m, MHNG 2410.1–6, 2409.95–100, 2273.48, 2273.61, 2273.81–82, 2273.84–97; QCAZ 266 (cleared and stained); *Provincia Cotopaxi:* Laguna de Limpiopungo, 4000 m, QCAZ 254, 385–86, 8797; Zumbagua, MHNG 2384.97–100, 2385.1–10; *Provincias Cotopaxi-Napo:* ca. 20 Km (airline) southeast of Latacunga, on road from San Miguel de Salcedo to Lagunas de Anteojos and towards the east, 01° 01' S and 78° 25' W, approximately between 3200–3800 m, QCAZ 702 (neotype), 703–16, 1857–58; *Provincia Chimborazo:* 20 km N Riobamba, QCAZ 9; *Provincia Bolívar:* ca. Chimborazo (Ambato-Guaranda road), QCAZ 641.

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SLOWLY-EVOLVING PROTEIN LOCI AND HIGHER-LEVEL SNAKE PHYLOGENY: A REANALYSIS

LARRY BUCKLEY[1,3], MAUREEN KEARNEY[2], AND KEVIN DE QUEIROZ[3]

[1]*Biology Department, Rochester Institute of Technology, Rochester, NY 14623, USA*
[2]*Department of Biological Sciences, George Washington University, Washington, DC 20052, USA*
[3]*Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA*

ABSTRACT: We reanalyzed data from a recently published study of higher-level snake relationships based on four slowly-evolving protein loci. The original study used phenetic clustering of genetic similarities and presented a single, highly resolved tree. Our reanalyses of these data reveal that the single published phenogram is only one of at least 10,000 equivalent UPGMA phenograms, the consensus of which is largely unresolved. Additive distance analysis and character-based parsimony analysis of the data also yield little resolution, indicating that these data are highly ambiguous regarding higher-level snake phylogeny. The high degree of resolution in the published phenogram is an analytical artifact resulting from the failure to consider alternative trees implied by tied distance values, which are numerous in the distance matrix derived from this particular data set. Although the published phenogram exhibits general agreement with traditional hypotheses about snake relationships, the same appears to be true for the thousands of equivalent phenograms, discrepancies among which sum to a substantial loss of resolution. Although the four loci sampled are evolving slowly relative to other commonly surveyed protein loci, they are nevertheless evolving too rapidly to be informative about the higher level phylogeny of snakes.

Key words: Allozymes; Genetic distances; Minimum evolution; Parsimony; Phenetic clustering; Phylogeny; Serpentes

IN a recent study of the higher-level relationships among snakes, Dowling et al. (1996) analyzed genetic similarities based on four protein-coding loci using average linkage phenetic clustering, specifically, the unweighted pair group method using arithmetic averages (UPGMA). Their result was a single, highly resolved tree (Fig. 1) that delineated 103 groups and exhibited general agreement with traditional