

A taxonomic revision of *Atelopus pachydermus*, and description of two new (extinct?) species of *Atelopus* from Ecuador (Anura: Bufonidae)

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Table of contents

Abstract	1
Resumen	2
Introduction	2
Materials and methods	3
Results	3
Taxonomic status and redescription of <i>Atelopus pachydermus</i> and description of a new species.....	3
<i>Atelopus pachydermus</i> (Schmidt, 1857)	4
<i>Atelopus petersi</i> sp. nov.....	11
New species from southern Ecuador	16
<i>Atelopus onorei</i> sp. nov.	16
Osteology of new species	23
Discussion	27
Acknowledgments	28
References	29
Appendix	32

Abstract

Atelopus pachydermus is redescribed on the basis of the retraced holotype and recently collected specimens. Comparisons with the holotype confirmed that this species occurs neither in Pacific Colombia, nor in the northeastern Cordillera of Ecuador, as proposed by previous authors. It occurs in the northwestern Andes of Peru and adjacent Ecuador. Populations from the Cordillera Oriental in northern Ecuador (some of them previously allocated to *A. pachydermus*) are described as a new species, which is distinguished from other *Atelopus* by size, coloration, and by having white digital pads that contrast with adjacent black phalanges. In addition, a population of *Atelopus* from the Andes of southwestern Ecuador, previously included in the *Atelopus bomolochos* complex, and having an aqua blue iris is described as a new species. We include osteological data of both new species. Predictions of numbers of species of *Atelopus* to be discovered and described, as well as of numbers for Ecuadorian amphibian diversity, indicates that these faunas are yet largely undescribed. Because recent records of *A. pachydermus* and the two new species are lacking despite search efforts, we assume that they are possibly extinct, similar to many other Andean *Atelopus*. Thus, we categorize these species either as

possibly extinct or, applying IUCN Red List criteria, as Critically Endangered. Current evidence suggests that amphibian extinctions in the Ecuadorian and Peruvian Andes have been more drastic than previously recognized.

Key words: Anura; Bufonidae; *Atelopus onorei* sp. nov.; *Atelopus bomolochos*; *Atelopus petersi* sp. nov.; *Atelopus pachydermus*; Ecuador; Extinction; Morphology; New species; Osteology; Peru; Systematics

Resumen

Se redescubre *Atelopus pachydermus* en base al holotipo y especímenes recientemente colectados. Al comparar este material con el holotipo, se confirma que esta especie no proviene de la zona Pacífica de Colombia, ni de la Cordillera nororiental de Ecuador, como había sido propuesto por otros autores. *Atelopus pachydermus* proviene de los Andes del noroeste de Perú y sureste de Ecuador. Las poblaciones de la Cordillera nororiental de Ecuador (algunas de ellas previamente incluidas en *A. pachydermus*) se redescubren como una especie nueva, la cual se distingue de otros *Atelopus* por características del tamaño, coloración y por poseer almohadillas digitales blancas que contrastan con las falanges adyacentes. Una población de *Atelopus* del suroeste de los Andes de Ecuador, previamente incluida en el complejo de *A. bomolochos*, es descrita como especie nueva; ésta es única en el género por poseer el iris azulado. Incluimos datos osteológicos de ambas especies nuevas. Al predecir el número de *Atelopus* por ser descubiertos y descritos, al igual que de los anfibios de Ecuador, es notorio que la descripción de estas faunas todavía es muy incompleta. Debido a la ausencia de registros recientes de *A. pachydermus* y las dos especies nuevas, asumimos que estarían extintas, de manera similar a lo ocurrido con otros *Atelopus* andinos. Por tanto, categorizamos a estas especies como posiblemente extintas o, aplicando las categorías de la UICN, como críticamente amenazadas. La evidencia disponible sugiere que las extinciones de anfibios en los Andes ecuatorianos y peruanos han sido mucho más drásticas que lo que se ha reconocido previamente.

Palabras claves: Anura; Bufonidae; *Atelopus onorei* sp. nov.; *Atelopus bomolochos*; *Atelopus petersi* sp. nov.; *Atelopus pachydermus*; Ecuador; Especies nuevas, Extinción; Morfología; Osteología; Perú; Sistemática

Introduction

Among the Neotropical bufonids, *Atelopus* is a remarkably large genus containing more than 115 species including at least 34 undescribed ones (La Marca *et al.*, 2005; Rueda-Almonacid *et al.*, 2005, and authors' unpubl. data). Apart from species awaiting description, there still exist several unsolved alpha-taxonomic problems among the described *Atelopus* (e.g., Lötters, 1996; Rueda-Almonacid *et al.* 2005). Difficulties in solving some of these problems arise because the type material is lost, or original descriptions do not provide accurate locality data. One of the long-lasting confusions of this kind is the status of *Atelopus pachydermus* (Schmidt, 1857). According to Savage (1970), Peters (1973), Frost (1985), and Lötters (1996), the type specimen of *A. pachydermus* is lost. A recent search at Muzeum Przyrodnicze, Uniwersytetu Jagiellońskiego of Kraków in Polonia (KM) revealed that the holotype of *A. pachydermus* still exists (Fig. 1). Its association to the original and a subsequent description by Schmidt (1857, 1858) and an illustration of the holotype (Schmidt, 1858:Fig. 26) is unequivocal. In addition, comparisons with specimens collected in the Andes of northeastern Peru and southeastern Ecuador suggest that the name *A. pachydermus* is applicable to populations in the Peruvian departamentos Cajamarca and Amazonas (compare Figs. 1, 3A; also see either Fig. 26 of Schmidt, 1858 or Fig. 6 of Cochran and Goin, 1970) and the Ecuadorian Provincia Zamora Chinchipe. In contrast, similar looking populations from provincias Napo (i.e., *A. pachydermus sensu* Peters, 1973) and Chimborazo in Ecuador are not conspecifics and we describe them as a new species. At the same time, we found that a population of *Atelopus* from the Andes of southwestern Ecuador, Provincia Azuay, previously referred to *A. bomolochos* Peters, 1973 (e.g. Lötters, 1996:Fig. 6) represents another undescribed taxon. The purpose of this paper is (1) to clarify the taxonomic status of *A. pachydermus* from Andean Peru and Ecuador including a redescription, and (2) to describe the two new species from Andean Ecuador mentioned.

Materials and methods

The redescription of *Atelopus pachydermus* is based on the examination, measurements, and photographs of the holotype (KM 1013/1356, Fig. 1) and additional specimens from northeastern Peru deposited in the MUSM (Museo de Historia Natural, Universidad Mayor de San Marcos, Lima). We complement the redescription by providing an English translation (from old-style German) of Schmidt's 1857 description.

Specimens examined and locality data other than type specimens are listed under Referred Specimens, before the diagnoses and in the Appendix. Institutional abbreviations other than KM and MUSM follow Leviton *et al.* (1985) and Frost (2006). Sexes of adults were determined by external features as defined by Coloma *et al.* (2000), or through dissection. We use the term spiculae to refer to pustular warts, and coni to refer to spiculae with pointed projections. Measurements are in millimeters (mm); they were taken on preserved adults with digital calipers to the nearest 0.1. We indicate webbing formulae in the manner described by Savage and Heyer (1969, 1997) and Myers and Duellman (1982). Cleared and stained material was prepared following Dingerkus and Uhler (1977). To facilitate comparisons, abbreviations and definitions of measurements, and diagnosis follow Coloma *et al.* (2000) and references therein. The template for the osteological description approximates Coloma (2002); however, only features that show variation considered systematically useful are described, whereas, general features are not described, but illustrated. Osteological nomenclature follows Coloma (2002) and references therein. Finger nomenclature follows Guayasamin and Trueb (2007). Thus, fingers are numbered preaxially to postaxially from II–V. Color transparencies cited in the text are deposited at QCAZ.

Multivariate analysis was used to assess the degree of morphometric differentiation among populations of the new species of *Atelopus* from eastern Ecuador, and between *A. bomolochos* and the new species from southwestern Ecuador. To remove the effect of covariation with SVL, Principal Components Analysis (PCA) was applied to the residuals of the linear regressions between SVL and seven other measured variables (cf. Vitt *et al.*, 2000). Only PCA components with eigenvalues >1 were retained. JMP IN 5.1, The statistical discovery software (© SAS Institute Inc., 1989–2003), was used to perform statistical analyses.

Results

Taxonomic status and redescription of *Atelopus pachydermus* and description of a new species

Atelopus pachydermus was labeled as collected by the Polish botanist Josef Ritter von Rawicz Warszewicz at “Neu-Granada” (Schmidt, 1857:15). Nueva Granada, an ancient political unit, comprised of parts of present Panama, Colombia, and Ecuador (Savage, 1970). Later, Schmidt (1858) amended that the species' country of origin was (translated from German): “West of New-Granada, near Bonaventura, at an altitude of 5000 feet” (= 3777 feet = 1150 m above sea level according to corrections done by Savage, 1970:278–279). Because this locality could not be located by Cochran and Goin (1970), Rivero (1968), or Peters (1973), all these contributors concluded that perhaps the type locality referred to the vicinity of the town of Buenaventura on the Pacific coast of Colombia, Departamento Valle del Cauca. However, at the same time, Rivero (1968) and Peters (1973) doubted that the holotype of *A. pachydermus* (which apparently was not available to the authors) originated from western Colombia. They concluded that the type locality might be in error (as noted for some other specimens collected by J. Warszewicz; cf. Savage, 1970) because the holotype descriptions by Schmidt (1857, 1858) were not referable to any population of *Atelopus* known from Colombia (see also more recent papers dealing with Colombian *Atelopus*; e.g., Lötters, 1996; Ruiz-Carranza *et al.*, 1996). In contrast, Rivero (1968) and Peters (1973) found that specimens of *Atelopus* from subparamos in the eastern Andes of northern Ecuador, Provincia Napo (although no town named “Bonaventura” has been located in the area),

were similar to the holotype descriptions by Schmidt (1857, 1858). Both authors provisionally assigned these Ecuadorian toads to *A. pachydermus*, which was followed by subsequent authors (e.g., Lötters, 1996; La Marca *et al.*, 2005). Rivero (1965) provided a brief account (based on Schmidt's 1858 figure) in a comparison of *A. pachydermus* to other taxa, whereas Peters (1973) provided a more detailed description mostly based on Ecuadorian specimens from Provincia Napo. More recently, Rodríguez *et al.* (1993) and Lötters (2005) reported *A. pachydermus* from humid montane forests in the departamentos of Amazonas, Cajamarca, and La Libertad, Peru.

Our search for the type locality of *Atelopus pachydermus* reveals that it is in error, as suggested by Lötters (1996), who noted that the nominal collector of the type material had likely not visited the region of the stated type locality. Nonetheless, there are two localities with a name similar to Bonaventura in Panama. These localities are located in what use to be called Western New Granada. Both are in eastern Panama. One is San Buenaventura (8°30' N, 78°30' W, Distrito Chimán, Provincia Panama, Panama, 55 m above sea level) on the Pacific Coast of Panama. Another is Buenaventura (9°31' N, 79°40' W, Provincia Panama, Panama, 29 m above sea level) on the Caribbean Coast of Panama. Neither of these localities fits the elevation given for the type locality of *A. pachydermus*. Additionally, there are no specimens of *Atelopus* from mountains nearby these towns (e.g., Cordillera de San Blas near Buenaventura) allocable to *A. pachydermus*.

Collections of *Atelopus* in the twentieth century (see Savage, 1972), on Warszewicz's route described by Savage (1970) in the Chiriquí region (Boquete-Róbalo trail) of Panama did not reveal the existence of any specimen that could be associated with the holotype of *A. pachydermus*. Also, we could not locate on maps any town or locality named Bonaventura in this region. Nevertheless, there are specimens from the Departamento Cajamarca, Peru, which are similar to *A. pachydermus* as originally described and by our comparisons with the holotype. Fortunately, an allocation of this name to the Peruvian specimens is reasonable considering that Warszewicz visited Peru in 1852. According to Savage (1970), on 28 December 1852, Warszewicz was at Huancabamba, Departamento Piura, Peru. Thus, the possibility that a mislabeling occurred and that the type originated from Peru is strengthened. Similar cases of mislabeling of at least four other species of South American anurans collected by Warszewicz has been demonstrated (see Savage and Heyer, 1969; Savage, 1969, 1970; Duellman, 1970; Duellman and De la Riva, 1999; De la Riva *et al.*, 2000; De la Riva, 2004).

A combination of unique SVL and features of the color pattern associates the type specimen of *Atelopus pachydermus* with the specimens from Cajamarca, Peru. The only Central American species of *Atelopus* that approximates the SVL of *A. pachydermus* (male holotype 52.9 mm SVL) is *A. zeteki* Dunn, 1933 (males 35.0–40.0 SVL; Lötters, 1996). In Central America, dorsal color patterns similar to the one present in the holotype of *A. pachydermus* are found in *A. senex* Taylor, 1952, *A. varius* (Lichtenstein and Martens, 1856), and *A. zeteki*. None of these has spots on the dorsal surfaces of the shanks except *A. zeteki*, a smaller species that differs by having more slender body shape and almost smooth skin. In contrast, the large SVL, body shape, skin texture, and color pattern, especially the presence of spots on dorsal surfaces of the shanks, associate the holotype of *A. pachydermus* with the specimens from Cajamarca.

***Atelopus pachydermus* (Schmidt, 1857)**

Phirix pachydermus Schmidt, 1857:15. Holotype: KM 1013/1356 from “Neu-Granada”; Schmidt, 1858:257.

Phryniscus pachydermus: Hoffmann, 1878:635 (by implication).

Phryniscus cruciger (non Lichtenstein and Martens): Boulenger, 1882:154 (partim).

Atelopus cruciger (non Lichtenstein and Martens): Nieden, 1926:84 (partim).

Phirix pachydermus: Dunn, 1931:397.

Atelopus subornatus (non Werner): Dunn, 1944:81.

A.[telopus]pachydermus: Rivero, 1963:107.

Atelopus pachydermus: Rivero, 1965:138 (partim); Peters, 1973:34–37 (partim); Lötters, 1996:39–40 (partim), 2005:97 (partim).

Referred specimens. Peru: MUSM 6524 from Camporedondo, Departamento Amazonas; MUSM (field number 890081a), MUSM (field number 890085), MUSM 13810–12, MUSM 5984, 6507 collected from nearby Grutas of Parque Nacional Cutervo, Departamento Cajamarca, obtained on March 1984 by Alfonso Miranda-Leiva; Ecuador: MHNG 2259.8–9 from Valladolid-Yangana, approximately 2600 m above sea level, Provincia Zamora Chinchipe, obtained on September 1985 by Giovanni Onore and Luis A. Coloma.

Diagnosis. (1) A large species with mean SVL in adult males 51.3 mm (44.2–56.4, $n = 7$) and in adult females 55.9–61.6 ($n = 2$); (2) hind limbs short, tibiotarsal articulation reaching to temporal region, when leg carried forward along body (tibia length/SVL = 0.375–0.439, $n = 9$); (3) phalangeal formula of hand 2–2–3–3 (suspected from external examination), basal webbing absent; (4) foot webbing formula $I(0^+)—(1^- \text{ to } 1^+)II(0^+ \text{ to } 1^-)—(1 \text{ to } 2^+)III(1 \text{ to } 2^-)—(2^+ \text{ to } 3)IV(2 \text{ to } 3^+)—(0^+ \text{ to } 1^-)V$; (5) snout acuminate, with tip gently rounded in dorsal view; upper jaw slightly protruding beyond lower; (6) tympanic membrane absent; (7) dorsum with widely scattered or dense well-defined, rounded warts; (8) scattered spiculae on posterior and ventrolateral surfaces of body or absent; (9) vertebral neural processes inconspicuous; (10) dorsum yellow with dark brown pattern of marks, blotches and/or lines (dorsum cream, tan, or olive with pale to dark brown pattern in preservative); (11) venter white, occasionally orange or red (venter tan to yellow with pale to dark brown blotches in preservative); (12) gular region without warts, spiculae, or coni.

Atelopus pachydermus is distinguished from all *Atelopus* by its large size, except *A. Boulengeri* Peracca, 1904, *A. arsyecue* Rueda-Almonacid, 1994, and *A. laetissimus* Ruiz-Carranza, Ardila-Robayo and Hernández-Camacho, 1994. It differs from all of them by a different color pattern. *Atelopus Boulengeri* usually has a uniform dorsum, and is larger than *A. pachydermus* (mean female SVL of *A. Boulengeri* [after data in Coloma, 1997]) = 65.9 vs. 55.9–61.6 in *A. pachydermus*). *Atelopus arsyecue* has large white, cream, creamy-yellow, round or elongated marks (Rueda-Almonacid, 1994; Renjifo and Renjifo, 2005:57). *Atelopus laetissimus* has a reticulated pattern usually bearing an X-mark on the anterior dorsum (Ruiz-Carranza *et al.*, 1994; Galvis, 2005:83).

Description of holotype. Adult male (Fig. 1), well preserved; original colors apparently bleached; forearm twice as thick proximally as distally; keratinized areas on thumb. Head slightly longer than wide; head length and head width each less than one third SVL; snout acuminate, tip of snout with swollen gland, rounded in dorsal view, slightly protruding beyond anterior margin of the jaw in profile; nostrils not protuberant, barely visible from above, situated slightly behind level of apex of lower jaw; canthus rostralis distinct, convex from tip of snout to nostril, concave from nostril to eye, swollen posteriorly; loreal region concave, upper lip slightly flared, interorbital and occipital regions flat, smooth, eyelid flared without distinct tubercles; postorbital crest glandular; tympanic membrane absent; choanae minute, rounded; tongue twice as long as wide, broader anteriorly, less than its posterior half not attached to mouth's floor. Forearm relatively short, length of forearm less than one third SVL; metacarpal tubercles distinct, round, outer about twice size of somewhat weaker inner; few weak supernumerary tubercles present; subarticular tubercles at joints of fingers IV and V; digital tips slightly broadened, with round pads; thumb relatively short, more than half length of hand, apparently having two phalanges; nuptial pads on inner or dorsal thumb absent; basal webbing and fringes on fingers absent; relative length of fingers $II < III < V < IV$. Tibia relatively short, 39 % of SVL; no fold on distal half of inner edge of tarsus; metatarsal tubercles distinct, rounded outer slightly larger than ovoid inner; supernumerary tubercles absent; subarticular tubercles present at joints of toes III–V, digital pads distinct; toe webbing formula $I(0^+)—(1)II(0^+)—(2)III(2^-)—(3)IV(3^+)—(0^+)V$, webbing always becoming fringe-like distally; relative length of toes $I < II < III < V < IV$.

Dorsum smooth, flanks wrinkled, both with scattered, round, flattened warts about 2 mm in diameter (no conspicuous spiculae); no warts on dorsum of head (present up to squamosal region) and sides of head including temporal region (warts behind angle of jaw and on postorbital crest). Wrinkling and warts on dorsum of upper arm, elbow, femur and knee. Ventral surfaces slightly wrinkled, without warts, spiculae or coni, except for smooth forearm and entire leg. Cloaca opening an inconspicuous tube slightly above midlevel of thighs,

directed posteriorly; no warts around cloacal opening.

In preservative (~70% ethanol; Fig. 1), dorsally and ventrally cream, with pale brown almost symmetrical linear pattern and some pale brown warts on dorsum. Pale brown, round blotch (about diameter of eye) each on thigh, shank, inner and outer heel, foot, ventral tibia, proximal metatarsus, and elbow (on dorsal parts of hind limbs, blotches may be duplicate); upper thumb light brown, ventral femur, and entire rest of arm and hand cream. Pale brown area below cloaca; nares cream; eyes black.

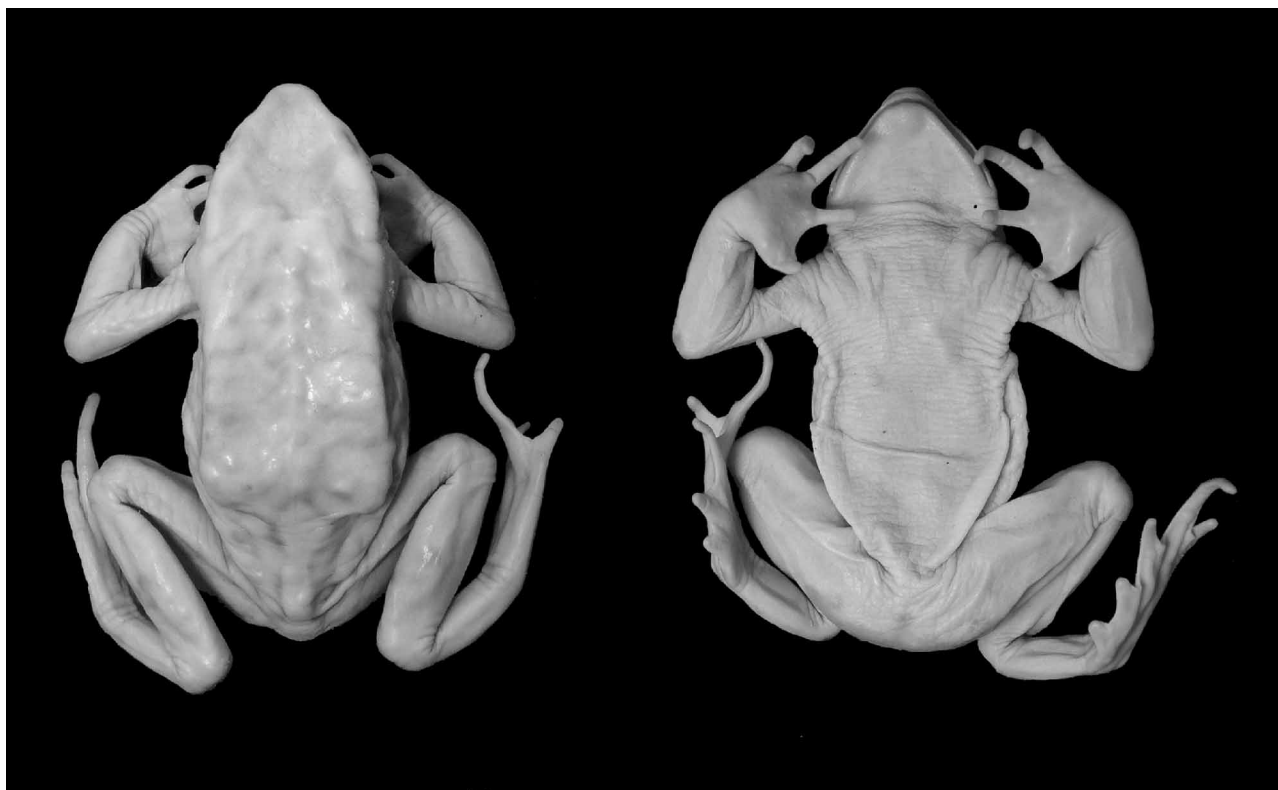


FIGURE 1. Holotype of *Atelopus pachydermus* (KM 1013/1356). Male, SVL = 52.9 mm.

Measurements (mm). SVL 52.9, TIBL 20.7, FOOT 23.5, HLSQ 14.9, HDWD 15.2, EYDM 4.6, EYNO 3.7, ITNA 4.5, SW 15.6, RDUL 16.7, HAND 14.8, THBL 9.3.

Variation. Meristic variation of seven adult males (including holotype) and two females is given in Table 1. Two juveniles from Ecuador (MHNG 2259.8–9) have SVL 29.7 and 21.7, respectively. They are tentatively assigned to *Atelopus pachydermus*. All specimens resemble the holotype. The two available females (MUSM 5984, 6524) are larger than the males; the forearm of females is not swollen; nuptial pads, present in adult males (but absent in MUSM 6507), cover dorsum and inner margins of Finger II. The number of warts is more or fewer than in the holotype. Warts, and spiculae are highly visible. In MUSM 6524 spiculae are present behind the eye, on posterior part of dorsum and on the thighs, and in MUSM 13812 also ventrolaterally on the body. In some specimens warts are present in the interorbital region, but never anterior to it; laterally warts are present in the temporal region; warts also are present around the cloaca opening. In MUSM 5984 (female) some warts are present on the chest, and in MUSM (field number 890085, male) warts are present on the chest and the ventral surfaces of the thighs. Subarticular tubercles are present on joints of phalanges of all toes and fingers. Scattered supernumerary tubercles are present on the soles and palms of all individuals. Foot webbing ranges as follows: **I**(0⁺)—(1⁻ to 1⁺)**II**(0⁺ to 1⁻)—(1 to 2⁺)**III**(1 to 2⁻)—(2⁺ to 3)**IV**(2 to 3⁺)—(0⁺ to 1⁻)**V**.

TABLE 1. Measurements of *Atelopus petersi* and *A. pachydermus*, respectively. Mean $\pm$ one SD, and range are given. Abbreviations follow Gray and Cannatella (1985) and Coloma *et al.* (2000). They are: SVL = snout-vent length; TIBL = tibia length; FOOT = foot length; HLSQ = head length; HDWD = head width; EY DM = eye diameter; EYNO = eye-nostril distance; ITNA = Internarial distance; RDUL = radio-ulna length; HAND = hand length; THBL = thumb length; SW = sacrum width. All measurements are in mm.

	<i>Atelopus petersi</i>			<i>Atelopus pachydermus</i>	
	Provincia Napo		Provincia Chimborazo	Departamentos Cajamarca & Amazonas	
	Males (n = 16)	Females (n = 7)	Females (n = 3)	Males (n = 7)	Females (n = 2)
SVL	38.9 $\pm$ 2.0 (35.2–42.1)	46.1 $\pm$ 2.08 (43.5–50.2) (n = 8)	45.6 $\pm$ 3.3 (43.3–49.3)	51.3 $\pm$ 3.9 (44.2–56.4)	58.8 (55.9–61.6)
TIBL	14.6 $\pm$ 1.14 (13.1–17.2)	16.5 $\pm$ 1.3 (14.2–17.9)	16.9 $\pm$ 0.8 (16.2–17.7)	21.2 $\pm$ 1.16 (19.4–23.1)	22.8 (22.4–23.1)
FOOT	15.9 $\pm$ 1.6 (13.8–18.4)	18.7 $\pm$ 1.1 (16.8–19.9)	16.6 $\pm$ 2.9 (14.7–19.9)	21.6 $\pm$ 1.86 (19.0–23.7)	23.3 (22.9–23.6)
HLSQ	11.7 $\pm$ 0.7 (10.5–12.8)	13.3 $\pm$ 0.7 (12.2–14.3)	13.1 $\pm$ 1.7 (11.5–14.8)	16.4 $\pm$ 1.38 (14.1–17.8)	17.1 (16.9–17.3)
HDWD	11.7 $\pm$ 0.8 (10.4–13.1)	12.9 $\pm$ 0.8 (12.0–14.0)	12.3 $\pm$ 1.3 (11.0–13.5)	15.6 $\pm$ 0.97 (13.8–16.9)	16.6 (16.4–16.7)
EYDM	3.7 $\pm$ 0.3 (3.3–4.1) (n = 8)	4.5 $\pm$ 0.7 (4.4–4.5) (n = 2)	4.4 $\pm$ 0.7 (3.9–5.2)	5.1 $\pm$ 0.51 (4.3–5.8)	5.1 (4.7–5.5)
EYNO			2.8 $\pm$ 0.1 (2.7–2.9)	3.7 $\pm$ 0.38 (3.2–4.1)	3.8 (3.6–4)
ITNA	4.3 $\pm$ 0.6 (3.5–5.4)	4.5 $\pm$ 0.6 (3.4–5.1)	4.6 $\pm$ 0.2 (4.4–4.7)	4.6 $\pm$ 0.27 (4.2–5.1)	5.15 (4.9–5.4)
RDUL	11.4 $\pm$ 1.3 (9.6–14.9)	13.8 $\pm$ 1.7 (11.6–17.2)	12.9 $\pm$ 1.1 (12.2–14.2)	16.1 $\pm$ 1.02 (14.9–17.9)	17.8 (17.3–18.3)
HAND	10.0 $\pm$ 0.75 (8.7–11.3)	12.1 $\pm$ 0.8 (10.9–12.9)	11.1 $\pm$ 1.0 (10.3–12.3)	13.8 $\pm$ 0.98 (12.5–15.2)	15.7 (15.4–15.9)
THBL	6.4 $\pm$ 0.5 (5.6–7.2) (n = 13)	7.8 $\pm$ 0.8 (6.7–8.7)	7.4 $\pm$ 0.9 (6.6–8.4)	8.7 $\pm$ 0.54 (8.0–9.5)	10.1 (9.9–10.3)
SW	12.6 $\pm$ 1.61 (10.7–15.3)	13.8 $\pm$ 0.1 (12.4–14.9) (n = 8)	12.5 $\pm$ 2.3 (9.9–14.0)	16.8 $\pm$ 1.36 (15.1–18.8)	19 (17.1–20.9)
TIBL/SVL	0.370 $\pm$ 0.019 (0.327–0.420, n = 26)			0.408 $\pm$ 0.020 (0.375–0.439, n = 9)	
HLSQ/SVL	0.295 $\pm$ 0.013 (0.266–0.321, n = 26)			0.314 $\pm$ 0.025 (0.281–0.356, n = 9)	
HDWD/SVL	0.290 $\pm$ 0.018 (0.254–0.322, n = 26)			0.300 $\pm$ 0.016 (0.271–0.327, n = 9)	
RDUL/SVL	0.292 $\pm$ 0.027 (0.261–0.374, n = 26)			0.311 $\pm$ 0.015 (0.286–0.337, n = 9)	
THBL/HAND	0.645 $\pm$ 0.026 (0.602–0.693, n = 23)			0.633 $\pm$ 0.016 (0.601–0.656, n = 9)	

Color variation in preservative (~70% ethanol): Dorsum and venter color pattern variation is depicted in Figure 2. The dorsum is tan or olive with a pale to dark brown pattern, or blackish brown with tan to pale yellow pattern. The dorsal pattern consists of irregular or semi-symmetrical markings, blotches and/or lines; the anterior head, or at least its periphery, and most parts of the feet and hands are tan or pale yellow. The arms and legs are tan or olive with pale to dark brown semi-symmetrical dots and blotches, or blackish brown with

tan or pale yellow markings. The venter is tan or yellow with few irregular pale to dark brown markings, most evident on the posterior part of the belly (at least brown markings below the cloaca); legs and arms always with markings, sole and palm in part or without markings, tarsal tubercles usually uniform yellow.

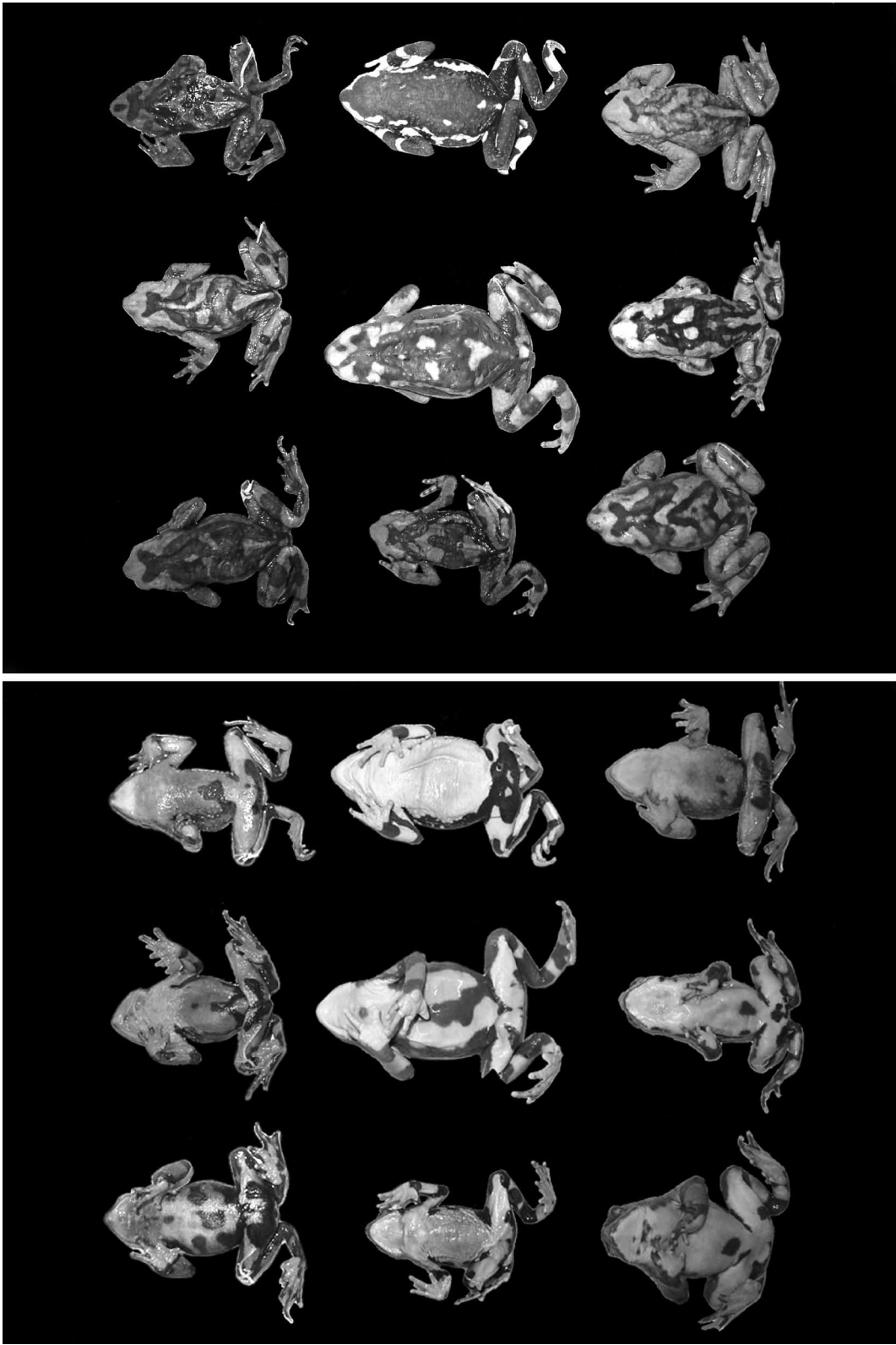


FIGURE 2. Color pattern variation of dorsum and venter of *Atelopus pachydermus*. Specimens are those listed under Referred specimens from Peru plus one individual (lower row at center), unnumbered at MUSM, which was neither measured nor examined in detail here.

Color in life (Fig. 3A): Lötters (2005:97) provided a color photograph of *Atelopus pachydermus* from Cutervo. As well, he provided a color in life description. “Dorsum very variable, mostly bright yellow with large black markings. The yellow color turns to white (occasionally orange or red) in ventral region.” Juveniles from Ecuador (MHNG 2259.8–9, color transparencies (QCAZ transparencies 2292–94, available at AmphibiaWebEcuador: <http://www.puce.edu.ec/zoologia/vertebrados/amphibiawebec/anfibiosecuador/bufonidae.html>) have dorsum, dorsal surfaces of limbs and flanks yellow-green with black marks. The iris has a yellow ring around the pupil.

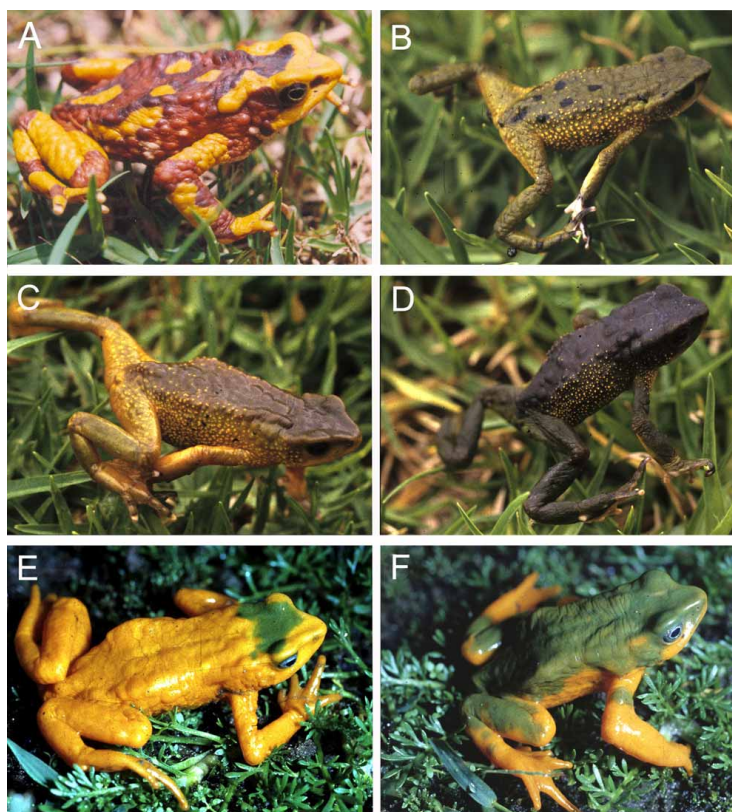


FIGURE 3. (A) *Atelopus pachydermus* from Cutervo, Peru (no museum number associated, photo AML); (B, C) *A. bomolochos* from 10 Km S Cutchil, Provincia Azuay (KU 217443–44, photos LAC); (D) *A. bomolochos* from 19 Km S Cutchil, Provincia Azuay (KU 217445, photo LAC); (E, F) *A. onorei* from Río Chipla, Provincia Azuay (no numbers associated, photos LAC).

Distribution, ecology and current population status. *Atelopus pachydermus* is known from the Cordilleras de Tarros (at Cordillera Occidental) and Central of the Andes of northern Peru, departamentos Cajamarca and Amazonas, and from Cordillera Oriental of the Andes in southern Ecuador, Provincia Zamora Chinchipe at about 2600 m above sea level (Fig. 4). In Peru, the area in which *A. pachydermus* occurs includes Humid Montane Forest, following the classification of types of vegetation of the Peruvian Andes as modified by Duellman (2004), who followed the system proposed by Tosi (1960). At the Peruvian Parque Nacional Cutervo (6° 00'–6° 20' S 78° 40'–78° 53' W, 2350–3350 m above sea level) annual mean temperature is 13.8 C. According to Duellman and Pramuk (1999), the vegetation in Peru of the humid montane forest of Cordillera Occidental is reduced to few trees, bushes (*Baccharis*) and bunch grasses; much of this forest has been cleared and cultivated, and at higher elevation *Eucalyptus* has been planted. In Ecuador, the locality is in Montane Cloud Forest (Valencia *et al.* 1999) in the Nudo de Sabanilla. In its proximities, 2000 hectares of forest and paramo habitats are protected within the Reserva Tapichalaca, which is located south of the Parque Nacional Podocarpus. Annual mean precipitation in this region is 1000–2000 mm and annual mean temperature is 12–18 C (Cañadas-Cruz, 1983).

ing inside the park. The only record from Ecuador is from September 1985. Searches at the Ecuadorian locality were carried out on February and September 2001 and on April 2004; they revealed no *Atelopus*.

Comments. Rodríguez *et al.* (1993) and Lötters (2005) reported *Atelopus pachydermus* from the Andes of northern Perú (departamentos Amazonas, Cajamarca, and La Libertad). They failed to provide museum and specimen numbers, and specific locality data. Listing Departamento La Libertad was an error and referred to an undescribed smaller, but otherwise similar species from Patate (see Catenazzi and Venegas, 2005:148).

Translation of the original description of *Phirix pachydermus* Oscar Schmidt (1857:14–15). "Phirix with robust fore- and hind limbs, head moderate; snout somewhat acute; skin thick, firm; color sulphur to whitish, light bluish pattern on dorsum and on femur as well as in cloacal region." For a translation from German into English of Schmidt's 1858 description see Cochran and Goin (1970:120).

Etymology. The specific name *pachydermus* is Greek and means thick skin.

Atelopus petersi sp. nov.

Atelopus pachydermus (non Schmidt): Rivero, 1963:107, 1968:23; Harding, 1983:58; Peters, 1973:34; Frost, 1985:31; Lötters, 1996:39; Coloma and Ron, 2001:38, La Marca *et al.* 2005:195.

Atelopus sp.: Almendáriz and Cisneros, 2005:155.

Holotype. QCAZ 300, from Ecuador: Provincia Napo: Cantón Quijos: near Oyacachi, (00°12'36" S, 78°42'00" W; approximately 3200 m above seal level), obtained on 3 April 1988 by Stella de la Torre-Salvador.

Paratypes. QCAZ 301 and 302 (cleared and double stained preparation), same data as holotype, collected by Manuel Pallares; QCAZ 298 (cleared and double stained preparation), 299, and 3154, same data as holotype, obtained on 30 March 1988 by Felipe Campos-Yáñez and Stella de la Torre-Salvador; QCAZ 4555 from Río Oyacachi, 2 Km east from Oyacachi, obtained on 19 August 1993 by Elicio Tapia; QCAZ 7678 from 1 km E of Oyacachi, 3150 m above sea level, obtained by Felipe Campos-Yáñez, Jorge Washington Izquierdo, and Diego Almeida-Reinoso, on 8 November 1996; USNM 193494, 193523, 193526–31 from Oyacachi, obtained by A. Proaño (no date); USNM 193521 from 2 Km E of Chalpi, 2755 m above sea level obtained on 7 July 1962 by James A. Peters; MHNG 2246.93–94 from 11 km (by road) east-southeast of Papallacta (00°03'S, 78°08' W), 2660 m above sea level, obtained on November 1985 by Giovanni Onore and Luis A. Coloma; KU 117874–79 from 3 Km east of Papallacta, 2900 m above sea level, obtained on 7 March 1968 by John D. Lynch, KU 142950 from 7.8 Km west-north-west of Cuyuja, KU 142951–2 from 5.7 Km east of Papallacta, KU 142953–54 from Río Papallacta, 4.6 Km east of Papallacta, 2890 m above sea level, obtained on 28 October 1971 by William E. Duellman; USNM 193496–502, 193506–18 from 0.5 km E of Papallacta, 3150 m above sea level, obtained on 5 July 1962 by James A. Peters and P. Spoecker; USNM 193503, from 1 km W of Papallacta, 3150 m above sea level, obtained on 6 July 1962 by James A. Peters *et al.*

Referred specimens. QCAZ 3870 and 3871 from Provincia Chimborazo: Lagunas de Atillo, obtained on 3 November 1990 by Anne Claire Desfossey; EPN 3307 from Laguna Cuyug (Cantón Guamote), 3318 m above sea level, 02° 10' 42" S, 78° 30' 30" W, obtained on 19 September 1986 by Ana Almendáriz.

Diagnosis. (1) A moderate-sized species with mean SVL in adult males 38.9 mm (35.2–42.1 mm, $n = 16$) and in adult females 46.0 mm (43.3–50.2, $n = 11$); (2) hind limbs short, mean tibia length/SVL 0.370 (0.327–0.420, $n = 26$); (3) phalangeal formula of hand 2-2-3-3, basal webbing absent; (4) foot webbing formula $I(0^+)—(0^{+1})II(0^{+1})—(0^{+1})III(0^{+1})—(2)IV(2^{-2})—(0^{+1})V$; (5) snout acuminate, slightly protruding beyond lower jaw; (6) tympanic membrane, tympanic annulus and stapes absent; (7) dorsal surfaces varying from smooth to warty; (8) white spiculae (cream in preservative) on forearms, flanks, and dorsal surfaces of thighs; (9) vertebral neural processes inconspicuous; (10) dorsum with yellow orange pattern to almost entirely black, flanks white (cream to cream and black in preservative); (11) venter yellow with or without black marks, or

uniform orange to reddish orange (cream to pale yellow, occasionally with black marks in preservative); (12) gular region without warts, spiculae or con.

Atelopus petersi is distinguished from all other species of *Atelopus* (except an undescribed species from southern Ecuador, Provincia Loja) by its white digital pads that contrast with adjacent black phalanges. *Atelopus petersi* is most similar to *A. bomolochos*, *A. pachydermus*, and *Atelopus* sp. (Provincia Loja) by having digital pads contrasting in color to adjacent phalanges. It differs from *A. bomolochos* and *Atelopus* sp. by having few spiculae on flanks (i.e., almost lacking); numerous spiculae present on flanks of *A. bomolochos* (Figs. 3B–D) and *A. sp.* It further differs from *A. bomolochos* by having white marks on flanks (absent in *A. bomolochos*). It differs from *A. pachydermus* by significantly smaller size (mean female SVL of *A. petersi* = 46.0 vs. 55.9–61.6 in *A. pachydermus*) and by lacking brown colors in life.

Description of holotype. (Figs. 5A–C). Head slightly longer than wide; head length and head width less than one third SVL (HLSQ/SVL = 0.284; HDWD/SVL = 0.262; snout truncate in dorsal view; barely protruding beyond anterior margin of jaw; tip of snout lacking swollen gland; nostrils slightly protuberant, directed laterally, situated behind level of apex of lower jaw; canthus rostralis distinct, slightly swollen from eye to nostril; loreal region concave, lips not flared, interorbital and occipital regions flat, smooth, eyelid flared without distinct tubercles; postorbital crest glandular; temporal areas warty; tympanic membrane and tympanic annulus absent; choanae small, rounded, widely separated; tongue more than twice as long as wide, slightly broader anteriorly, its posterior half not attached to mouth's floor; ostia pharyngea absent.

Forearm relatively short (RDUL/SVL = 0.297); palmar tubercle round, supernumerary palmar tubercles absent; thenar and subarticular tubercles distinct; digital tips with round pads; thumb relatively long (THBL/HAND = 0.628) having two phalanges; webbing on hands absent, fingers having lateral fringes; relative length of fingers II<III<V<IV.

Tibia relatively short (tibia/SVL = 0.360); no fold on distal half of inner edge of tarsus; outer metatarsal tubercle round, slightly raised, about two thirds length of oval inner metatarsal tubercle; supernumerary plantar tubercles absent; subarticular tubercles conspicuous, digital pads distinct; toes webbing formula I(0⁺)—(0⁺–1)II(0⁺–1)—(0⁺–1)III(0⁺–1)—(2)IV(2–2)—(0⁺–1)V; relative length of toes I<II<III = V<IV.

Dorsal surfaces varying from smooth to warty; scattered, irregularly distributed white spiculae and warts on flanks; warts on anterior and proximal dorsal surface of fore limb, throat, chest, and belly; undersides of hind limbs rugose, but free of warts; cloacal opening an inconspicuous tube at midlevel of thighs, directed posteriorly; low, elongated warts lateral to cloacal opening.

In preservative (~70% ethanol), cream with black, irregular marks on dorsum of body and limbs. Tips of fingers and toes cream dorsally and ventrally, contrasting to black adjacent phalanges. Dorsum of snout cream. Flanks cream and black, except infraorbital and canthal regions, which are cream. Venter cream anteriorly and cream with five scattered, irregular, black marks posteriorly. Limbs ventrally mostly cream, except at joints with irregular black marks. Palms and soles cream with black marks. Black mark below cloaca.

Measurements (mm). SVL 45.8, TIBL 165, FOOT 18.7, HLSQ 13.2, HDWD 12.0, ITNR 4.6, EYDM 4.5, EYNO 3.3, RDUL 13.8, HAND 12.2, THBL 7.6, SW 14.4.

Variation. Meristic variation is given in Table 1. Besides larger female size, the forearm in females is not swollen. Nuptial pads of adult males cover dorsum and inner margins of Fingers II and III. Nuptial pads vary from covering only Finger II (KU 117876) to Fingers II and III (KU 142950). When covering Finger III, nuptial excrescences can be more abundant proximally and at inner margin (KU 142954).

Color variation in preservative (~70% ethanol): Specimens from Napo, i.e., Oyacachi and Papallacta show large variation in dorsal and ventral patterns, from dorsum nearly entirely black (KU 117875) to mostly cream (QCAZ 299), and from venter white (KU 117875) to mostly marbled (KU 117879). Thus, they fit well descriptions and illustrations of color patterns in dorsal and ventral views provided by Peters (1973:Figs. 25–27, under *A. pachydermus*) of specimens from the same region. A juvenile (QCAZ 3154, SVL = 17.8 mm) has a fine mid-dorsal line.

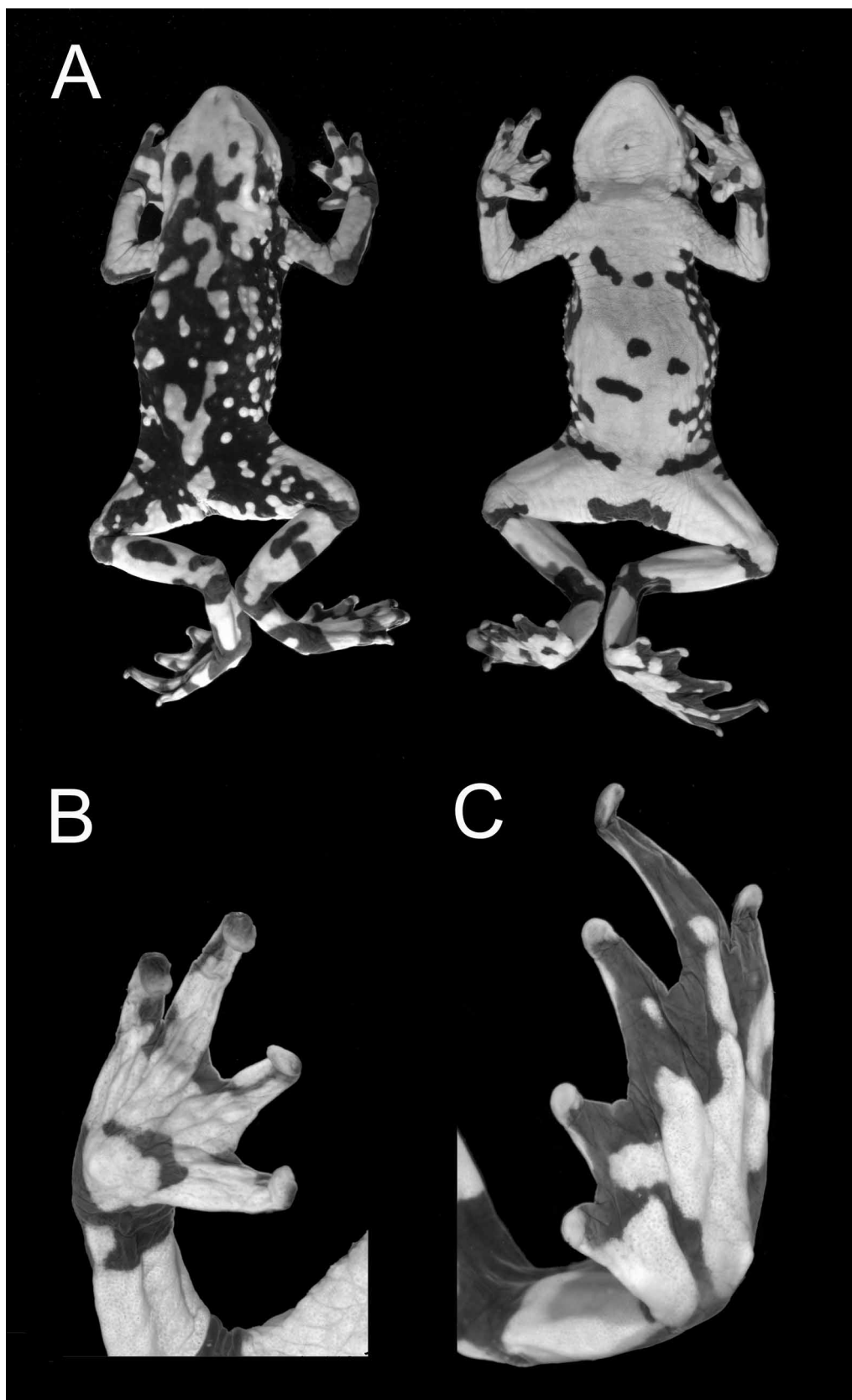


FIGURE 5. Holotype of *Atelopus petersi* (QCAZ 300): (A) female, SVL = 47.9 mm; (B) ventral view of right hand, enlarged 3.2 times of A; (C) ventral view of left foot; enlarged 3.2 times of A.

Referred Specimens from Provincia Chimborazo (QCAZ 3870, 3871, EPN 3307) are dorsally predominantly black, but have some cream blotches. QCAZ 3871 has a black dorsum with cream blotches, one on the snout, one on the upper eyelid, a small one on the interorbital region, two on the scapular region, and three on the sacral region; the flanks are black with minute white tips of spiculae. The loreal and suborbital regions are cream stippled with brown; the lower lip, throat, and chest are entirely white, whereas the belly and undersides of the limbs are black, except for a large white mark on belly. The palmar surfaces are white, and gray digits contrast with white tips of fingers dorsally, and all of Finger II is white dorsally. The dorsal surfaces of the feet, and soles are black; the ventral surfaces of Toe I, tips of toes, and metatarsal and subarticular tubercles are white. QCAZ 3870 differs from the previous individual by having the dorsum posterior to the head entirely black, whereas the dorsum of the head is mostly black with diffuse gray on the snout; the belly has four cream blotches and palms are mostly cream. EPN 3307 differs from QCAZ 3871 by having the dorsum of head mostly cream and four asymmetrical cream round blotches on the dorsum of the anterior part of body, the throat with a small black blotch, and the belly with a large white mark.

Color in life. Peters (1973:35) described specimens from Provincia Napo (Chalpi, Oyacachi and Papallacta) as follows: “The lighter dorsal areas are bright yellow. Many of the warts and pustules have white tops. The ventral surfaces are white in almost all individuals, but some may have orange areas or spots and some have red bellies.”

USNM 193518 has yellowish green spotting on dorsum and a bright orange belly (Field Notes of James A. Peters, 5 July 1962). KU 117874–75 is black above, 117874 is red below, 117875 is orange; metatarsal tubercles are yellow; KU 117876–79 juveniles are black above with dark faintly yellow blotches; black and white below. All specimens except 117879 are white below with black markings; in 117879 there is pale red pigment in the white areas posteriorly and dorsum black with few to many yellow spots. KU 117879 has yellow-white spots on back; flanks black with white spots; metatarsal tubercles white; iris dark brown (Field Notes of John D. Lynch, 7 March 1968). KU 142950, dorsum yellow and black; venter white and black; iris reddish brown (Field Notes of William E. Duellman, 27 October 1971). KU 142951–52, dorsum black with greenish yellow markings; venter black and white (Field Notes of William E. Duellman, 17 October 1971). KU 142953, dorsum green and black; KU 142954, yellow and black (Field Notes of William E. Duellman, 28 October 1971).

Lötters (1996:Fig. 11) and Coloma and Ron (2001:Fig. 29) provided color photographs of MHNG 2246.93 from 11 Km ESE of Papallacta. Almendáriz and Cisneros (2005:155) provided a color description and photograph of this species.

Referred specimen EPN 3307 from Provincia Chimborazo had a black dorsum, bearing scattered, small, greenish-yellow marks mostly on the cephalic region; venter with two yellow marks separated by a black stripe that extends toward dorsum (Field Notes of Ana Almendáriz, 19 September 1986).

Morphometric comparisons. SVL is not significantly different between females from Provincia Napo vs. Provincia Chimborazo ($t = 0.342$, $df = 9$, $P = 0.7402$). No males from Chimborazo are available for comparisons.

Two components with eigenvalues > 1.0 were extracted from the PCA of eight morphometric variables of 26 specimens from populations throughout the range of *Atelopus petersi*. The axes accounted for 57.5 % of the total variation. Along PC I, the highest loadings were for FL and HLSQ. Along PC II, the highest loadings were for SW and SVL. There is a wide overlap among the morphometric range of these populations.

Comments. The Provincia Chimborazo population seems conspecific with *Atelopus petersi*. However, at this time, further analyses are precluded by the small sample size (three females) from Provincia Chimborazo. Because this small sample size, we preferred to list the Provincia Chimborazo specimens as referred material and not as paratypes.

Peters (1973) discussed a series of specimens in the Gustavo Orcés collection (GOV 8698–700, currently USNM 236942–44) resembling *Atelopus petersi* (i.e., *A. pachydermus sensu* Peters, 1973), from the Andes of Provincia Loja in southern Ecuador. He stated that these specimens were identical to those from Oyacachi. However, these specimens are unicolor cream, in contrast to Oyacachi specimens. Because at that time *A. petersi* (*A. pachydermus sensu* Peters, 1973) was unknown from the area between Napo and Loja, Peters (1973:37) suggested that the locality data were erroneous. However, we prefer to assume that the Loja population may refer to a distinct (unnamed) taxon, although they are morphologically similar. Our PCA analysis

shows that morphometric variation between the Loja specimens and *A. petersi* widely overlaps. Our assumption is based on the large geographic gap between *A. petersi* and the Loja population. Nonetheless, resolution of this issue will require further analyses of *Atelopus* specimens and populations from intermediate areas and from Loja and Azuay.

Distribution, ecology and current population status. According to our data, *Atelopus petersi* occurs in the Cordillera Oriental of the Andes in Ecuador, Provincias Napo and – according to specimens tentatively referred to the new species – Chimborazo (Fig. 6), at elevations of 2660–3300 m above sea level. The area in which *A. petersi* occurs includes Cloud Montane Forest and High Montane Evergreen Forest, following the classification of the natural plant formations of the Ecuadorian Andes (Valencia *et al.*, 1999). Annual mean precipitation is about 1000–2000 mm and annual mean temperature is about 12–18°C (Cañadas-Cruz, 1983). According to Peters (1973), *A. petersi* (as *A. pachydermus*) occurs sympatrically with *A. ignescens sensu stricto* (Cornalia, 1849).

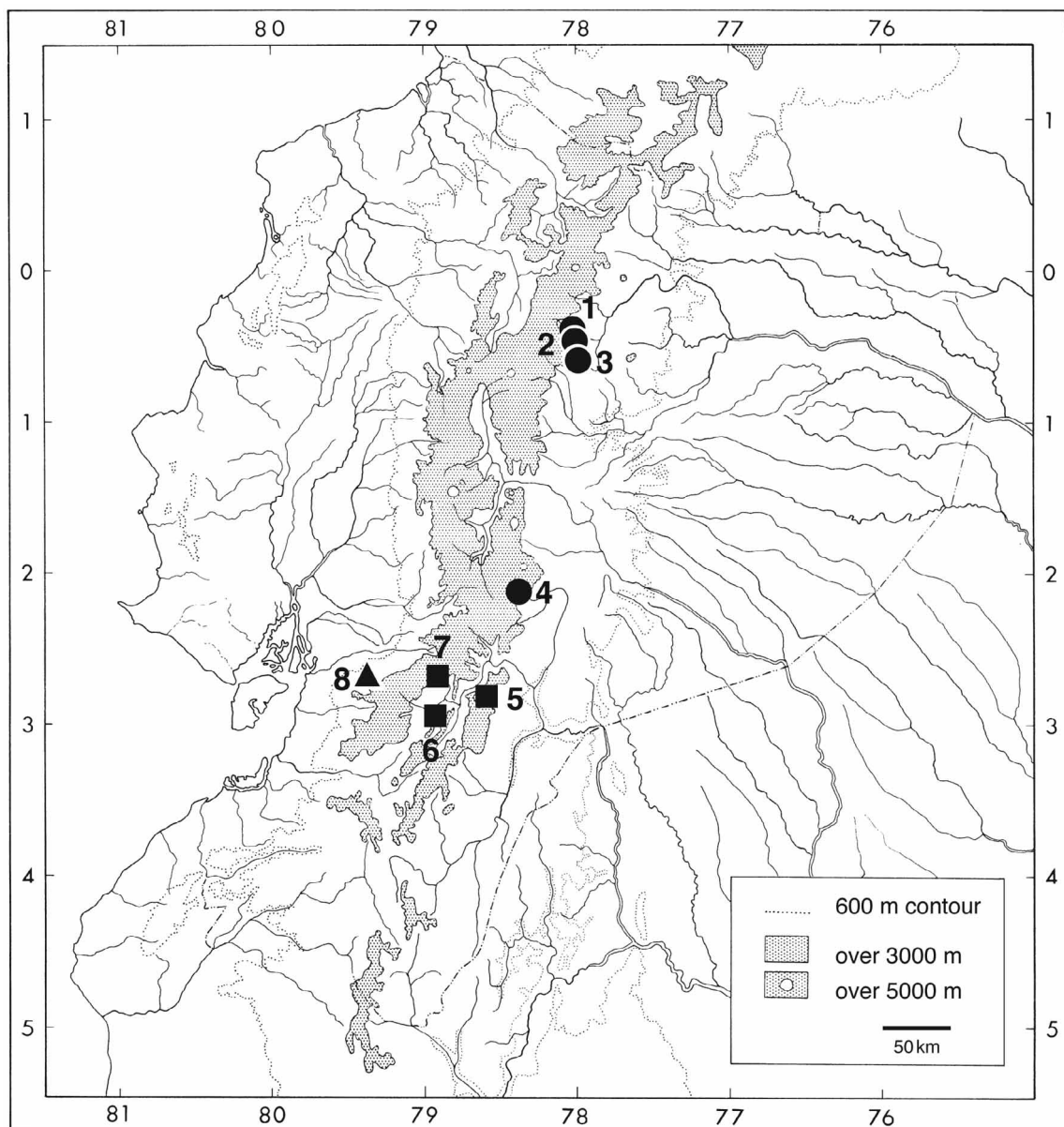


FIGURE 6. Map of Ecuador showing localities of *Atelopus petersi*, (circles), *A. bomolochos* (squares) and *A. onorei* (triangle). 1 = Provincia Napo: Oyacachi; 2 = Provincia Napo: Chalpi; 3 = Provincia Napo: 11 Km ESE Papallacta; 4 = Provincia Chimborazo: Lagunas de Atillo, Laguna Cuyug (specimens tentatively referred to *A. petersi*); 5 = Provincia Azuay: Sevilla de Oro; 6 = Provincia Azuay: Cuenca; 7 = Provincia Cañar: Juncal-General Morales; 8 = Provincia Azuay: Río Chipla, 10–15 Km E Luz María.

Knowledge on the life history of *Atelopus petersi* is poor. KU117874–79 were collected on 7 March 1968 under rocks at the edge of a stream. KU 142950 was collected in 27 October 1971 in streambed by day. KU 142951–54 were collected in 17, 27 and 28 October 1971 under logs on grassy hillside. The referred specimen EPN 3307 (female) was collected active on cushions plants in paramo habitat at 10:59 hrs on 19 September 1986. QCAZ 298–302 (two males, three females) were collected on April 1988 during the day when active on a trail. A juvenile (QCAZ 3154) was collected on 30 March 1988. QCAZ 4555 (female) was collected on 19 August 1993 when walking along the border of the Río Oyacachi. QCAZ 7678 was found dead, at 1 Km E of Oyacachi, on 8 November 1996. This is the latest record for this species from Provincia Napo. Despite occasional efforts to locate *A. petersi* subsequently (one visit to Oyacachi on September 2003, two visits to 11 Km East of Papallacta on January and August 1999, four visits to Atillo on May 2001, on 15 and 30 June 2002, and on April 2006), no additional individuals have been found. According to Peters (1973:36), in the past, *A. petersi* was “extremely common” in the vicinity of Papallacta, where it was found along the Río Papallacta, under rocks in moist, and spongy runoff areas. Interviewing local people at Oyacachi and Papallacta, they were familiar with these toads. Several different-aged persons revealed that these toads once were abundant but have not been seen for several years, although in Oyacachi some people claimed, on September 2003, that from time to time they still see single individuals.

Remarks. The color pattern of specimen JAP 2267 of *Atelopus petersi*, and depicted on Figs. 26–27 in Peters (1973) from the environs of Papallacta conforms well to the color pattern of the holotype of *A. bomolochos* (CAS 91930; Peters, 1973:Fig. 15). This resemblance might be homoplastic, plesiomorphic, or indicate a close phylogenetic affinity between them.

Etymology. The specific name is a noun in the genitive case and it is a patronym for James A. Peters, in recognition of his discovery of this species in 1962 and posterior detailed description in 1973. As well, we recognize his contribution to *Atelopus* taxonomy.

New species from southern Ecuador

The taxonomic status of *Atelopus bomolochos* has been uncertain mainly for two reasons: (1) Peters' (1973:16) statement that the specific status was “perhaps questionable” and his assumption of a close relationship to *A. ignescens* (*sensu* Peters, 1973), and (2) Grays' (1983) recognition of an *A. exiguus*-*bomolochos* complex including several populations of *Atelopus* from southern Ecuador. The recent clarification of the taxonomic status of *A. ignescens sensu stricto* (Coloma *et al.*, 2000; Ron *et al.*, 2003), *A. exiguus* (Coloma *et al.*, 2000), and *A. pachydermus* (this paper) prompted us to review the original description and type material of *A. bomolochos* (as listed in the Appendix). In doing so, we found that one of the populations previously allocated to *A. bomolochos* by Lötters (1996) and Coloma *et al.* (2000) from southwestern Ecuador is unique by displaying in life an aqua blue iris. Iris color has been suggested to represent a species-specific character in many bufonids including *Atelopus* (e.g., Lötters, 1996; Coloma *et al.*, 2000). We also found other differences (see below) and therefore conclude that the population with an aqua blue iris represents a taxon distinct from *A. bomolochos* and describe it as a new species.

Atelopus onorei sp. nov.

Atelopus bomolochos (non Peters): Lötters, 1996:Fig. 6; Coloma and Ron, 2001:Fig. 9.

Holotype. QCAZ 1860, adult female, from Ecuador: Provincia Azuay: 10–15 Km E Luz María, Río Chipla (2° 47' 24" S, 79° 21' 36" W), approx. 2500 m above sea level, obtained on 9 April 1990, by Stella de la Torre-Salvador, John J. Wiens, Felipe Campos-Yáñez, and Luis A. Coloma.

Paratypes. KU 217448–57, QCAZ 1861–63, 1865–67, 1868 (cleared and double stained preparation), 32258–59, same data as holotype; QCAZ 3440, 3442, same locality as holotype, obtained on 21 April 1990, by Fabián Toral, María Augusta Bravo, and Gustavo Morejón.

Diagnosis. (1) A moderate-sized species with mean SVL in adult males 38.8 mm (35.2–41.3 mm, $n = 9$) and in adult females 44.8 mm (41.9–47.9, $n = 4$); (2) hind limbs short, mean tibia length/SVL 0.381 (0.341–0.409, $n = 13$); (3) phalangeal formula of hand 2-2-3-3, basal webbing absent; (4) foot webbing formula I(0–1)—(0–2)II(1/2–2)—(1–3)III(1–3)—(2–4)IV(2–4)—(1–3)V; (5) snout acuminate, slightly protruding beyond lower jaw; (6) tympanic membrane absent; (7) dorsal surfaces of body usually smooth, (one [out of 13] individuals bears a few scattered small spiculae); (8) yellow spiculae (creamy white in preservative) present mostly on flanks; (9) vertebral neural processes inconspicuous; (10) dorsum yellow-orange to light green (creamy yellow to gray in preservative); (11) venter uniform cream to pale yellow in preservative; (12) gular region without warts, spiculae or con.

By having in life an aqua blue iris, *Atelopus onorei* is distinct from all other species of *Atelopus*. By displaying in life yellow-orange, green, or a combination of yellow-orange and green colors, *A. onorei* is most similar to *A. bomolochos*. Descriptions of the type specimens of *A. bomolochos* did not include colors in life. Nonetheless, Peters (1973) described the color in alcohol as “may be yellowish, yellow-green, or light brown.” Specimens assignable to *A. bomolochos*, collected near the type and paratype localities reveal large color variation as described by Peters. All of them have a predominantly black iris as depicted in Figs. 3B, C, D; although, specimens from 10 km S Cutchil show a fine green line around pupil (Field notes of John J. Wiens, 29 April 1990). Entirely yellow-orange individuals are most similar to *A. bomolochos* (from vicinities of Sigsig and Cutchil, Provincia Azuay; see Lötters 1996:Fig. 7), some specimens of *Atelopus* sp. from Departamento Nariño, Colombia (formerly referred to *A. ignescens*; for discussion see Coloma et. al., 2000), *A. guanujo* Coloma, 2002 from Provincia Bolívar, Ecuador, *A. carbonerensis* Rivero 1974, *A. chrysocorallus* La Marca, 1994, and *A. soriano* La Marca, 1983 all from the Andes of Venezuela (Estados Mérida and Trujillo). *Atelopus onorei* further differs from *A. bomolochos* by lacking minute black stippling regularly distributed on dorsum (Fig. 7), and by differences in hand and foot lengths of females. Herein, we compare *A. onorei* to populations described by Peters (1973) as *A. bomolochos* (specimens also used for morphometric analyses are indicated in the Appendix). The first two components with eigenvalues > 1.0 were extracted from the PCA of 7 morphometric variables of 15 males and 11 females from populations of *A. bomolochos* (Sevilla de Oro, Cuenca, and Juncal-General Morales) and *A. onorei* from Río Chipla. The axes accounted for 54.6 % of the total variation. There is no overlap among the morphometric space of females of *A. onorei* vs. *A. bomolochos* (Fig. 8), mostly because of hand and foot lengths, which are the highest loadings along PC II. Hand and foot lengths differ significantly between females of *A. onorei* vs. *A. bomolochos* (log comparisons of HAND of females t -test, $t = 5.165044$, $df = 6.4$, $P > 0.0009$; FOOT of females t -test, $t = 4.578094$, $df = 8.9$, $P > 0.0007$).

Atelopus onorei (mean SVL of females 44.8; mean SVL of males 38.8) is significantly larger (SVL of females t -test, $t = 2.992$, $df = 14$, $P < 0.097$; SVL of males t -test, $t = 7.320$, $df = 36$, $P < 0.0001$) than *A. guanujo* (mean SVL of females 39.6, 35.0–46.0, SD 3.0, $n = 12$; mean SVL of males 33.9, 29.9–37.1, SD 1.6, $n = 29$; after data in Coloma, 2002) and lacks white spiculae in life. *Atelopus onorei* differs from *Atelopus* sp. from Nariño by lacking a patch of black spiculae on females' gular-chest region. *Atelopus onorei* differs from *A. carbonerensis* and *A. soriano* in having a less protuberant snout and lacking a noticeably postocular crest. Furthermore, it differs from *A. carbonerensis* and *A. chrysocorallus* by having vocal slits in males and lacking a row of warts on the dorsolateral surfaces of the body in males (after data from La Marca, 1996; Rivero, 1974; Coloma, 1997).

Description of holotype. (Figs. 9A–C). Head about as long as wide, HLSQ and HDWD less than one third SVL (HLSQ/SVL = 0.280, HDWD/SVL = 0.282); snout acuminate, its margin slightly rounded in dorsal view; profile of tip of snout in lateral view curved and slightly protuberant to the anterior margin of jaw; no swollen gland on tip of snout; nostrils slightly protuberant, directed laterally, situated posterior to level of

apex of lower jaw; canthus rostralis distinct, weakly concave from eye to nostril; loreal region concave; lips not flared; interorbital and occipital regions flat, smooth; eyelid flared without tubercles; postorbital crest slightly raised, glandular; low pretympenic and post tympanic areas warty; tympanic membrane and tympanic annulus absent; temporal area smooth; choanae small, rounded, widely separated (28% of HW); tongue about twice as long as wide, its posterior half not attached to mouth's floor; ostia pharyngea absent.

Forearm relatively short ($RDUL/SVL = 0.278$); palmar tubercle round; palmar, supernumerary palmar, thenar and subarticular tubercles nearly indistinct; digital tips with round pads; thumb relatively long ($THBL/HAND = 0.717$), apparently having two phalanges; webbing on hands absent, fingers lacking lateral fringes; relative length of fingers $II < III < V < IV$. Tibia relatively short ($TIBL/SVL = 0.370$); fold on distal half of inner edge of tarsus absent; inner metatarsal tubercle oval, barely distinct; outer metatarsal tubercle conical, low raised, about two thirds length of inner metatarsal tubercle; supernumerary plantar and subarticular tubercles barely conspicuous; digital pads distinct; webbing formula of foot $I1-1II1-2III2-3IV3-2V$; relative length of toes $I < II < III = V < IV$.

Dorsal surfaces smooth; flanks rugose with scattered spiculae; anterior and proximal upper surfaces of fore limbs lacking spiculae; throat rugose, contrasting to smooth chest, belly, and undersides of hind limbs; cloacal opening a tube at nearly midlevel of thighs, directed posteriorly; skin lateral to cloacal opening rugose.

In preservative (~70% ethanol), dorsum of head mostly cream with diffuse gray marks, loreal region gray; dorsum of body gray extending onto upper flanks; dorsal and ventral surfaces of limbs creamy yellow, except tibia, fingers III, V, toes IV and V, which have gray marks with diffuse borders; minute gray stippling absent on dorsum of body (viewed at 8 X magnification); spiculae white; throat, chest, belly, ventral surfaces of limbs, palms and plants yellowish cream; proximal end of tongue lacking black pigmentation, inner margin of mandible with a fine gray line.

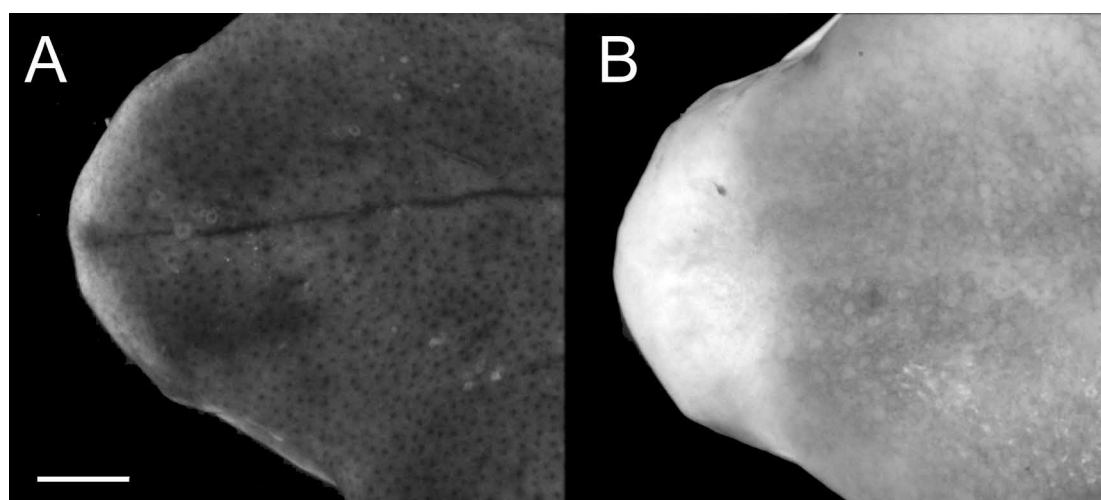


FIGURE 7. Skin of head of (A) *Atelopus bomolochos* (QCAZ 1900, 7.6 km S Cutchil, Provincia Azuay) and (B) *A. onorei* (QCAZ 1860) to show differences in pigmentation. Scale = 1 mm

Measurements (in mm). SVL 47.9, TIBL 17.7, FOOT 18.1, HLSQ 13.4, HDWD 13.5, ITNR 3.7, EYDM 4.5, EYNO 3.3, RDUL 13.3, HAND 10.6, THBL 7.6, SW 14.6.

Variation. Meristic variation is given in Table 1. The paratypes resemble the holotype with the following exceptions. Sexual dimorphism is evident in that females are larger than males (Table 1). Males have vocal slits and keratinized nuptial pads on the dorsal and inner surfaces of the thumb. Fore limbs are relatively long and slender in females only (Table 1). Spiculae are most abundant on the flanks in a female (QCAZ 3440) and some are scattered on the dorsum of the body in that specimen.

TABLE 2. Measurements (in mm) of adults of *Atelopus bomolochos* and *A. onorei*. Mean $\pm$ SD, and range are given. Abbreviations follow Gray and Cannatella (1985) and Coloma *et al.* (2000). They are: SVL = snout-vent length; TIBL = tibia length; FOOT = foot length; HL SQ= head length; HDWD = head width; EYDM= eye diameter; ITNA = Internarial distance; RDUL = radio-ulna length; HAND = hand length; THBL = thumb length; SW = sacrum width. All measurements are in mm.

	<i>Atelopus bomolochos</i>		<i>Atelopus onorei</i>	
	Males (n = 2)	Females (n = 5)	Males (n = 13)	Females (n = 6)
SVL	(38.4–40.8)	47.5 $\pm$ 2.7 (43.9–51.0)	38.6 $\pm$ 2.4 (34.2–41.9)	44.1 $\pm$ 2.5 (41.9–47.9)
TIBL	(13.6–15.7)	16.4 $\pm$ 0.5 (15.6–16.8)	15.1 $\pm$ 1.0 (13.0–16.4)	16.1 $\pm$ 0.85 (15.3–17.7)
FOOT	(15.7–16.0)	19.1 $\pm$ 0.9 (18.1–20.1)	16.1 $\pm$ 1.3 (13.6–18.0)	16.4 $\pm$ 1.0 (15.1–18.1)
HLSQ	(11.5–12.8)	13.0 $\pm$ 0.8 (11.8–13.8)	12.2 $\pm$ 0.8 (10.9–13.3)	13.1 $\pm$ 0.4 (12.6–13.6)
HDWD	(10.1–11.3)	12.6 $\pm$ 0.7 (11.9–13.5)	11.6 $\pm$ 0.8 (10.2–12.6)	12.4 $\pm$ 0.6 (11.9–13.5)
EYDM	(3.8–4.8)	4.6 $\pm$ 0.2 (4.4–4.8)	3.6 $\pm$ 0.5 (2.6–4.2)	3.7 $\pm$ 0.5 (3.1–4.5)
ITNA	(4.3–4.7)	4.3 $\pm$ 0.3 (3.8–4.5)	4.0 $\pm$ 0.2 (3.4–4.3)	4.0 $\pm$ 0.3 (3.6–4.5)
RDUL	(10.0–11.6)	13.4 $\pm$ 0.7 (12.4–14.4)	11.8 $\pm$ 1.0 (9.6–13.3)	12.7 $\pm$ 0.5 (12.1–13.3)
HAND	(9.5–10.2)	12.3 $\pm$ 0.9 (11.2–13.1)	9.7 $\pm$ 0.9 (7.7–10.7)	10.2 $\pm$ 0.4 (9.6–10.6)
THBL	(5.5–6.7)	7.5 $\pm$ 0.3 (7.0–7.8)	6.1 $\pm$ 0.6 (5.2–7.2)	6.6 $\pm$ 0.7 (5.9–7.6)
SW	(10.7–12.8)	14.7 $\pm$ 0.5 (14.1–15.5)	11.8 $\pm$ 0.9 (9.6–12.7)	13.4 $\pm$ 1.5 (10.7–15.2)
TIBL/SVL		0.353 $\pm$ 0.021 (0.327–0.384, n = 7)	0.383 $\pm$ 0.021 (0.341–0.418, n = 19)	
HLSQ/SVL		0.283 $\pm$ 0.019 (0.259–0.314, n = 7)	0.311 $\pm$ 0.014 (0.280–0.332, n = 19)	
HDWD/SVL		0.266 $\pm$ 0.011 (0.247–0.280, n = 7)	0.294 $\pm$ 0.014 (0.273–0.320, n = 19)	
RDUL/SVL		0.279 $\pm$ 0.013 (0.259–0.297, n = 7)	0.301 $\pm$ 0.014 (0.278–0.324, n = 19)	
THBL/HAND		0.614 $\pm$ 0.029 (0.579–0.653, n = 7)	0.637 $\pm$ 0.040 (0.576–0.717, n = 16)	

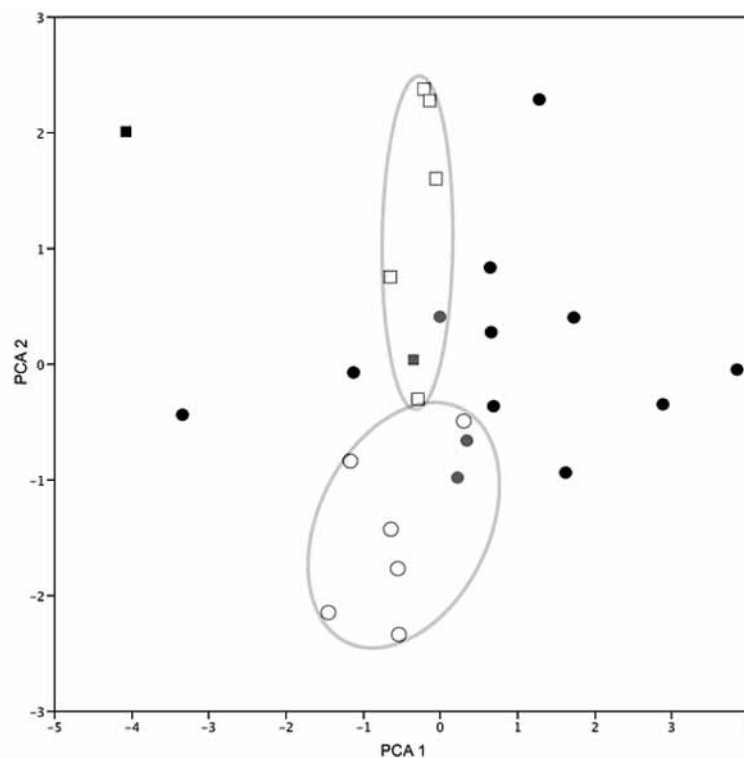


FIGURE 8. Axes I and II from Principal Components Analysis based on seven size-corrected morphological variables for populations of *Atelopus onorei* and of *A. bomolochos* from Azuay and Cañar Provinces, Ecuador. Squares = *A. bomolochos*; circles = *A. onorei*; open symbols = females.

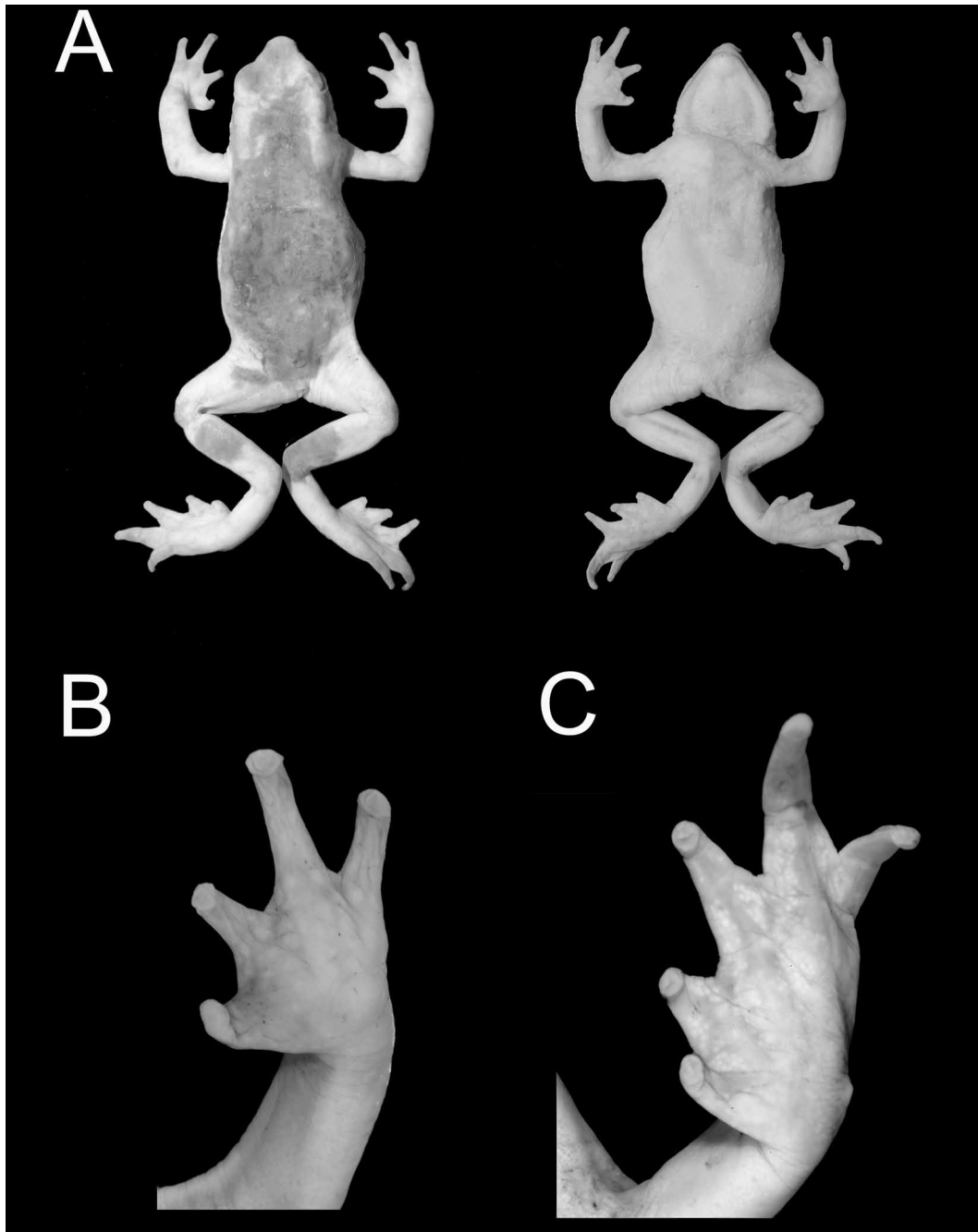


FIGURE 9. Holotype of *Atelopus onorei* (QCAZ 1860): (A) female, SVL = 47.9 mm; (B) ventral view of left hand, enlarged 3.5 times of A; (C) ventral view of left foot, enlarged 3.5 times of A.

Color variation in preservative (~70% ethanol): Dorsal colors vary from uniform yellow (QCAZ 3440) to mostly gray (QCAZ 3442). In QCAZ 2798, colors are faded because of poor preservation.

Color in life (Figs. 3E–F). Data from color transparencies (no museum numbers associated) and the senior author's field notes of specimens from the type locality. The dorsal ground color of body and limbs is orange yellow. The dorsum of one male is bright green, except the forearms, hands and feet, whereas other males and females show varying degrees of green coverage. In a few individuals the dorsum is pale yellowish brown with diffuse black blotches; the spiculae are yellow. The iris is conspicuously aqua blue with fine black reticulation and with a fine bluish-white stripe at the upper margin of pupil. Lötters (1996:Fig. 6) and Coloma and Ron (2001) published the same color photograph of an amplexant pair of *A. onorei* (as *A. bomolochos*). Nogales and Rueda-Almonacid (2005) also provided a painting and a color photo (under *A. bomolochos*).

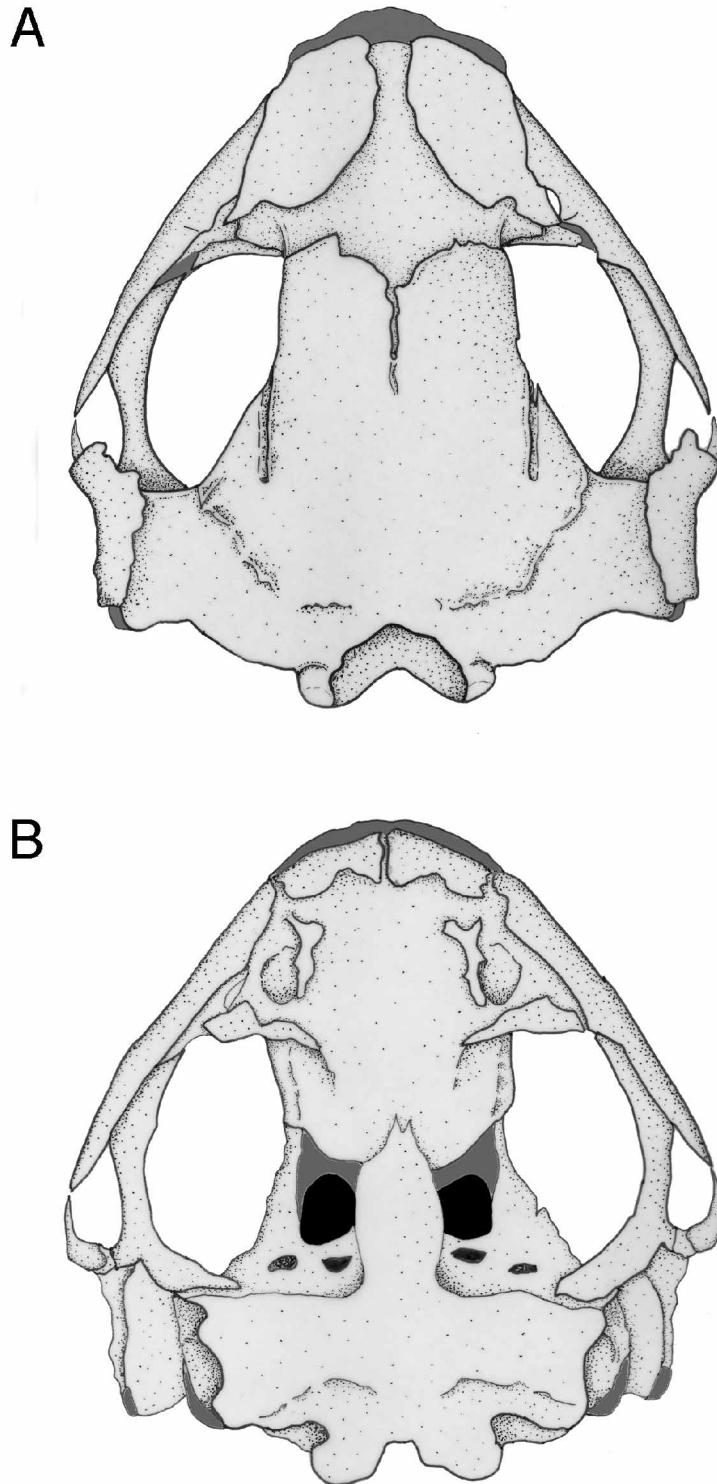


FIGURE 10. Skull of female *Atelopus petersi* from Oyacachi, Provincia Napo (QCAZ 302, SVL = 42.2 mm). (A) dorsal and (B) ventral views. Scale = 2 mm.

Distribution, ecology and current population status. *Atelopus onorei* is known only from the type locality in the Azuay Basin of the Cordillera Occidental of Ecuador, Provincia Azuay (Fig. 6) and a nearby creek (1–2 km West of Miguir, Morley Read pers. com. and his personal archive of photographs). At the latter locality, it occurs in sympatry with *A. nanay* Coloma 2002. The type locality is at about 2500 m above sea

level in humid cloud forest on the Pacific versant of the Cordillera Occidental. Annual mean rainfall is 1000–2000 mm and the annual mean temperature is 12–18 °C. Frogs were collected at Cloud Montane Forest areas (*sensu* Valencia *et al.* 1999), at the margin of the Río Chipla and near a small tributary. At the time of collection, during day at the type locality, most individuals were active and numerous pairs were in amplexus, while drizzle occurred (Field notes of L. A. Coloma, 9 April 1990). A female (QCAZ 3440) contained 133 ovarian eggs that are 2.14 mm in diameter (range = 1.67–2.58, $n = 20$, $SD = 0.219$).

Although this species previously was abundant at the type locality, no individuals have been found after 1990, despite at least four occasional search efforts by the senior author to locate this frog at the same site as before and surroundings on 28 November 1992, 20 February 1993, 21 April 1993, and 11 October 1993.

Etymology. The specific name is a noun in the genitive case and it is a patronym for Giovanni Onore, former Curator of Entomology at Pontificia Universidad Católica del Ecuador (PUCE). We recognize his invaluable contribution to the collections of Ecuadorian frogs and pioneer efforts on forming collections for scientific research at PUCE. His collecting efforts, especially during the eighties, resulted in the discovery of many new amphibians from Ecuador, among them *Atelopus*. As well, his amphibian collections in the Andean region of Ecuador provided key data, later used to document the amphibian extinctions and to shed light on its causes.

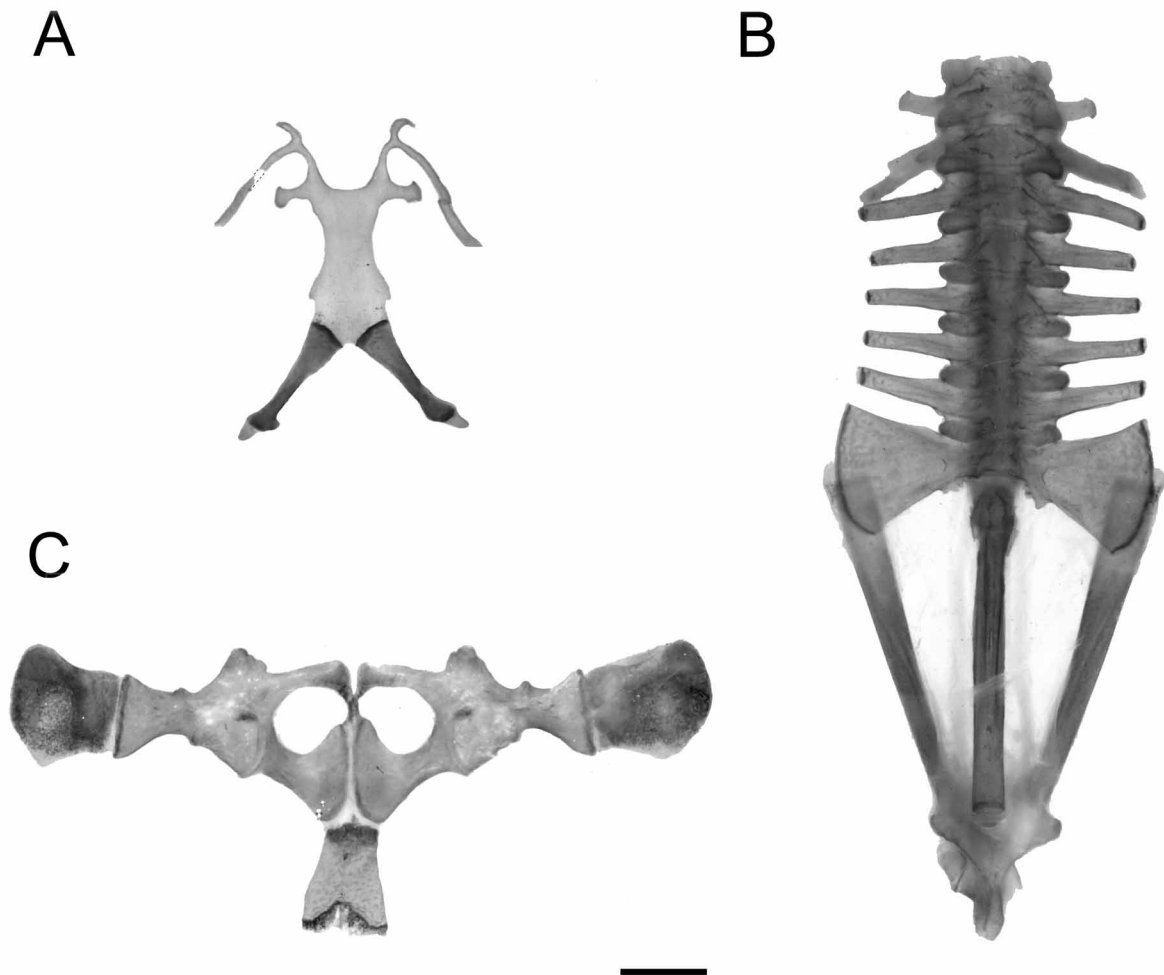


FIGURE 11. Skeletal features of female *Atelopus petersi* from Oyacachi, Provincia Napo (QCAZ 302, SVL = 42.2 mm). (A) ventral view of hyobranchium, (B) dorsal view of vertebral column and pelvic girdle, and (C) ventral view of pectoral girdle. Scale = 3 mm.

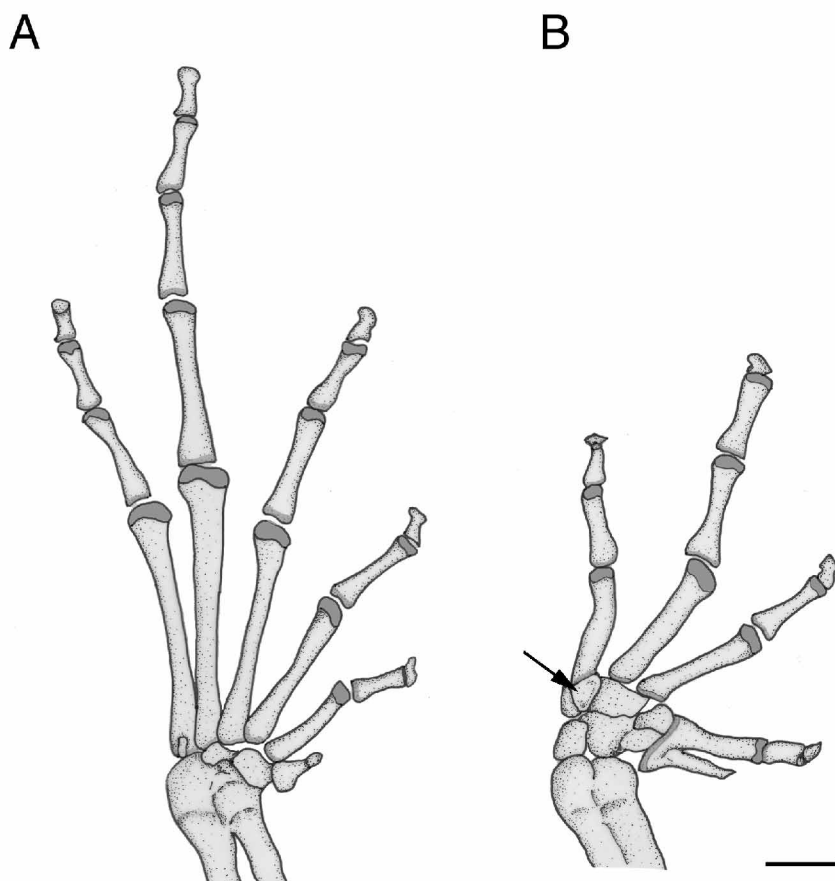


FIGURE 12. Manus (A) and pes (B), in ventral view, of female *Atelopus petersi* (QCAZ 302, SVL = 42.2 mm). The arrow designates the Sesamoid I. Stippled areas are bone; cartilage shown in gray. Scale = 2 mm.

Osteology of new species

The following description applies to two adult females of *Atelopus petersi* (QCAZ 298, SVL = 44.5, QCAZ 302, SVL = 42.2, both double C&S; from Oyacachi, Provincia Napo), and one adult female of *A. onorei* (QCAZ 1868, SVL = 43.6, double C&S; from Río Chipla, Provincia Azuay) unless otherwise indicated. General osteological features of *A. petersi* (QCAZ 302) and *A. onorei* are depicted in Figures 10–15. Anterior ramus of vomer larger than prechoanal ramus, directed ventrally toward anterior tip of maxilla; postchoanal ramus parallel to midline; rami pointed. Frontoparietals not articulated medially. Lateral borders of frontoparietals at level of posterior half of orbit with small, irregular flange. Occipital grooves nearly entirely roofed with anterior opening to level of about anterior margin of prootic, and posterior opening to level of about posterolateral margin of frontoparietal. Parasphenoid underlying sphenethmoid, posterior limits of ossification of which at about half-length of margin of orbit. Terminal end of cultriform process of parasphenoid serrate, with 2–3 points in *A. petersi*, 3 points in *A. onorei*. Posterior margin of parasphenoid curved with well-defined protrusion in QCAZ 302 and a less-defined in QCAZ 298 and in *A. onorei*. Surface of squamosal not sculptured. Otic ramus covering all but about posterior one fifth of crista parotica; zygomatic ramus small, triangular, barely protruding from anterior margin of dorsal portion of ventral ramus. Angle between otic ramus of squamosal and anterior margin of dorsal portion of ventral ramus variable, from acute to nearly perpendicular. Stapes absent. Operculum mineralized (QCAZ 298) or not mineralized (QCAZ 302) in *A. petersi*; mineralized in *A. onorei*. Medial palatine process of pars palatina of premaxilla well developed, triangular (length of outer

margin about or more than half length of medial edge when projected in imaginary line towards midline). Lower half of alary process of premaxilla slightly wider than upper half in *A. petersi*, about the same width in *A. onorei*. Posterior end of pars dentalis nearly truncate, articulating with maxilla (QCAZ 302) or not articulating (QCAZ 298) in *A. petersi*; not articulating in *A. onorei*. Dorsal margin of pars facialis of maxilla nearly even. Quadratojugals nearly in contact with maxilla. Ventral pars articularis of palatoquadrate associated with the quadratojugal mineralized.

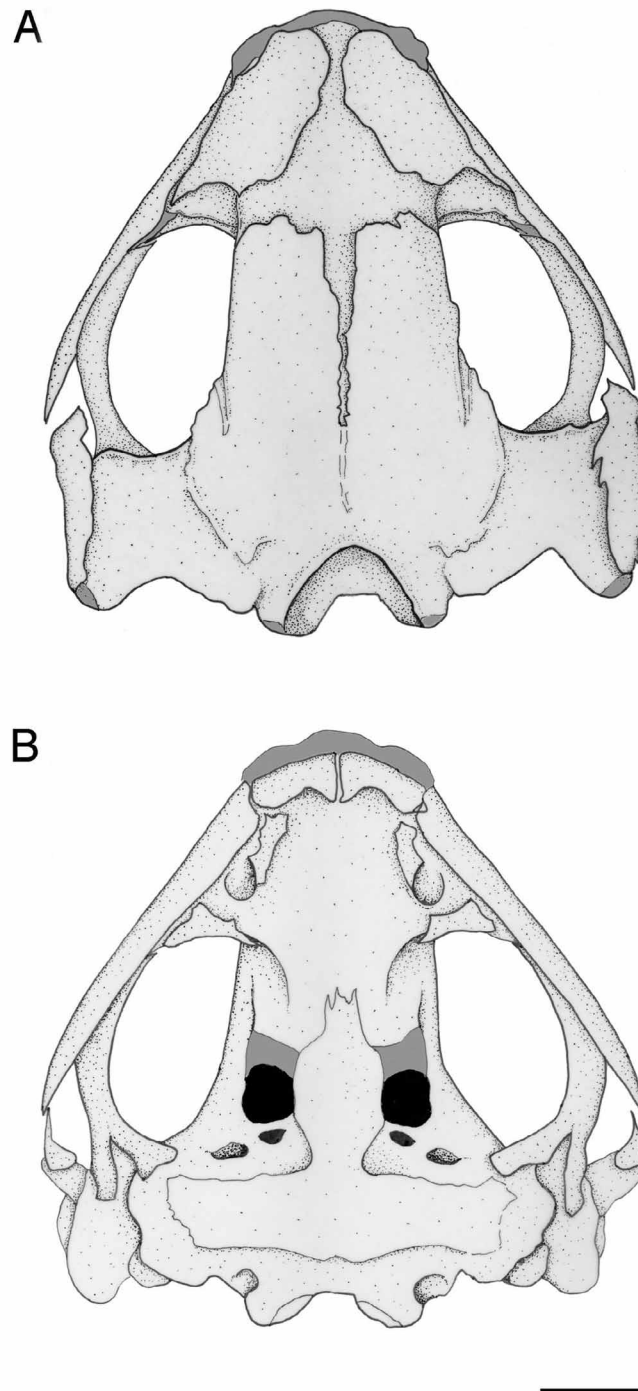


FIGURE 13. Skull of female *Atelopus onorei* from Río Chipla, Provincia Azuay (QCAZ 1868). (A) dorsal and (B) ventral views. Scale = 2 mm.

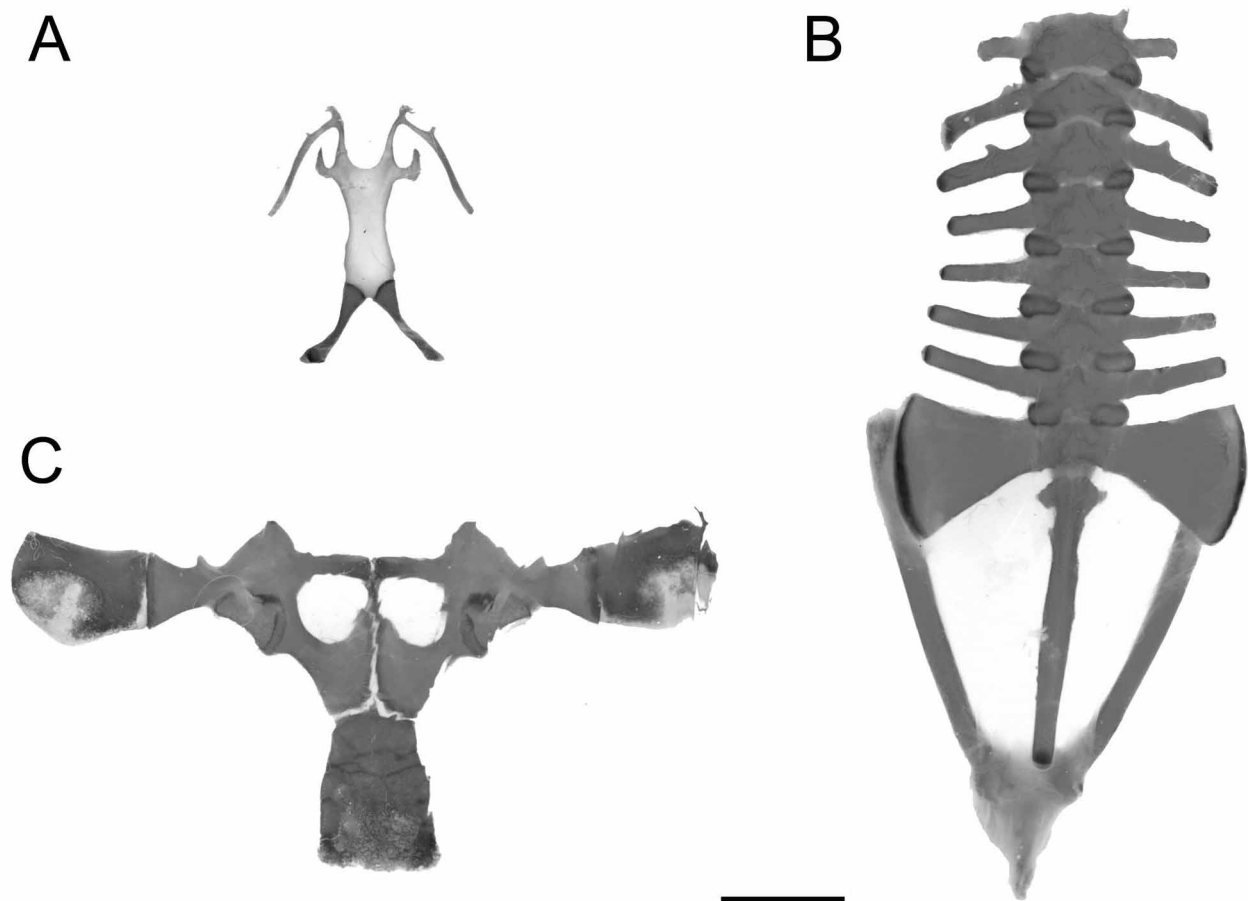


FIGURE 14. Skeletal features of female *Atelopus onorei* from Río Chipla, Provincia Azuay (QCAZ 1868). (A) ventral view of hyobranchium, (B) dorsal view of vertebral column and pelvic girdle, and (C) ventral view of pectoral girdle. Scale = 5 mm.

Hyoid plate longer than wide (*Atelopus petersi* 3.5, $n = 1$; *A. onorei* 2.6); cartilaginous, except mineralized anteriorly; lateral margins of hyoglossal sinus diverging anteriorly. Anterior process of hyale free anteriorly, not rejoining hyale, short; lateral process of hyale absent in *A. petersi*, present in *A. onorei*. Posterolateral process of hyoid small in *A. petersi*, absent in *A. onorei*; posterior flange at anterolateral hyoid process shorter than anterior in *A. petersi*, absent in *A. onorei*. Posteromedial hyoid process without ossified lateral expansion, except a bump at one side in one specimen of *A. petersi* (QCAZ 298). Cartilaginous suprascapula mineralized in *A. petersi*, only slightly mineralized in *A. onorei*.

Lateral borders of transverse processes on Presacrals II–VII even, lacking flanges and about the same width proximally and distally in *Atelopus petersi*, whereas in *A. onorei*, Presacral IV bearing a triangular flange and transverse processes slightly wider proximally than distally. Atlas complex (fused presacrals I and II) with one pair of transverse processes oriented anterolaterally. Presacrals III–IV with widest transverse processes in QCAZ 298 and *A. onorei*; in QCAZ 302 Presacral III with wider transverse processes than Presacral IV. All the transverse processes of Presacrals IV–VIII oriented nearly perpendicular to midline, but those on Presacrals VII–VIII slightly oriented anteriorly in QCAZ 302. In *A. onorei*, transverse processes of Presacrals II–IV slightly oriented posteriorly, V–VI oriented nearly perpendicular to midline, and those of VII–VIII slightly oriented anteriorly. Dorsal surfaces of neural arches raised, sculptured with a cross, nearly indistinct in QCAZ 302. Neural spines not elevated in *A. petersi*, elevated in *A. onorei*. Central and scattered pits absent on dorsum of most vertebrae in *A. petersi*, present in *A. onorei*. A central pit is most evident in Presacrals III–

VI of *A. onorei*. Sacrum and coccyx unfused. The anterior border of sacral diapophyses slightly concave, directed anterolaterally.

Clavicular acromium oriented nearly parallel in relation to the longitudinal axis in QCAZ 298, forming angle in QCAZ 302 and *Atelopus onorei*. Process of scapula at anterior margin pointed, triangular, well differentiated in QCAZ 298 and *A. onorei*, poorly developed in QCAZ 302. Ratio of sternum length to total length of girdle at midline 0.37–0.43 in *A. petersi*, 0.52 in *A. onorei*; ratio of maximum sternum width to minimum sternum width is 1.5–1.7 in *A. petersi*, 1.6 in *A. onorei*. Sternum entirely calcified, terminal end truncate and uncapitate in *A. petersi* (QCAZ 298), bicapitate with a less calcified area between capitates and less heavy calcification distally in *A. petersi* (QCAZ 302). In *A. onorei*, terminal end truncate and cartilaginous. Sesamoid bone anterior to distal end of ilium absent. Each ilium extending anteriorly beneath sacral diapophysis; distal end of ilium at anterior border of diapophysis in *A. petersi* (QCAZ 298), not reaching border in *A. petersi* (QCAZ 302) and *A. onorei*. Neural spines of coccyx and sacrum separated. Vestigial lateral processes on anterior end of coccyx in *A. petersi* (QCAZ 298) and *A. onorei*, not in *A. petersi* (QCAZ 302). No lateral flanges along nearly entire length of coccyx. Ratio of female tibio-fibula length to SVL 0.36 in *A. petersi* (QCAZ 298) and 0.38 in *A. onorei* (QCAZ 1868); phalangeal formula 2-2-3-3.

Sesamoids I and II (*sensu* Coloma, 2002) present. Prepollex has one calcified element. Single oval os sesamoides tarsale at level of distal head of fibulare. In *A. petersi*, the prehallux varies bilaterally; there is one element on one side and two on the other side of QCAZ 302, and only one element on both sides of QCAZ 298. In *A. onorei*, the prehallux has two elements.

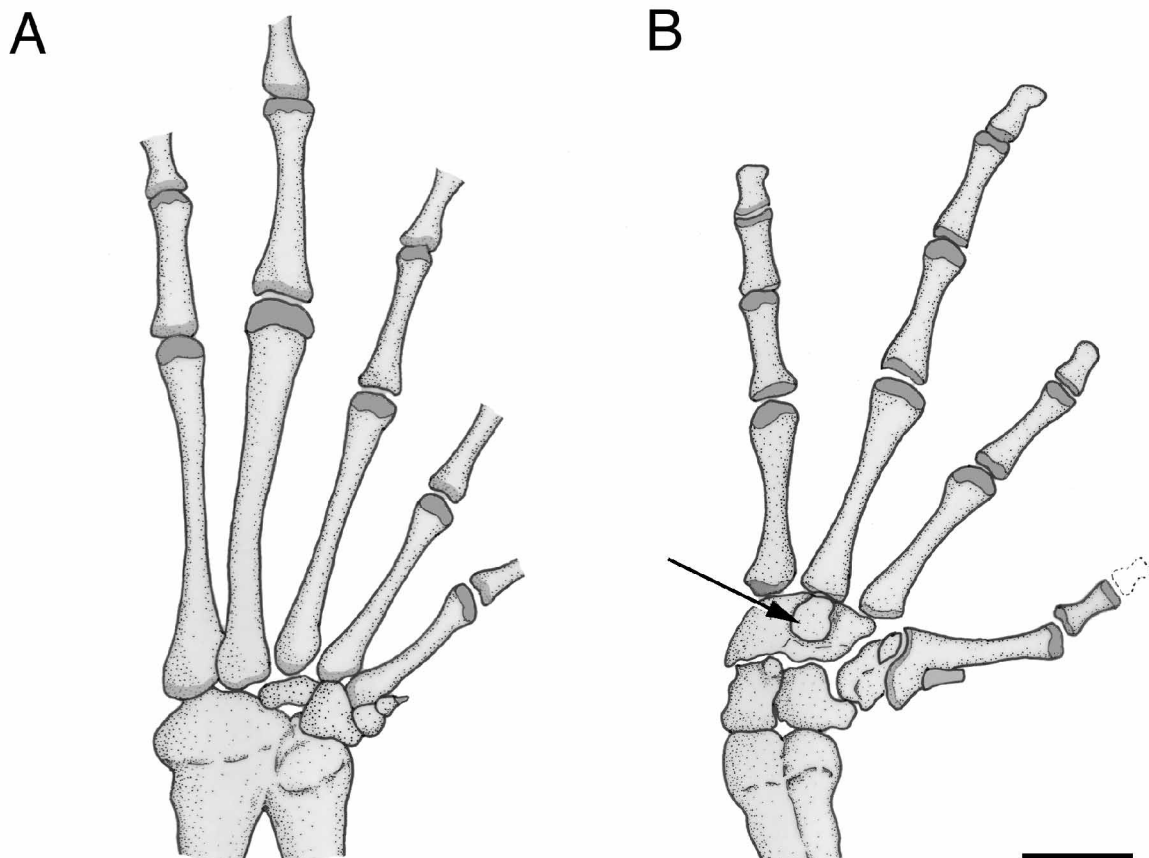


FIGURE 15. Manus (A) and pes (B), in ventral view, of female *Atelopus onorei* from Río Chipla, Provincia Azuay (QCAZ 1868). The arrow designates the Sesamoid I. Stippled areas are bone; cartilage shown in dark gray. Broken line indicates missing phalanx. Scale = 2 mm.

Discussion

Systematics

Species limits have been a matter of controversy along the history of systematic biology (e.g., Wiens and Servedio, 2000; Wiens, 2004). We are confident that the species proposed in this paper are distinct and that their diagnostic characters are indicative of allopatric isolation. However, our delimitation is constrained by small sample sizes for most of the populations, the lack of collections in intermediate areas, and the lack of phylogenetic information on the populations involved. The two former may no longer be solved given the disappearance of these frogs. The third aspect mentioned will require more detailed analyses, including morphological and molecular data. We hold the view that placement of *Atelopus onorei*, *A. petersi*, and *A. pachydermus* in the *A. ignescens* groups either *sensu* Peters (1973) or *sensu* Lynch (1993) is not informative, because these assemblages might be paraphyletic (Coloma 1997, 2002, authors' unpubl. data). To date, the only attempt to address the phylogeny of the entire genus *Atelopus* is the study by Coloma (1997). This study included *A. petersi* (as *A. pachydermus*), which was hypothesized to be the sister taxon of a clade containing *A. bomolochos* and *A. boulengeri* also from the eastern Andes of Ecuador plus *A. carrikeri* Ruthven, 1916, *A. eusebianus* Rivero and Granados Díaz, 1993, and *A. laetissimus* Ruíz-Carranza, Ardila-Robayo and Hernández-Camacho, 1994 from the eastern Andes and the Sierra Nevada de Santa Marta in Colombia.

Species numbers and extinction

The urgent call for completing the inventories of species and taxonomic work of amphibians has gained attention given the accelerated extinction rates that they are suffering, especially *Atelopus* (Stuart *et al.*, 2004; La Marca *et al.*, 2005). Because this genus is considered a "priority taxon," and Peru and Ecuador are included in priority regions (IUCN 2004), our efforts fill some of the gaps (see also Lötters *et al.*, 2005a,b).

This paper brings the total number of described *Atelopus* species from Peru to 14 and from Ecuador to 21. In addition, there remain several undescribed *Atelopus* from both countries based on morphological data: 8 from Ecuador (authors' unpubl. data) and 15 from Peru (Lötters *et al.*, 2005a). Estimates of diversity based on molecular systematics of Guianan *Atelopus* (Noonan and Gaucher, 2005) indicate remarkable diversification. These findings support the calculated increases within the range of 28–39 % of amphibian diversity based on molecular systematics, as calculated by Ron *et al.* (2006) for amphibians in the Neotropics. Thus, up to about 11 additional *Atelopus* species theoretically can be expected to exist in each country. If we apply the same criteria for the entire diversity in the genus (following La Marca *et al.*, 2005 and our unpubl. data), the number of species might be between 145 and 157, meaning that not least than 60–70 species of *Atelopus* are yet to be described.

Ecuador and Peru are among the countries holding the largest amphibian faunas of the world. Our knowledge on Peruvian amphibian taxonomy is widely behind Ecuador due to both taxonomic and collection gaps (e.g., Lötters *et al.*, 2005; Duellman, 2004). From Ecuador, to date, 458 species of amphibians are described (Coloma 2005–2007). Additionally, about 60 species from this country, morphologically diagnosed (senior author's unpubl. data), are awaiting description or to be recorded. This means an increase of about 12%. Thus, if we apply a conservative estimate of 20% (we assume an additional 8% of new discoveries) of increase of amphibian diversity based on morphology, plus the molecular systematics estimates of 28–39% by Ron *et al.* (2006), the numbers on Ecuadorian amphibian diversity might be between 677 and 728 species (for the moment, estimations for Peru can not be seriously given). Considering that Ecuadorian amphibian diversity is currently described and/or recorded at a rate of four species per year since 1990 (Coloma 2005–2007), the task of reporting the additional 219–270 species will take another 55–68 years, assuming no mayor changes on current rate of description. Similarly, in the case of Ecuadorian *Atelopus*, and assuming that *Atelopus* descriptions are prioritized (at a rate of two species per year) over other taxa, it will be necessary about 10 years to complete this task (i.e., to describe 19 new species of *Atelopus*) in Ecuador. From these numbers and consider-

ing that more than 70 species of *Atelopus* (La Marca, *et al.*, 2005) and that not least than 141 (31%) of the Ecuadorian amphibian species are under categories of extinction risk (Ron *et al.*, in press), we emphasize on the challenge of a rapid response and fundamental changes in policies and actions that are required in order to address the amphibian crisis. The latter has being claimed elsewhere (IUCN/SSC Global Amphibian Specialist Group, and Declining Amphibian Populations Task Force, 2005; Mendelson III *et al.*, 2006), given the novel threats mostly imposed by global warming and pathogens (Pounds *et al.*, 2006, 2007; Lips *et al.*, 2006, Seimon *et al.* 2006).

Atelopus pachydermus, *A. petersi* and *A. onorei* are herein considered as possibly extinct or – applying IUCN Red List criteria (version 3.1 from 2001) – Critically Endangered. A suspected reduction in population sizes is inferred by occasional searches that revealed no specimens since ten or more years; also the geographic range is severely fragmented in all cases; furthermore, *A. onorei* is known from a single locality that was severely affected by a road construction, between Cuenca and Naranjal, Ecuador, which violated regulations of environment protection by throwing all road material to the adjacent creeks.

The areas of occurrence of *Atelopus onorei* and *A. petersi* are close to areas where climate abnormalities have occurred and *Atelopus* and *Telmatobius* extinctions have been reported (Ron *et al.*, 2002; Bustamante *et al.* 2005, Merino-Viteri *et al.*, 2005). Also, they are close to areas where the chytrid fungus has occurred or its presence is highly predicted (Ron, 2005). Also, *A. pachydermus* occurs in an area close to the range of *A. peruensis* Gray and Cannatella, 1985, which disappeared in 1999/2000 (Lötters *et al.*, 2005a). Miranda-Leiva (1995) already expressed his concern regarding the possible extinction of *A. pachydermus*. In this scenario and considering the overwhelming evidence that *Atelopus* has been affected by these two key factors in the highlands (Pounds *et al.*, 2006, 2007; Lips *et al.*, 2006), it seems reasonable to consider *A. pachydermus* and the two new species not as Critically Endangered, but as possibly extinct. Same criteria might apply for many of the *Atelopus* species currently as Critically Endangered. On the other hand, it cannot be dismissed the fact that relictual or isolated individuals or populations of some species of Andean *Atelopus* still survive and have been recorded in recent years from southern Ecuador. To the best of our knowledge, since 1997, there are two species recorded in paramo habitats: a single adult female of *Atelopus* sp. (aff. *bomolochos*) found in 2002 at the Sangay National Park, Provincia Chimborazo; and 29 individuals (1 female, 18 males, 10 juveniles) of *A. exiguus* Boettger, 1892 found at Mazán, Provincia Azuay (Toral and Frenkel, 2006). These records might represent species whose density was drastically affected, and require rapid response actions that should prioritize ex-situ conservation management, as claimed elsewhere (Mendelson III *et al.* 2006a,b).

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References

- Almendáriz, A., & Cisneros, D. (2005) *Atelopus* sp. 19. In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T. & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 155.
- Boettger, O. 1892. *Katalog der Batrachier-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft*, Frankfurt/Main, Germany, 73 pp.
- Boulenger, G.A. (1882) *Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum*. London: Taylor & Francis. xvi + 495 pp., 30 pl.
- Bustamante, M.R., Ron, S.R. & Coloma, L.A. (2005) Cambios en la diversidad en siete comunidades de anuros en los Andes de Ecuador. *Biotropica*, 37, 180–189.
- Cañadas-Cruz, L. (1983) *El mapa bioclimático y ecológico del Ecuador*. Ministerio de Agricultura y Ganadería. Programa Nacional de Regionalización Agraria. Banco Central del Ecuador, Quito, Ecuador, 209 pp.
- Catenazzi, A. & Venegas, P.J. (2005) *Atelopus* sp. 12. In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T., & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 148.
- Cochran, D.M. & Goin, C.J. (1970) Frogs of Colombia. *United States National Museum Bulletin*, 288, 1–655.
- Coloma, L.A. (1997) *Morphology, systematics and phylogenetic relationships among frogs of the genus Atelopus (Anura: Bufonidae)*. Ph. D. dissertation, Lawrence, University of Kansas, 287 pp.
- Coloma, L.A. (2002) Two new species of *Atelopus* (Anura: Bufonidae) from Ecuador. *Herpetologica*, 58(2), 229–252.
- Coloma, L.A. (ed). (2005–2007) Anfibios de Ecuador. Ver. 2.0 (29 October 2005). Museo de Zoología, Pontificia Universidad Católica del Ecuador. Quito, Ecuador. Available from <http://www.puce.edu.ec/zoologia/vertebrados/amphibiawebe/index.html> (accessed 19 June 2007).
- Coloma, L.A. & Ron, S. (2001) *Ecuador megadiverso. Anfibios, reptiles, aves y mamíferos/Megadiverse Ecuador. Amphibians, reptiles, birds, and mammals*. Serie de Divulgación del Museo de Zoología. Centro de Biodiversidad y Ambiente, Pontificia Universidad Católica del Ecuador, 1, 140 pp.
- Coloma, L.A., Lötters, S. & Salas, A.W. (2000) Taxonomy of the *Atelopus ignescens* complex (Anura: Bufonidae): designation of a neotype of *Atelopus ignescens* and recognition of *Atelopus exiguus*. *Herpetologica*, 56, 303–324.
- Cornalia, E. (1849) Vertebratorum synopsis in Museo Mediolanense extantium quae per novam orbem Cajetanus Osculati Collegit Annis 1846–47–48. *Museo Mediolanense*, 304–315.
- De la Riva, I. (2004) Taxonomic Status of *Bufo simus* O. Schmidt, 1857 (Anura: Bufonidae). *Journal of Herpetology*, 38(3), 431–434.
- De la Riva, I., Köhler, J., Lötters S. & Reichle, S. (2000) Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetología*, 14, 19–164.
- Dingerkus, G. & Uhler, L.D. (1977) Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology*, 52, 229–232.
- Duellman, W.E. (1970) Hylid frogs of Middle America. *Monograph of the Museum of Natural History University of Kansas*, 1, 1–753.
- Duellman, W.E. (2004) Frogs of the genus *Colostethus* (Anura; Dendrobatidae) in the Andes of northern Peru. *Scientific Papers Natural History Museum The University of Kansas*, 35, 1–49.
- Duellman, W.E. & De la Riva, I. (1999) Rediscovery and taxonomic status of *Hyla splendens* Schmidt, 1857 (Anura: Hylidae). *Copeia*, 1999, 197–199.
- Duellman, W.E. & Pramuk, J.B. (1999) Frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae) in the Andes of northern Peru. *Scientific Papers Natural History Museum The University of Kansas*, 13, 1–78.
- Dunn, E.R. (1931) New frogs from Panama and Costa Rica. *Occasional Papers of the Boston Society of Natural History*, 5, 385–401.
- Dunn, E.R. (1944) Herpetology of the Bogotá area. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 6, 68–81.
- Frost, D.R. (Ed.). (1985) *Amphibian Species of the World. A Taxonomic and Geographical Reference*. Allen Press and the Association of Systematics Collections, Lawrence, Kansas, U.S.A., 732 pp.
- Frost, D.R. (2006) *Amphibian Species of the World: an Online Reference*. Version 4 (17 August, 2006). American Museum of Natural History, New York, USA. Available from <http://research.amnh.org/herpetology/amphibia/index.php> (accessed 26 January 2007).
- Galvis, P.A. (2005) *Atelopus laetissimus*. In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T. & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 83.
- Gray, P. (1983) Morphometrics of the *Atelopus ignescens* Complex (Anura: Bufonidae). M. S. Thesis, University of Kansas, Lawrence, Kansas, U.S.A.
- Gray, P. & Cannatella, D.C. (1985) A new species of *Atelopus* (Anura: Bufonidae) from the Andes of northern Peru.

- Copeia*, 1985, 910–917.
- Guayasamin, J.M. & Trueb, L. (2007) A new species of glass frog (Anura: Centrolenidae) from the lowlands of north-western Ecuador, with comments on centrolenid osteology. *Zootaxa*, 1447, 27–45.
- Harding, K.A. (1983) *Catalogue of new world amphibians*. Oxford, New York, Toronto, Sidney, Paris, Frankfurt, Pergamon Press, 420 pp.
- Hoffmann, C.K. (1878) In Bronn (ed.), *Die Klassen und Ordnungen des Thier-Reichs*, 6(2), pp. 635.
- IUCN, Conservation International & NatureServe. (2004) *Global Amphibian Assessment*. Available from <http://www.globalamphibians.org> (accessed 19 June 2007).
- JMP IN 5.1. (1989–2003) The statistical discovery software. SAS Institute Inc. USA.
- La Marca, E. (1983) A new frog of the genus *Atelopus* (Anura: Bufonidae) from Venezuelan cloud forest. *Contributions in Biology and Geology. Milwaukee Public Museum*, 54, 1–12.
- La Marca, E. (1996 “1994”) Descripción de una nueva especie de *Atelopus* (Amphibia: Anura: Bufonidae) de selva nublada andina de Venezuela. *Memoria Sociedad de Ciencias Naturales La Salle*, LIV (142), 101–108.
- La Marca, E., Lips, K.R., Lötters, S., Puschendorf, R., Ibáñez, R., Rueda-Almonacid, J.V., Schulte, R., Marty, C., Castro, F., Manzanilla-Puppo, J., García-Pérez, J.E., Bolaños, F., Chaves, G., Pounds, J.A., Toral, E. & Young, B.E. (2005) Catastrophic population declines and extinctions in Neotropical harlequin frogs (Bufonidae: *Atelopus*). *Biotropica*, 37, 190–201.
- Leviton, A.E., Gibbs, Jr., R. H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. *Copeia*, 1985, 802–832.
- Lips K.R., Brem, B., F., Brenes, R., Reeve, J.D., Alford, R.A., Voyles, J., Carey, C., Livo, L., Pessier, A.P. & Collins, J.P. (2006) Emergin infectious disease and the loss of biodiversity in a neotropical amphibian community. *Proceedings of the National Academy of Sciences*, 103, 3165–3170.
- Lötters, S. (1996) The Neotropical Toad Genus *Atelopus*. Checklist — Biology — Distribution. M. Vences & F. Glaw, Cologne, Germany, 143 pp.
- Lötters, S. (2005) *Atelopus pachydermus* (Schmidt, 1857). In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T. & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 97.
- Lötters, S., Schulte, R., Córdova, J.H. & Veith, M. (2005a) Conservation priorities for harlequin frogs (*Atelopus* spp.) of Peru. *Oryx*, 39 (3), 343–346.
- Lötters, S., Schulte, R. & Duellman, W.E. (2005b) A new and Critically Endangered species of *Atelopus* from the Andes of northern Peru (Anura: Bufonidae). *Revista Española de Herpetología*, 18, 101–109.
- Lynch, J.D. (1993) A new harlequin frog from the Cordillera Oriental of Colombia (Anura, Bufonidae, *Atelopus*). *Alytes*, 11, 77–87.
- Mendelson III, J.R., Lips, K.R., Diffendorfer, J.E., Gagliardo, R.W., Rabb, G.B., Collins, J.P., Daszak, P., Ibáñez D., R., Zippel, K.C., Stuart, S.N., Gascon, C., da Silva, H.R., Burrowes, P.A., Lacy, R.C., Bolaños, F., Coloma, L.A., Wright, K.M. & Wake, D.B. (2006a). Response to Comment on “Confronting amphibian declines and extinctions.” Letters. *Science*, 314, 1541–1542.
- Mendelson III, J.R., Lips, K.R., Gagliardo, R.W., Rabb, G.B., Collins, J.P., Diffendorfer, J.E., Daszak, P., Ibáñez D., R., Zippel, K.C., Lawson, D.P., Wright, K.M., Stuart, S.N., Gascon, C., da Silva, H.R., Burrowes, P.A., Joglar, R.L., La Marca, E., Lötters, S., du Preez, L.H., Weldon, C., Hyatt, A., Rodriguez-Mahecha, J.V., Hunt, S., Robertson, H., Lock, B., Raxworthy, C.J., Frost, D.R., Lacy, R.C., Alford, R.A., Campbell, J.A., Parra-Olea, G., Bolaños, F., Calvo Domingo, J.J., Halliday, T., Murphy, J.B., Wake, M.H., Coloma, L.A., Kuzmin, S.L., Stanley Price, M., Howell, K.M., Lau, M., Pethiyagoda, R., Boone, M., Lanoo, M.J., Blaustein, A.R., Dobson, A., Griffiths, R.A., Crump, M.L., Wake, D.B. & Brodie Jr., E.D. (2006b) Confronting amphibian declines and extinctions. *Science*, 313, 48.
- Merino-Viteri, A., Coloma, L.A. & Almendáriz, A. (2005) Los *Telmatobius* (Leptodactylidae) de los Andes del Ecuador y su declive poblacional. In Lavilla, E.O. & De la Riva, I. (Eds.), *Estudios sobre las ranas andinas de los géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*. Asociación Herpetológica Española, Monografías de Herpetología 7, Valencia, España, pp. 9–37.
- Miranda-Leiva, A. (1995) Inventario preliminar de anfibios y reptiles del Parque Nacional de Cutervo. *Revista Biovisión del Departamento de Ciencias Biológicas de la Universidad Nacional de Cajamarca*, 3.
- Myers, C.W. & Duellman, W.E. (1982) A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates*, 2752, 1–32.
- Nieden, F. (1926) *Anura II. Das Tierreich*. Walter de Gruyter & Co., Berlin and Leipzig, Germany, 110 pp.
- Nogales, F. & Rueda Almonacid, J.V. (2005) *Atelopus bomolochos* Peters, 1973. In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T. & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 60.
- Noonan, B.P. & Gaucher, P. (2005) Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. *Molecular Ecology*, 14, 3017–3031.
- Peracca, M.G. (1904) Viaggio del Dr. Enrico Festa nell’Ecuador e regioni vicine: rettili ed amfibii. *Bolletino dei Musei di*

- Peters, J.A. (1973) The frog genus *Atelopus* in Ecuador (Anura: Bufonidae). *Smithsonian Contributions to Zoology*, 145, 1–49.
- Pounds, J.L., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167.
- Pounds, J.L., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2007) Response to Comment on “Widespread amphibian extinctions from epidemic disease driven by global warming.” Brief communications arising. *Nature*, 447:doi:10.1038/nature05941.
- Renjifo, J.M. & Renjifo, C. (2005) *Atelopus arsyecue*. In Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T., & Angulo, A. (Eds.), *Ranas arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia, pp. 57.
- Rivero, J.A. (1963) Five new species of *Atelopus* from Colombia, with notes on other forms from Colombia and Ecuador. *Caribbean Journal of Science*, 3, 103–124.
- Rivero, J.A. (1965) Notes on the Andean salientian (Amphibia) *Atelopus ignescens* (Cornalia). *Caribbean Journal of Science*, 5, 137–140.
- Rivero, J.A. (1968) More on the *Atelopus* (Amphibia, Salientia) from western South America. *Caribbean Journal of Science*, 8, 19–29.
- Rivero, J.A. (1974 “1972”) On *Atelopus oxyrhynchus* Boulenger (Amphibia, Salientia), with the description of a new race and a related new species from the Venezuelan paramos. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, 29, 600–612.
- Rivero, J.A. & Granados Díaz, H. (1993) Nueva especie de *Atelopus* (Amphibia: Bufonidae) del departamento del Cauca, Colombia. *Caribbean Journal of Science*, 29, 12–17.
- Rodríguez, L.O., Córdova, J. & Icochea, J. (1993) Lista preliminar de los anfibios del Perú. *Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (A)*, 45, 1–22.
- Ron, S.R. (2005) Predicting the distribution of the amphibian pathogen *Batrachochytrium dendrobatidis* in the New World. *Biotropica*, 37(2), 209–221.
- Ron, S.R., Duellman, W.E., Coloma, L.A. & Bustamante, M.R. (2003) Population decline of the jambato toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *Journal of Herpetology*, 37, 116–126.
- Ron, S.R., Santos, J.C. & Cannatella, D.C. (2006) Phylogeny of the túngara frog genus *Engystomops* (= *Physalaemus pustulosus* species group; Anura: Leptodactylidae). *Molecular Phylogenetics and Evolution*, 39, 392–403.
- Ron, S.R., Guayasamin, J.M., Coloma, L.A. & Menéndez-Guerrero, P. (In press) Status and Decline of Amphibians of Ecuador. In H. Heatwole and J. W. Wilkinson (Eds.), *Amphibian Biology. Decline and conservation, Vol. IX*. Surrey Beatty & Sons Pty. Ltd. Australia.
- Rueda-Almonacid, J.V. (1994) Una nueva especie de *Atelopus* Duméril & Bibron 1841 (Amphibia: Anura: Bufonidae) para la Sierra Nevada de Santa Marta, Colombia. *Trianea*, 5, 101–108.
- Rueda-Almonacid, J.V., Rodríguez-Mahecha, J.V., Lötters, S., La Marca, E., Kahn, T. & Angulo, A. (Eds.). (2005) *Ranas Arlequines*. Conservación Internacional. Panamericana Formas e Impresos S. A., Bogotá, Colombia.
- Ruíz-Carranza, P.M., Ardila-Robayo, M.C. & Hernández-Camacho, J.I. (1994) Tres nuevas especies de *Atelopus* A. M. C. Duméril & Bibron 1841 (Amphibia: Bufonidae) de la Sierra Nevada de Santa Marta, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 19, 153–163.
- Ruiz-Carranza, P.M., Ardila-Robayo, M.C. & Lynch, J.D. (1996) Lista actualizada de la fauna de Amphibia de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 20, 365–415.
- Ruthven, A.G. (1916) Description of a new species of *Atelopus* from the Santa Marta mountains, Colombia. *Occasional Papers of the Museum of Zoology, University of Michigan*, 8, 1–69.
- Savage, J. (1969) Clarification of the status of the toad, *Bufo veraquensis* O. Schmidt, 1857. *Copeia*, 1969, 178–179.
- Ruthven, A.G. (1970) On the trail of the golden frog: with Warszewicz and Gabb in Central America. *Proceedings of the California Academy of Sciences*, 38, 273–338.
- Ruthven, A.G. (1972) The systematic status of *Bufo simus* O. Schmidt with description of a new toad from western Panama. *Journal of Herpetology*, 6, 25–33.
- Savage, J.M. & Heyer W.R. (1969) Variation and distribution of the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. *Beitrag zur Neotropischen Fauna*, 5, 111–131.
- Savage, J.M. & Heyer W.R. (1997) Digital webbing formulae for anurans: a refinement. *Herpetological Review*, 28, 131.
- Schmidt, O. (1857) Diagnosen neuer Frösche des Zoologischen Cabinets zu Krakau. *Sitzungsberichte der Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse*, 24, 10–15.
- Schmidt, O. (1858) Deliciae herpetologicae musei zoologici cracoviensis. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse*, 14, 237–258.
- Seimon, T.A., Seimon, A., Daszak, P., Halloys, S.R.P., Schloegel, L.M., Aguilar, C.A., Sowell, P., Hyatt, A.D., Konecky,

- B. & Simmons, J.E. (2006). Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology*, 12, 1–12.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, 306, 1783–1786.
- Toral, E., & Frenkel, C. (2006) Population state of *Atelopus exiguus* in the South Ecuadorian Andes. In: Donnelly, M.A. & K.E. Cooper (Eds.). *Abstracts-2006. Joint Meeting of Ichthyologists & Herpetologists. New Orleans, USA*, pp: 111–112.
- Tosi, J. A., Jr. (1960) *Zonas de vida natural en el Perú*. Instituto Interamericano de Ciencias Agrícolas, Zona Andina, Boletín Técnico 5, Lima, Perú.
- Valencia, R., Cerón, C., Palacios, W. & Sierra, R. (1999) Las formaciones naturales de la Sierra del Ecuador. In Sierra, R. (Ed.), *Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental*. Proyecto INEFAN/GEF-BIRF y Ecociencia, Quito, Ecuador, pp. 79–108.
- Vitt, L. J., Sartorius, S.S. , Avila-Pires, T.C.S., Espósito, M.C. & Miles, D.B. (2000) Niche segregation among sympatric Amazonian teiid lizards. *Oecologia*, 122, 410–420.
- Wiens, J.J. (2004) What is speciation and how should we study it? *The American Naturalist*, 163, 914–923.
- Wiens, J.J. & Servedio, M.R. (2000) Species delimitation in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London*, 267, 631–636.

Appendix

Type specimens of *Atelopus bomolochos* examined

ECUADOR: *Provincia Azuay*: CAS 85139–41, Vic. E of Cuenca, 2535 m above sea level; CAS 85341–42, 93912, paratopotypes from Sevilla de Oro, 2800 m above sea level, 82 km E of Cuenca; *Provincia Cañar*: CAS 93906, paratype from between Juncal and General Morales, 2500 m above sea level.