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TWO NEW SPECIES OF *ATELOPUS* (ANURA: BUFONIDAE) FROM ECUADOR

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ABSTRACT: Two new species of *Atelopus* from Ecuador are described; both are from the highlands of the Cordillera Occidental of the Andes, one from the Chimbo Basin and the other from the Páramos del Cajas. I include osteological data of both species and the description of the gastromyzophorous tadpoles of one of the new species. Patterns of diversity and endemism of *Atelopus* justify the necessity of further research and conservation efforts directed toward Andean habitats.

Key words: Anura; Bufonidae; *Atelopus*; *A. guanujo* new species; *Atelopus nanay* new species; Taxonomy; Osteology; Tadpole; Andes; Ecuador

THE speciose neotropical bufonid genus *Atelopus* contains about 70 recognized species (Frost, 2000). Individuals of *Atelopus* are easily collected because they are diurnal, slow-moving, sometimes abundant, and often conspicuously colored. Therefore, many specimens have been deposited at scientific collections since the 19th century. Nevertheless, ongoing explorations in the neotropics and more detailed analyses of museum specimens continue to reveal previously unknown species.

Most species of *Atelopus* occur in the northern Andes (Lötters, 1996), and seven nominal species have been recorded from the Cordillera Occidental of Ecuador: *Atelopus arthuri* Peters, 1973; *A. coynei* Miyata, 1980; *A. exiguus* (Boettger, 1892); *A. ignescens* (Cornalia, 1849); *A. longirostris* Cope, 1868; *A. lynchi* Cannatella, 1981; and *A. mindoensis* Peters, 1973. All of these species are endemic to the Cordillera Occidental except *A. ignescens,* which also occurs in the Cordillera Oriental (Coloma et al., 2000).

Herein, I describe two new species from the Cordillera Occidental of the Ecuadorian Andes; one is from Chimbo Valley and the other is from Páramos del Cajas.

MATERIALS AND METHODS

Specimens examined, other than type specimens, are listed in Appendix I. Museum acronyms follow Leviton et al. (1985), Frost (1985), and Duellman (1993). Sexual maturity was determined by the presence of eggs or convoluted oviducts in females, and by the presence of nuptial excrescences covering the dorsum of Finger I in males. Throughout the text, I use the term "spiculae" to refer to pustular warts and "coni" to refer to spiculae with pointed projections (Duellman and Trueb, 1986). Measurements were taken following Gray and Cannatella (1985), with the addition of sacrum width (SW = the length from the outer margin of the sacral diapophysis to the outer margin of the contralateral side). Measurements are given only for adults. Abbreviations of measurements follow Coloma et al. (2000); they are SVL (snout–vent length), TIBL (tibia length), FOOT (foot length), HLSQ (head length from the squamosal to snout), IOD (interorbital distance), HDWD (head width), EYDM (eye diameter), EYNO (eye to nostril distance), ITNA (internarial distance), RDUL (length of flexed forearm), HAND (hand length), THBL (thumb length), and SW (sacrum width). Measurements of frogs and tadpoles were made to the nearest 0.1 mm with MAX-CAL® digital calipers. Measurements of tadpoles were made under a dissecting microscope. When comparing SVL of *Atelopus,* raw data were log transformed and a Student's unpaired *t*-test was used to assess the significance of differences between means. Measurements (mean, sample size, and standard deviation) for *A. sorianoi* (females and males) and *A. chrysocorallus* (females) were taken from La Marca (1996, 1983), respectively. Data on skeletons were taken from cleared and alizarin-red–alcian-blue stained specimens, and they were prepared following a modified version of the technique of Dingerkus and Uhler (1977). Osteological nomenclature follows Duellman and Trueb (1986), Trueb and Cloutier (1991), and Trueb (1993), but nomenclature for the skeletal elements of the hand follows Fabrezi and Alberch (1996).

Webbing formulae are indicated in the manner described by Savage and Heyer (1969), with modifications suggested by Myers and Duellman (1982) and Savage and Heyer (1997). The webbing formula is a subjective approximation, because in some cases the distinction between webbing and lateral fringes is ambiguous; in such cases, a range is indicated when a single specimen is described. In the diagnoses, a range also indicates intraspecific variation. Staging of larvae follows Gosner (1960). Drawings were made using a camera lucida attached to a Wild® M3B microscope. Ecological distributions of each species follow the Natural Formations of Ecuadorian Sierra defined by Valencia et al. (1999). Climatological data for the natural formations were taken from Cañadas-Cruz (1983).

SYSTEMATICS

Atelopus **guanujo** sp. nov.

Holotype.—QCAZ 11103, adult female, from Guanujo (01° 33′ 20″ S, 79° 00′ 24″ W; 2900 m), Provincia Bolívar, Ecuador, obtained on 13 April 1983 between 0945 h and 1030 h, by Marinus S. Hoogmoed and Luis A. Coloma.

Paratypes.—MHNG 2271.11–38 from Guanujo, 2600 m, obtained in December 1985 by Luis A. Coloma; QCAZ 1884, 1885 (cleared-and-stained preparation), 1905, obtained at the same locality in December 1986 by Luis A. Coloma; QCAZ 1886–92, 11205 (cleared-and-stained preparation), 11250–1 (cleared-and-stained preparation), 11253 (cleared-and-stained preparation), KU 289426 (cleared-and-stained preparation), obtained at the same locality in 10 April 1988 by Mario Tapia and Giovanni Onore; KU 193267 from near Guaranda, Provincia Bolívar, Ecuador, obtained by unknown collector in June 1980; KU 178388–89 from Guanujo, 2923 m, obtained in 15 January 1978 by John D. Lynch; MHNG 1151.21 from Gallo Rumi, Provincia Bolívar, Ecuador, obtained in April 1964 by Karl Von Sneidern.

Diagnosis.—(1) A moderate-sized species (SVL in females 35.0–46.0, $\bar{x}$ = 39.6, n = 12; males 29.9–37.1, $\bar{x}$ = 33.9, n = 29); (2) hindlimbs short (tibia length/SVL = 0.322–0.409, n = 41); (3) phalangeal formula of hand 2-2-3-3, basal webbing absent; (4) foot webbing formula **I**(0–1)—(0–2)**II**(½–2)—(1–3)**III**(1–3)—(2–4)**IV**(2–4)—(1–3)**V**; (5) snout acuminate, protruding beyond lower jaw; (6) tympanic membrane, tympanic annulus and stapes absent; (7) dorsal surfaces of body usually smooth, eight (out of 38) individuals bear a few scattered small warts and spiculae, (8) white spiculae (cream in preservative) present on forearm, flanks and dorsal surfaces of thighs; (9) vertebral neural processes inconspicuous; (10) dorsum orange to dark brown (cream to dark brown in preservative); (11) venter uniform orange (cream to pale yellow in preservative); (12) gular region without warts, spiculae or coni.

In having a plain orange-red dorsum, *Atelopus guanujo* is most similar to *A. bomolochos* (populations from Cutchil and Chilpe, Provincia Azuay, Ecuador), *A.* sp. (from Laguna La Cocha, Departamento Nariño, Colombia; see Coloma et. al., 2000, for a discussion of the taxonomic status of this population therein included under the name *A. ignescens*), *A. carbonerensis, A. chrysocorallus,* and *A. sorianoi* from the Andes of Venezuela. It differs from *A.* sp. and *A. bomolochos* by having white spiculae (in life) on forearm, flanks, and dorsal surfaces of thighs (black in *A.* sp., yellow in *A. bomolochos*). *Atelopus guanujo* is significantly smaller than *A. carbonerensis, A. chrysocorallus, A. sorianoi, A.* sp. and *A. bomolochos* (Table 2). Further, *A. guanujo* differs from *A.* sp. by lacking a patch of spiculae and coni on the gular and pectoral regions, from *A. bomolochos* in lacking green or greenish orange dorsal coloration, from *A. carbonerensis* and *A. sorianoi* in having a less protuberant snout and lacking 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.

Description of holotype.—(Figs. 1, 2A). Head about as long as wide, HLSQ and HDWD less than one third SVL (HLSQ/SVL = 0.293, HDWD/SVL = 0.283); snout acuminate in dorsal view; in lateral view, profile of tip of snout to the anterior margin of jaw curved and slightly protuberant; swollen gland on tip of snout absent; nostrils slightly protuberant, directed laterally, situated at level of apex of lower jaw; canthus rostralis distinct, weakly concave from eye to nostril; loreal region concave; lips not flared; interorbital region and occiput flat, smooth; eyelid flared without distinct tubercles; postorbital crest slightly raised, glandular; pretympanic and tympanic areas covered with warts; tympanic membrane and tympanic annulus absent; temporal area with spiculae; choanae small, rounded, widely separated; tongue twice as long as wide, broadest anteriorly, free for half its length posteriorly; ostia pharyngea absent.

Forearm relatively short (RDUL/SVL = 0.290); palmar tubercle round; supernumerary palmar tubercles distinct; thenar and subarticular tubercles distinct; digital tips with round pads; thumb relatively long (THBL/HAND = 0.621), apparently having two phalanges; webbing on hands absent, fingers lacking lateral fringes; relative length of fingers III > IV > II > I. Tibia relatively short (TIBL/SVL = 0.376); fold on distal half of inner edge of tarsus absent; inner metatarsal tubercle oval; outer metatarsal tubercle round, raised, about two thirds length of inner metatarsal tubercle; supernumerary plantar and subarticular tubercles conspicuous; digital pads distinct; webbing formula of foot **I**1—1**II**1—(1–2)**III**(1–2)—2**IV**(2–3)—(1–1½)**V**; relative length of toes IV > V = III > II > I.

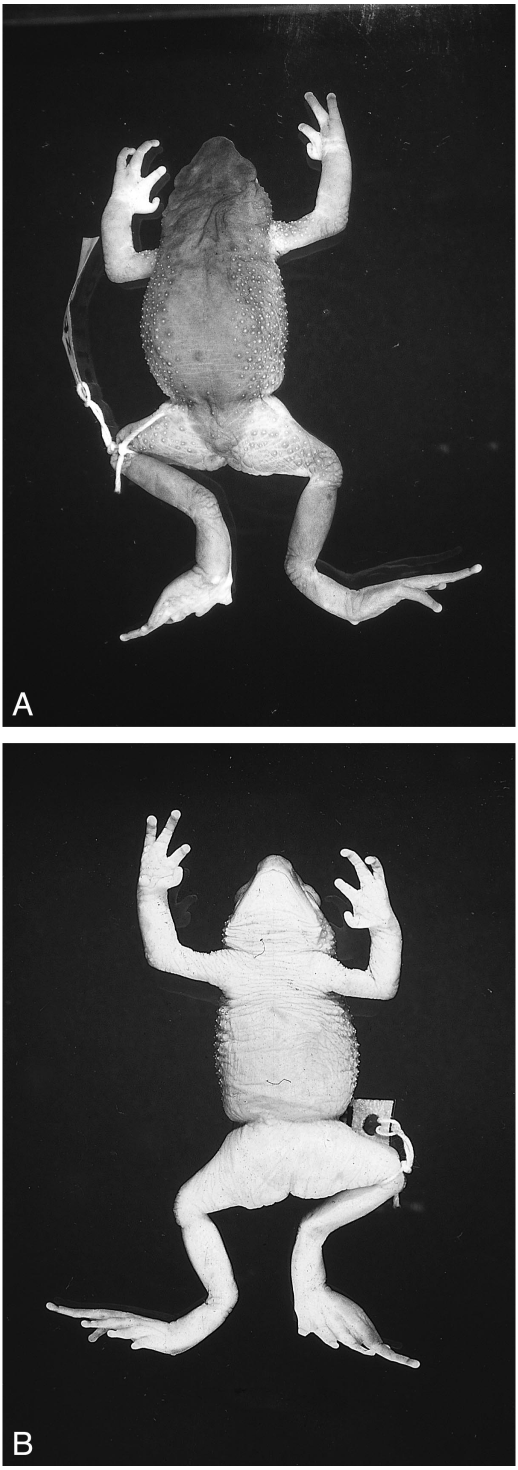

FIG. 1.—Holotype of *Atelopus guanujo* (QCAZ 11103): (A) dorsal and (B) ventral views. Female SVL = 37.5 mm.

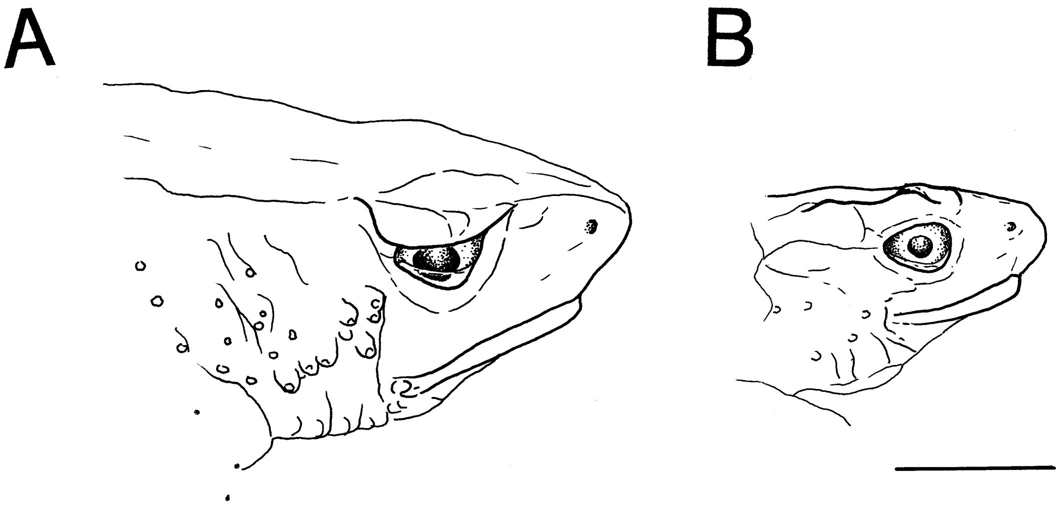

FIG. 2.—Lateral view of head of holotype of (A) *Atelopus guanujo* and (B) *A. nanay* (QCAZ 1922). Scale = 5 mm.

Dorsal surfaces smooth with scattered spiculae, increasing in number toward the flanks; flanks and anterior and proximal upper surfaces of forelimbs bearing numerous, evenly distributed spiculae; throat, chest, belly, undersides of hindlimbs rugose, but free of warts; cloaca opens as an inconspicuous tube at midlevel of thighs, directed posteriorly; warts present lateral to cloacal opening, low.

Coloration in preservative (70% ethanol): dorsal surface of head and body brown, becoming paler brown posteriorly on body, flanks, dorsal surfaces of limbs; minute gray stippling regularly distributed on dorsum of body (viewed at 8× magnification); spiculae cream; dorsal surfaces of Fingers I and II cream; tips of digits of hand cream dorsally, brown adjacent articular region of phalanges; throat, chest, belly, and ventral surfaces of limbs yellowish cream; outer metatarsal tubercle cream, brown surrounding plantar areas; proximal end of tongue lacking black pigmentation.

Measurements (in mm): SVL 37.5, TIBL 14.1, FOOT 16.9, HLSQ 11.0, HDWD 10.6, ITNR 3.4, EYDM 3.0, EYNO 2.7, RDUL 10.9, HAND 10.3, THBL 6.4, SW 11.0.

Variation.—Meristic variation is described in Table 1. The paratypes resemble the holotype with the following noteworthy exceptions. The proximal undersides of thighs and pelvic area have a patch of areolate skin in all but holotype. 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 and inner side of the proximal phalanx of Finger II. Forelimbs are long and slender in females, but short and robust in males (Table 1). Morphological features of hand and foot of a female paratype (KU 178389) are depicted in Fig. 3. MHNG 2271.28 and 2271.30 have abnormal right and left hindlimbs, respectively; they lack shanks and distal elements.

All paratypes possess a brown, narrow middorsal line; in most specimens, it is conspicuous, but in 7 (QCAZ 1886–87, 1905, MHNG 2271.13, 2271.16, 2271. 25, 2271.28) of 38 it is indistinct. Dorsal coloration varies in preservative from uniform yellowish cream to dark brown. Some individuals have one to three small dark brown marks on dorsum. One specimen (MHNG 2271.16) possesses a creamy yellow dorsum with ill-defined brown marks. Two specimens (QCAZ 1884, 1886) have dark brown areas on the flanks. The venter varies from uniform pale cream to pale yellow in preservative. A young female (KU 193267) possesses a dark brown patch

TABLE 1.—Measurements (in mm) of adults of *Atelopus guanujo* and *A. nanay*; n = sample size. Mean and one standard deviation are listed above range.

	A. guanujo		*A. nanay*	
	Males (n = 29)	Females (n = 12)	Males (n = 17)	Females (n = 2)
SVL	33.9 ± 1.6 (29.9–37.1)	39.6 ± 3.0 (35.0–46.0)	25.2 ± 1.0 (23.6–27.3)	35.7 (31.7–39.6)
TIBL	12.8 ± 0.9 (10.1–14.4)	14.2 ± 0.3 (13.8–14.8)	9.2 ± 0.6 (7.9–10.1)	11.6 (9.9–13.3)
FOOT	14.9 ± 1.0 (12.5–16.8) (n = 28)	16.5 ± 0.9 (15.3–18.0)	9.4 ± 0.7 (8.5–10.8)	13.1 (10.7–15.4)
HLSQ	10 ± 0.4 (9.0–11.3)	11.3 ± 0.5 (10.5–12.1)	7.8 ± 0.5 (7.0–8.9) (n = 16)	10.2 (8.9–11.4)
HDWD	10.1 ± 0.5 (8.8–11.1)	10.7 ± 0.5 (9.7–11.3)	7.8 ± 0.3 (7.5–8.6)	9.7 (8.6–10.7)
EYDM	3.4 ± 0.3 (2.7–4.1)	3.5 ± 0.3 (3.0–4.1) (n = 11)	2.9 ± 0.2 (2.6–3.2) (n = 16)	3.3 (3.1–3.4)
EYNO	2.3 ± 0.2 (1.9–2.7)	2.7 ± 0.2 (2.5–3.0) (n = 11)	2.0–0.2 (1.7–2.2) (n = 16)	2.4 (2.1–2.6)
ITNA	3.6 ± 0.2 (3.2–3.9) (n = 28)	3.8 ± 0.6 (3.3–4.2)	2.9 ± 0.3 (2.6–3.3) (n = 16)	3.6 (3.3–3.9)
RDUL	9.6 ± 0.6 (8.7–10.8) (n = 16)	11.1 ± 0.7 (9.9–11.7)	7.8 ± 0.5 (7.1–8.5) (n = 16)	9.5 (8.6–10.4)
HAND	8.5 ± 0.5 (7.6–9.4) (n = 27)	10.5 ± 0.6 (9.6–11.3)	6.3 ± 0.3 (5.8–7.0) (n = 16)	8.5 (6.9–10.1)
THBL	5.7 ± 0.4 (4.6–6.4)	6.7 ± 0.5 (6.1–7.5)	4.0 ± 0.2 (3.6–4.2) (n = 16)	5.5 (4.4–6.6)
SW	9.4 ± 0.6 (7.7–10.2) (n = 28)	11.7 ± 1.4 (9.1–14.0)	6.4 ± 0.4 (5.8–7.1) (n = 16)	9.4 (8.2–10.5)

on the undersides of the thighs and pelvic region.

Color in life (Fig. 4): Color transparencies of specimens (no museum numbers associated) from Guanujo reveal that the dorsum, dorsal surfaces of limbs (except fingers and toes) and flanks are nearly uniform reddish orange to uniform orange or brownish orange. Dorsal surfaces of fingers and toes are yellowish orange with brown areas on the articular regions of phalanges. Creamy white spiculae are present on the flanks and forelimbs. The iris is black and lacks a conspicuous pupilary ring.

Tadpoles.—Tadpoles of this species are unknown.

Distribution and natural history.—*Atelopus guanujo* is known only from the type locality and its vicinity (Guaranda, Gallo Rumi) in the Chimbo Basin of the Cordillera Occidental of Ecuador, Provincia Bolívar (Fig. 5). These localities are between 2600 and 2923 m in humid cloud forest in the upper Río Chimbo Valley. Annual mean rainfall is 1000–2000 mm, and the annual mean temperature is 12–18 C. Frogs were collected at disturbed Cloud Montane Forest areas near the Río Salinas and Río Illangama. Formerly, this species

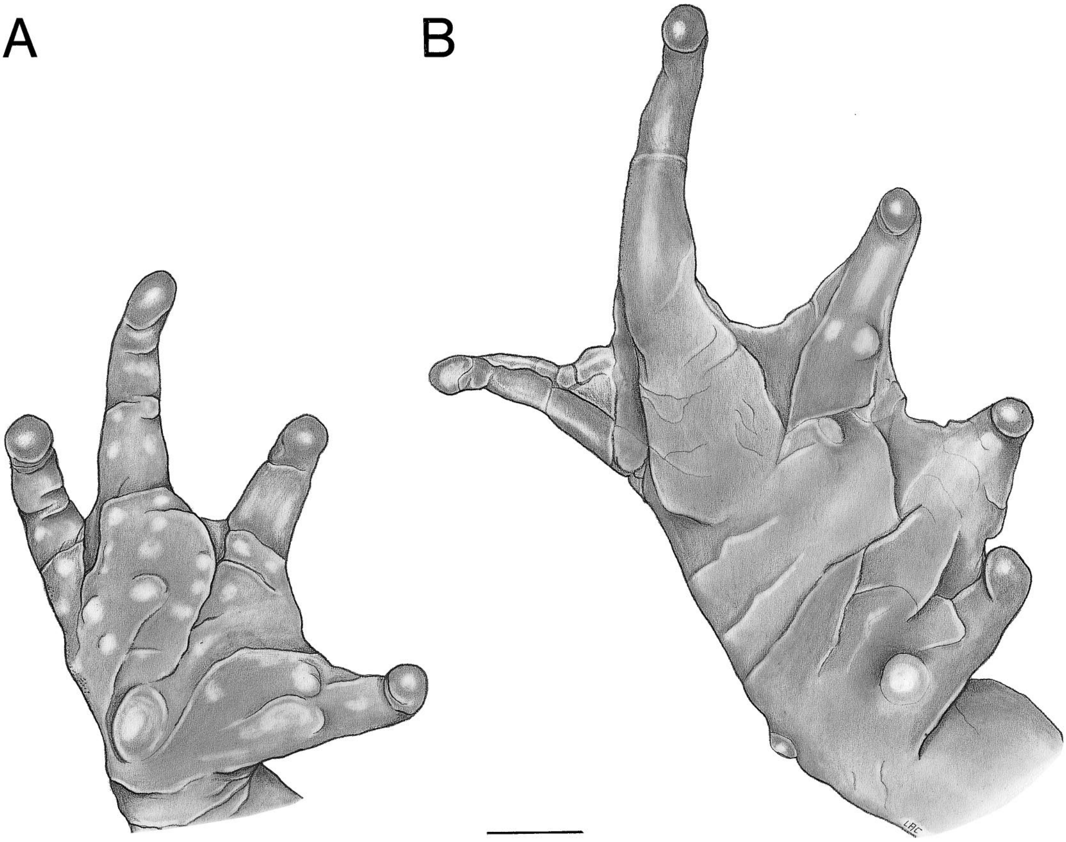

FIG. 3.—Ventral view of (A) right hand and (B) right foot of paratype (KU 178389, female) of *Atelopus guanujo.* Scale = 2 mm.

was abundant (personal observation); however, despite repeated efforts to locate this frog, the last living individuals were seen in 10 April 1988 by Mario Tapia. Some of these individuals were in amplexus (Mario Tapia, personal communication).

FIG. 4.—*Atelopus guanujo* (no number associated) from Guanujo.

Etymology.—The specific name is a noun in apposition and is dedicated to the Guanujo, a Quechua people inhabiting part of the region where this species formerly was abundant. The specific name also refers to the type locality, near the town that bears the same name as the indigenous group. This species is known locally as "puca sapo," Quechua and Spanish words, respectively; meaning "red toad".

Atelopus **nanay** sp. nov.

Holotype.—QCAZ 1922, adult male, from Las Tres Cruces (4 km W of Laguna Toreadora; 2° 46′ S, 79° 14′ W; Parque Nacional del Cajas; 4000 m), Provincia Azuay, Ecuador, obtained on 28 July 1989 by

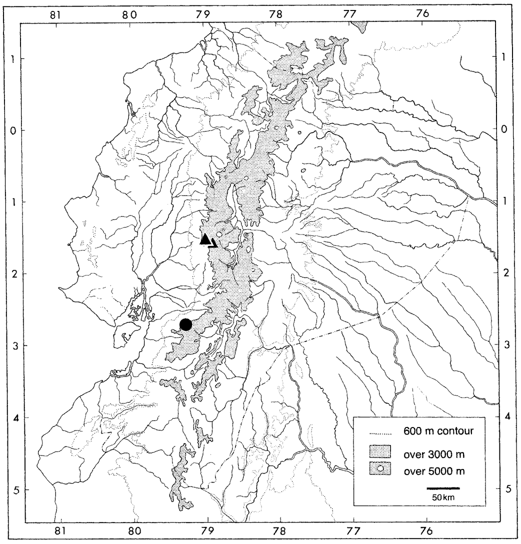

FIG. 5.—Map of Ecuador showing localities of *Atelopus guanujo* (triangles) and *A. nanay* (circle).

Stella de la Torre, Felipe Campos-Yánez, and Luis A. Coloma.

Paratypes.—QCAZ 1916–21, 1923 (cleared-and-stained skeletal preparation), 1924–27, KU 217474–78, same data as holotype; CM 117018 from 35 km WNW of Cuenca, Provincia Azuay, Ecuador, collected 9 November 1987 by an unknown collector; QCAZ 13938 from road Cuenca-Molleturo, Provincia Azuay, Ecuador, collected 31 December 1981 by Fernando Ortiz-Crespo.

Diagnosis.—(1) A small *Atelopus* (SVL in females 31.7–39.6, $\bar{x}$ = 35.7, n = 2; males 23.6–27.3, $\bar{x}$ = 25.2, n = 17); (2) hindlimbs short (tibia length/SVL in females 0.312–0.336, n = 2; males = 0.331–0.402, n = 17); (3) phalangeal formula of hand 1-2-3-3, webbing absent; (4) foot webbing formula **I**(0–½)—(½–1)**II**(½–1)—(1–2)**III**(1–2)—(2–3)**IV**(2–3)—1**V**; (5) snout acuminate, protruding beyond lower jaw; (6) tympanic membrane, tympanic annulus and stapes absent; (7) dorsal surfaces usually smooth, in some cases bearing few scattered, flat warts; (8) scattered white spiculae (cream in preservative) in flanks, limbs, and dorsum; (9) vertebral neural processes absent; (10) dorsum black (cream to dark brown in preservative); (11) venter cream with green and brown marks in life; plantar and palmar tubercles cream; (12) gular region without warts, spiculae or coni.

In having a black dorsum, *Atelopus nanay* resembles *A. ignescens* (as redefined by Coloma et al., 2000) from the northern Ecuadorian Andes, and has a size similar to that of *A. exiguus* from the southern Ecuadorian Andes in Provincia del Azuay. It differs from these taxa by having a 1-2-3-3 phalangeal formula (as observed in QCAZ 1923; skeletal preparation) instead of 2-2-3-3 (*A. ignescens, n* = 4; *A. exiguus, n* = 4; data taken from Coloma, 1997, and Coloma et al., 2000, respectively). *Atelopus nanay* is significantly smaller than *A. ignescens* (Table 2). Also, *A. nanay* lacks coni on flanks, and lacks a triangular mark with black spiculae and coni in the gular-pectoral region (present in *A. ignescens*). *Atelopus exiguus* has a green dorsum, yellow spiculae, and a yellow venter in life, whereas *A. nanay* has a black dorsum, white spiculae, and a venter black to cream with green and brown marks. Furthermore, *A. nanay* differs from *A. exiguus* by lacking pigmentation of proximal end of tongue and by having minute dark spots regularly distributed on dorsum of (viewed at 8× magnification).

Description of holotype.—(Figs. 2B, 6, 7). Head about as long as wide, HLSQ and HDWD slightly less than one third SVL (HLSQ/SVL = 0.328, HDWD/SVL = 0.316); snout truncate in dorsal view; in lateral view, profile of tip of snout to anterior margin of jaw curved and slightly protruding beyond lower jaw; swollen gland on tip of snout absent; nostrils slightly protuberant, directed laterally, situated at level of apex of lower jaw; canthus rostralis distinct, weakly concave from eye to nostril; loreal region concave; lips not flared; interorbital region and occiput flat, smooth; eyelid and canthus rostralis flared without distinct tubercles; postorbital crest flared; tympanic region without warts; tympanic membrane and tympanic annulus absent; warts in temporal area present, barely raised; choanae small, rounded, widely separated; tongue twice as long as wide, broadest anteriorly, free for half its

TABLE 2.—Results of Student's unpaired *t*-test showing significant differences between SVL of *Atelopus guanugo* and each of five species of *Atelopus* (above) and SVL of *A. nanay* and *A. ignescens* (below). Range, mean, standard deviation (SD), and samples size (*n*) are indicated above results.

Species	Females	Males
A. bomolochos	38.3–50.4 $\bar{x} = 44.7$, SD $\pm$ 3.2, $n = 13$ $t = 4.078$, df = 23, $P < 0.001$	32.1–42.1 $\bar{x} = 36.9$, SD $\pm$ 3.8, $n = 5$ $t = 2.960$, df = 32, $P = 0.0057$
A. carbonerensis	45.6–54.1 $\bar{x} = 49.4$, SD $\pm$ 4.3, $n = 4$ $t = 4.981$, df = 14, $P < 0.001$	—
A. chrysocorallus	47.1–50.4 $\bar{x} = 48.9$, SD $\pm$ 1.2, $n = 8$ $t = 6.062$, df = 18, $P < 0.001$	—
A. sorianoi	42.2–49.1 $\bar{x} = 44.9$, SD $\pm$ 2.6, $n = 5$ $t = 6.415$, df = 15, $P < 0.001$	38.2–39.8 $\bar{x} = 38.9$, SD $\pm$ 0.8, $n = 5$ $t = 6.779$, df = 32, $P < 0.001$
A. sp.	40.3–52.2 $\bar{x} = 45.2$, SD $\pm$ 3.6, $n = 10$ $t = 4.090$, df = 20, $P < 0.001$	36.7–41.0 $\bar{x} = 38.1$, SD $\pm$ 1.6, $n = 6$ $t = 5.664$, df = 33, $P < 0.001$
A. ignescens	35.6–48.2 $\bar{x} = 42.5$, SD $\pm$ 3.3, $n = 15$ $t = 3.552$, df = 15, $P < 0.0029$	34.2–41.4 $\bar{x} = 37.8$, SD $\pm$ 1.9, $n = 15$ $t = 24.911$, df = 30, $P < 0.001$

length posteriorly; vocal slits present; ostia pharyngea absent.

Forearm length nearly one third SVL (RDUL/SVL = 0.328); fingers not webbed, lacking lateral fringes; thenar, palmar, and subarticular tubercles distinct; palmar tubercle round; supernumerary palmar tubercles absent; digit tips with round pads; keratinized nuptial pad covering entire dorsal and lateral surfaces of thumb and inner side of Finger II; forearm swollen; thumb relatively short (THBL/HAND = 0.641), apparently with one phalanx; relative length of fingers III > IV > II > I. Tibia relatively short (TIBL/SVL = 0.402); no fold on distal half of inner edge of tarsus; inner metatarsal tubercle oval; outer metatarsal tubercle round, noticeably raised, slightly smaller than inner metatarsal tubercle; supernumerary plantar tubercles absent; subarticular tubercles at base of digits barely raised; digital pads distinct, round; webbing covering all digits except two or three phalanges of Toe IV; foot webbing formula **I**0—½**II**½—1**III**1—(2–3)**IV**2—1**V**; relative length of toes IV > V = III > II > I.

Dorsal surfaces smooth with few wrinkles on head and limbs; flanks with few, scattered, barely-raised spiculae, most numerous ventrolaterally; throat, chest, belly, and undersides of forearm rugose, but free of warts; cloacal patch with few wrinkles, but not differentiated from adjacent skin on undersides of thighs; cloacal opening at midlevel of thighs with surrounding skin heavily wrinkled.

Color in life: dorsum black; spiculae on flanks white; palmar and plantar tubercles cream; venter cream with large green marks; gular region with brown marks (Field Notes of L. A. Coloma, 28 July 1989).

Coloration in preservative (70% ethanol): dorsum, flanks and dorsal surfaces of limbs black; minute gray stippling regularly distributed on dorsum of body (viewed at 8× magnification); spiculae cream; upper lip cream suffused with brown; well-defined black stripe bordering the lower labium at inner and outer margins; undersides of limbs black with cream flecks; throat cream with brown marks; chest and abdomen cream; palmar, thenar, metatarsal, and subarticular tubercles on palmar and plantar surfaces cream contrasting with black on surrounding surfaces; a black, elliptical cloacal patch on undersides of thighs; proximal end of tongue lacking black pigmentation. The iris is

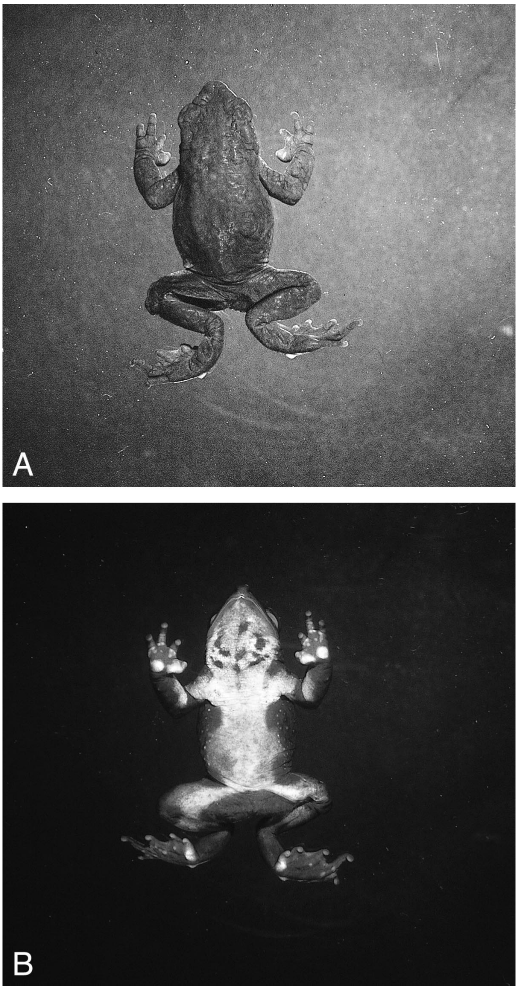

FIG. 6.—Holotype of *Atelopus nanay:* (A) dorsal and (B) ventral views. Male SVL = 24.4 mm.

black and lacks a conspicuous pupilary ring.

Measurements (in mm): SVL 24.4, TIBL 9.8, FOOT 8.0, HLSQ 8.0, HDWD 7.7, ITNR 2.7, EYDM 2.6, EYNO 2.1, RDUL 8.0, HAND 6.4, THBL 4.1, SW 6.9.

Variation.—Meristic variation is described in Table 1. The paratypes resemble the holotype, with the following noteworthy exceptions: females are larger than males; the snout of females is less protuberant than in males; the forearm of females is not swollen; and nuptial pads are absent in females. One female (CM 117018) differs in having more numerous spiculae on the flanks, anterodorsal surface of the arm and dorsal surfaces of the thighs, and a few scattered spiculae on the dorsum of body (not on head); another female (QCAZ 13938) lacks spiculae.

In males, the snout is acuminate in dorsal view; the top of the snout is sloped anteroventrally in lateral view. A few spiculae are present on the anterior surface of the arm in three males (QCAZ 1917–18, 1926) (out of 12), and spiculae are virtually absent on the flanks in four males (QCAZ 1916, 1920, 1924–25). Malformations are apparent on QCAZ 1921 and 1927: the former lacks Toe III on the left foot, and the latter has two toes on the right foot.

In preservative, ventral color in males varies from uniform cream (e.g., QCAZ 1918) to cream with dark brown marks (e.g., QCAZ 1927), to nearly uniform dark brown (e.g., QCAZ 1925). In one specimen (QCAZ 1921), the entire palmar surface is cream; thus, there is no marked contrast between tubercles and adjacent surfaces. In one female (CM 117018), the venter is cream with black marks, whereas in another (QCAZ 13938) the venter and ventral surfaces of limbs are entirely black, except the border of the mandible, which is brownish. In life, color variation mainly is on the venter. QCAZ 1923 had a cream venter washed with diffuse green and large, brown marks; QCAZ 1924 had an entirely green venter and QCAZ 1925 had a brown venter with diffuse white marks.

Tadpoles.—Measurements (mm) of developmental stages of a series of 14 larvae (QCAZ 3672) with the same data as the holotype are given in Table 3. The following description is based on an individual in Stage 28 (QCAZ 3672) (Fig. 8B). Type-IV tadpole of Orton (1953). Tadpoles belong to the gastromyzophorous ecomorphological guild defined by Altig and Johnston (1989).

Body length (tip of snout–base of vent tube) 5.9 mm, total length 16.2 mm. Body elongately ovoid, dorsoventrally compressed, about two thirds as high as wide, greatest width at anterior half of body. Snout bluntly rounded in dorsal view and in profile; body constricted at level of eyes and at spiracle; nostrils small, about one-

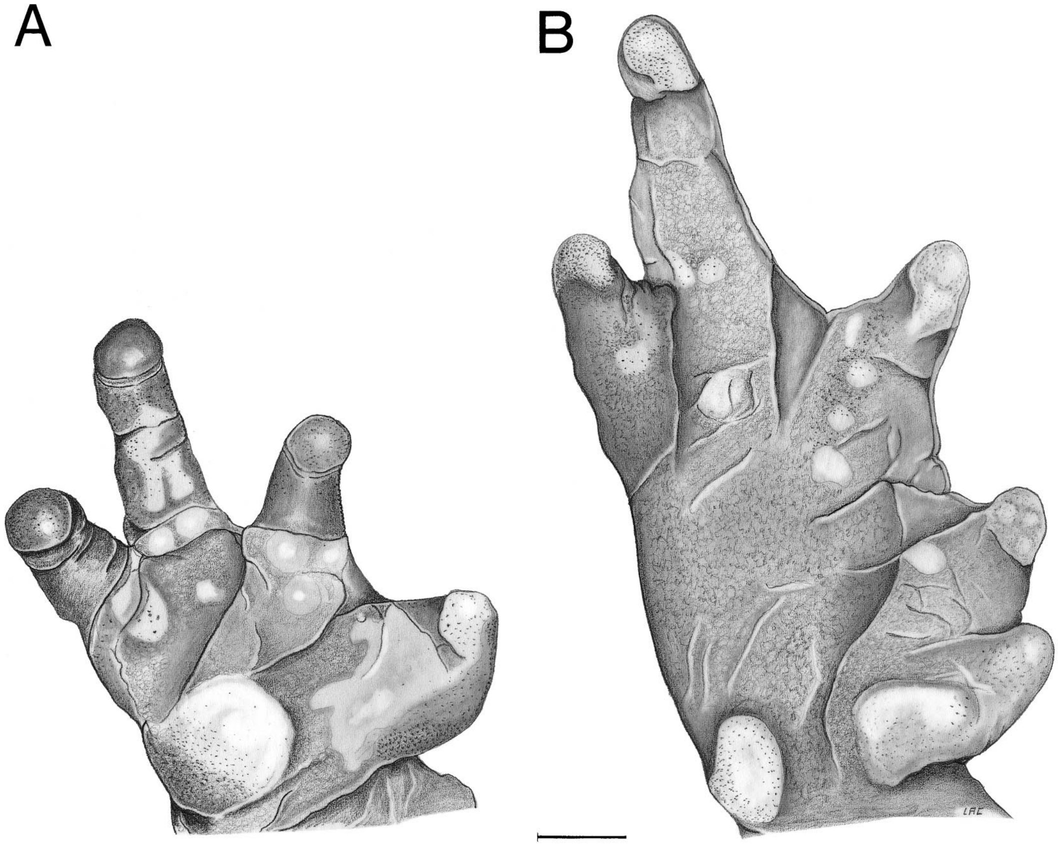

FIG. 7.—Ventral view of (A) right hand and (B) right foot of holotype of *Atelopus nanay.* Scale = 1 mm.

third the distance from eyes to tip of snout; eyes dorsal, directed dorsolaterally, diameter 0.7 mm; interocular distance 1.3 mm (taken from the medial edges of the corneas). Spiracle sinistral, half free, elongate, ventral to horizontal body axis, directed posterodorsally, originating at midbody; diameter of opening about equal to length of free tube; vent tube short, medial. Caudal musculature robust anteriorly, narrowing abruptly posterior to midlength of tail, terminating in a narrow strip just anterior to end of tail; dorsal fin highest posterior to midlength of tail; tail length 36.4% of total length; dorsal and ventral fin heights 0.7 mm at midlength of tail, dorsal fin beginning well posterior to body, ventral fin beginning posterior to vent tube, tip of tail rounded.

TABLE 3.—Measurements (in mm) of developmental stages sensu Gosner (1960) of 14 tadpoles of *Atelopus nanay* (QCAZ 3672); *n* = sample size, SD = standard deviation.

Stage	*n*	Body length mean ± SD (range)	Total length mean ± SD (range)
25	2	4.4 ± 0.1 (4.3–4.5)	11.2 ± 0.4 (10.0–11.4)
26	3	4.9 ± 0.4 (4.5–5.2)	13.0 ± 0.7 (12.4–13.8)
27	7	5.2 ± 0.4 (4.8–5.9)	14.2 ± 1.1 (12.7–15.5)
28	2	5.7 ± 0.3 (5.5–5.9)	15.0 ± 1.7 (13.8–16.2)

Mouth ventral, surrounded by labia forming complete oral disc 3.8 mm wide; one row of marginal papillae on upper labium, on vertex between upper and lower labia, and on one-fourth of lower labium; papillae on rest of lower labium absent; one submarginal papilla anterior to vertex

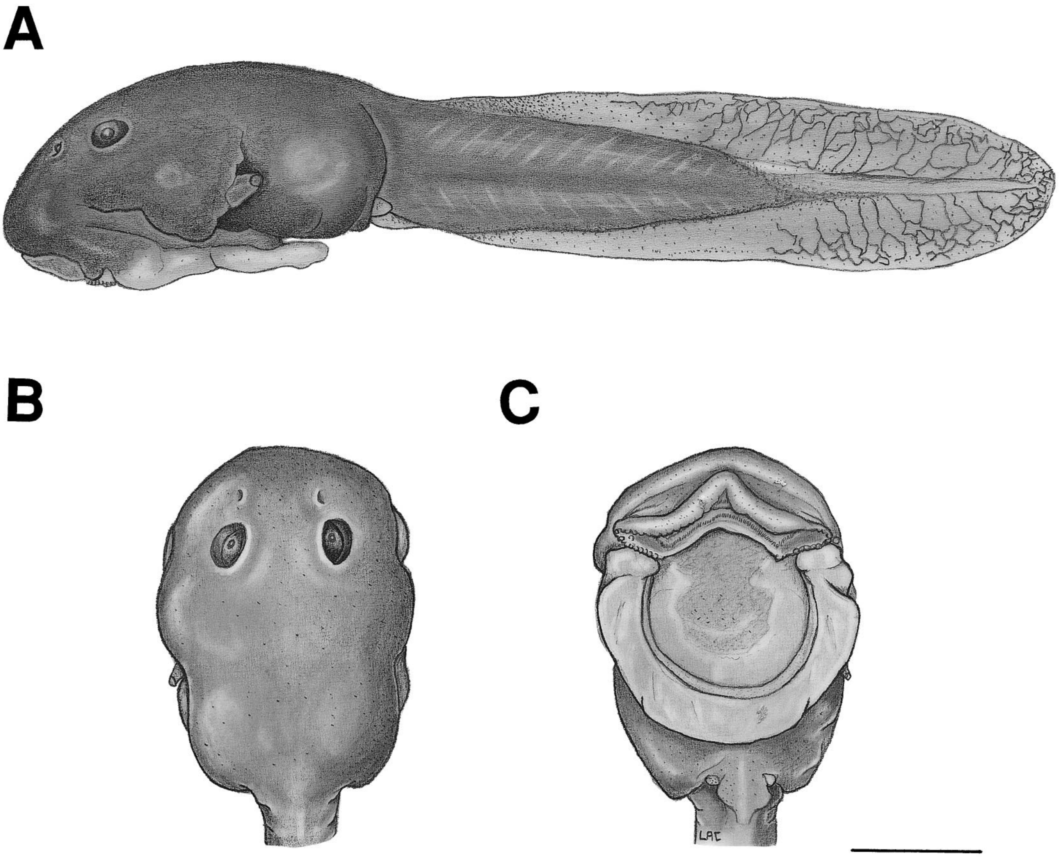

FIG. 8.—Tadpole of *A. nanay* (QCAZ 3672): (A) lateral, (B) dorsal, and (C) ventral views. Scale = 2 mm.

on upper labium; one submarginal papilla just posterior to vertex on lower labium. Labial tooth row formula 2/3; rows complete, about equal in length; jaw sheaths about equal in length, upper jaw sheath narrow, but wider medially; lower jaw sheath V-shaped. Large ventral suctorial disc covering area from posterior labium to just anterior to end of body (at base of vent tube), forming a complete, round disc with raised edges; suctorial disc broadened at juncture with labium, few wrinkles present just posterior to juncture; roof of suctorial disc bearing an elliptical fold posteriorly; skin on edge and roof of disc smooth, skin on posterior margin of roof finely rugose.

In preservative, dorsum, sides of body, and belly uniform brown; spiracle brown; tail musculature uniform brown for two thirds of its length, whereas distal one-third white with scattered brown pigment. Dorsal fin brown at base, with numerous flecks posteriorly forming a reticulate pattern; scattered flecks on anterior half of ventral fin and reticulate pattern posteriorly; oral disc brown; suctorial disc translucent, except for brown flecks on roof. In life (based on color transparencies), body entirely black and fins translucent with black flecks.

Comparisons: The tadpole of *Atelopus nanay* is similar to that of *A. ignescens* (Duellman and Lynch, 1969) and *A. carrikeri* (senior synonym of *A. leoperezii* Ruíz-Carranza, et al., 1994 fide Coloma, 1997), which are the only larvae of *Atelopus* (among 30 species for which information is available; Coloma et al., 2000) having an entirely black body. Tadpoles of *A. nanay* are slightly smaller (total length of tadpoles in Stage 25 = 10.0–11.4, $\bar{x}$ =

11.2, n = 2) than larvae of *A. ignescens* (total length of tadpoles in Stage 25 = 11.5–14.7, $\bar{x}$ = 13.2, n = 10; data from Duellman and Lynch, 1969), and much smaller than those of *A. carrikeri* [Ruíz-Carranza et al. (1994) stated that the length of tadpoles of *A. carrikeri* is twice the length of previously known *Atelopus* larvae]. Furthermore, tadpoles of *A. nanay* possess a white blotch on the distal third of the tail musculature, whereas the tail musculature of *A. ignescens* is entirely black. Tadpoles of *A. nanay* resemble those of *A. exiguus* and *A. peruensis* in having a shallow tail. However, the latter two have pale (in life, pale golden and bluish white, respectively) marks on dorsum of body and caudal musculature (Coloma et al., 2000).

Distribution and natural history.—This species is known only from paramo habitats at the type locality, which is in Herbaceous Paramo in the Cordillera Occidental in Ecuador (Fig. 5). Annual mean precipitation is 1000–2000 mm and annual mean temperature is 3–6 C. By day, on 28 July 1989, some specimens were active close to streams and springs in an area of many interconnected pools; others were on land under rocks. A female, collected on 9 November 1987, has convoluted oviducts with large ovarian eggs. *Atelopus nanay* was found syntopically with *Eleutherodactylus cryophilius, Telmatobius niger,* and *Gastrotheca pseustes.* Tadpoles were found in a stream close to a spring where adults of this species also were present. Some of the specimens described herein are the last seen alive at that locality (in 1989), despite subsequent efforts (28 November 1992, 19 February 1993, 19 December 1998) to find them.

Etymology.—The specific name *nanay* is a Quechua word, which means "sadness." The name is used in reference to the sadness that Ecuadorian indigenous peoples often express when referring to the disappearance of highland *Atelopus.* This name is used to call attention to catastrophic extinction of frogs of the genus *Atelopus* in the Ecuadorian Andes.

Osteology

The following description applies to adults of *Atelopus guanujo* and *A. nanay,* except when indicated otherwise. Intraspecific variation was not assessed in *A. nanay.* Descriptions are based on cleared and double-stained skeletal preparations [QCAZ 1885 (male), 11205 (female), 11250–51 (males), 11253 (male) of *A. guanujo* and QCAZ 1923 (male of *A. nanay*)], except as indicated otherwise [for some features, I include specimen KU 289426 (male of *A. guanujo*)].

Skull.—(Figs. 9, 10). In dorsal view, the skull is triangular. A cartilaginous medial septum nasi, paired tectum nasi, and paired oblique cartilages are visible dorsally as a continuous, thin strip at the anterior end of the sphenethmoid and at the anterolateral border of nasals. The solum and septum nasi are synchondrotically (or synostotically) fused to the sphenethmoid. The septum nasi contributes to the medial, anterodorsal configuration of the snout that is protruding relative to the anterior margin of maxilla. Between the tectum nasi and the premaxilla are the alary and prenasal cartilages.

The septomaxilla is a U-shaped bone with medial and lateral rami; the anterior end is closed. The lateral ramus is broad and bears a nasal process. The latter varies in shape from an elongate, cylindrical and well-differentiated process in *Atelopus nanay* to a pyramidal, poorly differentiated process in *A. guanujo. Atelopus guanujo* and *A. nanay* have a foramen in the lateral ramus.

The entire surfaces of the single sphenethmoid are sculptured with a rough appearance, except its posterior fourth, which is cartilaginous and borders the anterolateral margins of the optic foramina. The posterior limits of ossification of sphenethmoid are at about one-third the length of the margin of the orbit in *Atelopus nanay,* and at varying levels from one-third to slightly posterior to midway of orbital region in *A. guanujo.*

Paired prootics are synostotically united ventromedially; dorsally, they are fused to the posterolateral margins of frontoparie-

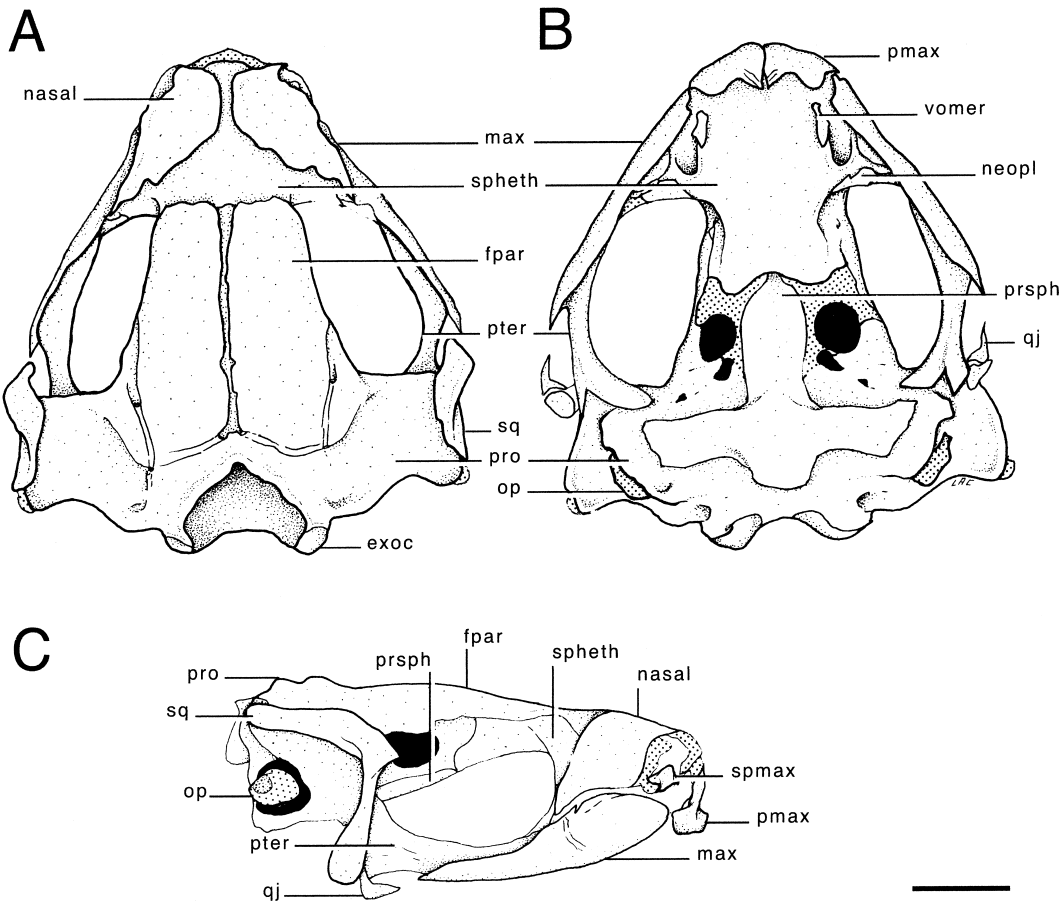

FIG. 9.—Skull of *Atelopus guanujo* (QCAZ 1885, male) in (A) dorsal, (B) ventral, and (C) lateral views. Scale = 2 mm. Abbreviations: exoc = exoccipital; fpar = frontoparietal; max = maxilla; neopl = neopalatine; op = operculum; pmax = premaxilla; pro = prootic; prsph = parasphenoid; pter = pterygoid; spmax = septomaxilla; qj = quadratojugal; spheth = sphenethmoid; sq = squamosal.

tals. Prootic surfaces are slightly rugose. The lateral portion (crista parotica) lacks a posterodorsal projection beyond the end of the posterior margin of the cranium. The anterior margin of prootic forms the posterior edge of the optic foramen. The oculomotor and prootic foramina are located at the anteroventral portion of the prootic. The posteroventral margin of the prootic surrounds the ventral margins of the postotic foramen.

Both paired exoccipitals are synostotically united dorso- and ventromedially completely encircling the foramen magnum in bone. The posterior margins of exoccipitals form the posteromedial wall of the otic capsule, the occipital condyle, and the margin of the foramen magnum. A postotic foramen is located just lateral to the occipital condyle. The anteroventral margins of exoccipitals are in contact with the medial posteroventral margin of the parasphenoid.

A tympanic membrane, tympanic annulus, and stapes are absent. A well-developed cartilaginous operculum lies in the fenestra ovalis. The operculum is conical and oval in lateral view. The operculum is entirely cartilaginous in *Atelopus nanay*, whereas it is mineralized in *A. guanujo* (except in QCAZ 1885, in which it is mostly cartilaginous).

The nasals are broadly triangular and separated at midline; each possesses an

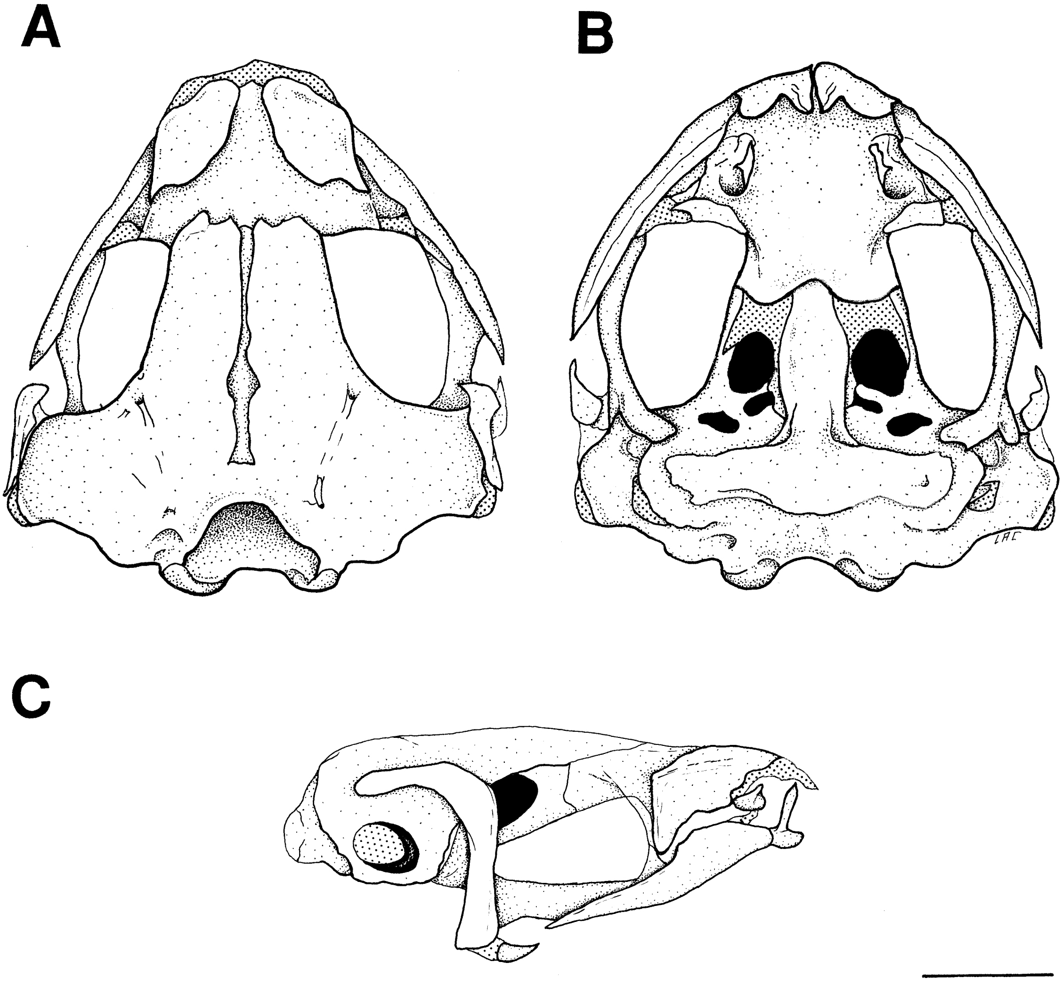

FIG. 10.—Skull of *Atelopus nanay* (QCAZ 1923, male) in (A) dorsal, (B) ventral, and (C) lateral views. Scale = 2 mm.

elongate maxillary process that extends ventrolaterally toward the maxilla. The maxillary process is pointed; the process is narrowly separated from the maxilla.

The frontoparietals are paired, rectangular bones that roof the dorsal and dorsolateral surfaces of the braincase, from the level of the anterior margin of the orbit to close to the margin of the foramen magnum. Medial articulation of the frontoparietals is absent in *Atelopus nanay* and varies intraspecifically in *A. guanujo*; in three specimens, more than half the length of the bones is articulated whereas in three others a medial articulation is absent. A suture line is visible in the specimens with an articulated condition. The lateral border of the frontoparietal, at level of posterior half of orbit, lacks a flange, except in two specimens (out of five) of *A. guanujo* that possesses a small flange. Occipital grooves are present; the grooves in *A. guanujo* are partially roofed, the posterior half of the groove is covered; the left groove in *A. nanay* is completely roofed whereas the right groove is covered along the posterior three-fourths of its length. Posteriorly the frontoparietals are synostotically fused posterolaterally to the prootics, and posteromedially to the medial anterodorsal margins of the exoccipitals.

The paired medially-separated vomers

are crescent-shaped, triradiate, and edentate. The anterior ramus of the vomer is directed parallel to the midline in *Atelopus nanay* and anterolaterally and ventrally toward the anterior tip of the maxilla in *A. guanujo*; the terminus of the anterior ramus is pointed in *A. nanay* whereas is either pointed (QCAZ 11250, 11253) or truncate in *A. guanujo.* In *A. guanujo,* the anterior ramus varies from long to short; it is long and nearly reaches the maxillae in QCAZ 11251; it is shorter or as long as the prechoanal ramus in QCAZ 1885. In *A. nanay,* the anterior ramus is about as long as prechoanal ramus. Pre- and postchoanal rami surround the medial, antero-, and posteromedial margins of the choana. The prechoanal ramus is directed towards the maxillae, whereas the postchoanal ramus is either parallel to the midline or directed posterolaterally. The rami are pointed in *A. nanay,* but in *A. guanujo* their distal ends may be rounded or truncate. The vomers do not contact the overlying sphenethmoid.

The neopalatine is an elongate, triangular, or subarcuate bone that underlies the planum antorbitale and sphenethmoid orbital margin; it extends from the sphenethmoid toward the maxilla. A gap exists between the lateral margin of neopalatine and maxilla. The maxillary half of neopalatine is widest and its lateral border is usually pointed; the medial end is pointed and the amount of overlap with sphenethmoid is variable. The anterior border of the neopalatine is slightly rounded in *Atelopus nanay* and two specimens (QCAZ 1885, 11251) of *A. guanujo,* whereas it has an apex in the other three specimens (QCAZ 11205, 11250, 11253) of *A. guanujo.*

The parasphenoid has an inverted T-shape and invests the ventral surface of the neurocranium; it extends from the level posterior to neopalatines (from the anterior half of the orbit) toward, but not reaching the margin of the foramen magnum; its surfaces are smooth. The cultriform process abuts [in *Atelopus nanay,* and one specimen (QCAZ 1885) *A. guanujo*] or underlies the posterior part of the sphenethmoid. The terminal end of the cultriform process is rounded in *A. nanay* and in three individuals of *A. guanujo*; it is acutely pointed in other three of *A. guanujo.* The parasphenoid alae are oriented perpendicular or slightly posterolateral to the cultriform process. The posterior margin of parasphenoid is nearly straight, bearing a subquadrangular (*A. guanujo*) or rounded (*A. nanay*) posterior process medially.

Each premaxilla consists of a dorsal alary process, a biradiate pars palatina, and an edentate, pars dentalis in the anterior margin. The alary process projects anterolaterally. In *Atelopus guanujo,* the lower half of the alary process is wider than the upper half, whereas in *A. nanay,* it is only slightly wider. The pars palatina has two well-differentiated processes, a medial (palatine) and a lateral process; the lateral process is almost as twice the length of the palatine process. The medial process of the pars palatina is a well-developed, triangular, pointed ramus in *A. nanay.* In *A. guanujo,* there is intraspecific variation; the medial process varies from well-developed in QCAZ 1885 to not well-differentiated in QCAZ 11253. A foramen is present along the length of the medial process of the pars palatina, and a ridge is evident on its ventral surface. The inner margin of the pars palatina, where the palatine and lateral processes come together, forms a concave border. The posterior end of the pars dentalis is pointed in *A. guanujo* (except in QCAZ 11205, in which it is truncate) and *A. nanay* and articulates with the maxillae. In one specimen of *A. guanujo* (QCAZ 1885), a small, sesamoid oval bone lies at the contact zone between the pars palatina of premaxillae and maxillae.

The maxilla is an elongate, edentate bone located between the premaxilla and the quadratojugal. A horizontal pars palatina of the maxilla extends along the lingual margin of the maxilla; posteriorly this shelf contacts the anterior ramus of the pterygoid. The maxilla is deepest anteriorly and bears the pars facialis which is subtriangular and directed medially; its dorsal margin is nearly even in *Atelopus nanay* and bears small bumps that nearly contact the neopalatine or the maxillary process of the nasal in *A. guanujo.* The anterior end of the maxilla is truncate, whereas the posterior end is pointed. The anterior end slightly overlaps the posterior end of premaxilla. The posterior end of the maxilla is separated from the quadratojugal; in *A. nanay,* it is separated by a length similar to that of the quadratojugal, whereas in *A. guanujo,* the distance of separation varies from one third to the full length of quadratojugal.

The quadratojugal is a small, L-shaped bone underlying the margin of the ventral arm of the squamosal; the posterior ramus articulates with the pars articularis of the palatoquadrate and the anterior ramus is separated from the maxilla.

The squamosal bears one or two dorsal rami, and a ventral ramus. The otic ramus (posterior, dorsal ramus) is moderately expanded towards the dorsolateral surface of the prootic; the otic ramus varies in the degree to which it overlaps the prootic; sculpturing on this element is nearly absent. The otic ramus overlaps nearly the entire length of the crista parotica (QCAZ 11253) or leaves only about one fourth of the posterior end free. *Atelopus nanay* and one specimen of *A. guanujo* (QCAZ 1885) lack a clearly differentiated zygomatic ramus (anterior, dorsal ramus) whereas four specimens of *A. guanujo* bear a small triangular zygomatic ramus. In one specimen (QCAZ 11250), there is a small foramen located in the zygomatic ramus. The angle between the dorsal part of the squamosal and the anterior margin of the dorsal portion of the ventral ramus varies from acute to nearly perpendicular in *A. guanujo* and is nearly perpendicular in *A. nanay.* The lower portion of the ventral ramus is flat and blade-like and invests the palatoquadrate laterally. The squamosal has a keel that extends from the outer side of dorsal arm toward the outer, upper half of the ventral arm.

The triradiate pterygoid bears anterior, medial, and posterior rami; the anterior ramus articulates with the maxilla anteriorly; the medial ramus invests the pseudobasal process of the prootic, and a short, posterior ramus invests the medial surface of the palatoquadrate. The articulation of the medial pterygoid ramus with the prootic involves two poorly differentiated heads that articulate with the ventrolateral surface of the pseudobasal process of the otic capsule.

The palatoquadrate is primarily cartilaginous and is invested by the ventral arm of the squamosal laterally and the posterior ramus of pterygoid medially and posteromedially. The ventral pars articularis associated with the quadratojugal is cartilaginous with a slight mineralization in two specimens of *Atelopus guanujo* (QCAZ 11205, 11250).

The lower jaw is composed of four paired elements. Anteriorly, the mentomeckelian bone bears a cartilaginous medial margin that forms a symphysis with the opposite medial margin. Posteriorly the dorsal portion of the mentomeckelian bone is fused to the dentary; the latter is thin when viewed laterally. The edentate dentary overlaps the angulosplenial dorsally at the anterior portion and extends laterally toward the posterior region. The angulosplenial is located at the lingual surface of the mandible from a point behind one length of mentomeckelian bone and to the posterior end of the mandible. Between the dentary and angulosplenial a Meckel's cartilage extends from a point just behind the mentomeckelian bone to the posterior end of the mandible. Meckel's cartilage is invested by the dentary anterodorsally and anterolaterally, and by the angulosplenial posteroventrally and posteromedially. The dentary terminates posteriorly at a level just anterior to the beginning of the curve of angulosplenial.

Hyobranchium.—(Fig. 11). The hyobranchium consists of a cartilaginous plate, two hyalia, a pair of basally narrow alary (anterolateral) processes, usually a pair of posterolateral processes, and two ossified posteromedial processes. There is variation in shape of the plate (= corpus), as well as in the presence of the posterolateral processes. The plate is longer than wide in *Atelopus guanujo* (ratio of hyoid plate length/hyoid plate minimum width 2.17–3.91, *n* = 6) and *A. nanay* (3.54, *n* = 1). Endochondral mineralization in corpus of hyoid plate are present in two speci-

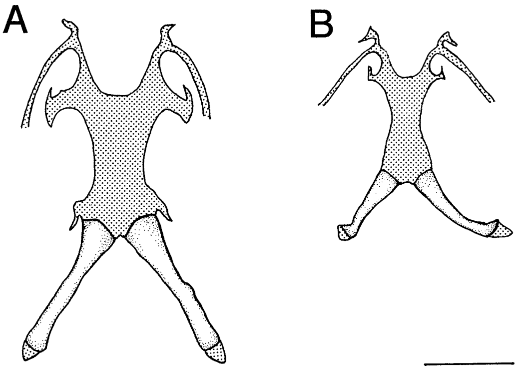

FIG. 11.—Ventral view of hyobranchium of (A) *Atelopus guanujo* (QCAZ 1885, male) and (B) *A. nanay* (QCAZ 1923, male). Dotted pattern indicates cartilage. Drawings of posteromedial processes may be distorted because they are not in a horizontal plane. Scale = 2 mm.

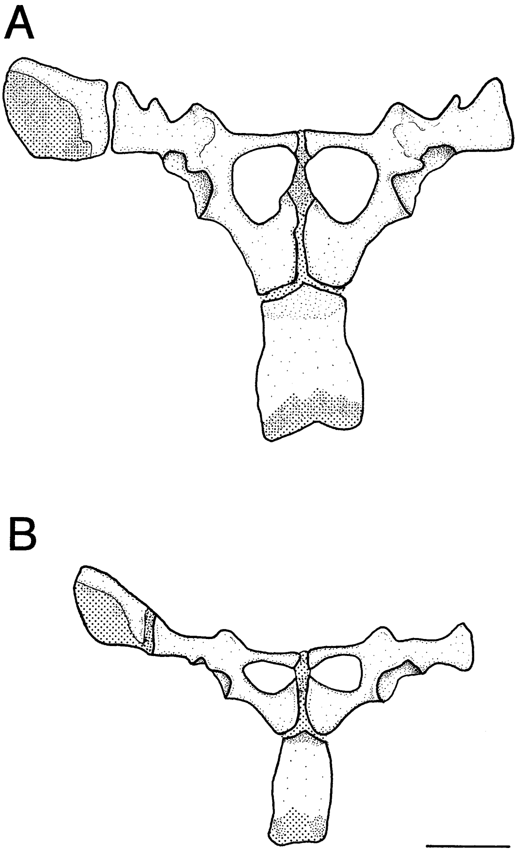

FIG. 12.—Ventral views of pectoral girdles of (A) *Atelopus guanujo (*QCAZ 1885, male) and (B) *A. nanay* (QCAZ 1923, male). Dotted pattern indicates cartilage. Calcified areas are indicated by irregular stippling on the overlay. Scale = 5 mm.

mens of *A. guanujo*: QCAZ 11250 possesses mineralization, which covers the entire corpus, whereas QCAZ 11251 possesses mineralization at lateral and posterior margins of corpus. Each hyale bears a short anterior process, which may be straight or deflected laterally. The length of the anterior process varies intraspecifically in *A. guanujo,* but it does not rejoin the hyale. Two specimens of *A. guanujo* (QCAZ 11251, 11253) also bear a small process on the hyale lateral to the anterior process; in *A. nanay,* this process is absent. As described by the configuration of the hyalia, the shape of the hyoglossal sinus varies; the lateral margins of the hyoglossal sinus diverge anteriorly except in one specimen of *A. guanujo* (QCAZ 11250) in which they are almost parallel. The anterolateral processes always are present, and vary in shape. The narrow base in both species supports an anterior flange and another smaller posterior flange. Posterolateral processes vary in length in three specimens of *A. guanujo* and are absent in three, whereas in *A. nanay* they are absent. The long, bony posteromedial processes bear cartilaginous ends. In four specimens (QCAZ 1885, 11205, 11251, KU 289426) (out of six) of *A. guanujo,* each posteromedial process bears a small lateral expansion at about half its length.

Pectoral girdle.—(Fig. 12). Each half of the firmisternal pectoral girdle is composed of the suprascapula, scapula and zonal area. The cartilaginous suprascapula is fan shaped and is mineralized. Variation exists in degree of mineralization from scattered to heavy in *Atelopus guanujo,* and with little mineralization in *A. nanay.* A bony, bicapitate cleithrum is present on the anterior margin of the suprascapula. The cleithrum is L-shaped, with the elongate arm located along the anterior margin and the short arm along the scapular border of suprascapula. The scapula is short and stocky, and fused to clavicle and coracoid at its medial end. The pars acromialis and pars glenoidalis of scapula are not well defined; but their margins are evident by virtue of a separation zone that forms a small oval fenestra located at the inner margin of glenoid cavity. A prezonal element (= omosternum) is absent. Zonal components are clavicles, procoracoids, coracoids and epicoracoids. The clavicle is oriented transversely or slightly anteromedially; it is fused at its distal end with the pars acromialis of the scapula and distal end of coracoid.

At midline, the epicoracoid cartilages are synchondrotically fused throughout their lengths and lack any trace of a suture. Anteriorly, at midregion, the epicoracoids are fused to procoracoid cartilages and form an epicoracoid bridge. Posteriorly, the mineralized epicoracoid cartilages are not fused to the sternum. A suture line is visible between the platelike epicoracoids and the sternum. The shape of this suture line possess a triangular projection at midlength that extends anteriorly, except in two specimens (QCAZ 11250–51) of *Atelopus guanujo* on which the suture line is nearly straight. A calcified procoracoid cartilage extends from midlength to medial end of clavicles; the clavicle borders it dorsally and ventrally. Epicoracoids and coracoid margins form the medial margin of the pectoral fenestra.

Other differences in the pectoral girdle include the degree of development of processes along the anterior margin of the clavicle and scapula, and the length and shape of the sternum. There are two triangular processes; the proximal, a clavicular acromium, is larger than the distal. The former lies at the joint between the clavicle and scapula; its orientation varies from nearly parallel in relation to the longitudinal axis in two (out of five) *Atelopus guanujo* to forming an angle in *A. guanujo* and *A. nanay.* The distal process is well differentiated in *A. guanujo* but absent in *A. nanay.*

The sternum varies in length. The ratios of sternum length to total length of girdle at midline are 0.45–0. 54 (*n* = 6) in *Atelopus guanujo,* and 0.58 for *A. nanay.* There is no clear differentiation between a mesosternun and a xiphisternum. The sternum is entirely calcified, except for a distal cartilaginous terminus. One specimen of *A. guanujo* (QCAZ 11250) has a distal mineralized terminus. In a specimen of *A. guanujo* (QCAZ 1885), cartilaginous regions are present at the anterior and posterior ends. The sterna are expanded distally in *A. guanujo* and about uniform in width throughout its length in *A. nanay*; the ratios of sternum maximum width to sternum minimum width are 1.25–2.05 (*n* = 6) in *A. guanujo,* and 1.34 for *A. nanay.* The terminal end of the sternum is truncate and unicapitate in both species.

Pelvic girdle.—(Fig. 13). The pelvic girdle is V-shaped in dorsal aspect in both species; it is composed of paired ilia, ischia, and pubes. The ilial shafts are cylindrical and bear cartilaginous anterior tips. Each ilium extends anteriorly beneath the sacral diapophysis; the distal end of the ilium lies at the anterior border of the diapophysis in one specimen (QCAZ 1885), whereas in others it does not reach the border. Posteriorly, the ilia are united in a medial symphysis with the ischia and pubes; the pubis is ossified. The iliosacral articulation is Type IIA (sensu Emerson, 1979), thus the ilium is attached to the diapophysis by a broad, transverse ligament. There is a small, sesamoid bone anterior to the distal end of the ilium in one specimen of *Atelopus guanujo.*

Vertebral column.—(Fig. 13). The vertebral column contains nine elements. The atlas complex is formed by the complete fusion of Presacrals I and II. There are six independent trunk vertebra (Presacrals III–VIII), the sacrum, and the coccyx. Vertebral centra are procoelus, and the sacrum bears a bicondylar articulation with the coccyx. The holochordal centra are cylindrical and solid. The neural arches of Presacrals IV–VIII are not imbricate. Vertebral shields and free ribs are absent.

In the atlas complex, one pair of transverse processes is present and they are oriented anterolaterally in *Atelopus guanujo,* whereas in *A. nanay,* the transverse processes are oriented nearly perpendicular to the midline. In Presacrals III–VIII, the anterior and posterior margins of the transverse processes are even in both species. The proximal end of the transverse processes is slightly wider than the terminal end in *Atelopus guanujo* (except in one

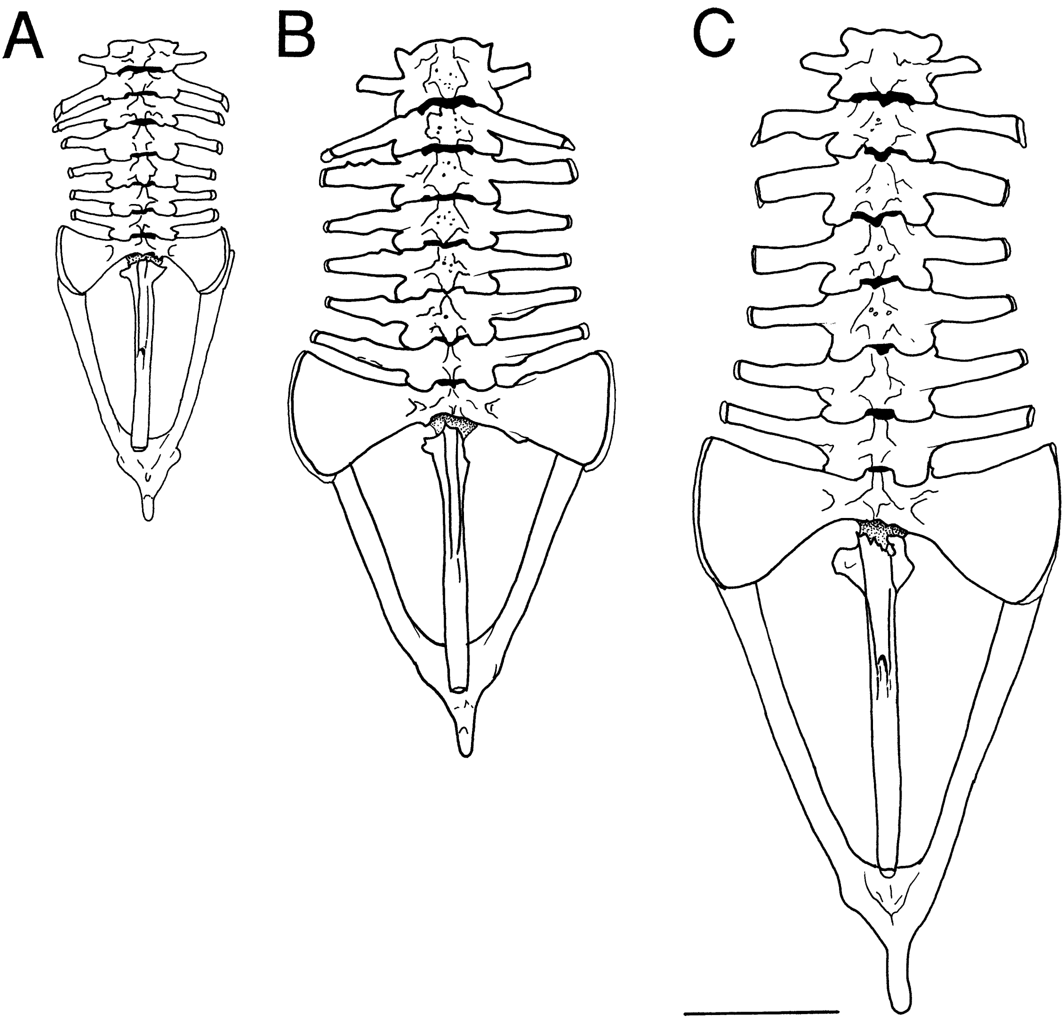

FIG. 13.—Dorsal views of vertebral columns and pelvic girdles of (A) *Atelopus nanay* (QCAZ 1923, male), (B) *A. guanujo* (QCAZ 1885, male), and (C) *A. guanujo* (QCAZ 11205, female). Scale = 5 mm.

specimen, QCAZ 1885) and *A. nanay* owing to the presence of a flange, which diminishes in size distally. The transverse processes are slightly shorter than the sacral diapophyses and their ends form a slightly concave line. The transverse processes of Presacrals III and VIII are the largest. Presacral IV bears the widest transverse processes in *A. guanujo*; however, in *A. nanay,* Presacral III bears wider transverse processes than Presacral IV. Orientation of the transverse processes varies markedly. The processes of Presacral III project posteroventrally, whereas those of Presacral IV have less pronounced posterior orientation; the processes of Presacrals V–VIII become oriented more anteriorly. In one specimen of *A. guanujo* (QCAZ 11250), all the transverse processes are oriented nearly perpendicular to the midline. In *A. guanujo,* the spacing among transverse processes between vertebra varies intraspecifically because of sexual dimorphism, with males having smaller spaces than females (Fig. 13B,C). Sculpturing on the dorsal surfaces of neural arches is indistinct in both species. A central pit in most vertebrae is absent; there are scattered small pits in one individual (QCAZ 1885) of *A. guanujo.*

The shape of the sacrum varies and is related to the sacral diapophyses, which are expanded. One specimen of *Atelopus guanujo* (QCAZ 11250) bears a nearly horizontal anterior and posterior border, whereas in *A. nanay* and others of *A. guanujo,* the anterior border is more angular and directed anterolaterally, and the posterior border extremely angular. In *A. nanay,* the sacrococcygeal articulation is bicondylar; in *A. guanujo,* the sacrum and coccyx are fused dorsally and ventrally in two specimens, and unfused in four. The coccyx is an elongate, subcylindrical bone that has an inverted triangular anterior end, which is formed by small vestigial lateral processes. Lateral processes are absent in one specimen (QCAZ 11253) of *A. guanujo,* whereas in other specimens (QCAZ 1885, 11205) are present only at one side. Lateral flanges along nearly entire length of coccyx are absent.

Forelimb.—A humerus, radioulna, carpal elements, four digits (II–V), and a prepollex make up the forelimb. Intercalary elements are absent. Torsion is absent in Digit II (first finger). The following carpal elements were observed: a postaxial centrale (= radiale), an ulnare, the Element Y, distal Carpals 3, 4, and 5 fused in a single bone, and distal Carpal 2. Additionally, two other elements were identified. Because their origin and homologies to carpal elements in other taxa are uncertain, I provisionally consider these two bones to be sesamoid bones (Sesamoids I and II). Sesamoid I is located under distal Carpal 3 + 4 + 5; it is round. Sesamoid II is a smaller, round bone located at the distal end of the radius at the posterior upper side of the postaxial centrale, and is larger in *Atelopus guanujo* than in *A. nanay.* Terminal phalanges on the digits are T-shaped. The phalangeal formula is 2-2-3-3 in *Atelopus guanujo,* whereas *A. nanay* has a reduced Digit II (= Finger I) with a formula of 1-2-3-3. The prepollex is calcified. It possesses two elements in *Atelopus nanay* and one to three elements in *A. guanujo.* In QCAZ 1885, the prepollex consists of two elements on the left hand and three on the right hand. In one specimen (QCAZ 11250), the prepollex is a single bone with the proximal end nearly completely fused to the adjacent proximal end of the first phalanxe of Finger I. In QCAZ 11251, the prepollex of the right hand is similar to the latter, but the left hand has a prepollex with two elements.

Hind limb.—The hind limb comprises a femur, tibiofibula, calcified cartilago plantaris, tarsal elements, five metatarsals, five digits, and prehallux. The tibiofibula is smaller in *Atelopus nanay* than in *A. guanujo.* The ratios of female tibiofibula lengths to snout–vent lengths are 0.32–0.39 (n = 13) in *A. guanujo,* and 0.31 for *A. nanay.* The tarsal elements include the tibiale (= calcaneum), fibulare (= astragalus), Tarsal I, Tarsals 2 + 3 (fused), centrale, and os sesamoides tarsale. *Atelopus nanay* has one os sesamoides tarsale that is elliptical to round in shape and is located ventral to the distal head of the fibulare. The same bone also is present in *A. guanujo,* and a smaller one is located ventral to Tarsal I. In some specimens of *A. guanujo* (e.g., QCAZ 11205, 11251, 11253), two to four additional os sesamoides tarsale are located close to the two larger ones. The phalangeal formula of the pes is 2-2-3-4-3. The prehallux is ossified with the distal end cartilaginous in *A. nanay,* whereas is either completely ossified or bears a cartilaginous end in *A. guanujo.* In *A. nanay,* the number of elements varies bilaterally, and there is one element on one side and two on the other side. In *A. guanujo,* there are one to three elements, and intraindividual bilateral variation occurs.

DISCUSSION

Knowledge of the alpha-level systematics of *Atelopus* continues to increase with species descriptions (Ardila-Robayo and Ruiz-Carranza, 1998; Ibañez et al., 1995; Lötters and Henzl, 2000; Rivero and Morales, 1995). However, hypotheses of relationships among *Atelopus* include few species and/or are poorly supported (La Marca, 1983; Lescure, 1973, 1981; Lynch, 1993; McDiarmid, 1971, 1973; Peters, 1973; Rivero, 1963*a,b,* 1984; Rivero and Serna, 1993; Rivero and Morales, 1995). Placement of the new species described herein in any of the species groups proposed by several authors (e.g., Lynch, 1993; Peters, 1973) is ambiguous. The *A. flavescens* group of Lynch (1993) would accommodate *A. nanay* based on its phalangeal formulae; however, the historical reality of this group has been questioned (Coloma, 1997; Vélez-Rodríguez and Ruiz-Carranza, 1997) because of intra-individual and intraspecific variation noted in the lack of a terminal phalanx on thumb, which defines it. The phylogenetic allocation of *A. guanujo* within the *A. ignescens* groups—either sensu Peters, 1973 or sensu Lynch, 1993—is doubtful because of lack of evidence of their monophyly, a problem which was already recognized by both authors. The *A. ignescens* group sensu Peters (1973) is diagnosed based on the length of limbs relative to body length, whereas the *ignescens* group sensu Lynch (1993) lacks diagnostic characters. Although I could allocate the new species to phenetic groupings, I prefer not to do so, because I think that such assignment might introduce bias to future attempts to infer phylogenetic relationships.

The description of two new species in this paper brings the total number of *Atelopus* from Ecuador to 18. Among these, 15 species occur in the Andes at elevations >1000 m (Coloma and Quiguango, 2000). The endemism and diversity of *Atelopus* corroborates a pattern of biodiversity which resides primarily in montane components when contrasted to lowland ecosystems (Lötters, 1996; see also Peterson et al., 1993 for similar biodiversity patterns in Mexico). In lowland ecosystems, although alpha diversity (number of species at a single site) may be high, beta diversity (in two or more sites in a given region) of some groups of plants and animals is less than in the Andes: for example, in Ecuadorian bamboos (Clark, 1997), Ecuadorian Compositae (Funk, 1997), South American amphibians (Duellman, 1999), Colombian frogs (Lynch et al., 1997), and Ecuadorian frogs (Coloma and Quiguango, 2000). Alpha and beta diversity are higher in the Andes than in lowland ecosystems in Ecuadorian frogs such as Centrolenidae (Duellman and Burrowes, 1989; Lynch and Duellman, 1973), *Colostethus* (Coloma, 1995), and *Eleutherodactylus* (Lynch and Duellman, 1980, 1997), among others. These patterns suggest the need for further biological research and conservation efforts directed to Andean habitats, where disappearance of frog populations are a matter of concern.

RESUMEN

Se reconocen dos especies de *Atelopus* de Ecuador nuevas para la ciencia; la una de la Hoya de Chimbo, la otra de los Páramos del Cajas; ambas provienen de regiones altas en la Cordillera Occidental de los Andes. Se proveen descripciones osteológicas de ambas especies y del renacuajo de torrente de una de las especies nuevas. Los patrones de diversidad y endemismo de *Atelopus* justifican la necesidad de mayores investigaciones biológicas y esfuerzos de conservación dirigidos a habitats andinos.

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APPENDIX I

Specimens Examined

Atelopus bomolochos.—ECUADOR: *Provincia Azuay:* Vic. E of Cuenca, 2535 m, (CAS 85l39–41); Sevilla de Oro, 2800 m, 82 km E of Cuenca, (CAS 85341, 93912; paratopotypes); 3 km E of Sigsig, 2460 m, (QCAZ 1893–94); 10 km S Cutchil, 2900 m, (QCAZ 1861–69, 1896–99); 7.6 km S Cutchil, 2880 m, (QCAZ 1900); 6.2 km S Cutchil, 2800 m, (QCAZ 1901); Río Chilpe, 10–15 km E Luz–María, aprox. 2500 m, (QCAZ 1860); 13 km NE Nieves, (CM 117039); *Provincia Cañar:* Between Juncal and General Morales, approx. 2500 m, (CAS 93906, paratype);

Provincia Loja: Loja (locality questioned by Peters [1973:37]), (USNM 236942–44); *Provincia Morona Santiago:* Sucúa, (USNM 283538–41).

Atelopus carbonerensis.—VENEZUELA: *Estado Mérida:* 32 km NW Mérida, road to Azulita, 2010 m, (KU 132857, KU 132860, KU 132864, KU 132867–68, KU 132871).

Atelopus ignescens.—ECUADOR: *Provincias Napo and Pichincha:* Páramo de Guamaní, La Virgen, 3800–4200 m, (MHNG 2410.1–6, 2409.95–100, 2273.48, 2273.61, 2273.81–82, 2273.84–97).

Atelopus sorianoi.—VENEZUELA: *Estado Mérida:* Paramito de San Francisco, 2450 m [QCAZ 4910, 4911 (C&S)].

Atelopus sp.—COLOMBIA: *Departamento Nariño*: 8 Km E Pasto, 3050 m, (KU 169267); 12 Km E Pasto, 3050 m, (KU 169284, 169292); Vereda de San Fernando, 7.5 Km E Pasto, 2800 m, (KU 169267); Hacienda San Gerardo, 2900–3000 m, [ICN 450, 459, 469, 471, 472 (C&S), 473, 481 (C&S)]; El Encano, 2800 m, [ICN 3633 (C&S), 3636–38]; Volcán Galeras, 3200 m, [ICN 3406].