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The amphibian community at Yanayacu Biological Station, Ecuador, with a comparison of vertical microhabitat use among *Pristimantis* species and the description of a new species of the *Pristimantis myersi* group

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Abstract

We provide information regarding the composition of the amphibian community at Yanayacu Biological Station, on the Amazonian slopes of the Andes of Ecuador, and describe a new species of *Pristimantis* that is referred to the *P. myersi* group. The new species is distinguished from other species of the group mainly by its color pattern, and by lacking ulnar and tarsal tubercles. The advertisement call of the new species has two distinct call types, a short call with 1–3 pulses and a long call with a mean of 15.5–18.9 more rapid pulses, which are often produced together in long call series. Finally, we analyze the microhabitat use of *Pristimantis* species found at Yanayacu and find that there is significant variation in vertical habitat use among *Pristimantis*, highlighting the ecological diversity of sympatric species.

Key words: Anura, Ecuador, microhabitat, new species, *Pristimantis bicantus*, *Pristimantis myersi,* Strabomantidae, Yanayacu Biological Station

Resumen

Se presenta información sobre la composición de la anfibios de la Estación Biológica Yanayacu, ubicada en la vertiente amazónica de la Cordillera de los Andes del Ecuador. Se describe una nueva especie de *Pristimantis*, asignada al grupo *Pristimantis myersi*. Esta especie se distingue de otras similares principalmente por su patrón de coloración y por carecer de tubérculos ulnares y tarsales. La nueva especie tiene dos tipos de cantos de anuncio claramente diferenciables, un canto corto de 1–3 pulsos y uno largo con una media de 15.5–18.9 pulsos producidos más rápidamente, los cuales están agrupados en prolongadas series de cantos. Finalmente, se analiza el microhábitat de las especies simpátricas de *Pristimantis* de Yanayacu y se concluye que existe una variación significativa en el uso del estrato vertical del bosque. Estos resultados resaltan la diversidad ecológica de este grupo de anuros.

Palabras clave: Anura, Ecuador, Especie Nueva, microhabitat, *Pristimantis bicantus*, *Pristimantis myersi,* Estación Científica Yanayacu, Strabomantidae

Introduction

South America maintains an incredible diversity of amphibians (Duellman 1999). Among them, a clade of direct-developers, the terraranans, usually are the most abundant and species-rich group in Andean cloud forests (Lynch & Duellman 1997; Heinecke *et al*. 2007; Hedges *et al*. 2008). The taxonomy of terraranans, especially that of *Pristimantis,* is a challenge taxonomically because of their high diversity, intraspecific variation, the relatively few external morphological characters available to distinguish among them, and the lack of field guides. In Ecuador, there are few studies that attempt to report information on the diversity and

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ecology of amphibian communities (Lynch 1976a, 1979; Duellman 1978; Lynch & Duellman 1980, 1997; Duellman & Lynch 1988), a limitation that also impacts conservation efforts since very few people have the necessary resources to identify a *Pristimantis* to the species level, severely limiting information on population trends, distribution, and diversity.

Herein, we present the results of a two-year study at the Yanayacu Biological Station, a cloud forest locality on the Amazonian slope of the Andes of Ecuador. We provide brief diagnoses for 15 amphibian species, describe the morphology and vocalization of a new species of *Pristimantis,* which we tentatively place in the *P. myersi* group, and discuss the vertical microhabitat use of sympatric *Pristimantis* species.

Methods

The diagnosis and description of the new species follow those of Lynch and Duellman (1997). We examined alcohol-preserved specimens from the herpetological collections at the Museo de Zoología of the Pontificia Universidad Católica del Ecuador, Quito (QCAZ) and the Natural History Museum of The University of Kansas, Lawrence (KU). In addition to the type series of the new species, specimens examined are listed in Appendix I.

Morphological traits are as defined by Lynch and Duellman (1997). Morphological measurements were taken as described in Guayasamin (2004) and are: (1) snout–vent length (SVL); (2) tibia length; (3) foot length; (4) head length; (5) head width; (6) interorbital distance; (7) upper eyelid width; (8) internarial distance; (9) eye-to-nostril distance; (10) snout-eye distance; (11) eye diameter; (12) tympanum diameter; (13) eye- to-tympanum distance; (14) radioulna length; (15) hand length; and (16) Finger-I length. Sexual maturity was determined by the presence of eggs or convoluted oviducts in females or by the presence of vocal slits in males. Color patterns in life were taken from field notes and color photographs.

Recordings were made with a Sennheiser SE66 microphone (frequency response 40–20,000 Hz) and a Sony WM-D6C professional analog tape recorder (frequency response 40–15,000 Hz). Calls were digitized in COOL EDIT 2000 (Syntrillium Software Corporation, Phoenix, AZ) and analyzed in RAVEN PRO 1.3 (Cornell Lab of Ornithology, Ithaca, NY). Calls were digitized at a sample rate of 44100 Hz, sample size of 16 bits, and input speed of 1×. The sonogram analyses used settings of window type Hann, window size 256 samples, and filter bandwidth 248 Hz; time grid resolution of 2.9 ms and 50% overlap; and frequency grid resolution of 172 Hz and DFT size 256 samples. Dominant frequency was determined using the spectrogram slice view of RAVEN PRO. Call terminology follows Heyer *et al*. (1990).

From December 2000 to October 2002, we conducted an inventory of amphibian species at the Yanayacu Biological Station (YBS) near Cosanga, Provincia Napo, Ecuador (0°36' S, 77°53'W) as part of a monitoring program. Amphibians were inventoried using Visual Encounter Surveys (VES), distance sampling, and capture-mark recapture methods (Funk *et al*. 2003). All main habitat types were sampled at YBS, including primary cloud forest, secondary cloud forest, bamboo forest, overgrown pasture, forest edges, streams, ponds and small lakes, and roadside ditches. In forest, we sampled from a trail network and from three 50 × 50 m grids, each composed of ten 50 m long transects spaced 5 m apart from each other. A random number generator was used to determine where to set up each grid within a 500 × 500 m block of primary, secondary, and bamboo forest. The 500 × 500 m block of forest was surveyed, divided into 100 different 50 × 50 m grids, and then three grids were randomly chosen. Although the main inventory was completed in October 2002, opportunistic collections of previously missed or rare species were continued through June 2009.

When a *Pristimantis* species was encountered, its perch height was measured using a measuring tape. Height was rounded to the nearest 10 cm. The significance of differences in nocturnal perch height among the six *Pristimantis* species at Yanayacu with $N \geq 25$ was tested using a one-way analysis of variance (ANOVA). Pairwise differences in mean perch height were tested using the Tukey-Kramer method. The significance of differences in perch height between juvenile and adult frogs was tested using T-tests. All statistical analyses were performed using MINITAB 15 (Minitab Inc., State College, PA).

Species accounts

Family: Bufonidae

This group of toads contains some of the most familiar anurans, including the cane toad (*Rhinella marina;* previously *Bufo marinus*) and the jambato (*Atelopus ignescens*). Most of them have a warty appearance and are diurnal, terrestrial, and have aquatic larvae (e.g., *Rhinella, Atelopus*), but others are nocturnal, arboreal, and undergo direct development (e.g., *Osornophryne*). Bufonids are found natively in all continents, except Australia (where it has been introduced) and Antarctica. The family Bufonidae contains 538 species (AmphibiaWeb 2009). The taxonomy of amphibians has undergone several recent changes and there is debate on which names should be used. For bufonids, we follow the general proposal by Frost *et al*. (2006), as modified by Chaparro *et al*. (2007). In YBS, there are two species of bufonids, *Osornophryne guacamayo* and *Rhinella margaritifera* (previously *Bufo margaritifer*).

Osornophryne guacamayo (Plate 1)**.** Described by Hoogmoed (1987). This species can be easily recognized by having a blackish dorsal coloration with, usually, two yellow-gray dorsolateral lines, which are not clearly differentiated from the rest of the dorsum; yellow venter with dark brown to black spots; dorsal skin of body and limbs with numerous tubercles of different sizes; limbs long and slender; fingers connected by a thick web; feet heavily webbed with Toe IV and V much longer than Toes I, II, and III; and by lacking parotoid glands and tympanum (Hoogmoed 1987) . At YBS, SVL in adult females is 36.1–39.3 mm (n = 3) and 22.7 mm in one adult male. *Osornophryne guacamayo* has been found on leaves during the night (Table 1). Although most bufonids reproduce in water, *O. guacamayo* places its eggs on the ground, where they undergo direct development into froglets. At YBS, the only species that is likely to be confused with *O. guacamayo* is *Rhinella margaritifera,* which has a visible tympanum, parotoid glands, dorsolateral row of red tubercles (traits absent in *O. guacamayo*), and lacks conspicuous webbing among fingers (present in *O. guacamayo*). Additionally, in *R. margaritifera,* only Toe IV is elongated, whereas in *O. guacamayo* Toes IV and V are conspicuously longer that the rest of the toes.

Rhinella margaritifera (Plate 1)**.** Described by Laurenti (1768). A moderate-sized toad distinguished by having dorsal skin scattered with tubercles, and a row of red conical tubercles that begins on the posterior edge of the parotoid gland and ends on the groin. The fingers lack webbing, whereas the toes are about one-half webbed. This is a terrestrial and diurnal species that has a dorsal coloration that mimics leaf litter. At YBS, SVL in adult females is 57.4–68.7 mm (n = 4) and 40.9–46.1 mm (n = 5) in adult males. Within YBS, *Rhinella margaritifera* can only be confused with *Osornophryne guacamayo* (see previous species account).

Remarks: One of the oldest problem in the taxonomy of South American amphibians is the *Rhinella margaritifera* species complex. Hoogmoed (1986, 1989) recognized several species within this complex (previously referred to as the *Bufo typhonius* complex), but he did not formally recognize most of them. More recently, Fouquet *et al*. (2007) suggested that *R. margaritifera* might be composed of as many as 11 species. Herein, we use the name *R. margaritifera* realizing that it represents a species complex until the systematics of this group of toads is resolved.

Family: Centrolenidae

Glassfrogs have a Neotropical distribution and are particularly diverse in the northern Andes. All centrolenids have a partial or complete ventral transparency, a dilated medial process on Metacarpal III, and deposit their eggs out of water (usually on the upper or under sides of leaves; Hayes & Starrett 1980; Ruiz-Carranza & Lynch 1991; Guayasamin *et al*. 2009). They are usually found at night on vegetation along streams when reproducing. Herein, we follow the taxonomy proposed by Guayasamin *et al*. (2009) that recognizes 12 genera and 147 species within Centrolenidae. In YBS, there are five identified (*Centrolene bacatum, C. buckleyi, Nymphargus posadae, N. siren, N. wileyi*) and two unidentified (*Centrolene* sp, *Cochranella* sp) species of glassfrogs.

TABLE 1. Amphibian species found at Yanayacu Biological Station (0°36' S, 77°53' W). Elevation refers only to the distribution of species at Yanayacu Biological Station. Abundance refers to numbers of adult females, adult males, adults of unknown sex, juveniles/subadults, and animals of unknown stage and unknown sex, in this order.

Family	Species	Elevation (m)	Habitat	Microhabitat	Abundance	Activity
Bufonidae	*Osornophryne guacamayo*	2300–2500	Primary forest	Leaves, ferns	1/1/0/0/0	Nocturnal
	Rhinella margaritifera	2000–2200	Open pasture, disturbed habitat	Small ponds, ditches, and pools in pasture	3/4/2/0/1	Nocturnal
Centrolenidae	*Centrolene bacatum*	2000–2200	Primary forest and bamboo along streams	Leaves	1/9/0/0/0	Nocturnal
	Centrolene buckleyi	2000–2200	Primary forest along streams	Leaves	0/2/0/0/1	Nocturnal
	Centrolene sp 1	2100	Primary forest along streams	Leaves	0/3/0/0/0	Nocturnal
	Cochranella sp 1	2100	Primary forest along streams	Leaves	1/0/0/0/0	Nocturnal
	Nymphargus posadae	2000–2200	Primary forest along streams	Ferns, leaves	1/3/0/0/0	Nocturnal
	Nymphargus siren	2100	Primary forest along streams	Leaves	0/2/0/0/0	Nocturnal
	Nymphargus wileyi	2000–2200	Primary forest along streams	Leaves, ferns	1/5/0/0/0	Nocturnal
Dendrobatidae	*Hyloxalus pulchellus*	2000–2200	Primary and secondary forest	Forest floor and leaf litter; often hidden in dense vegetation	0/2/1/1/3	Diurnal
Strabomantidae	*Pristimantis bicantus*	2100–2300	Primary and secondary forest	Low vegetation, forest floor	33/32/0/24/5	Nocturnal
	Pristimantis eriphus	2000–2300	Primary and secondary forest	Leaves, ferns, bromeliads	10/3/9/14/27	Nocturnal
	Pristimantis cf. eriphus	2000–2200	Primary and secondary forest	Leaves	0/1/1/0/1	Nocturnal
	Pristimantis inusitatus	2000–2200	Primary and secondary forest	Leaves, ferns	10/7/2/2/14	Nocturnal
	Pristimantis gladiator	2270–2500	Primary forest	Low vegetation, forest floor	0/0/0/0/2	Nocturnal
	Pristimantis leucopus	2000–2200	Primary forest	High leaves above streams	1/2/0/0/0	Nocturnal
	Pristimantis cf. petersi	2000–2200	Primary forest	Leaves and low vegetation	7/6/9/49/27	Nocturnal
	Pristimantis w-nigrum	2000–2200	Pasture, forest edge, secondary and primary forest	Hidden in grass in pastures, forest floor, low vegetation	0/7/3/7/8	Nocturnal
	Pristimantis sp 1	2000–2200	Primary forest	Low vegetation	0/0/0/36/0	Nocturnal
Caeciliidae	*Caecilia orientalis*	2100	Pasture and secondary forest	Fossorial, under rotten logs, comes to surface during hard rains	1/3/0/1/2	Unknown

Centrolene bacatum (Plate 1)**.** Described by Wild (1994). This species is easily distinguished from other amphibians in YBS by having a green dorsal coloration with few white tubercles, some of which form a line that extends from below the eye to the insertion of the arm (Wild 1994; Guayasamin *et al*. 2006a). As all species included in the genus *Centrolene, C. bacatum* has a venter that is posteriorly translucent. Also, adult males of this species have a humeral spine (absent in all *Nymphargus* species, except *N. grandisonae* and

some individual in *N. griffithsi*, both species found on the western slope of the Andes). *Centrolene bacatum* is smaller than *C. buckleyi* [25.3–30.5 mm (*n* = 23) in adult males of *C. buckleyi*]. In YBS, SVL in *C. bacatum* males, 19.3–21.8 mm (*n* = 11); SVL = 20.4 mm in one adult female. Active, calling males of *Centrolene bacatum* are frequently heard in YBS during the night; however, they usually call from areas close to the canopy; females deposit the egg masses on the upper and undersides of leaves, in vegetation along streams.

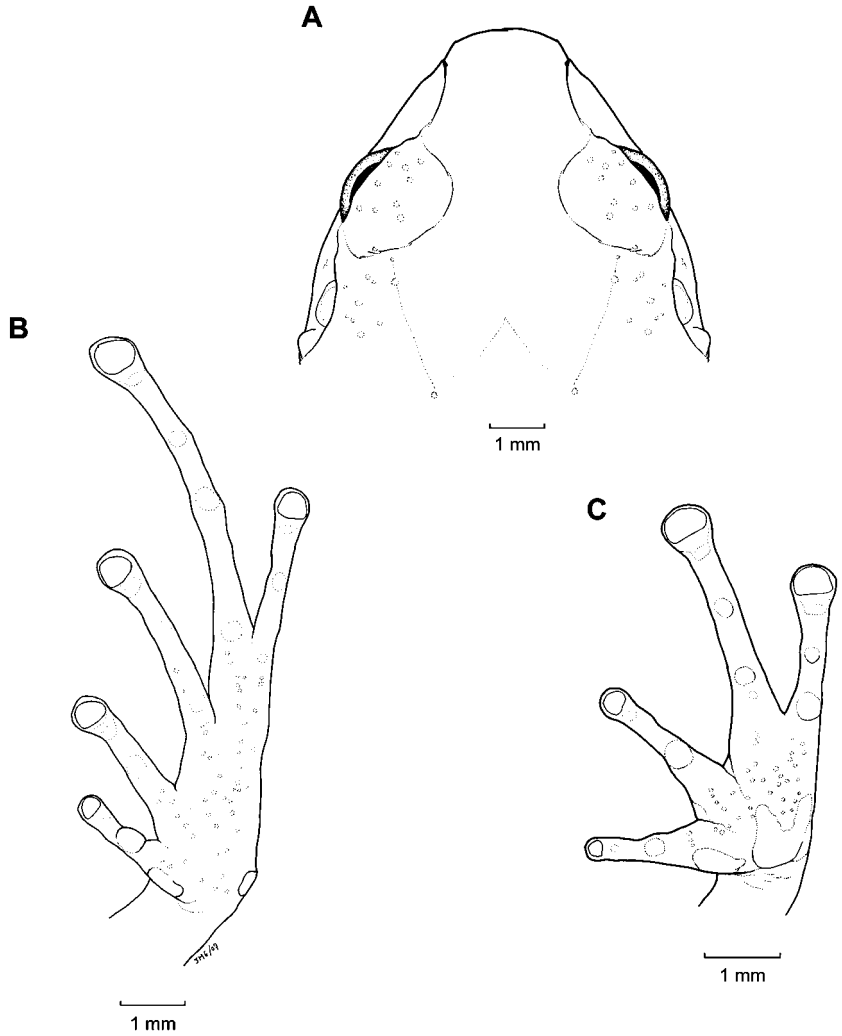

FIGURE 1. **(A)** Head, **(B)** hand, and **(C)** foot of *Pristimantis bicantus*, holotype, adult female, QCAZ 19024.

Centrolene buckleyi (Plate 1).—Described by Boulenger (1882). Among the glassfrogs found at YBS, *Centrolene buckleyi* is easily distinguished by having green dorsal surfaces sharply demarcated laterally from white lower flanks, a humeral spine (in males), white upper lip, a moderate adult size (SVL in males 25.3–30.5 mm; in females 29.8–34.4 mm) and a sloping snout in lateral profile (Guayasamin *et al*. 2006a).

Remarks: Genetic analyzes suggests that *Centrolene buckleyi* represents a species complex (Guayasamin *et al*. 2008), a hypothesis that needs further examination with a dense sampling in Ecuador and Colombia.

Nymphargus posadae (Plate 2).—Described by Ruiz-Carranza and Lynch (1995). This species can be differentiated from other glassfrogs by lacking webbing between fingers, lacking humeral spines, having a green dorsum with small greenish-white warts, and by having a white upper lip, and a white line on the ventrolateral border of arm, Finger IV, tarsus and Toe V (Guayasamin *et al*. 2006a). *Nymphargus posadae* is differentiated from *Centrolene buckleyi* and *C. bacatum* mainly by lacking humeral spines, which are present in the adult males of the two *Centrolene* species. Also, *N. posadae* lacks webbing between fingers, whereas there is some webbing between the two externalmost fingers of *C. bacatum* and *C. buckleyi*. At YBS, there are

two additional glassfrogs that belong to the genus *Nymphargus* (i.e., *N. siren* and *N. wileyi*). These three species share the absence of webbing between fingers. *Nymphargus siren* differs from the other two species (and any other amphibian in YBS) by presenting small yellow spots on the dorsum, whereas *N. wileyi* has a uniform green dorsum (in *N. posadae*, green dorsum with small greenish-white warts). SVL in males is 30.7–34.1 mm ($\bar{x}$ = 32.3, *n* = 6); in females 30.2–33.3 mm ($\bar{x}$ = 31.4, *n* = 4).

Remarks: Males of *Nymphargus posadae* collected in YBS are smaller (SVL = 30.7–31.9 mm, *n* = 3) than Colombian specimens (SVL = 32.7–34.1 mm, *n* = 3; Ruiz-Carranza & Lynch 1995; Guayasamin *et al*. 2006a).

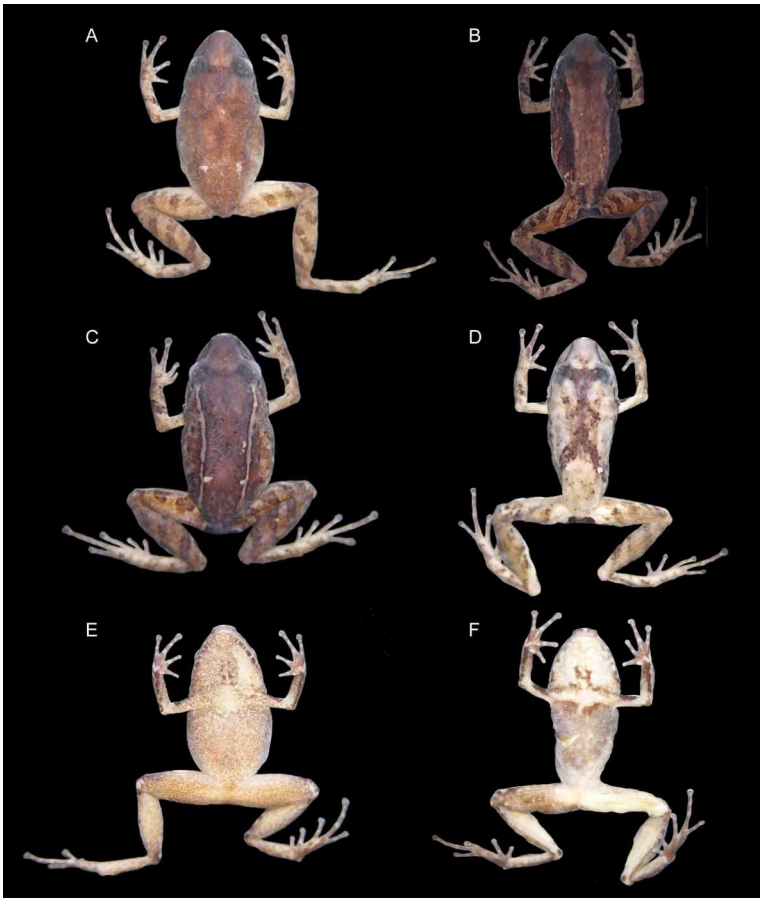

FIGURE 2. Dorsal and ventral color variation of *Pristimantis bicantus* in ethanol. **(A, E)** QCAZ 19024 (female holotype); **(B)** QCAZ 16186, adult female; **(C)** QCAZ 18988, adult female; **(D, F)** QCAZ 16201, adult female.

Nymphargus siren (Plate 2).—Described by Lynch and Duellman (1973). In YBS, this glassfrog is the only amphibian that has a green dorsum with small yellow spots. Additionally, *N. siren* lacks webbing between fingers, lacks humeral spines, and is relatively small (SVL < 22.0 mm). *Nymphargus siren* seems to be a rare species in YBS; only two males have been found during the two years of surveys.

Nymphargus wileyi (Plate 2).—Described by Guayasamin *et al*. (2006a). *Nymphargus wileyi* differs from other Glassfrogs by having a uniform green dorsum, white renal peritoneum, and by lacking membranes between Fingers III and IV. In adult males, SVL 23.4–26.5 mm ($\bar{x}$ = 24.6; *n* = 11); 25.1–28.1 mm in adult females ($\bar{x}$ = 26.3; *n* = 4).

Family: Dendrobatidae

The family Dendrobatidae is distributed in the Neotropics and contains 267 species (AmphibiaWeb 2009; including species of Aromobatidae and Dendrobatidae *sensu* Grant *et al*. 2006). Unlike most anurans, poison dart frogs are diurnal and often times show colorful, aposematic coloration. Also, dendrobatids present

elaborated reproductive modes, with different types of parental care (Zimmerman, 1990). In YBS, only one species of dendrobatid has been found, *Hyloxalus pulchellus*. We follow the taxonomy proposed by Grant *et al*. (2006), as modified by Santos *et al*. (2009).

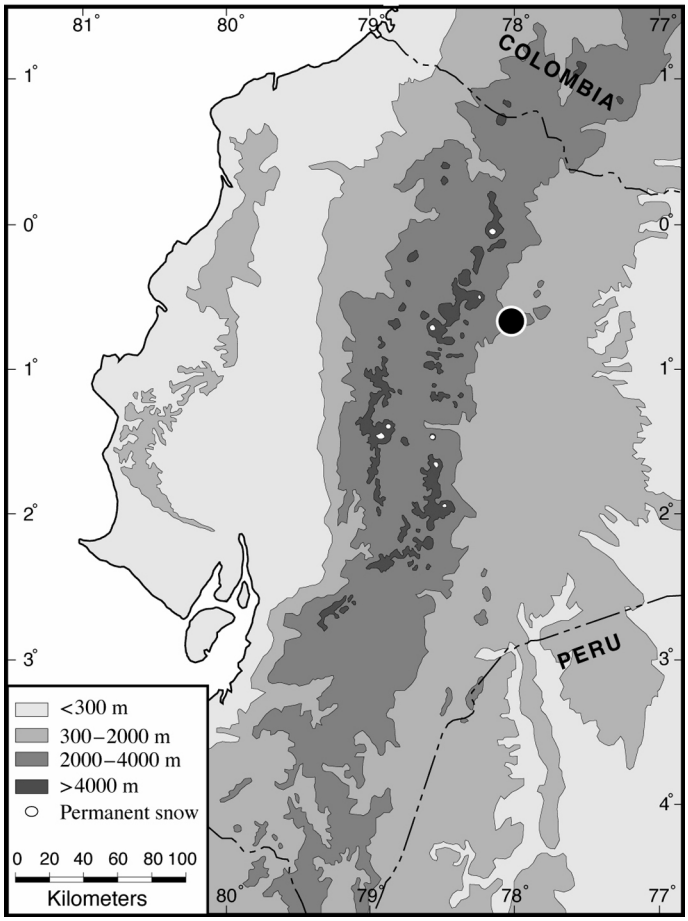

FIGURE 3. Map of Ecuador showing the type locality of *Pristimantis bicantus* (Yanayacu Biological Station, 0°36' S, 77°53' W, 2100–2300 m).

Hyloxalus pulchellus (Plate 2). Described by Jiménez de la Espada (1871). This species is characterized by having a dark brown dorsum, thin cream lateral stripe, dark brown to black flanks, and a bluish-white venter with grayish-black reticulation. In adult males, SVL 17.3–21.5 mm (n = 44); 19.6–24.4 mm (n = 16) in adult females (Coloma 1995).

Remarks. *Hyloxalus pulchellus* exhibits morphological and color variation along its distribution —inter-Andean páramos of southern Colombia and northern Ecuador, and on the eastern slopes of the Andes from southern Colombia to the headwaters of the Río Pastaza in Ecuador, at elevation between 1590 and 2970 m) — and it has been suggested that it might represent a complex of species (Coloma 1995).

Family: Strabomantidae

This family is restricted to tropical and subtropical South America (Hedges *et al*. 2008) and has a recognized diversity of 556 species (AmphibiaWeb 2009). All strabomantids seem to have direct development, a trait that might have facilitated their diversification in moist areas where standing water is rare (e.g., cloud forests). Most species in this family lack webbing between fingers and toes. Strabomantids represent the most diverse clade in YBS, with 6 described and 3 undescribed species. We follow the taxonomy proposed by Heinicke *et al*. (2007) and Hedges *et al*. (2008).

Pristimantis eriphus (Plate 3)**.** Described by Lynch and Duellman (1980). This species is distinguished from other anurans by having many small conical tubercles on dorsal skin, one prominent tubercle on the upper eyelid, conical ulnar and tarsal tubercles, and a conical tubercle on heel. In life, *Pristimantis eriphus* has a pale green dorsum with dark olive to green-brown markings; its flanks and hidden surfaces of limbs have a black and white pattern; the venter is white to greenish-white with dark brown to black reticulations; the iris is orange-red to reddish copper. At YBS, SVL in adult males is 16.3–21.4 mm (n = 16); in adult females, SVL 18.6–33.2 mm (n = 16).

Pristimantis gladiator (Plate 4)**.** Described by Lynch (1976b). In life, *Pristimantis gladiator* has a brown to orange-brown dorsum with dark brown markings, and a black groin with orange to red spots. Other diagnostic traits of *P. gladiator* include the presence of low ulnar and tarsal tubercles and low, non-pungent tubercles on the upper eyelid. In adult males, SVL 14.9–16.9 mm (n = 5); adult females unknown (updated from Lynch 1976b). None of the other frogs at YBS have a black groin with orange-red spots. This small species has been found by day under rocks and logs (Lynch 1976b).

Pristimantis inusitatus (Plate 4)**.** Described by Lynch and Duellman (1980). This species is distinguished from other frogs mainly by its dorsal color pattern (see below) and by having conical ulnar and tarsal tubercles, a conical tubercle on heel, and a conical tubercle on the upper eyelid. In life, *Pristimantis inusitatus* has a sexually dimorphic coloration. Females have a green dorsum with yellow to yellow-green tubercles, a pale lemon yellow to yellow groin, white throat with green markings, white venter, and yellow-cream to yellow iris with black reticulations. Males differ by having a brown-green to pink-brown dorsum with dark brown marks, clearly banded limbs, a pale yellow throat with small white spots, and a white venter (translucent on its posterior portion). At YBS, SVL in adult males is 13.1–17.5 mm (n = 15); in adult females, SVL 22.2–26.0 mm (n = 10).

Pristimantis leucopus (Plate 5)**.** Described by Lynch (1976c). A species diagnosed by having an upper eyelid with few small flat tubercles or lacking tubercles, low and inconspicuous ulnar and tarsal tubercles, and by lacking tubercles on the dorsum. In life, this species has a green to brown dorsum with dark brown marks, flanks mostly dark gray with greenish-brown mottling, and throat, chest, and belly reddish-orange with brown mottling that is most conspicuous on the throat. The groin and ventral surfaces of legs are dark gray to black. *Pristimantis leucopus* is one the largest species found at YBS; SVL in adult males is 29.7–37.8 mm; in adult females, SVL 39.2–44.0 mm (Lynch & Duellman 1980; this work).

Pristimantis* cf. *petersi (Plate 5)**.** Described by Lynch and Duellman (1980). This species is characterized by having smooth dorsal skin, a papilla at the tip of the snout, and one conical tubercle on the upper eyelid. In life, *Pristimantis petersi* usually has a pale green to dull green dorsum with no distinct markings (Lynch & Duellman 1980), but individuals found at YBS have a brown to orange-brown dorsum with dark brown markings. At YBS, SVL in adult males is 15.7–21.2 mm (n = 10); in adult females, SVL 24.0–27.5 mm (n = 5).

Remarks. Because of the differences in color pattern between the usual *Pristimantis petersi* and the population found at YBS, we consider the identification as tentative. Additionally, individuals (especially females) found at YBS are larger than those reported in the literature (in 35 males, SVL = 14.5–19.9 mm; in 8 females, SVL = 20.3–23.1 mm; Lynch & Duellman 1980). In Funk *et al*. (2003), *Pristimantis* cf. *petersi* was referred to as *Eleutherodactylus* sp. 2.

Pristimantis w-nigrum (Plate 5)**.** Described by Boettger (1892). This frog is easily recognized by having, in life, a color pattern of yellow with black markings on the groin, anterior and posterior surfaces of thighs, and concealed shank. Other distinctive traits include having a light brown dorsum with brown markings, a prominent tympanum, and a first finger that is longer than the second. At YBS, SVL in adult males is 31.9–40.2 mm (n = 5); no adult females have been found. Lynch and Duellman (1980) report the following body size for the species: in adult males, SVL = 29.3–46.8 mm (n = 32); in adult females, SVL = 44.4–56.6 mm (n = 15).

Remarks. *Pristimantis w-nigrum* is unusual among Andean amphibians by having a broad distribution that includes the Pacific and Amazonian slopes of the Andes, as well as the high Andes of Colombia and Ecuador

(800–3200 m; Lynch & Duellman 1997). Given the importance of the Andes in the speciation of amphibians (Lynch & Duellman 1997; Guayasamin *et al*. 2008), it is likely that *P. w-nigrum* actually represents a species complex.

Caecilia orientalis (Plate 5).—Described by Taylor (1968). Family Caeciliidae. Caecilians are subterranean or aquatic amphibians found throughout much of the tropics (Duellman & Trueb 1994). At YBS, only one species of caecilian has been reported, *Caecilia orientalis* (Funk *et al*. 2004), which is easily identified by having an elongated and limbless body with a blue-gray to lavender dorsal coloration. Funk *et al*. (2004) described the egg clutch and nest site of *C. orientalis,* confirming that this caecilian is oviparous. *Caecilia orientalis* is the main prey item of the Barred Hawk, *Leucopternis princeps* (Greeney *et al*. 2008). At YBS, SVL in adult males is 320–356 mm (n = 2); in females, SVL = 348–458 mm (n = 2).

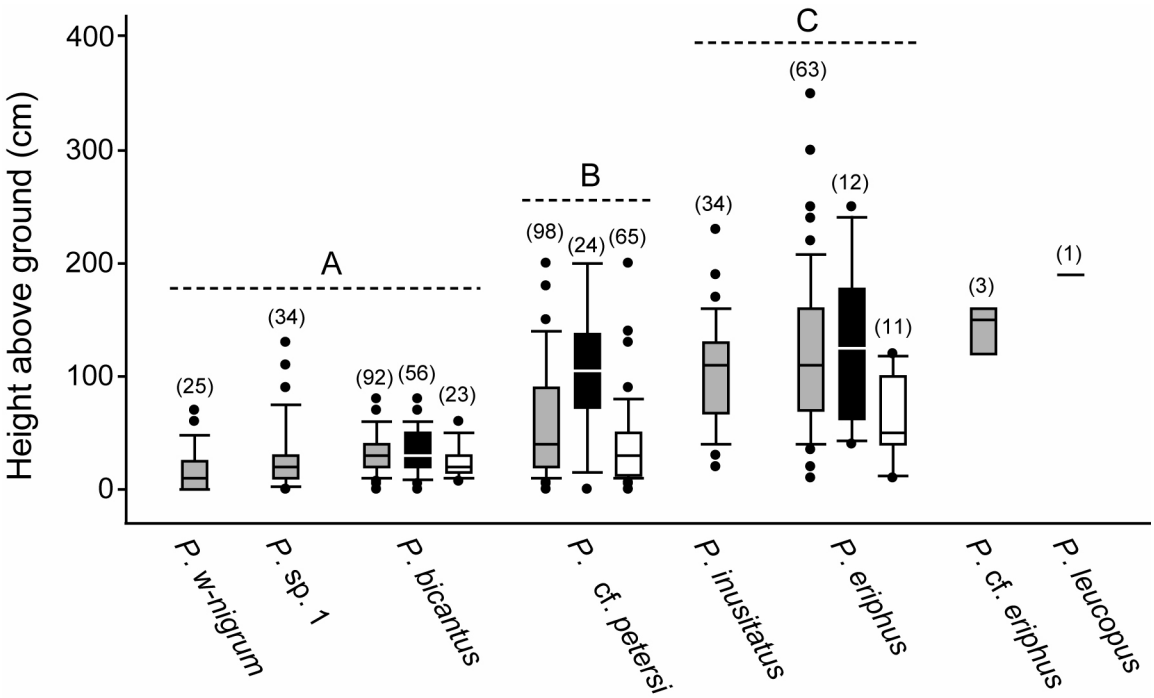

FIGURE 4. Microhabitat use of sympatric species of *Pristimantis* at Yanayacu Biological Station. Box plots of the vertical distance above the ground where frogs were encountered at night. Separate box plots are shown for adults and juveniles for species in which at least 10 individuals of each stage were found. Grey = all individuals; black = adults; and white = juveniles. The boundaries of boxes indicate the 25th and 75th percentiles; the line within the box is the median; error bars are the 10th and 90th percentiles; and points below and above error bars are outliers. Sample sizes (numbers of frogs) are shown above plots in parentheses. Species grouped with a horizontal dashed line and letter did not have significantly different height means (for all individuals; Tukey-Kramer method, $P > 0.05$).

Pristimantis bicantus, new species

Holotype. Adult female QCAZ 19024, collected at Yanayacu Biological Station, trail to San Isidro Lakes (0°36' S, 77°53'W; 2150 m), Provincia Napo, Ecuador, on 10 January 2001 by Fernando Nogales and Diego Almeida-Reinoso.

Paratopotypes. All specimens were collected along different trails within Yanayacu Biological Station, Provincia Napo, Ecuador, or nearby the scientific station, at elevations between 2100 and 2300 m: High trail, QCAZ 19003–08, collected by Martín R. Bustamante on 2 January 2001; QCAZ 19021–23, collected by Claudia Arcanjo on 2 January 2001; QCAZ 19025–28, collected by WCF on 2 January 2001; QCAZ 39813, 39818–19, collected by Martín R. Bustamante on 3 January 2005. Macuca loma, QCAZ 18996, 18999, collected by Martín R. Bustamante and WCF on 29 December 2000; QCAZ 19044–45, 19056–57, collected

by Martín R. Bustamante on 14 January 2002; QCAZ 18979, 18985–89, 18997, collected by WCF on 11 January 2001; QCAZ 18990–91, 18998, collected by WCF on 01 January 2001; QCAZ 18983–84, collected by WCF on 11 January 2001; QCAZ 18997–98, 19000–002, collected by Martín R. Bustamante and WCF on 01 January 2001. Macuca loma creek number 4, QCAZ 22379, collected by Martín R. Bustamante and Galo Diaz on 25 October 2002. San Isidro lakes, QCAZ 19017–18, collected by Fernando Nogales and Diego Almeida-Reinoso on 10 January 2001; QCAZ 39820, collected by Fernando Nogales and Diego Almeida-Reinoso on 11 January 2005. Small San Isidro lake, QCAZ 18980, 18981, collected by WCF on 10 January 2001. Trail to San Isidro lakes, QCAZ 18982, 18993, 19019–20, collected by WCF on 10 January 2001. Upper old station creek, QCAZ 19039–43, 19046–55, collected by Martín R. Bustamante on 17–18 January 2002. Upper trail, QCAZ 19030–38, collected by Martín R. Bustamante on 15 January 2002; QCAZ 22378, 22380–81, collected by Martín R. Bustamante and Galo Diaz on 15 August 2002. Waterfall trail, QCAZ 19029, collected by WCF on 5 January 2002; QCAZ 39814–17, collected by Martín R. Bustamante, Diego Almeida-Reinoso, and Fernando Nogales on 06 January 2005. Nearby scientific station, QCAZ 18978, collected by Diego Almeida-Reinoso and Fernando Nogales on 16 January 2001.

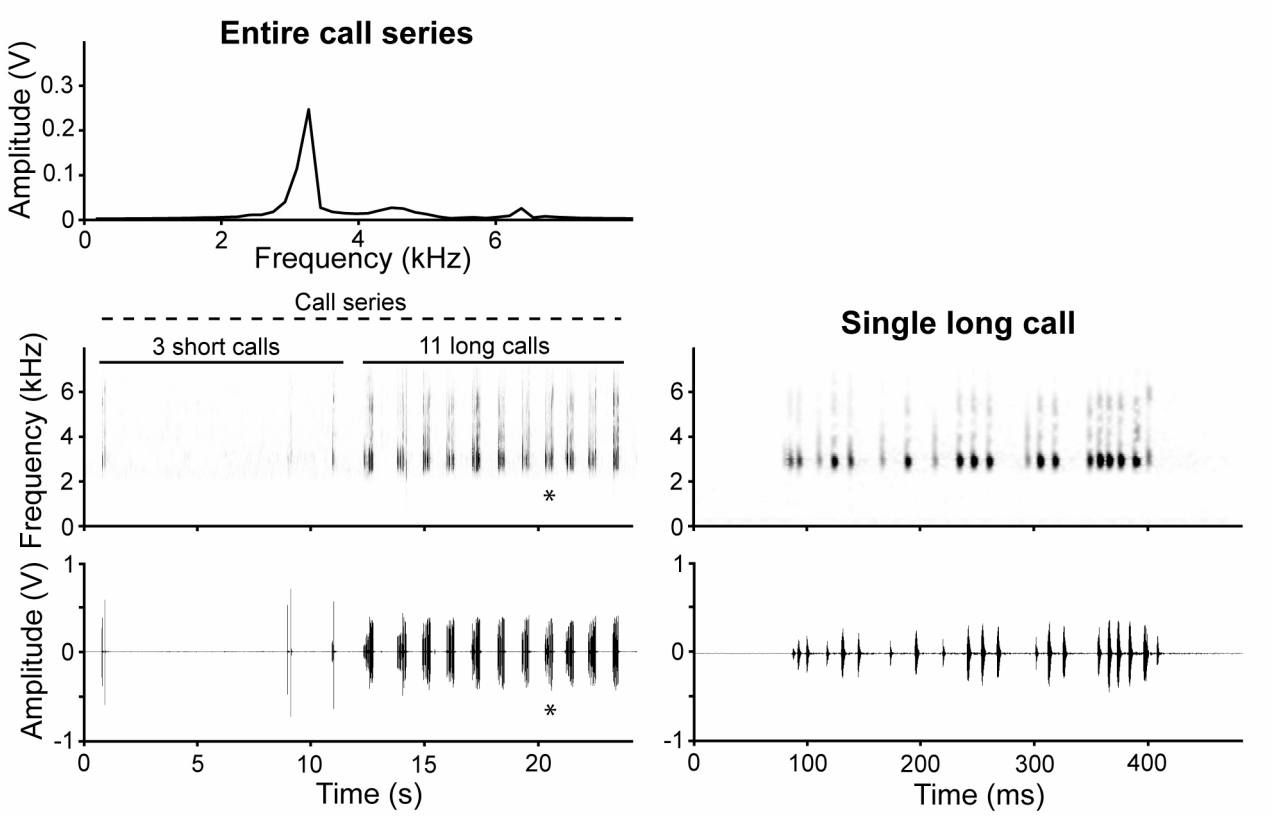

FIGURE 5. Left side shows a power spectrum (top), sonogram (middle), and oscillogram (bottom) of a series of advertisement calls of *Pristimantis bicantus* (QCAZ 18983). Right side shows a sonogram (middle) and oscillogram (bottom) of a single long call (the eighth of the 11 long calls shown on the left, marked with an asterisk). This is an example of a call series consisting of three short calls (each with two pulses) and 11 long calls (each with 17–23 more rapid pulses). The power spectrum was measured along the entire duration of the call series.

Generic placement. As defined by Lynch and Duellman (1997) and Hedges *et al*. (2008), the *Pristimantis (Pristimantis) myersi* group contains small frogs (adult females < 28 mm), with robust bodies, short snouts, and relatively narrow heads; limbs are short to moderately long; Finger I is shorter than Finger II, and Toe V is only slightly longer than Toe III and does not extend to the proximal edge of the distal subarticular tubercle of Toe IV; the digital discs are narrow and rounded; the tympanic membrane is differentiated (except in *P. leoni* and *P. ocreatus*); cranial crests are absent; vocal slits are present (except in *P. floridus*); and vomerine

teeth are present. The morphology of *Pristimantis bicantus* agrees with all the diagnostic traits of the *P. myersi* species group (Lynch & Duellman 1997; Hedges *et al*. 2008), except that the tympanic annulus is relatively larger in males than in females, and tarsal tubercles are absent.

Diagnosis. (1) Skin on dorsum shagreen with small scattered, rounded warts; upper flanks with numerous low warts; occipital and dorsolateral folds usually absent (but see variation; Figs. 1, 2); (2) tympanic membrane and tympanic annulus well differentiated (Fig. 1); tympanic annulus sexually dimorphic; tympanum in males 6.87–10.22% ($\bar{x}$ = 7.99, *n* = 32) SVL, tympanum in females 4.28–6.15% ($\bar{x}$ = 5.23, *n* = 33) SVL; (3) snout rounded in dorsal and lateral views (Figs. 1, 2); (4) upper eyelid bearing many low tubercles; upper eyelid about 43.5–85.7% ($\bar{x}$ = 70.2) IOD; cranial crests absent; (5) dentigerous processes of the vomer evident, each processes bearing 2–8 teeth; (6) males with vocal slits, nuptial pads absent; (7) Finger I shorter than Finger II; discs on Finger I and II not expanded, discs on Finger III and IV slightly expanded (Fig. 1); (8) fingers lack lateral fringes; (9) ulnar tubercles absent; (10) heel and inner and outer edges of tarsus lacking tubercles; (11) inner metatarsal tubercle oval, about 1.5–2.5× the length of round outer metatarsal tubercle; (12) toes lack lateral fringes; webbing absent; Toe V slightly longer than Toe III; discs slightly expanded, disc on Toe IV slightly larger than those on outer fingers (Fig. 1); (13) in preservative, dorsum brown with darker markings, throat whitish cream to pale brown with two dark brown marks on center, venter whitish cream to pale brown, groin cream, posterior surfaces of thighs cream to pale brown (Fig. 2); (14) SVL in males 12.0–15.8 mm ($\bar{x}$ = 14.2 ± 1.013, *n* = 32), in females 17.0–21.7 mm ($\bar{x}$ = 19.0 ± 1.117, *n* = 33).

Pristimantis bicantus is distinguished from most species in the genus *Pristimantis* by having a Toe V slightly longer than Toe III, a Toe V that reaches about to the level of the penultimate subarticular tubercle on Toe IV, and discs on fingers and toes not expanded or slightly expanded. *Pristimantis bicantus* is most likely to be confused with species of the *myersi* group (Lynch & Duellman 1997; Hedges *et al*. 2008), which contains the following species: *Pristimantis festae* (Peracca, 1904), *P. floridus* (Lynch & Duellman, 1997), *P. gladiator* (Lynch, 1976b), *P. hectus* (Lynch & Burrowes, 1990), *P. leoni* (Lynch, 1976b), *P. myersi* (Goin & Cochran, 1963), *P. ocreatus* (Lynch, 1981), *P. pyrrhomerus* (Lynch, 1976b), *P. repens* (Lynch, 1984), *P. scopaeus* (Lynch, Ruiz-Carranza & Ardila-Robayo, 1996), and *P. xeniolum* (Lynch, 2001). The main characters distinguishing *Pristimantis bicantus* from *P. floridus, P. myersi,* and *P. pyrrhomerus* are the absence of tarsal tubercles (present in *P. floridus, P. myersi,* and *P. pyrrhomerus*); these species also occur in different biogreographic areas (Table 2). Additionally, *Pristimantis bicantus* differs from *P. hectus* and *P. myersi* by lacking ulnar tubercles (present in *P. hectus* and *P. myersi*). *Pristimantis bicantus* is distinguished from *P. leoni* by lacking ulnar and tarsal tubercles (present in *P. leoni*), and bearing low tubercles on upper eyelid (subconical tubercles in *P. leoni*). *Pristimantis bicantus* differs from *P. festae* by having slightly expanded discs on outer fingers (fingers not expanded in *P. festae*), lacking lateral fringes on toes (present in *P. festae*), and having a pale cream venter in preservative (black venter usually with cream spots in *P. festae*). *Pristimantis bicantus* can be distinguished from *P. ocreatus* by possessing pads on fingers (pads absent on inner fingers in *P. ocreatus*), and having slightly expanded discs on toes and outer fingers (fingers and toes not expanded in *P. ocreatus*). *Pristimantis bicantus* differs from *P. repens* by lacking a single subconical tubercle on the upper eyelid (present in *P. repens;* Lynch 1984), having, in life, a translucent venter with a gray-orange hue (olive-brown venter in *P. repens;* Lynch 1984); additionally, *P. repens* is found in páramo and subpáramo habitats (Lynch 1984), whereas *P. bicantus* inhabits cloud forests. *Pristimantis bicantus* is distinguished from *P. scopaeus* by having an evident tympanic membrane and tympanic annulus (not visible in *P. scopaeus;* Lynch *et al*. 1996). *Pristimantis bicantus* is distinguished from *P. xeniolum* by having dentigerous process of the vomer with teeth (teeth absent in *P. xeniolum;* Lynch 2001), lacking ulnar and tarsal tubercles (present in *P. xeniolum;* Lynch 2001), and, in males, having vocal slits (absent in *P. xeniolum;* Lynch 2001). Finally, *P. bicantus* is most likely to be confused with *P. gladiator*. Differences between these two species are subtle, but not overlapping. *Pristimantis bicantus* has teeth on the vomers (teeth absent in *P. gladiator*), lacks ulnar and tarsal tubercles (low tubercles present in *P. gladiator*), and, in life has a gray groin with or without reddish or

salmon hue (groin black with red-orange spots in *P. gladiator*). Additionally, *P. gladiator* is found at elevations between 2270 and 2910 m (Lynch 1976b; personal observation), whereas *P. bicantus* seems to be restricted to elevations between 2100–2300 m. Given the importance of the Andean mountains in promoting allopatric speciation (Lynch & Duellman 1997; Guayasamin *et al*. 2008; Bonaccorso 2009), it is relevant to note that only three species of the *Pristimantis myersi* group (i.e., *P. bicantus, P. festae, P. gladiator*) inhabit the same biogeographical region (Amazonian slope of the Andes; Table 2); therefore, comparisons between the new species and *P. festae* and *P. gladiator* are, likely, more important when testing the validity of the new species.

TABLE 2. Distribution of species in the *Pristimantis myersi* group.

Species	Distribution	Elevation (m)	Source
Pristimantis bicantus	Central Ecuador: Amazonian slope of the Andes	2100–2300	This work
Pristimantis festae	Northern and central Ecuador: High Andes and Amazonian slope of the Andes	2360–4400	Lynch and Duellman (1980) as *Eleutherodactylus trepidotus;* this work
Pristimantis floridus	Northern Ecuador: Pacific slope of the Andes	700–2000	Lynch and Duellman (1997)
Pristimantis gladiator	Northern and central Ecuador: Amazonian slope of the Andes	2270–2910	Lynch and Duellman (1980); this work
Pristimantis hectus	Southern Colombia and northern Ecuador: Pacific slope of the Andes	1200–1780	Lynch and Burrowes (1990); Lynch and Duellman (1997)
Pristimantis leoni	Southern Colombia and Northern Ecuador: Pacific slope of the Andes	1960–3400	Lynch and Duellman (1997)
Pristimantis myersi	Southern Colombia: High Andes of Nudo de Pasto and southern end of Cordillera Central	2900–3275	Lynch (1981)
Pristimantis ocreatus	Northern Ecuador: High Andes	3500–4150	Lynch (1981); Stuart *et al*. (2008)
Pristimantis pyrrhomerus	Central Ecuador: Pacific slope of the Andes	2075–3000	Lynch and Duellman (1997)
Pristimantis repens	Southern Colombia: High Andes of the Cordillera Central, Volcán Galeras	3150–3720	Lynch (1984); Stuart *et al*. (2008)
Pristimantis scopaeus	Central Colombia: High Andes of the Cordillera Central	3580–3600	Lynch *et al*. (1996)
Pristimantis xeniolum	Central Colombia: High Andes of the Cordillera Occidental	3300–3600	Lynch (2001)

Description of holotype. Adult female (QCAZ 19024, SC 408) with head narrower than widest part of body; head longer than wide (head width 91.1% head length); snout rounded in dorsal and lateral views, relatively short (snout-to-eye distance 18.6% SVL), without papilla at tip (Fig. 1); in lateral view, canthus rostralis distinct; loreal region slightly concave; nostrils slightly protuberant, directed laterally; interorbital area flat, broader than upper eyelid (upper eyelid width 69.6% interorbital distance); cranial crests absent; upper eyelid bearing several nonconical tubercles; tympanic membrane well-defined, with dark brown pigmentation on upper third; tympanic annulus distinct, round; supratympanic fold obscuring anterodorsal and posterodorsal edges of annulus (Fig. 1); tympanum diameter 47.6% eye length; two nonconical postrictal tubercles. Choanae small, nearly elliptical, not concealed by palatal shelf of maxillary; dentigerous process of the vomer oblique, widely separated, posteromedial to choanae, each bearing 3–5 small teeth; tongue slightly longer than wide, granular, without notch in posterior border.

Skin of head shagreen; dorsum shagreen, with scattered small tubercles, some of which are aligned over a W-shaped occipital mark, but not forming folds; upper flanks with numerous low warts; venter slightly areolate; discoidal fold absent; anal sheath absent. Forearm slender; radio-ulna length 24.5% SVL; ulnar tubercles absent; ulnar fold absent; hand length longer than radio-ulna length (hand length 26.1% SVL); fingers without lateral fringes; finger lengths I < II < IV < III; palmar tubercle bifid, thenar tubercle oval (Fig. 1); subarticular tubercles round, not prominent; supernumerary palmar tubercles not evident; disc cover of Finger I not expanded; those of Fingers II–IV slightly expanded; outer discs of fingers slightly narrower than Toe IV; all disc covers with nearly elliptical ventral pads defined by grooves (Fig. 1).

Hind limbs relatively robust; tibia length 54.3% SVL; foot length slightly smaller than tibia length (foot length 47.9% SVL); tarsal tubercles absent; no tubercle on heel; toes without lateral fringes (Fig. 1); subarticular tubercles round, not prominent; inner metatarsal tubercle oval, two times size of outer tubercle; supernumerary plantar tubercles not evident (Fig. 1); disc cover of Toe V not expanded, disc covers of Toes I–IV slightly expanded; toes with defined pads; disc pads nearly elliptical; toe lengths I < II < III < V < IV (Fig. 1); tip of Toe V almost reaches distal border of penultimate subarticular tubercle of Toe IV; tip of Toe III reaches proximal border of penultimate subarticular tubercle of Toe IV.

In ethanol, dorsum brown with darker interorbital bar, occipital W-shaped mark, and weakly defined chevron at the level of sacrum. Upper and lower lips with dark brown bars, supratympanic stripe dark brown. Flanks pale brown with small darker marks. Dorsum of limbs pale brown with dark brown bars. Cloacal region dark brown. Groin cream brown, anterior and posterior surfaces of thighs pale brown. Throat cream brown with darker marks on center (Fig. 2E). Venter pale brown. Most of ventral surfaces of arms and feet dark gray. Palms and soles dark grayish brown, tubercles on palms and soles unpigmented (Fig. 2A, E).

Measurements of holotype (mm).—Adult female (QCAZ 19024); SVL = 18.8; tibia length = 10.2; foot length = 9.0; head length = 7.9; head width = 7.2; interorbital distance = 2.3; upper eyelid width = 1.6; internarial distance = 2.4; eye-to-nostril distance = 1.8; snout-to-eye distance = 3.5; eye diameter = 2.1; tympanum diameter = 1.0; eye-to-tympanum distance = 0.9; radio-ulna length = 4.6; hand length = 4.9; and Finger-I length = 2.9.

Variation in external morphology. Meristic variation of the type series is presented in Table 4. There is conspicuous variation in the number of teeth on the dentigerous process of the vomer (2–8 teeth), usually larger individuals have more teeth. Tympanum in males larger than in females (tympanum in males 6.9–10.2% SVL, tympanum in females 4.3–6.2% SVL). Snout with small papilla at tip (females, QCAZ 10103, 16209, 19029). Some individuals (QCAZ 16203, 16209, 19031, 19040–2, 19045, 19048, 19051, 19053, 19057) present a series of low tubercles that form low occipital and dorsolateral folds (Fig. 2).

Color in life. The following description includes the color variation found in *Pristimantis bicantus*. Dorsum light to dark brown usually with an indistinct dark interorbital bar and with or without dark chevron markings; some individuals with light dorsolateral line and some with pale snout; dorsal surfaces of legs with contrasting dark and light bars; distinct dark line extending from posterior edge of eye, through top half of tympanum, to above insertion of arm; flanks light brown or gray with or without diagonal dark bars extending towards groin; uniform dark brown patch with lighter colored border on posterior surface of thighs below cloacal opening; groin and hidden surfaces of thighs gray with or without a reddish or salmon hue; venter translucent with a light gray-orange hue and small white and black speckles, especially laterally and anteriorly; iris pale yellow with dark red medial horizontal bar and orange ring around pupil (Plate 3).

Color variation (in ethanol).—Dorsally, anterior half of head cream (females, QCAZ 19042, 19051; males, QCAZ 19026). Dorsum grayish cream (females, QCAZ 16201, 19039; males, QCAZ 18981, 18983–84, 19019, 19027, 19035, 19038, 19044), pale brown (female QCAZ 19005), or uniform pale brown (female, QCAZ 19056; males, QCAZ 18994, 18997). Interorbital bar, W-shaped mark, and chevron absent (females, QCAZ 16186, 19056; males, QCAZ 18994, 18997). Dorsolateral stripes, external border of upper eyelid, and canthal stripe cream (female, QCAZ 10102, 19029, 19049, 19051; males, QCAZ 18980, 18982, 18996, 19004, 19031, 19036, 19052). Dorsolateral stripes dark gray (males, QCAZ 18994, 18997). Flanks whitish cream (females, QCAZ 16209, 19049; males, QCAZ 18981, 19030, 19032, 19035, 19038, 19044), grayish

cream (female, QCAZ 19039; males, QCAZ 18980, 18983, 19052, 18984), or brown (female, QCAZ 19001). Groin and flanks brown with cream flecks (female, QCAZ 19001). Posterior surfaces of thighs creamy gray (female, QCAZ 16201; males, QCAZ 19019, 19030–02, 19035, PUCE 330, 334), or brown with cream flecks (females, PUCE 335, QCAZ 19001). Throat, venter, and groin whitish cream (females, PUCE 329, 344, QCAZ 16186, 16209, 19003, 19005–06, 19029, 19033, 19046, 19048–49; males, QCAZ 18981, 18984, 18986, 19004, 19019, 19026, 19030–02, 19038, 19044), creamy gray (females, QCAZ 16201, 19039, 19042; males, QCAZ 18980, 19052), whitish gray (females, QCAZ 19050–51), pale brown (female, QCAZ 18978), or brown (female, QCAZ 10102). Throat with no dark brown marks (females, QCAZ 10102, 19003, 19048, 19029, 19050; males, QCAZ 18992–94, 19004, 19019, 19025–26, 19030, 19036, 19038), brown with darker marks and cream flecks (males, QCAZ 18982, 18996–97, 19034), or whitish cream (male, QCAZ 18983). Venter gray (male, QCAZ 18983). Palms and soles gray (females, QCAZ 19001, 19029, 19051; male, QCAZ 19001).

Etymology. The specific name *bicantus* is derived from the Latin *bi-*, meaning "two" and *cantus*, meaning "song" in reference to the species' call, which has two distinct call types.

Distribution. *Pristimantis bicantus* is known only from the cloud forests surrounding Yanayacu Biological Station (0°36′S, 77°53′W) at elevations between 2100 and 2300 m (Fig. 3).

Ecology. *Pristimantis bicantus* is one of the two most abundant frog species at Yanayacu (*Pristimantis* cf. *petersi* is the other most abundant frog; Table 1). Ninety-four individuals were found at night during approximately two years of inventory work (2000–2002), of which 65 were adults, 23 were juveniles, one was a subadult, and stage was not determined for the remaining five. Most were found in primary forest, although 31% were found in secondary forest, suggesting this species is more tolerant of disturbance than most other *Pristimantis* at Yanayacu. *Pristimantis bicantus* used low leaves 0–80 cm ($\bar{x}$ = 32 cm) above the ground as substrate at night (Fig. 4). Of the eight *P. bicantus* females dissected to count and measure ovarian ova, the number of large ova was 13–20 ($\bar{x}$ = 16.3), each with a diameter of 1.1–2.6 mm ($\bar{x}$ = 2.1 mm). Some females also had a few to several very small ova.

TABLE 3. Means and ranges of call parameters of *Pristimantis bicantus* sp. nov. from Yanayacu Biological Station. Abbreviations are QCAZ = Museo de Zoología de la Pontificia Universidad Católica del Ecuador; *n* = number of calls analyzed.

	Museum number	
Call parameter	QCAZ 18983 (*n* = 35)	QCAZ 18984 (*n* = 167*)
Recording T (°C)	13.0	13.0
SVL (mm)	16.1	16.5
Fundamental frequency (Hz) of short calls	3186 (2918–3350)	3134 (2939–3313)
Fundamental frequency (Hz) of long calls	2831 (2804–2857)	2973 (2917–3093)
Number of harmonics	2	2
Call series duration (s)	2.7 (0.01–22.7)	7.6 (0.01–43.1)
Short call duration (ms)	153 (10–272)	112 (5–159)
Long call duration (ms)	344 (296–401)	315 (239–395)
Number of short calls per call series	1.4 (1–3)	1.9 (1–6)
Number of long calls per call series	5.3 (2–11)	17.1 (7–24)
Number of pulses per short call	2.1 (1–3)	1.9 (1–3)
Number of pulses per long call	18.9 (16.0–20.5)	15.5 (11.6–17.1)
Pulses per sec for short calls	10.8 (0.6–15.2)	9.3 (0.5–13.9)
Pulses per sec for long calls	21.8 (19.2–26.5)	16.5 (14.5–17.7)
Call series per min	2.3	2.3

TABLE 4. Morphological variation of adult males and females of *Pristimantis bicantus*. Range (in mm) is followed by mean, standard deviation, and sampling size (*n*).

	Females	Males
SVL	17.0–21.7	11.8–15.8
	18.9 ± 1.1	14.2 ± 1.0
	n = 36	*n* = 32
Foot	8.0–9.5	5.5–6.8
	8.7 ± 0.3	6.4 ± 0.4
	n = 26	*n* = 12
Head length	7.2–8.6	5.1–6.5
	8 ± 0.3	6.0 ± 0.4
	n = 26	*n* = 12
Head width	6.2–7.8	5.0–6.2
	7.2 ± 0.3	5.3 ± 0.3
	n = 26	*n* = 12
Interorbital distance	2.0–2.6	1.7–2.2
	2.3 ± 0.1	1.9 ± 0.1
	n = 36	*n* = 32
Upper eyelid width	1.0–1.9	1.0–1.7
	1.6 ± 0.2	1.3 ± 0.2
	n = 36	*n* = 32
Eye-to-nostril distance	1.5–2.2	1.3–1.7
	1.9 ± 0.1	1.4 ± 0.1
	n = 26	*n* = 12
Snout-to-eye distance	3.0–3.9	2.2–2.9
	3.3 ± 0.2	2.5 ± 0.2
	n = 26	*n* = 12
Eye diameter	2.1–2.8	1.7–2.5
	2.4 ± 0.2	2.0 ± 0.3
	n = 26	*n* = 12
Tympanum	0.8–1.4	0.9–1.5
	1 ± 0.2	1.2 ± 0.2
	n = 36	*n* = 32
Radioulna length	4.4–5.3	2.9–3.9
	4.8 ± 0.2	3.6 ± 0.3
	n = 26	*n* = 12
Hand length	4.3–5.1	3.0–3.9
	4.8 ± 0.2	3.5 ± 0.3
	n = 26	*n* = 12
Finger I length	2.4–3.0	1.6–2.0
	2.7 ± 0.1	1.9 ± 0.1
	n = 26	*n* = 12
Finger II length	2.7–3.6	1.9–2.5
	3.2 ± 0.2	2.3 ± 0.2
	n = 26	*n* = 12

Vocalization. We recorded the calls of two *Pristimantis bicantus* males at Yanayacu Biological Station on 11 January 2001 (see Table 3 for details). Two call types were recorded, short calls and long calls (Fig. 5). Males often produced call series consisting of a few to several short calls followed by many long calls. Short

calls were also heard without long calls, but long calls were always preceded by short calls as part of a call series. Short calls consisted of 1–3 pulses with a mean fundamental frequency of 3134–3186 Hz. Long calls consisted of a mean of 15.5–18.9 more rapid pulses and a slightly lower mean fundamental frequency of 2831–2973 Hz. The fundamental frequency was equivalent to the dominant frequency for both short and long calls. The long calls sound like a fingernail being dragged across the teeth of a comb. Some call series were exceptionally long, lasting up to 43.1 s. Theses calls are likely advertisement calls since the males recorded were part of a large breeding chorus of *P. bicantus*.

Remarks. In Funk *et al*. (2003), *Pristimantis bicantus* was referred to as *Eleutherodactylus* sp. 3.

Amphibian inventory and *Pristimantis* vertical microhabitat use

We found thirteen described and seven undescribed species of amphibians at Yanayacu Biological Station (Table 1; Appendix I). One of these unknown species has subsequently been described (*Nymphargus wileyi*; Guayasamin et al., 2006a) and herein we describe a second unknown species, *Pristimantis bicantus*. Five families of amphibians were represented: Bufonidae (2 species), Centrolenidae (7), Dendrobatidae (1), Strabomantidae (9), and Caeciliidae (1). All of these species are nocturnal except for the dendrobatid, *Hyloxalus pulchellus*. and the bufonid *Rhinella margaritifera*. In terms of species richness and abundance, the amphibian community at Yanayacu is dominanted by *Pristimantis* species. The species richness of centrolenids was also relatively high, but they are rare with the exception of *Centrolene bacatum* and *Nymphargus wileyi*. Amphibians were found in all habitat types surveyed, but species richness was highest in primary cloud forest. Amongst the abundant species, both adults and juveniles were found except in the case of *Pristimantis* sp. 1. Thirty-five juveniles and one subadult female of this species were found, but no adults were found.

Substrate height differed significantly among the six species of *Pristimantis* that were analyzed from Yanayacu Biological Station (ANOVA, $F_{5,340} = 42.58$, $P < 0.001$; Fig. 4). Substrate height of *Pristimantis bicantus* was significantly lower than *P. eriphus*, *P. inusitatus*, and *Pristimantis* cf. *petersi* (Tukey-Kramer method, $P < 0.05$), but was not significantly different than the perch height of *P. w-nigrum* or *P.* sp. 1 ($P > 0.05$). Juvenile *P. bicantus* used significantly lower perches (juvenile $\bar{x} = 26$ cm) than adults (adult $\bar{x} = 34$ cm, T-Test, $T_{54} = 2.17$, $P = 0.034$; Fig. 4). Juvenile *P. eriphus* (juvenile $\bar{x} = 65$ cm) and *Pristimantis* cf. *petersi* (juvenile $\bar{x} = 38$ cm) also used significantly lower substrates than adults (*P. eriphus*: adult $\bar{x} = 130$ cm, $T_{17} = 2.91$, $P = 0.010$; *Pristimantis* cf. *petersi*: adult $\bar{x} = 107$ cm, $T_{30} = 5.64$, $P < 0.001$).

Discussion

Systematics.— The morphology of *Pristimantis bicantus* agrees with all the diagnostic traits of the *myersi* species group (Lynch & Duellman 1997; Hedges *et al*. 2008), except that the tympanic annulus is relatively larger in males than in females, and tarsal tubercles are absent.

Amphibian species inventory.—With 20 species of amphibians, Yanayacu Biological Station has one of the richest known amphibian faunas of any site of comparable altitude in the Tropical Andes. Unfortunately, few amphibian inventories have been conducted in this region, so there are few sites available for comparison. The amphibian fauna of the Bosque Integral Otonga, found on the Pacific slopes of the Ecuadorian Andes from 1000–2300 m, has also been extensively sampled and includes 18 species in the families Bufonidae (1 species), Centrolenidae (2), Dendrobatidae (1), Hylidae (2), Strabomantidae (8), Hemiphractidae (2), Caeciliidae (1), and Rhinatrematidae (1; Quiguango *et al*. 2005). Thus Otonga has a greater diversity of amphibian families, but Yanayacu has more species in fewer families, particularly for centrolenids and strabomantids. Lynch and Duellman (1997) provided *Pristimantis* species lists for several sites on the Pacific slopes of the Ecuadorian Andes. Two sites were at similar altitudes as Yanayacu: Quebrada Zapadores at

2010 m with ten *Pristimantis* species and Pilaló at 2400 m with six *Pristimantis* species. The species richness of *Pristimantis* at these sites is similar to that observed at YBS (9).

We found fewer amphibian species in disturbed habitat types than in primary forest (Table 1). Eighteen species were found in primary forest, eight in secondary and bamboo forest, and only three in overgrown pasture. This is a well-known pattern observed in many tropical amphibian faunas. For example, Lynch and Duellman (1997) and Pearman (1997) also reported the highest diversity of *Pristimantis* species in primary forest in western Ecuador and Amazonian Ecuador, respectively. Primary forest was particularly important at Yanayacu for *Pristimantis* and centrolenid species. Six out of seven centrolenid species were only encountered only in primary forest along streams. All nine *Pristimantis* species were found in primary forest and were generally more abundant in primary forest than other habitat types. Undisturbed primary forest is clearly critical habitat for the amphibian community of Yanayacu and other cloud forest and rainforest sites.

Adults and juveniles of most of the abundant amphibian species were found at Yanayacu. A notable exception to this was *Pristimantis* sp. 1 in which only juveniles were found in two years of inventory work and six subsequent years of ongoing herpetological investigations. Moreover, juvenile *Pristimantis* sp. 1 are relatively abundant, making it even more surprising that no adults have yet been found. This suggests that adults are using a habitat type that has not yet been surveyed sufficiently. One possibility is that the adults use the canopy, a habitat that we did not inventory (Guayasamin *et al*. 2006b). This seems unlikely, however, because at least juvenile *Pristimantis* sp. 1 do not appear to be canopy species morphologically. In particular, it has narrow toe pads and discs, suggesting it is not an arboreal species. Finding adult representatives of this species will require additional fieldwork in under-surveyed microhabitats.

Vertical microhabitat use.—We found significant differences among species in the height of substrate used while the frogs were active at night (Fig. 4). In general, there were three different classes of vertical habitat use at Yanayacu: ground or low vegetation (mean perch height below 50 cm; *P. bicantus*, *P. w-nigrum*, and *P.* sp. 1); high vegetation (mean perch height above 100 cm; *P. eriphus* and *P. inusitatus*); and intermediate vegetation (mean perch height between 50 and 100 cm; *Pristimantis* cf. *petersi*). Moreover, *Pristimantis* species were generally the only frog species in the forest at Yanayacu with the exception of an occasional centrolenid species that had wandered far from streams. Thus partitioning of perch height among *Pristimantis* species is likely primarily mediated by interactions with congeners. Others have also observed vertical habitat partitioning among *Pristimantis* species in western Ecuador (Lynch & Duellman 1997) and *Pristimantis*, *Craugastor*, and *Diasporus* in Costa Rica (Miyamoto 1982). Lynch and Duellman's (1997) observations were not quantitative, however, and Miyamoto's (1982) analysis was over a much shorter time frame (2 months) than ours (2 years) and subsequently had smaller sample sizes. Several hypotheses could explain among species variation in vertical habitat use, including partitioning of calling (Miyamoto 1982) or foraging sites. Although some species share the same vertical zone, in these cases, they generally differ in some other dimensions of habitat use. For example, although both *P. bicantus* and *P. w-nigrum* use the ground or low vegetation, *P. bicantus* uses primary and secondary forest, whereas *P. w-nigrum* is also found in pasture and tends to be found near stream edges. *Pristimantis w-nigrum* is also much larger than *P. bicantus*, and therefore likely forages on larger prey.

We also found that juveniles used significantly lower perches at night than adults in the three species with sufficient samples sizes to test this hypothesis (*P. bicantus*, *P. eriphus*, and *Pristimantis* cf. *petersi;* Fig. 4). This difference was most pronounced in *P. eriphus* and *Pristimantis* cf. *petersi*, due in part to being more arboreal than *P. bicantus,* resulting in a greater potential for vertical habitat partitioning between juveniles and adults. Lower vertical habitat use in juveniles than adults is also seen in the *Pristimantis* and *Craugastor* species shown in Table 2 of Miyamoto (1982), but he did not discuss this result or test whether these differences were statistically significant. As with variation among species in perch height, several hypotheses could explain differences between juveniles and adults in perch height. For example, adults may ascend higher than juveniles to call (males) and find mates (females). Adults also tend to consume larger prey items than juveniles and the larger prey used by adults may be more abundant on higher substrates and the smaller prey used by juveniles may be more abundant on lower substrates. Resource partitioning due to interspecific

and intraspecific competition has been documented previously in amphibians (Schoener 1974; Duellman & Pyles 1983; Toft 1985) and could play a role in the interspecific and intraspecific variation in perch height observed here.

The observation of significant variation in vertical habitat partitioning among *Pristimantis* species highlights the ecological diversity of this exceptionally diverse clade of frogs and how little is known about how this diversity evolved. Streelman and Danly (2003) argued that many vertebrates diverge along axes of habitat, morphology, and communication. Is this the order in which adaptive radiation occurred in *Pristimantis*? Only a thorough analysis integrating ecology, morphology, and phylogenetics will reveal the patterns and mechanisms of radiation in this legendary, but poorly understood, group of frogs.

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APPENDIX I: Specimens examined

Centrolene bacatum: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 16212, 17807, 22387, 22728, 26025–27, 26056, 37973, 37976–78.

Centrolene buckleyi: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 22388, 26031–32.

Centrolene sp: Ecuador: Napo: Yanayacu Biological Station, 2100 m: QCAZ 25744–46.

Cochranella sp*:* Ecuador: Napo: Yanayacu Biological Station, 2100 m: QCAZ 37230.

Hyloxalus pulchellus: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 16196, 18652, 20923–24.

Nymphargus posadae: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 25090, 26023.

Nymphargus siren: Ecuador: Napo: Yanayacu Biological Station, 2100 m: QCAZ 37971, 37975.

Nymphargus wileyi: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 22367–69, 22389–90, 26024, 26028–30, 26057, 28494–96, 32725, 37972, 37974.

Osornophryne guacamayo: Ecuador: Napo: Yanayacu Biological Station, 2300–2500 m: QCAZ 26047–49, 31081.

Pristimantis cf. *eriphus*: Ecuador: Napo: Yanayacu: High trail behind Yanayacu, QCAZ 10617; Yanayacu, QCAZ 19063; Upper trail, QCAZ 19064.

Pristimantis eriphus: Ecuador: Napo: Yanayacu: High trail, QCAZ 19066, 19068; Macuca loma, QCAZ 19071–72; Richmond creek, QCAZ 19069; Terrestrial transect 1, Macucaloma trail, QCAZ 22280–81; Terrestrial transect 2, waterfall trail, QCAZ 22282; Upper trail, QCAZ 19070; Waterfall trail, QCAZ 19067.

Pristimantis festae.—Ecuador: Napo: 1 km W Papallacta, 3170 m, KU 106938–42 (paratypes).

Pristimantis gladiator.—Ecuador: Napo: 3.3 km ESE Cuyuja, 2350 m, KU 143516 (holotype); 5.7 km E Papallacta, 2910 m, KU 143513–15 (paratypes).

Pristimantis hectus.—Colombia: Nariño: Reserva Natural La Planada, 7 km S Chuchunés, 1780 m, KU 212539–44 (paratypes).

Pristimantis inusitatus: Ecuador: Napo: Yanayacu: CMR grid C, QCAZ 22285; CMR grid Charapa B, QCAZ 19074–76, 19078–79; Macuca loma, QCAZ 19094–95, 19098; Macuca loma trail, QCAZ 19083, 19096–97; Yanayacu, QCAZ 19081–82; Terrestrial transect 2, waterfall trail, QCAZ 22286; Trail from San Isidro to Rio Yanayacu, QCAZ 19091–093; Trail to San Isidro lakes, QCAZ 19510; Waterfall trail, QCAZ 19080, 19084, 19088–90.

Pristimantis leucopus: Ecuador: Napo: San Isidro, QCAZ 19065.

Pristimantis leoni.—Ecuador: Imbabura: Nudo de Mojanda, N slope, 3400 m, KU 130870 (holotype).

Pristimantis myersi.—Colombia: Cauca: 23–30 km E Puracé, 3030–3275 m, KU 168432–39.

Pristimantis ocreatus.—Ecuador: Carchi: Volcán Chiles, 10 km W Tufiño, 3500–3800 m, KU 117573 (holotype), 17574–81 (paratypes).

Pristimantis pyrrhomerus.—Ecuador: Cotopaxi: Pilaló, 2580 m, KU 131606 (holotype); 6 km E Pilaló, KU 142167–70 (paratypes).

Pristimantis sp. 1: Ecuador: Napo: Yanayacu: CMR grid Charapa A, QCAZ 18897–98, 18901–03, 18909–10, 18914; CMR grid Charapa B, QCAZ 18900, 18904, 18911; High trail, QCAZ 18922–23, 18926; Macuca loma, QCAZ 18929–33; Macuca loma trail, QCAZ 18916–17, 18919, 18924, 22382; Terrestrial transect 2, waterfall trail, QCAZ 18915, 18920–21, 18925, 22384; Trail to San Isidro lakes, QCAZ 18899; Upper trail, QCAZ 18928.

Pristimantis cf. *petersi*: Ecuador: Napo: Yanayacu: Above the waterfall, QCAZ 19059–60; CMR grid B, QCAZ 22373, 22376–77; CMR grid C, QCAZ 22375; High trail, QCAZ 19058; Macuca loma, QCAZ 18935–36, 18950, 18952, 18956, 19506–07, 19509; Isidro, QCAZ 19508; Macuca loma trail, QCAZ 18937, 18941–42, 18944–49, 18951, 18953–55, 18957–58, 18960–70, 39822, 39833; San Isidro lakes, QCAZ 18992; Stream by old house, QCAZ 22372; Terrestrial transect 2, waterfall trail, QCAZ 22374; Trail to San Isidro lakes, QCAZ 18938–40, 18943, 18959, 19015–16, 39823–24; Waterfall trail, QCAZ 18971–77, 19009–14, 19061–62, 19498–505, 39825.

Pristimantis w-nigrum: Ecuador: Napo: Yanayacu: CMR grid A, QCAZ 22272; Macuca loma trail, QCAZ 22270, 22279; Terrestrial transect 1, Macuca loma, QCAZ 22273–77; Terrestrial transect 2, waterfall trail, QCAZ 22271.

Rhinella margaritifera: Ecuador: Napo: Yanayacu Biological Station, 2000–2200 m: QCAZ 22189–92, 31418–19, 31422–24.

Caecilia orientalis: Ecuador: Napo: Yanayacu Biological Station, 2100 m: QCAZ 21417–19.

Osornophryne guacamayo. Female, QCAZ 40101. SVL= ca. 34.0 mm. Ecuador: Provincia de Napo: Cordillera de los Guacamayo, 2050 m. Photos by Luis A. Coloma.

Rhinella margaritifera. Male, QCAZ 31418. SVL= 42.8 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Centrolene bacatum. Male, QCAZ 26056. SVL= 19.9 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Centrolene buckleyi. Male, QCAZ 26032. SVL= 26.0 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

***Cochranella* sp**. Female, QCAZ 37230. Yanayacu Biological Station, 2100 m. SVL= 28.7 mm. Photo by Esther Cole.

Nymphargus posadae. Female, QCAZ 25090. SVL= 29.6 mm. Yanayacu Biological Station, 2100 m. Photos by Martín R. Bustamante.

Nymphargus siren. QCAZ 37971. SVL= 20.5 mm. Yanayacu Biological Station, 2123 m. Photo by Luis A. Coloma.

Nymphargus wileyi. Male, QCAZ 26057. SVL= 26.0 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Hyloxalus pulchellus. Male, QCAZ 16196. SVL= 20.4 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Pristimantis bicantus. Female, QCAZ 32997. SVL= 20.0 mm. Yanayacu Biological Station, 2200 m. Photo by Luis A. Coloma.

Pristimantis bicantus. Juvenile female, QCAZ 33001. SVL = 17.7 mm. Yanayacu Biological Station, 2200 m. Photo by Luis A. Coloma.

Prisitmantis eriphus. Female, QCAZ 32705. SVL= 28.9 mm. Yanayacu Biological Station, 2123 m. Photos by Luis A. Coloma.

Pristimantis* cf. *eriphus. Adult male, QCAZ 19064. SVL = 17.8. Yanayacu Biological Station, 2100 m. Photo by WCF.

Pristimantis sp 1. Subadult female, QCAZ 18932. SVL = 18.3 mm. Yanayacu Biological Station, 2100 m. Photo by WCF.

Pristimantis inusitatus. Female, no number associated. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Pristimantis inusitatus. Female, QCAZ 32710. SVL= 20.2 mm. Yanayacu Biological Station, 2100 m. Photo by Luis A. Coloma.

Prisitmantis inusitatus. Adult male, QCAZ 32711. Yanayacu Biological Station, 2123 m. Photos by Luis A. Coloma.

Pristimantis gladiator. Female, QCAZ 40808, SVL= 19.8 mm. Provincia de Napo: Cordillera de los Guacamayos, 2270 m. Photos by Luis A. Coloma.

Pristimantis leucopus. Female, QCAZ 16189. SVL= 38.9 mm. Yanayacu Biological Station, 2100 m. Photos by Martin R. Bustamante.

Pristimantis* cf. *petersi. Adult male, QCAZ 18970. SVL= 17.7 mm. Yanayacu Biological Station, 2100 m. Photo by Martín R. Bustamante.

Pristimantis w-nigrum. Adult male, QCAZ 42892. Provincia Bolívar: Reserva Cashca-Totoras, 2936 m. Photo by Luis A. Coloma.

***Caecilia orientalis*.** Male, QCAZ 22385. SVL= 331 mm. Yanayacu Biological Station, 2100 m. Photos by Martín R. Bustamante.