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Two New Species of Frogs of the Genus *Colostethus* (Dendrobatidae) from Peru and a Redescription of *C. trilineatus* (Boulenger, 1883)

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ABSTRACT

Colostethus trilineatus (Boulenger, 1883) is widespread in the lowlands of Amazonian Peru and Ecuador. It is characterized, in part, by small size, gray throat and Finger III strongly swollen in adult males, and an advertisement call of 10 notes with emphasized frequencies at 4920–6040 Hz. Material examined revealed extensive variation in dorsal, ventral, and thigh coloration. In numerous adult males from several localities Finger II is also swollen. The swelling of Finger II varies intraspecifically, possibly as a function of male reproductive activity.

Vocalizations of *Colostethus trilineatus* recorded at the type locality are temporally distinct from those reported from other localities. At the type locality, advertisement calls are composed of single notes (i.e., not couplets) of (usually) > 40 msec duration and < 90 msec between notes, whereas other calls consist of notes of < 30 msec duration produced as couplets repeated at roughly 200 msec intervals. Although these differences in amplitude modulation could indicate the existence of two species, the calls at the three localities are spectrally identical (all have emphasized frequencies primarily between 5 and 6 kHz) and the specimens examined from these localities are morphologically indistinguishable. For the time being, we interpret the differences in temporal patterning as intraspecific variation.

Colostethus melanolaemus is a new species known from the type locality near the mouth of the Napo River and the upper Ampiyacu River. *Colostethus melanolaemus* most closely

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resembles *C. trilineatus* and *C. juanii* Morales, 1994, but it differs from them in male throat color, swelling of Finger III, snout-vent length, and advertisement call. Although this species reaches a snout-vent length of nearly 24 mm, Finger IV is shorter than or equal to Finger II, and the distal subarticular tubercle is absent. The advertisement call of *C. melanolaemus* usually consists of four notes with emphasized frequencies of 3840–4560 Hz. For comparative purposes, the advertisement call of *C. juanii* is also described.

The oblique lateral stripe, found in many dendrobatids, occurs as a diffuse, inconspicuous, pale region or group of small spots that extends from the groin to midway along the flank in *Colostethus brunneus* (Cope, 1887), *C. juanii*, *C. melanolaemus*, *C. trilineatus*, and several other similar species of *Colostethus*. This pattern differs from the states found in most species of *Colostethus*.

Colostethus alessandroi is a new species found between about 800–1500 m on the eastern slopes of the Andes of southern Peru. This species is most similar to *C. mcdiarmidi* Reynolds and Foster, 1992, but differs in amount of toe webbing, ventral coloration, snout-vent length, dorsal coloration, shank length, and tympanum diameter. Both *C. alessandroi* and *C. mcdiarmidi* have swollen third fingers in adult males. The call of *C. alessandroi* is composed of couplets repeated rhythmically in series of over 300 calls. Spectral energy is concentrated between 3400 and 4320 Hz, with the greatest energy peaks usually below 4.0 kHz. The first note of each couplet is longer than the second.

RESUMEN

Colostethus trilineatus (Boulenger, 1883) está ampliamente distribuido en las tierras bajas de la Amazonia peruana y ecuatoriana. Se caracteriza, en parte, por su tamaño reducido, garganta gris y tercer dedo manual fuertemente expandido en machos adultos, y una vocalización que consiste en 10 notas con frecuencias enfatizadas de 4920–6040 Hz. El material examinado indica que este taxón varía en su coloración dorsal, ventral y de los muslos. Varios machos adultos provenientes de distintas localidades presentan el segundo dedo expandido además del tercero. La expansión del segundo dedo manual varía intraespecíficamente, posiblemente en relación con la actividad reproductiva.

Los patrones temporales de las vocalizaciones de *Colostethus trilineatus* grabadas en la localidad típica difieren de los que se han reportado para otras localidades. En la localidad típica, los cantos de anuncio consisten en notas solitarias (i.e., no producidas en pares) de (usualmente) $>$ 40 msec de duración separadas por $<$ 90 msec, mientras que los de las otras localidades presentan notas de $<$ 30 msec de duración producidas en pares que se repiten en intervalos de unos 200 msec. Aunque estas diferencias en la modulación de amplitud podrían indicar la existencia de dos especies, los cantos en las tres localidades son espectralmente idénticos (todos presentan frecuencias enfatizadas principalmente entre 5 y 6 kHz) y los especímenes examinados de estos sitios son morfológicamente indistinguibles. Por el momento, interpretamos estas diferencias en los patrones temporales como variación intraespecífica.

Colostethus melanolaemus es una especie nueva conocida de la localidad típica cerca de la desembocadura del Río Napo y en el alto Río Ampiyacu. Comparte su mayor parecido con *C. trilineatus* y *C. juanii* Morales, 1994, pero difiere de éstos en las características de la garganta en machos adultos, longitud rostro-cloacal, dilatación del tercer dedo, color de los flancos, y el canto de anuncio. Aunque esta especie alcanza una longitud rostro-cloacal de casi 24 mm, el cuarto dedo manual es más corto o de igual longitud que el segundo y el tubérculo subarticular distal está ausente. El canto de anuncio de *C. melanolaemus* usualmente consiste en cuatro notas con frecuencias enfatizadas de 3840–4560 Hz. Para permitir una comparación acústica, se describe el canto de anuncio de *C. juanii*.

La franja oblicua lateral, presente en muchas especies de dendrobátidos, ocurre como una inconspicua región pálida difusa o un grupo de puntos diminutos que se extiende desde la ingle hasta la mitad de los flancos en *Colostethus brunneus* (Cope, 1887), *C. juanii*, *C. melanolaemus*, *C. trilineatus*, y varias especies similares más. Esta morfología difiere de la que se encuentra en la mayoría de las especies de *Colostethus*.

Colostethus alessandroi es una especie nueva distribuida entre los 800–1500 m en la vertiente oriental de los Andes del sur del Perú. Se parece a *C. mcdiarmidi* Reynolds y Foster, 1992, pero difiere en la extensión de la membrana pedial, el color del vientre, la longitud rostro-cloacal, la coloración dorsal, la longitud de la tibia, y el diámetro del tímpano. Los machos adultos de ambas especies presentan el tercer dedo expandido. El canto de advertencia de *C. alessandroi* está compuesto por pares de notas que se repiten rítmicamente en series de hasta más de 300 cantos. La energía espectral se distribuye entre 3400 y 4320 Hz, con los principales picos de energía menores de 4.0 kHz. La primera nota de cada par es más larga que la segunda.

INTRODUCTION

Significant advancement in dendrobatid systematics is hindered in part by the inadequacy of alpha taxonomy of *Colostethus*, resulting in an underestimation of the diversity of species and the variation within each. Herein, we describe two new species of *Colostethus* and discuss intraspecific variation in similar taxa.

Among the species that most resemble one of the new species, *Colostethus trilineatus* (Boulenger, 1883) is found in the same region of northern Amazonian Peru and occurs in sympatry at one locality. Despite recent attempts to clarify its identity, the diagnosis of *C. trilineatus* remains problematic. Morales (1994) provides a brief account based on his examination of the holotype and extensive material, but his aim is primarily to distinguish *C. trilineatus* from *C. brunneus* (Cope, 1887) and *C. marchesianus* (Melin, 1941), and he does not provide a complete redescription or assess the extensive variation exhibited by this species. Indeed, Duellman and Mendelson (1995: 338) report several discrepancies among the specimens Morales (1994) refers to *C. trilineatus* (see also Köhler and Lötters, 1999; Gonzalez et al., 1999). In light of the confusion surrounding the identity of this species and its relevance to the diagnosis of a number of species of Amazonian *Colostethus*—including one described herein—we begin by providing a detailed redescription of *C. trilineatus* based on 123 specimens from throughout most of its reported range (fig. 1).

Unless otherwise noted, measurements and proportions are given only for adults, as determined by examination of gonads and secondary sex characters. Males with vocal slits on both sides of the mouth were scored as adult, those with only one as subadult, and those lacking slits on both sides as juvenile. Females with expanded, convoluted oviducts and enlarged ova were scored as adult, those with only weakly expanded and non- or weakly convoluted oviducts and weakly differentiated ova as subadult, and those with small, undifferentiated ova and unexpanded, straight oviducts as juvenile. Statistical summaries are reported as the mean ± standard error. Description of pale stripes along the body follows Edwards (1974a). Collection abbreviations are: **AMNH** (American Museum of Natural History), **AMNH FS** (American Museum of Natural History, Field Series, uncataloged specimens collected by LOR), **BMNH** (Natural History Museum, London), **IAvH** (Instituto Alexander von Humboldt), **ICN** (Instituto de Ciencias Naturales, Universidad Nacional de Colombia), **KU** (Natural History Museum, the University of Kansas), **MUSM** (Museo de Historia Natural de la Universidad Mayor de San Marcos), **NKA** (Museo de Historia Natural Noel Kempff Mercado), and **USNM** (National Museum of Natural History, Smithsonian Institution). Bioacoustic analyses were performed using a Kay 5500 DSP Sona-Graph.

As currently defined, there is no evidence for the monophyly of *Colostethus*. The species discussed herein are therefore referred to *Colostethus* only because they cannot be referred to any other dendrobatid genus. Most of the species groups of Rivero (‘‘1988’’ [1990]) and Rivero and Serna (‘‘1988’’ [1989]) are not supported by synapomorphy and therefore are not recognized in the present study.

Colostethus trilineatus (Boulenger)

Figures 2–7

Phyllobates trilineatus Boulenger, 1883: 636. Holotype BMNH 1947.2.14.20 from ‘‘Yurimaguas, [Departamento Loreto,] Huallaga River, Northern Peru.’’

DIAGNOSIS: A very small *Colostethus* (males to about 18 mm SVL; females to about 19 mm SVL); Finger III (and often Finger II) of adult males strongly swollen;

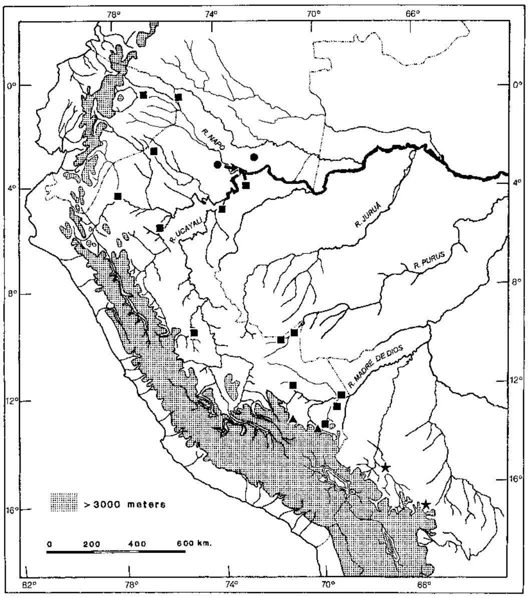

Fig. 1. Map of western South America showing localities for material examined of *Colostethus trilineatus* (■), *C. melanolaemus* (●), *C. alessandroi* (▲), and *C. mcdiarmidi* (★).

Fig. 2. A specimen of *Colostethus trilineatus* from Cocha Cashu, Parque Nacional del Manu, Depto. Madre de Dios, Peru, ca. 380 m. [From color transparency by LOR.]

throat evenly stippled gray in adult males; testes white (unpigmented) in adult males; Toes II–IV basally webbed; dorsolateral stripe present; oblique lateral stripe present as diffuse, inconspicuous, pale region or group of small spots extending from groin to midway along flank (see Remarks, below); ventrolateral stripe present; one or two subarticular tubercles on Finger IV; median lingual process absent; cloacal tubercles absent; anal sheath absent; black armband absent.

Colostethus trilineatus most resembles six nominal species from the Amazon basin: *C. beebei* (Noble, 1923); *C. brunneus*; *C. juanii* Morales, 1994; *C. marchesianus*; *C. peruvianus* (Melin, 1941); and *C. stepheni* Martins, 1989. *Colostethus beebei* is most easily distinguished from *C. trilineatus* by the possession of a median lingual process. Adult male *C. brunneus* lack a dark throat, swollen Finger III, and ventrolateral stripe. *Colostethus juanii* is a larger species (tables 1–2) in which the gray stippling on the throat of adult males is concentrated into spots or mottling and Finger III of adult males is not swollen. Adult male *C. marchesianus* have an immaculate throat (Morales, 1994). According to Morales's (1994) account and photographs of the holotype in the possession of TG, *C. peruvianus* has a complete oblique lateral stripe and lacks a ventrolateral stripe. *Colostethus stepheni* has a median lingual process, a well-defined, complete oblique lateral stripe, and lacks the dorsolateral and ventrolateral stripes.

MEASUREMENTS OF HOLOTYPE (in mm): BMNH.1947.2.14.20 is an adult male with vocal slits and large, unpigmented (white) testes. SVL, 17.2; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow, 4.0; hand length from proximal edge of palmar tubercle to tip of Finger III, 3.8; shank length from outer edge of flexed knee to heel, 8.0; foot length from

TABLE 1
Adult SVL (in mm) of Four Similar Amazonian Species of *Colostethus*

Species	Sex	*n*	Range	Mean ± SE
brunneus	♀	5	14.6–17.2	16.40 ± 0.49
	♂	6	15.7–17.0	16.76 ± 0.21
juanii	♀	10	19.3–24.3	21.72 ± 0.52
	♂	7	18.7–21.7	19.99 ± 0.41
melanolaemus	♀	14	21.3–23.6	22.24 ± 0.22
	♂	11	21.1–23.4	22.16 ± 0.22
trilineatus	♀	57	15.2–19.3	17.09 ± 0.12
	♂	48	15.0–17.7	16.45 ± 0.09

TABLE 2

Results (P-values) of ANOVA Comparing SVL of Adult Males and Adult Females of Four Similar Amazonian Species of *Colostethus* (see table 1 for data)[a]

		brunneus	*juanii*	*melanolaemus*	*trilineatus*
brunneus	♂	—			
	♀	—			
juanii	♂	0.0001*	—		
	♀	0.0001*	—		
melanolaemus	♂	0.0001*	0.0001*	—	
	♀	0.0001*	0.2090	—	
trilineatus	♂	0.6930	0.0001*	0.0001*	—
	♀	0.1411	0.0001*	0.0001*	—

[a]The general hypotheses of no difference among the four samples of males and four samples of females were both strongly rejected (P = 0.0001). An asterisk (*) indicates significance at P < 0.05 after correction with sequential Bonferroni (Rice, 1989).

proximal edge of outer metatarsal tubercle to tip of Toe IV, 7.2; head width between angle of jaws, 6.0; head length diagonally from corner of mouth to tip of snout, 5.3; eye length from posterior to anterior corner, 2.5; eye to naris distance from anterior corner of eye to center of naris, 1.5; distance between centers of nares, 2.5; snout length from anterior corner of eye to tip of snout, 2.8; interorbital distance, 1.9; diameter of tympanum immeasurable (due to preservational artifact).

REDESCRIPTION

A composite redescription is provided based on 123 specimens from one Ecuadorian and 13 Peruvian localities. Many of these localities and/or their anuran assemblages have been described in detail (Toft and Duellman, 1979; Aichinger, 1987; Duellman and Koechlin, 1991; Rodríguez, 1992; Duellman and Mendelson, 1995; Duellman and Thomas, 1996; Wild, 1996; Parmelee, 1999). All localities are below 900 m. Given that several of the most crucial diagnostic characters are restricted to adult males, the four localities for which adult males were not available are marked with an asterisk and are only tentatively referred to *Colostethus trilineatus* (number of specimens examined in parentheses; see fig. 1 and appendix): Aguas Negras* (5); Río Alto Purús (1); Candamo* (2); Cocha Cashu (26); Río Curanja (4); Cuzco Amazónico (16); Explornapo* (1); Genaro Herrera (4); Limoncocha, Ecuador (3); Panguana (50); Río Santiago (1); Tambopata (2); Teniente López* (3); Yurimaguas (5). *Colostethus trilineatus* also has been reported from Bolivia (Morales, 1994; De la Riva et al., 1996; Köhler and Lötters, 1999; Gonzalez et al., 1999), but Bolivian material was not examined in this study.

MORPHOLOGY: Adult males 15.0–17.7 mm SVL ($n = 48$, $\bar{x} = 16.45 \pm 0.09$ mm), adult females 15.2–19.3 mm SVL ($n = 57$, $\bar{x} = 17.09 \pm 0.12$ mm). The holotype is larger than the other two males from Yurimaguas (MUSM 15611 = 16.1 mm SVL; AMNH FS 8689 = 16.0; see fig. 3), but the difference in SVL is less than that observed within some other populations (e.g., Panguana). Testes unpigmented (white) in all males. Mature ova pigmented black or brown. Most of dorsal and ventral surfaces smooth, except variably expressed tubercles scattered over posterior part of body and dorsal surfaces of legs and a weak, low tubercle on each eyelid in well preserved specimens. A weak to strong postrictal bulge present, reminiscent of postrictal spicules or tubercles found in many *Colostethus*.

Head width between angle of jaws 31–36% of SVL, 1.02–1.25 times head length in males and 0.95–1.14 in females. Interorbital distance 27–38% of head width. Snout sloped, rounded in dorsal aspect, sharply

Fig. 3. Ventral and dorsal views of adult male *Colostethus trilineatus* from the type locality (Yurimaguas). Holotype BMNH 1947.2.14.20 (left), AMNH FS 8689 (center), MUSM 15611 (right). ×1.2.

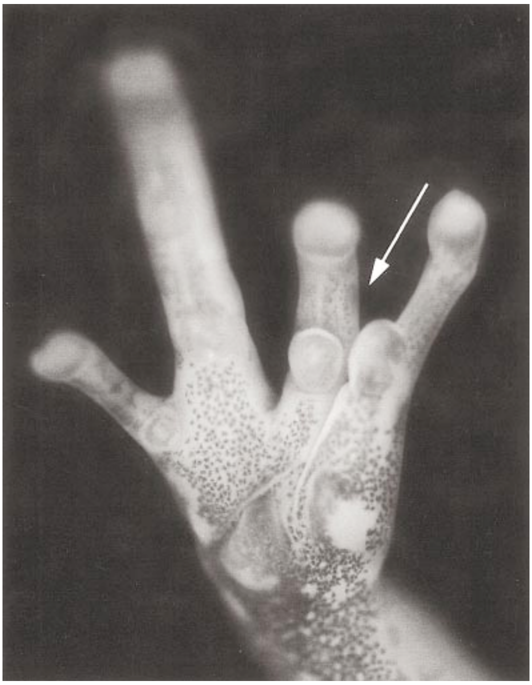

Fig. 4. Palmar view of right hand of *Colostethus trilineatus*, MUSM 15618. Note the swelling of the preaxial side of the Finger II. ×20.

rounded in profile, protruding beyond jaws. Loreal region flat or weakly concave, not sloping outward to lip. Canthus rostralis sharply rounded and well defined. Eye length 39–53% of head length. Eye-naris distance 50–64% of snout length and 54–80% of eye length. Nares directed posteriorly in profile, protuberant in dorsal aspect. Tympanum small; greatest diameter 33–48% of eye length. Teeth on maxillary arch straight, moderate in length, not curved and fanglike.

Hand length (fig. 4) 20–26% of SVL, 0.89–1.15 times forearm length. Finger I > Finger II when appressed. Relative lengths of appressed fingers III > I > II > IV. Fingers weakly keeled distally. Metacarpal fold absent. A single, protuberant subarticular tubercle on each of Fingers I and II, two on Finger III, and one or two on Finger IV. Palmar tubercle well defined, elliptical or subtriangular. Thenar tubercle weak, elliptical. Digital discs weakly expanded. A pair of strong dorsal scutes on each disc.

Finger III swollen in all adult males (contra Duellman and Mendelson, 1995: 338), not distally exaggerated. Degree of swelling somewhat variable, but strong and conspicuous along entire length of preaxial side of digit in all but a few adult males. Finger II also swollen along preaxial side between level of subarticular tubercle and finger disc (fig. 4) in five (of 11) adult males from Cocha Cashu, two (of six) from Cuzco Amazónico, and 12 (of 20) from Panguana (Finger II of several other specimens from these and other localities could not be unequivocally coded as swollen or not). Not all males from a locality had Finger II swollen, and no specimen had Finger II swollen and Finger III not swollen.

Shank length and foot length 41–49 and 37–47% of SVL, respectively. Relative lengths of appressed toes IV > III > V > II > I. Basal webbing between Toes II–IV (webbing formula **II** 1½–3½ **III** 2½–4 **IV,** following Myers and Duellman, 1982). Weak keels or fringes present on both edges of all toes. Outer metatarsal fold[3] present, often forming small tubercle. Tarsal keel on distal third of tarsus well defined, tuberclelike, arising roughly one-third to one-fourth tarsus length from the distal end of the tarsus, not extended distad to reach outer edge of inner metatarsal tubercle. Toe discs weakly expanded; each with pair of well-defined scutes on dorsal surface. One subarticular tubercle on Toes I and II, two on III and V, and three on IV. Outer metatarsal tubercle round; inner metatarsal tubercle elliptical; both tubercles well-defined and protuberant.

COLOR IN PRESERVATIVE: The dorsal coloration (figs. 2, 3, 5) is tan to dark brown, either uniform or with small, dark spots scattered over the dorsum. Within-population variation in the expression of a narrow, pale vertebral stripe is as follows (present:absent): Aguas Negras (0:5); Río Alto Purús (0:1); Candamo (0:2); Cocha Cashu (19:7); Río Curanja (1:3); Cuzco Amazónico (8:8); Explornapo (0:1); Genaro Herrera (0:4); Limoncocha (0:3); Panguana (0:50); Río Santiago (0:1); Tambopata (1:1); Teniente López (0:3); Yurimaguas (1:4); total for all localities (30:93).

All specimens have a pale dorsolateral stripe from the posterior corner of the eyelid to almost the end of the urostyle, although it is inconspicuous in specimens that are dorsally very light (e.g., MUSM 9186 and 9195, both from Cocha Cashu). In one specimen (AMNH FS 8689 from the type locality; see fig. 3) the pale dorsolateral stripes broaden medially just behind the eyelids to form the outline of an hourglass pattern. The eyelid is blackish brown in all specimens.

Ventral coloration among adult males is somewhat variable (figs. 3, 5). In most specimens, the throat and chest are stippled gray, but in some (e.g., MUSM 9196 and 15611) the stippling is much heavier, making the throat and chest dark gray or brown (but never solid black). In females, the throat, chest, and medial belly are immaculate or nearly so (very weak stippling often occurs on the chin). In all specimens examined, the belly is more strongly pigmented laterally than medially. In some specimens (e.g., MUSM 9184) the lateral belly ventral (medial) to the ventrolateral stripe is dark brown with whitish spots, whereas in others (e.g., KU 194916) it is stippled brown or gray with a variable number of elongate brown spots.

Thigh coloration is highly variable (figs. 3, 5). Dorsally, thighs are tan or light brown, free of dark markings (e.g., AMNH FS 8689, fig. 3) or with numerous, irregular, small spots or blotches, one or more well-defined blotches, or one well-defined transverse band of variable width. In most specimens, the anterior surface of the thigh exhibits a diffuse pale brown, brown, or black (in dark specimens, e.g., MUSM 15611) stripe from the knee through the groin and continuous with the dark coloration of the flank. A few specimens (e.g., KU 194916) lack a dark anterior thigh stripe; in these, the anterior surface is the same color as the dorsal surface. A flash mark is absent from the groin. The posterior surface of the thigh is gray, pale brown, brown, or dark brown and invariably with minute, diffuse, whitish dots. The white spot on either side of the cloaca that Boulenger (1883) described is present in all well-preserved specimens, although it varies from a prominent, well-defined spot (e.g., AMNH FS 8689) to an inconspicuous narrow line (e.g., MUSM 9184; much of the variation in this character is shown in fig. 5). Thighs are usually ventrally immaculate, although they occasionally have a few diffuse gray or brown specks of pigment.

The dorsal surface of the shank has one poorly to well-defined transverse band in most specimens, although in some (e.g., MUSM 9183) the shank is covered in irregular, dark brown blotches that fail to define a transverse band. Concealed surfaces of the shank are invariably pigmented pale brown or gray (i.e., flash marks absent). The inner surface of the foot is immaculate creamy white, free of melanophores. The plantar surface is brown or gray with creamy white blotches and spots; contact surfaces of tubercles are dark gray. Webbing between Toes III–IV is creamy white or brown.

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[3] Following Edwards (1974b), this structure is often incorrectly referred to as the ‘‘outer tarsal fold’’ (e.g., Duellman and Lynch, 1988; Duellman and Simmons, 1988; Kaiser et al., 1994; Coloma, 1995). At its strongest, this fold runs between the postaxial edge of the base of Toe V and the outer metatarsal tubercle, but it never extends beyond the metatarsal tubercle onto the tarsus.

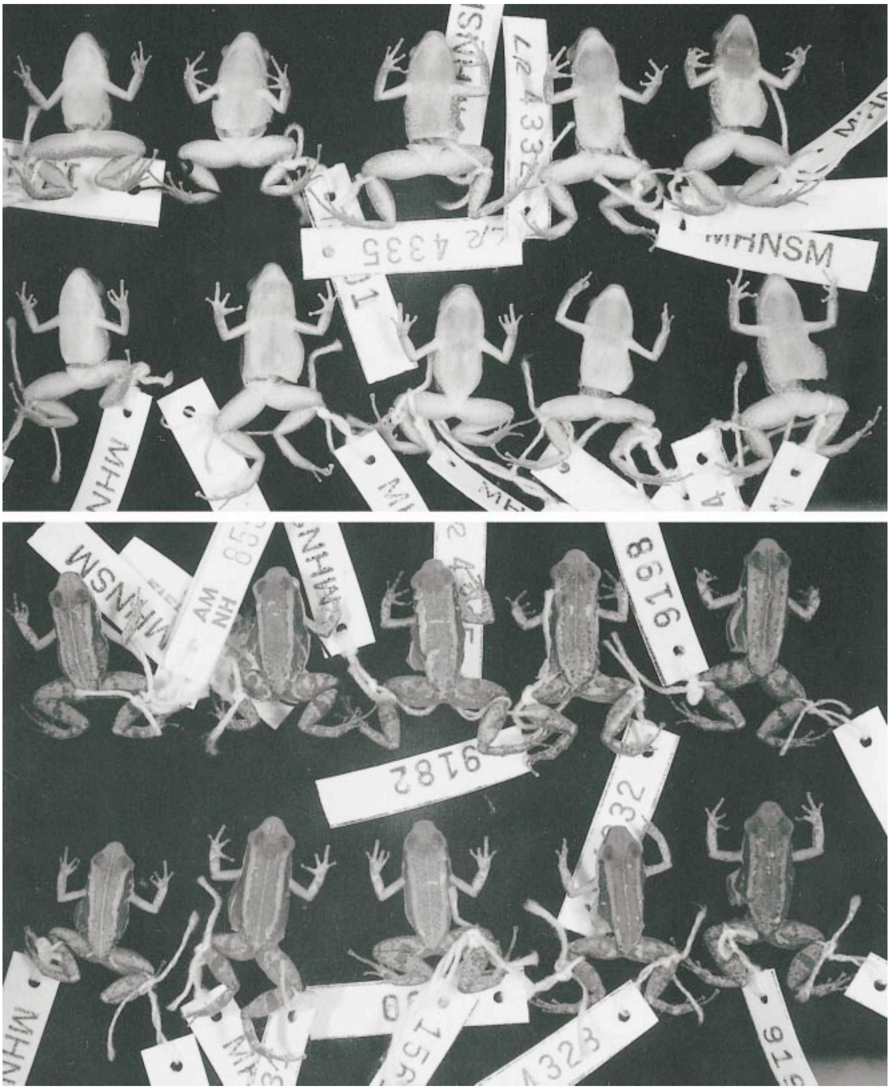

Fig. 5. Variation in ventral and dorsal coloration among adult male *Colostethus trilineatus* from Cocha Cashu. All specimens in top row have only Finger III swollen; those of bottom row have Fingers II and III swollen. From left to right, top row: AMNH 153038, MUSM 9201, MUSM 9184, MUSM 9182, MUSM 9198; bottom row: MUSM 9183, MUSM 9188, MUSM 15618, MUSM 9200, MUSM 9191. Slightly larger than life size.

The arm is dorsally gray or tan with variably expressed darker brown blotches that extend from the anterior and posterior surfaces. The anterior and posterior surfaces of the upper arm have well-defined, dark brown, longitudinal stripes. The anterior stripe extends from near the base of the arm almost to the elbow; the posterior stripe extends from the axilla around the elbow, where it meets the dark brown mottling on creamy white ground of the outer and ventral sides of the forearm. Palmar surfaces are brown.

The flank is dark brown or blackish brown with or without pale flecks and spots (fig. 6). The dark coloration of the flank is delimited ventrally by a moderately to well-defined ventrolateral stripe passing just dorsal to the

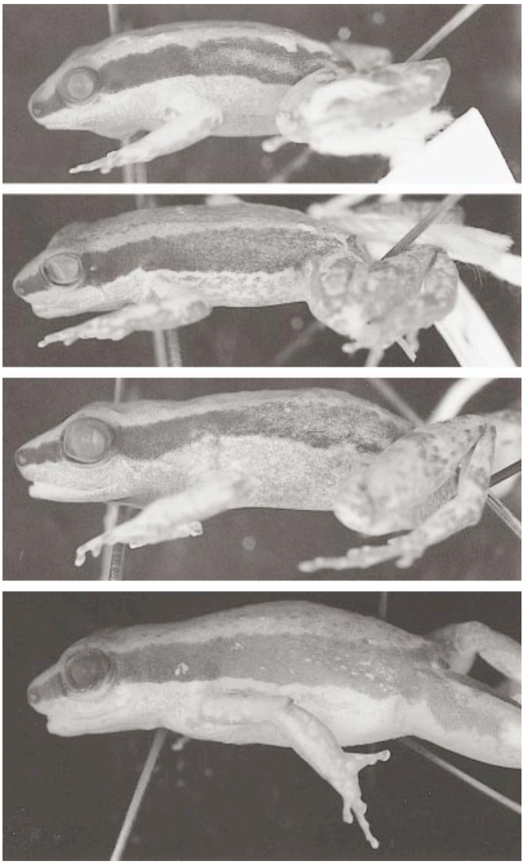

Fig. 6. Lateral view of two similar Amazonian species of *Colostethus*. Note the variation in the pale area anterior to the groin and the distance of the pale ventrolateral stripe from arm. From top to bottom, *C. trilineatus* (AMNH FS 8689 ♂; MUSM 15618 ♂), and *C. melanolaemus* (AMNH FS 11920 ♂; AMNH 114944 ♀). ×2.8.

arm, present in all specimens. Most specimens in all populations have a diffuse pale area anterior to the groin that extends anterodorsad to a point no further than half the distance to the arms (figs. 2 and 6). In some (e.g., MUSM 9201), this pale area includes several diffuse, whitish spots. In a few specimens (e.g., KU 194916), the area anterior to the groin is not obviously lighter than the rest of the flank, but this is probably a preservational artifact, as all well-preserved and living frogs have this pale region (e.g., fig. 2). The dark coloration of the flanks continues anteriad from the eye, through the loreal region, and around the snout (encompassing nares) to form a face mask. Below this, the face is creamy white with gray stippling or a blackish brown stripe along the upper lip (e.g., MUSM 15611). Dark lower lip line absent.

COLOR IN LIFE: Color in life was described for specimens from Teniente López (Duellman and Mendelson, 1995) and Río Curanja (Duellman and Thomas, 1996), and color photographs of Bolivian specimens were published in Gonzalez et al. (1999). Photographs taken by LOR of material from Cocha Cashu (e.g., fig. 2) and Genaro Herrera agree with the published accounts except that the spots on either side of the cloaca and the vertebral stripe are yellowish bronze and the vertebral stripe is bordered by black.

NATURAL HISTORY: *Colostethus trilineatus* is a forest-dwelling species not closely associated with bodies of water. Numerous aspects of its ecology have been reported (usually under the name *C. marchesianus*) by Toft and Duellman (1979), Aichinger (1987), Rodríguez (1992), Duellman and Mendelson (1995), Wild (1996), and Parmelee (1999).

VOCALIZATIONS

AMNH FS 8689 (16.0 mm SVL) was collected at Yurimaguas, the type locality. A recording of this frog (AMNH herpetology reel 272, made by Javier Icochea at 15:18 h on 25 September 1993, 27°C) includes 27 calls in 3.08 min of continuous tape (0.15 calls per sec). The advertisement call (fig. 7) is a series of short, high-pitched peeps. Calls consist of 9–13 notes ($n = 26$, $\bar{x} = 11.2 \pm 0.3$ notes, mode = 10 notes; one obviously anomalous call of four notes is excluded). Call duration is 972–1550 msec ($n = 26$, $\bar{x} = 1260 \pm 29.8$ msec). Detailed data were taken from the first two calls on the tape, constituting 12 and 11 notes, respectively. In both calls, the first two notes are shortest (both 41.8 msec in call 1; 39.5 and 41.0 msec, respectively, in call 2). Similarly, internote duration between the first two notes of both calls is less than half of that of the other notes (25.8 msec in call 1; 29.9 msec in call 2). Video spectrographic scrolling revealed that in 17 of the 27 calls the internote duration between the first two notes is conspicuously less than between the remaining

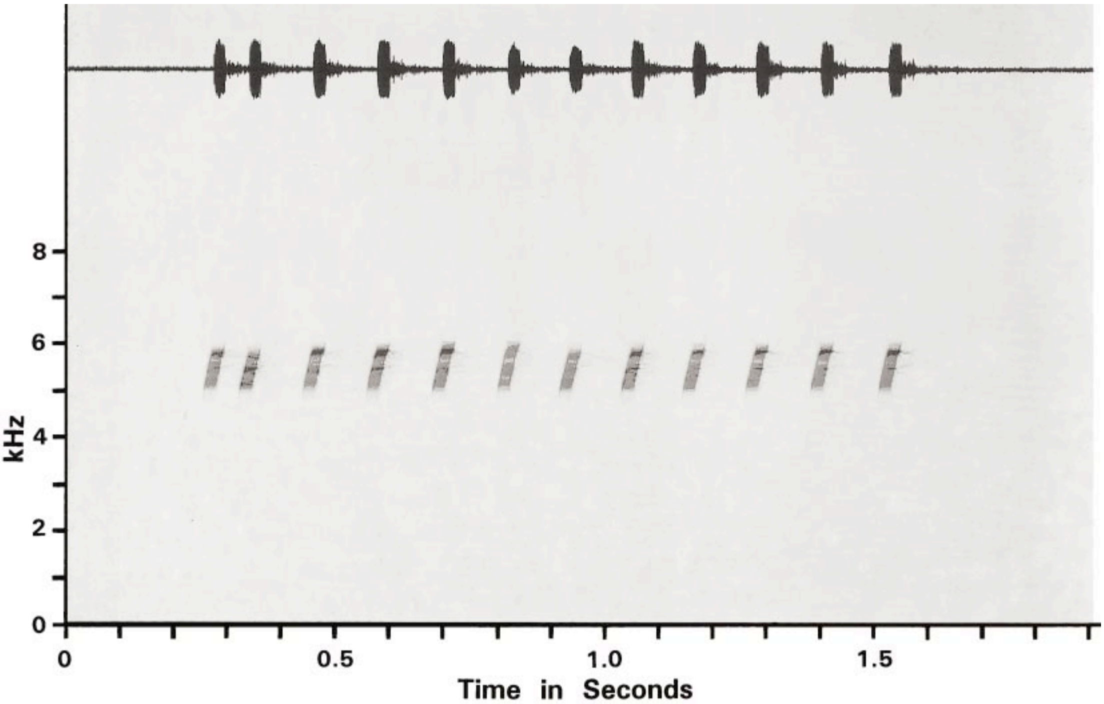

Fig. 7. Narrow-band (59 Hz) spectrogram and waveform of advertisement call of *Colostethus trilineatus* from Yurimaguas, the type locality (AMNH FS 8689).

notes. For the remaining notes, note duration is 43.0–45.3 msec (n = 19, $\bar{x}$ = 43.79 ± 0.15 msec); internote duration is 71.1–88.7 msec (n = 17, $\bar{x}$ = 77.92 ± 1.25 msec). Each note weakly frequency modulated from lower to higher, with emphasized frequencies of the 23 notes between 4920 and 6040 Hz. Minor frequency modulation is detected among the notes of each call, in which notes are emitted at increasing frequencies, then decreasing frequencies, and again increasing frequencies, before terminating at a relatively high frequency.

REMARKS

Colostethus brunneus and *C. marchesianus* have been reported from Peru (Duellman and Toft, 1979; Toft and Duellman, 1979; Schlüter, 1980; Frost, 1985; Rodríguez, 1992; Rodríguez et al., 1993; Rodríguez and Duellman, 1994; Wild, 1996; Parmelee, 1999). However, none of the material we examined is referable to those taxa, and we suspect that previous reports were based on erroneously determined specimens of *C. trilineatus*.

The diffuse, pale region extending from the groin to midway along the flank is located in the same area as the oblique lateral stripe and is presumably homologous with it. However, this pattern does not conform to any of the previously delimited states (i.e., complete from groin to eye, e.g., *C. nubicola* [Dunn, 1924]; broken into series of spots, e.g., *C. agilis* Ruiz-Carranza and Lynch, 1985; partial or incomplete, e.g., *C. kingsburyi* [Boulenger, 1918]), and it is frequently overlooked. It is often difficult to code unambiguously, as it is hard to distinguish from chafing, fading, and other preservational artifacts, or from the white spots and flecks that are roughly uniformly scattered over the flank of many species of *Colostethus*. Nevertheless, all well-preserved and live exemplars of a number of similar species possess this diffuse, pale area on the flank, and we have not noticed it in any species west of the Amazonian slopes of the Andes. In the Amazon basin, we have observed this state in *C. brunneus*, *C. juanii* (in which it is usually quite prominent), *C. trilineatus*, *C. melanolaemus* (named below), and at least five unnamed species.

The discovery of the swollen second finger in some specimens was initially taken as evidence for the recognition of two species. However, related evidence indicates that this interpretation was spurious. Specimens with the swollen second finger were all found in sympatry with specimens that exhibit swelling only of the third finger. Field notes and other data do not indicate differences in microhabitat selection, and the specimens are otherwise indistinguishable (e.g., fig. 5). Similarly, both conditions were found at localities separated by > 700 km (Panguana in the middle portion of the range, and Cocha Cashu and Cuzco Amazónico in the southern portion), and the swollen second-finger morphology was detected only in the three largest samples. The expression of swelling of the third finger is known to vary among males taken in large series (Myers et al., 1991; personal obs., TG), probably as a function of reproductive activity, and it is likely that the swollen second finger would serve the same function and undergo the same kind of variation. This claim is further supported by our observation of apparently continuous variation in the amount of swelling of the second finger (which prevented us from clearly assigning several specimens to either of the morphological classes). It should be noted, however, that swelling of Finger II does not appear to covary with age (inferred from SVL) or other secondary sex characters that often vary with reproductive activity (e.g., throat color; fig. 5).

Several differences in temporal patterning are observed between the vocalizations recorded at the type locality and those reported for Panguana (Schlüter, 1980) and Cuzco Amazónico (Coloma, 1995; De la Riva et al., 1996).[4] Calls recorded at the latter two localities consist of couplets repeated at roughly 200 msec intervals; each note of the couplets has a duration of < 30 msec. Rodríguez and Duellman (1994: 16) report a similar call of "two chirplike notes produced at a rate of about 72 per minute", but no further data are provided. In contrast, the calls recorded at the type locality are composed of single notes (i.e., not couplets) of usually > 40 msec duration, repeated at < 90 msec intervals. Although these differences in amplitude modulation could conceivably indicate the existence of two species, the calls of the three populations are spectrally identical and no significant morphological differences were detected among the specimens examined.[5] It has long been known that signal structure may vary greatly among populations, individuals, and even calls of the same individual (Bogert, 1960; see Juncá, 1998 and Myers et al., 1998, as well as the discussion of *C. juanii*, below, for examples of variation of temporal patterning in dendrobatids). When acoustic samples are small and the differences between them unaccompanied by morphological or other correlates, taxonomic interpretations should be conservative. For this reason, we continue to refer to all these frogs as *C. trilineatus*.

In contrast to the above, another similar species occurs in the same vicinity as *Colostethus trilineatus*, but differs in both temporal and spectral call parameters as well as in morphology. Consequently, we name it

Colostethus melanolaemus, new species

Figures 6, 8–11

HOLOTYPE: MUSM 17741 (field number AMNH FS 11921), an adult male collected

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[4] Köhler and Lötters (1999) also reported calls for *C. trilineatus* and an unidentified species of *Colostethus* from Cobija, Departamento Pando, Bolivia, that are almost identical to those of *Colostethus trilineatus* at Panguana and Cuzco Amazónico.

[5] AMNH FS 8689, the specimen recorded at the type locality, differs from other examined *Colostethus trilineatus* in having an hourglass dorsal color pattern. Although the possibility exists that this specimen is not conspecific with the other material taken at the type locality, in all other respects it falls well within the range of variation seen in other populations of *C. trilineatus*, and this hourglass dorsal pattern occurs commonly as part of the repertory of intraspecific variation in numerous species of *Colostethus*, including *C. brunneus* (Cope, 1887; Morales, 1994; personal obs., TG), *C. juanii* (Morales, 1994; personal obs., TG), *C. mandelorum* Schmidt, 1932 (Rivero, "1982" [1984]; La Marca, 1993), and *C. sanmartini* Rivero, Langone, and Prigioni, 1986. Gonzalez et al. (1999: 185, fig. 5A) also provide a photograph of an unidentified specimen with this dorsal pattern. Based on available data, we are unable to conclude that more than one species occurs at the type locality of *C. trilineatus*.

by Lily O. Rodríguez, 11 March 1999, Explornapo Lodge, ACEER, Lower Río Napo near Quebrada Sucusari, Departamento Loreto, Peru, GPS coordinates 72°55′W, 3°14′S.

PARATYPES: MUSM 15607, collected by Lily O. Rodriguez, 24 March 1993 at the type locality. AMNH FS 11920 and AMNH FS 11922, collected by Lily O. Rodríguez, 10–11 March 1999 at the type locality. AMNH 114924–114945, collected by Borys Malkin, 28 March–9 April 1970 at Estirón, Río Ampiyacu, Departamento Loreto, Peru.

ETYMOLOGY: The specific epithet is an adjective derived from the Greek *melanos* (black) and *laemos* (throat), in reference to the pure black throat of adult males of this species.

DIAGNOSIS: A small species (males to about 23 mm SVL, females to about 24 mm SVL); Finger III weakly swollen in adult males; throat black in adult males, immaculate white in females; testes white (unpigmented) in adult males; Toes II–IV basally webbed; dorsolateral stripe present; oblique lateral stripe present as a diffuse, inconspicuous, pale region or group of small spots that extends from the groin to midway along the flanks; ventrolateral stripe present (poorly defined); one subarticular tubercle on Finger IV; median lingual process absent; cloacal tubercles absent; anal sheath absent; black armband absent.

Colostethus melanolaemus is most similar to *C. trilineatus* and *C. juanii*.[6] It differs from both in having (1) throat pure black in adult males (gray in *C. trilineatus*; gray stippling concentrated into spots, mottling, or reticulated pattern in *C. juanii*), (2) significantly greater adult SVL (tables 1, 2), and (3) weakly swollen Finger III in adult males (strongly swollen in *C. trilineatus*; not swollen in *C. juanii*). *Colostethus melanolaemus* further differs from *C. trilineatus* in having an advertisement call of 1–6 notes, mode = 4 (couplets or 9–13 notes, mode = 10, in *C. trilineatus*), and emphasized frequency of 3840–4560 Hz (emphasized frequency 4920–6040 Hz in *C. trilineatus*). *Colostethus melanolaemus* is further diagnosed from *C. juanii* in having significantly shorter internote duration (*C. melanolaemus*: n = 11, range = 123.4–236.7, $\bar{x}$ = 153.15 ± 10.26 msec; *C. juanii*: n = 11, range = 271.9–468.7 msec, $\bar{x}$ = 389.12 ± 18.89 msec; P = 0.0001).

Fig. 8. A specimen of *Colostethus melanolaemus* from the type locality. [From color transparency by LOR.]

MEASUREMENTS OF HOLOTYPE (in mm): The holotype, MUSM 17741, is an adult male with vocal slits and enlarged, white (unpigmented) testes. SVL 22.7; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow, 5.2; hand length from proximal edge of palmar tubercle to tip of Finger III, 5.6; shank length from outer edge of flexed knee to heel, 10.6; foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV, 9.7; head width between angle of jaws, 7.3; head length diagonally from corner of mouth to tip of snout, 7.2; eye length from posterior to anterior corner, 3.0; eye to naris distance from anterior corner of eye to center of naris, 2.3; distance between centers of nares, 3.2; snout length from anterior corner of eye to tip of snout, 3.8; interorbital distance, 2.2; greatest diameter of tympanum, 1.3.

DESCRIPTION OF TYPE SERIES

MORPHOLOGY: Adult males 21.1–23.4 mm SVL (n = 11, $\bar{x}$ = 22.16 ± 0.22). Adult females 21.3–23.6 mm SVL (n = 14, $\bar{x}$ = 22.24 ± 0.22). Ventral surfaces smooth. Dorsal surfaces smooth or weakly granular, with

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[6] Four specimens (AMNH 114946–114949) of an undescribed species of *Colostethus* were collected in sympatry with *C. melanolaemus* at Estirón, Río Ampiyacu. This species can be distinguished from *C. melanolaemus*, in part, by its smaller size and paler throat in adult males. We prefer to await additional, better preserved material to thoroughly describe and name this species.

low, conical tubercles scattered over posterior part of body and dorsal surfaces of thighs and shanks. Weak bulge present immediately posterior to rictus.

Head width between angle of jaws 31–34% of SVL, 0.96–1.11 times head length. Interorbital distance 26–30% of head width. Snout sloped, gently rounded or almost truncate in dorsal aspect, bluntly rounded in profile, protruding beyond jaws (fig. 6). Loreal region flat, vertical or weakly sloped outward to lips. Canthus rostralis sharply rounded, well defined. Eye 40–48% of head length. Eye-naris distance 56–61% of snout length and 61–77% of eye length. Nares directed posteriorly in profile, protuberant in dorsal aspect. Tympanum small; greatest diameter 30–43% of eye length. Teeth on maxillary arch straight, moderately long, not curved and fanglike.

Hand length 20–25% of SVL, 0.89–1.09 times forearm length. Relative lengths of fingers III > I > II ≥ IV, with Finger II usually longer than IV. Finger IV extended to midpoint between proximal and distal subarticular tubercles of Finger III in most specimens; Finger IV extended to base of distal subarticular tubercle in a few specimens, in which Fingers II and IV are subequal (e.g., MUSM 15607; fig. 9). All fingers free of lateral fringes, with only faint trace of lateral keeling visible under high magnification. Metacarpal fold very weak, forming small, inconspicuous tubercle proximally. One well defined subarticular tubercle on Fingers I, II, and IV; two on Finger III. Palmar tubercle round, low. Thenar tubercle weak, fairly small, slightly elongate. Digital discs weakly expanded. Each finger with pair of prominent dorsal scutes.

Condition of Finger III sexually dimorphic. In adult males, preaxial surface of Finger III with glandular appearance, thicker and "meatier" than other fingers, often with irregular outline in palmar view, enlarged, with subarticular tubercles closer to postaxial than preaxial side of finger (i.e., Finger III of males weakly swollen along entire length). Preaxial surface unexpanded and nonglandular in females.

Shank and foot length 41–47 and 38–46% of SVL, respectively. Relative lengths of appressed toes IV > III > V > II > I (fig. 9). Basal webbing between Toes II–III and III–IV; no webbing between IV–V; preaxial lateral fringe of Toe II well-defined but not expanded into webbing (webbing formula **II** 1½–3½ **III** 2½–4 **IV,** following Myers and Duellman, 1982). Weak keels barely discernible on each edge of Toe V, but well-developed fringes present on both edges of all other toes. Weak outer metatarsal fold present, forming weak tubercle proximally in some specimens (e.g., MUSM 17741). Tarsal keel well defined, curved proximally, distally faint but extended to reach inner metatarsal tubercle. Toe discs weakly expanded, each with well-defined dorsal scutes. One subarticular tubercle on Toes I and II, two on III and V, three on IV; all well-defined and protuberant except proximal tubercle on right Toe IV, which is less prominent but always present. Round, protuberant outer metatarsal tubercle and elliptical inner metatarsal tubercle separated by slight bulge.

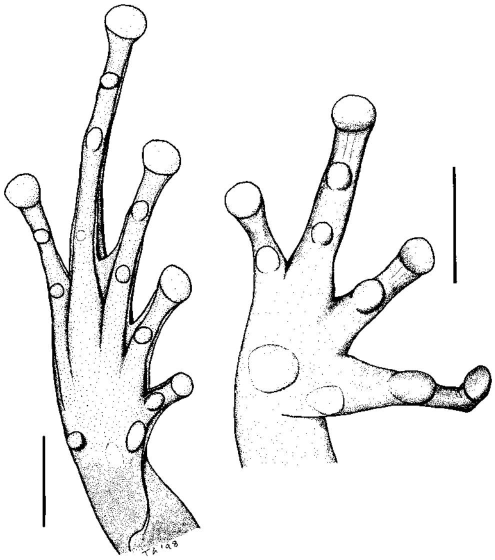

Fig. 9. Right foot and hand of *Colostethus melanolaemus* (MUSM 15607). Scale bars = 2 mm.

COLOR IN PRESERVATIVE: The dorsum (fig. 10) is grayish brown. The dorsolateral stripe is stippled gray. In males, the throat is conspicuously solid black, and the chest, most of the belly, and the ventral surface of the upper arm are all stippled gray. Females are ventrally immaculate. Ventral surfaces of

Fig. 10. Ventral and dorsal views of adult male *Colostethus melanolaemus* from the type locality. From left to right, top row: AMNH FS 11920, MUSM 17741 (holotype); bottom row: AMNH FS 11922, MUSM 15607. ×2.8.

legs and groin are free of pigmentation in both sexes. Palmar and plantar surfaces are brown. Contact surfaces of tubercles are gray.

The dorsal thigh color is pale brown, with one dark brown or gray crossband or spot that aligns with a similar band or spot on the dorsal surface of the shank. The anterior surface of the thigh has a diffuse, dark brown stripe from near the knee through the groin and continuous with the dark coloration of the flank. A conspicuous, curved, whitish spot occurs on each side of the cloaca. The shank is dorsally pale brown with a well-defined dark brown transverse band. Concealed surfaces of the thigh (= posterior surfaces of thigh) and shank are dark brown with minute whitish flecks and spots. The preaxial portion of each foot is whitish, free of melanophores. The foot is dorsally brown with one or more dark brown blotches. The posterior surface of the tarsus and plantar surface are dark brown. Contact surfaces of tubercles and digital discs are gray.

The arm is tan or gray with scattered darker spots and blotches. The elbow is conspicuously dark brown. The anterior and posterior surfaces of the upper arm are darker in MUSM 15607, forming dark brown longitudinal stripes.

A broad, blackish brown stripe extends along the flank (fig. 6), through the loreal region, and around the tip of the snout (encompassing the nares). Along the flank, this dark coloration is bordered ventrally by a narrow, moderately defined, white ventrolateral stripe that extends from the groin, above the arm, to the posteroventral border of the eye. Below the ventrolateral stripe, the flank is stippled gray or pale brown, as is the face below the blackish brown face mask. The oblique lateral stripe is present as a diffuse, inconspicuous, pale region or group of small spots extending from the groin to midway along the flank (fig. 6).

NATURAL HISTORY: The four specimens from the type locality were collected in the forest along a trail leading from the Explornapo Lodge to the Amazon Center for Environmental Education and Research (ACEER). Like *Colostethus juanii* and *C. trilineatus*, *C. melanolaemus* occurs near streams but extends at least 25 m into the forest, therefore differing from strictly riparian species confined to the streamside, such as *C. abditaurantius* and *C. imbricolus*. *Colostethus melanolaemus* and *C. trilineatus* both occur at the type locality of *C. melanolaemus* near the junction of the Río Napo and the much smaller Río Sucusari.

VOCALIZATIONS

MUSM 15607 (21.5 mm SVL) was recorded for audiospectrographic analysis by Lily O. Rodríguez at 08:00 h from leaf litter at the type locality (AMNH herpetology reel 271). Two uninterrupted sequences of calls were recorded approximately 3–4 m from the frog; temperature data were not taken. The first series includes 14 calls (72 notes) in 27 sec (0.52 calls per sec; 5.14 notes per sec); the second section of tape includes 39 calls (140 notes) in 71 sec (0.28 calls per sec; 1.97 notes per sec). Temporally, calls are highly variable. Each call consists of 1–6 notes ($\bar{x}$ = 3.6 ± 0.2 notes; mode = 4 notes) separated by intervals of variable duration. Similarly, the time between calls varies from a few to many seconds, with no apparent pattern. Signal interference due to conspecific call overlap obscures many of the temporal parameters in most calls. Nevertheless, examination of isolated calls reveals that the signal is nonpulsatile.

Detailed data were taken from one call composed of four notes (call duration = 751.2 msec), two of five (844.8 msec and 843.7 msec, respectively), and one single-note call (54.7 msec). As shown in figure 11, emphasized frequencies lie between 3840–4560 Hz. Notes are weakly frequency modulated from lower to higher. Note duration ranges from 47.3–59.8 msec (n = 15, $\bar{x}$ = 53.98 ± 1.12 msec). Internote duration ranges from 123.4–236.7 msec (n = 11, $\bar{x}$ = 153.15 ± 10.76 msec). No pattern of spectral or amplitude modulation within or among calls was discerned.

Throughout the recording, the voucher specimen chorused with another male, heard in the background. Either of the two males initiated calling, but the background male consistently called at a slightly faster rate and emitted longer calls (up to 14 notes per call).

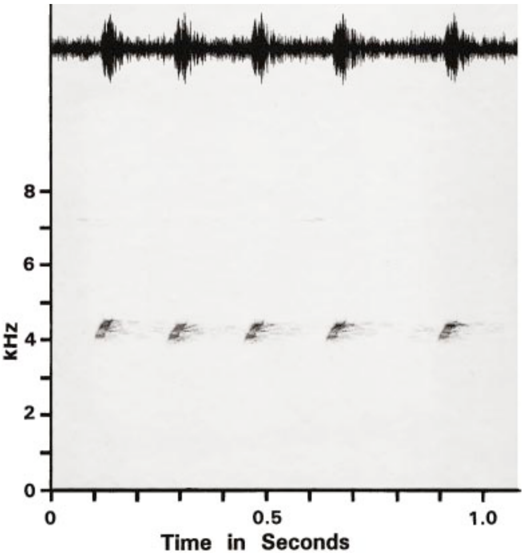

Fig. 11. Narrow-band (59 Hz) spectrogram and waveform of advertisement call of *Colostethus melanolaemus* (MUSM 15607).

REMARKS

Many species of dendrobatids that are <19 mm SVL lack the distal subarticular tubercle on Finger IV and have Fingers IV ≤ II (TG, unpublished data). However, *Colostethus melanolaemus* is the first species larger than 19 mm that we have seen with this morphology, and it indicates that finger length and number of subarticular tubercles vary independently of body size.

As described above, we coded Finger III as weakly swollen in adult male *Colostethus melanolaemus*. In some dendrobatids the swelling is conspicuous, either exaggerated distally (e.g., *C. nubicola*) or along the entire length of the digit (e.g., *C. trilineatus*). In others, including *C. melanolaemus*, the swelling of Finger III is much more subtle, and in some cases the only way to unambiguously code this character is to compare directly well-prepared, sexually active males and females.

Although the call of *Colostethus melanolaemus* differs in a number of aspects from that of *C. trilineatus*, it is nearly indistinguishable from the temporally highly variable call of *C. juanii*. Insofar as the call of *C. juanii* has not been described previously, and it bears on the diagnosis of *C. melano-*

laemus, we describe it here. Call data for *C. juanii* derive from recordings TG 9903 (ICN 44487, 20.8 mm SVL, recorded at 09:45 h, 15 August 1999, air temperature 21.9°C, microphone 60 cm from frog; called from atop a moss-covered boulder immediately adjacent to the stream, overhung by vegetation) and TG 9904 (ICN 44486, 20.3 mm SVL, recorded at 08:20 h, 16 August 1999, air temperature 21.4°C, microphone 25 cm from frog; frog perched on an almost horizontal portion of a moss-covered tree trunk of about 7 cm diameter, approximately 4 m from the stream up a very steep-walled canyon), both made by TG at Villavicencio (type locality; see appendix for details), copied on AMNH herpetology reel 290. Although these two frogs called out in the open, most calling *C. juanii* were secluded in the leaf litter and other debris from this secondary forest. Calling began at daybreak and abruptly tapered off at around 09:00 h, with only sporadic calling produced infrequently throughout the rest of the daylight hours.

TG 9903 includes two continuous trains of notes separated by a pause of 19 sec. The first continuous train consists of 93 calls (175 notes) in 2.95 min (0.52 calls per sec; 0.99 notes per sec) emitted as single notes, couplets, triplets, and quadruplets; the second train includes 20 calls in 1.17 min (0.28 calls per sec), all produced as single notes. TG 9904 includes one single train of 90 calls (138 notes) in 4.0 min (0.38 calls per sec; 0.58 notes per sec), a second train of 16 calls (32 notes) in 50 sec (0.32 calls per sec; 0.64 notes per sec), and a third train of 63 calls (140 notes) in 3.5 min (0.30 calls per sec; 0.67 notes per sec); the three trains on TG 9904 are all mixtures of single notes, couplets, triplets, and quadruplets. The time between the second and third trains is 63 sec (time between the first and second trains undetermined). Of 284 calls pooled from both recordings, 41.9% are single notes, 35.2% are couplets, 17.6% are triplets, and 5.3% are quadruplets ($\bar{x}$ = 1.86 ± 0.05 notes per call). No pattern was detected in the sequence of single notes, couplets, triplets, and quadruplets, except that trains begin with a series of single notes. Notes vary continuously from being nonpulsatile to consisting of two or three pronounced pulses.

Detailed analysis was carried out on the first 23 notes of the second train of recording TG 9904 (fig. 12). The first three notes are notably softer than the rest of the train, and they increase in duration (37.5, 46.9, and 62.5 msec, respectively) and emphasized frequency (3560–3720, 3600–3880, and 3720–4080 Hz, respectively); as such, they appear to be typical ''warm-up'' calls and are excluded from further analysis. The remaining 20 notes were emitted in 10 calls as two single notes (duration of each 59.4 msec), six couplets (duration 478.1–581.3 msec), one triplet (duration 1093.6 msec), and one quadruplet (duration 1256.2 msec; fig. 12). Signals are frequency modulated from lower to higher, with minimum emphasized frequencies of 3880–4160 Hz and maximum emphasized frequencies of 4120–4560 Hz. Note duration is 53.1–68.8 msec (n = 20, $\bar{x}$ = 62.03 ± 0.94 msec). Time between calls (groups of notes) is 2–4 sec, and time between notes within a single call (internote duration) is 271.9–468.7 msec (n = 11, $\bar{x}$ = 389.12 ± 18.89).

***Colostethus alessandroi*, new species**

Figures 13–18

HOLOTYPE: MUSM 15609 (field number AMNH FS 11862), an adult male collected 17 January 1998 by Lily O. Rodríguez, Alessandro Catenazzi, and Fredy Qertehuari at San Pedro, Cosñipata, Paucartambo, Departamento de Cuzco, Peru, GPS coordinates 13°03′S, 71°32′W, 1480 m. The specimen was taken from atop a rock beside a stream.

PARATYPES: AMNH 157004, collected with the holotype. AMNH 159110, MUSM 17737, collected 21–22 February 1999 by Alessandro Catenazzi at the type locality. MUSM 15608, collected 23 June 1994 by Fonchii Chang 3 km from Pueblo San Gabán, Departamento de Puno, Peru, 13°27′S, 70°27′W, ca. 820 m.

ETYMOLOGY: The specific epithet is a patronym for Alessandro Catenazzi in recognition of his field studies of the Peruvian herpetofauna.

DIAGNOSIS: A small species (adult males to roughly 22 mm SVL, adult females unknown); Finger III swollen in adult males; venter stippled pale gray; testes white (un-

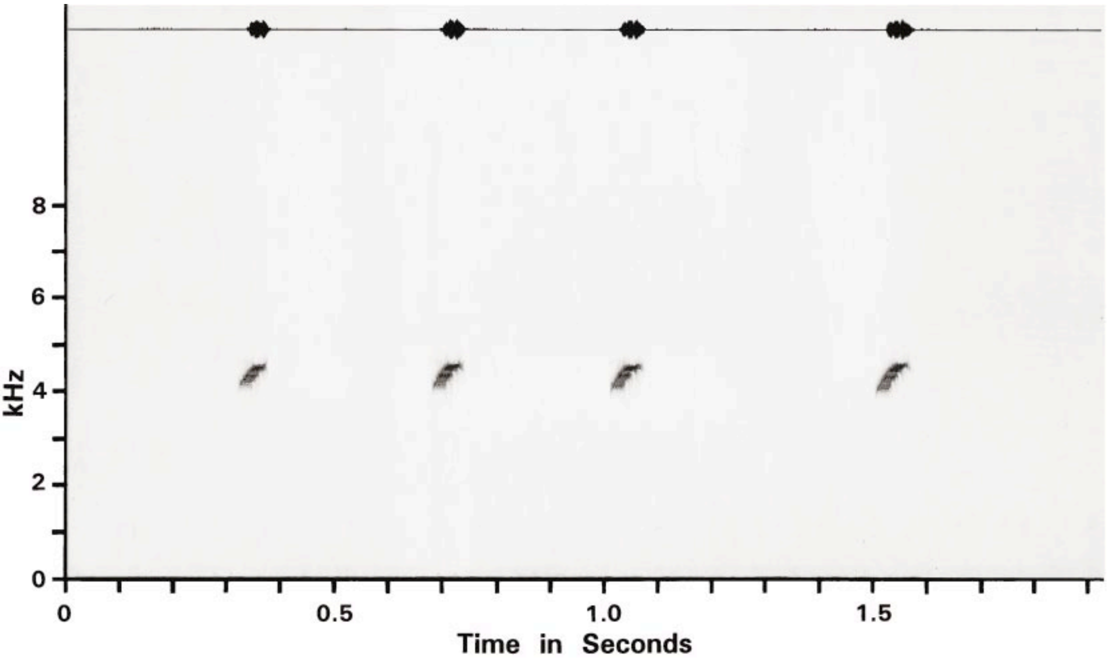

Fig. 12. Narrow band (59 Hz) spectrogram and waveform of advertisement call of *Colostethus juanii* (ICN 44486). This is the first quadruplet of the second train of recording TG 9904.

pigmented) in adult males; toes moderately webbed; dorsolateral stripe present; oblique lateral stripe present as a pale region or group of one or more elongate spots near the groin; ventrolateral stripe present; median lingual process absent; cloacal tubercles absent; anal sheath absent; black armband absent.

Colostethus alessandroi is most similar to *C. mcdiarmidi* Reynolds and Foster, 1992, but differs in having (1) more extensive toe webbing (fig. 14); (2) a darker venter (usually; fig. 15); (3) slightly smaller adult male SVL (*C. alessandroi* = 21.3–22.1 mm; *C. mcdiarmidi* = 22.5–24.3 mm); (4) different dorsal coloration (*C. alessandroi* lacks discrete light spots on the posterior dorsum and has darker, more diffuse dorsolateral stripes and darker thigh coloration; fig. 16); (5) pro-

Fig. 13. *Colostethus alessandroi* AMNH 157004 (SVL = 21.3 mm). (From color transparency by Alessandro Catenazzi.)

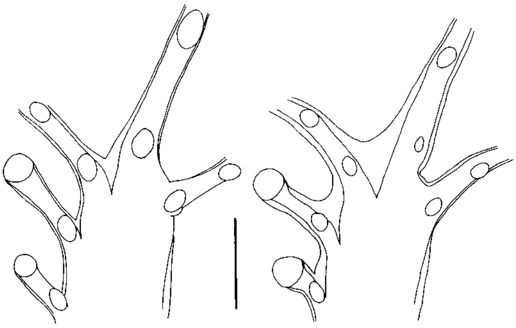

Fig. 14. Plantar view of feet with toes splayed. Left: *C. mcdiarmidi* (holotype USNM 257805). Right: *C. alessandroi* (AMNH 157004). Scale bar = 2 mm.

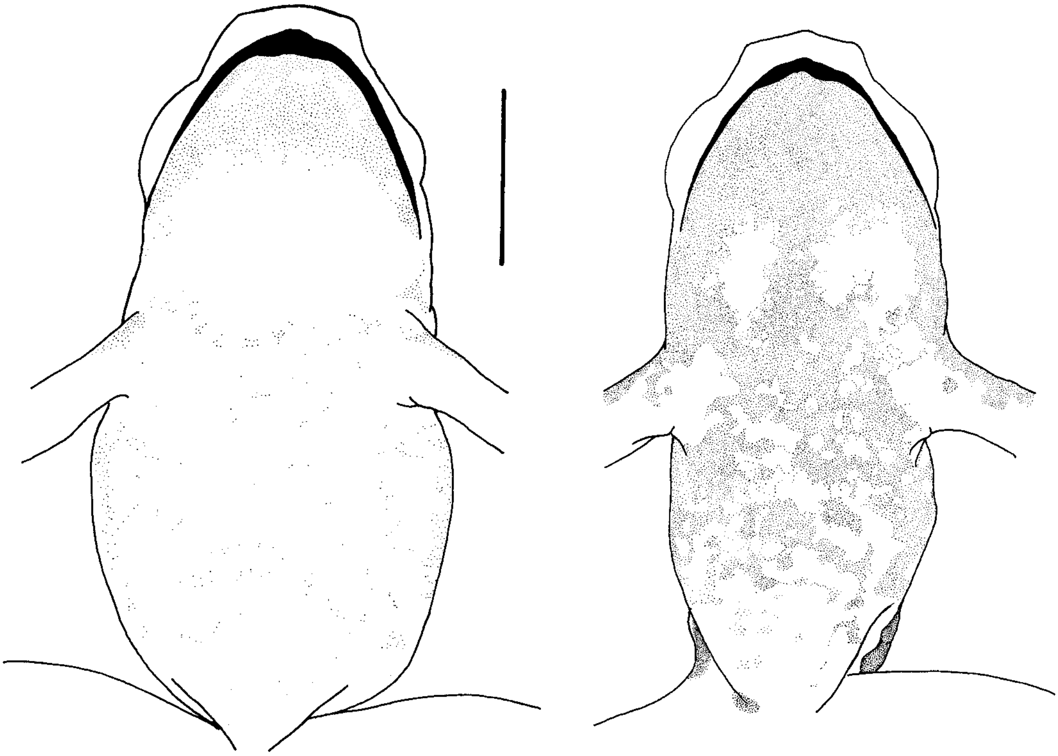

Fig. 15. Ventral view of adult males of *Colostethus mcdiarmidi* holotype USNM 257805 (left) and *C. alessandroi* AMNH 157004 (right). Scale bar = 5 mm.

portionately longer shanks (shank length/SVL = 0.46–0.50 in *C. alessandroi*, 0.43–0.46 in *C. mcdiarmidi*); and (6) slightly smaller tympana, both absolutely (1.1–1.3 mm in *C. alessandroi*, 1.5–1.8 mm in *C. mcdiarmidi*) and proportionately (e.g., tympanum/eye = 0.37–0.41 in *C. alessandroi*, 0.45–0.56 in *C. mcdiarmidi*). Finger III is swollen in adult males of both species (contra Reynolds and Foster, 1992; fig. 17).

Colostethus kingsburyi, from northern Peru and Ecuador, is most easily distinguished from *C. alessandroi* by lacking webbing and having a conspicuous, incomplete oblique lateral stripe (see photo in Coloma, 1995: plate 1C) and a black venter with pale reticulations or irregular spots in adult males.

MEASUREMENTS OF HOLOTYPE (in mm): The holotype MUSM 15609 is an adult male with vocal slits and enlarged, white (unpigmented) testes. SVL 22.0; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow, 4.7; hand length from proximal edge of palmar tubercle to tip of Finger III, 5.8; shank length from outer edge of flexed knee to heel, 10.2; foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV, 9.6; head width between angle of jaws, 7.6; head length diagonally from corner of mouth to tip of snout, 7.0; eye length from posterior to anterior corner, 3.0; eye to naris distance from anterior corner of eye to center of naris, 2.0; distance between centers of nares, 3.0; snout length from anterior corner of eye to tip of snout, 3.9; interorbital distance, 2.3; greatest diameter of tympanum, 1.1.

DESCRIPTION OF TYPE SERIES

The type series consists of five specimens, four adult males with enlarged, granular, white (unpigmented) testes, and one subadult female.

MORPHOLOGY: Males 21.3–22.1 mm SVL ($n = 4$, $\bar{x} = 21.90 \pm 0.20$ mm). Adult fe-

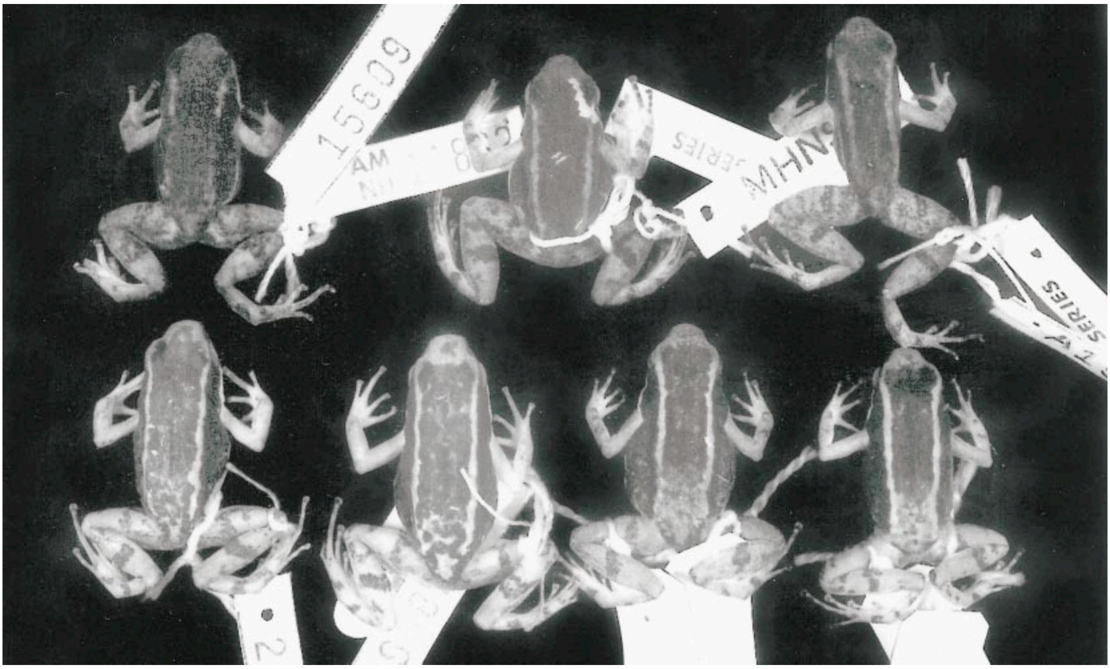

Fig. 16. Dorsal view of similar species of *Colostethus*. From left to right, top row: *C. alessandroi* MUSM 15609 (♂), MUSM 15608 (♂), AMNH 157004 (♂); bottom row: *C. mcdiarmidi* USNM 257805 (♂), USNM 257806 (♀), NKA 3712 (♀), NKA 3708 (♂). ×1.3.

males unknown (subadult female MUSM 17737 is 23.4 mm SVL). A few small, low, weak tubercles scattered over eyelids, lower back, and upper surfaces of legs. A pair of elongate preaxilar tubercles extended toward ventral edge of tympanum. Cloacal tubercles absent. Ventral surfaces smooth.

Head width between angle of jaws 34–35% of SVL and 1.05–1.09 times head length. Interorbital distance 30–35% of head width. In profile, snout gently rounded above and bluntly pointed, protruding beyond jaws. In dorsal aspect, snout bluntly pointed. Loreal region flat and weakly sloping outward to lip. Canthus rostralis sharply rounded and well defined. Eye length 43–48% of head length. Eye-naris distance 51–57% of snout length and 63–67% of eye length. Nares directed posteriorly in profile; protuberant in dorsal aspect. Tympanum small, its greatest diameter 37–41% of the eye length. Teeth on maxillary arch straight, moderate in length, not curved and fanglike.

Hand length (fig. 17) 26–28% of SVL, 1.11–1.23 times forearm length. Relative

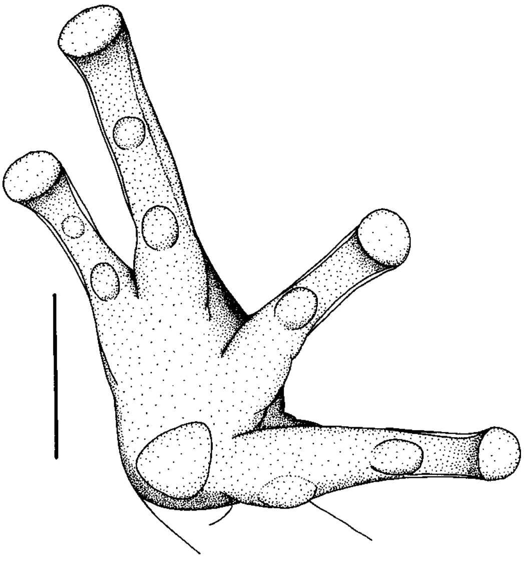

Fig. 17. Palmar view of right hand of *Colostethus alessandroi* (AMNH 157004). Scale bar = 2 mm.

lengths of appressed fingers III > IV > I > II. All fingers with well-defined keellike lateral fringes, most prominent distally. Metacarpal fold short. A single subarticular tubercle on Fingers I and II, two on Fingers III and IV; distal tubercle of Finger IV diffuse, all others well defined and protuberant. Palmar tubercle subtriangular and well defined. Thenar tubercle elongate, small, poorly defined. Digital discs weakly expanded. Paired scutes on dorsal surface of each disc prominent. Preaxial side of Finger III swollen along entire length in adult males.

Shank length 46–50% of SVL. Foot length 42–47% of SVL. Relative lengths of appressed toes IV > III > V > II > I. Well-developed webbing between all toes except Toes IV–V (webbing formula **I** 1½–2 **II** 1½–3 **III** 2½–3½ **IV**; fig. 14). Well-developed fringes on both edges of all toes. Weak outer metatarsal fringe present, as is curved tarsal keel. Toe discs weakly expanded with well-defined scutes on dorsal surface of each. One subarticular tubercle on Toes I and II, two on III and V, and three on IV; proximal tubercle on Toe III smaller than others and offset from midline. Inner metatarsal tubercle round, outer metatarsal tubercle elliptical, both well developed.

COLOR IN PRESERVATIVE: Dorsal coloration (figs. 13, 16) is dark gray to black, with minute pale spots scattered over the dorsum. The snout is somewhat paler than the surrounding area. A diffuse, gray dorsolateral stripe extends from the posterior corner of the eyelid to the pelvic region (broken and inconspicuous posterior to the level of the arms in MUSM 15609).

Ventral coloration is somewhat variable. In all, the throat, chest, and belly have gray stippling (fig. 15). In MUSM 15608 the stippling on the belly is limited to a few fairly discrete spots, but the venter is still darker than in *C. mcdiarmidi*. In AMNH 159110 the venter is much more sparsely pigmented than in other specimens, similar to *C. mcdiarmidi*. The subadult female also has extensive ventral stippling.

Thigh coloration is variable. Dorsally, the thigh is gray with one diffuse dark gray or blackish transverse band of variable width and numerous poorly defined dark gray and black blotches and spots (fig. 16). The anterior surface of the thigh has a diffuse dark gray or black stripe from the knee to the groin. The groin appears to be free of flash marks. The posterior surface of the thigh is gray and black with minute, diffuse whitish spots and flecks. A conspicuous white spot is present on each side of the cloaca. The thigh is ventrally immaculate.

The dorsal surface of the shank has one or two blackish transverse bands and numerous diffuse dark blotches and spots. The concealed surface of the shank is pale, free of melanophores. The inner surface of the foot is immaculate creamy white or faintly stippled pale gray; the plantar surface is gray with creamy white blotches and spots. Toe webbing is immaculate or stippled gray.

The dorsal surface of the arm is gray with variably expressed darker blotches. The anterior surface of the arm is also gray in AMNH 157004 and MUSM 15608, but the holotype (MUSM 15609) has a black spot at the base of each arm and a very weak, darker gray longitudinal stripe. The posterior surface of the arm is uniform gray, fading proximally. The arm is ventrally immaculate. The palmar surface is gray.

The flank is black with an inconspicuous paler area or one or more elongate spots near the groin. The dark coloration of the flank is delimited ventrally by a poorly defined, pale ventrolateral stripe consisting of a wavy stripe or series of elongate spots. In ventral view, the lateral portions of the belly (i.e., medial and/or ventral to the ventrolateral stripe) are stippled gray.

The black coloration of the flanks continues anteriad through the loreal region and around the snout (encompassing the nares). Below this the face is stippled gray.

COLORATION IN LIFE: AMNH 157004 (fig. 13) was greenish brown on the dorsum and flanks. The arms and legs had a yellowish tinge, especially the posteroproximal surface of the upper arm. The dorsolateral stripe was pale brown with a bronze tinge anteriorly. The iris was black with golden flecks with a conspicuous golden ring around the pupil.

NATURAL HISTORY: *Colostethus alessandroi* is riparian. All the specimens collected to date were taken from habitats in early stages of succession. Males were observed calling beside streams, perched on moss-cov-

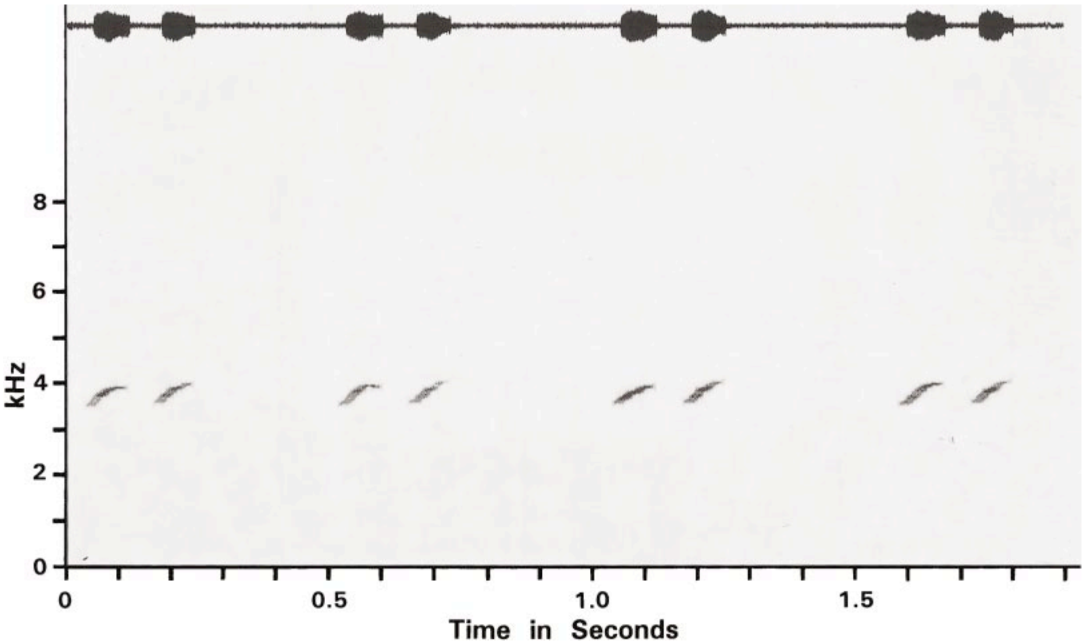

Fig. 18. Narrow-band (59 Hz) spectrogram and waveform of advertisement call of *Colostethus alessandroi* from the type locality.

ered rocks or fallen vegetation, or hidden among rocks and vegetation. Calling activity was greatest in early morning and tapered off by midday, although it also was observed to continue into the afternoon, especially during the rainy season.

VOCALIZATIONS

An uncollected individual was recorded by Alessandro Catenazzi at a creek at the type locality at 10:00 h on 21 February 1999, 17.4°C (AMNH herpetology reel 289). Although the specimen evaded capture, it was clearly observed calling from a moss-covered rock overhung by tree roots; many other specimens were also observed calling, and all emitted the same vocalization. Data were taken from a continuous train of 321 couplets and two single notes in 1.40 min of continuous tape. Couplets are produced rhythmically at an average rate of 1.58 couplets per sec. Detailed data were taken from the first 35 vocalizations of this series; the two single notes were pooled with the first notes of couplets.

The duration of the first note of each couplet is significantly longer than the second note ($P = 0.0001$); the first note ranges from 84.4–103.1 msec ($n = 35$, $\bar{x} = 91.96 \pm 0.62$ msec), whereas the second note is 75.0–87.5 msec ($n = 33$, $\bar{x} = 81.06 \pm 0.64$ msec). Internote duration is 34.4–53.1 msec ($n = 33$, $\bar{x} = 46.69 \pm 0.65$ msec). Time between couplets is 212.5–596.9 msec ($n = 33$, $\bar{x} = 365.4 \pm 19.6$ msec). Notes are weakly or nonpulsatile.

Spectral energy is concentrated between 3400–4320 Hz with the greatest energy peak at 3720–4160 Hz ($n = 68$, $\bar{x} = 3881 \pm 10$ Hz); all but four of the 35 calls exhibit greatest energy peaks below 4.0 kHz. Each note is strongly frequency modulated from lower to higher (fig. 18). The two notes of each couplet overlap almost completely in all spectral parameters and are only statistically distinguishable in that the minimum frequency of the first note is slightly higher than the second note (first note: $n = 35$, $\bar{x} = 3512 \pm 9$ Hz; second note: $n = 33$, $\bar{x} = 3484 \pm 9$ Hz; $P = 0.0351$).

REMARKS

Given the overall morphological similarity and geographic distributions of *Colostethus* *alessandroi* and *C. mcdiarmidi*, it is likely that they are closely related. Indeed, the possibility exists that they are geographic variants of a single species, such as extremes in a cline. However, although few specimens are presently available, we compared directly equivalent semaphoronts (adult males) from several localities and found no evidence of clinal variation along either a latitudinal or altitudinal gradient,[7] and a number of characters distinguish the two groups. Additional specimens, especially from intermediate localities, are required to further assess intraspecific variation and test our hypothesis. Similarly, the inclusion of additional lines of evidence (e.g., vocalizations, osteology, DNA sequence data) could further elucidate this problem, although failure to discover differences in them would not necessarily prove these populations to be conspecific.

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[7] The specimens of *Colostethus alessandroi* were obtained from localities at 1480 m and 820 m, separated by over 100 km; the specimens of *C. mcdiarmidi* are from localities at 1693 m and 1350 m, more than 300 km apart (fig. 1).

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APPENDIX: SPECIMENS EXAMINED

See text for specimens of new species.

Colostethus brunneus (*N* = 12): BRAZIL: **Mato Grosso**: Chapada dos Guimaraes, KU 93154–93155. **Pará**: Río Mapuera, AMNH 53331–53333. COLOMBIA: **Amazonas**: Leticia, Internado de Nazareth (Selva al E), IAvH 2871, 2872; Amazonas, margen izquierda Río Loreto Yacu (límites con Perú), ca. cacerío San Juan, ca. 100 m, ICN 11153–11357.

Colostethus juanii (*N* = 20): COLOMBIA: **Meta**: Villavicencio, KU 189426 (paratype), 189427 (holotype); Villavicencio, Pozo Azul, ICN 42576; Villavicencio, Caño Parado, ICN 2463–2464; Acacías, km 13 Villavicencio–Acacías, 650 m, ICN 14154; Acacías, Vereda Alto Acacías, carretera antigua Acacías–Guamal, ca. 730 m, ICN 14155; Acacías, vereda "Vista Hermosa", 100 m; Villavicencio, km 2, carretera Villavicencio–Restrepo, 600 m, ICN 44486–44487, 44489–44490; Restrepo, Salinas, seccional UPIN, a 500 m de la cabina administrativa, ICN 17311–17314; Restrepo, Salinas de UPIN, Quebrada Salinas, 750–760 m; Cubarral, El Dorado, ICN 39494–39496. **Cundinamarca**: Medina, Vereda Choapal, ca. 6–7 km NNO Medina, 580–630 m, ICN 15644–45.

Colostethus trilineatus (*N* = 123): ECUADOR: **Sucumbíos**: Limoncocha, 243 m, KU 182124–182125, 183529. PERU: **Amazonas**: Headwaters of Río Santiago, AMNH 42065. **Huánuco**: Finca Panguana, Río Llullapichis, 4 km upstream from Río Pachitea, elev. approx. 200 m, KU 154925–154930, 17952–171992, MUSM 14134, 14138–13140. **Loreto**: Explornapo Lodge, jct. Río Sucusari and Río Napo, KU 220407; Aguas Negras, Río Napo, AMNH FS 8764, 8772–8774, 8831; Santander, Río Alto Purús, AMNH FS 11545; Río Curanja, Balta, 300 m, KU 196706–196709; Genaro Herrera, MUSM 15612–15613, 15615–15616; Teniente López, 200 m, KU 221831–221833; Yurimaguas, BMNH 84.2.18.22, 84.2.18.23, 1947.2.14.20 (holotype), AMNH FS 8689, MUSM 15611. **Madre de Dios**: Cocha Cashu, Parque Nacional del Manu, ca. 380 m, MUSM 9180, 9182–9201, 15614, 15618–15621; Cuzco Amazónico 15 km E Puerto Maldonado, 200 m, KU 194916, 205270–205273, 205275–205282, 207547, 207549–207550; Tambopata Wildlife Reserve, jct. Río Torre and Río Tambopata, 12°50′S, 69°17′W, BMNH 1987.596, 1987.599. **Puno**: Candamo (13°30′S, 69°41′W), 825 m, MUSM 15617, 16569.

Colostethus mcdiarmidi (*N* = 4): BOLIVIA: **La Paz**: Territorio Comunitario y Reserva de la Biósfera "Pilón Lajas" (15°06′S, 67°32′W), 1350 m, NKA 3708, 3712. **Cochabamba**: 0.25 km E road to San Onofre from Cochabamba to Villa Tunari at point 97.5 km from Cochabamba, 1693 m, USNM 257805 (holotype), 257806.