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Leaf-frogs of the *Phyllomedusa perinesos* Group (Anura: Hylidae)

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The *Phyllomedusa perinesos* group consists of four species (*P. perinesos*, *P. baltea*, *P. duellmani*, n. sp., and *P. ecuatoriana*, n. sp.) from cloud forests of the Amazonian slopes of Perú and Ecuador. The new species are described from the Cordillera de Matanga of southern Ecuador and from the Cordillera Oriental of northern Perú. The group is diagnosed by purple flanks and concealed surfaces, and a purple belly with white granules, a unique condition among phyllomedusine frogs. It appears to be the only cloud forest radiation of pond-breeding phyllomedusines. The evolution of this monophyletic assemblage seems to be associated with the Andean orogeny and the formation of the Huancabamba Depression.

SPECIES of phyllomedusine frogs occur in southern México, Central America, and throughout South America except for Chile and southern Argentina. They inhabit mesic forests from sea level up to 2,100 m altitude, although a few species such as *Pachymedusa dacnicolor* are found in desert scrub forests.

Most phyllomedusines are brightly colored, and the color patterns are usually species-specific. The identification of preserved specimens can be difficult, whereas in life, species are easily distinguished. Such an example is *Agalychnis annae*, which was long identified as *Agalychnis moreletii* until live specimens of both species were compared (Duellman, 1963).

Being largely pond breeders, most leaf-frogs are found in lowland rainforests. A few species, such as *Phyllomedusa lemur*, are found in Central American cloud forest. At the time of the most recent revision (Duellman, 1968) only *Phyllomedusa buckleyi* was known from northern Andean cloud forests. However, four new species have been discovered in the last decade: Duellman (1973) described *Phyllomedusa perinesos* from montane rainforests of Ecuador, a striking new species characterized by purple belly and concealed surfaces. Duellman and Toft (1979) described a second, closely related species, *Phyllomedusa baltea*, from cloud forest in Perú. In this paper I describe two new cloud forest species that are closely related to the aforementioned, and I present additional data on the biology of *Phyllomedusa perinesos*, which was described from a single specimen. I informally designate this assemblage as the *Phyllomedusa perinesos* group.

Measurements of morphological characters and calls were made as described by Duellman (1970). Recordings were made on a Uher-4000 Recorder and the Sonagrams were produced by a Sona-Graph 7029A (Kay Electric Company). The term "concealed surfaces" refers to those parts of the body that are pressed against one another and thus hidden while the frog is in a resting position with limbs flexed. The specimens examined are part of the collections of the University of Kansas Museum of Natural History (KU), the National Museum of Natural History (USNM), the Academy of Natural Sciences of Philadelphia (ANSP), the University of Michigan Museum of Zoology (UMMZ) and the Field Museum of Natural History (FMNH).

SYSTEMATICS

The *Phyllomedusa perinesos* group

Members of the *P. perinesos* group differ from all other phyllomedusines in having purple hands, feet, flanks and concealed surfaces, variously marked with orange, and a uniformly purple belly with white granules.

Definition.—Sexual dimorphism in size; maximum snout–vent length of 55.4 mm in males, 63.5 mm in females; 1) hands and feet not webbed; 2) parotoid glands moderately well-developed; 3) white dorsal warts never present; 4) males having thin horny nuptial excrescences; 5) males having vocal slits and single, median subgular vocal sac; 6) first toe about equal in length to second; 7) first metatarsal about equal in length to second; 8) iris silver-gray with greenish cast; 9) prevomerine teeth

present; 10) posterior portion (pars scapularis) of depressor mandibulae present; 11) nektonic tadpoles having oval bodies and moderately deep tail fins; 12) mouths of larvae anteroventral, lacking labial papillae anteromedially; 13) larvae with two upper and three lower rows of denticles.

Content.—Four species: *Phyllomedusa baltea* Duellman and Toft; *P. perinesos* Duellman; *P. duellmani,* n. sp.; *P. ecuatoriana,* n. sp.

Distribution.—The combined distributions of the four species include the Amazonian slopes of Perú and Ecuador from 0° to 10°S, at elevations of 1,280 to 1,910 m.

Phyllomedusa baltea Duellman and Toft

Holotype.—KU 154746, an adult female, from Laguna, west slope of the Serranía de Sira, Departamento Huánuco, Perú, 1,280 m, 09°32'S, 74°48'W.

Paratypes.—KU 154747–48, collected with the holotype.

Diagnosis.—1) Dorsal surfaces of hands and feet uniform purple with a salmon line extending to end of third and fourth fingers and to end of fourth and fifth toes; digital discs purple; 2) two distinct para-anal tubercles present (not as distinct as in *P. perinesos*); 3) salmon stripe extending from corner of jaw to flank; 4) anterior and posterior surfaces of thighs uniform purple, without orange blotches; salmon stripe present anterior and posterior to the green dorsal surface of thigh; 5) concealed surfaces of shanks and tarsi uniform purple, without orange blotches; 6) palpebrum finely reticulated.

Tadpoles.—Duellman and Toft (1979) described and illustrated a tadpole (KU 174714, N = 2) at Stage 25 (Gosner, 1960), not Stage 21 as stated in their paper. This larva is typical of most phyllomedusine larvae: eyes lateral; mouth small, terminal; tail narrowing gradually to a fine tip; spiracle slightly sinistral of midventer; median portion of upper lip lacking papillae; as many as five rows of papillae laterally; two upper and three lower rows of denticles; second upper row interrupted medially, others unbroken. The venter is bluish gray; the dorsum and caudal musculature, brown, and the fins, brownish gray.

Distribution and ecology.—Known only from a small pond in the lower cloud forest of the isolated Serranía de Sira of central Perú (Fig. 1).

Etymology.—The specific name (Latin) means border, and refers to the distinctive salmon line that separates the dorsal and ventral colors of the frog (Duellman and Toft, 1979).

Remarks.—The mating call is not known. The holotype laid eggs in the collecting bag, but these were discarded. Other species collected in the same area as *P. baltea* include *Bufo nesiotes, B. poeppiggi, Eleutherodactylus ockendeni* and *E. peruvianus* (Duellman and Toft, 1979).

Phyllomedusa ***duellmani,*** n. sp.
Fig. 2

Holotype.—KU 181813, an adult male, from 8 km NNE (by road) Balzapata, Depto. Amazonas, Perú, 1,850 m, 05°47'S, 77°48'W, obtained on 3 March 1979, by Thomas J. Berger and David C. Cannatella.

Paratype.—KU 181814, an adult male, same data as the holotype.

Diagnosis.—1) Dorsal surfaces of hands and feet orange (in life) with irregular purple markings; 2) two distinct para-anal tubercles present, not as prominent as in *P. perinesos*; 3) white stripe extending from corner of jaw posteriorly to flank; 4) anterior and posterior surfaces of thigh purple with irregular orange markings; 5) concealed surfaces of shanks and tarsi purple with irregular orange markings; 6) palpebrum moderately reticulated.

Description.—See Tables 1, 2 for measurements. Head wider than body; snout short, acutely rounded in dorsal view; in lateral view, sloping and slightly rounded from lip to nostril; canthus rostralis distinct, rounded; loreal region concave; lips thin, unflared; nostrils not protuberant, directed laterally; internarial region flat; eyes large and protuberant, pupil vertically elliptical; palpebrum with fine silvery reticulation and scattered flecks; parotoid gland weakly differentiated; supratympanic fold indistinct,

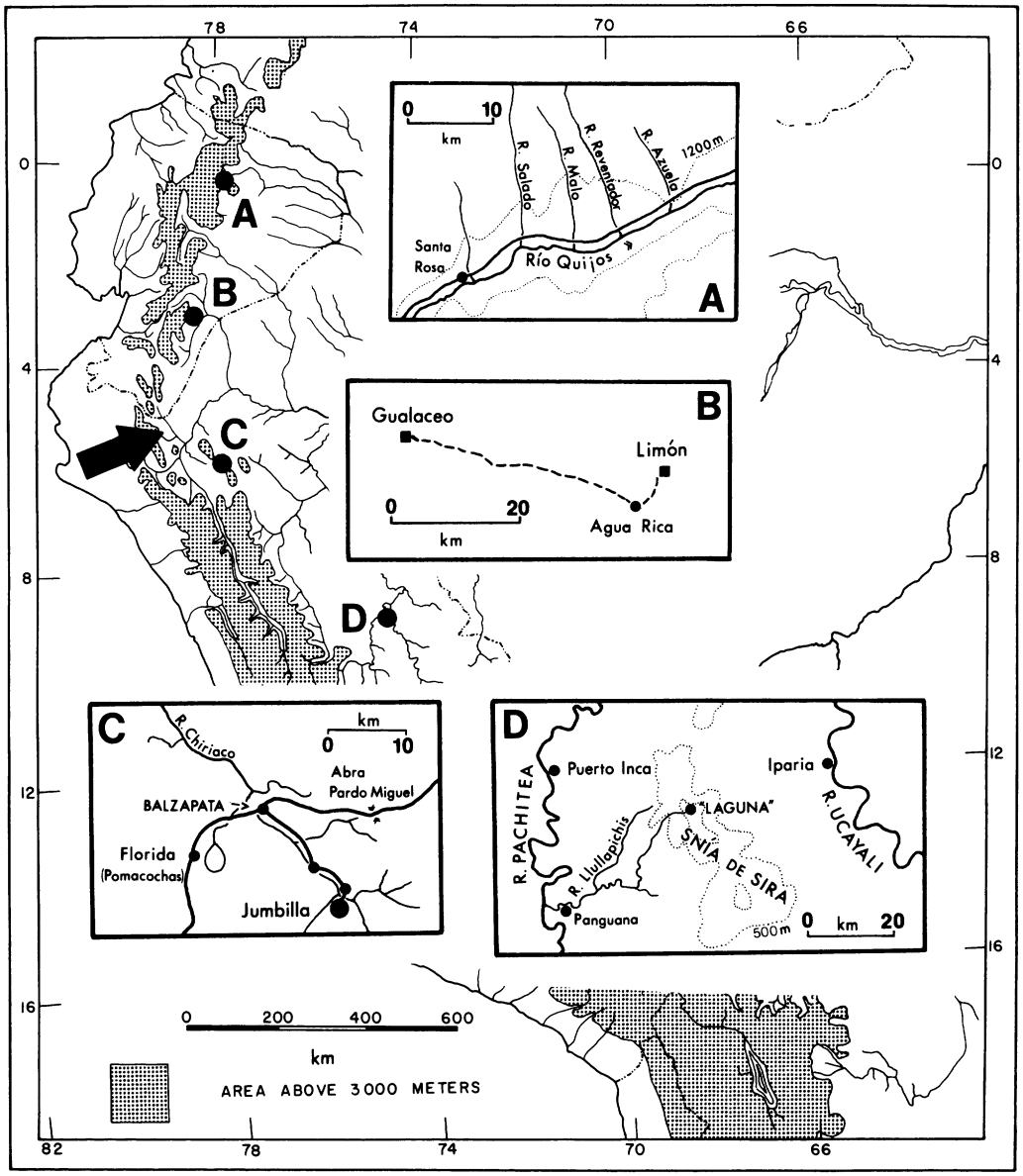

Fig. 1. Distribution of the *P. perinesos* group in Perú and Ecuador. Large arrow indicates region of Huancabamba Depression. A) *P. perinesos*; B) *P. ecuatoriana*; C) *P. duellmani*; D) *P. baltea.*

slightly obscuring dorsal margin of tympanum; tympanum distinct, slightly oval, separated from eye by distance equal to one-half diameter of tympanum.

Axillary membrane absent; brachium slender; antebrachium more robust; ulnar fold distinct, extending from elbow to tip of fourth finger; fingers moderately long; relative length from shortest to longest 1-2-4-3; discs of moderate size, rounded; subarticular tubercles moderately large, subconical; supernumerary tubercles lacking on fingers; palmar tubercle weakly developed, round; prepollex distinct, bearing thin keratinous nuptial pad; fingers lacking webbing or fringes.

Legs moderately long, slender; heel with

TABLE 1. MEASUREMENTS OF SPECIES OF THE *Phyllomedusa perinesos* GROUP. In mm; mean ± 2 SE, range.

Species	Sex	N	SVL	TIB	FOOT	HLEN	HWID
P. perinesos	♂	21	48.8 ± 0.70 46.2–51.5	23.6 ± 0.31 22.3–25.0	19.2 ± 0.42 17.5–21.3	17.1 ± 0.25 16.5–18.4	16.3 ± 0.28 15.0–17.4
	♀	5	63.9 ± 1.17 62.2–65.2	30.4 ± 0.84 29.1–31.7	24.3 ± 0.80 22.9–25.2	21.7 ± 0.50 20.8–22.2	21.1 ± 0.61 20.0–21.6
P. duellmani (range only)	♂	2	51.7–54.2	23.0–23.8	19.9–21.4	18.5–18.7	17.0–18.8
P. baltea	♂	1	45.2	23.0	17.8	16.8	16.4
	♀	1	63.5	29.5	23.6	22.1	21.8
P. ecuatoriana	♂	1	55.4	23.4	18.4	18.5	17.3

slight tubercle, but no distinct calcar; outer tarsal fold distinct; toes of moderate length; relative length from shortest to longest 2-1-3-5-4; first toe only slightly longer than second; discs rounded, slightly longer than those on fingers; inner metatarsal tubercle low, flattened, slightly elliptical, outer metatarsal tubercle indistinct; subarticular tubercles rounded, subconical to conical; a few smaller supernumerary tubercles present along metatarsals 3–5; webbing absent between toes.

Anal opening tubular, directed posteriorly at midlevel of thighs; anal flap absent; prominent supra-anal fold; peri-anal region tubercular; skin on dorsum generally smooth, minutely granular along parotoid glands; white dorsal warts absent; skin on throat, belly, anal region, anterior flanks, ventral aspects of arms and tarsi distinctly granular; skin on concealed surfaces of limbs and flanks smooth; tongue cordiform, notched posteriorly; prevomerine teeth present; dentigerous processes small, separated medially; oriented almost horizontally at posterior plane of elliptical choanae; vocal slits present in both males, short, parallel to mandible, extending from posterolateral margin of tongue to corner of mouth; vocal sac single, median, subgular.

In preservative, dorsal surfaces of head, body, forearms, fourth fingers, thighs, shanks, tarsi and fifth toes pale to dark blue; lower lip, ulnar, tarsal and supra-anal folds white; concealed surfaces of limbs and dorsal surfaces of hands and feet cream with few irregular purple markings; flanks cream with two irregular purple bars; anal region purple-brown; belly, throat, ventral surfaces of limbs, hands and feet light to dark purple; many prominent white granules on throat, belly, anterior flanks, anal region and ventral surfaces of thighs; a few scattered white granules on ventral aspects of forearms and tarsi.

TABLE 2. RATIOS OF MEASUREMENTS OF THE *P. perinesos* GROUP, MALES ONLY. For *P. perinesos* the data are the mean ± 2 SE, range. For the other species the ratio is given along with the probability (*P*) of this bivariate observation being sampled from the *P. perinesos* population. See text for details.

Species	N	TIB/SVL	FOOT/SVL	HLEN/SVL	HWID/SVL
P. perinesos	21	0.484 ± 0.0043 0.468–0.503	0.392 ± 0.0062 0.368–0.421	0.351 ± 0.0034 0.338–0.369	0.335 ± 0.0039 0.314–0.357
P. duellmani (KU 181814)	1	0.445 $P < 0.01$	0.385 $P > 0.05$	0.358 $0.05 > P > 0.01$	0.329 $P > 0.05$
P. duellmani (KU 181813)	1	0.439 $P < 0.01$	0.395 $0.05 > P > 0.01$	0.345 $0.05 > P > 0.01$	0.347 $P < 0.01$
P. baltea	1	0.509 $0.05 > P > 0.01$	0.394 $P > 0.05$	0.372 $0.05 > P > 0.01$	0.363 $P < 0.01$
P. ecuatoriana	1	0.422 $P < 0.01$	0.332 $P < 0.01$	0.334 $P < 0.01$	0.312 $P < 0.01$

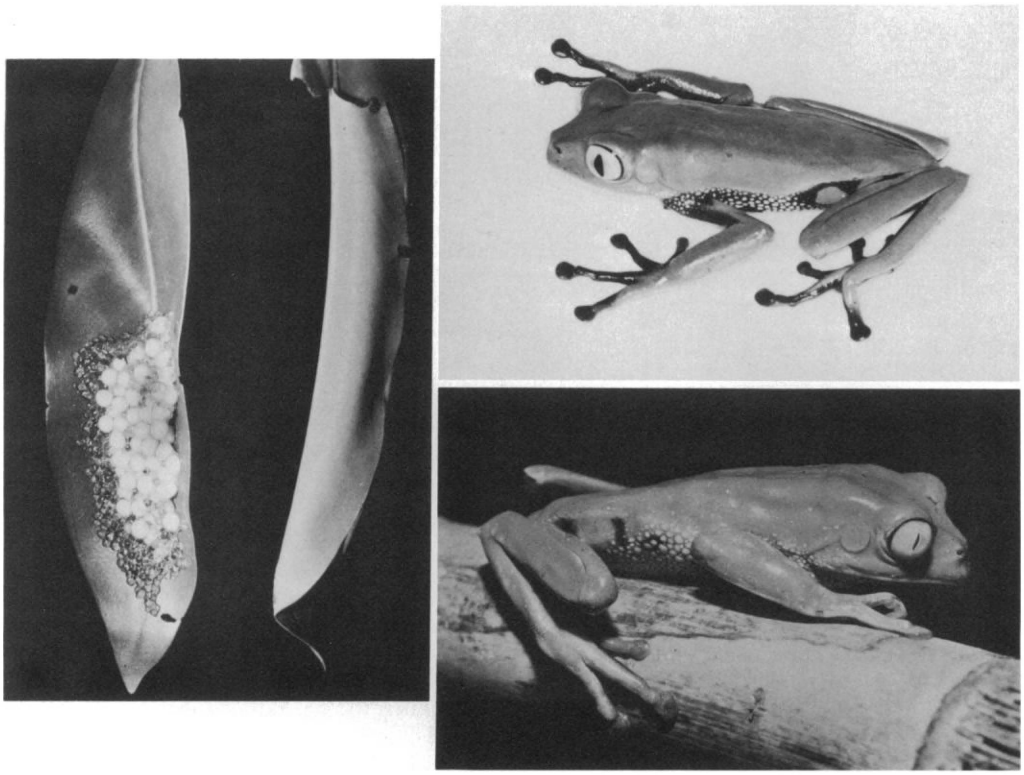

Fig. 2. Left: Eggs of *P. duellmani.* Clutch on left (KU 181887) opened to expose eggs; clutch on right (KU 181888) intact. Top right: *P. perinesos,* male, KU 164450, SVL 49.4 mm. Bottom right: *P. duellmani,* male, KU 181813, holotype, SVL 54.2 mm.

In life, dorsum green; hidden surfaces deep orange with purple markings; throat and belly orange with purple between granules; anal, heel, labial stripes creamy white; iris silvery gray with greenish cast; palpebrum lightly reticulated with white.

Measurements of holotype.—In mm: snout–vent length (SVL) 54.2; tibia length (TIB) 23.8; foot length (FOOT) 21.4; head length (HLEN) 18.7; head width (HWID) 18.8; interorbital distance (IOD) 5.0; internarial distance (IND) 3.7; diameter of tympanum (TYMP) 3.4; distance from anterior corner of eye to nostril (EYE-NOS) 5.0.

Tadpoles.—A representative tadpole at Stage 37 is illustrated in Fig. 3. The total length of the larva is 52.9 mm; the body length is 23.4 mm. KU 181886 consists of 29 tadpoles, the smallest of which is at Stage 25 and has a total length of 21.1 mm and body length of 8.6 mm. The largest tadpole in the lot is the one at Stage 37 mentioned above. KU 181885 consists of a single tadpole. Both lots of larvae were collected from a shallow (0.3 m) roadside ditch, over which vegetation was hanging. Larvae of *Ololygon* sp. were also collected from the ditch. The *Phyllomedusa* larvae were observed to orient head up at about at a 45° angle, in typical phyllomedusine fashion. At the time of collection at dusk the water temperature was 19 C.

The following larval description is based on KU 181885–86: Body about as wide as deep; eyes dorsolateral, directed laterally; spiracle a flap-like tube, ventral and sinistral to midline; mouth terminal; caudal musculature slender, tapering gradually to a point; at midlength of tail the depth of caudal musculature is about equal to depth of ventral fin, but greater than that of dorsal fin; cloacal tube short. Mouth small; medial portion of upper lip lacking papillae; elsewhere, papillae present in two to five rows along margin of mouth; two upper and

Fig. 3. Tadpoles of *P. perinesos* (top) and *P. duellmani* (bottom).

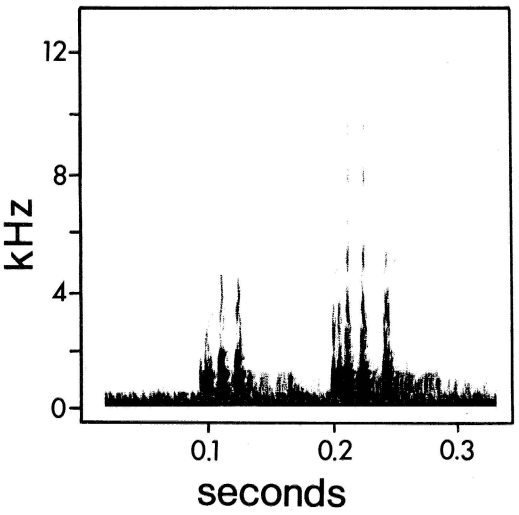

Fig. 4. Audiospectrogram of the presumed mating call of *P. duellmani,* KU 181813 (KU Tape 1356), wide band filter.

three lower rows of denticles; second upper row interrupted medially; other rows unbroken; upper beaks broadly arched; lower beak V-shaped, both serrate.

In preservative, body almost pigmentless in all individuals; a few diffuse dusky blotches on tail and fins of some larger larvae; edges of fins dark gray in some. In life, dorsum pale gold, venter silvery white; caudal musculature unpigmented; fins very pale gold; iris pale gold; edges of fins gray.

Eggs.—Two clutches of unpigmented eggs were collected with the type specimens. Each clutch was concealed completely by the folded edges of the leaf on which it was deposited (Fig. 2). The clutches were about 10 cm apart at a height of about 1 meter over the small ditch where the larvae were collected. The egg masses had assumed a roughly cylindrical shape within the leaf cases; numerous small jelly capsules were concentrated at the top and bottom of the clutch. This mode of egg deposition—the eggs enveloped within a leaf—is found in some, but not all, species currently assigned to the genus *Phyllomedusa.* Pyburn (1980) has shown that in *P. hypocondrialis* such an arrangement of leaf and eggless capsules prevents desiccation of the eggs. One clutch (KU 181887) contains 78 eggs at the blastopore stage. The mean diameter of ten randomly selected eggs is 3.7 mm, with a range of 3.5–3.8. The second clutch (KU 181888) consists of 126 eggs; the mean diameter is 3.6 mm, range 3.4–3.8 mm.

Mating call.—The presumed mating call of *P. duellmani* was recorded from KU 181813, calling from a plastic bag on the night of collection; the air temperature was 15 C. The call-group is a short "puh-dup," consisting of a primary and a single secondary note (Fig. 4). Eighteen call-groups were produced during a 30 sec period. Ten call-groups were analyzed. The mean duration of a call-group is 0.152 sec (0.139–0.164). The mean duration of the primary note is 0.037 sec (0.032–0.040); that of the secondary is 0.043 (0.032–0.057). The mean duration between the first pulse of the primary and the first pulse of the secondary note is 0.109 sec (0.103–0.113). The primary note consists of 3–4 pulses (mode = 4); the secondary has 3–5 pulses (mode = 3).

The most intense energy distribution of the call is from 0–2,000 Hz. The fundamental frequency of the primary note is 80 Hz; the dominant frequency occurs at 930–970 Hz, and the other most intense energy bands are at 170, 580–600, and 1,000–1,050 Hz. The fundamental frequency of the secondary is also 80 Hz. There appears to be equally intense dominant frequencies at 700–710 and 920–940 Hz. Other intense energy frequencies exist at 170, 750–780, 1,020–1,030, and 1,070–1,090 Hz.

Distribution.—Phyllomedusa duellmani is known only from the upper Río Chiriaco, Depto. Amazonas, Perú, at altitudes of 1,850 and 1,910 m (Fig. 1).

Ecology.—The two adult specimens were taken by night on vegetation overhanging a water-filled ditch along the road. The adults, larvae,

and eggs were collected along a 5 m strip of the ditch. Both adults were calling when they were captured; the evening was rainless and slightly windy. Other species collected at 8 km NNE Balzapata include *Bufo typhonius, Colostethus* sp., *Hyla* sp., *Ololygon* sp. and *Eleutherodactylus* sp.

Etymology.—I associate the name of William E. Duellman with this new species in recognition of his contributions to the systematics of phyllomedusine frogs.

Remarks.—The only other phyllomedusine frog known from the mountains of northern Perú (Moyobamba) is *Phyllomedusa coelestis,* which is known only from the holotype (ANSP 11384). I have compared that holotype with the holotype of *P. duellmani* and the two definitely are not conspecific. *Phyllomedusa coelestis* is a species closely related to *P. tarsius* and *P. trinitatis.* In *P. coelestis,* the palpebrum is not reticulated, there is no purple pigmentation, and the foot is more specialized, the first toe being much longer than the second.

Additional specimens examined.—Perú: Amazonas:8 km NNE Balzapata, 1,850 m, 181886 (larvae), 181887–88 (eggs); 10 km NNE Balzapata, 1,910 m, 181885 (larvae).

Phyllomedusa ***ecuatoriana,*** n. sp.

Holotype.—USNM 215750, an adult male, from Agua Rica, a one-house posada on the trail between Limón and Gualeceo, slightly south and west of Limón, Provincia de Morona-Santiago, Ecuador, 1,890 m, 03°02′S, 78°27′W, obtained on 19 August 1962, by James A. Peters.

Paratypes.—None.

Diagnosis.—1) Dorsal surfaces of hands and feet purple with irregular cream (orange in life?) markings; digital discs uniform purple; 2) enlarged para-anal tubercles absent; 3) white stripe extending from corner of jaw to flank; 4) a large cream (orange in life?) blotch on anterior and posterior surfaces of thighs; 5) concealed surfaces of shanks and tarsi uniform purple, without discrete blotches or markings; 6) palpebrum with scattered silvery flecks, not reticulated.

Description.—See Tables 1, 2 for measurements. Head slightly wider than body; snout short, acutely rounded in dorsal view; in lateral view, sloping from lip to nostril; canthus rostralis distinct, rounded; loreal region slightly concave; lips thin, not flared; nostrils directed laterally, slightly protuberant; pupil vertically elliptical (presumed); palpebrum not reticulated, bearing a few scattered silvery flecks; parotoid glands weakly differentiated; supratympanic fold weak, slightly obscuring upper edge of tympanum; tympanum distinct, slightly oval, separated from eye by distance equal to one-third diameter of tympanum.

Axillary membrane absent; brachium slender, antebrachium more robust; ulnar fold distinct, extending from elbow to tip of fourth finger; fingers moderately long; relative length from shortest to longest 1-2-4-3; discs of moderate size, rounded; subarticular tubercles not very distinct, rounded; one or two smaller supernumerary tubercles along metacarpals 2–4; palmar tubercle not evident; prepollex distinct, bearing thin keratinous nuptial pad; fingers lacking webbing; slight lateral fold present on fingers.

Legs moderately long, slender; heel bearing weak tubercle, not a distinct calcar; outer tarsal fold distinct; toes of moderate length; relative length from shortest to longest 2-1-3-5-4; first toe only slightly longer than second; discs rounded, slightly smaller than those on fingers; inner metatarsal tubercle low, flattened, oval; outer metatarsal tubercle not evident; subarticular tubercles rounded, flattened, subconical; a few smaller supernumerary tubercles along metatarsals 2–5; webbing absent between toes; toes with slight lateral fringe.

Anal opening tubular, directed posteriorly at midlevel of thighs; anal flap absent; supra-anal fold distinct; peri-anal region tubercular; skin on dorsum smooth; white dorsal warts absent; skin on throat, belly, anal region and anterior flanks granular; skin on concealed surfaces of limbs and posterior flanks smooth; tongue cordiform, notched posteriorly; prevomerine teeth present; dentigerous processes small, separated medially, oriented almost horizontally at posterior level of elliptical choanae; vocal slits present, short, parallel to mandible, extending from posterolateral margin of tongue to corner of mouth; vocal sac single, median, subgular.

In preservative, dorsal surfaces of head, body, forearms, fourth fingers, finger and toe pads, thighs, shanks, tarsi and fourth and fifth toes dark blue; lower lip, ulnar, tarsal and supra-anal folds off-white; dorsal surfaces of hands and feet purple with irregular cream markings; flanks cream with two large diffuse

purple blotches, the posterior one extending onto thigh; cream stripe extending from angle of jaw posteriorly to flanks, merging with cream blotches; anal region purple with cream tubercles; concealed surfaces of hind limbs purple; a single large cream blotch on anterior and posterior surfaces of thighs; cream spots absent elsewhere on hind limb; belly, throat, ventral surfaces of limbs, hands and feet purple; distinct cream granules on belly, anterior flanks, and anal region.

Measurements of holotype.—In mm: SVL 55.4; TIB 23.2; FOOT 18.4; HLEN 18.5; HWID 17.3; IOD 5.6; IND 3.7; TYMP 3.2; EYENOS 4.6.

Distribution.—Known only from the type-locality in the drainage of the upper Río Santiago on the Amazonian slopes of the Cordillera Oriental, Ecuador (Fig. 1).

Ecology.—The unique specimen was taken in a large swampy area strewn with logs and large rocks.

Etymology.—I name this new leaf-frog in honor the country of its origin, the Republic of Ecuador. The specific epithet is an adjective modifying *Phyllomedusa,* and thus feminine.

Remarks.—Eggs, tadpoles, and mating call of the species are unknown. Peters (1973) discussed the *Atelopus* from his transects across the slopes of the Cordillera de Matanga and Cerro El Picacho, east of Cuenca. Lynch (1979) described several species of *Eleutherodactylus* from the same region.

Overall, this species is most similar to *P. perinesos,* but differs from that species in the first three characters of the diagnosis. Furthermore, the possibility that the holotype of *P. ecuatoriana* is simply an aberrant specimen of *P. perinesos* is refuted by the morphometric data.

Phyllomedusa perinesos Duellman
Fig. 2

Holotype.—KU 146562, an adult male, from the Río Salado, about 1 km upstream from its confluence with the Río Coca, Provincia Napo, Ecuador, 1,410 m, 00°13'S, 77°44'W.

Paratypes.—None.

Diagnosis.—1) Dorsal surfaces of hands, feet, and digital discs uniform purple; 2) two enlarged para-anal tubercles, with numerous smaller surrounding tubercles, 3) no stripe extending from corner of jaw posteriorly to flank; 4) a large orange blotch on both anterior and posterior surfaces of thighs; 5) concealed surfaces of shanks and tarsi with or without discrete orange blotch (see *Variation*); 6) palpebrum with scattered flecks, not reticulated.

Variation.—The holotype of *P. perinesos* has one large orange spot (in life) on the dorsal surface of the upper arms, two spots on the left flank, one on the right flank, one on each of the anterior and posterior surfaces of each thigh, and one spot on the inner surfaces of the left shank, but none on the right. I have examined 33 randomly selected specimens to ascertain variation in the distribution of spots. Thirty-two of 33 have brachial spots on the left and right sides; 23 (of 33) have one spot on the left flank; 10 have two spots. Eighteen have one spot on the right flank; 15 have two spots. All 33 specimens have one spot on each of the anterior and posterior surfaces of both thighs. Nine specimens have one spot on both the left and right inner shank; three have a spot only on the left side, and three others have a spot only on the right. Eighteen frogs lack spots on either shank. Thirteen specimens have a spot on each tarsus; one specimen, only on the left tarsus, and two specimens, only on the right. Seventeen lack spots on either tarsus.

Metamorphic young.—Three newly metamorphosed young were collected on the night of 17 July 1977. They were taken on low vegetation within a few meters of the pond. The froglets still retained a 5 mm vestige of the larval tail. The dorsal surfaces were green; diffuse yellow-orange blotches were present on the concealed surfaces. The ventral surfaces were off-white, with no traces of the adult purple pigmentation; however, the digits of the hands and feet were dull purple. Apparently the complete adult color pattern is not realized until later in ontogeny. Starrett (1960) noted a similar situation in *Agalychnis callidryas.*

Newly metamorphosed young are distinguishable from those of the syntopic *Phyllomedusa buckleyi* by the foot structure. In *P. perinesos* the first toe is about equal in length to the second; in *P. buckleyi* the first toe is distinctly short-

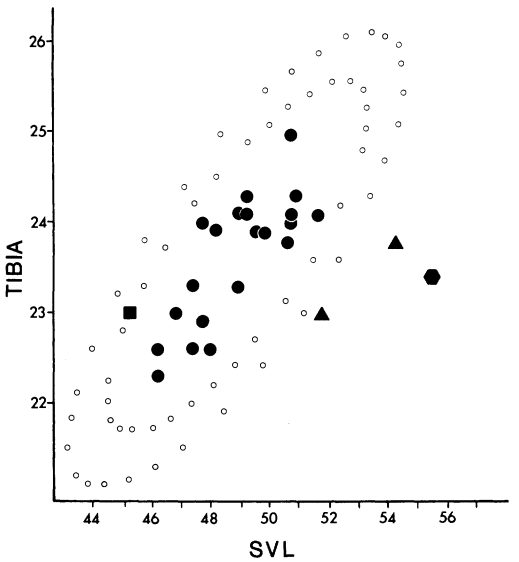

Fig. 5. Plot of tibia length vs snout–vent length for *P. perinesos* (dots), *P. baltea* (square), *P. duellmani* (triangles) and *P. ecuatoriana* (hexagon). The small circles represent calculated points that define the 95% (inner) and 99% (outer) confidence ellipses for the observations of *P. perinesos*.

typhonius, B. marinus, Colostethus sp., *Hyla phyllognatha, H. sarayacuensis, Ololygon rubra, Osteocephalus verrucigerus, Centrolenella siren, C. audax, C. cochranae,* and *C. pipilata.* Lynch and Duellman (1980) listed seven species of *Eleutherodactylus* from the Río Salado: *E. cremnobates, E. incomptus, E. peruvianus, E. petersi, E. prolatus, E. quaquaversus,* and *E. w-nigrum.* Duellman (1979) included the Río Salado community in his analysis of the Andean herpetofauna.

Etymology.—The name *perinesos* (Greek) means edged with purple, in allusion to the purple color of the flanks and concealed surfaces of the limbs (Duellman, 1973).

Remarks.—Duellman (1973) commented on the type-locality. He visited the area immediately after the Papallacta–Lago Agrio road was opened in October 1971. Since then much of the forest along the road has been cleared by settlers. The small group of buildings on the west side of the Río Salado bridge has become known by the natives simply as Salado. This settlement is within 50 m of the type-locality; thus, KU specimens labelled as "Salado" and "Río Salado" are from essentially the same locality.

I have shown (Cannatella, 1980) that *P. perinesos* is not related to the *P. buckleyi* group, as suggested by Duellman (1973), but rather is part of the larger assemblage of the more derived species of *Phyllomedusa,* including such species as *P. tarsius, P. tomopterna, P. hypochondrialis* and several others.

The palpebrum of the holotype of *P. perinesos* was originally described as unpigmented. In all the individuals of *P. perinesos* the palpebrum bears a few silvery flecks on its anterior portion. This condition is shared with *P. ecuatoriana*; *P. baltea* and *P. duellmani* have finely reticulated palpebra.

Additional specimens examined.—Ecuador: Napo: Río Salado, ±1 km upstream from Río Coca, 1,410 m, KU 164450–73, 166318–19, 178851–87, 179569–72, 184953–54 (eggs), FMNH 204283–86, UMMZ 143363; 2 km SSW Río Reventador, 1,490 m, KU 164474; Salado (km 124), 1,420 m, KU 179176, 180363–64 (eggs); Río Azuela, 1,740 m, KU 179177 (larvae).

Discussion

Morphometrics.—Four ratios were analyzed in an effort to assess differences in some body proportions among the species (Table 2). *Phyllomedusa perinesos* was used as the reference population to which the other species were compared. Certain distributional assumptions were met by the *P. perinesos* data: the data were judged to be normally distributed if the correlation coefficient for the raw data and their normal scores was greater than a critical value—0.950 for N = 21 (Ryan et al., 1978). Each variable for *P. perinesos* in Tables 1 and 2 was found to be normally distributed. Also, each pair of ratio variables (e.g., TIB and SVL) was found to be highly correlated ($P < 0.01$). To ascertain whether the ratio data of *P. baltea, P. duellmani,* and *P. ecuatoriana* were different from that of *P. perinesos,* 95 and 99% confidence ellipses were computed for the individual observations of the bivariate plot of each ratio for *P. perinesos* (Sokal and Rohlf, 1969). This procedure is analogous to setting the 95% confidence limits on a Dice-gram, using limits of two standard deviations. The results are summarized in Table 2.

As a graphic example, Fig. 5 demonstrates

er than the second. Metamorphic young of *P. buckleyi* may have white dorsal warts; these are not present in *P. perinesos*.

Tadpoles.—A representative tadpole at Stage 40 is illustrated in Fig. 3. The total length of the tadpole is 57.2 mm; the body length is 24.5 mm. KU 179177 consists of three tadpoles—including the one illustrated—all at Stage 40. The body lengths of the other two larvae are 22.3 and 22.7 mm.

The following description is based on KU 179177: Body about as wide as deep; eyes dorsolateral, directed laterally; spiracle a flap-like tube, ventral and sinistral to midline; mouth terminal; caudal musculature moderately slender, tapering to a point; dorsal fin shallower than ventral fin. Mouth small; median portion of upper lip without papillae; elsewhere, papillae present in two to four rows; two upper and three lower rows of denticles; second upper row interrupted medially; other rows unbroken; upper beak broadly arched, lower beak V-shaped; both serrate.

In preservative, dorsum of body and anterior portion of tail dark brown, fading laterally; sides of body and caudal musculature cream with irregular dark brown spots; venter off-white with a bluish cast; fins with dark brown blotches and black edges.

Larvae of *P. perinesos* have been collected syntopically with those of *P. buckleyi* at the Río Azuela site. Fortuitously, advanced larvae of both species, with well-developed feet were collected, and the species were easily distinguished by the relative lengths of the first and second toes (see *Metamorphic young*). Concomitantly, differences in pigmentation and relative size of the oral disc were noted in the advanced tadpoles. Larvae of *P. buckleyi* have been described previously (Cannatella, 1980). The tadpoles of *P. buckleyi* lack the dark brown mottled pigmentation of *P. perinesos*; also, the oral disc of *P. buckleyi* is relatively larger than in *P. perinesos* (or *P. duellmani*), but this is best discerned by direct comparison of larvae of both species. No larvae of *P. perinesos* have been found at the Río Salado site, although several lots of *P. buckleyi* tadpoles are known (Cannatella, 1980). My assignment of these lots to *P. buckleyi* is based on comparison with the Río Azuela specimens; the Salado specimens all lack mottled pigmentation, and have relatively larger oral discs (as judged by casual inspection) than the Río Azuela *P. perinesos*. Moreover, they agree quite readily in most features with the *P. buckleyi* from the Río Azuela. I have not been able to identify with confidence very young tadpoles (pre-Stage 24).

Eggs.—Four clutches were examined. Two clutches (KU 180363–64) were found on 17 July 1977 at the type-locality over the edge of a pond, 0.5–1.0 m above the water. As in *P. duellmani*, the unpigmented eggs were concealed within a rolled leaf and numerous empty jelly capsules formed a plug at each end. KU 180363 consists of 62 eggs at the yolk plug stage; the mean diameter of 10 eggs is 3.2 mm (2.9–3.5); KU 180364 has 52 eggs with a mean diameter of 3.6 mm (3.3–3.9).

Two other clutches (KU 184953–54) were laid by amplectant pairs maintained overnight in plastic bags on 17 July 1977. In both clutches many of the eggs appear to be unfertilized, and numerous empty jelly capsules were deposited with the eggs on the side of the bag. KU 184953–54 consist of 74 and 62 eggs, with mean diameters (N = 10) of 3.6 (3.2–3.9) and 3.7 (3.3–3.9), respectively. Neither of the females (KU 178853 and 178855) that laid the clutches had any eggs remaining in the ovisacs.

Mating call.—The mating call of *P. perinesos* has not been recorded. I have heard individuals calling the field and the call is a single "cluck."

Distribution.—*P. perinesos* is known from three localities along the Quito–Lago Agrio road in the valley of the upper Río Coca (Río Quijos) on the Amazonian slopes at elevations of 1,410–1,740 m. Almost all known specimens are from the type-locality at the Río Salado; one specimen has been taken near the Río Reventador (Fig. 1). *P. buckleyi* is sympatric with *P. perinesos* at the Río Salado and the Río Azuela sites. The presence of *P. perinesos* at the latter locality is based solely on larval specimens (see *Tadpoles*); only *P. buckleyi* is known from the Río Azuela by adult specimens.

Ecology.—*P. perinesos* is found in subtropical rainforest. Most of the specimens have been collected near a pond in cutover area near the Río Salado. I have commented previously (Cannatella, 1980) on the occurrence of *P. perinesos* and *P. buckleyi* at the same pond. Other anuran species collected at the Río Salado include *Bufo*

that for the TIB/SVL ratio, the probability that the bivariate observation for *P. duellmani* or *P. ecuatoriana* was drawn from the *P. perinesos* population is less than 0.01, and for *P. baltea* $0.05 > P > 0.01$. I interpret a P of less than 0.05 as supportive evidence for the hypothesis that a given species is distinct from *P. perinesos*; however, lack of a significant difference does not falsify the hypothesis.

It is curious that *P. ecuatoriana,* which is most similar in color pattern to *P. perinesos,* is nonetheless very different in the morphometric ratios. Because an error in the measurement of SVL in *P. ecuatoriana* would produce a systematic deviation in the ratio data, I have used "Standard length"—the distance from the tip of the snout to the tip of the urostyle—as an additional assessment of body length. For *P. perinesos* the correlation coefficient of SVL and standard length was 0.99 ($P \ll 0.001$). A reanalysis of the ratio data for *P. perinesos* and *P. ecuatoriana* yielded results virtually identical to those obtained previously—the ratios of *P. ecuatoriana* are all significantly different from those of *P. perinesos* at $P < 0.01$.

Ecology.—Duellman (1979) compared the herpetofaunas of seven cloud forest communities. Three of these assemblages (Calima, Dos Ríos and Zapadores) are on the Pacific versant of Ecuador and Colombia; no phyllomedusines are present in these three communities. The four other communities—El Pepino in Colombia, Azuela and Salado in Ecuador and Cosnipata in Perú—are Amazonian versant groups. Of these, the Azuela and Salado communities both include *P. perinesos* and *P. buckleyi*; no phyllomedusines are known from the other two sites.

The species of these latter four communities can be divided into groups based on reproductive mode, type of water in which the larvae live, and whether the species is endemic to cloud forests or not. One obvious pattern in the data is that certain taxonomic groups belong exclusively to one category and are characterized by distinct reproductive patterns: *Eleutherodactylus* and hemiphractine and amphignathodontine hylids have only direct development; *Centrolenella* are stream-breeders. A second significant feature is that few of the pond-breeding frogs are endemic to, or occur in, cloud forests. Duellman (1970) noted that for the total number of Middle American hylids occurring at given altitudes from 0–2,000 m, the number of pond-breeders is indirectly proportional to the number of stream-breeders. Among the Middle American hylids, only *Hyla ebraccata* and the phyllomedusines deposit their eggs on foliage hanging over ponds.

Of the endemic cloud forest pond-breeders of the four cloud forest communities, only *P. perinesos* deposits its eggs on vegetation over lentic water. *Phyllomedusa buckleyi* also oviposits in this fashion, but is not endemic to cloud forests (Cannatella, 1980). With the exception of the stream-adapted *Phyllomedusa guttata* group, all phyllomedusines for which the data are known oviposit in this way. Thus, the reproductive mode of these *Phyllomedusa* species is not an adaptive novelty related to the paucity of pond-breeders in cloud forests, but rather is a primitive constraint of their phylogeny. Although the data are lacking for *P. baltea* and *P. ecuatoriana,* the *Phyllomedusa perinesos* group is probably the only group of cloud forest pond-breeding frogs that oviposit on vegetation.

Relationships and biogeography.—The purple coloration on the hands, feet, flanks and concealed surfaces; and the purple belly with white granules is a derived character (synapomorphy) for the species of the *P. perinesos* group. No other phyllomedusines are colored in this way.

The data that might clarify relationships within the *P. perinesos* group are meager. *P. ecuatoriana* and *P. perinesos* possess single, discrete orange blotches on the anterior and posterior thighs (Fig. 6). This may be a derived character-state; no other phyllomedusines possess such spots. However, one could consider the absence of orange spots on the uniformly purple thighs of *P. baltea* to be derived from the character-state of orange spots on otherwise purple thighs. In this case the orange spots of *P. perinesos* and *P. ecuatoriana* would be a shared primitive feature.

The most recent diagnoses of the phyllomedusine genera (Duellman, 1970) state that *Phyllomedusa* lack reticulated palpebra, and *Agalychnis* (except *A. calcarifer*) and *Pachymedusa* possess reticulated palpebra. However, both *P. baltea* and *P. duellmani* have lightly reticulated palpebra, and *P. perinesos* and *P. ecuatoriana* have scattered pigment flecks on the palpebrum, a condition that appears to be an incomplete reticulation. In addition, *P. guttata, P. tom-*

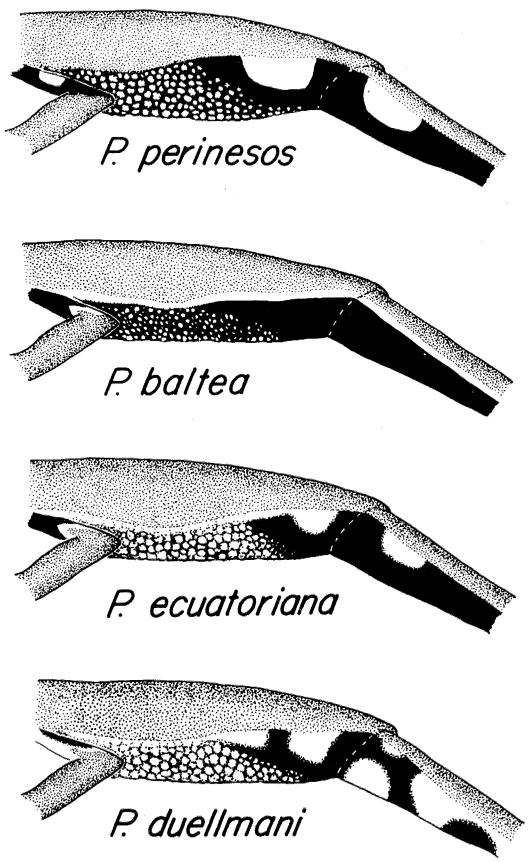

Fig. 6. Color pattern of the *P. perinesos* group. Solid black is purple in life, stippled regions are green, and the white areas of the flanks and limbs are orange. The belly granules are white.

opterna and a few other *Phyllomedusa* have scattered flecks. The presence of a reticulated palpebrum is probably a primitive character for phyllomedusines, because *Agalychnis* and *Pachymedusa,* which are among the most primitive phyllomedusines, possess that character state. The reduction of the network to scattered flecks of pigment, or to no pigment at all is a derived state; this loss possibly has occurred several times within the Phyllomedusinae. On the basis of scattered flecks on the palpebrum, *P. perinesos* and *P. ecuatoriana* can be considered to be sister-species. The relationships of *P. baltea* and *P. duellmani* to each other or to the other species is not clear, however.

To account for the presence of *P. baltea* in the Serranía de Sira, Duellman and Toft (1979) postulated a southward migration along the Andes of a *Phyllomedusa* stock during times of Pleistocene climatic depression. An alternative scenario is equally reasonable: the immediate ancestor of the *P. perinesos* group was present along the proto-Andean slopes of Ecuador and Perú. The fragmentation and speciation of this ancestral species possibly was associated with the major orogenies of the Andes and the formation of the Huancabamba Depression. Data from microcomplement fixation studies of serum albumin indicate that *P. perinesos* diverged from other phyllomedusines about 35–40 mybp, about 60–70 immunological distance units (Linda Maxson, pers. comm.). The correlation of immunological distances with geologic time is possible only if one assumes that the rate of albumin evolution is constant. The assumption has been contested recently (Farris et al., 1979), but because the issue is not settled, I have accepted the evolutionary clock hypothesis for the purposes of this discussion. Because the species is a member of a monophyletic species group, the group itself must be at least as old. The *P. perinesos* group thus probably had its origin in the Eocene.

Current trends in biogeographic analysis emphasize the vicariance of biotas with subsequent allopatric speciation. If such a mechanism obtains, then one can expect that the cladograms of relationships of various groups of organisms will be largely congruent and will indicate the broad historical patterns of the evolution of the biota (Rosen, 1978). In the specific case at hand, one can expect that if the formation of the Huancabmba Depression was significant in the vicariance of a species clade, then the species on at least one side of the barrier will be each others' closest relatives. This is the case with *Gastrotheca*; microcomplement fixation studies have shown that the Andean *Gastrotheca* north of the Huancabamba Depression are more closely related to each other than they are to *Gastrotheca* south of the Depression (Scanlan et al., 1980). The meager data suggest that this may also be the case with the *P. perinesos* group when intra-group relationships are better understood. Analysis of relationships by both morphological and biochemical studies of other groups such as *Atelopus, Telmatobius,* and the *Bufo spinulosus* complex would add valuable insights into the biogeography and evolution of the northern Andes.

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Specimens Examined

Phyllomedusa baltea.—PERÚ: Huánuco: West slope Serranía de Sira, "Laguna," 1,280 m, KU 154746 (holotype), 154747–48 (paratypes), 174714 (larvae).

Phyllomedusa duellmani.—PERÚ: Amazonas: 8 km NNE Balzapata, 1,850 m, KU 181813 (holotype), 181814 (paratype), 181886 (larvae), 181887–88 (eggs); 10 km NNE Balzapata, 1,910 m, 181885 (larvae).

Phyllomedusa ecuatoriana.—ECUADOR: Morona-Santiago: Agua Rica, 1,890 m, USNM 215750 (holotype).

Phyllomedusa perinesos.—ECUADOR: Napo: Río Salado, ±1 km upstream from Río Coca, 1,410 m, KU 146562 (holotype), 164450–73, 166318–19, 178851–87, 179569–72, 184953–54 (eggs), FMNH 204282–86, UMMZ 143363; 2 km SSW Río Reventador, 1,490 m, KU 164474; Salado (km 124), 1,420 m, KU 179176, 180363–64 (eggs); Río Azuela, 1,740 m, KU 179177 (larvae).

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