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A New Poison Frog from Manu National Park, Southeastern Peru (Dendrobatidae, *Epipedobates*)

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ABSTRACT

Epipedobates macero is a new species of dendrobatid poison frog from lowland rain forest of the Manu National Park, in the upper Madre de Dios drainage of southeastern Peru. It is most sim-

ilar to a few other species occurring along the Andean front in eastern Peru, namely *E. petersi* and *E. cainarachi*, which differ in details of coloration, morphology, and vocalization.

RESUMEN

Epipedobates macero, especie nueva, es un dendrobátido venenoso de la selva pluvial baja del Parque Nacional del Manu, en el drenaje del Río Alto Madre de Dios, al sudeste del Perú. Es similar a otras dos especies que ocurren en los bosques

del llano amazónico al pie de los Andes orientales peruanos, a saber, *E. petersi* y *E. cainarachi*, las cuales difieren en detalles de coloración, morfología, y vocalización.

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INTRODUCTION

The western edge of Amazonia, at low to moderate elevations along the Andes, may have been an important region of speciation or refuge³ for dendrobatid frogs of the genus *Epipedobates*. Eleven of 24 species recently assigned to this genus (Myers, 1987; Schulte, 1989; Jungfer, 1989) have fairly restricted distributions within that segment of the Andean front between parallels 2° North (southern Colombia) and 16° South (northern Bolivia). With a few exceptions, the other species are either more widespread in the Amazonian basin or else occur on the Pacific versant of Colombia and Ecuador.⁴

A twelfth species of *Epipedobates* (fig. 1) endemic to extreme western Amazonia is named here: It came to the attention of the first author in 1985 during a preliminary faunal survey of Manu National Park, in the upper Madre de Dios drainage of southeastern Peru. It has since been listed by Rodríguez (1987; see also Rodríguez and Cadle, 1990) as a new species being described by Rodríguez and Myers. Schulte (1987) and Jungfer (1989) also mentioned its existence on the basis of a photograph taken by one of the Park's early visitors.

³ These two concepts of course are not mutually exclusive, inasmuch as postulated refugia may be theorized as centers of speciation. But virtually every part of mainland tropical South America has been designated a Pleistocene refuge for one kind of organism or another, usually without supporting data other than current distributions. Distribution maps alone cannot differentiate between recent speciation, impending extinction, or a range of other possibilities.

⁴ The genus *Epipedobates* Myers was erected explicitly to accommodate the basal, plesiomorphic assemblage of lipophilic-alkaloid producing dendrobatids. These species can be arranged in species groups (although only one is demonstrably monophyletic), but relationships among the groups are unknown. As recommended by Myers (1987: 303), "further splitting is inadvisable unless two or more separate lineages can be objectively [i.e., phylogenetically] determined." For that reason (with further comments by Myers et al., 1991: 18), we follow Schulte (1989) in considering, for the time being, the 1988 names *Allobates* Zimmermann and Zimmermann and *Phobobates* idem as junior synonyms of *Epipedobates*.

Epipedobates macero, new species

Figures 1–9

HOLOTYPE: MHNSM 0726 (formerly MHNJP 2001), an adult female collected on October 21, 1985, by Lily Rodríguez, on west side Río Manu across from Cocha Cashu Biological Station,⁵ Parque Nacional del Manu, about 380 m elev., Department of Madre de Dios, Peru (fig. 2).

PARATYPES: A total of 17 adults—plus juveniles and larvae—all from Parque Nacional del Manu in Depto. Madre de Dios, as follows: AMNH A-129473, 129474 (juv.), 129475 (4 dorsal tadpoles from 129473), 133205, 133206 (6 froglets), 133207 (2 free-living tadpoles); 134159–134163; MHNSM 3834 (skinned carcass), 3837, 3838, 3841 (skinned carcass), 9093; MHNNP (Paris) 1989.3605–1989.3607; USNM 322909, 322910 (juv.)—preceding all collected at the type locality across river from Cocha Cashu Biological Station, 1986–1989, by Lily Rodríguez et al. AMNH A-134088, near Tayakome (Machiguenga Indian village), 450 m, 11°53'S, 71°25'W, collected on August 9, 1986, by André Bärtschi.

ETYMOLOGY: The species name *macero*, a noun in apposition, is the Machiguenga Indian word for "frog." The Machiguenga are one of the indigenous tribes of the Río Manu region.

DEFINITION AND DIAGNOSIS: A medium-size dendrobatid with an adult snout-to-vent length (SVL) of about 24–30 mm. Head and back bright red and strongly granular; sides black, with a bright yellow stripe extending obliquely from groin to above shoulder; yellow labial stripe not reaching snout; a yellow spot on anterodorsal base of thigh; ventral surfaces blue with black reticulum. Lacking axillary and groin spots and lacking a concealed calf spot on proximoventral part of

⁵ Stephens and Traylor (1983: 57) placed Cocha Cashu at approximately 11°51'S, 71°19'W, at an elevation of about 400 m above sea level. Terborgh et al. (1984) stated that Cocha Cashu is "located about 45 km northwest (= 80 river km upstream) from the mouth of the Río Manu . . . 11°55'S, 77°[error for 71°]18'W; elev. approx. 380 m."

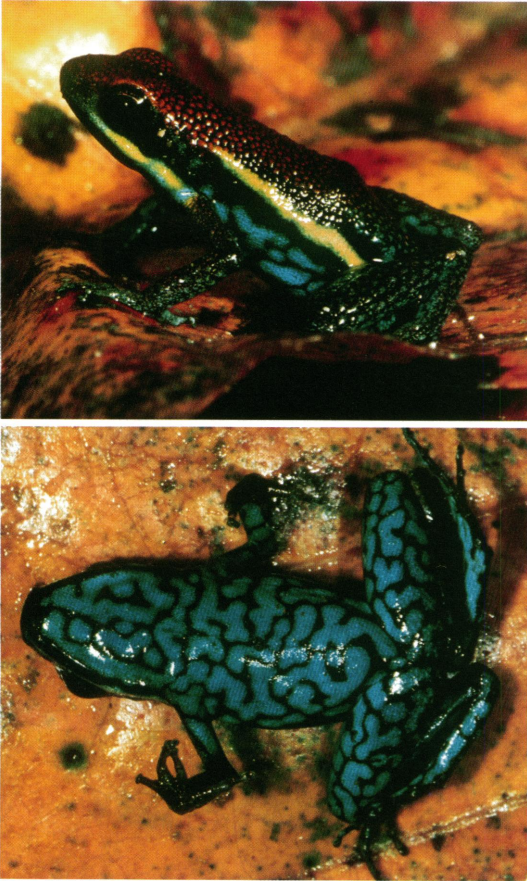


Fig. 1. *Epipedobates macero*, new species. Lateral and ventral views of a living specimen photographed on September 8, 1986, at Tayakome, Parque Nacional del Manu. [Courtesy André Bärtschi]

shank. Teeth present on maxillary arch. Appressed first finger about equal to second; finger discs weakly to moderately expanded; third finger disc of adults about 1.3–1.7 times wider than finger. Toes completely without webbing. Advertisement call a train of short, harsh notes at a dominant frequency of 3500 Hz; terrestrial. Defensive skin alkaloids include a pyrrolizidine oxime and members of the decahydroquinoline and histrionicotoxin classes of dendrobatid alkaloids.

Epipedobates macero is a member of the *E. petersi* species group (sensu Schulte, 1989). It is similar in morphology and basic color pattern (fig. 1) to *E. cainarachi* (fig. 11) and

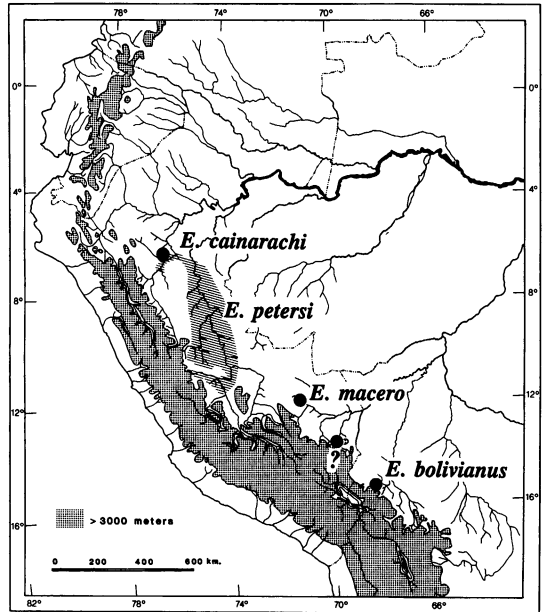


Fig. 2. Western Amazonia, showing distributions of the species of *Epipedobates* discussed in this paper. Distribution of *E. petersi*—in the Río Ucayali and part of the Río Huallaga drainages—is based mainly on the type specimens mapped and listed in Silverstone (1976: 19, 37). The questioned locality is for *petersi* paratypes from La Union in the Río Tambobata drainage (Madre de Dios drainage), Depto. Puno, extreme southeastern Peru. See footnote 10.

E. petersi (fig. 12), but *E. macero* differs from these in that the oblique lateral stripe and the labial stripe are both incomplete. In *E. macero*, the anterior terminus of the oblique lateral stripe lies above or slightly anterior to the shoulder (conspicuously short of the eye) and the labial stripe usually does not extend rostrad from the eye (conspicuously short of the narial region). Also, there are differences in color in life: The central Peruvian *E. petersi* has a brown dorsum, a pale (yellowish, perhaps with greenish tinge) oblique lateral stripe continuous to the eye, and a pale (white or yellowish) labial stripe extending anteriorly to the end of the snout. *Epipedobates macero* is more similar to the geographically distant *E. cainarachi* (NW Peru, fig. 2) in that both have red dorsa and yellow stripes, but *E. cainarachi* has a slightly longer first finger,

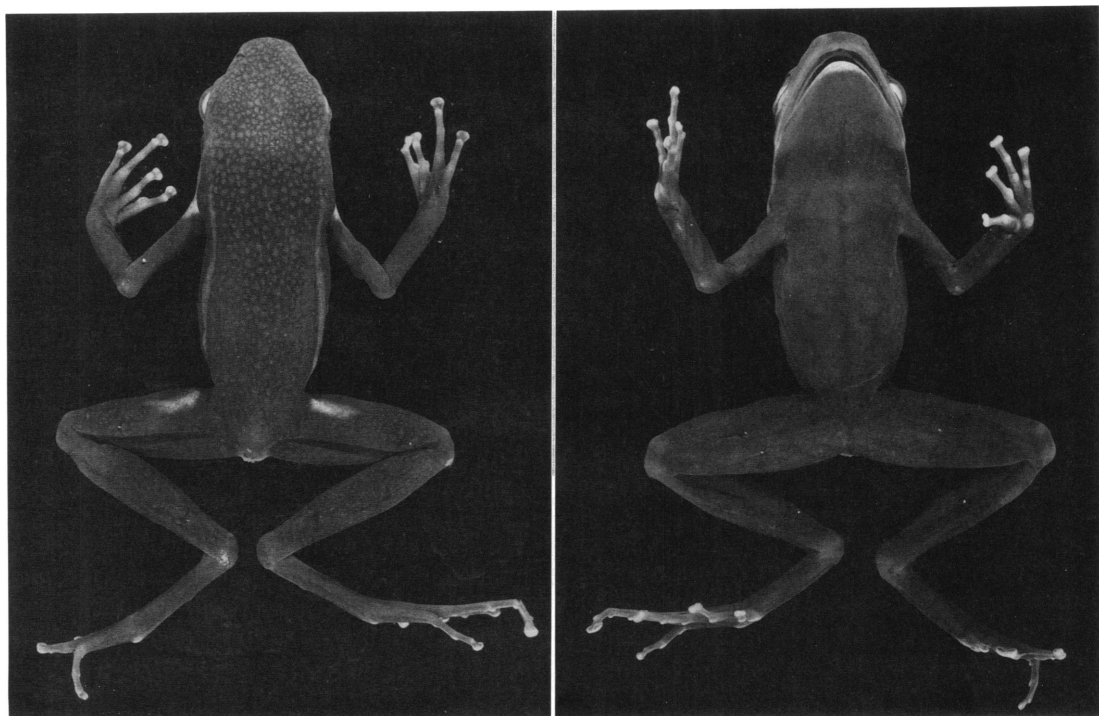


Fig. 3. *Epipedobates macero*, new species. Dorsal and ventral views of holotype (MHNSM 07269), $\times 2$.

its coloration seems less bright and/or more variable, and its stripes are complete as in *E. petersi*. See Notes on Other Species for further comment and apparent differences in vocalizations.

MEASUREMENTS OF HOLOTYPE (in mm): The undissected holotype (fig. 3) is a female judged to be sexually mature because of its size; it has toes 2–3 aberrantly fused on the left foot but appears normal in all other respects. Length from snout to vent 27.3; tibia length between heel and outer surface of flexed knee 14.8; greatest width of body 8.4; head width between angles of jaws, and between outer edges upper eyelids, 8.5, 7.6 respectively; approximate width of interorbital area 3.0; head length (sagittal) from tip of snout to angle of jaw 7.3; tip of snout to center of naris (sagittal) 0.8; center of naris to anterior edge of eye 2.8; distance between centers of nares 3.5; eye length from anterior to posterior edge 3.5; horizontal diameter of tympanum roughly 1.6; corner of mouth to lower edge of tympanic ring 0.7; hand length from proximal edge of large medial palmar tubercle to tip of

longest (third) finger 7.6; width of disc of third finger (and width of penultimate phalanx below disc) 1.0 (0.6); width of discs (and penultimate phalanges below discs) of third and fourth toes 1.0 (0.6) and 1.2 (0.7), respectively.

DESCRIPTION OF TYPE SERIES

External Morphology: A medium-size dendrobatid, with adult males attaining a size of about 27 mm SVL and adult females about 30 mm SVL (measurements and proportions summarized in table 1). Dorsal skin of head, body, and hind limbs coarsely and conspicuously granular; skin smooth on forelimbs, sides of head and body, and ventral surfaces. Head wider between jaw articulations than between outer edges of upper eyelids; head somewhat narrower than body (usually) or about as wide. Head width between angles of jaws 30–38 percent of SVL. Snout sloping, bluntly pointed or rounded in profile, truncately rounded (usually) or bluntly pointed in dorsal and ventral aspect. Nares situated

TABLE 1
Size and Proportions of Adult *Epipedobates macero*, New Species, from the Type Locality

Character	N	Mean \pm 1 SE	SD	CV (%)	Range
Snout-vent length (SVL) in mm ^a	5♂	25.70 \pm 0.29	0.64	2.49	25.0–26.5
	12♀	28.59 \pm 0.18	0.62	2.16	27.3–29.5
Tibia length ^b /SVL	4♂	0.510 \pm 0.008	0.017	3.24	0.49–0.53
	11♀	0.503 \pm 0.006	0.021	4.08	0.47–0.54
Head width ^c /SVL	4♂	0.338 \pm 0.016	0.032	9.38	0.31–0.38
	11♀	0.316 \pm 0.003	0.008	2.68	0.30–0.33
Center naris to edge eye/eye length	4♂	0.748 \pm 0.034	0.067	9.01	0.69–0.84
	11♀	0.793 \pm 0.012	0.039	4.96	0.72–0.85
Hand length ^d /SVL	4♂	0.277 \pm 0.009	0.019	6.70	0.26–0.30
	11♀	0.273 \pm 0.003	0.009	3.39	0.25–0.29
Hand length/head width	4♂	0.822 \pm 0.022	0.045	5.44	0.77–0.87
	11♀	0.864 \pm 0.008	0.028	3.21	0.81–0.90
Width 3rd-finger disc/finger width below disc ^e	4♂	1.387 \pm 0.048	0.096	6.92	1.29–1.50
	11♀	1.526 \pm 0.037	0.121	7.94	1.33–1.67

^a An additional 55 living frogs were measured in the field, including 11♂ (24–26 mm SVL), 6♀ (28–29 mm), 38 small juveniles (9.9–12.8 mm, \bar{x} = 10.7 \pm 1.4 mm), and two larger juveniles 14 and 15.8 mm SVL.

^b Tibia length is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating the length of the tibiofibula.

^c Greatest head width as measured between jaw articulations.

^d Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.

^e Digit width measured near distal end of penultimate phalanx.

near tip of snout and directed posterolaterally; nares visible from front and from below but not from above. Canthus rostralis rounded; loreal region nearly vertical, slightly concave to flat. Interorbital distance wider than upper eyelid. Eye nearly equal to snout length; distance from center of naris to eye 69–85 percent of eye length. Tympanum nearly half of eye size, concealed dorsally and postero-dorsally.

Hand (fig. 4) moderately large, its length 25–30 percent of SVL and 77–90 percent of head width between jaw articulations. Relative lengths of *appressed* fingers 3 > 4 \approx 2 \approx 1; fingers 1, 2, and 4 all approximately equal when appressed, with overlapping discs; appressed first finger varies from slightly shorter to barely longer than second. Finger discs weakly to moderately expanded; third finger disc averaging 1.4–1.5 times wider than distal end of adjacent phalanx. A large outer metacarpal tubercle on base of palm and a smaller inner metacarpal tubercle on base of first finger, these being relatively low, with rounded surfaces. One subarticular tubercle

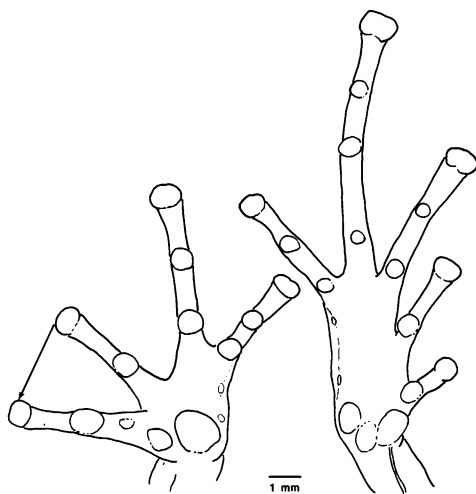


Fig. 4. Left hand and right foot of *Epipedobates macero*, new species (MHNSM 3837, ♀ paratopotype). Arrow indicates position of shorter digit when the first two fingers are appressed; finger 1 varies from slightly shorter than finger 2 to slightly longer (as in this specimen).

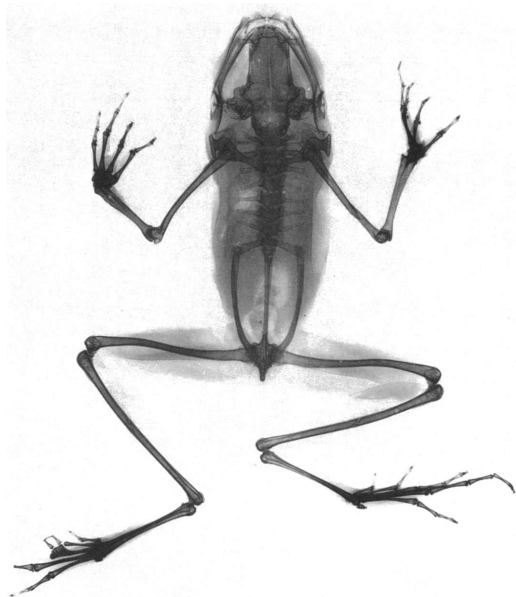


Fig. 5. *Epipedobates macero*, new species. Radiograph of female holotype, $\times 1.8$.

on fingers 1, 2, and two subarticular tubercles on fingers 3, 4; all subarticular tubercles well developed and prominently raised. Several other very small tubercles discernible on hands of some specimens, as on proximal part of first finger between subarticular tubercle and inner metacarpal tubercle, and on lateral side of palm on a faint outer metacarpal fold. Keel along sides of fingers extremely faint, not forming fringe.

Hind limbs long, with heel of adpressed limb reaching to eye or between eye and tip of snout. Tibia 47–54 percent of SVL. Relative lengths of appressed toes $4 > 3 > 5 > 2 > 1$; first toe reaching base of subarticular tubercle of second. No basal webbing or toe fringes (ventrolateral keeling very weak); keel from lateral side of toe 5 sometimes forming a weak outer metatarsal fold, extending onto sole toward outer metatarsal tubercle. Toes with moderately expanded discs as wide or wider than finger discs (fig. 4). One to three prominently raised subarticular tubercles (one each on toes 1, 2, two each on 3, 5, and three on 4); no basal webbing. Two or three large metatarsal tubercles, with low, rounded surfaces: inner metatarsal tubercle slightly larger than outer metatarsal tubercle; a smaller me-

dian metatarsal tubercle, sometimes absent or faint, situated between and slightly proximal to the inner and outer tubercles. Several other very small tubercles discernible on some specimens, especially on the weak outer metatarsal fold (these tiny tubercles tending to occur even if the outer metatarsal fold is absent).

Distal half of tarsus with tarsal keel bearing a slightly raised tubercle at proximal end; ventrolateral side of tarsus tending to be rugose or tubercular.

COLOR PATTERN: In life, the noticeably granular dorsum is dark, bright red in adult frogs (fig. 1); the flanks are black, with a distinct bright yellow stripe that extends obliquely from the groin to a dorsolateral terminus above the shoulder or between arm and tympanum (not reaching eye). A yellow labial stripe commences below the middle or anterior edge of eye (rarely in front of eye) and extends posteriorly under eye and tympanum to the anteroproximal part of upper arm; there may be a suffusion of light green on the side of the snout anterior to the eye. There is a bright yellow spot on the anterodorsal base of thigh above groin (see fig. 3); there is no calf spot and no pale markings in axilla or groin. The limbs are basically black but may be extensively suffused with green and bronze speckling and spotting (fig. 1). The ventral surfaces are overall blue, sometimes bright, in a dark reticulum that varies in life from boldly black (fig. 1) to weak blackish gray.

In preservative, the bright yellow and red pigments fade to pale gray; the blue ventral surfaces fade to gray in a dark reticulum of variable distinctness.

OSTEOLOGY

Teeth are present on the maxillary arch, as confirmed for most of the type specimens.

Additional data are obtainable from an X-ray photograph of the holotype (fig. 5): The skull is nearly as wide as long. Frontoparietals in medial contact throughout. Sphenethmoid large, in close contact with anterior ends of frontoparietals. Small teeth present on maxillae and premaxillae. Mandible with a pronounced retroarticular process. Eight presacral vertebrae, with no obvious fusions; sacral diapophyses barely dilated. Phalangeal for-

mula of hands 2-2-3-3, of right foot 2-2-3-4-3 (left foot malformed). Each normal digit with a short, prominently T-shaped terminal phalanx, with the transverse process lying nearly at the middle of the fleshy disc.

MYOLOGY

Examination of two skinned carcasses (MHNSM 3834, 3841), showed jaw and thigh musculature typical of most dendrobatids (e.g., see Myers et al., 1991: 8-9). Flesh color of the preserved carcasses is light gray (in a range of white to black among species and species groups within the Dendrobatidae).

The massive superficial slip of the m. depressor mandibulae originates from the dorsal fascia and overlaps the posterodorsal margin of the tympanic ring. A largely concealed, deeper slip of this muscle originates dorsally from the otic ramus of the squamosal and anteriorly from the posterior margin of the tympanic ring.

There is no m. adductor mandibulae externus superficialis. The mandibular branch of the trigeminal nerve laterally crosses the deeper m. adductor mandibulae posterior subexternus, which apparently originates partly from the anterior edge of the squamosal (zygomatic ramus abbreviated) and partly from the anterior margin of the tympanic ring. (Intrafamilial variation in the origin of this muscle is presumably correlated with degree of development of the squamosal zygomatic ramus.)

On the thigh, the distal end of the m. gracilis complex is pierced by the tendon of insertion of the deep m. semitendinosus, as is typical of dendrobatids.

DORSAL TADPOLES

One male had four tadpoles (AMNH A-129475) on its back, but these were dislodged and died in the collecting container before preservation; consequently they are in poor condition, but some basic data are obtainable.

The larvae are in stage 25 of the Gosner system (external gills absorbed, limb buds not evident). The following description is a composite but mainly based on the best preserved individual (fig. 6), which has the following measurements in mm: head-body length 4.8;

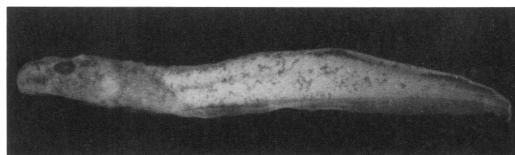


Fig. 6. Tadpole of *Epipedobates macero*, new species. Stage 25 larva (AMNH A-129475, 1 of 4) from back of male paratopotype, $\times 4.5$.

greatest body width > 2.2 (shriveled); total length 14.1; greatest tail depth from top of dorsal fin to bottom of ventral fin 2.0; width of oral disc about 1.

HABITUS: Head-body in dorsal perspective an elongated ellipse rounded at both ends; head and body depressed (width distinctly greater than depth), slightly convex above, flat or slightly concave below. Eyes and nostrils in a dorsal position, with eyes directed anterolaterally. Sinistral spiracle positioned nearly midway between dorsum and venter; anus dextral. Long, low-finned tail about 66 percent of total length, with a depth of about 14 percent of total length. Dorsal fin very low anteriorly, barely reaching body. Tail tip bluntly pointed (i.e., not conspicuously rounded).

PIGMENTATION: Head and body medium gray in preservative, with rather uniformly distributed melanophores. Tail much paler: caudal musculature sparsely pigmented with irregularly distributed small cluster of melanophores; nearly unpigmented tail fins bearing few melanophores, mostly on dorsal fin.

MOUTH PARTS: The tooth-row formula is $2/3$, with the second upper row broken above the beak. The beak is narrowly keratinized and has very finely serrated cutting edges. The lateral and posterior edges of the laterally indented oral disc bear a single row of at least 19 or 20 large, bluntly pointed papillae.

FREE-LIVING TADPOLES

Free-living larvae occur in shallow streams (see under Natural History following). Two specimens (AMNH A-133207), in Gosner stages 30 and 31, are available for this description. They agree rather well with the above description of dorsal, stage-25 tadpoles (from the back of a nurse frog), with few points of departure.

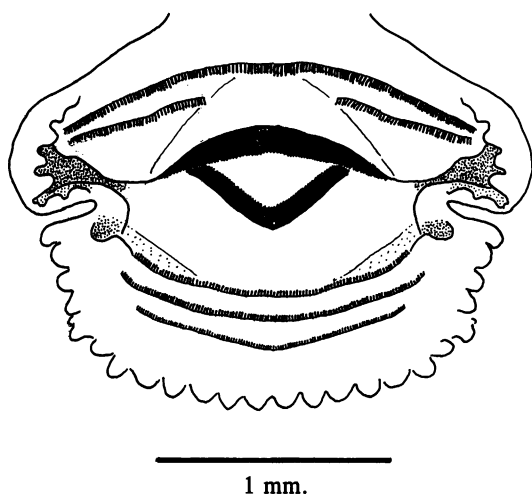


Fig. 7. Mouth of *Epipedobates macero* tadpole, stage 30 (AMNH A-133207, 1 of 2). Semi-diagrammatic, with broken upper beak reconstructed in drawing.

Measurements of the two are as follows (stage 30/stage 31): head-body lengths 8.0/8.2 mm; greatest body widths 4.9/5.0 mm; total lengths 23.5/23.4 mm; greatest tail depths from top of dorsal fin to bottom of ventral fin 3.8/4.0 mm; width of oral discs 2.3/2.3 mm. Tail length/total length 0.66/0.65; tail depth/total length 0.16/0.17. Eyes dorsolaterally located, directed anterolaterally; nostrils directed laterally or anterolaterally. Spiracle positioned somewhat ventral to midpoint between dorsum and venter. Low-finned tail *not* reaching body. Tail sparsely pigmented with clumps of melanophores (but see color change under Natural History).

Mouth parts (fig. 7) similar to those of dorsal tadpoles. The beak remains narrowly keratinized and the third lower (posteriormost) tooth row remains weakly keratinized. There seem to be about twice the number of blunt labial papillae along the posterior edge of the oral disc, but the dorsal larvae are in too poor condition for accurate counts and verification. These papillae form a single row in both early (25) and later (30–31) stages (i.e., no ontogenetic change to a double row).

POSTMETAMORPHIC CHANGES

Recently metamorphosed froglets of 9.9–10.5 mm SVL (caliper measurements in life)

are totally black. Pale lateral lines and a pale thigh spot then appear, followed by a blue coloration ventrally; a few granulations turn brown-red on the head. Finally, the lateral line and thigh spot turn bright yellow-green; pigmentation on dorsal granules is now red and extending posteriorly over the dorsum. By this time, the froglets exceed 10.5 mm SVL.

SKIN TOXINS

Methanolic extract of a single skin of topotypic *Epipedobates macero* contained 20 dendrobatid alkaloids in an estimated total amount of 100–150 $\mu\text{g}/100$ mg skin (J. W. Daly, personal commun.).

The one major compound present was dendrobatid alkaloid **236**, an uncommon pyrrolizidine oxime⁶ previously reported only from two populations of the *Dendrobates pumilio* complex (Daly et al., 1987, tables 4–5). Half of the minor and trace alkaloids (10 of 20) belonged to the histrionicotoxin class, including alkaloid **259A**, histrionicotoxin (**283A**), isodihydrohistrionicotoxin (**285A**), neodihydrohistrionicotoxin (**285B**), and alodihydrohistrionicotoxin (**285C**). Other minor and trace alkaloids (cis- and trans-**243A**, cis- and trans-**219A**, and a **223F**) belonged to the decahydroquinoline class of dendrobatid alkaloids.

VOCALIZATION

The advertisement call (fig. 8) of *Epipedobates macero* is a train of uniform notes that are heard as short (≈ 0.03 – 0.05 sec), high-pitched, rather harsh “peeps,” which are closely spaced and emitted at a rate of 10 notes per second. Call length varies in the range of 2.5–16.4 sec ($\bar{x} = 9.64$ sec, $S.D. = 4.01$ sec) for 29 recorded calls of two or more frogs (AMNH herpetology reel 259). The dominant frequency is held rather constant at about 3500 Hertz throughout the call.

In one call (fig. 8A), the wide-band spectrogram suggests that each note comprises several poorly resolved pulses, an interpretation consistent with the waveform of a sin-

⁶ Such compounds previously were classified as amine alkaloids but their structures were recently revised (Tokuyama et al., 1992).

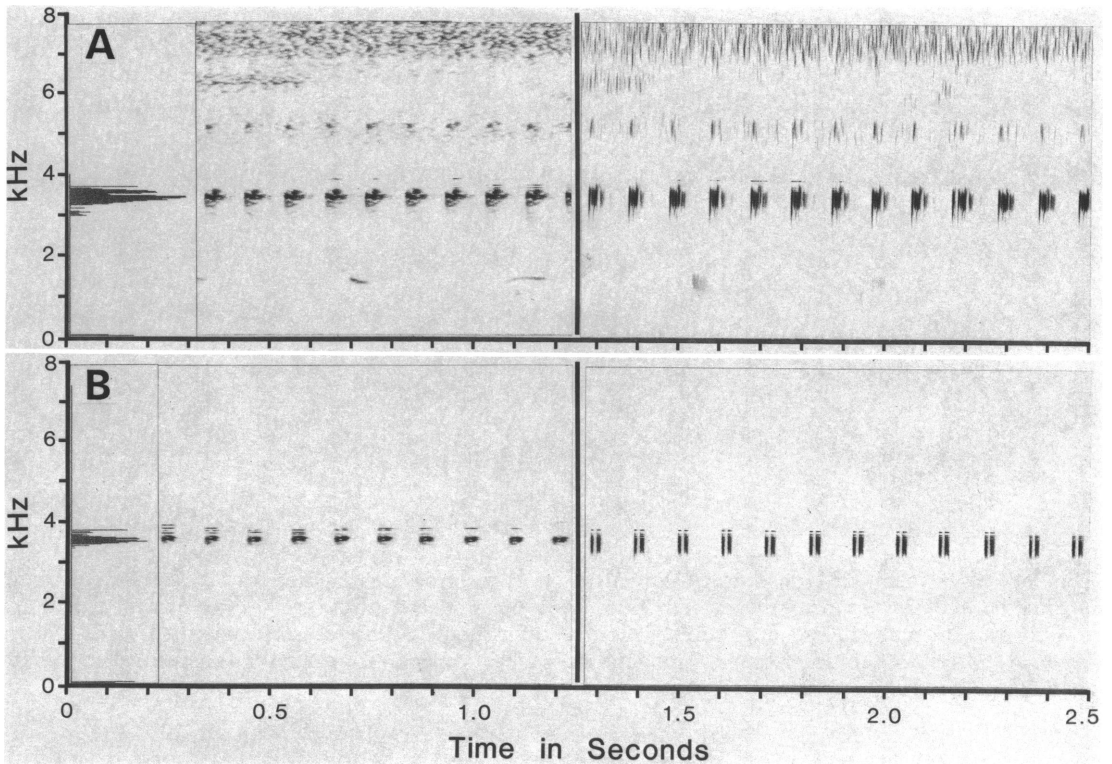


Fig. 8. Advertisement calls from two specimens of *Epipedobates macero*. Sound spectrograms (with sections of first notes) graphed with narrow-band, 45-Hz filter on left side of vertical line and with wide-band, 300-Hz filter on right side. **A.** From middle section of 14.9-sec call, recorded near Tayakome, Parque Nacional del Manu, August 9, 1986, by André Bärtschi; calling frog sitting exposed on dead branch on forest floor, on shore of small stream, 4 p.m., temperature not noted (AMNH herpetology reel 259). **B.** From 5.5-sec call, recorded by L. Rodríguez at type locality, November 5, 1989, in afternoon, at air temperature about 27°C (AMNH herpetology reel 260).

gle note from this sequence of notes (fig. 9A). The wide-band spectrogram in figure 8B, however, shows shorter, "cleaner" notes solely comprising two distinct pulses, one short and one longer (fig. 9B).⁷

Although closely spaced (internote interval ≈ 0.06 sec), the notes are individually perceived; they are poorly tuned and have an unmusical, rather metallic quality. The un-

musical aspect distinguishes this "harsh peep train" kind of call from spectrographically similar "trill calls" (Myers and Daly, 1979).

The preceding description is made in the absence of temperature data for most of the available recordings, so caution is required when comparing new data. Even within lowland rain forest, normal diurnal temperature fluctuation can be expected to cause changes in the vocalization of *E. macero*. For example, note repetition rate is likely to show a positive correlation with temperature, whereas note duration might be negatively correlated.

NATURAL HISTORY

Epipedobates macero is a terrestrial frog of crepuscular calling habits. Calling males were

⁷ Zweifel (1972: figs. 19, 38) similarly showed contrasting sets of "muddy" vs. clean sound spectrograms of New Guinea microhylid frogs. In one case, Zweifel noted (p. 453) that such differences "may in some instances be attributable to the degree of inflation of the vocal sac, but here it seems to be a matter of entire local populations behaving consistently, not just individual variation." In the other case (p. 483), the two kinds of calls were heard at the same locality.

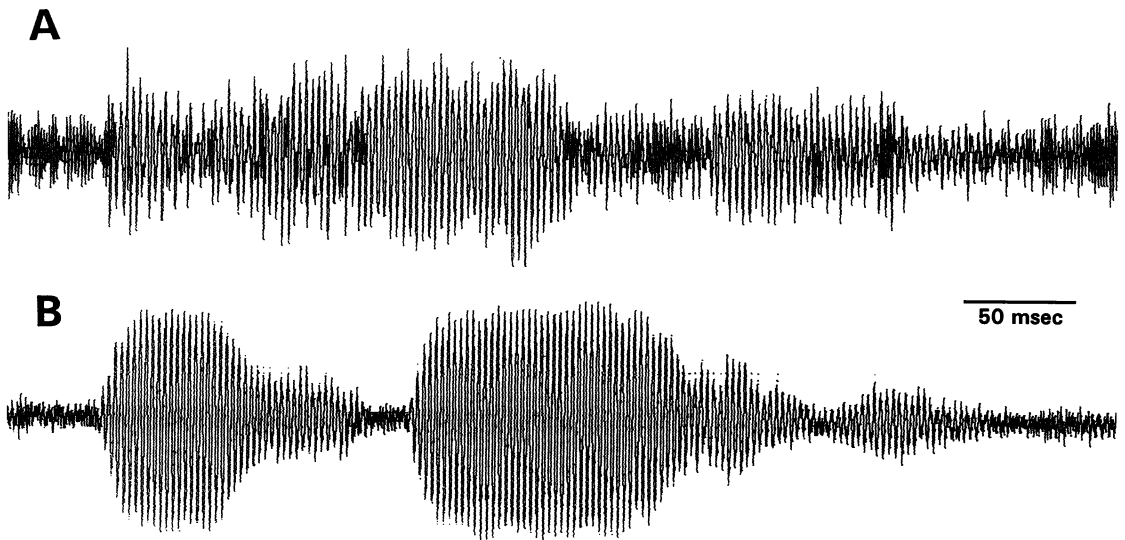


Fig. 9. Waveforms of typical notes shown in sound spectrograms, figures 8A, B. A. This vertically magnified waveform confirms perception from wide-band spectrogram (fig. 8A, right side) that notes are only weakly pulsatile (several "pulses" weakly indicated). B. Waveform (magnified on Y-axis as above) of shorter note comprising two strong pulses, which are clearly shown in the wideband spectrogram (fig. 8B, right side).

observed on the ground or on logs no more than 0.4 m aboveground, near forest streams at places about 1 m above stream level. Calling occurs mainly within a few hours after dawn and a few hours before darkness; it may occur at other times of day, especially on rainy days, but is less frequent.

Two censuses a year apart were made at the end of the dry season (Sept. 9, 1988, and Oct. 2, 1989) in order to assess streamside population density in an area of about 5 m along each side of a forest stream for a distance of 100 m. Average population density along this stream bank was calculated at 9.5 adults + 19 juveniles per 1000 m² (10 ad. [6♂:4♀] + 15 juv. in 1988, 9 ad. [5♂:4♀] + 23 juv. in 1989). *Epipedobates macero* seemed to have disappeared from this habitat when it was subsequently visited during the rainy season (February and March). Evidently it moves away from the stream and more into the forest during the rainy season, but, whether near the stream or in deeper forest, calling has been heard most months of the year.

Stomach contents of one female (26 mm SVL) consisted of 33 prey items, including 13 ants, 12 beetles, 5 unidentified larvae, and 3 other unidentified items. Prey size was in the range of 1.9–7.0 mm, with a mean of 3.4 mm.

Only two tadpole-carrying nurse frogs (both males) have been found, both near streams in October (1986, 1989); one had two and the other had four tadpoles.

Tadpoles were found in shallow, slow moving clear-water streams having sandy tan bottoms, with deposits of dead leaves. The free-living larvae can be distinguished from other, sympatric *Epipedobates* in having a golden metallic stripe along the upper edge of the tail musculature; an interorbital bar is sometimes evident. The free-living larvae appear able to vary color somewhat according to the natural background (pale sand or dark, dead leaves): The tails turned uniformly light tan when a few tadpoles were placed in a white plastic container; the same tadpoles next day acquired a darkening of brown tail spots after being transferred to a dark background of dead leaves.

NOTES ON OTHER SPECIES

Epipedobates bolivianus (Boulenger)

Figure 10

Prostherapis bolivianus Boulenger, 1902: 397. Syntypes: Two specimens [BMNH 1947.2.13.89–90] from San Carlos, 1200 m, [Depto. La Paz], Bolivia, and one [BMNH 1947.2.13.91] from S. Ernesto, 800 m, [Depto.

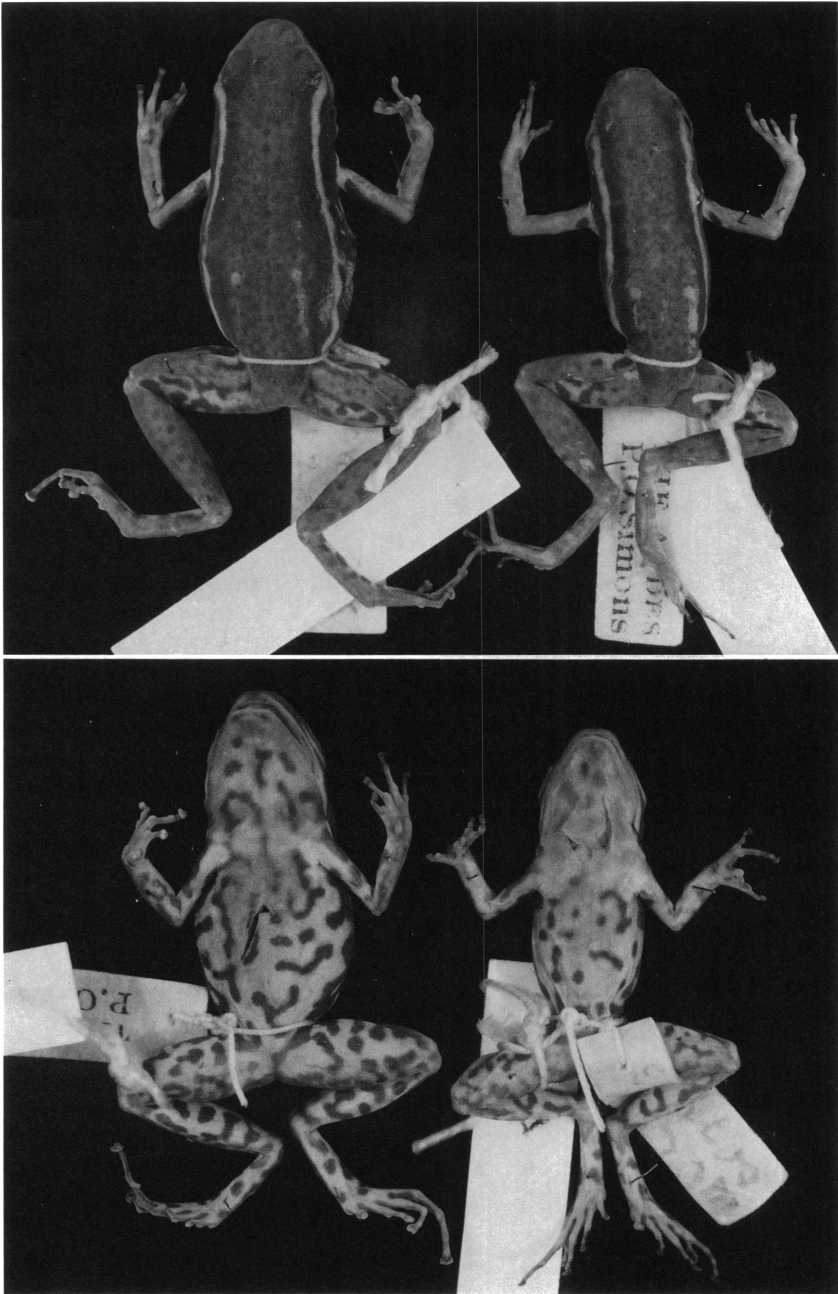


Fig. 10. *Epipedobates bolivianus* (Boulenger, 1902). **Left**, BMNH 1947.2.13.89 (lectotype); **Right**, BMNH 1947.2.13.90 (paralectotype), $\times 2$.

La Paz], Bolivia; collected by P. O. Simons. Lectotype = BMNH 1947.2.13.89, designated by Silverstone (1976: 35).

Epipedobates bolivianus is a poorly known species that occurs at higher elevations, several hundred kilometers to the southeast of

E. macero (see map, fig. 2). Direct comparison showed that resemblance between the two species is only superficial, but we take this opportunity to publish photographs of two type specimens of *E. bolivianus* for permanent record (fig. 10).



Fig. 11. *Epipedobates cainarachi* Schulte, 1987. Specimen (KU 211973) from 14 km Shapaja, Depto. San Martín, Peru. [Courtesy William E. Duellman]

The two specimens of *E. bolivianus* compared with specimens of *E. macero* were the adult female lectotype (25.6 mm SVL) and an adult male paralectotype (22.3 mm SVL). These specimens differ from *macero* in having conspicuously paler venters that were probably white or yellow in life (rather than blue as in *macero*), anterior and posterior surfaces of thighs conspicuously marbled like ventral surfaces (thighs dark in *macero* except for anterodorsal yellow spot at base of thigh), complete labial and oblique lateral lines, in lacking teeth, and in smaller size. Based on the preserved types, *Epipedobates bolivianus* probably also differs in being dorsally brown or (at most) red-brown rather than bright red.

Epipedobates cainarachi Schulte

Figure 11

Dendrobates zaparo, not of Silverstone. Schulte, 1987: 17–18, 1 fig. (color photo).

Epipedobates cainarachi Schulte, 1989 (May): 41–46. Holotype: AMNH A-136282 (original no. CRS 10550), from km 33 on road from Tarapoto to Yurimaguas, valley of upper Río Cainarache, Cordillera Oriental, Depto. San Martín, Peru; collected by Rainer Schulte, January 4, 1982.

Epipedobates ardens Jungfer, 1989 (August): 89–91, fig. 3 (color). Holotype: ZFMK 49084, from km 28 on Tarapoto-Yurimaguas road, ca. 600

m elev., Depto. San Martín, Peru; collector and date not given.

Schulte (1987) published the first color photograph of this species, showing medium yellow labial and oblique lateral stripes that are complete; the dorsum appears as a rather light reddish brown, but Schulte (in litt., July 20, 1987) said that this was due to poor printing and that the dorsum was actually “deep brick red.” Jungfer (1989, fig. 3) published another photograph (of holotype of *E. ardens*), showing a darker red dorsum much like that of *E. macero*, but the oblique lateral stripe is very pale yellowish on the flanks and the labial stripe is white. Figure 11 herein shows a third specimen of *E. cainarachi*; both the lateral and labial stripes are yellow and the dorsum is red-brown. It would seem that the stripes and the dorsum are sometimes paler and less vivid in *E. cainarachi* as compared with *E. macero*, but it is uncertain whether the variation is individual, inter-populational, or simply due to the perils of color photography and printing.⁸

Schulte (1989: 44) stated that the most common vocalization of *Epipedobates cainarachi* (in captivity?) is a group of 5–6 rapid, frequency-modulated whistles, repeated with a pause between each group. This is very different from the field recordings of *E. macero* shown herein.

Epipedobates cainarachi differs from *E. macero* in relative lengths of fingers 1 and 2 (when both are pressed together), although the average difference is hard to quantify. In nine specimens of *cainarachi* examined (AMNH A-136282–136286 [the type series] and KU 211973–211975⁹), the first finger is always longer; commonly, the tip of the second finger only reaches the base of the subdigital pad of the first finger, although it sometimes reaches halfway up. The last condition seems to approximately represent the

⁸ Note added in Proof: The proofs for the three color figures in the present paper agreed well with the color prints (made from internegatives) that were sent to the printer. The prints in turn had agreed well with the original 35 mm transparencies. More than this one cannot do without having a living frog for final comparison.

⁹ Collected by Dr. Duellman's party on February 10, 1989, 14 km ESE Shapaja, 360 m, San Martín, Peru (see fig. 11).

maximum when finger 1 > 2 in *E. macero*, in which variation includes 1 = 2 and 2 > 1.

Epipedobates petersi (Silverstone)

Figure 12

Phylllobates petersi Silverstone, 1976: 37–38, figs. 6F, 9B, frontisp. 2 (color). Holotype: USNM 166763, upriver from Santa Isabel[la] (village on Río Nevati, tributary of Río Pichis, Pachitea drainage), 35 km SE Puerto Bermúdez, 80 km ENE Oxapampa, Depto. Pasco, Peru; collected by G. R. Noonan, July 16, 1968.

Epipedobates petersi has a much larger distribution than the other species discussed in this paper. As originally defined by Silverstone (1976), *E. petersi* occurs mainly in the lowlands of the Río Ucayali drainage and part of the Río Huallaga drainage of central Peru. But we regard as questionable Silverstone's assignment, to this species, of specimens found over 700 km to the southeast of the Río Ucayali basin (see map caption, fig. 2).¹⁰

Color in life seems to provide good diagnostic characters for species of morphologically similar *Epipedobates*, and the combination of a brown dorsum and a pale yellowish or greenish yellow oblique lateral line is assumed to be characteristic of *petersi*. These colors were present in the holotype of *E. petersi*, as seen in figure 12. Schlüter (1987: 19) published a photograph of a similarly colored specimen (but with a whitish labial stripe) from the Panguana area in the Río Pachitea drainage (Ucayali tributary). The pale markings of *E. petersi* seem to be less bright than those of *E. macero*. The ventral surface of *petersi* is blue with black marbling (Silverstone, 1976: 38) as in *cainarachi* and *macero* (the vividness of the ventral blue coloring varies at least in the last species).

Schlüter (1980: 154–155) described the call of *Epipedobates petersi* from the Panguana



Fig. 12. *Epipedobates petersi* (Silverstone, 1976). View of holotype (USNM 166763) in life, from Río Nevati (Pachitea drainage), Depto. Pasco, Peru. [From color transparency made in July 1968, courtesy Asa C. Thoresen (see Silverstone, 1976, frontisp. 2, for color painting based on same transparency)]

region as “tütü-tü-tütütü.” His sound spectrograph (from a recording of a confined specimen) shows a different sequence of notes at the end of the call—the call starts with a close grouping of two contiguous notes followed in about 0.05 sec by a single note; then, at intervals of nearly 0.1 sec. the call ends with two groups of contiguous paired notes. The call is given at about the same frequency (3500 Hz) as in *E. macero*, but individual notes are roughly 0.12 sec long, more than twice as long as in *macero*.

The grouping of notes in the above *petersi* call also is very different from the continuous train of notes in *E. macero*. Schulte (1989: 44), however, stated that *E. petersi* also has a much longer call, exceeding 30 sec and comprising single (ungrouped) notes. One might anticipate that individual notes in such a call also would be of longer duration than those in *E. macero*.

ETHNOZOOLOGICAL NOTE

Dr. Gerald Weiss preserved a dendrobatid frog as a voucher specimen for an observa-

¹⁰ Note added in Proof: The three British Museum paratypes of *E. petersi* from Depto. Puno and two additional specimens recently obtained there by the first author have now been examined. Although they have most of the characteristics of northern *petersi*, the southern specimens appear to represent a distinguishable, unnamed population of smaller-size frogs. They differ from *Epipedobates macero* of this paper in smaller size (♂ about 21 mm, ♀ about 25 mm SVL), in possessing a complete oblique lateral line, and in lacking red pigmentation.

tion made during his intensive field work with the Campa Indians of central Peru (Weiss, 1975). The specimen (AMNH A-111000), identified by Myers as *Epipedobates petersi*, is an adult female (without color notes) obtained by Weiss from a Campa Indian on October 9, 1980, at Otica on the Río Tambo, Department of Junín, Peru. The locality Otica (approx. 11°18'S, 73°47'W) is situated about 4.5 km downriver from the *Otíka* (a dangerous river pass), which is shown on a map in Weiss (op. cit., fig. 5). Weiss (personal commun.) said that the Campa name for *Epipedobates petersi* is "*tentékiti*," after the sound of its call (*tenté, tenté . . .*).

Weiss preserved this frog along with specimens of several other genera of frogs eaten by the Campa. According to Weiss (*in litt.*, March 1982), *Epipedobates* is prepared as follows: "Whatever quantity collected is salted, wrapped in a leaf, and roasted in the campfire ashes—well roasted to remove the poison, and eaten with manioc. After roasting, they may be chewed, the bones removed, and fed to a baby to make it talkative."

The various skin alkaloids in the defensive secretions of *Epipedobates petersi* (see Daly et al., 1987: 1082, under *D. petersi*) are probably better described as noxious than toxic (op. cit.: 1024, fn.) and, in any case, cooking would be expected to lessen pharmacological activity. Nonetheless, this is the only instance known to us where a species of dendrobatid frog—cooked or uncooked—is eaten by humans.

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for permission to publish their transparencies of related species of *Epipedobates*.

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