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Distribution of the Dendrobatid Frog *Colostethus chocoensis* and Description of a Related Species Occurring Macrosympatrically

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ABSTRACT

Colostethus lacrimosus is a new species of small, web-footed dendrobatid from lowland rain forest of western Colombia. It occurs macrosympatrically with the similar, but larger, *Colostethus chocoensis* (Boulenger, 1912). Excluding a few published misidentifications, *C. chocoensis* heretofore was known only from the holotype, which is redescribed and illustrated. The range of *C. chocoensis* is extended north to east-central Panama and south to northwestern Ecuador. The population in Ecuador conceivably represents a different species but, if so, it cannot be reliably diagnosed at this time. *Colostethus chocoensis* and *C. lacrimosus* seem to be rare compared with certain other riparian species, possibly a reflection of unusually secretive behavior as well as relatively low population densities.

RESUMEN

Colostethus lacrimosus, especie nueva, es un pequeño dendrobátido palmeado, de la selva pluvial baja de Colombia occidental. Aparece macrosimpátricamente con la similar, pero mas grande, *Colostethus chocoensis* (Boulenger, 1912). Excluyendo identificaciones falsas, *C. chocoensis* se conocía antes solamente del espécimen holotipo, el cual se redescribe e ilustra. Basándose en nuevos especímenes, se extiende la distribución geográfica de *C. chocoensis* hacia al norte hasta Panamá oriental, y hacia el sur hasta Ecuador noroeste. La población ecuatoriana representa posiblemente una especie distinta, pero, si así es, no se puede diagnosticar por ahora con certeza. *Colostethus chocoensis* y *C. lacrimosus* parecen muy raras comparadas con otras especies ribereñas, posible reflejo de su comportamiento secreto así como de sus pequeñas poblaciones.

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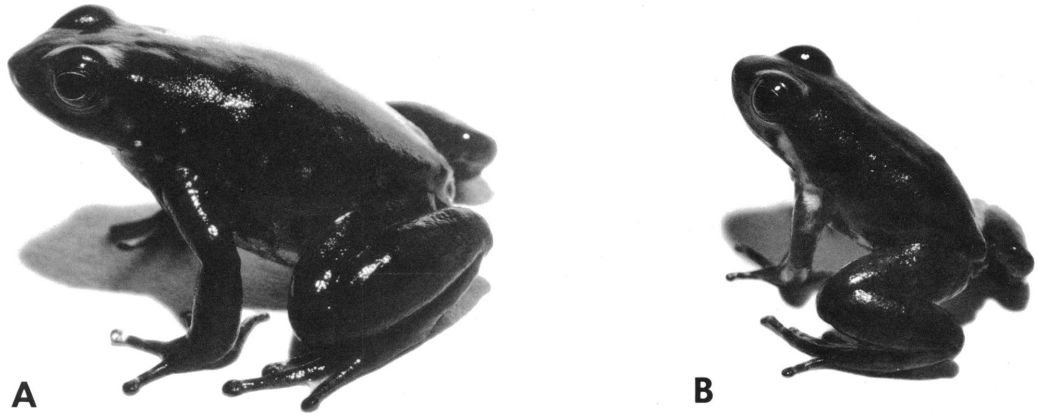

Fig. 1. Two related, web-footed *Colostethus* in life, both adult females; about 2.5× life size. **A.** A specimen (AMNH 104819, 24 mm SVL) from northwestern Ecuador tentatively assigned to *C. chocoensis* (Boulenger). **B.** Holotype (AMNH 88828, 18 mm SVL) of *C. lacrimosus*, new species, from western Colombia.

INTRODUCTION

Despite their cryptic coloration (most are brown), the dendrobatid frogs of the genus *Colostethus* sensu lato often are conspicuous animals because of their abundance, diurnal activity, and frequent vocalization. The riparian species *C. inguinalis* and *C. trinitatis*, for example, are at least superficially familiar to hundreds of biologists and are fascinating subjects for comparative study (see Wells, 1980a, 1980b).

Colostethus, however, also contains rare and highly secretive species about which virtually nothing is known. The present paper provides basic taxonomic and distribution data for two such species, the result of an investigation into the status of 19 specimens from western Colombia and Ecuador and a single one from Panama. Identification of the last specimen was particularly needed for a survey of amphibians and reptiles on the Isthmus of Panama, for which fieldwork has been completed. The Panamanian frog was taken from a large spider by Catherine A. Toft, in 1974, and I hope that this report will stimulate the search for a population from which additional specimens and natural history data can be obtained.

ACKNOWLEDGEMENTS: For help at various times in the field, I am grateful to Catherine A. Toft, John W. Daly, and Eugene W. Schupp. Drs. Toft, John D. Lynch, and Richard G. Zweifel kindly read and commented on the manuscript. For lending critical specimens used in this study I am indebted to Drs. Barry Clarke, British Museum (Natural History) (BMNH), William E. Duellman, University of Kansas Museum of Natural History (KU), and John W. Wright, Los Angeles County Museum of Natural History (LACM).

Colostethus chocoensis (Boulenger)

Figures 1A, 2, 3A, B

Hylixalus chocoensis Boulenger, 1912: 190 (holotype, BMNH 1947.2.14.27, from "Noanama, Rio San Juan, Choco, S.W. Colombia, about 100 feet, from the collection of Mr. M. G. Palmer."

DIAGNOSIS: A moderate-size *Colostethus* (to about 25 mm SVL) having extensively webbed feet, narrowly fringed fingers with appressed first finger shorter than second, third finger of male not swollen, a complete outer metacarpal fold, a pale marking atop base of upper arm; lacking pale ventrolateral, oblique lateral, or dorsolateral lines. See Diagnosis under *C. lacrimosus* following for differentiation of *chocoensis* from its smaller, macrosympatric sibling.

SPECIMENS EXAMINED: **Colombia:** Chocó: Noanamá [near mouth Quebrada Vicordó,

70 m elev.], middle Río San Juan (BMNH 1947.2.14.27, holotype). **Ecuador:** Bolívar-Cotopaxi border: about 7 km airline SSW El Corazón, 800 m elev. (AMNH 104819–104824).[2] **Panama:** Panama: El Llano-Cartí Road, km 11.7, 150 m elev. (KU 172790).

Redescription of Holotype

The type specimen is a female of 24.3 mm SVL (26 mm as measured by Boulenger); it is a subadult or sexually inactive adult female, with a flat, nonconvoluted oviduct about 0.5 mm wide and compact ovaries containing unpigmented ova < 0.5 mm. The specimen is in fairly good condition; the body had previously been opened both midventrally and on the right side.

Morphology: Skin smooth overall (i.e., finely pitted but nongranular). Greatest head width (between angles of jaws) 40 percent of SVL. Snout sloping, rounded in profile, acutely rounded (nearly pointed, fig. 8C) in dorsal and ventral view. Front of snout somewhat deformed, with naris on left side farther from tip of snout than naris on right (but both are same distance from eye). Nares visible from in front, barely visible from above or below; posterior rim of naris raised slightly and bearing a low, rounded tubercle-like prominence posterodorsally to naris. Canthus rostralis rounded; loreal region flat and nearly vertical, almost imperceptibly sloping outward to lip. Interorbital region much wider than upper eyelid. Length of snout in lateral view nearly equal to eye length; center naris-edge eye/eye = 0.64. Tympanum small and inconspicuous, seemingly less than one-third of eye length and concealed posterodorsally.

Hand moderate, its length 30 percent of SVL, 75 percent of greatest head width. Relative lengths of appressed fingers 3 > 4 > 2 > 1; tip of first finger nearly reaching disc of second (fig. 2). Discs of all fingers moderately expanded; third finger disc 1.7 times wider than distal end of adjacent phalanx. Base of palm with a large median metacarpal tubercle whose distal side is very slightly concave; a smaller elliptical inner metacarpal tubercle on base of first finger; one or two subarticular tubercles (one each on fingers 1, 2, two each on fingers 3, 4); all tubercles low, with rounded surfaces. A weak (narrow), fleshy keel-like fringe along sides of fingers; fringe on median side of first finger extending faintly to inner metacarpal tubercle; fringe on lateral side of fourth finger continuous with a weak outer metacarpal fold extending to large palmar (outer metacarpal) tubercle (fig. 2).

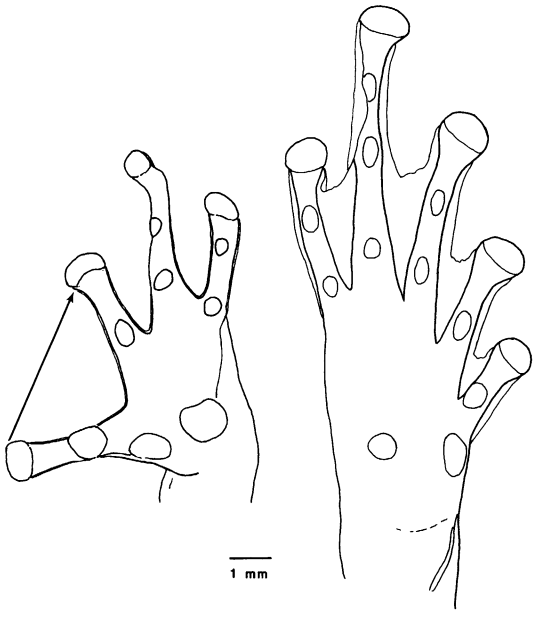

Fig. 2. Left hand and right foot of holotype (BMNH 1947.2.14.27?) of *Colostethus chocoensis* (Boulenger), ×5.5 (cf. fig. 5).

Hind limbs relatively long, with heel of appressed limb reaching past eye nearly to tip of snout; tibia 53 percent of SVL. Relative lengths of appressed toes 4 > 3 > 5 > 2 > 1; first toe reaching middle of subarticular tubercle of second. Toe discs noticeably expanded, those on third and fourth toes 1.6–1.75 times wider than adjacent phalanges. Feet extensively webbed to base of each toe disc, although web is reduced to a broad fringe on medial sides of toes 2–4 (fig. 2); a well-developed fringe along the outer free edges of toes 1 and 5. One to three nonprotuberant subarticular tubercles; a small round outer metatarsal tubercle and a slightly larger elliptical inner metatarsal tubercle. A strong tarsal

[2] I superficially examined (but did not take data from) some USNM specimens collected in this region of Ecuador by the late Kenneth Miyata.

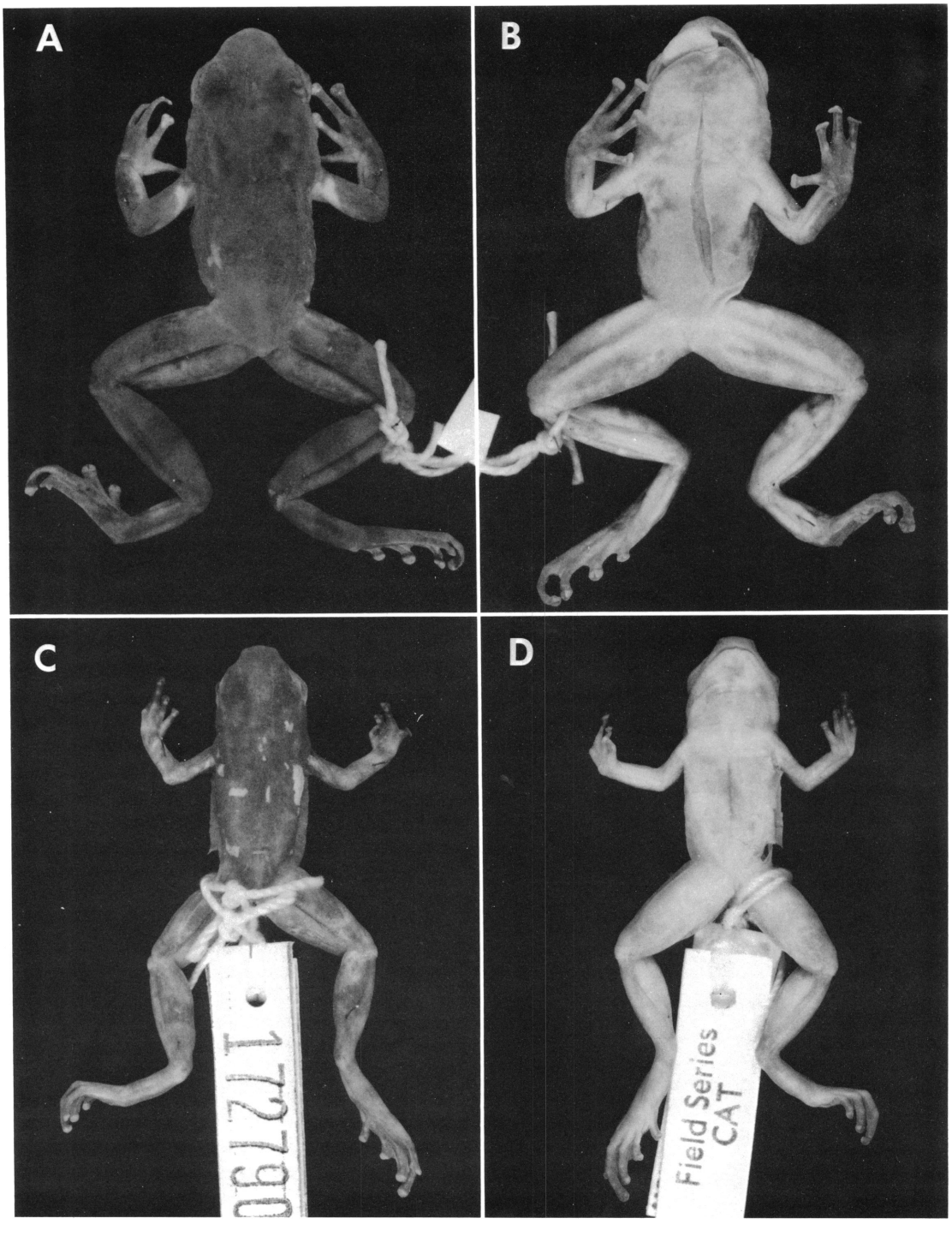

Fig. 3. *Colostethus chocoensis* (Boulenger). **A, B.** Dorsal and ventral views of Colombian holotype (BMNH 1947.2.14.27), a subadult or sexually inactive female. **C, D.** An adult male from eastern Panama (KU 172790). Both ×2.2.

keel, on distal third of tarsus, is continuous with fringe on free edge of first toe; no tubercle or elevation at proximal end of tarsal keel.

Teeth present on maxillary arch.

COLOR PATTERN: In 1912, Boulenger described the preserved specimen as:

> Blackish grey above, with a rather indistinct grey streak along each side of the back and a fine grey vertebral line; upper lip with a row of small white spots; a white spot on the upper surface of the arm, near its base; a black bar across the thigh and another across the tibia; lower parts white, with a few blackish spots or marblings.

Nearly 80 years later, this specimen (fig. 3A, B) has faded from "blackish grey" to dark brown and a few ill-defined blackish brown markings are now discernible on the dorsum as follows: When the specimen is in liquid and under the proper light, two broad V-shaped dark markings are visible, one positioned between the eyes and the other between the upper arms. There also are a few dark smudges of indefinite shape posteriorly on the dorsum. The dorsolateral gray streaks mentioned by Boulenger are now seen as areas of ground color between the darker dorsal markings and the equally dark sides. Boulenger's "fine grey vertebral line" is equivalent to a very narrow median break in the dorsal dark markings but is too vague to be called a definite hairline such as appears in some anurans. The lower sides have pale spots that merge into the ventral color. The ventral surfaces are whitish, irregularly smudged with brown.

The upper lip is brown, with a white-scalloped lower edge forming the small white spots mentioned by Boulenger. An oblique area extending from the lower rear edge of the eye across the tympanum to the forelimb is a somewhat paler brown than adjacent areas, but it does not form a discrete postocular stripe nor was it mentioned by Boulenger.

The forelimbs are brown, without crossbands or longitudinal dark bars; the tops of fingers 1, 2 and the disc of finger 3 are whitish. The conspicuous pale marking at the base of the upper arm is the dorsal extension of a pale axillary spot. The hind limbs are brown with a single broad crossband on thigh and shank each and with a few smaller bands on tarsus and foot; rear of thighs lighter brown with a few dark dots but no definite pattern.

VARIATION AND COLOR IN LIFE

PANAMA: The one specimen (KU 172790, fig. 3C, D) is an adult male (vocal slits open) of 19.5 mm SVL. It was described in life as being chocolate brown above, with a yellow flash mark atop base of upper arm, and with a tinge of metallic blue on the venter. There are a few details of color pattern in which the Panamanian specimen differs from the Colombian holotype: The dark-smudged dorsum lacks a definite pattern in that the darker pigmentation does not form V-shaped markings. There is no oblique pale postocular area but rather a distinct, albeit not sharply defined, *horizontal* white line, which starts above the corner of the mouth and extends under the tympanum to the upper arm. Only finger 1 is mostly white above; the arms have vague blotching reminiscent of crossbanding; the flash mark on the base of the upper arm is discrete and not confluent with the pale axillary area.

Except for sex-correlated size (table 1) and a more truncate snout (figs. 3, 8), the Panamanian frog agrees in morphology with the preceding description of the female holotype, including the details of hand and foot structure.

ECUADOR: Two adult females and four juveniles were dark olive green—appearing black in some light—with a few tan dots scattered on the sides and with vague limb bars. The color of the pale mark atop the base of the arm was not noted but, based on a color transparency, seems to have been golden bronze with a small area of pale blue. The throat and venter were very pale blue; the undersides of the limbs were grayish brown; several had a slight suffusion of orange underneath the hind limbs. Iris pale bronze or, in one, pale green, with dense black venation.

The Ecuadorian specimens are darker in preservative and apparently were darker in life than the one specimen from Panama, but the preserved frogs from Ecuador might be described as "blackish grey" as in the original description of *chocoensis*. The feet appear slightly less webbed than in the holotype of *chocoensis* (see fig. 2) simply because the dis-

TABLE 1

Measurements (in mm)[a] of Holotype of *Colostethus chocoensis* (Boulenger) and of Two Additional Specimens Assigned to that Species

Character	Holotype, BMNH 1947.2.14.27 Adult (?) ♀	AMNH 104819 Adult ♀	KU 172790 Adult ♂
Snout–vent length	24.3	23.9	19.4
Tibia length[b]	12.9	12.1	9.3
Head width between angles of jaws	9.7	8.2	6.8
Head width between outer edges upper eyelids	7.9	7.1	5.7
Width of interorbital area (approximate)	3.5	3.5	2.2
Head length (sagittal), tip snout to angle of jaw	7.5	6.9	5.0
Snout length (sagittal) to edge of eye	3.0	2.7	2.2
Center naris to anterior edge of eye	2.3	2.0	1.7
Distance between centers of nares	3.9	3.3	2.6
Eye length anterior to posterior edge	3.6	3.2	3.0
Horizontal diameter of tympanum[c]	>1	>1.4	>1
Corner of mouth to lower edge of tympanic ring	0.9	0.5	0.8
Hand length[d]	7.3	6.9	5.0
Width of 3rd finger disc	1.2	1.1	0.8
Width of 3rd finger below disc[e]	0.7	0.7	0.5
Width of 3rd toe disc	1.3	1.2	0.9
Width of 3rd toe below disc	0.8	0.8	0.7
Width of 4th toe disc	1.4	1.3	0.9
Width of 4th toe below disc	0.8	0.8	0.7

[a] Measurements <10 mm made with ocular micrometer in Wild M7-S stereomicroscope switched to vertical-beam mode (mono-position); dimensions >10 mm taken with digital calipers.

[b] Tibia measured between heel and outer surface of flexed knee.

[c] An estimated measurement (tympanum concealed dorsally and posterodorsally).

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

[e] Digit width measured near distal end of penultimate phalanx.

tally narrowed web (or "fringe") is relatively narrower on the medial sides of toes 2–3 and on both sides of toe 4. The Ecuadorian frogs were like the Panamanian one in having pale bluish venters in life. The tympanum varies in distinctness in the Ecuadorian series, but, in the two adult females, it seems to be nearly half the diameter of the eye. These females, which are sexually mature at 23.0 and 23.9 mm SVL, are slightly smaller than the 24.3 mm holotype which was either subadult or sexually inactive. In other respects, the Ecuadorian specimens agree with the preceding description of the holotype.

Distribution and Habitat

As here conceived, *Colostethus chocoensis* is distributed—whether continuously or discontinuously—from eastern Panama through Colombia west of the Andes to northwestern Ecuador, at about 70 to 800 m above sea level. Known localities are few, however, and are separately discussed below.

Panama: The only known isthmian locality (fig. 4) is in the low hills that carry the continental divide close along the Atlantic coast of eastern Panama, in *Am* climate of the Köppen system (Myers, 1969). The forest is moderate-height monsoon rain forest covering a topography of ridges and steep hillsides, with drainage by clear-water rocky streams. Compared with adjacent Pacific lowland vegetation, this is a very humid seasonal evergreen forest of reduced deciduousness—late in one dry season I estimated that forest above the 200 m contour was no more than about 10 percent leafless. At this time (March 21–22, 1974) I took specimens of the following eight species of dendrobatid frogs at km 12.8–14.6, elevation 290–370 m, on the then new road being constructed from El Llano in the Pacific drainage north to Cartí on the Atlantic coast: *Colostethus flotator*, *C.*

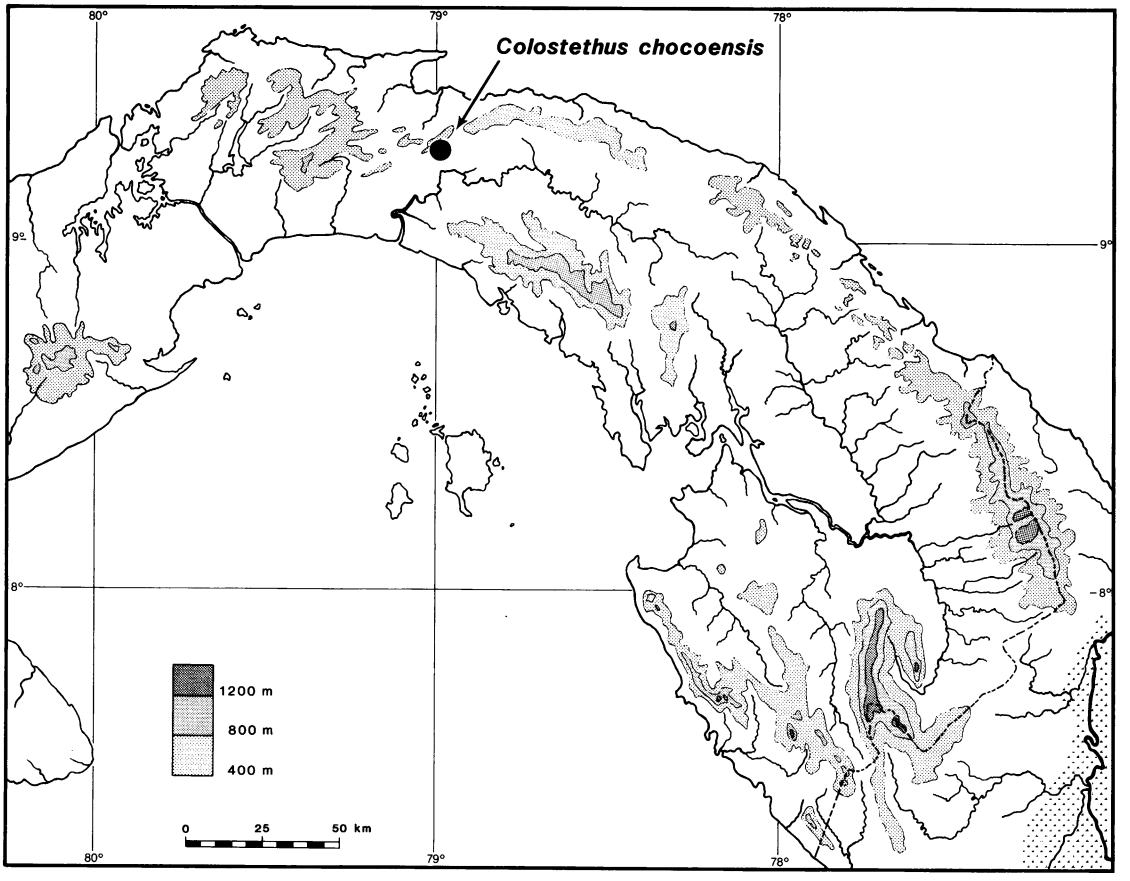

Fig. 4. Eastern Panama, showing approximate location of collecting site for the first isthmian specimen of *Colostethus chocoensis* (see fig. 3C, D).

inguinalis, *C. nubicola*, *C. pratti*, *C. talamancae*, *Dendrobates auratus*, *Minyobates fulguritus*, *M. minutus*. A few months later, in July, Catherine Toft added to this rich dendrobatid fauna a specimen of a ninth species, here determined as *C. chocoensis*.

Dr. Toft and I returned to this area in 1976 but were unable to rediscover the precise spot of capture, which was a stream located in heavy forest to the west and downslope (150 m elev.) from km 11.7 (380 m elev.) on the El Llano-Cartí road.

Colombia: Noanamá, the type locality (fig. 7) of *C. chocoensis*, is situated in west-central Colombia at 70 m elevation (by altimeter), at the mouth of Quebrada Vicordó on the west bank of the Río San Juan. It seems most likely to me that *chocoensis* occurs a bit inland from this great river, on the sides of low ridges where there are clear-water, gravel-bottomed forest streams.

Colostethus chocoensis conceivably occurs continuously from Noanamá north through the San Juan–Atrato lowlands to eastern Panama, but two previous reports of *chocoensis* in northwestern Colombia are based on other species: (1) Cochran and Goin reported (1970: 46–48, 581 [pl. 9A, B]) several specimens of "*Phyllobates*" *chocoensis* from south of Santa Barbara, Dept. Antioquia, Colombia. This locality, above 1500 m in the Río Cauca drainage of the Cordillera Central, seems likely to be too high for *chocoensis* and must be based on misidentification of a *Colostethus* characterized by less webbing than *chocoensis*, as indicated by the illustration in Cochran and Goin and by their statement that the toes were only "one-half webbed."

Unfortunately, the specimens (BMNH 1929.2.1.3–6) are no longer identifiable; an entry in the British Museum catalog states that they were "destroyed by fungus at USNM, 1962 Dr. D. Cochran" (B. T. Clarke, in litt.). (2) Edwards (1974: 137–138, 354) based his account of *C. chocoensis* on a single specimen from the Río Atrato drainage, but that specimen (LACM 55815) is here included in the type series of *C. lacrimosus*.

ECUADOR: A small series (AMNH 104819–104824) of frogs tentatively assigned to *chocoensis* was obtained in November 1979, at 800 m elevation on the Pacific versant of northwestern Ecuador. This locality, on the border between Bolívar and Cotopaxi provinces, lies about 700 km SSW of the Colombian type locality. The habitat was a clear-water rocky stream, in a steep-sided ravine planted in bananas. The frogs were found mainly under rocks along the edge of the stream, although a few were seen out from cover. Another species of *Colostethus* (see Myers et al., 1991, fig. 15A) occurred microsympatrically with the *chocoensis* but was active on rocks and was more conspicuous. The dendrobatid *Epipedobates tricolor* occurred also in this ravine.

Colostethus lacrimosus, new species

Figures 1B, 5, 6

HOLOTYPE: AMNH A-88828 (field no. CWM 11897), an adult female collected by C. W. Myers and John Daly on February 17, 1973, at Quebrada Guanguí, about 0.5 km above its junction with Río Patia,[3] 100–200 m elev., in upper Río Saija drainage, Department of Cauca, Colombia. The type locality is roughly 2°50′N, 77°25′W.

PARATYPES (11): AMNH 88829–88830, from the type locality, collected by an Emberá Chocó Indian for Myers and Daly in February 1973. AMNH 110747–110753, 110789, collected by Noanamá Chocó Indians for Borys Malkin, in June 1969, January 1971, and January 1972, on both east and west sides of lower Río San Juan at Quebrada Pangala (about 4°15′N, 77°00′W), Department of Chocó, Colombia. LACM 55815, collected by Philip A. Silverstone on August 21, 1966, upper Río Buey [trib. Río Atrato, 6°05′N, 76°45′W], above Tambos, 110–160 m.

ETYMOLOGY: The name is a Latin adjective meaning "tearful," in reference to the conspicuous white stripe extending from the lower rear edge of the eye.

DIAGNOSIS: A small dendrobatid (to nearly 20 mm SVL) resembling the macrosympatric *Colostethus chocoensis* in having extensively webbed feet, weakly fringed fingers with appressed first finger shorter than second, third finger not swollen in male, a complete outer metacarpal fold, a pale marking atop base of upper arm; and in lacking pale ventrolateral, oblique lateral, or dorsolateral lines.

Colostethus lacrimosus differs from *C. chocoensis* in being appreciably smaller in size (adult females < 20 mm, vs. ≥ 23 mm SVL in female *chocoensis*), in the presence of a distinct white postocular stripe (fig. 1B), slightly less extensive foot webbing (cf. figs. 2, 5), and apparently also in having white (vs. blue tinged) ventral surfaces in life.

MEASUREMENTS (in mm) OF HOLOTYPE: The specimen is an adult female as determined by the presence of enlarged ova and oviducts. Length from snout to vent 18.0; tibia length between heel and outer surface of flexed knee 8.3; greatest width of body 6.4; head width between angles of jaws, and between outer edges upper eyelids, 6.5, 5.3, respectively; approximate width of interorbital area 2.6; head length (sagittal) from tip of snout to angle of jaw 5.0; snout length from tip to edge of eye (sagittal) 2.0; center of naris to anterior edge of eye 1.5; distance between centers of nares 2.5; eye length from anterior to posterior edge 2.9; horizontal diameter of tympanum about 0.8 (concealed posterodorsally); corner of mouth to lower edge of tympanic ring 0.3; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 4.9; width of disc of third finger (and width of penultimate phalanx below disc) 0.7 (0.5); width of discs (and penultimate phalanges below discs) of third and fourth toes 0.7 (0.5) and 0.8 (0.6), respectively.

DESCRIPTION

The type series comprises 12 specimens from three localities. Inasmuch as the series

[3] This is the same as "Río Patía del Norte," a cartographic invention. Not to be confused with the Río Patía; see Myers et al. (1978: 313) for comments on the orthography of *Patia* vs. *Patía*.

TABLE 2
Size and Proportions[a] of Specimens of Adult *Colostethus lacrimosus*, New Species, from Three Localities in Western Colombia

Character	N	Mean ± 1 SE	SD	CV (%)	Range
Snout–vent length (SVL) in mm	1 ♂	15.8	—	—	—
	9 ♀	18.66 ± 0.24	0.71	3.78	17.7–19.6
Tibia length/SVL	1 ♂	0.500	—	—	—
	9 ♀	0.464 ± 0.006	0.019	4.03	0.43–0.51
Head width/SVL	1 ♂	0.392	—	—	—
	9 ♀	0.367 ± 0.005	0.014	3.90	0.35–0.39
Center naris-edge eye/eye length	1 ♂	0.519	—	—	—
	9 ♀	0.539 ± 0.011	0.034	6.36	0.48–0.59
Hand length/SVL	1 ♂	0.278	—	—	—
	8 ♀	0.250 ± 0.006	0.018	7.31	0.22–0.27
Hand length/head width	1 ♂	0.710	—	—	—
	8 ♀	0.688 ± 0.020	0.056	8.21	0.59–0.77
Width 3rd-finger disc/finger width below disc	1 ♂	1.750	—	—	—
	8 ♀	1.581 ± 0.057	0.162	10.27	1.40–1.75

[a] Measurements as in table 1.

is morphologically uniform and appears clearly to represent a single taxon, a composite description is provided. Eleven specimens, including the holotype, are females, of which nine are sexually mature. The smallest specimen (AMNH 110753) is 15.5 mm SVL and is a juvenile, with uniformly tiny ova and narrow oviducts; the next largest female (AMNH 88829) is 16.0 mm SVL and judged to be a subadult just approaching maturity, as indicated by enlarging ova and relatively large but nonconvoluted oviducts. The remaining nine all have large oviducts and enlarged ova of various size (up to 2.5 mm diameter). The size range for the adult females is 17.7–19.6 mm SVL (table 2). The single male (LACM 55815), with vocal slits opened, is adult at 15.8 mm SVL.

MORPHOLOGY: Skin overall smooth in preservative. Greatest head width (between angles of jaws) 35–39 percent of SVL. Snout sloping, bluntly pointed to rounded in profile, nearly truncate (broadly rounded) in dorsal and ventral view. Nares situated near tip of snout and directed posterolaterally; nares visible from front, not or but barely visible from above or below; posterior rim of naris raised slightly and bearing a low, rounded tubercle-like prominence posterodorsally to naris. Canthus rostralis rounded; loreal region flat, sloping moderately outward to lip. Interorbital region much wider than upper eyelid. Snout appreciably shorter than eye length; center naris-edge eye/eye = 0.48–0.52. Tympanum small and inconspicuous, less than one-third of eye length and concealed posterodorsally.

Hand moderate, its length 22–28 percent of SVL, 59–77 percent of greatest head width. Relative lengths of appressed fingers 3 > 4 > 2 > 1; tip of first finger reaching (fig. 5) or failing to reach disc of second. Discs of all fingers slightly to moderately expanded; third finger disc 1.4–1.8 times wider than distal end of adjacent phalanx. Base of palm with a large median metacarpal tubercle, flattened or slightly concave along its distal edge; an elliptical inner metacarpal tubercle on base of first finger; one or two subarticular tubercles (one each on fingers 1, 2, two each on fingers 3, 4); all tubercles low, with rounded surfaces. A weak (narrow), fleshy keel-like fringe along sides of fingers; fringe on median side of first finger extending as a weak keel or fold to inner metacarpal tubercle; fringe on lateral side of fourth finger continuous with a weak outer metacarpal fold extending continuously to large palmar (outer metacarpal) tubercle (fig. 5).

Hind limbs of moderate length, with heel of appressed limb reaching or failing to reach eye; tibia 43–51 percent of SVL. Relative lengths of appressed toes 4 > 3 > 5 > 2 > 1; first toe reaching middle of subarticular

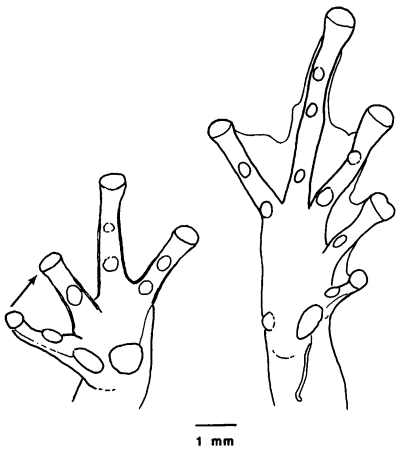

Fig. 5. Left hand and right foot of holotype (AMNH 88828, ad.♀) of *Colostethus lacrimosus*, new species, ×5.5 (cf. fig. 2).

tubercle of second. Toe discs moderately expanded. Feet extensively webbed, but web reduces to a very narrow fringe distally on toes 2–4—giving an approximate webbing formula[4] of **I** 1–2 **II** 1–2½ **III** 1 or 1½–3 **IV** 3–1 **V** (fig. 5); a weak indication of fringe along the outer free edges of toes 1 and 5. One to three nonprotuberant subarticular tubercles; a small round outer metatarsal tubercle and a slightly larger elliptical inner metatarsal tubercle. A strong tarsal keel, on distal third to half of tarsus, is continuous with the narrow fringe on free edge of first toe; no tubercle or elevation at proximal end of tarsal keel.

Teeth present on maxillary arch.

COLOR PATTERN: In life (fig. 1B), the holotype and two paratopotypes were greenish brown above, with the oblique postocular stripe and flash mark atop upper arm both being white. The ventral surfaces were white, turning pale gray underneath the limbs.

In preservative (fig. 6), the dorsum is brown with a vague to bold blackish brown pattern, which includes a dark head cap that terminates posteriorly as a V-shaped point. The posterior terminus of this cap may narrowly connect with a large scallop-edged blotch (as in the holotype) or the midtrunk markings may consist only of a few discrete spots (fig. 6). The upper sides tend to be dark or blackish brown, becoming lighter brown with some white mottling below. The hind limbs vary from indistinctly to distinctly banded, with a tendency for a distinct narrow white mark on the dorsal base of each thigh on each side of the cloaca; the rear of the thigh is brown without definite pattern.

An oblique white postocular stripe starts at the lower rear edge of the eye and extends across the lower three-fourths of the tympanum to the upper arm, where it connects with a white flash mark atop the base of the arm (fig. 1B); the dorsal flash mark in turn is posteriorly confluent with a pale axillary spot. The lower edge of the postocular white stripe is bordered by a blackish brown streak or stripe that extends across the corner of the mouth to the arm, where it is confluent (or nearly so) with a longitudinal dark stripe on the front edge of the upper arm. Anterior to the dark border of the postocular stripe, the upper lip is dusky white continuously around the tip of the snout. The edge of the lower lip is brown as are the undersides of the hands and feet; the ventral surfaces otherwise are nearly immaculate white.

DISTRIBUTION AND HABITAT

Colostethus lacrimosus appears to have a lowland (< 200 m elev.) rain-forest distribution. I know it from three localities in a north-south distance of about 360 km in western Colombia. The northernmost locality, Río Buey, is a west-bank tributary of the north-flowing Río Atrato. The two more southern localities, in different drainage systems on the Pacific coast, are about 160 km apart; one of these, Pangala on the lower Río San Juan, is only about 50 km downstream from the type locality of *C. chocoensis* (see map, fig. 7). See Myers et al. (1978) for information on the type locality, Quebrada Guanquí in the Río Saija drainage.

A paratype collected by P. A. Silverstone in the Río Atrato drainage lacks an explicit field note (fide J. W. Wright). The AMNH paratypes from the two southern localities were brought into camp by Indians. Consequently, the only datum on behavior is that for the holotype, which was found by moving rocks along a clear-water forest stream. The apparent rarity of *Colostethus lacrimosus*

[4] This is the standard notational device of Savage and Heyer, as modified by Myers and Duellman (1982: 6).

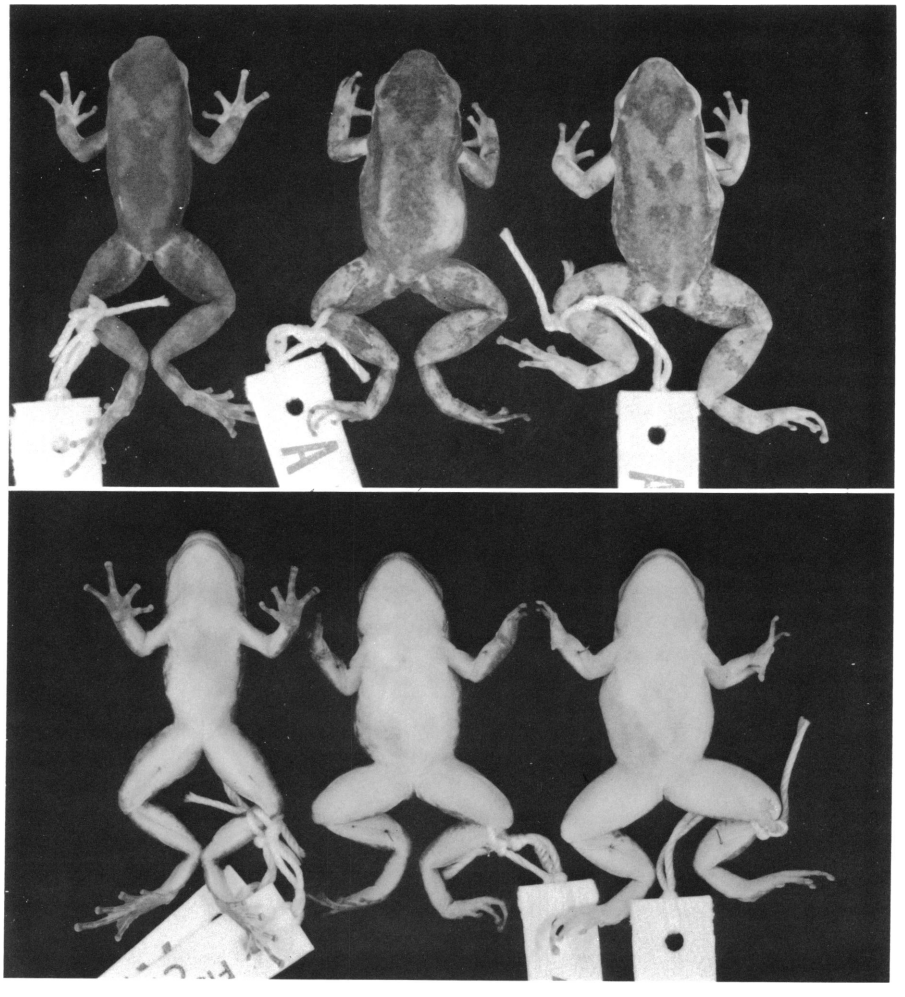

Fig. 6. *Colostethus lacrimosus*, new species, × 1.8. From left to right: AMNH 88828 (holotype), AMNH 110752, AMNH 110789, all adult females.

might therefore be largely due to extremely secretive habits, although low population densities or patchy distribution seem also likely to be contributing factors. These same remarks seem applicable to *C. chocoensis*.

DISCUSSION

In life, at least in certain populations, both taxa have some green in the dorsal coloration, as based on my color notes for Ecuadorian *chocoensis* and topotypic *lacrimosus*. Both are riparian species of evidently secretive habits (compared with many other species of *Colostethus*), and both share an unstriped color pattern, a similar habitus, and similar hand-and-foot morphology, including a complete outer metacarpal fold. Some part of this resemblance must reflect more than plesiomorphy and I assume a phylogenetically close relationship between *C. chocoensis* and *C. lacrimosus*. Color pattern variation in each species, namely in the interorbital and middorsal dark blotching (figs. 3, 6), is suggestive of a relationship with *C. fuliginosus* (sensu lato) of Amazonian South America.

Colostethus chocoensis and *C. fuliginosus* are phenetically similar (fide Edwards, 1974: 36, 38, phenograms), and both species are placed in Rivero's Group VI (Rivero and Serna, 1988: 150). Edwards' (1974: 137–138, 354) concept of *Colostethus chocoensis*, how-

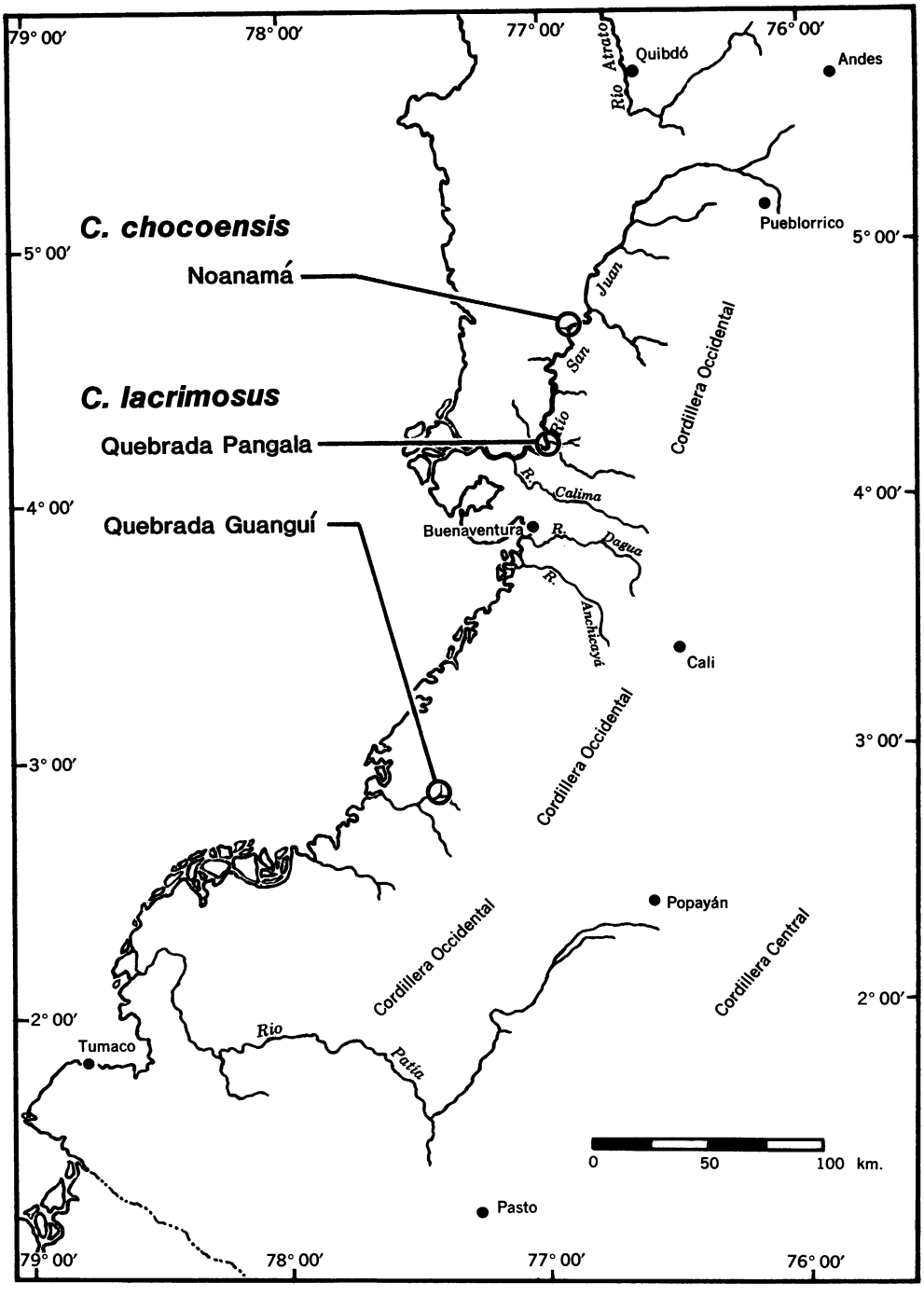

Fig. 7. Western Colombia, showing proximity of type locality of *Colostethus chocoensis* (Boulenger) to southern localities for *Colostethus lacrimosus*, new species.

ever, was based essentially on a single adult male that is here included in the type series of the new *C. lacrimosus*; he ignored the much greater size of the female holotype of *chocoensis* (a difference of 10 mm as published, 8 mm by my measurements). Rivero and Serna ("1988" [1989]: 147) used Edwards' monograph extensively, but they paid more attention to Boulenger's original 1912 description of *chocoensis*:

> *Colostethus chocoensis*. Esta especie, claramente asignable al Grupo VI, es el único miembro colombiano del grupo al oeste de los Andes. Es claramente distinguible por su tímpano pequeño e inconspicuo y por tener dos rayas difusas y cortas en la parte anterior del dorso.

However, a small tympanum is shared with the macrosympatric *lacrimosus*, and the two short lines described for the anterior part of the dorsum of *chocoensis* are, as previously mentioned (under Redescription of the Holotype), only areas of ground color between vague dorsal markings and the dark sides. But despite the inadequacy of the type description of *chocoensis* and confusion with *lacrimosus*, these two species are so similar that the placement of *chocoensis* is unaffected in the species groupings of Edwards and of Rivero—although the identification of *chocoensis* is not as simple as assumed by Rivero and Serna. Nor, for that matter, can I be confident that I have correctly adduced the taxonomic limits of *Colostethus chocoensis*.

The problem is that of correctly interpreting variation in inadequate samples from geographically distant populations. The new species *lacrimosus* can readily be separated from specimens assigned to *chocoensis* because of its small size, immaculate white venter, and postocular white stripe. Of the remaining specimens considered, the single male from east-central Panama makes a good match with the Colombian female holotype of *chocoensis* (fig. 3). The conclusion that *chocoensis* occurs in Panama seems unavoidable and a western Colombia–central Panama distribution, whether continuous or disjunct, has parallels in such frogs as *Hyla palmeri*, *Minyobates fulguritus*, and *M. minutus*.

Extending the range of *Colostethus chocoensis* to northwestern Ecuador is also geographically plausible but perhaps more questionable. My Ecuadorian sample is from a higher elevation (800 m) than the Colombian type locality (70 m), an elevational range similar to that of a few other dendrobatids on the Pacific versant of northwestern South America, and they had pale blue venters as did the specimen collected by Toft in Panama. The Ecuadorian specimens tend to have the snout unusually pointed for a dendrobatid (figs. 1A, 8A), but a similar point is discernible in the holotype when it is viewed at the right inclination (fig. 8C), and Ecuadorian specimens with more rounded snouts approach the somewhat truncated appearance of the Panamanian specimen (cf. fig. 8B, D). Nonetheless, an unusually pointed snout, particularly as viewed in profile (fig. 1A), may be a defining character of the Ecuadorian population, but nothing can be done with such a character without knowledge of intrapopulational variation in undisputed *chocoensis*.

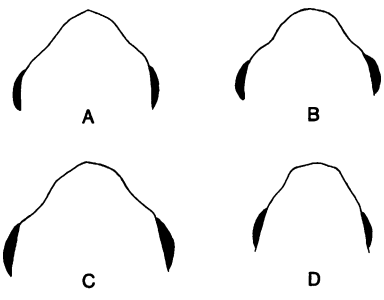

Fig. 8. *Colostethus chocoensis* (Boulenger): variation in snout shape in dorsal view, as shown by camera lucida tracings. **A, B.** From same population in NW Ecuador (AMNH 104819♀, 104820♀, respectively). **C.** Western Colombia (♀ holotype). **D.** Eastern Panama (KU 172790♂).

The Ecuadorian population may also have a larger tympanum than in the holotype and Panamanian specimens of *C. chocoensis*, as reflected not only in *estimated* measurements of horizontal diameter but also in proximity of the lower edge of the tympanum to the corner of the mouth (table 1). The tympanum appears to be no more than one-third the size of the eye in the holotype and Panamanian specimens of *chocoensis* (and also in *lacrimosus*), but it seems to be nearly half of eye size in some Ecuadorian specimens. I am rea-

sonably confident that there is a difference but must stress that the preceding comparisons are inadequate quantification because the dendrobatid tympanum can only be accurately measured if exposed by dissection (which I have not done on the sparse material available). Externally, the distinctness of the tympanum varies according to the extent to which it is subcutaneously covered by the anterior edge of the massive superficial slip of the m. depressor mandibulae—a topology shared by all dendrobatids and a synapomorphy for the family. Without resorting to dissection, a measurement between the lower edge of the tympanic ring and the corner of the mouth is sometimes useful, although differences of < 0.5 mm may be obtained (table 1) and, in any case, intraspecific variation cannot be ruled out a priori.

A few other apparent differences between the holotype and Ecuadorian specimens (see under Variation and Color in Life) might also represent either variation within a species or minor differences between related species. I originally thought that the Ecuadorian population represented a new species, but I cannot confidently differentiate it from *chocoensis* and therefore prefer not to introduce a new name without more corroboration than is available at present.

The two trans-Andean species discussed in this paper belong to *Colostethus* in the broad sense. They seem more closely related to cis-Andean *C. fuliginosus* than to the type species of *Colostethus* (*latinasus*). Further study may well necessitate formal resurrection of the old genus *Hyloxalus*, of which the type species is *fuliginosus*. In the absence of an adequate character analysis, however, the name *Colostethus* sensu lato should be continued for *fuliginosus* and its relatives, particularly in light of the following correction.

Note on the Definition of *Colostethus* Cope

Myers et al. (1991: 18) recently commented on the partitioning of *Colostethus*. They continued using this name in the loose sense while suggesting that, "A restricted *Colostethus* can be resolved by the novel third-finger synapomorphy, although use of this sexually dimorphic character is not without problems." The unusual condition of a swollen third finger in adult males, which characterizes a dozen or so species of *Colostethus*, was claimed to be "unknown elsewhere in the Dendrobatidae." This was a serious lapsus on my part, since I have observed the presence of a slightly swollen third finger in males of certain *Epipedobates*. Whether its occurrence in *Epipedobates* owes to homoplasy or homology remains to be determined. The first possibility would not invalidate the character as a defining one for *Colostethus* s.s., whereas the second might help to elucidate relationships at the base of the lipophilic alkaloid-producing group of dendrobatids (see Myers et al., 1991: 28–29).

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