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Volume: 84 Issue: 1

Month/Year: 1971 Pages: 1470-162

Article Author: Edwards, S. R.

Article Title: Taxonomic notes on South American Colostethus with descriptions of two new species.

ISSN: 0006-324X

Odyssey TN: 737302



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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

TAXONOMIC NOTES ON SOUTH AMERICAN
COLOSTETHUS WITH DESCRIPTIONS OF TWO
NEW SPECIES (AMPHIBIA, DENDROBATIDAE)

BY STEPHEN R. EDWARDS

University of Kansas, Lawrence, Kansas 66044

The family Dendrobatidae can be divided into two groups—those species lacking maxillary teeth (*Dendrobates*) and those species having maxillary teeth (*Phyllobates* and *Colostethus*). Savage (1968) studied Central American dendrobatids and separated *Phyllobates* from *Colostethus* as follows: *Phyllobates* has scattered "punctations" of black pigment in the flesh; the dorsal and ventral ground color is black; and the skin is poisonous. *Colostethus* lacks black pigmentation in the flesh; the dorsal ground color is dark brown, and the venter is white to yellow (males of some species have a black wash on the throat); and the skin is non-poisonous. The criteria of ventral coloration utilized by Savage to distinguish *Colostethus* must be amended to include species with extensive black coloration of the venter. Some of those species that Savage considered to be in the genus *Colostethus* were named in the genera *Prostherapis* and *Hyloxalus*, both of which are now placed in synonymy of *Colostethus*. Therefore, by implication, all those South American species originally described in *Prostherapis* and *Hyloxalus* also must be referred to *Colostethus*. Savage also indicated that many South American species named in the genus *Phyllobates* belong in *Colostethus*. Examination of type specimens, study of preserved specimens, and critical analysis of original descriptions has led me to refer the following 43 nominal species to the genus *Colostethus* (the original generic allocation is given in parentheses):

alagoanus (*Phyllobates*) Bokermann, 1967
alboguttatus (*Phyllobates*) Boulenger, 1903
anthonyi (*Phyllobates*) Noble, 1921
beebei (*Hylixelus*) Noble, 1923
bocagei (*Hyloxalus*) Jiménez de la Espada, 1871
bromelicola (*Phyllobates*) Test, 1956
brunneus (*Prostherapis*) Cope, 1887
capixaba (*Phyllobates*) Bokermann, 1967
carioca (*Phyllobates*) Bokermann, 1967
chocoensis (*Hylixelus*) Boulenger, 1912
collaris (*Hylixelus*) Boulenger, 1912
dunni (*Prostherapis*) Rivero, 1961
festae (*Prostherapis*) Peracca, 1904
fuliginosus (*Hyloxalus*) Jiménez de la Espada, 1871
granuliventris (*Hylixelus*) Boulenger, 1919
herminae (*Prostherapis*) Boettger, 1893
infraguttatus (*Phyllobates*) Boulenger, 1898
inguinalis (*Prostherapis*) Cope, 1868
intermedius (*Phyllobates*) Andersson, 1945
kingsburyi (*Phyllobates*) Boulenger, 1918
latinasus (*Phyllobates*) Cope, 1868
mandelorum (*Phyllobates*) Schmidt, 1932
marchesianus (*Phyllobates*) Melin, 1941
mertensi (*Phyllobates*) Cochran and Goin, 1964
neblina (*Prostherapis*) Test, 1956
olfersoides (*Eupemphix*) Lutz, 1925
palmatum (*Phyllobates*) Werner, 1899
peruvianum (*Phyllobates*) Melin, 1941
pratti (*Phyllobates*) Boulenger, 1899
pulchellum (*Phyllodromus*) Jiménez de la Espada, 1871
ranoides (*Dendrobates*) Boulenger, 1918
riocosangae (*Phyllobates*) Andersson, 1945
riveroi (*Prostherapis*) Donoso-Barros, 1964
shrevei (*Prostherapis*) Rivero, 1961
subpunctatum (*Prostherapis*) Cope, 1899
sylvatica (*Phyllobates*) Barbour and Noble, 1920
taeniatus (*Phyllobates*) Andersson, 1945
trilineatum (*Phyllobates*) Boulenger, 1913
trinitatum (*Phyllobates*) Garman, 1888

variabilis (*Prostherapis*) W
vergeli (*Hyloxalus*) Hellmi
vertebralis (*Phyllodromus*)
whimperi (*Prostherapis*) B

The purpose of this paper is the revision of specific taxonomy of *Colostethus* in Ecuador, to describe two new species from the Andean region of Ecuador. *Colostethus vertebralis* (Boulenger, 1912) is considered together because of its geographic distribution in the Andean, southern Ecuador. The paucity of information available on *C. vertebralis*. Recent collections of this species now make it possible to describe the variation of a number of characters.

Colostethus elaeagnus

(Figs. 1a, 1b)

Holotype: KU 120540, from Loja, Ecuador, collected on 9 June 1968 by John D. Lynch.

Paratypes: KU 120515-539, collected on 9 June 1968 from 9 km E Loja, Loja Province, Ecuador, by John D. Lynch.

Diagnosis: The following number of characters in the diagnosis propose of standardizing diagnoses in the genus *Colostethus*, 18.0 to 25.7 (1) sexual dimorphism in color (2) sexual dimorphism in color dorsally and laterally, smooth ventral surface; (3) tympanic fold heavy, covering dorsal surface; (4) first finger longer than second; (5) first and second fingers expanded; (6) third finger of male with glands distinct; (7) tarsal fold distinct; (8) tubercle along inner margin of dorsal surface; (9) basally, continuous with lateral fold; (10) all toes; (11) toe discs slightly enlarged; (12) lateral stripe yellow to gray-white, bordered above and below by irregular white ground color pale yellow-gray to yellow, with or without white spots; (13) across the chest; (14) gray bars, interspaces gray to yellow; (15) small, body length 11.2 to 14.2 (mean 22.4) mm in stages 31 to 40; (16) not umbrelliform; (17) tooth rows

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 sson, 1945
 ger, 1918

variabilis (*Prostherapis*) Werner, 1899
vergeli (*Hyloxalus*) Hellmich, 1940
vertebralis (*Phyllodromus*) Boulenger, 1899
whimper (*Prostherapis*) Boulenger, 1882

The purpose of this paper is to establish a working foundation of specific taxonomy in the genus *Colostethus* in South America, to describe two new species, and to redescribe *Colostethus vertebralis* (Boulenger). The three species are considered together because of their similar distributions in high Andean, southern Ecuador. In the past there has been a paucity of information available on the widespread species, *C. vertebralis*. Recent collections from throughout the range of this species now make it possible to consider the geographic variation of a number of characters.

Colostethus elachyhistus new species

(Figs. 1a, 2a, 3, 4, and 6)

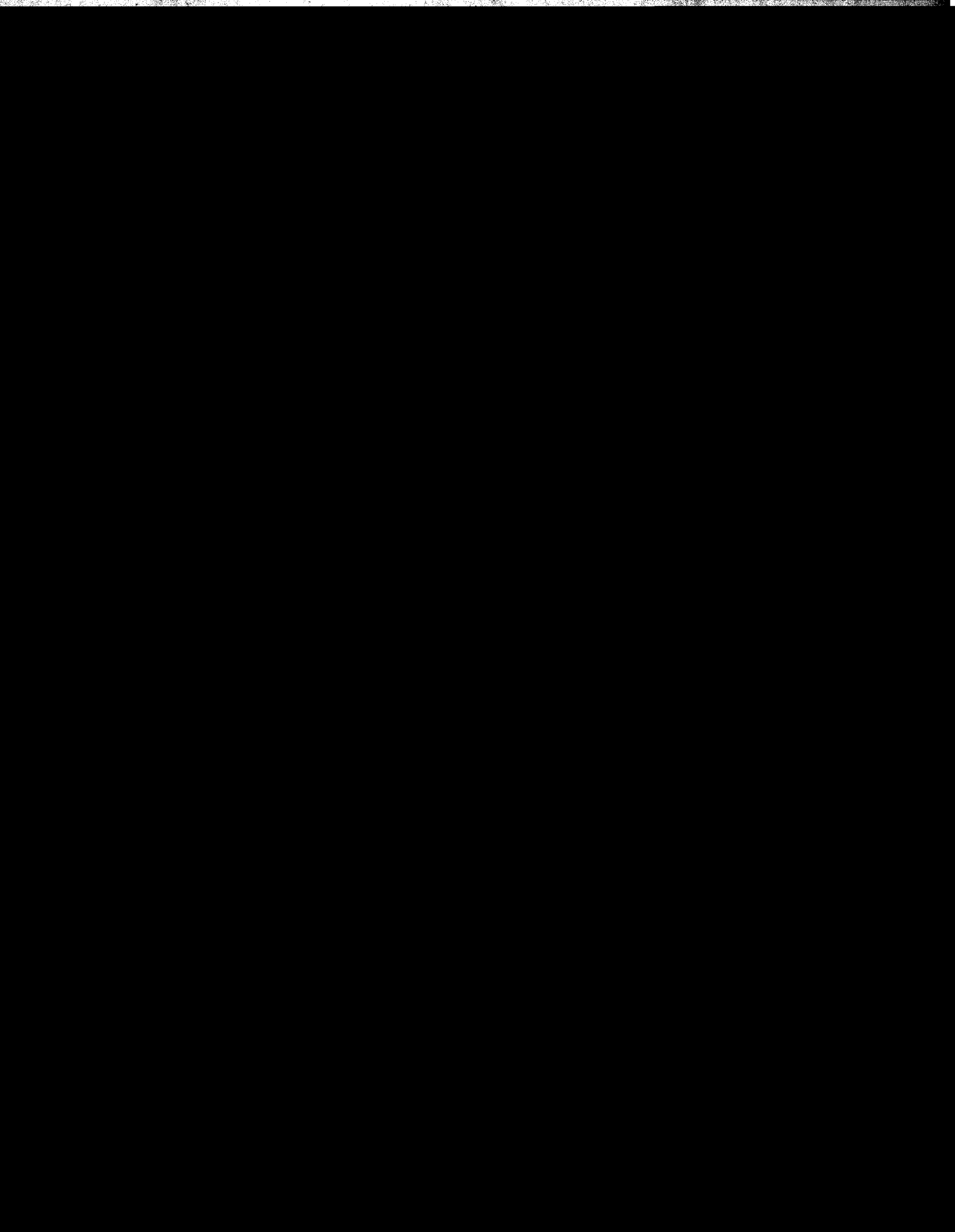
Holotype: KU 120540, from Loja, Loja Province, Ecuador, 2150 m, collected on 9 June 1968 by John D. Lynch.

Paratypes: KU 120515-539, collected with the type; and KU 120541, from 9 km. E. Loja, Loja Province, Ecuador, 2660 m, collected by John

The following nomenclature designations are given for the purpose of standardizing diagnoses in forthcoming descriptions: (0) median caudal fin absent; (1) snout-vent length 18.0 to 25.7 (mean 22.4) mm; (2) sexual dimorphism in color and size absent; (3) skin granular dorsally, smooth ventrally; (4) tympanum distinct; (5) supraorbital fold heavy, covering dorsal one-third of tympanum; (6) first finger longer than second; (7) finger discs subequal in size, not expanded in males; not swollen; (8) digital scutes; (9) dorsal fin oblique, extending from inner metatarsal margin of distal half of tarsus; (10) toes webbed with lateral fringes extending along both margins of web; (11) toes lightly expanded, subequal in size; (12) dorsal ground color gray-white, extending from upper eyelid to groin, overlain by irregular black reticulations; (13) dorsal ground color gray to gray-black; (14) venter creamy white with white on black marbling extending medially to thighs, shanks and feet marked by irregular dark gray to yellow-gray; (15) free-swimming tadpole with body length 14.2 (mean 12.7) mm, tail length 21.0 to 24.5 mm, tail width 31 to 41; (16) mouth directed anteroventrally, with both rows 2/3 with second upper and first lower

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fourth diameter of tympanum; first finger longer than second; third finger of males not swollen.

Ratio of shank to snout-vent length 0.378-0.548 (mean 0.500); inner tarsal fold short, oblique, present on distal half of tarsus, thickened and curving abruptly near end of fold; inner metatarsal tubercle ovoid; outer metatarsal tubercle conical, subequal in size to inner metatarsal tubercle; supernumerary tubercles absent; subarticular tubercles simple, round; digital pads slightly expanded, larger than those of fingers; webbing between toes vestigial; lateral fringes extending to bases of discs along both margins of all toes; webbing and lateral fringes indistinct or absent in juveniles.

Coloration: In preservative, dorsal ground color of adults pale yellow-gray to gray-black with irregular black blotches in two parallel rows

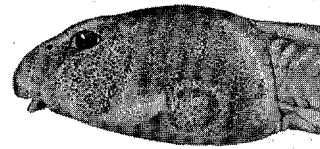


FIG. 3. Lateral view of free-swimming tadpole of *Colostethus elachy* (one of series KU 12137).

expanded laterally just anterior to eye; moderately separated slightly closer to eyes than to midline at about midlength of body; dextral-caudal musculature gray body, extending nearly to tip of from point just posterior to tail point of tail; dorsal fin extending

Mouth small, anguiform, with two rows of papillae on fleshy lip; upper and first lower rows separated medially by beak; beak

In preservative, black above; gray anterior to eyes; papillae are creamy white with black reticulation anteriorly on dorsal half of tail; pigment; ventral fin colorless, fourth.

Etymology: From the Greek *elachy* meaning web, referring to the rudimentary web.

Natural history: The specimen collected by day in or around stream calling by night and day. No male was found guarding a clutch of Loja. The embryos were in the sac was visible and the head and

Comparisons: The presence of distinguishes *Colostethus elachy* webbing (*anthonyi*, *bromelicola*, *marchesianus*, *nubicola*, *ofersioi*, *mancae*, *taeniatus*, *tricolor*, and *ve* have the toes more than one-third *dunni*, *fuliginosus*, *granuliventris*,

Those species having the toes

sloping gradually posterior to tip of snout; snout rounded to along back; dorsal fin extending anterior margin of caudal stripe black, narrowing or terminating near tip of snout; stripe indistinct, formed by enamel white flecks; lips with patches of gray; dorsolateral stripe narrow anteriorly, broad yellow to gray-white, extending from upper eyelid to groin, with pale stripe of same color along anterior surface of thigh; dorsal stripe bordered above and below by dark gray to black reticulation extensive below; upper arm with or without gray to black mottling dorsally; longitudinal black stripe along anterior margin of proximal one-third of arm; forearm colorless or dark gray, mottled or marbled; thigh, shank, tarsus, and foot marked dorsally by irregular transverse black bars, with yellow to creamy interspaces; venter creamy to yellow, with or without white on black marbling extending medially across chest; yellow patch on chin and in groin in some specimens.

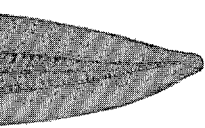
In preservative, juveniles having a more pastular dorsum, with dark gray to black ground color; dorsolateral stripe faint; venter lacking marbling; transverse bars on legs more distinct with creamy-white interspaces; forearm, and tail-stub when present, faintly barred.

In life dorsal ground color of adults pale olive to reddish brown with brown to black flecks; few specimens have reddish-brown spots dorsally; dorsolateral stripes pale cream to creamy yellow, bordered by greenish brown to dark brown; limbs dull gray-green with black spots or bands; groin and light areas on hind limbs yellow to brown; venter pale yellow-green with white spots, or solid white, with or without pale gray mottling; lips bronze; iris coppery bronze with black reticulations.

The above description is based on specimens from Loja. Those specimens from 9 km E of Loja were similarly colored, except that they had a distinct black area above the dorsolateral stripe; and the throat was dull yellow.

Tadpoles: (Figs. 3 and 4). Description based on a series of tadpoles from developmental stages 31 to 41 (free-swimming). Developmental stages for embryos and tadpoles are based on the system proposed by Gosner (1960).

Body depressed, flattened ventrally for half body length; dorsal contour



Colostethus elachy-

of adults pale yellow-
in two parallel rows
with darker specimens;
at tip of snout; labial
lips with or without
ly, broad posteriorly,
to groin, continuous
of thigh; dorsolateral
black reticulations, most
to black stippling or
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lar dorsum, with dark
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dorsal fringes indistinct or absent

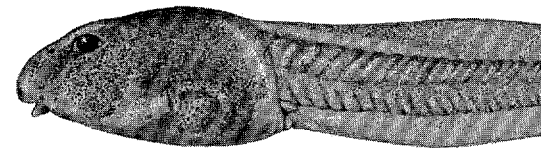


FIG. 3. Lateral view of free-swimming tadpole of *Colostethus elachyhistus* (one of series KU 121377), $\times 7.2$.

sloping gradually posterior to eyes, curving abruptly anterior to eyes to tip of snout; snout rounded to subovoid in dorsal view; body abruptly expanded laterally just anterior to eyes; body widest at midpoint; eyes distinct, moderately separated medially, directed dorsolaterally; nostrils slightly closer to eyes than to tip of snout; spiracle sinistral, slightly below midline at about midlength of body; anal tube distinct, median to slightly dextral; caudal musculature gradually tapering in width and depth from body, extending nearly to tip of narrowly rounded tail; dorsal fin tapering from point just posterior to tail insertion to deepest point at about midpoint of tail; dorsal fin extending onto body; ventral fin narrower than dorsal fin.

Mouth small, anteroventral, bordered anterolaterally and posteriorly by two rows of papillae on fleshy lips; tooth rows 2/3, equal in length; second upper and first lower rows divided medially, second upper tooth row separated medially by beak; beak rough, edges serrated.

In preservative: black above, dark gray to black below, becoming pale gray anterior to eyes; papillae and lips unpigmented; caudal musculature creamy white with black reticulations concentrated into small blotches anteriorly on dorsal half of tail; dorsal fin with fine reticulations of black pigment; ventral fin colorless, except for a few black flecks on distal fourth.

Etymology: From the Greek *elachys*, meaning little, and *histos*, meaning web, referring to the rudimentary webbing on the feet.

Natural history: The specimens from the vicinity of Loja were collected by day in or around small pools of water. Males were heard calling by night and day. No amplexing adults were found. A single male was found guarding a clutch of 19 eggs beneath a rock 9 km E of Loja. The embryos were in developmental stages 19 and 20; the yolk sac was visible and the head and tail were well developed.

Comparisons: The presence of basal webbing between the toes readily distinguishes *Colostethus elachyhistus* from those species which lack webbing (*anthonyi*, *bromelicola*, *infraguttatus*, *intermedius*, *kingsburyi*, *marchesianus*, *nubicola*, *olfersioides*, *pratti*, *ranoides*, *riocosangae*, *talamancae*, *taeniatus*, *tricolor*, and *vertebralis*) and from those species which have the toes webbed basally but not webbed between the toes (*poagei*, *pacobensis*, *coarctatus*, *caunni*, *fuliginosus*, *granuliventris*, *palmatus*, *riveroi*, and *vergeli*).

Those species having the toes webbed basally are distinguished from

on a series of tadpoles
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The specimen from the wet Pacific lowlands (MCZ 3214, Río Chanchan, Chimborazo Province, Ecuador) is indistinguishable from *C. inguinalis*.

This species is referred to *inguinalis* because of the unique dorsal color pattern consisting of distinct, round white spots on a light brown ground color, the distinctly expanded discs on the toes. This identification is supported by data taken on the types of *inguinalis* by Liam E. Duellman.

The majority of the specimens reported by Barbour and Noble were in localities at 500 to 800 m elevation in the relatively dry Upper Río Chanchan drainage. I have examined specimens from each of the localities reported by Barbour and Noble (total 39 specimens) and found that they are the same as *inguinalis*. The poor condition of the Barbour specimens that I have examined precludes specific identification. However, as a group, they can be distinguished from *elachyhistus* by the lack of the unbarred legs, the narrower and frequently discontinuous dorsal stripe, the greatly expanded discs on the fingers, and the blunt snout when viewed in dorsal profile.

Colostethus elachyhistus has a known distribution along the western margin of the Andes. Elevations are 150 to 2600 m, from 1 to 5 degrees S to 5 degrees 30' S latitude. Specimens examined: Ecuador—Loja: KU 120515 (neotype), KU 121516–540 (paratopotypes); KU 121379 (20 juveniles); KU 121373–376 (adherent tadpoles), KU 121377–378 (free-swimming tadpoles); 9 km E Loja; KU 120541, 121380 (eggs); 3 km SW Malacatos; MCZ 56256–257; 10 km N Celica; MCZ 56259, 56265.

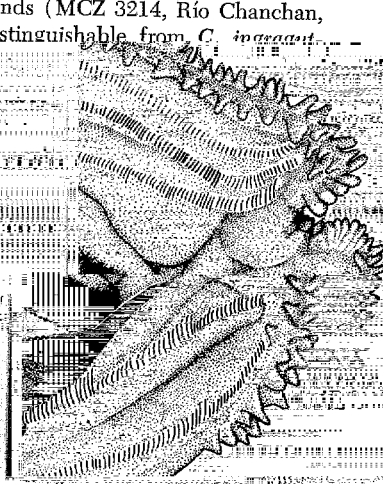
Colostethus anthracinus new species

(Figs. 1b, 5, and 6)

Holotype: KU 120639, from Páramo de Raranga, 12 km S Cutchil, Morona-Santiago Province, Ecuador, 3400 m, collected 18 June 1968 by John D. Lynch.

Paratypes: KU 120640–658, collected with the holotype.

Diagnosis: (1) Small *Colostethus*, 17.2 to 19.9 (mean 18.3) mm snout-vent length; (2) sexual dimorphism exhibited in ventral coloration of males; (3) skin granular anterodorsally, pustular to areolate in area around vent and on dorsal surfaces of thighs; (4) tympanum indistinct, completely covered in some males; (5) supratympanic fold well developed; (6) first finger longer than second; (7) discs of fingers not expanded; (8) third finger of males not swollen; (9) digital glands distinct, with enamel white pigmentation; (10) tarsal fold sigmoid, not associated with inner metatarsal tubercle; (11) webbing and lateral fringes of toes absent; (12) discs of toes not expanded; (13) dorsolateral stripe yellow to gray, narrow, most conspicuous in females; (14) dorsal ground color pale gray to dark brownish black; (15) venter yellow to creamy white in females, dark gray to solid black with yellow groin in males; (16) limbs colored like dorsum, with or without dark bars restricted to thighs.



tadpole (one of series KU

rixaba and *carioca* from Brasil their small size (14 to 18 mm) between the third and fourth pharyngeal teeth (15 mm snout-vent length only between the outer four pharyngeal teeth). *Colostethus* differ from *elachyhistus* in the absence of a distinct tympanum, the concealed tympanum. Further, in 30 mm snout-vent length), *Colostethus* possess three plantar tubercles and that surrounding the first is tuberculate. Although *C. anthracinus* it has a concealed tympanum, the first and second fingers are sub-

over 1000 specimens of *C. inguinalis* in the lowlands of Ecuador. Geographic provinces (relatively wet Pacific lowlands, Ecuador).

Description and variation: (Figs. 1b, 5a, 5b, and 6). Head wider than long, same width as body; ratio of head width to snout-vent length 0.335–0.403 (mean 0.368); snout rounded, blunt, slightly projecting in lateral profile; canthus rostralis obtusely angular, slightly constricted; loreal

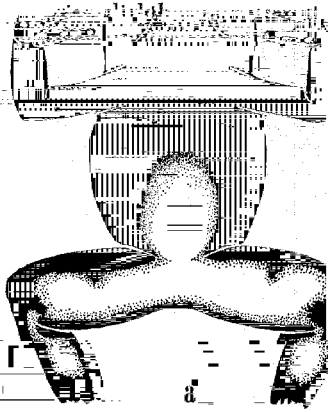


FIG. 5. Diagrammatic ventral view showing extremes in ventral coloration

(darker specimens); ventral part of legs black in all males examined.

In life, dorsum deep chocolate yellow brown (females from Loja Loja Province) with varying anteroposterior stripe creamy bronze, posterior 1/3 in all specimens from Morona-Santiago Province; males from Loja Province flanks of all specimens blue-gray; venter of males from both localities of thighs and in groin; venter of both males and females orange black flecking; iris reddish brown.

Etymology: From the Latin *coloratio*, reference to the ventral coloration.

Natural history: The type locality is páramo; the vegetation consists of cloud forest; specimens in the KU collection were collected along rivulets by day, during clear days with cloud cover. A second locality, with vegetation consisting of shrub forest, was found under rocks adjacent to a stream, a sign of breeding activity.

region faintly concave; nostrils lateral, much closer to eye than to snout; diameter of eye much greater than distance from eye to nostril; tympanum indistinct; one half to fully covered by heavy supratympanic fold; tongue round to oval, entire behind, posterior one-half to three-fourths free; choanae small, not visible when viewed from directly below; males with a single, median, subgular vocal sac; vocal slits short, oblique, near base of tongue.

Skin of dorsum finely granular anteriorly; dorsal ridges or folds absent; skin surrounding vent and on dorsal surfaces of thighs coarsely granular; venter smooth; anal opening unmodified; forearm lacking tubercles; two palmar tubercles; outer tubercle rounded to subtriangular; inner tubercle oval, equal in size to outer tubercle; subarticular tubercles round, simple, larger proximally; first finger longer than second; third finger of males not swollen.

Ratio of shank to snout-vent length 0.430–0.488 (mean 0.459); inner tarsal fold short, sigmoid, not associated with inner metatarsal tubercle; inner and outer metatarsal tubercles oval, slightly elevated, equal in size; supernumerary tubercles absent; subarticular tubercles simple, round; toes lacking webbing and lateral fringes; toe discs slightly expanded or not.

Coloration: In preservative, males from Morona-Santiago Province solid dark gray to black dorsally; indistinct black vertebral stripe visible in paler specimens; dorsal coloration of single male from Loja Province pale gray with large black spots at level of scapula; black lateral stripe in this specimen extending from groin to level of arm, being separated from black flanks by a narrow, dorsolateral creamy white stripe extending anteriorly from groin.

Females from both localities paler dorsally; dorsal ground color dark brown with black vertebral stripes (Morona-Santiago Province) or gray with dorsal black blotches (Loja Province); distinct dorsolateral stripe of light yellow present on all females; black canthal stripe, extending around snout, present in all females and single male from Loja Province; upper lip and labial area yellow with enamel white spots in all females and some males from Morona-Santiago Province; remaining males having black lips; upper surfaces of limbs dark gray to black in all males from both localities; females with yellow-gray to black forearms (Morona-Santiago Province) or pale gray with darker transverse bars along dorsal thighs and shanks (Loja Province); anterior surface of arms yellow in some females.

Ventral coloration sexually dimorphic, irrespective of locality; females having yellow-white venter, with gray wash on ventral surfaces of limbs; males having varying degrees of uniform black pigmentation on chin, throat, and chest as isolated spots (lighter specimens), or extending over entire venter, excluding groin and proximal portion of ventral thighs

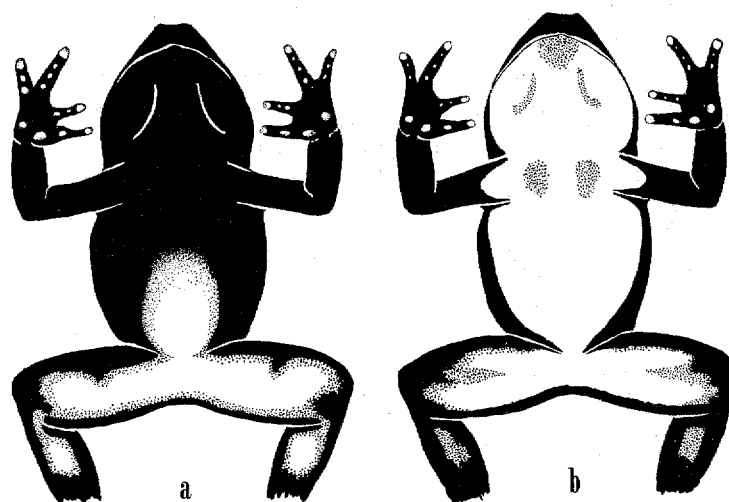


FIG. 5. Diagrammatic ventral views of *Colostethus anthracinus* showing extremes in ventral coloration in males.

(darker specimens); ventral parts of hands, feet, arms, and distal portion of legs black in all males examined; palmar and plantar tubercles unpigmented.

In life, dorsum deep chocolate brown (Morona-Santiago Province), yellow brown (females from Loja Province), or bronze brown (males from Loja Province) with varying amounts of flecking or spotting; dorsolateral stripe creamy bronze, posterior half of stripe bordered dorsally by black in all specimens from Morona-Santiago Province and females from Loja Province; males from Loja Province with reddish bronze labial stripe; flanks of all specimens blue-gray to black with blue or green flecking; venter of males from both localities black, with orange on ventral surface of thighs and in groin; venter of females yellow to orange; axillae of both males and females orange; thighs variably black to brown with black flecking; iris reddish bronze.

Etymology: From the Latin *anthracinus* meaning "coal-black," in reference to the ventral coloration in the males.

Natural history: The type locality, at an elevation of 3400 m, is in páramo; the vegetation consists of short grasses and cushion plants. All specimens in the KU collections were collected from beneath stones along gullies, by day, during cold rainy conditions with 100 percent clear cover. A second locality, 500 m lower in elevation, is subpáramo with vegetation consisting of small bushes and grasses. Specimens were found under rocks adjacent to a small, water-filled ditch. There was no sign of breeding activity.

Distribution: *Colostethus anthracinus* has an Andean distribution in southern Ecuador at elevations between 2500 and 3500 m, and 3 degrees S and 4 degrees S latitude. Specimens examined: ECUADOR: *Morona-Santiago*: Páramo de Raranga, 12 km S Cutchil, KU 120639 (holotype), KU 120640-658 (paratopotypes); *Loja*: 13 to 14 km E Loja (by road), KU 120635-638; *Azuay*: vicinity of Gualaceo, CAS 94772.

Comparisons: *Colostethus anthracinus* can be distinguished from all previously described species in the genus except *C. talamancae*, *nubicola*, and *pratti* (all of Central America) on the basis of the black ventral coloration in the males. *Colostethus nubicola* can be distinguished on the basis of the reduced ventral coloration, and inconsistency in the color dimorphism; Savage (1968) described the venter of males as being immaculate in some specimens. *Colostethus pratti* differs in having the third finger of the males swollen, and a mottling on the throat. *Colostethus talamancae* is larger (males to 22 mm and females to 24 mm snout-vent length) and lacks a tarsal fold; furthermore, the nostril lies one-half the distance between the eye and the tip of the snout, and the dorsum is smooth.

Colostethus vertebralis (Boulenger)

1899 *Phyllodromus vertebralis* Boulenger, Ann. Mag. Nat. Hist., London (73: 456) Cañar (8400 ft), Ecuador.
 1904 *Prostheropsis vertebralis* Peracca, Bol. Mus. Zool. Anat. Comp. Torino (456) 19: 17.
 1920 *Phyllobates vertebralis* Barbour and Noble, Bull. Mus. Comp. Zool., Cambridge 63: 401.

(Figs. 1c and 6)

Diagnosis: (1) Small to medium *Colostethus*, 14.6 to 19.7 (mean 17.1)

mm, (2) sexual dimorphism in size, males being smaller than females; (3) skin smooth dorsally, becoming areolate around vent in some specimens; (4) tympanum indistinct; (5) supratympanic fold heavy, covering dorsal half of tympanum; (6) first finger equal to, or slightly longer than tip of snout; (7) distance between eye and tip of snout greater than eye diameter; (8) diameter of eye; (9) ratio of tympanum width to eye; (10) supratympanic fold broad, indistinctly blotched behind; posterior tibiae partially hidden by maxillae which having conspicuous vocal slits and skin of dorsum smooth to fine granular laterally; weak middorsal fold present unmodified; forearm of a few specimens bearing one or two poorly defined palmar tubercles; outer palmar tubercle ovoid; palmar tubercle; two or three

TABLE 1. Intraspecific morphological variation from different localities, illustrated as a ratio to size (mm)

Locality	Sex
Cuenca, Azuay Province	
8 km S Cutchil, Morona-Santiago Province	
8-9 km N San Lucas, Loja Province	
Laguna de Zurucuchu, Azuay Province	♂
	♀

width to snout-vent length; (11) dorsal view, bluntly defined, concave, not swollen; (12) digital gland distinct; (13) toes present on distal half of tarsus extending from inner margin abruptly at midpoint; (14) webbing and membrane from toes; (15) discs of toes expanded, greater than diameter of toe; (16) dorsolateral stripe broad, greenish yellow, extending from margin of eye to groin, passing over upper eyelid to tip of snout; (17) dorsal ground color lemon yellow to yellow-gray, with pale cream vertebral stripes; (18) venter greenish yellow with black specks of varying densities extending from flanks to chest; (19) thighs and shanks colored as dorsum with black flecks, tarsi and feet with indistinct dark gray bars.

Description and variation: (Figs. 1c; 6; Table 1). Males smaller than females; head width equal to or narrower than body width

morphometric variation in *Colostethus vertebralis* species, illustrating sexual dimorphism with respect to size (means in parentheses).

Sex	N	Elev. (m)	Snout-vent length (mm)	Shank	
				Snout-vent length	
♂♂	6	2540	15.6-17.6 (16.7)	0.436-0.493 (0.473)	
♀♀	3		18.1-19.7 (18.8)	0.441-0.456 (0.448)	
♂♂	8	3040	14.6-17.2 (15.9)	0.430-0.493 (0.456)	
♀♀	7		15.8-18.5 (17.5)	0.403-0.453 (0.429)	
♂♂	10	3100	14.4-17.0 (15.7)	0.430-0.490 (0.460)	
♀♀	16		17.0-19.7 (17.7)	0.410-0.477 (0.437)	
♂♂	4	3200	15.1-17.6 (16.3)	0.430-0.481 (0.451)	
♀♀	6		16.9-19.6 (18.3)	0.413-0.443 (0.430)	

length 0.30-0.40 (mean 0.348); snout rounded in lateral profile; canthus rostralis moderately well defined; (8) hind-finger of males from inner tubercle; (10) inner tarsal fold distinct; (11) lateral tubercle; (12) lateral tubercle; (13) greater than disc of fingers; (14) yellow, extending from posterior per. eyelid to tip of snout or not; (15) to yellow-gray, with or without inter greenish yellow with gray or black dorsal tubercles; (16) black spots or dark gray bars. (6; Table 1). Males smaller than females; head wider than body width; ratio of head

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has an Andean distribution in 2500 and 3500 m, and 3 degrees examined: ECUADOR: Morona-Cutichil, KU 120639 (holotype), 13 to 14 km E Loja (by road), alaceo, CAS 94772.

It can be distinguished from all other species except *C. talamancae*, *nubicola*, and *ibicola* on the basis of the black ventral mottling, and inconsistency in the color of the venter of males as being immixt with *pratti* differs in having the dorsal mottling on the throat. *Colostethus* 22 mm and females to 24 mm old; furthermore, the nostril lies behind the tip of the snout, and the

snout (Boulenger) 1901, Ann. Mag. Nat. Hist., London 27: 100. *Bol. Mus. Zool. Anat. Comp. Madrid* 1901, 1: 100. *and Noble, Bull. Mus. Comp. Zool.*

id 6) *Colostethus* 14.6 to 19.7 (mean 17.1) mm; males being smaller than females; snout-vent length moderate around vent in some specimens; supratympanic fold heavy, covering

tip of snout; distance from eye to nostril about three-fourths eye diameter; nostril slightly depressed; ratio of tympanic width to eye diameter 0.38-0.82 (mean 0.556); supratympanic fold broad, extending to tongue; large, oval, generally not blotched behind; posterior three-fourths free; choanae small, wholly or partially hidden by maxillae when viewed from directly below; males having conspicuous vocal slits and median, subgular vocal sac. Skin of dorsum smooth to finely granular becoming areolate around vent; venter finely granular laterally and in area of groin, smooth medially; weak mid-dorsal fold present in some specimens; anal opening unmodified; forearm of a few specimens from 8500 m N San Lucas bearing one or two poorly defined tubercles; absent in all other specimens; outer palmar tubercle oval, equal to or slightly larger than inner palmar tubercle; two or three supernumerary tubercles infre-

TABLE 1. Intraspecific variation from different localities to species

Locality
Cuenca, Azuay Province
8 km S Cutichil, Morona-Santiago Province
8-9 km N San Lucas, Loja Province
Laguna de Zurucuchu, Azuay Province

width to snout-vent length; dorsal view, blunt in lateral view

present; subarticular tubercles round, distinct, larger proximally; fingers lacking webbing or lateral fringes; digital pads slightly expanded; dorsal digital glands distinct; digital pad of third finger about half diameter of tympanum; first finger equal to or slightly longer than second.

Ratio of shank to snout-vent length 0.403–0.493 (mean 0.448); tarsal fold indistinct, extending from inner metatarsal tubercle, bending abruptly at midpoint; outer metatarsal tubercle conical, equal to inner metatarsal tubercle; subarticular tubercles of toes simple, round, larger proximally; toe pads slightly expanded, more so than pads of fingers; toes lacking webbing or lateral fringes.

Coloration. In preservative, dorsal ground color of adults yellow-gray to brownish-black, lighter brown color occurs in specimens from Laguna de Zurucuchu and Cuenca; specimens from 8–9 km N San Lucas darker; specimens from 8 km S Cutchil exhibit both extremes in coloration; middorsal thin creamy white stripe present in darker specimens; canthal stripe solid black; lips colorless; gold stripe extending below eye in all specimens; flanks flecked with light to dark gray.

Dorsolateral stripe distinct, broad, greenish yellow, extending from posterior margin of eye to groin where it expands slightly; dorsolateral strips extending across upper eyelid to tip of snout or not, forming a dorsal border to black canthal stripe; forearm colorless in lighter specimens and speckled with dark gray in darker specimens; upper arm colored

as forearm, with black longitudinal stripe at elbow; thighs and shanks pale yellow to dark brown, with varying amounts of dark flecking; tarsi and feet indistinctly barred in lighter specimens; venter greenish yellow with gray to black flecking extending medially across throat and chest from flanks; two distinct black spots on chest at level of pectoral girdle in most specimens from Laguna de Zurucuchu; chest spots absent in all other specimens.

In life, dorsum pale rose to light brown; specimens from 8–9 km N San Lucas with black vertebral and paravertebral stripes, with or without a creamy white middorsal stripe; specimens from 8 km S Cutchil have black, irregular spots on dorsum; dorsolateral stripe broad, creamy white, expanding in groin as bright lemon yellow flash color in all specimens; flanks pale blue-gray to blue-green; sides of head chocolate brown, labial stripe white to bronze; specimens from 8 km S Cutchil have yellow throat and pale green-yellow venter; specimens from 8–9 km N San Lucas have off-white throat and venter, with pale gray wash; posterior surface of thighs pale green to creamy yellow with brownish-gray reticulations; iris bronze, lacking reticulation.

Natural history. Specimens of *Colostethus vertebralis* were found under rocks or in open areas, usually near small streams, and at high altitudes. Actively calling males were observed only at 8–9 km N San Lucas, Loja Province, by day.

Distribution. *Colostethus vertebralis* has an inter-Andean distribution from 2 degrees 30' S to 40 degrees S latitude at elevations between 2500 m and 3200 m. Specimens examined: ECUADOR: Loja: 8–9 km N San

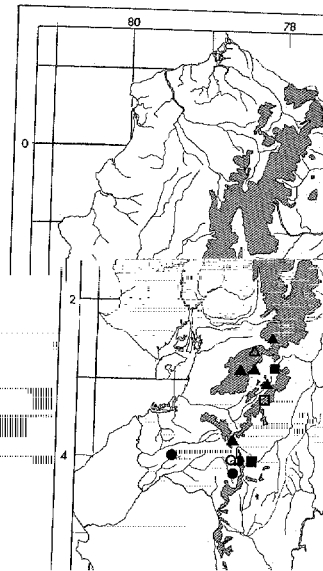


FIG. 6. Locality records for *C. (squares)*, and *C. vertebralis* (circles).

Lucas, KU 120545–569. Azuay: Zurucuchu, KU 120612–631. M... 20570–602. Chimborazo: 30 m

Comparisons. Absence of toe... from those species which posse... Comparisons" under *C. elachyhi*... webbing, all but four can be disti... their larger size (greater than 2... distinct difference in lengths of... species are: *anthonyi*, *bromelicola*, *archesianus*, *nubicola*, *olferioides*. The remaining four species can... *alis* as follows: 1) *Colostethus*... amazonian slopes of the Andes, are... mottled, and the dorsal color patt... elongate spots. The skin of the do... m Panamá and Colombian Ch... y wash on the throat in males

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low flash color in all specimens;
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3 km S Cutchil have yellow throat
s from 8–9 km N San Lucas have
gray wash; posterior surface of
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Colostethus vertebralis were found under
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only at 8–9 km N San Lucas, Loja

has an inter-Andean distribution
titude at elevations between 2500
ECUADOR: Loja: 8–9 km N San

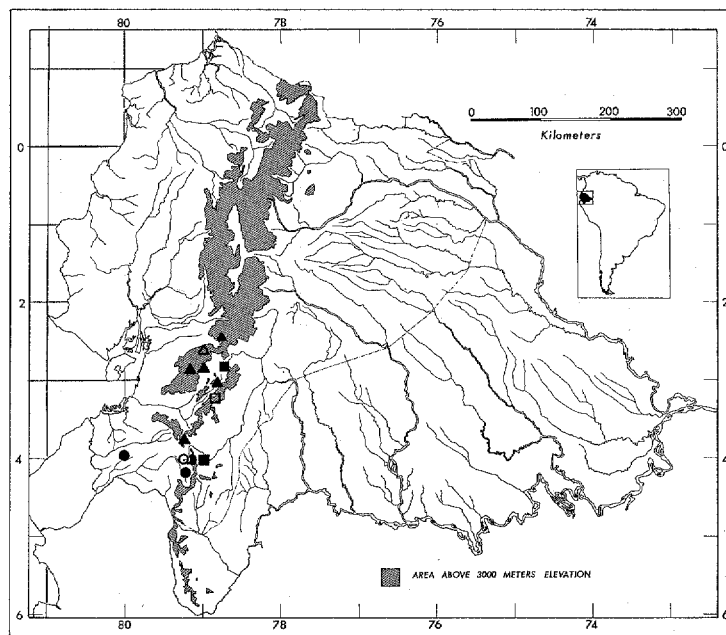


FIG. 6. Locality records for *C. elachyhistus* (circles), *C. anthracinus* (squares), and *C. vertebralis* (triangles)—open symbols denote type localities.

Lucas, KU 120545–569. Azuay: Cuenca, KU 120603–611; Laguna de Zurucuchu, KU 120612–631. Morona-Santiago: 8 km S Cutchil, KU 120570–602. Chimborazo: 30 miles S (by road) Alausi, CAS 85179.

Comparisons: Absence of toe webbing distinguishes *C. vertebralis* from those species which possess webbing (for species involved see "Comparisons" under *C. elachyhistus*). Of those species which lack toe webbing, all but four can be distinguished from *vertebralis* on the bases of their larger size (greater than 20.0 mm snout-vent length) and/or the distinct difference in lengths of the first and second fingers. These species are: *anthonyi*, *bromelicola*, *infraguttatus*, *intermedius*, *kingsburyi*, *marchesianus*, *nubicola*, *olfersioides*, *ranoides*, *talamancae*, and *tricolor*.

The remaining four species can be separated from *Colostethus vertebralis* as follows: 1) *Colostethus riosangae* and *taeniatus*, from the Amazonian slopes of the Andes, are slightly larger. The legs are distinctly barred, and the dorsal color pattern consists of a series of blotches or elongate spots. The skin of the dorsum is smooth. 2) *Colostethus pratti*, from Panamá and Colombian Choco, has a swollen third finger and a gray wash on the throat in males. 3) *Colostethus brunneus*, from the

