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**Ecuadorian Frogs
of the Genus *Colostethus*
(Anura: Dendrobatidae)**

Luis A. Coloma

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Ecuadorian Frogs of the Genus *Colostethus*
(Anura: Dendrobatidae)

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ABSTRACT The present knowledge of dendrobatid frogs of the genus *Colostethus* in Ecuador is summarized. The taxonomic history of the genus is discussed and taxonomically useful characters (e.g., external morphology, gonads, tadpoles, and calls) are described. Thirty-one species are recognized, including five new species described herein. Eight nominal species are assigned to its synonymy; they are—viz., *Colostethus citreicola* (*C. nexipus*), *C. festae* (*Epipedobates parvulus*), *C. intermedius* (*C. kingsburyi*), *C. maculosus* (*C. bocagei*), *C. parvus* (*C. exasperatus*), *C. taeniatus* (*C. pulchellus*), *C. terogranularis* (*C. pulchellus*), and *C. torrenticola* (*C. jacobuspetersi*). Lectotype designations are made for *C. bocagei* and *C. infraguttatus*, and a neotype is proposed for *C. pulchellus*. Several species are redescribed, and taxonomic accounts with data on variation are given for each species. New locality records and distribution maps are provided. The ranges of species previously known from other countries (*C. breviquartus*, *C. lehmanni*, and *C. talamancae*) are extended to Ecuador. New ecological data are presented, and descriptions of tadpoles of eight species and calls of six species are provided. A dichotomous key is included to assist in the identification of specimens. Systematic, distributional, natural history, and extinction trends summaries are presented.

Key words: Dendrobatidae; *Colostethus*; Ecuador; Systematics; Ecology; Distribution; Natural history; Extinction.

INTRODUCTION

The cryptically colored and nonpoisonous dendrobatid frogs of the genus *Colostethus* (sensu lato) are highly diversified in the neotropics; 92 species currently are recognized. *Colostethus* ranges from Costa Rica and the Lesser Antilles to Bolivia and Brazil; the elevational distribution extends from sea level to about 4000 m. The frogs are associated with vegetational types varying from dry and humid tropical forests to montane forest and páramo.

Edwards (1974a) performed a phenetic analysis to clarify the systematics of *Colostethus*. Attempts to recognize natural species groups and the evolutionary history of its members also were made by Rivero (1989), Rivero and Serna ("1988"), Myers et al. (1991), and La Marca (1992). However, these

analyses were hampered by the lack of detailed information on *Colostethus* in regions such as Ecuador. Detailed information that is pivotal to a comprehensive systematic analysis of the genus is presented herein.

In the last three decades, increased collecting efforts in the Andes and adjacent lowlands have revealed the existence of many species, some of which have been described only recently (Rivero, 1984, 1991a,b; La Marca, 1985, 1989; Péfaur, 1984, 1985; Lynch and Ruíz-Carranza, 1985; Rivero et al., 1986; Rivero and Serna, 1986, 1991; Frost, 1986; Duellman and Simmons, 1988; Duellman and Lynch, 1988; Rivero and Granados-Díaz, 1989; Morales and Schulte, 1993).

HISTORICAL RÉSUMÉ

The first descriptions of *Colostethus* from Ecuador (*Hyloxalus fuliginosus*, and *H. bocagei*) were published in 1871 by the Spanish naturalist and explorer Marcos Jiménez de la Espada, who traversed Ecuador and much of Latin America. The type material of these species was deposited in the Museo Nacional de Ciencias Naturales in Madrid, Spain. Jiménez de la Espada (1875:pl. 3) provided illustrations of both *Hyloxalus fuliginosus* and *Hyloxalus bocagei*, and an illustration (but no description) of a third species, *Phyllodromus pulchellum*.

By the end of the 19th Century and the first half of the 20th Century, several other species and new locality records were added through the efforts of several naturalists and professional collectors who sent specimens to European museums. George A. Boulenger described *Prostherapis whymperi*, *Phylllobates infraguttatus*, *Phyllodromus vertebralis*, and *Phylllobates kingsburyi* (1882, 1898, 1899, 1918, respectively) based on collections deposited in the British Museum of Natural History that were made by naturalists and explorers such as Edward Whymper, W. F. H. Rosenberg, P. O. Simmons, and

M. G. Palmer. Peracca (1904) added new locality records for several Ecuadorian *Colostethus* based on collections made by an Italian naturalist, Dr. Enrico Festa.

Between the time of the significant contributions of Boulenger until 1945, there were no remarkable additions to our knowledge of *Colostethus* in Ecuador. Andersson (1945), described several new Ecuadorian frogs based on collections made by an American collector W. Clarke-MacIntyre and a Swedish traveler Rolf Blomberg. Andersson described three *Colostethus* (*Phyllobates taeniatus*, *P. intermedius*, and *P. riososangae*); the types are deposited in the Swedish Museum of Natural History.

After 1945, about 25 years elapsed before the advent of a new period of systematic work on Ecuadorian *Colostethus*. Edwards (1971) described *C. elachyhistus* and *C. anthracinus*, and provided a redescription of *C. vertebralis*. Edwards (1974b) redescribed *C. taeniatus*, *C. marchesianus*, and *C. intermedius*, and described *C. sauli*. Edwards (1974a) recognized 22 nominal species from Ecuador (including several new species). Most of Edwards' contributions are based primarily on material collected by field parties led by William E. Duellman and John D. Lynch and deposited in the Museum of Natural History at The University of Kansas. Subsequently, Frost (1985) listed 14 species of *Colostethus* from Ecuador with taxonomic and geographical references, and described *C. nexipus* (Frost, 1986).

Duellman et al. (1989a, b) described three species of *Colostethus* from the eastern side of the Andes. Myers (1991) recorded *C. chocoensis* from Ecuador.

Rivero ("1988") and Rivero and Serna ("1988") recognized several putative monophyletic groups within *Colostethus*; five of these groups (*C. brunneus*, *C. fuliginosus*, *C. inguinalis*, *C. subpunctatus*, and *C. vertebralis* groups) include Ecuadorian species. Coloma (1991) listed 18 species of Ecuadorian *Colostethus* in a geographical checklist. Rivero (1991a, b) described 12 species based on material collected by several persons (e.g., members of the Olalla family and James A. Peters) and deposited in the collections of the Smithsonian Institution and the Museum of Comparative Zoology. Rivero and Almendáriz (1991) and Almendáriz ("1991") summarized the systematics and distribution of 30 nominal species plus 10 unnamed Ecuadorian *Colostethus*. Finally, Morales and Schulte (1993) described *C. fugax*.

The previous studies provided a baseline for my work on Ecuadorian *Colostethus*, the objectives of which are to (1) describe five new taxa, (2) re-describe poorly known species, and (3) add new data on the morphology, biology, ecology, and distribution of all species. Ultimately, it is expected that the data presented herein will help to provide a better understanding of the evolution of this important component of the neotropical herpetofauna, as well as a basis for further ecological studies and conservation efforts.

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ously shared data with me that contributed significantly to the completion of this project.

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MATERIALS AND METHODS

Specimens examined in the course of this study are listed in the Appendix. Throughout the text and Appendix, specimens are listed with their catalog numbers. Museum abbreviations are taken from Frost (1985) and Duellman (1993); they are, as follow:

AMNH American Museum of Natural History, New York.
 ANSP Academy of Natural Sciences, Philadelphia.
 BM British Museum (Natural History), United Kingdom.
 CAS California Academy of Sciences, San Francisco.
 CSJ Museo de Historia Natural, Colegio San José, Medellín, Colombia.
 EPN Escuela Politécnica Nacional, Quito, Ecuador.
 KU University of Kansas, Natural History Museum, Lawrence.
 LACM Natural History Museum of Los Angeles County, Los Angeles.
 MCZ Museum of Comparative Zoology, Harvard University, Cambridge.
 MECN Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.

MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland.
 MNCN Museo Nacional de Ciencias Naturales, Madrid, Spain.
 MZU Museo Regionale di Scienze Naturali, Torino, Italy.
 NHMG Naturhistoriska Museet, Göteborg, Sweden.
 NMW Naturhistorisches Museum Wien, Vienna, Austria.
 NRM Swedish Museum of Natural History, Stockholm, Sweden.
 QCAZ Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito.
 RMNH Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.
 USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 UMMZ University of Michigan, Museum of Zoology, Ann Arbor.

Measurements were obtained with Helios dial calipers and recorded to the nearest 0.1 mm in the manner described by Duellman and Simmons (1988). Throughout the text SVL = snout-vent length. Sex was determined by dissection and the presence of

sexually dimorphic characters. Sexual maturity of females was determined by the presence of eggs or convoluted oviducts.

Webbing formulae are described in the manner of Duellman and Simmons (1988). The webbing formula $II-1\frac{1}{2}III-1\frac{1}{2}III-2IV2-IV$ is illustrated in Figure 1. In some cases, the webbing formulae are subjective because the distinction between the webbing and lateral fringe is ambiguous. Drawings of specimens immersed in alcohol were made using a Wild M-8 stereo microscope equipped with a camera lucida.

Because *Colostethus* has not been diagnosed by uniquely derived characters, species placement in the genus is a matter of convenience based on a taxon's lack of the apomorphies that characterize monophyletic groups within the Dendrobatidae. The recently described genus *Mannophryne* (La Marca, 1992) accommodates several Ecuadorian *Colostethus* that have either one or several of the putative synapomorphies of the new genus (e.g., bandlike marks on throat; complex, aggressive and mating behavior; yellow throats); however, I think that the unique characters that define *Mannophryne* should be studied in more detail and corroborated within a phylogenetic analysis of all *Colostethus* and *Colostethus*-like forms. Thus, I place within *Colostethus* several species that possess one or several of the characters that define *Mannophryne* pending phylogenetic analyses.

In delimiting species, I relied on characters currently used in dendrobatid taxonomy and additional ones that I found to be constant within populations. In agreement with Frost and Hillis (1990), binomials are expected to reflect lineages, the components of which are not incontrovertibly in different phylogenetic trajectories. However, because of the lack of adequate information for some species, errors of either underestimation or overestimation of the real historical species are plausible.

To aid readers with the applications of names by authors dealing with Dendrobatidae, I present in Table 1 a list of the trivial and present names of *Colostethus* and *Epipedobates* reported from the Ecuadorian fauna. *Colostethus brunneus* and *C. sylvaticus*, that were included in the Ecuadorian fauna by Almendáriz ("1991"), are excluded from this report, because no records were provided.

In the species accounts, synonymies include the

numbers and depository of primary types and the type locality. Diagnoses follow closely the format of Duellman and Simmons (1988) with the addition of other character, which is the color of the testes in males. Data of the diagnoses are taken from the specimens examined, unless otherwise indicated. Measurements of *Colostethus pumilus* and *C. fallax* were taken from the original descriptions. *Colostethus fugax* and *C. peculiaris* were not examined and all data are taken from the original descriptions. Because it is difficult to distinguish adults and juveniles males, I do not report a mean SVL for adults; rather, I present the range of SVL for all males of each species (excluding recently metamorphosed juveniles); mean SVL for females is reported for adults. Each species is compared with, and distinguished from, similar Ecuadorian species to facilitate identification. Descriptions of holotypes are provided for the new taxa and for poorly described taxa. Data on intraspecific variation are presented for most species. Coloration in life, larvae morphology, vocalization, etymology, distribution, and ecology are provided for each species. A dichotomous key is included to aid in identification of specimens.

I chose to describe and compare back-riding tadpoles in Stages 24 and 25 (Gosner, 1960) (except the tadpoles of *Colostethus anthracinus* and *C. awa*, which were reared in captivity) because they can be identified with confidence. The occurrence of several species of Dendrobatidae in sympatry causes uncertainty in assigning free-swimming tadpoles to a particular species in the absence of complete developmental series.

Ecological distributions of each species are given in the Ecuadorian life zones defined by Cañadas-Cruz (1983). Unless otherwise indicated, climatological data for the life zones are taken from Cañadas-Cruz (1983). Distribution maps with locality records are based on specimens examined and reliable literature records. The ranges of most species do not necessarily reflect their actual distribution (see Extinction Trends for more detail). Illustrations of relevant characters and color photographs are provided for most of the species.

Calls of six species were recorded. Recordings of all species except *Colostethus jacobuspetersi* were obtained with a Marantz stereo cassette recorder and a Sennheizer K3U microphone. Two recordings of *C. jacobuspetersi* were obtained with a Sony cas-

sette recorder and a Uher (Model 4000-S) recorder. Periods during which the frog appeared to be undisturbed by the investigator were chosen for analysis. Audiospectrograms were made on a Vibralizer (Kay Electric Company) using the narrow band frequency (45 Hz). Frequency measurements of the calls were obtained by using a grid marked on a plastic overlay on top of the audiospectrograms. Call rates (number

of calls per minute) were measured with a stopwatch directly from the tapes. Notes per call, call length, note duration, and phase (time between notes) were measured from wave forms generated by SoundEdit of the Farallon MacRecorder Sound System software. Original tapes are on file in the tape archive, Division of Herpetology, Natural History Museum, The University of Kansas.

Table 1. Alphabetical synonymy of Ecuadorian *Colostethus* and *Epipedobates*.

Trivial name	Original generic name, author, and date			Present name
<i>anthonyi</i>	<i>Phyllobates</i>	Noble	1921	<i>Epipedobates tricolor</i>
<i>citricola</i>	<i>Colostethus</i>	Rivero	1991b	<i>Colostethus nexipus</i>
<i>festae</i>	<i>Prostherapis</i>	Peracca	1904	<i>Epipedobates parvulus</i>
<i>intermedius</i>	<i>Phyllobates</i>	Andersson	1945	<i>Colostethus kingsburyi</i>
<i>maculosus</i>	<i>Colostethus</i>	Rivero	1991a	<i>Colostethus bocagei</i>
<i>paradoxus</i>	<i>Colostethus</i>	Rivero	1991a	<i>Epipedobates tricolor</i>
<i>parcus</i>	<i>Colostethus</i>	Rivero	1991b	<i>Colostethus exasperatus</i>
<i>riocosangae</i>	<i>Phyllobates</i>	Andersson	1945	<i>Colostethus pulchellus</i>
<i>taeniatus</i>	<i>Phyllobates</i>	Andersson	1945	<i>Colostethus pulchellus</i>
<i>terogranularis</i>	<i>Colostethus</i>	Rivero	1991b	<i>Colostethus pulchellus</i>
<i>torrenticola</i>	<i>Colostethus</i>	Rivero	1991b	<i>Colostethus jacobuspetersi</i>

CHARACTERS

Following is a summary of the characters used, or that are potentially useful, in the diagnoses of the species.

Size.—The species of *Colostethus* from Ecuador generally are small-to-medium-sized (Table 2), compared to other dendrobatid frogs, such as *Aromobates*, which reaches 64 mm SVL. The smallest species is *C. machalilla*, attaining a maximum SVL of 17.6 mm. The largest species, *C. fuliginosus*, has a maximum SVL of 32.5 mm. The smallest recently metamorphosed juvenile of *C. chocoensis* is 6.7 mm in SVL. Males usually are smaller than females (Table 2).

Discs on fingers and toes.—Some *Colostethus* have greatly expanded terminal discs on the digits; others have small discs about the same diameter as the width of the digits. Species at higher elevations, such as *C. anthracinus*, *C. jacobuspetersi*, and *C.*

vertebralis, have discs about equal in width to the digits. Species at lower elevations usually have expanded discs. A similar elevational trend occurs among populations assigned to *C. elachyhistus*. In the diagnoses, discs of the third finger and fourth toe were used to assess disc size.

Relative lengths of first and second finger.—In most Ecuadorian *Colostethus*, the first finger is about equal in length to the second finger (I = II), when the fingers are adpressed. In *C. chocoensis*, *C. nexipus*, and *C. punilus*, the first finger is shorter than the second; in *C. kingsburyi*, *C. machalilla*, *C. marchesianus*, *C. talamancae*, and *C. toachi*, the first finger is longer than the second.

Fringes on fingers and toes.—The fringe is a lateral dermal fold on the digits. Some species (e.g., *Colostethus elachyhistus*, *C. exasperatus*, *C. talamancae*, and *C. sauli*) clearly have this charac-

Table 2. Snout-vent lengths (mm) of Ecuadorian *Colostethus*. Range is given for adult females. Range for males includes adult and subadult individuals.

Species	Females			Males		Recently metamorphosed
	Range	(mean)	<i>n</i>	Range	<i>n</i>	(<i>n</i> = 1)
<i>anthracinus</i>	17.1–23.6	(19.4)	15	16.2–19.0	14	12.9
<i>awa</i>	19.1–25.9	(22.5)	38	16.1–22.4	26	12.1
<i>bocagei</i>	23.9–28.2	(26.1)	20	17.0–24.7	20	13.4
<i>breviquartus</i>	15.4–16.8	(16.3)	3	—	—	—
<i>cevallosi</i>	20.6–21.0	(20.8)	2	18.2	1	—
<i>chocoensis</i>	22.9–27.0	(25.3)	6	21.5–22.1	3	6.7
<i>delatorrae</i>	19.3–20.5	(19.9)	2	17.5–20.8	8	—
<i>elachylistus</i>	21.5–24.8	(23.4)	22	17.8–24.1	20	—
<i>exasperatus</i>	20.7–21.2	(21.0)	2	17.5–20.1	6	—
<i>fallax</i>	16.8	(16.8)	2	16.2–18.5	4	—
<i>fugax</i>	19.3–20.1	—	—	17.0–19.5	—	—
<i>fuliginosus</i>	27.8–32.5	(30.0)	12	23.6–24.3	4	—
<i>infraguttatus</i>	19.5–23.4	(21.1)	20	16.7–20.5	20	11.5
<i>jacobuspetersi</i>	22.3–29.5	(26.1)	28	19.3–25.1	23	13.0
<i>kingsburyi</i>	22.7–26.2	(24.8)	6	22.3–24.5	6	—
<i>lehmanni</i>	17.0–22.8	(20.0)	40	15.4–20.0	24	—
<i>machalilla</i>	15.0–17.6	(15.8)	28	14.4–16.0	22	—
<i>maquipucuna</i>	23.5–24.1	(23.8)	2	21.2	1	—
<i>marchesianus</i>	16.5–18.7	(17.4)	22	15.5–18.5	20	7.0
<i>marmoreoventris</i>	—	—	—	21.7	1	—
<i>mystax</i>	19.2–21.8	(20.6)	3	19.5–21.5	3	—
<i>nexipus</i>	18.8–23.0	(21.6)	5	20.0–23.9	4	11.6
<i>peculiaris</i>	29.0–29.8	(29.4)	2	26.5	1	—
<i>pulchellus</i>	19.6–24.4	(21.4)	16	17.3–21.5	44	11.4
<i>pumilus</i>	12.4–18.1	(16.6)	4	16.8	1	—
<i>sauli</i>	21.9–25.2	(24.0)	8	19.5–22.8	9	—
<i>shuar</i>	25.0–31.5	(27.4)	10	24.2–30.8	12	—
<i>talamancae</i>	23.8–24.1	(23.9)	2	20.4	—	—
<i>toachi</i>	24.6–28.2	(26.2)	3	18.1–23.1	6	9.5
<i>vertebralis</i>	17.0–20.2	(18.5)	20	14.1–17.5	21	9.4
<i>whynperi</i>	—	—	—	20.8–22.6	3	—

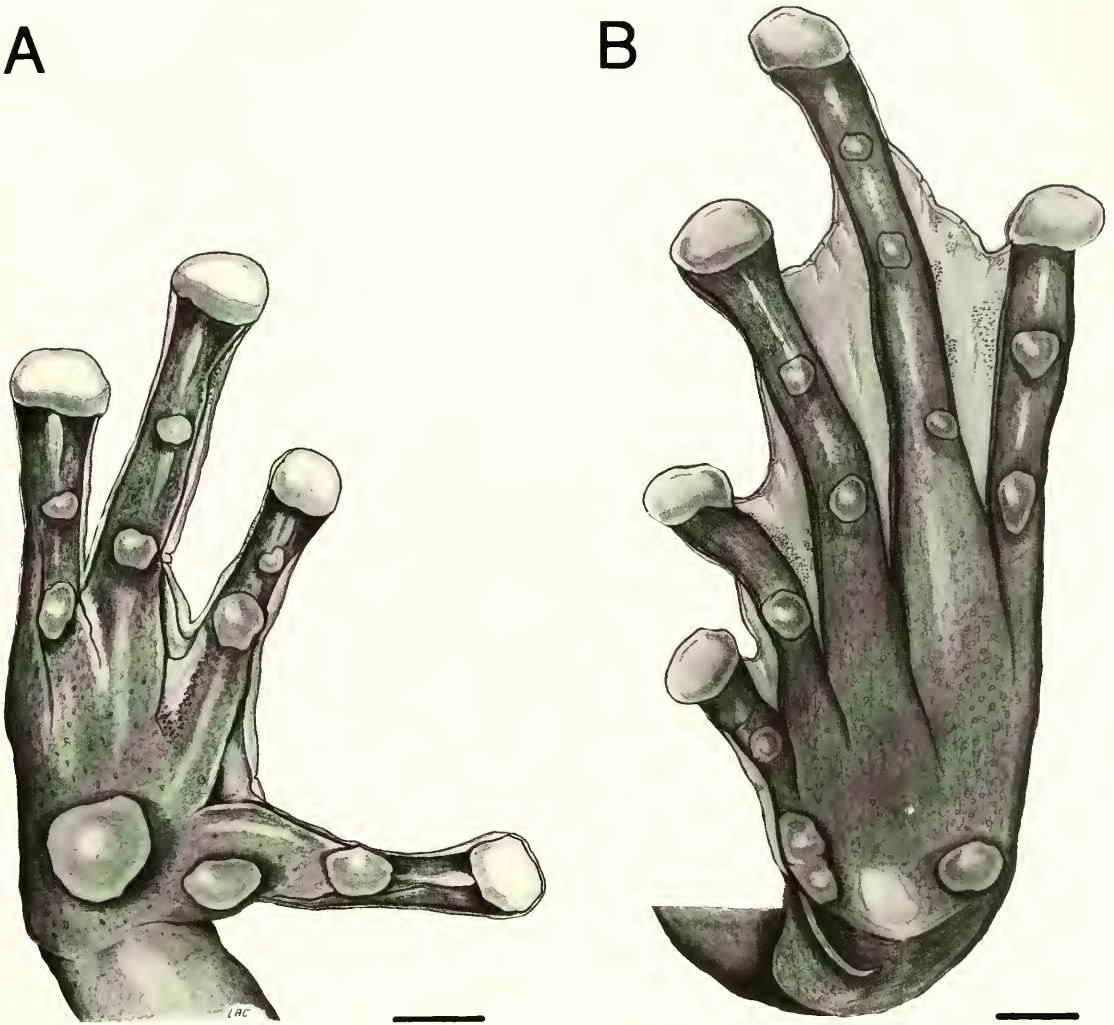


Fig. 1. *Colostethus chocoensis*. **A.** Right hand (MNHG [GO 47]). **B.** Left foot (MNHG 19107). Notice webbing between fingers on hand. Foot illustrates a webbing formula of $\text{II}-1\frac{1}{2}\text{II1}-1\frac{1}{2}\text{III1}-2\text{IV2}-1\text{V}$. Lines equal 1 mm.

ter, whereas others (e.g., *C. bocagei*, *C. chocoensis*, *C. fuliginosus*, and *C. nexipus*) have well-developed fringes on hands, but the fringes on the feet are continuous with the interdigital webbing. Most species lack fringes; in some, such as *C. awa*, *C. kingsburyi*, *C. mystax*, and *C. shuar*, fringes are poorly developed. In some cases, the intraspecific variation observed may be an artifact of preservation that tightens the skin to the digit. When it was difficult to distinguish between a real fringe and a preservation artifact, I describe the dermal modification as a "keel."

Third finger in males.—The distal segments of the third finger in males is distinctly swollen in several *Colostethus* and *Epipedobates*. Myers et al (1991) indicated that this character is expressed more strongly in some species, and that in some species at least, it is not expressed in all adult males. Of the Ecuadorian *Colostethus*, only *C. fugax* and *C. machalilla* have this character.

Tarsal folds.—There are two kinds of folds. A dermal fold may occur along the outer ventral edge of the tarsus. About half of the Ecuadorian *Colostethus* lacks this fold; however, it is well

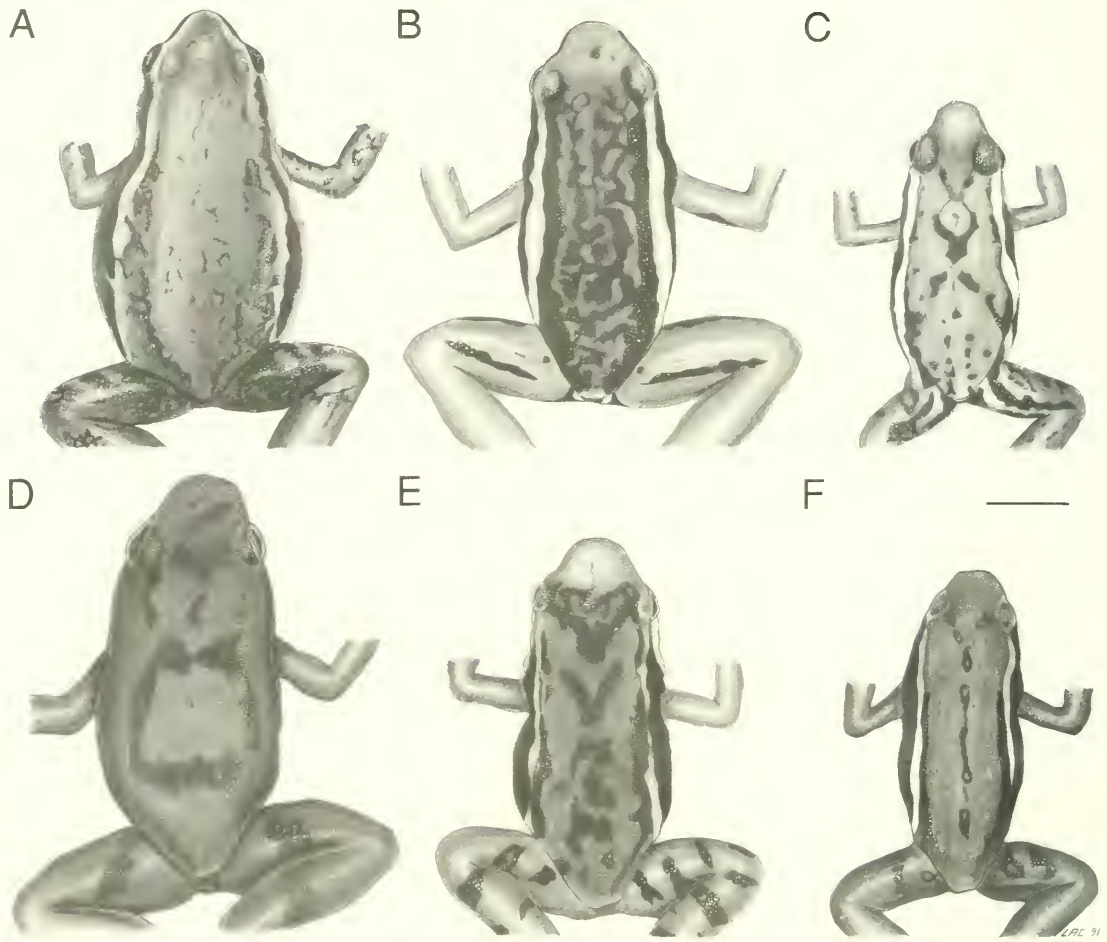


Fig. 2. Dorsal color patterns of *Colostethus*. **A.** *C. jacobuspetersi*, QCAZ 1378. **B.** *C. maquipucuna*, KU 202882. **C.** *C. machalilla*, KU 132330. **D.** *C. chocoensis*, MNHG (GO 47). **E.** *C. infraguttatus* KU 142401. **F.** *C. anthracinus*, KU 120653. Lines equal 5 mm, except in A, in which it is 2 mm.

developed in *C. bocagei*, *C. elachyhistus*, *C. fuliginosus*, *C. talamancae*, *C. sauli*, and *C. shuar*. In other species, it is weakly developed. A sigmoid or straight inner tarsal fold is present in most species; it extends from the distal half or two thirds of the tarsus to the inner metatarsal tubercle.

Webbing between fingers and toes.—Webbing is absent between the fingers in most Ecuadorian *Colostethus*; however, some species, such as *C. chocoensis* (Fig. 1) and *C. peculiaris* possess a small webbing between Fingers II and III that is continuous with a lateral fringe. The amount of webbing between the fingers in *C. chocoensis* varies. The extent of webbing between toes varies from

unwebbed to almost completely webbed. Also, intraspecific variation in foot webbing exists among populations of *C. infraguttatus* and *C. elachyhistus*, and within populations of *C. toachi*.

Dorsal color patterns.—Several *Colostethus* have a uniform brown dorsum; however, most species have dark marks or dark stripes on the dorsum (Fig. 2). Dark marks may be in an irregular or reticulate pattern as in *C. maquipucuna*, some specimens of *C. pulchellus*, and *C. jacobuspetersi*. Some populations of *C. elachyhistus* and *C. shuar* have irregularly distributed dark spots. The most common pattern is that of a transverse mark between the eyes, followed posteriorly by a “V”-shaped mark

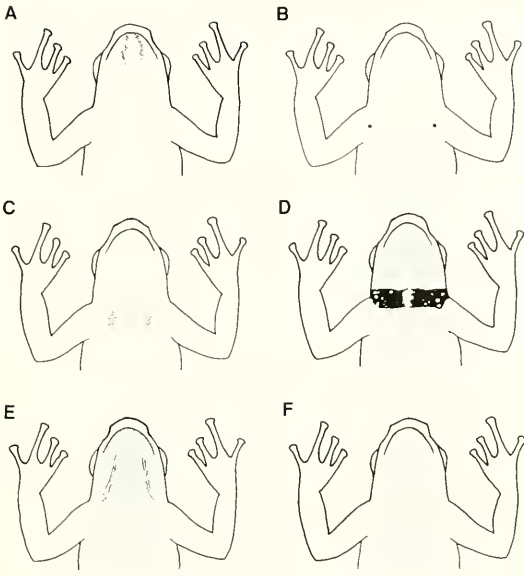


Fig. 3. Schematic representation of gular-chest markings in *Colostethus*. **A**. Marks on mental region. **B**. Small spots at base of arm. **C**. Two discrete dark marks. **D**. Band-like marks. **E**. Unspotted throat of male. **F**. Spotted throat of female.

and other scattered marks or short longitudinal stripes in the sacral region. An "X"-shaped mark in the scapular region of dorsum is characteristic of *C. machalilla*.

Usually a black dorsolateral stripe extends from scapular region to the anal region; the stripe may be interrupted or vary in intensity within populations. In some specimens of *Colostethus elachyhistus*, *C.*

pulchellus, and *C. delatorreae*, there are two short, dark paravertebral stripes in the sacral region. A cream vertebral stripe characterizes *C. vertebralis* and some specimens of *C. elachyhistus* and *C. breviquartus*.

Most species have dark transverse bars on the fore- and hind limbs. Longitudinal black stripes occur on the anterior surface of the upper arm. Longitudinal black or white stripes are present anteriorly and posteriorly on the thigh. Usually there also is a short oblique white stripe across the proximodorsal surface of the thigh. This stripe sometimes is connected to the oblique lateral stripe anteriorly and to a white longitudinal stripe on the posterior surface of the thigh.

Dorsolateral stripe.—White or cream dorsolateral stripes occur in several species. The stripes usually extend from the tip of snout or the occiput along the dorsolateral margin of the body posteriorly to the cloacal region. In *C. nexipus*, this stripe is pink and incomplete.

Oblique lateral stripe.—Many Ecuadorian *Colostethus* have a pale cream or white stripe extending along the lateral body from behind the eye to the groin. Several kinds of oblique lateral stripes can be distinguished among the species. In some species (e.g., *C. bocagei*), the stripe is washed anteriorly with darker colors so that it is barely visible. In others (e.g., *C. awa*), the stripe is constricted or interrupted in some populations and absent in others. Also, in some species (e.g., *C. kingsburyi* and *C. marchesianus*), the stripe is short and restricted to the inguinal region. Intrapopulation variation in

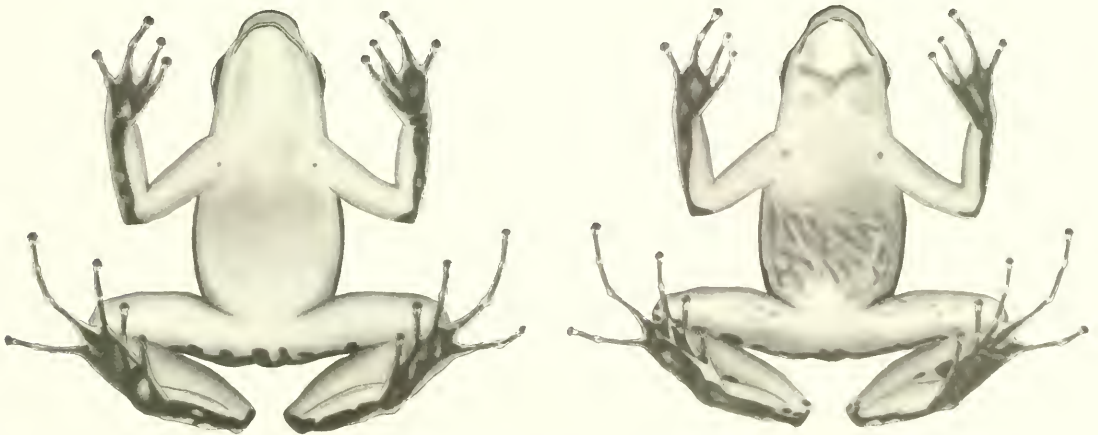


Fig. 4. Sexual dimorphic coloration on the venter of *Colostethus maquipucuna*. **A**. KU 202882, female. **B**. KU 202881, male. Line equals 5 mm.

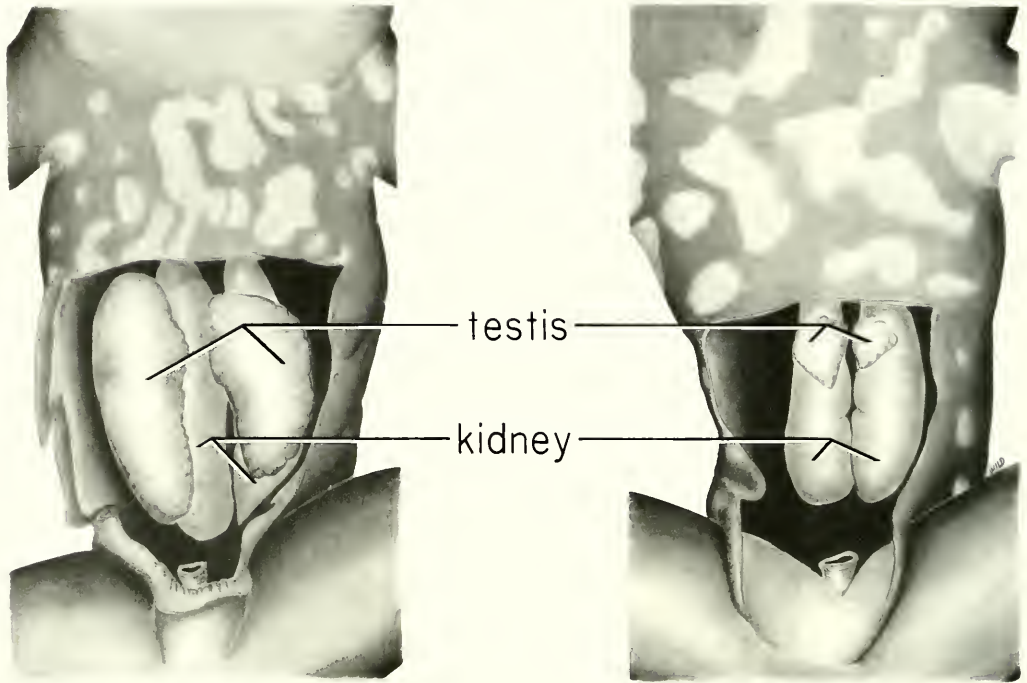


Fig. 5. Testes of (A) *Colostethus chocoensis* (MNHG 19107), and (B) *C. fuliginosus* (KU 182105), showing differences in size. Line equals 5 mm.

the oblique lateral stripe occurs in *C. nexipus*, in which the stripe may be absent, interrupted, or continuous, and connected or not with the dorsolateral stripe.

Ventrolateral stripe.—This white or cream stripe usually extends from the axilla to the groin. In some species, it is continuous with a cream labial stripe. It is complete or incomplete, with variation occurring within and among populations. This stripe is barely visible in some preserved specimens. In some species (e.g., some populations of *C. awa*), it is continuous with the lateral and/or ventral color. The ventrolateral stripe is most conspicuous in species having a dark venter; however, it also occurs in species with immaculate venters, such as *C. marchesianus* and *C. toachi*.

Markings on gular-chest region.—Dark marks in the gular-chest region characterize many Ecuadorian *Colostethus* (Fig. 3). These marks may be irregularly distributed and continuous with markings on the abdomen or throat or restricted to the gular and chest region. The dark marks may form a

diffuse band (*C. bocagei*), a white-spotted band (*C. awa*, and *C. infragutatus*), two large spots (*C. elachyhistus*), or two small spots (*C. vertebralis*, *C. pulchellus*, and *C. shuar*). Ontogenetic changes occur in this character, with some species having white-spotted bands as adults but completely dark bands as juveniles. *Colostethus delatorreae* and *C. maquipucuna* have two small black spots ventrally on the lateral part of the chest at the level of the insertion of the arm (Figs. 3B, 4).

Ventral coloration.—Ventral coloration varies inter- and intraspecifically. Interspecific variation ranges from immaculate venters, cream, yellow, orange, red, to black washes, heavy black darkening, black reticulations, or white or black spots. Ventral coloration is sexually dimorphic in most species (Fig. 4). In males of most species, throat is uniformly washed with gray; this contrasts to white, paler, or spotted patterns in the mental region, and on the chest and abdomen. This character is clearly visible in adult males (Fig. 3E). Males usually have darker venters than females; in species in which

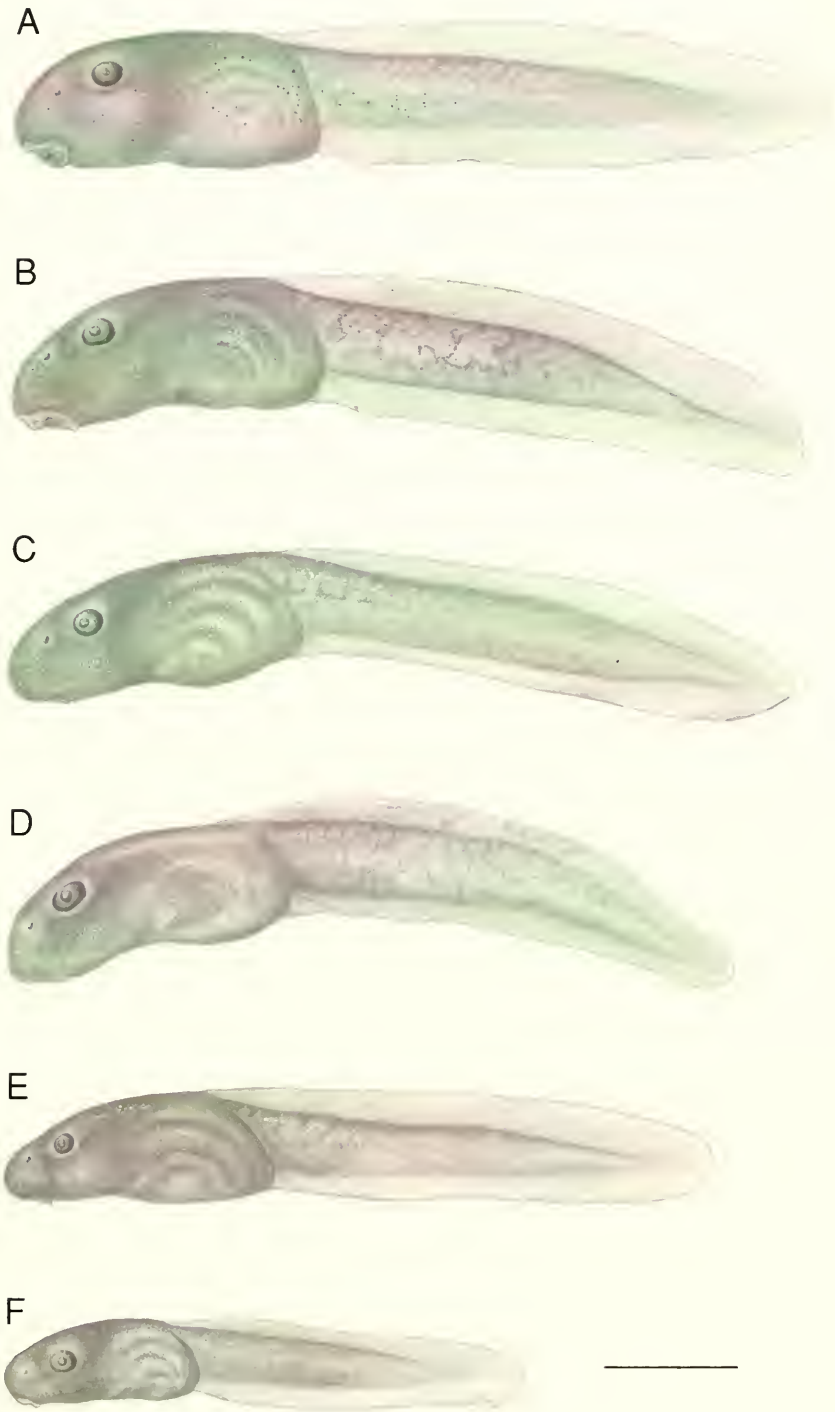


Fig. 6. Tadpoles of (A) *Colostethus infraguttatus*, QCAZ 1341; (B) *C. vertebralis*, QCAZ 1447; (C) *C. delatorrei*, KU 202977; (D) *C. toachi*, RMNH 25248; (E) *C. pulchellus*, KU 118113; and (F) *C. machalilla*, KU 142833. Line equals 2 mm.

spotted abdomen patterns occur in both sexes, the pattern in males is usually more distinct. In species having a gular-chest band, females always possess the band, whereas males lack it or possess a diffuse darkening of the region. However, in at least one population of *C. infraguttatus*, the band is clearly visible in males.

Granulation and spicules.—Most species of *Colostethus* possess granules (verrucae, warts) on the skin. Usually they are located dorsally in the sacral region. Granules are present on dorsal surfaces of hind limbs in some species (e.g., *C. toachi* and *C. infraguttatus*). Species having extensively granulated skins include some populations or specimens of *C. bocagei*, *C. elachyhistus*, *C. infraguttatus*, *C. shuar*, and *C. pulchellus*. Spicules (conical, pointed projections) occur behind the corner of the mouth in some species (e.g., *C. awa*, *C. jacobuspetersi*, and *C. sauli*), and usually are white or cream.

Male gonads.—The testes of males differ in size and coloration. *Colostethus chocoensis* has large testes that extend along the entire length of the kidneys, whereas other species examined have testes that cover about one-third the length of the kidney (Fig. 5A). Males of *C. toachi*, *C. mystax*, and *C. machalilla* have brown testes, in contrast to the white testes of other Ecuadorian species.

Tadpoles.—Because few *Colostethus* tadpoles are known, their taxonomic value is limited. Before detailed analyses of ontogenetic variation are undertaken, comparisons among tadpoles of different species at different stages may be misleading; thus, I compared only those in Stages 24–26 (Gosner, 1960); in Stages 24–25 they are back-riding tadpoles. Of the seven species for which back-riding tadpoles have been described, the largest tadpoles

are those of *C. infraguttatus* (total length 11.8 mm) and the smallest, those of *C. machalilla* (total length 7.6 mm). Most of the interspecific variation involves differences in pigmentation (Figs. 6–7). The tadpole of *C. anthracinus* has smaller eyes than other Ecuadorian *Colostethus* (Figs. 6–7) and is remarkable because after Stage 26 these larvae lose cornified beak and denticles.

The generalized *Colostethus* tadpole has an oval body that is moderately depressed and about two thirds as deep as wide. (The body and tail are arched in some specimens, possibly as a result of their position on the parent's back.) The snout is rounded in dorsal view and profile. The nostrils are located about midway between the eyes and the tip of snout. The eyes are directed dorsolaterally. The spiracle is sinistral and the vent tube is short, conical, and dextral to ventral fin. The caudal musculature is robust and gradually tapers toward the end of the tail, which is rounded. The oral disc is directed ventrally and not umbelliform. It bears two upper and three lower rows of denticles, the second upper row of which is narrowly interrupted medially; all rows are subequal in length, except the third lower row, which is shorter than others. The beaks are slender and serrate. The upper beak is broadly arched with long lateral processes, whereas the lower beak is "U"-shaped. (The beaks and dentition are relatively poorly developed in back-riding tadpoles of *C. pulchellus*.) The median part of the upper lip is bare and the posterior lip is bordered by one row of marginal papillae. The dorsum and sides of body are pigmented; the venter is pigmented or not. The caudal musculature has varying amounts of pigment; brown flecks are present or not. The fins are translucent with flecks on the dorsal fin in some species.

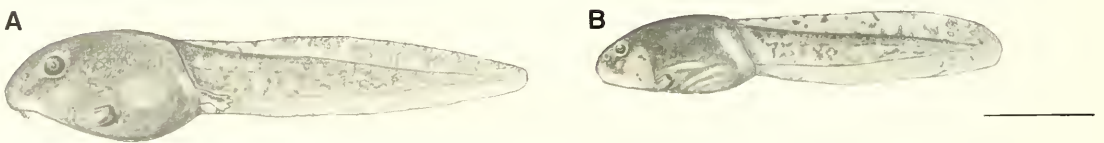


Fig. 7. Tadpoles of (A) *Colostethus awa*, QCAZ 3350; and (B) *C. anthracinus*, QCAZ 2697. Line equals 5 mm.

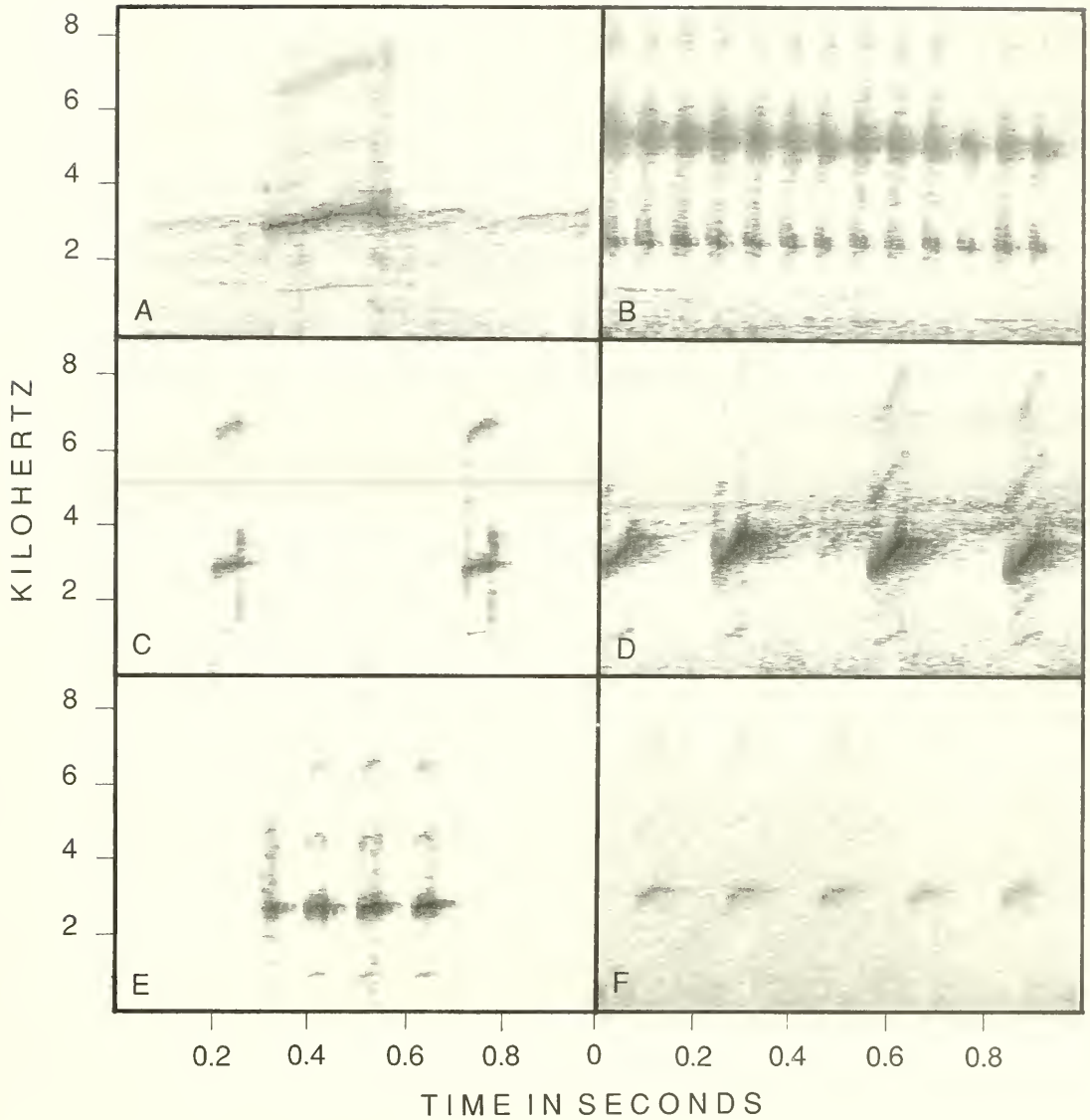


Fig. 8. Audiospectrograms of calls of (A) *Colostethus jacobuspetersi*, (B) *C. nexipus*, (C) *C. vertebralis*, (D) *C. marchesianus*, (E) *C. pulchellus*, and (F) *C. awa*. Figures B, D, and F depict only parts of the call.

Calls.—Because the calls of few *Colostethus* are known, an assessment of their phylogenetic significance is not possible. However, a wealth of potentially useful systematic characters exists in the calls, the physical parameters of which are summarized in Table 3 and displayed in Figure 8.

The call repertoire of *Colostethus* is composed of three kinds of calls—(1) peep- or trill-like calls, (2) buzz calls, and (3) single-note calls (Zimmerman,

1990; Kaiser et al., 1994). The calls of *C. jacobuspetersi* and *C. vertebralis* are composed of single notes emitted at a constant rate over a relatively long period of time. *Colostethus awa*, *C. nexipus*, and *C. marchesianus* produce trills. *Colostethus pulchellus* emits a buzz call. The behavioral significance (advertisement, courtship, or aggression) of these calls is unknown.

Table 3. Parameters of calls of six species of *Colostethus*. Values are given as means and ranges. Sample size for call length and notes per call is given as total number of calls sampled/total number of frogs sampled. Length and time in sec, frequencies in Hz.

Parameter	Species					
	<i>C. awa</i>	<i>C. jacobspetersti</i>	<i>C. marchesianus</i>	<i>C. nevipus</i>	<i>C. pulchellus</i>	<i>C. vertebralis</i>
Call length	2.8-4.8	0.23-0.31	5.3-8.1	1.4-2.4	0.4-0.6	0.07
Call rate	6	8	1	6-7	18	93
Notes per call	14-23	1	22-23	20-29	4-6	1
Note length	0.05	0.23 - 0.30	0.11	0.03-0.04	0.05	0.07
Phase	0.15-0.18	5.40-12.60	0.11-0.24	0.05-0.06	0.06-0.12	0.50-0.83
Fundamental frequency	See text	1300-1500	800-1300	See text	1000-1100	1100-1200
Dominant frequency	3000-3400	2900-3400	2600-3800	See text	2700-3000	2700-3100
Harmonics	1	2	2	1	2	2
Sample size	8/1	5/2	5/1	8/2	8/1	1/1

KEY TO SPECIES OF *COLOSTETHUS* FROM ECUADOR

1. White or pale dorsolateral stripe present 2
White or pale dorsolateral stripe absent 7
2. White ventrolateral stripe absent 3
White ventrolateral stripe present 5
3. Toes webbed *C. nexipus*
Toes unwebbed 4
4. Diffuse gray and white spots on abdomen in males *C. exasperatus*
Solid black darkening on abdomen in males *C. whymperi*
5. Fringes absent on Toe IV *C. kingsburyi*
Fringes present on Toe IV 6
6. Fringes absent on Finger II
..... *C. marchesianus*
Fringes present on Finger II
..... *C. talamancae*
7. White or pale oblique lateral stripe complete, constricted, or interrupted 8
White oblique lateral stripe absent, inconspicuous, or short 25
8. Two discrete dark marks on gular-chest region 9
No discrete dark marks on gular-chest region 14
9. Toes webbed at least basally 10
Toes unwebbed 12
10. Oblique lateral stripe constricted or interrupted *C. awa* (part)
Oblique lateral stripe complete 11
11. Webbing present between all toes
..... *C. elachyhistus*
Webbing present only between Toes II, III, and IV *C. infraguttatus*
12. Vertebral white or cream line present
..... *C. vertebralis*
Vertebral white or cream line absent 13
13. Adult SVL less than 25 mm
..... *C. pulchellus* (part)
Adult SVL more than 25 mm *C. shuar*
14. Abdomen reticulated, marbled, or spotted ...
..... 15
Abdomen white or blackish 18
15. Two small spots ventrally at base of arm ... 16
No small spots ventrally at base of arm ... 17
16. No dark marks on dorsal surfaces of thighs; oblique lateral stripe wide
..... *C. maquipucuna*
Dorsal surfaces of thigh with dark marks; oblique lateral stripe narrow
..... *C. delatorreae*
17. Discs on fingers and toes not expanded
..... *C. jacobuspetersi*
Discs on fingers and toes moderately expanded
..... *C. pulchellus* (part)
18. Toes webbed at least basally, 19
Toes unwebbed 22
19. Adult SVL less than 20 mm; Finger III swollen in males 20
Adult SVL more than 20 mm; Finger III not swollen in males 21
20. "X"-shaped mark on dorsum *C. machalilla*
Uniform brown dorsum *C. fugax*
21. Webbing between toes well developed; fringes on Finger II *C. sauli*
Webbing basal between toes; no fringe on Finger II *C. toachi*
22. Venter immaculate, white or cream 23
Venter black or suffused with black 24
23. Fringe absent on fourth toe *C. cevallosi*
Fringe present on fourth toe
..... *C. breviartus*
24. Discs on fingers not expanded
..... *C. anthracinus*

- Discs on fingers expanded *C. lehmanni*
25. Oblique lateral stripe absent 26
 Oblique lateral stripe inconspicuous or short
 30
26. Toes webbed 27
 Toes unwebbed 28
27. Venter distinctly marbled *C. peculiaris*
 Venter blackish, lightly spotted
 *C. chocoensis*
28. Venter distinctly marbled
 *C. marmoreoventris*
 Venter blackish 29
29. Finger I shorter than Finger II *C. pumilus*
 Finger I = II *C. mystax*
30. Toes unwebbed *C. fallax*
 Toes webbed 31
31. Venter with diffuse dark and/or white spots
 *C. bocagei*
 Venter distinctly marbled 32
32. Bandlike gular-chest mark present
 *C. awa* (part)
 No bandlike gular-chest mark
 *C. fuliginosus*

SPECIES ACCOUNTS

Colostethus anthracinus Edwards Plate 2E

Colostethus anthracinus Edwards, 1971:155.—
 Holotype: KU 120639 from Páramo de Raranga,
 12 km S Cutchil, Provincia Morona Santiago
 Ecuador, 3400 m.

Diagnosis.—A species characterized by (1) SVL, males 16.2–19.0, $n = 14$; females, 17.1–23.6 ($\bar{x} = 19.4$; $n = 15$); (2) disc on Finger III not expanded; (3) Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV not expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toes unwebbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) discrete marks absent on gular-chest region; (13) solid black darkening on abdomen in males, venter white in females; (14) Finger III not swollen in males; (15) testes white.

Colostethus anthracinus is compared with those species that lack toe webbing, have an oblique lateral stripe extending from the eye to the groin, and lack expanded digital tips (*C. jacobuspetersi* and *C. vertebralis*). *Colostethus anthracinus* is distinguished from both species by having a solid dark darkening on the venter of males. Females of *C. anthracinus* can be confused with females of *C. vertebralis*; however, *C. anthracinus* lacks a clear middorsal stripe and two spots on chest. *Colostethus anthracinus* is further distinguished from *C.*

jacobuspetersi by lacking a spotted or reticulated venter and by its smaller size.

Description and variation.—The original description is adequate except that Edwards' (1971) "dorsolateral stripe" is an oblique lateral stripe, and Finger I is considered to be about equal in length to second herein, whereas Edwards (1971) reported Finger I longer than Finger II. Dorsal coloration varies. In some specimens from the type locality, the dorsum is uniformly patterned in having a triangular shaped mark on the dorsum of head, followed by a black middorsal stripe. The middorsal stripe is shorter in specimens from Mazán and southeast of Gualaceo, and it is absent in some specimens from the Abra de Zamora. A black dorsolateral stripe extending from scapular region to the vent is always present; however, in two specimens from the Abra de Zamora this stripe is diffuse. The dorsum is speckled with minute, elongated pale marks that are imbedded in the black stripes and marks in some specimens. Ventral coloration varies ontogenetically; thus, larger males have blacker venters than smaller ones, and females have increased minute black stippling on the throat with age.

A recently metamorphosed juvenile (QCAZ 2697) has a SVL of 12.9 mm.

Tadpoles.—The following description is based on an individual in Stage 26 (Fig. 7B) (QCAZ 2697). Total length 20.5 mm; body moderately depressed, about two thirds as deep as wide; body uniform in

width; snout bluntly rounded in dorsal and lateral profiles; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.5 mm; spiracle sinistral, not raised; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin slightly higher than ventral fin; tail length 58% total length, tail height 18% total length, dorsal fin height 1.2 mm at midlength of tail, not extending onto body; ventral fin height 0.9 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform, but noticeably raised from the body; oral disc width 1.7 mm; tooth row formula 2/3; second upper row narrowly interrupted medially; first and second lower rows subequal in length to upper rows; third lower row interrupted, weakly developed, shorter than other rows; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by two rows of marginal papillae.

Dorsum and sides of body dark brown; abdomen transparent; caudal musculature cream with dark brown flecks along entire length; dorsal fin translucent with dark brown flecks, ventral fin translucent with scattered brown flecks distally.

Other tadpoles in stages after Stage 26, show variation in their lack of a cornified beak and denticles. Also, a lateral line system is clearly visible; it extends around the eyes, along the body and the length of the tail musculature.

Calls.—Unknown.

Distribution and ecology.—*Colostethus anthracinus* occurs in a narrow altitudinal zone (2710–3500 m) on the Cordillera Oriental (Cordillera Real or Central), and the Mazán River in southern Ecuador (Fig. 9). The distribution lies mainly within the Very Humid Montane Forest and Lower Humid Montane Forest; the former has annual mean temperatures of 7–12°C and the second 12–18°C; annual mean precipitation is 1000–2000 mm in both zones.

Colostethus anthracinus occurs sympatrically with *C. vertebralis* at the Mazán River, and at higher elevations of the Cordillera de Boliche and Cordoncillo in the northern part of the range of *C. anthracinus*. The distribution of *C. anthracinus* is parapatric at the northern extreme of the range of *C.*

elachyhistus in Cordillera Cordoncillo.

Comments.—As suggested by Rivero (1989), the ventral coloration illustrated by Edwards (1971:157, Fig. b) is not accurate, because it shows two gular-chest marks. Confusion may have arisen because either the specimen is a misidentified *C. vertebralis* or the drawing overemphasizes a more diffuse stippling of the area in juveniles of *C. anthracinus*.

Colostethus awa new species

Plate 2C

Holotype.—QCAZ 1327 from 15 km NW Alluriquín (5 km NW La Florida), Finca Gloria, 0°15' S, 79°01' W, 950 m, Provincia Pichincha, Ecuador, collected on 3 July 1989 by Luis E. López and Luis A. Coloma.

Paratypes.—QCAZ 1326, 1328, KU 220602–03, 220605–06 with the same data as the holotype; KU 220607, QCAZ 1329 topotypes collected on 30 December 1989 by D. Kizirian, F. Campos, J. Wiens, and L. Coloma; QCAZ 3251–54 topotypes collected 12 October 1991 by L. Coloma; RMNH 25224–32, topotypes collected on 9 April 1983 by M. S. Hoogmoed and L. Coloma.

Diagnosis.—A species characterized by (1) SVL, males 16.1–22.4, $n = 26$; females, 19.1–25.9 ($\bar{x} = 22.5$; $n = 38$); (2) disc on Finger III expanded; (3) Finger I shorter or about equal to length of Finger II; (4) fringe present or absent on Finger II; (5) disc on Toe IV expanded; (6) fringe present or absent on Toe IV; (7) outer tarsal fold present or absent; (8) toe webbing formula $I2-2(2\frac{1}{2})II1\frac{1}{2}(2)-3III2\frac{1}{2}(3)-4IV4-3V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe usually absent; when present, extending to eye, sometimes short, constricted or broken at scapular level; (11) ventrolateral stripe generally present; (12) white spotted band on gular-chest region; (13) white spots on abdomen in both sexes, throat white spotted in females, uniform gray in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus awa is compared with those species that have basal webbing, an oblique lateral stripe extending from the eye to the groin, and discrete dark marks on gular-chest region (*C. infraguttatus* and *C. elachyhistus*). *Colostethus awa* is distinguished from both by having an interrupted, oblique

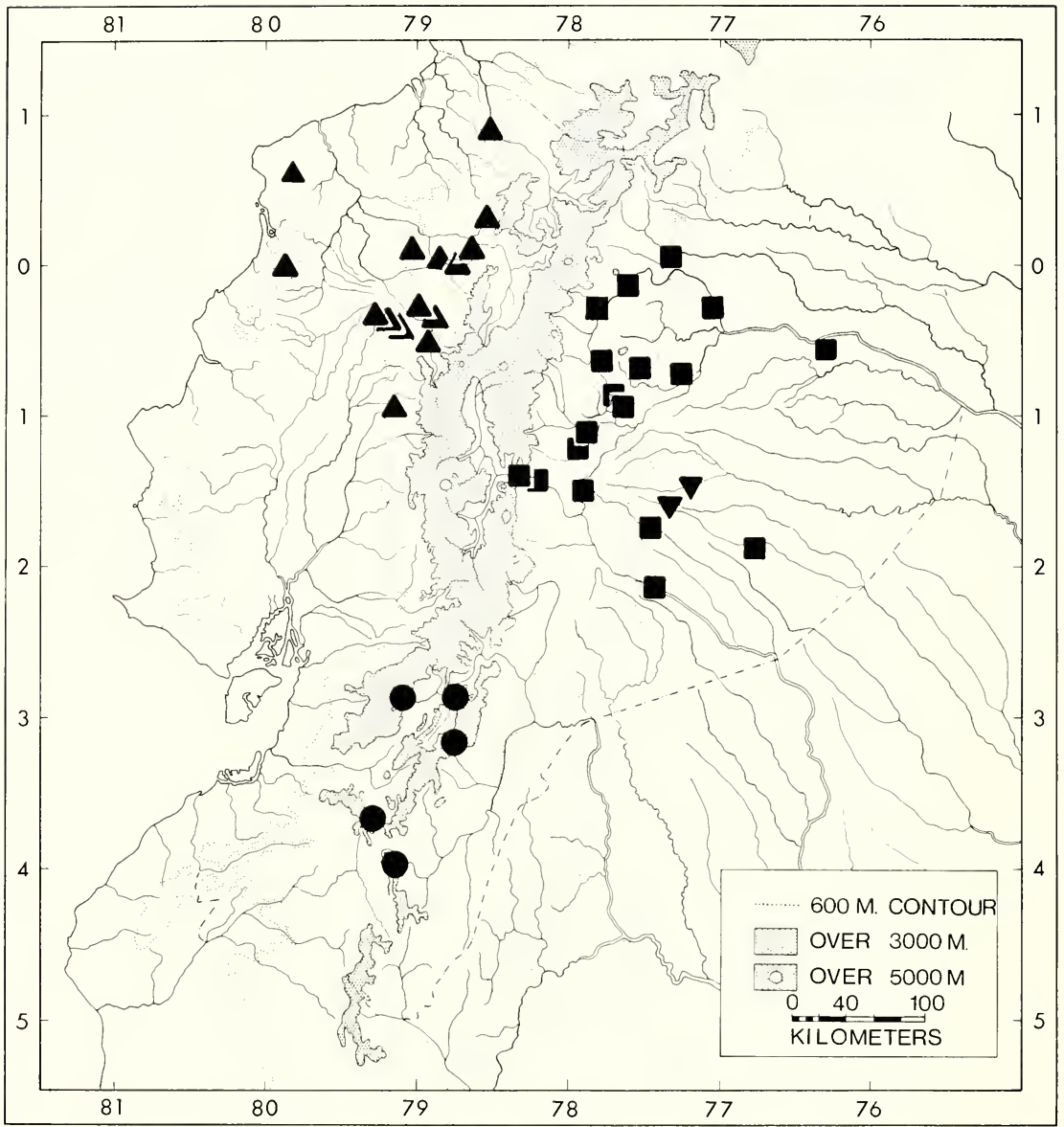


Fig. 9 Distributions of *Colostethus anthracinus* (●), *C. awa* (▲), *C. bocagei* (■), and *C. fugax* (▼).

lateral stripe at the scapular level or by lacking the stripe.

Colostethus awa also is compared with those species having a short oblique lateral stripe and webbing between the toes (*C. bocagei* and *C. fuliginosus*). It is distinguished from *C. fuliginosus* in profile; loreal region concave; nostrils slightly protuberant laterally; eye-nostril distance half length of eye; supratympanic fold inconspicuous, obscuring posterodorsal part of tympanum; tympanum

Description of holotype.—Female, 22.0mm in SVL; body moderately robust; head longer than wide; head length 38.6% SVL; head width 35.9% SVL; snout bluntly rounded in dorsal view, truncate in profile; loreal region concave; nostrils slightly protuberant laterally; eye-nostril distance half length of eye; supratympanic fold inconspicuous, obscuring posterodorsal part of tympanum; tympanum

diameter 45.6% length of eye. Forelimbs moderately long; Finger I slightly shorter than Finger II; fingers unwebbed with lateral fringes poorly developed; terminal discs expanded; subarticular tubercles large, round; palmar tubercle large, round, elevated; thenar tubercle moderately rounded; hind limbs moderately robust; tibia length 50.9% SVL; foot length 49.1% SVL; outer tarsal fold absent; inner tarsal fold sigmoid on distal half of tarsus; outer metatarsal tubercle round, half size of elliptical inner metatarsal tubercle; toes webbed with narrow lateral fringes; terminal discs expanded, about twice width of digits; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum, flanks, and venter smooth; anal opening directed posteroventrally at midlevel of thighs; anal flap moderately long; tongue narrowly triangular, shallow distally, free posteriorly for approximately half of its length.

Color in preservative: Dorsum with black blotches visible on dark brown ground color; dorsum of snout dark brown, "V"-shaped mark on the occipital region followed posteriorly by a "V"-shaped mark and four rounded blotches, flanks dark brown with white spots; short white stripe on groin; tympanic region dark brown above and white with brown stippling below; short white stripe behind tympanum extending to level of insertion of arm; upper lip brown mottled with pale cream marks; dorsal surfaces of forearms cream with brown cross marks; anterior surfaces of upper arms with white spots on brown; dorsal surfaces of hind limbs with six brown bars (through the heel); digital scutes gray and white; throat and chest cream marbled with gray; a black with white spots bandlike mark on gular-chest region; abdomen black with white spots; ventral surfaces of hind limbs white; palmar and plantar surfaces gray.

Measurements of holotype (mm): SVL 22.0; tibia length 11.2; foot length 10.8; head length 8.4; head width 7.9; eye diameter 3.5; eye-nostril distance 2.2; tympanum diameter 1.6.

Variation.—The ventral coloration is sexually dimorphic. Females have marbled venters and throats, with a spotted bandlike mark on the throat; males lack this mark, and have a uniform black throat. Specimens from Lita at the northernmost part of the range are similar to topotypes except for the following features: (1) Finger I is slightly shorter

than Finger II; (2) Finger II lacks a fringe; (3) an outer tarsal fold is present; (4) a ventrolateral stripe is present; (5) a cream oblique lateral stripe, which may be constricted or interrupted occurs at the scapular level; (6) the top of the head bears a triangular mark that lies anterior to a "V"-shaped mark, and an irregular pattern of extensive mottling; (7) a black dorsal stripe borders a narrow, oblique lateral stripe, which is widest anteriorly and generally interrupted or constricted along the body; and (8) in some specimens the upper lip is white with few or no obscure dark marks. One specimen has black blotches on the ventral surfaces of legs. Specimens from Cordillera de la Costa resemble topotypic material and specimens from vicinities of Santo Domingo de los Colorados, but differ in having a weakly defined oblique lateral stripe, slightly less webbing among toes, and the muscles of ventral surfaces of thighs are pale yellowish; specimens from West of Pilaló also have a weakly defined oblique lateral stripe.

Recently metamorphosed juveniles have a dark bandlike mark on throat. A recently metamorphosed juvenile (KU 133291) has a SVL of 12.1 mm.

Color in life: Male (QCAZ 1325): dorsum reddish brown with diffuse dark marks; flanks dark gray; white spicules in post-tympanic region; dorsum of legs dark brown; brown stripe on anterior surface of upper arm; throat black; abdomen with white spots, black anteriorly and orange posteriorly; ventral surfaces of thighs orange; palmar and plantar surfaces gray with orange tubercles; iris golden (L. A. Coloma, field notes, 23 June 1989), KU 133285–305 from Lita, Provincia Imbabura; dorsum bronze with irregular black spots; flanks black; discontinuous dorsolateral stripe pale yellow; upper lip pale yellow with black flecks; legs brown with black bars; venter pale blue-green in females, marbled blue-green and black, with solid black throat in males; ventral surfaces of legs rose or pale red (S. R. Edwards, field notes, 13 August 1970).

Tadpoles.—The following description is based on an individual in Stage 35 (Fig. 7A) (QCAZ 3350) which was hatched and reared in captivity.

Total length 26.1 mm; body moderately depressed, about two thirds as high as wide; body approximately uniform in width; snout bluntly rounded in dorsal and lateral profiles; nostrils about midway between eyes and tip of snout; eyes directed

dorsolaterally, diameter 1.0 mm; spiracle sinistral; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; fins subequal in height at midlength of tail, dorsal fin narrow proximally, increasing in height at about one third of tail length; tail length 60.5% total length, tail height 15.3% total length, dorsal and ventral fin height 1.2 mm at midlength of tail, dorsal fin not extending onto body; distal end of tail acuminate, tip of fin rounded. Oral disc directed ventrally, not umbelliform; oral disc width 3.0 mm; tooth row formula 2/3; second upper row narrowly interrupted medially; lower rows subequal in length to upper rows; third lower row not interrupted; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by one row of marginal papillae.

Dorsum and sides of body dark brown; abdomen transparent with scattered dark brown pigment; caudal musculature cream with dark brown flecks; fins translucent with scattered dark brown flecks on dorsal fin.

Calls.—A male (QCAZ 1325, SVL 22.1 mm) was recorded at Río Intag, 1200 m, Provincia Imbabura, on 23 June 1989 at 16:20 h (Fig. 8F). Air temperature was 24°C and the microphone was located approximately 3 m from the frog. The call is a trill with a 2.8–4.8 sec duration, emitted at a rate of six calls per minute. Each call consists of 14–23 notes. Note length is 0.05 sec and time between notes 0.15–0.18 sec. It is not clear if the fundamental frequency is the same as dominant frequency because background noise obscures the analysis. The dominant frequency is about 3000–3400 Hz and there is one harmonic above the dominant frequency.

Distribution and ecology.—*Colostethus awa* is known from elevations of 265–1220 m on the western Andean slopes and in the western Pacific lowlands (Fig. 9). The distribution lies within Humid Tropical Forest, Very Humid Premontane Forest and Humid Premontane Forest. Annual mean precipitation is 2000–4000 mm in the two former life zones, and 1000–2000 mm in Premontane Humid Forest. Annual mean temperature is 24–25°C in Humid Tropical Forest and 18–24°C in Very Humid Premontane Forest and Humid Premontane Forest.

At Lita, the annual mean temperature is 22°C and annual mean precipitation is 3100 mm (IGM, no date); precipitation is evenly distributed throughout the year (Cañadas-Cruz, 1983).

Eleutherodactylus crenunguis was found during the day feeding on juveniles of *Colostethus awa*.

A male *Colostethus awa* (QCAZ 1325) showed aggressive behavior when exposed to a playback recording of his call. He was calling from inside a crevice between rocks on the bank of the Río Intag. His call was recorded and played; he came out of the crevice and jumped over the recorder.

Specimens were collected by day from a drainage ditch and from leaf litter adjacent to railroad tracks just outside, and near the entrance to, a tunnel at the type locality (S. R. Edwards, field notes, 13 August 1970). Other specimens were collected in creeks close to a water tank and to a small waterfall.

A clutch with 21 eggs was laid by a captive female. A captive male from the type locality was observed transporting 11 tadpoles on its back.

Colostethus awa has been found sympatrically with *Epipedobates boulengeri* at the lowlands and with *C. lehmanni*, *C. toachi*, *C. chochoensis*, and *C. whymperei*, on the slopes of the Andes in Provincia Pichincha, and with *C. machalilla* at the northern part of the Cordillera de la Costa.

Etymology.—The specific name refers to the Awá territory in the vicinity of Lita in northern Ecuador. This protected natural area is the home of the last remaining members of the Awá tribe. Translated literally, the word "Awá" means "people."

Comments.—*Colostethus awa* closely resembles members of the *C. trinitatis* and the *C. vertebralis* groups of Rivero ("1988") and *Mannophryne* (La Marca, 1992); *C. awa* shares with them the presence of bandlike marks on the gular-chest region.

The polymorphism evident in most of the characters (see diagnosis) reflects interpopulational variation. However, there are some samples from Cordillera de La Costa and from the vicinity of Pilaló which exhibit intrapopulational polymorphisms; thus, it is difficult to interpret the taxonomic status of these parapatrically distributed populations. I suspect that several species may be involved, particularly, the Lita population may not be conspecific, but further analyses are required.

Colostethus bocagei (Jiménez de la Espada)
Plate 1G

Hyaloxalus bocagei Jiménez de la Espada, 1871:59.—

Syntypes: MNCN 1583–84 from San José de Moti [Cantón de Quijos], Provincia Napo, Ecuador [collected in June 1865]; MNCN 1583 herein designated as lectotype.

Hylivalus bocagei—Boulenger, 1882:138.

Colostethus bocagei—Edwards, 1971:148.

Colostethus maculosus—Rivero, 1991a:17–20.—

Holotype: MCZ-A 99558 from Puyo, between Turingia and Theatre, 950 m, Provincia Pastaza, Ecuador. New synonymy.

Diagnosis.—(1) SVL, males 17.0–24.7, $n=20$; females, 23.9–28.2 ($\bar{x} = 26.1$; $n = 20$); (2) disc of Finger III expanded; (3) length of Finger I = II; (4) fringe present on Finger II; (5) disc of Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present; (8) toe webbing formula $I1-1\frac{1}{2}II1-2\frac{1}{2}III1\frac{1}{2}-2\frac{1}{2}IV2\frac{1}{2}-IV$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, sometimes diffuse, or absent; (11) ventrolateral stripe absent; (12) discrete marks present on gular-chest region, but sometimes diffuse; (13) diffuse white or dark spots on abdomen; (14) Finger III not swollen in males; (15) testes white.

Colostethus bocagei is compared with those species that lack a dorsolateral stripe and have an oblique lateral stripe that is diffuse anteriorly or absent (*C. awa*, *C. fuliginosus*). *Colostethus bocagei* is distinguished from *C. awa* by its more extensive webbing on the toes, and from *Colostethus fuliginosus* by having less toe webbing, less defined ventral color patterns, and a smaller size.

Description.—The lectotype (MNCN 1583) and paralectotype (MNCN 1584) are in poor condition. A redescription of these specimens is not useful because few external diagnostic characters can be described precisely. MNCN 1583 and 1584 of undetermined sex are approximately 26.5 and 22.5 mm in SVL, respectively. A combination of SVL and characters of the original description allows the association of this species with material collected in this century near the type locality in eastern Ecuador. Herein, I describe a specimen (KU 166106) from a series collected 2 km SSW of the Río Reventador, 1490 m, Provincia de Napo, on 20 March 1975 by J. E. Simmons.

Female, 27.3 mm SVL; body moderately robust; head slightly longer than wide; head length 38.1% SVL; head width 34.8% SVL; snout bluntly rounded in dorsal view and profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance about half diameter of eye; supratympanic fold weak, diffuse, obscuring posterodorsal part of tympanum; diameter of tympanum 42.8% diameter of eye. Forelimbs moderately long; first finger shorter than second; fingers unwebbed, having narrow keel-like lateral fringe; terminal discs expanded; disc on Finger III twice width of distal end of adjacent phalange; subarticular tubercles large, oval; metacarpal median tubercle large, rounded, barely elevated; inner metacarpal tubercle on base of Finger I elliptical. Hind limbs moderately robust; tibia length 46.9% SVL; foot length 41.4% SVL; outer tarsal fold present; inner tarsal keel sigmoid on distal two thirds of tarsus, continuous with fringe on free edge of first toe; outer metatarsal tubercle round, more than half size of elliptical inner metatarsal tubercle; toes webbed with lateral fringes; terminal discs expanded, about twice width of digits; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum, flanks, and venter smooth; tubercle elevated slightly behind the corner of the mouth; anal opening directed posteroventrally at midlevel of thighs, anal sheath moderately long; tongue elongately elliptical, slightly indented posteriorly, free posteriorly for about two thirds of its length.

Color in preservative: Dorsum dark brown with many darker blotches; dorsum of snout dark brown; flank brown with oblique lateral stripe from groin to posterior corner of eye, constricted in some regions and interrupted in others, obscured distally; tympanic region whitish; upper lip white with gray stippling; dorsal surfaces of forearms with three transverse bars; anterior surfaces of upper arm with dark mark spotted with white; dorsal surfaces of hind limbs distinctly barred with at least nine transverse bars on thigh, shank, and tarsus. Inner two fingers and inner three toes whitish gray; other toes and fringes with brown marks; gray scutes on tips of fingers and toes, except white on inner two fingers and inner three toes; ventral surfaces of hind limbs gray and palmar surfaces gray; plantar surface dark gray; throat and chest white with minute gray stip-

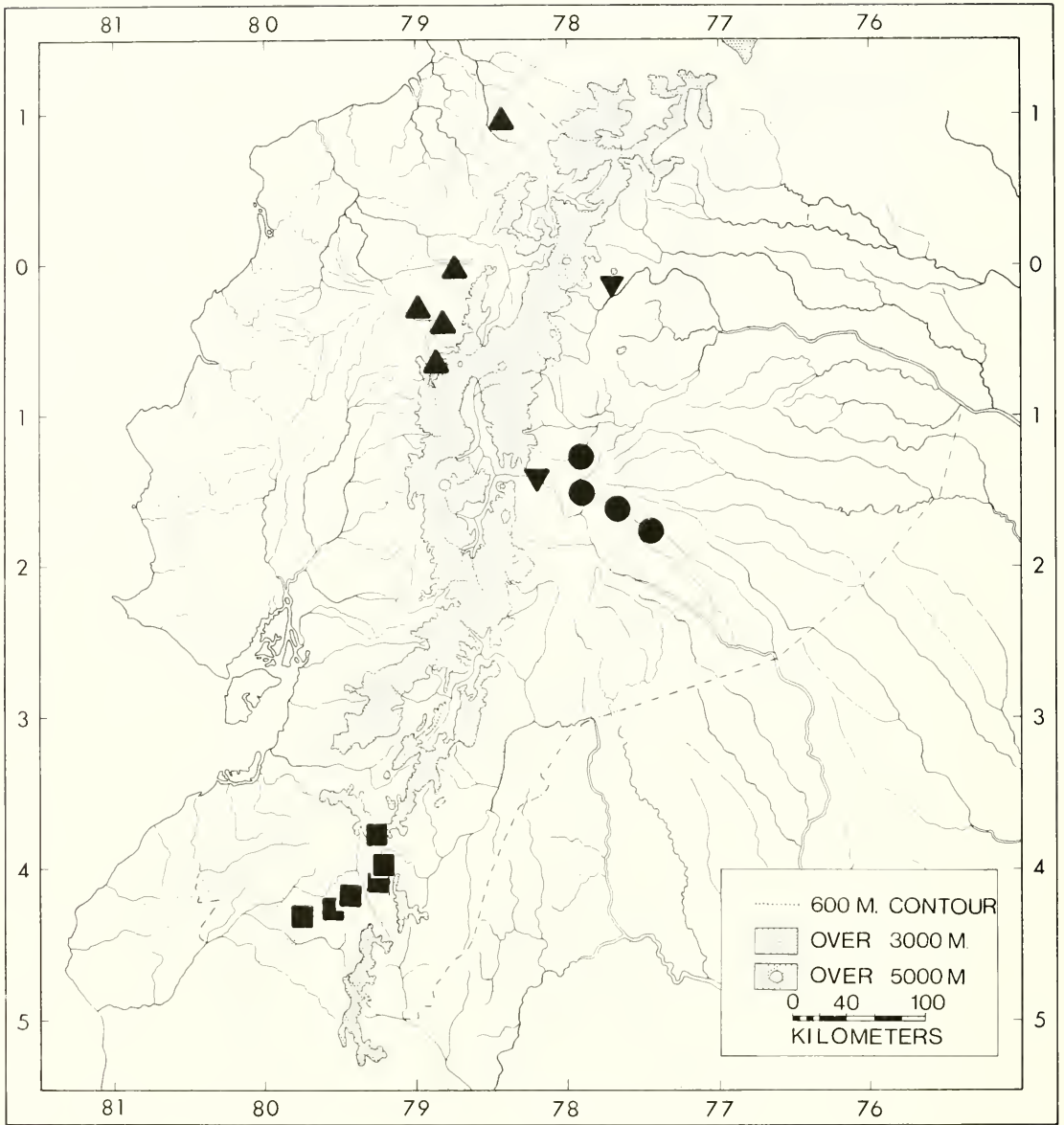


Fig. 10. Distributions of *Colostethus cevallosi* (●), *C. chocoensis* (▲), *C. elachylistus* (■), and *C. kingsburyi* (▼).

pling; abdomen white; white mark in axilla.

Variation.—Specimens from 2 km SSW of Río Reventador differ only in that smaller individuals have smaller discs on the first toe. A female (KU 166109) has white marks on a gray throat. Among a series from Azuela (near the former locality), one female has white marbling on the venter and throat, and one male has dark gray on the venter with diffuse small white spots except on the gular-chest

region, which is gray without spotting. Males vary ontogenetically in ventral coloration; the venter is white with fine gray stippling in small individuals and darker in the larger males.

A series from Lumbaqui (Provincia Napo) differs in coloration, as follows. The dorsum lacks numerous black blotches, but has a "V"-mark in the scapular region. The oblique lateral stripe is indistinct, but white spots are present in the groin; fe-

males have white venters and gray throats, and a male has a darker gray throat than do females and a slight concentration of dark pigment in the gular-chest region.

Five other series from 20.8 km S of Cosanga, 37.4 km E of Baños, Río Negro, Mera, and Sarayacu show the following intraspecific variation in color patterns. The oblique lateral stripe is complete in some specimens but is represented by spots in others. In some specimens, dorsal blotches are present, whereas in others discrete "V"-shaped marks occur between the eyes and the occiput. The tympanum is brown or white. The vocal sac is uniform gray. In males, the gray venter may be uniform or have white spots. Females have whitish venters contrasting with a gray throat with white spots. In specimens from north of Montalvo, the dorsal skin of the body is tubercular; discrete bandlike marks on throat are present and an oblique lateral stripe is absent.

Juveniles have small white spots dorsally. A recently metamorphosed juvenile (KU 189935) has a SVL of 13.4 mm.

Color in life: KU 166100–01: dorsum olive-tan with dark brown marks; venter gray; iris grayish brown (W. E. Duellman, field notes, 6 October 1974). KU 166106–07: dorsum olive-tan with brown spots; venter bluish gray; iris dull bronze (W. E. Duellman, field notes, 20 March 1975). KU 122222–24: brown dorsally with black marks; anterior and posterior surfaces of thighs and flanks mottled gray and brown; ventral surfaces of limbs gray; abdomen and throat white; iris coppery red with dark brown reticulations (W. E. Duellman, field notes, 28 June 1968).

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus bocagei* occurs at elevations between 300 and 1740 m on the eastern side of the Andes in the provincias Sucumbíos, Napo, Tungurahua, and Pastaza (Fig. 9). The distribution lies within the Tropical Humid Forest, and Very Humid Premontane Forest. Both zones have an annual mean precipitation between 2000–4000 mm; annual mean temperature is 24–25°C in Tropical Humid Forest, and 18–24°C in Very Humid Premontane Forest.

Three specimens were found at night sleeping at the end of a mossy log and on rocks in a river. Others were found during the day under and among rocks

near rocky streams; some of them among rocks under a short waterfall (W. E. Duellman, field notes, 28 June 1968, 6 October 1974, and 20 March 1975; J. D. Lynch, field notes, 26 July 1968).

At the Río Azuela *Colostethus bocagei* has been collected with four other species of *Colostethus*—*C. fuliginosus*, *C. kingsburyi*, *C. pulchellus*, and *C. shuar*. Also *C. bocagei* occurs sympatrically with *C. sauli* and *C. marchesianus* in the lowlands of eastern Ecuador.

Comments.—Andersson (1945) suggested that *Colostethus bocagei* was the same as *C. fuliginosus*. Both were described in the same paper and from the same locality by Jiménez de la Espada (1871); however, the sympatric occurrence near the type locality of two species, and the fact that these two species differ in the extent of the webbing on the toes and body size, almost certainly allows the recognition of both taxa. The type material of both nominal taxa is poorly preserved; however, they can be distinguished by differences in size—*C. fuliginosus* is larger (MNCN 1585 with a SVL of 32.2 mm; MNCN 1586, 32.5 SVL) than *C. bocagei* (MNCN 1583 with a SVL of 26.5 mm; MNCN 1584, 22.5 mm), and the latter species has less webbing on the toes (Jiménez de la Espada, 1871).

The gular-chest marks of specimens from lowland populations of *C. bocagei* are not as well defined as in members of *Mannophryne*, and the *C. vertebralis* group of Rivero ("1988").

Rivero (1991a) described *C. maculosus* based on two specimens. The type specimen (MCZ-A91558), a male from Puyo, corresponds well with the series from Mera and adjacent localities; and the paratype (MCZ-A 104946), from El Reventador, corresponds well with the specimens from Reventador and surrounding localities herein described. Rivero (1991a) also discussed differences between the type and paratype of *C. maculosus*. He stated his opinion that "they belong to the same species although they may eventually be found to be subspecies of each other." The variation exhibited by the type material of *C. maculosus* falls well within the range of variation of *Colostethus bocagei* populations described herein; therefore, I consider *C. maculosus* (Rivero, 1991a) to be a junior synonym of *C. bocagei* (Jiménez de la Espada, 1871).

Colostethus breviquartus Rivero and Serna
Plate 3B

Colostethus breviquartus Rivero and Serna, 1986:529.—Holotype: CSJ 0298, from Urrao (Parque de las Orquídeas), 1700–1800 m, Departamento Antioquia, Colombia.

Diagnosis.—(1) SVL, males unknown in the Ecuadorian sample; females, 15.4–16.8 (\bar{x} = 16.3; n = 3); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) discrete marks absent on gular-chest region; (13) abdomen white; (15) third finger not swollen in males (reported for a Colombian population by Rivero and Serna, 1988:147); (16) testes color unknown.

Colostethus breviquartus is compared with those species that have a complete oblique lateral stripe, have rudimentary or no webbing on the toes, and have an immaculate white venter (*C. cevallosi*, *C. fugax*, and *C. machalilla*). It is distinguished from *C. fugax* and *C. machalilla* by males lacking a Finger III swollen. Furthermore, *C. breviquartus* differs from *C. machalilla* by a different dorsal color pattern (an “X”-shaped mark in *C. machalilla* and a uniform dorsum in *C. breviquartus*) and from *C. cevallosi* by having fringed toes.

Description and variation.—The original description (Rivero and Serna, 1986) is appropriate and corresponds to Ecuadorian specimens examined, except that the first and second fingers are equal in length (Finger I slightly longer than Finger II in holotype), and the largest Ecuadorian specimen is an adult female having a SVL of 16.8 mm, in contrast to the holotype that has a SVL of 21.2 mm.

There is variation in dorsal coloration in Ecuadorian specimens. One specimen has small dark flecks on the dorsum, but the others lack flecks. One has a well-defined black band bordering the oblique lateral stripe in contrast to diffuse bands in the others. Also, one has a well-defined transverse band on the dorsal surface of the shank.

Color in life: MECN 735: dorsum pale brown to olive and dark brown; brown to black dorsolateral

band; white oblique lateral stripe, cream-colored behind the eye; flanks brown or black with small white spots; upper lip cream yellow; dorsal surfaces of forelimbs pale yellow with black marks at the insertion of the forelimb; dorsal surfaces of hind limbs varying from pale yellow to brown (QCAZ, Color Transparencies 531–32).

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus breviquartus* is known from elevations of 600–900 m from two localities in Provincia Carchi in north-western Ecuador (Fig. 11); about 600 km (airline) from the type locality on the western slopes of the Cordillera Occidental in Departamento de Antioquia in northern Colombia. The distribution in Ecuador lies within the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm, and annual mean temperature is 18–24°C.

MECN 734 and 736 were collected in the leaf litter in undisturbed forest at 15:00 h. MECN 735 was collected near a stream.

Colostethus breviquartus was collected with a juvenile assigned to *C. chocoensis*. It also occurs in the same general area with *C. awa* and *Epipedobates boulengeri*.

Comments.—The characters of the type material of *Colostethus breviquartus* correspond closely with those of Ecuadorian specimens, except for size. There are not intermediate records of the species in an area of about 670 km airline. The Ecuadorian population may not be conspecific with *C. breviquartus*; however, the few available specimens from the type locality and Ecuador preclude extensive comparisons.

Colostethus cevallosi Rivero

Colostethus cevallosi Rivero, 1991b:7–8.—Holotype: USNM 282648, from Palanda, E of Sarayacu, Río Bobonaza, around 700 m, Provincia Pastaza, Ecuador.

Diagnosis.—(1) SVL, male 18.2 mm, females, 20.6–21.0 mm (\bar{x} = 20.8; n = 2); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe ab-

sent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe present; (12) two discrete marks absent on gular-chest region; (13) abdomen white in females, gray in males; (14) Finger III not swollen in males (15) testes white.

Colostethus cevallosi is compared with those species that have a complete oblique lateral stripe, white venter (in females), and rudimentary or no webbing on the toes (*C. fugax*, *C. machalilla*, *C. toachi*, and *C. breviquartus*). It is distinguished from *C. fugax*, and *C. machalilla* by males lacking a swollen Finger III and from *C. breviquartus* by lacking a fringe on Toe IV. *Colostethus cevallosi* closely resembles *C. toachi*, but differs by the males having white testes and gray venter.

Description and variation.—Rivero's description (1991b) is adequate.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus cevallosi* occurs between 480 and 970 m in Provincia Pastaza on the eastern side of the Andes (Fig. 10). The distribution lies mainly within the Very Humid Premontane Forest and Pluvial Premontane Forest. Annual mean temperature is 18–24°C in both zones; annual mean precipitation is 2000–4000 mm in Very Humid Premontane Forest and 4000–8000 mm in Pluvial Premontane Forest.

Colostethus cevallosi has been collected in sympatry with *C. bocagei*, and *C. fugax*; its range overlaps the distribution of *C. marchesianus*.

Colostethus chocoensis (Boulenger)

Hylaxalus chocoensis Boulenger, 1912:190.—Holotype: BM 1947.2.14.27, from Noanama, Río San Juan, about 30 m, Departamento Chocó, Colombia.

Hylaxalus chocoensis—Hellmich, 1940:27.

Prostherapis chocoensis—Gorham, 1963:25.

Phyllobates chocoensis—Cochran and Goin, 1970:46.

Colostethus chocoensis—Edwards, 1971:148.

Diagnosis.—(1) SVL, males 21.5–22.1, $n = 3$; females, 22.9–27.0 ($\bar{x} = 25.3$; $n = 6$); (2) disc on Finger III expanded; (3) Finger I shorter than Finger II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer

metatarsal fold present; (8) toe webbing formula II—1½III—1½(2)III(1½)I—2IV2½—1V; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) discrete marks absent on chest; (13) light spots on abdomen, unspotted gular-chest region in males; (14) Finger III not swollen in males; (15) testes white, enlarged.

Colostethus chocoensis is distinguished from those species lacking white stripes (*C. awa*, *C. pumilus*, and *C. mystax*) by having extensive webbing between the toes. *Colostethus chocoensis* closely resembles *C. fuliginosus* and *C. bocagei*, from which it differs by lacking oblique lateral stripes. Some specimens of *C. fuliginosus* and *C. bocagei* may lack conspicuous stripes, but *C. chocoensis* also differs by having Finger I shorter than Finger II. Also, *C. chocoensis* resembles *C. peculiaris* from which it is distinguished by lacking a pair of large pectoral spots.

Description and variation.—A redescription of the holotype is provided by Myers (1991). Also, Myers (1991) described and compared Ecuadorian material with other populations. The Ecuadorian specimens examined agree with these descriptions.

There are dark marks on the head and a square mark on the dorsum of the body (Fig. 2D). The venter has light spots or reticulations. Males have unspotted throats and females have white marks on their throat.

Males of this species have large elongately ovoid testes 4.5–5.4 mm in diameter; the left testis is smaller than the right (Fig. 5A). In some specimens, Fingers II and III are webbed basally (Fig. 1A). A recently metamorphosed juvenile (MECN 757) is 6.7 mm SVL.

Color in life: KU 166157–58: dorsum brown with dark brown marks and bluish cream flecks laterally; throat and ventral surfaces of limbs pale gray; abdomen bluish white with gray reticulations; iris dull bronze (W. E. Duellman, field notes, 8 April 1975).

Tadpoles.—Unknown

Calls.—Unknown.

Distribution and ecology.—*Colostethus chocoensis* ranges from southern Panama to west-central Ecuador. In Ecuador it is known at elevations between 600–1540 m on the western slopes of the Andes in provincias Carchi, Pichincha, and Cotopaxi (Fig. 10). The distribution lies within the

Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm, and annual mean temperature is 18–24°C.

A female and a male (KU 166157–58) were found perched on leaves of herbs 10 cm over water at night (W. E. Duellman, field notes, 8 April 1975). A juvenile (MECN 757) was found at the edge of a stream at 15:00 h.

Colostethus chocoensis has been found in sympatry with *C. breviquartus* in northwestern Ecuador, and with *C. awa*, *C. toachi*, and *Epipedobates spinosai* in west-central Ecuador.

Comments.—The assignment of Ecuadorian specimens to this species is tentative. Myers (1991) reported differences between the Ecuadorian specimens and the holotype of *C. chocoensis*, a female. Size and shape of the testes for specimens at the type locality of *C. chocoensis* are unknown.

Colostethus delatorreae new species

Plate 3D

Holotype.—KU 202825, a male, from ca. 5 km W El Laurel, approx. 25 km E Maldonado, 2340 m, Provincia Carchi, Ecuador, collected on 26 February 1984 by David M. Hillis.

Paratypes.—All from Provincia Carchi, Ecuador. KU 202826 same data of holotype; KU 182197–99, KU 182201–02 from 14 km (airline) SE Maldonado, 2500 m; KU 220618–21, QCAZ 1436 from 18.5–27.3 km E Maldonado, ca. 2420 m.

Diagnosis.—A species characterized by (1) SVL, males, 17.5–20.8, $n = 8$; females, 19.3–20.5 ($\bar{x} = 19.9$; $n = 2$); (2) disc on Finger III expanded; (3) length of Finger I = Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV wider than diameter of toe; (6) fringe absent on Toe IV, keel present; (7) outer tarsal fold absent; (8) toes unwebbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe present; (12) discrete markings absent on chest-gular region; two small black spots at base of arms; (13) abdomen white in females, reticulated or white spotted in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus delatorreae is compared with *C. maquipucuna*, both of which have a complete oblique lateral stripe, a reticulated or spotted venter, two small spots at the ventral part of the arm inser-

tion, and lack bandlike marks on the gular-chest region. *Colostethus delatorreae* is distinguished from *C. maquipucuna* by having more marks on the dorsal surfaces of thighs and a narrow oblique lateral stripe. *Colostethus delatorreae* is similar to *C. pulchellus*; however, *C. pulchellus* lacks a ventrolateral stripe and black spots ventrally, and has less expanded discs on fingers.

Description of holotype.—Adult male, 19.8 mm SVL; body slender; head slightly longer than wide; head length 34.3% SVL; head width 32.8% SVL; snout bluntly rounded in dorsal view and in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance about half diameter of eye; supratympanic fold weak, diffuse, obscuring posterodorsal part of tympanum; tympanum diameter 48.2% diameter of eye. Forelimbs moderately long; Finger I and II about equal in length; fingers unwebbed, lacking lateral fringes, but keels present; Finger III not swollen; terminal discs expanded moderately; subarticular tubercles low, round; palmar tubercle large, rounded, barely elevated; thenar tubercle elliptical; nuptial excrescences absent. Hind limbs long; tibia length 49% SVL; foot length 43.4% SVL; outer tarsal fold absent; inner tarsal fold sigmoid on distal half of tarsus, barely elevated; outer metatarsal tubercle round, about half size of elliptical inner metatarsal tubercle; toes unwebbed without lateral fringes, but keels present; terminal discs expanded moderately; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum smooth anteriorly and slightly granulated above anal region; skin on flanks and venter smooth; anal opening directed posteroventrally at midlevel of thighs; anal sheath short; tongue elongately elliptical, widest posteriorly, free posteriorly for about two thirds of its length; vocal sac single, not well developed.

Color in preservative: Dorsum dark brown; dorsum of snout pale brown; black band on flanks, narrow white oblique lateral stripe extending from point behind eye to groin; tympanic region brown, lighter than surrounding areas; upper lip creamy white with minute black stippling on lower border; dorsal surfaces of forearms cream with minute gray stippling; distinct blackish-brown longitudinal stripes on anterior and posterior surfaces of upper arm, posterior stripe on posterior surface continuing onto

ventral surface of forearm; dorsal surfaces of hind limbs mottled dark brown and with cream; dark gray longitudinal stripe on anterior surface of thigh continuous with brown shank; distinct transverse bars on tarsi and feet; tips of Fingers I and II and of Toes I–III cream; other digits brown; minute black stippling making gray tint on throat and chest; brown stripe on cream border of lower jaw, not reaching corner of mouth; two discrete gray spots on chest at level of insertion of arms; abdomen reticulated brown and white; ventrolateral white line; ventral surfaces of hind limbs with diffuse brown spots; ventral surfaces of tarsi, plantar and palmar surfaces brownish gray.

Measurements of holotype (mm): SVL 19.8, tibia length 9.7, foot length 8.6, head length 6.8, head width 6.5, length of eye 2.9, eye-nostril distance 1.6, tympanum diameter 1.4.

Variation.—Other males are similar to the holotype. The two discrete spots at the base of arm are clearly defined in two other males; in others, the spots are incorporated into the marbled pattern of the abdomen. In males, the abdomen usually has white spots anteriorly and reticulations posteriorly. A juvenile male lacks the two discrete spots. Females resemble the holotype, except that only one individual has a clearly defined ventrolateral stripe. Spots are present at the base of the arm. The dorsum is diffusely marbled; a black stripe borders the oblique lateral stripe medially and extends from the eye to the anal region. The oblique lateral stripe is continuous with a white stripe on the posterodorsal surface of the thigh. Usually there is a brown spot on the dorsal wrist.

Color in life: Males (KU 182197–98, KU 220618–19): dark grayish-brown or pale brown dorsum with golden or cream oblique lateral stripe; labial stripe cream or yellowish bronze; flanks brown; posterior surfaces of thighs dull yellow with brown or brownish-black markings; throat dirty creamy yellow (nearly unpigmented in one specimen); venter with a mosaic pattern of black and white spots; ventrolateral stripe white, interrupted. Female (QCAZ 1436): black and gray markings on flanks, venter yellowish cream; ventral surfaces of limbs tinted with orange. Juvenile (QCAZ 1457): like males, but with white venter. Adults (KU 182199–202): dorsum brown with indefinite brown mottling, a coppery-white oblique lateral stripe; bronze face

stripe; throat yellow, venter white with blue wash; ventrolateral stripe white; flanks black (J. D. Lynch, field notes, 31 May 1977; L. A. Coloma, field notes, 10 June 1989).

Tadpoles.—The following description is based on a back-riding tadpole (KU 202977) in Stage 25 (Fig. 6C).

Total length 11.6 mm; body moderately depressed, about two thirds as high as wide; widest at about three-fourths length of body; snout bluntly rounded in dorsal and lateral profiles; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.5 mm; spiracle sinistral, its opening directed posterodorsally at a point slightly below the midline at approximately two-thirds length of body; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin low on anterior one fourth of tail, slightly higher than ventral fin; tail length 67% total length, tail height 14% total length, dorsal fin height 0.4 mm at midlength of tail, not extending onto body; ventral fin height 0.3 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform; 1.2 mm wide; tooth row formula 2/3; second upper row narrowly interrupted medially; lower rows subequal in length to upper rows; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak “V”-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip having one row of marginal papillae.

Dorsum and sides of body dark brown; abdomen transparent cream with pigmentation laterally on throat; caudal musculature cream with dark brown flecks; fins translucent with dark brown flecks on dorsal fin.

Calls.—Unknown.

Distribution and ecology.—*Colostethus delatorrae* is known only from elevations of 2340–2500 m on the western slopes of the Andes in northern Ecuador (Fig. 15). Its distribution lies within the Low Very Humid Montane Forest, where annual mean precipitation is 2000–4000 mm, and annual mean temperature is 12–18°C.

Specimens were active, under stones, and a log along roadside rivulets. Males, KU 202885–26 and either 182197 or 182198, were carrying one, one, and unknown number of larvae, respectively.

Colostethus delatorrae has not been found sym-

patrically with any other dendrobatid frog.

Etymology.—The specific name is a patronym for Stella de la Torre, one of the collectors of paratype specimens, and an enthusiastic Ecuadorian biologist who has made significant contributions to the collections of frogs from Ecuador.

Colostethus elachyhistus Edwards
Plate 2B

Colostethus elachyhistus Edwards, 1971:149.—

Holotype: KU 120540 from Loja, 2150 m, Provincia Loja, Ecuador.

Diagnosis.—(1) SVL, males 17.8–24.1, $n=20$; females, 21.5–24.8 ($\bar{x}=23.4$; $n=22$); (2) disc on Finger III not expanded or slightly expanded; (3) length of Finger I = II; (4) fringe present on Finger II; (5) disc on Toe IV slightly wider than diameter of toe; (6) fringe present on Toe IV; (7) outer tarsal fold present; (8) toe webbing formula I(1½)2—2II2—3III(2½)3—3½(4)IV4—2½(3)V; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) two discrete marks present on gular-chest region; (13) white spots on abdomen; (14) Finger III not swollen in males; (15) testes white.

Colostethus elachyhistus is compared with those species having a complete oblique lateral stripe, two discrete marks on gular-chest region, and basal webbing (*C. infraguttatus* and *C. awa*). It differs from *C. awa* by having a complete and well-defined oblique lateral stripe, and from *C. infraguttatus* by having more extensive webbing on the toes.

Description and variation.—Edwards' (1971) original description is appropriate; however, the dorsolateral stripe of the original description here is considered to be an oblique lateral stripe. The dorsal pattern was described as irregular blotches (Edwards, 1971). A generalized dorsal pattern consists of a small mark on a pale gray snout, a mark between eyes, a "V"-shaped mark behind the former continuous with two black parallel paravertebral stripes. In some specimens the marks are diffuse. Males have white spots on dark abdomen with the gular-chest region unspotted gray. The venter may be marbled or spotted in females. Two gular-chest spots are present in both sexes.

Specimens from continuous localities ranging

from 850 to 2760 m over a distance of approximately 90 km from Sabiango to San Lucas in southern Ecuador show the following variation from low to high elevations. The color pattern is the same as that described previously, but specimens from the lowest elevations have more marks on the dorsum than those from higher elevations. Also, some specimens from the higher localities have an indication of a pale middorsal stripe, and more defined black lines on the anterior and posterior surfaces of the forearms and anterior surfaces of the thighs. Interrupted ventrolateral stripes are present in all the samples, but in some specimens from higher elevations the oblique lateral stripe is wider than in all specimens from lower elevations. In populations from lower elevations, the tips of the fingers are more expanded than are those from higher elevations, in which the discs on the fingers are about equal in size to the adjacent phalanges. Also, webbing is more extensive at lower elevations (see diagnosis).

Tadpoles.—Edwards (1971) described a series of free-swimming tadpoles in Stages 31–41.

Calls.—Unknown.

Distribution and ecology.—*Colostethus elachyhistus* occurs on the western slopes of the Andes at elevations of 850–2760 m in southern Ecuador (Fig. 10). The distribution lies within the Dry Premontane Forest, Dry Lower Montane Forest, and Humid Lower Montane Forest. Annual mean temperature is 18–24°C in Dry Premontane Forest, 12–18°C in Dry Lower Montane Forest, and Humid Lower Montane Forest; annual mean precipitation is 500–1000 mm in Dry Premontane Forest and Dry Lower Montane Forest, and 1000–2000 mm in Humid Lower Montane Forest.

Edwards (1971) reported a male guarding a clutch of 19 eggs beneath a rock. *Colostethus elachyhistus* occurs sympatrically with *Epipedobates tricolor* at lower elevations. Its distribution is parapatric to the distribution of *C. infraguttatus* in the Pacific lowlands, and to the distribution of *C. vertebralis* and *C. anthracinus* in inter-Andean valleys.

Comments.—Intraspecific variability in *Colostethus elachyhistus* is greater than in other species; the variation exhibited by the Loja Basin populations may represent geographic variation. Duellman and Wild (1993) reported differences in webbing and coloration in adults and coloration of tadpoles among populations from Canchaque and

Huancabamba from Peru and from the Loja Basin in Ecuador. I agree with their suggestion that more than one species may be included in this nominal taxon; however, in the absence of estimates of gene flow among different populations, it is difficult to test this hypothesis using morphological evidence.

In some parts of the range at lower elevations, individuals of *Colostethus elachyhistus* resemble the parapatric *C. infraguttatus*. For example, toe webbing, disc size and ventral color patterns are similar in nearby populations belonging to these two species. Either intergradation or hybrid zones occurs between them. At higher elevations, in the vicinity of Urdaneta in the Cordillera de Cordoncillo individuals assigned to *C. elachyhistus* herein, are similar to the parapatric *C. vertebralis*. For example, they have a pale middorsal stripe, small pectoral spots, and the tips of fingers are only slightly expanded. Tentatively, I recognize these nominal taxa (*C. elachyhistus*, *C. infraguttatus*, and *C. vertebralis*); this recognition draws attention to the differences among populations.

Colostethus exasperatus Duellman and Lynch
Plate 1B

Colostethus exasperatus Duellman and Lynch, 1988:129.—Holotype: ANSP 29218, an adult male from Camp 2, "Yapitya," 1700 m, on the trail from Logroño to Yaupi, west slope of the Cordillera de Cutucú, Provincia Morona Santiago, Ecuador.

Colostethus parvus Rivero, 1991b:8–10.—Holotype: USNM 282819 from Limón and Gualaceo, on trail between Agua Rica and San Juan Bosco, 1981 m, Provincia Morona-Santiago, Ecuador. New synonymy.

Diagnosis.—(1) SVL, males 17.5–20.1, $n = 6$; SVL, females 20.7–21.2 ($\bar{x} = 21.0$, $n = 2$); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV wider than diameter of toe; (6) fringe absent on Toe IV; toes slightly keeled; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe present; (10) short oblique lateral stripe present; (11) ventrolateral stripe absent; (12) discrete marks absent on gular-chest region; (13) white venter in females; dark brown spots ventrally, laterally marbled in

males; (14) third finger not swollen in males; (15) testes white.

Colostethus exasperatus is compared with those species that lack toe webbing, and a white ventrolateral stripe, and have a pale dorsolateral stripe (*C. whympersi*). It is distinguished from *C. whympersi* by lacking a heavy dark darkening on the abdomen of males.

Description and variation.—The original description (Duellman and Lynch, 1988) is adequate, except in that fringes are absent on fingers and toes (fringes present on fingers and toes according to Duellman and Lynch, 1988); I prefer to consider Toe IV as a laterally keeled rather than fringed; also, I am unable to distinguish two discrete marks on the chest as originally stated. On the dorsum, a blackish band borders the inner side of the dorsolateral stripe. There is a swollen black gland on the inner surface of the elbow.

Two males (KU 146240–41) from an elevation of 970 m in Provincia Pastaza are structurally similar to specimens from Morona Santiago; however, they differ in several features of coloration. (1) The venter is uniformly dark gray in preservative; (2) the hind limbs have fewer marks, and (3) a swollen dark gland at the inner join of upper and lower arm is absent. In life, a male (KU 146240) had a dark brown dorsum with yellow dorsolateral stripes and upper arms; the throat was black, abdomen grayish yellow, hind limbs orange with dark brown bars dorsally, and iris brown (W. E. Duellman, field notes, 23 April 1972).

Tadpoles.—Duellman and Lynch (1988) described a series of back-riding tadpoles in Stages 23–25. In life, back-riding tadpoles (KU 146776) carried by a male (KU 146241) had a dark brown body and caudal musculature, translucent tail, and cream gut (W. E. Duellman, field notes, 23 April 1972).

Calls.—Unknown.

Distribution and ecology.—*Colostethus exasperatus* occurs between 970 and 1981 m on the eastern slopes of the Andes in southern Ecuador in provincias Pastaza and Morona Santiago (Fig. 11). The distribution lies within the Pluvial Premontane Forest and Very Humid Premontane Forest. Annual mean temperature is 18–24°C in both zones; annual mean precipitation is 4000–8000 mm in Pluvial Premontane Forest, and 2000–4000 mm in Very Humid Premontane Forest.

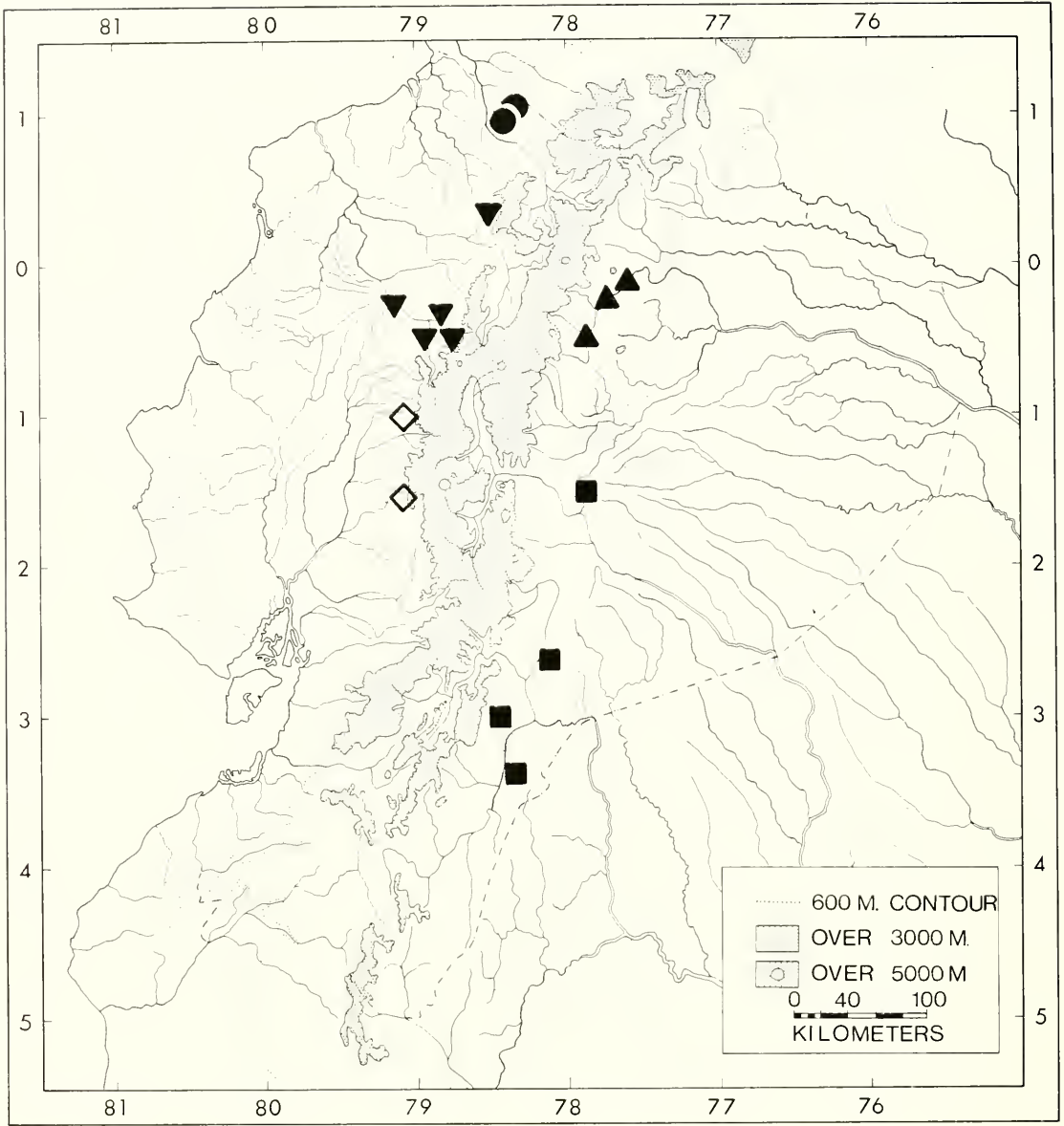


Fig. 11. Distributions of *Colostethus breviquartus* (●), *C. exasperatus* (■), *C. fallax* (◆), *C. fuliginosus* (▲), and *C. lehmanni* (▼).

Colostethus exasperatus occurs sympatrically with *C. mystax* and *C. shuar* in Cordillera del Cóndor.

Comments.—Rivero (1991b) described *Colostethus parvus* from Limón and Gualaceo, on a trail between Agua Rica and San Juan Bosco, 1981 m, Provincia Morona Santiago (Provincia Zamora-Santiago indicated in the original description is an error). I have examined three paratypes (USNM

282532–34) and I do not find any differences between these specimens and type material of *C. exasperatus*. Rivero reported *C. parvus* to have an oblique lateral stripe; however, a close examination of the stripe reveals that it is the same as the dorso-lateral stripe of *C. exasperatus*. Therefore, I relegate the nominal *C. parvus* (Rivero, 1991b) to the synonymy of *C. exasperatus* (Duellman and Lynch, 1988).

The specimens from Provincia Pastaza may represent a different species, but at this time, I am unwilling to recognize them taxonomically because few specimens are available.

Colostethus fallax Rivero

Colostethus fallax Rivero, 1991b:12–13.—Holotype: USNM 282670, from 3 km W Pilaló, on Quevedo-Latacunga Road., 1760 m, Provincia Cotopaxi, Ecuador.

Diagnosis.—(1) SVL, males 16.2–18.5, $n = 4$; females, 16.8 ($\bar{x} = 16.8$, $n = 2$); (2) disc on Finger III not or barely expanded; (3) length of Finger I = Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV not or barely expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) short oblique lateral stripe sometimes present; (11) ventrolateral stripe absent; (12) two discrete marks absent on gular-chest region; (13) venter white; (14) Finger III not swollen in males; (15) testes color unknown.

Colostethus fallax is distinguished from all other Ecuadorian *Colostethus* by lacking or having a short, oblique lateral stripe, and lacking a pale dorsolateral stripe and webbing between toes.

Description and variation.—Rivero's description (1991b) is appropriate.

Tadpoles.—Unknown.

Calls.—Rivero (1991b) described the call as a single, sharp "peep."

Distribution and ecology.—*Colostethus fallax* is known from the type locality and a nearby site on the western slopes of the Andes, between 1760–2430 m (Fig. 11). The distribution lies within the Very Humid Premontane Forest and Low Humid Montane Forest. Annual mean precipitation is 2000–4000 mm in Very Humid Premontane Forest, and 1000–2000 mm in Low Humid Montane Forest; annual mean temperature is 18–24°C in Very Humid Premontane Forest and 12–18°C in Low Humid Montane Forest.

Colostethus fugax Morales and Schulte

Colostethus fugax Morales and Schulte, 1993:97–106.—Holotype: USNM 282831, from Cabeceras

del Río Bobonaza (approx. 01°31' S, 77°19' W), 686 m, Provincia Pastaza, Ecuador.

Diagnosis.—(1) SVL, males 17.9–19.5; females, 19.3–20.1; (2) disc on Finger III expanded; (3) Finger I > Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV, keel present; (7) outer tarsal fold absent; (8) basal webbing present, toe webbing formula $I2-3\frac{1}{2}II3-4III4-3IV4\frac{1}{2}-3V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe inconspicuous; (12) discrete marks absent on gular-chest region; (13) venter cream in both sexes; (14) Finger III swollen in males; (15) testes color unknown (not stated in original description).

Colostethus fugax is compared with those species that have a complete oblique lateral stripe and immaculate venter, and lack or have basal webbing on the toes (*C. breviquartus*, *C. cevallosi*, *C. machalilla*, and *C. toachi*). It is distinguished from *C. breviquartus*, *C. cevallosi*, and *C. toachi* by males lacking a Finger III swollen. *Colostethus machalilla* resembles *C. fugax* in having a Finger III swollen in males, and immaculate venters in both sexes; however, *C. machalilla* has an "X"-shaped dorsal color pattern.

Description and variation.—Morales and Schulte's description (1993) is adequate.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus fugax* is known from elevations of 600–700 m at the type locality and a nearby site on the Amazon Basin (Fig. 9). The distribution lies in a transition zone between Humid Tropical Forest and Very Humid Premontane Forest. Both zones have an annual mean precipitation of 2000–4000 mm; annual mean temperature is 24–25°C in Humid Tropical Forest and 18–24°C in Very Humid Premontane Forest. *Colostethus fugax* occurs sympatrically with *C. cevallosi* and probably with *C. bocagei* and *C. marchesianus*.

Colostethus fuliginosus (Jiménez de la Espada)
Plate 1E

Hyloxalus fuliginosus Jiménez de la Espada, 1871:59.—Lectotype: MNCN 1585 (old number 276) (designated by Savage, 1968:753) from San

José de Moti (Cantón Quijos), Provincia Napo, Ecuador [collected in June 1865].

Hylixalus fuliginosus—Boulenger, 1882b:138.

Hyloxalus fuliginosus—Savage, 1968:747.

Colostethus fuliginosus—Edwards, 1971:148.

Diagnosis.—(1) SVL, males, 23.6–24.3, $n = 4$; females, 27.8–32.5 ($\bar{x} = 30.0$; $n = 12$); (2) disc on Finger III expanded; (3) Finger I slightly shorter or equal than Finger II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer metatarsal fold present; (8) toe webbing formula $I1\frac{1}{2}$ — $2III1\frac{1}{2}$ — $2\frac{1}{2}(3)III2$ — $3(3\frac{1}{2})IV3\frac{1}{2}$ — $2V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, inconspicuous in some specimens; (11) ventrolateral stripe absent; (12) discrete marks absent on chest; (13) throat dark in males, white spots on dark ground color on venter of females; (14) Finger III not swollen in males; (15) testes white.

Colostethus fuliginosus is compared with those species that have extensive toe webbing and either have or lack an inconspicuous oblique lateral stripe (*C. chocoensis* and *C. bocagei*). It is distinguished from them by having well-defined spotted or marbled patterns on the venter, and a larger size.

Description.—An appropriate description of the lectotype and paralectotype (MNCN 1585–86, both females) is not possible because they are poorly preserved. Measurements of these specimens are—MNCN 1585: SVL 32.2, tibia length 15.1, head length 11.2, head width 12.3, eye diameter 4.9, eye-nostril distance 2.1; MNCN 1586: SVL 32.5, tibia length 14.6, head length 10.2, head width 10.6, eye diameter 4.7.

Following is a description of KU 143087 from a series of specimens from the Río Azuela, 1740 m, Provincia Napo. An adult female, 29.5 SVL; body robust; head about as long as wide; head length 34.0% SVL, head width 34.1% SVL; snout bluntly rounded in dorsal view, and in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance 48.8% diameter of eye; supratympanic fold weak, diffuse, obscuring posterodorsal part of tympanum; tympanum diameter 40% diameter of eye; forelimbs moderately long; Finger I slightly shorter than Finger II; fingers having lateral keel-like fringes; fringes between Fingers II and III extending proximally as a small

web; terminal discs moderately expanded; disc on Finger III about 1.6 times wider than distal end of adjacent phalange; subarticular tubercles low, round, oval; palmar tubercle large, rounded, barely elevated; thenar tubercle moderately rounded, small, bordered at inner side by three smaller, rounded tubercles; hind limbs moderately robust, tibia length 47.1% SVL, foot length 45.1% SVL; outer tarsal fold absent; inner tarsal fold nearly straight on distal half of tarsus; outer metatarsal tubercle round, about half size of elliptical inner metatarsal tubercle; toes webbed without narrow lateral fringes $I1\frac{1}{2}$ — $2III1\frac{1}{2}$ — $2\frac{1}{2}III2$ — $3IV3\frac{1}{2}$ — $2V$; terminal discs expanded, about twice width of digits; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum and venter smooth, flanks smooth, angle of jaw tubercular; anal opening directed posteroventrally at midlevel of thighs; anal sheath short; tongue elongately elliptical, narrow proximally, not indented posteriorly, free posteriorly for about one fourth of its length.

Coloration in preservative: Dorsum dark brown with small darker marks on scapular region; flanks dark brown mixed with white ventrolaterally; tympanic region pale brown with white line bordering lower border of tympanum; upper lip gray; tubercles white at angle of jaw; dorsal surfaces of forearms uniform brown with slightly visible darker, longitudinal stripes; anterior and posterior surfaces of upper arm uniform brown; dorsal surfaces of hind limbs brown with darker transverse bars along the entire length; throat and chest cream with brown spots; abdomen cream with few brown spots laterally; groin with few small white spots; ventral surfaces of limbs brown, inner fingers and toes with less brown pigment than outer ones; scutes white on Fingers and Toes I–III, brown on IV–V.

Variation.—In some specimens, a diffuse oblique lateral stripe is present; in others, this stripe is replaced by small white spots. All specimens have a dark interorbital bar and scattered dark spots are present on the dorsum, and two to four transverse bars on the thighs. White marks across the digits are less conspicuous on outer digits. Some individuals have small supernumerary tubercles on hands.

Ventral coloration is sexually dimorphic. Males have a black abdomen with white spots; the gular-chest region is uniform gray. The throat in females

varies from cream with minute stippling to gray and gray with small dark spots; the abdomen is pale or diffusely spotted, but always less conspicuously marked than in males.

Color in life: A female (KU 143087): dorsum dark olive-brown; venter dull yellow; iris reddish bronze. A male (KU 166156): dorsum dull olive-brown with tan supratympanic stripe and bars on limbs; venter greenish gray with creamy yellow spots; iris grayish brown. A juvenile (KU 143086): dorsum brown with dark brown marks; dorsolateral stripe reddish brown; flanks olive-tan; venter yellow; iris dark bronze (W. E. Duellman, field notes, 20 October 1971 and 6 October 1974).

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus fuliginosus* is restricted to the Amazonian slopes of the Andes in northern Ecuador at elevations between 1660 and 1910 m (Fig. 11). The distribution lies within Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 18–24°C.

Specimens have been found by day, usually under rocks or logs at the edge of fast-flowing streams and rivers; others were in grass in a culvert, along a roadside ditch, and on a large leaf above a stream. At night, a juvenile was found under the edge of a rock on the bank of a stream in cloud forest; two females were on a sandy bank of stream and others were sleeping on low vegetation less than 10 cm high beside a stream (J. D. Lynch, field notes, 15–16 July 1977; and W. E. Duellman, field notes, 20–21 October 1971, 7 April 1972, and 6 October 1974).

Colostethus fuliginosus has been collected sympatrically with *C. bocagei*, *C. kingsburyi*, *C. pulchellus*, *C. shuar*, and *Minyobates abditus*.

Comments.—Savage (1978) indicated that the type locality, San José de Moti, is on the north slope of Volcán Sumaco. See additional taxonomic comments under *C. bocagei*.

Colostethus infraguttatus (Boulenger)

Plate 2F

Phyllobates infraguttatus Boulenger, 1898:118.—Syntypes: BM 1947.2.14.7–8 (BM 1947.2.14.7 herein designated as lectotype). From Puente del Chimbo, the railway terminus about 112 km E

Guayaquil, about 304 m. Provincia Chimborazo, Ecuador.

Colostethus infraguttatus—Edwards, 1971:148.

Diagnosis.—(1) SVL, males, 16.7–20.5 ($n = 20$); females, 19.5–23.4 ($\bar{x} = 21.1$; $n = 20$); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present in some specimens; (8) toe webbing formula $I2-3\frac{1}{2}II2-3(3\frac{1}{2})III3-4IV4\frac{1}{2}-3V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe present or absent; (12) discrete marks usually present on gular-chest region; (13) white spots on throat and abdomen in males and females; (14) Finger III not swollen in males; (15) testes white.

Colostethus infraguttatus is compared with those species that have discrete marks on gular-chest region, and basally webbed toes (*C. awa* and *C. elachyhistus*). It is distinguished from *Colostethus awa* by having a complete oblique lateral stripe and from *C. elachyhistus* by having less webbing among toes.

Description and variation.—The two syntypes (BM 1947.2.14.7–8) are well preserved and the original description is adequate, except that the dorsal pattern has not been described because the syntypes are darkened owing to preservation. Measurements of lectotype (mm): SVL 22.2, tibia length 10.1, head length 8.5, head width 7.9, eye diameter 3.5, eye-nostril distance 1.8, tympanum diameter 1.4.

In the most southern *Colostethus infraguttatus* from the vicinity of Piñas, Provincia El Oro, the skin above the anal region is granulated and the toes are webbed basally. An interorbital dark triangle and a scapular “V”-shaped mark are present in all individuals examined (Fig. 2E). In some specimens the “V”-shaped mark is separated at the vertex. Black dorsolateral stripes are present in all individuals, but in some, they are discontinuous in the scapular region. The posterior part of the dorsum is irregularly spotted. The dorsal coloration of juveniles is like that of adults. The forelimbs are gray with a distinct or diffuse brown longitudinal stripe on the anterior surface of the upper arm; the stripe does not extend to the forearm, which has diffuse bars dor-

sally. The hind limbs have generally three or four transverse bars on each segment, sometimes the bars are inconspicuous or their number varies between the sides of the same individual; transverse bars also are present on hands and feet. There is a rather diffuse, longitudinal gray stripe on the anterolateral surface, and in some specimens another on the posterior surface of the thigh. White spots or marbling occur on the throat and abdomen, and females have two discrete dark spots or irregular marks on the gular-chest region. The inner two fingers and inner three toes have white scutes. Specimens from Uzhcurrumi and Vía Pasaje, Provincia El Oro, are similar to the preceding, except that males have two discrete spots on the chest, and juveniles have a few pale spots on the dorsal surfaces of the body and limbs.

Series of frogs from 13.5 km W Luz María differs by having less-defined dorsal markings—especially the “V”-shaped mark. Both sexes have poorly defined bandlike mark on the gular-chest region; males have a uniformly gray throat, whereas females have white spots in the gular-chest region. Recently metamorphosed young have black stippling concentrated in the region of gular-chest marks of adults, the abdomen is white, toes are unwebbed, and fringes on the toes are inconspicuous. Specimens from Balsapamba, one of the most northern localities, show less defined dorsal markings; however, the marks are still discernible and similar to the previously described pattern. Also the marks on thighs are less defined and the tips of the digits are less expanded and toe webbing is absent. Specimens from Pallatanga are similar to the preceding but males have darker venters.

A recently metamorphosed juvenile (KU 152064) has a SVL of 11.5 mm.

Color in life: A female from Balsapamba (KU 142382): dorsum metallic tan; dorsolateral and labial stripes bronze-cream; forelimbs and dorsal surfaces of hind limbs tan; ventral surfaces of limbs and posterior surfaces of thighs orange-yellow; throat white; abdomen dark gray with white spots; flanks black with yellow spots in groin; iris black with minute golden flecks (W. E. Duellman, field notes, 13 July 1971). Other specimens from the same locality and surrounding areas were described as having a dorsum varying from greenish to pale and dark brown spotted with dark brown, dorsolateral

stripe bronze-gold anteriorly becoming lemon-yellow in the groin; labial stripe yellow with bronze cast; thighs pale orange or yellow with dark brown marks; concealed surfaces of shanks lemon-yellow; throat of males dusky brown; venter white-blue with hint of green and spotted with white or very pale blue in females (J. D. Lynch, field notes, 14–20 July 1970).

Tadpoles.—The following description is based on an individual in Stage 24 (Fig. 6A) from a series of 15 back-riding tadpoles (QCAZ 1341).

Total length 11.8 mm; body moderately depressed, about two thirds as deep as wide; about equal width along entire length of body; snout bluntly rounded in dorsal view and in profile; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.5 mm; spiracle sinistral; no spiracular opening identified; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin low on anterior one fourth of tail; fins subequal in height; tail length 64% total length, tail height 17% total length; dorsal fin height 0.6 mm at midlength of tail, not extending onto body; ventral fin height 0.6 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform, 1.3 mm wide; tooth row formula 2/3; second upper row narrowly interrupted medially; first and second lower rows subequal in length compared to upper rows; third lower row weakly developed, shorter than other rows; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak “V”-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by one row of low marginal papillae.

Dorsum and sides of body dark brown; dark stripe along proximal half of dorsal edge of caudal musculature; venter pigmented anterolaterally, unpigmented posteriorly; caudal musculature cream with scattered dark brown flecks, most numerous proximally; fins translucent.

Calls.—Unknown.

Distribution and ecology.—*Colostethus infraguttatus* occurs in a relatively wide altitudinal zone (70–1500 m) on the western slopes of the Ecuadorian Andes and the Coastal Cordillera (provincias Manabí, Guayas, Bolívar, Los Ríos, Azuay, and El Oro) (Fig. 12). The distribution lies within the Humid Premontane Forest, Tropical Deser-

tic Thicket, Tropical Thorny Scrub, and Very Dry Tropical Forest. Annual mean precipitation is 1000–2000 mm in Humid Premontane Forest, and 125–1000 in the other life zones; annual mean temperature is 18–24°C in Humid Premontane Forest and 24–26°C in the other zones.

Specimens were found at the shore of Río Ayampe and on road rivulets near Luz María.

Colostethus infraguttatus occurs in sympatry with *Epipedobates tricolor*, in southwestern Ecuador and with *C. machalilla* in the coastal regions. Its distribution is parapatric to the distributions of *C. vertebralis* on the western slopes of the Andes in the Molleturo region and to *C. elachyhistus* at lower elevations.

Comments.—The interpopulational variation exhibited by *Colostethus infraguttatus* suggests that several species may be included in this nominal taxon. However, absence of discrete differences between populations precludes recognition of more than one species at this time. Also, *C. infraguttatus* closely resembles *C. elachyhistus*; additional data may reveal that the two nominal taxa are conspecific. (See comments under *C. elachyhistus*.)

Colostethus jacobuspetersi Rivero
Plate 2G

Colostethus jacobuspetersi Rivero, 1991b:2–3.—Holotype: USNM 282893, from Quito, Barrio Villa Flora, in south part of the city, 2800 m, Provincia de Pichincha, Ecuador.

Colostethus torrenticola Rivero, 1991b:4–6.—Holotype: USNM 282603 from 5 km N Pallatanga, at waterfall and Saint Mary Sanctuary, 2450 m, Provincia Chimborazo, Ecuador. New synonymy.

Diagnosis.—(1) SVL, males, 19.3–25.1, $n = 23$; females, 22.3–29.5 ($\bar{x} = 26.1$; $n = 28$); (2) disc on Finger III not expanded; (3) Finger I slightly shorter than Finger II; (4) fringe present on Finger II; (5) disc on Toe IV not expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) two discrete markings absent on chest-gular region; (13) abdomen with white spots or diffuse reticulated patterns; (14) Finger III not swollen in males; (15) testes white.

Colostethus jacobuspetersi is compared with *C. pulchellus* that has a complete oblique lateral stripe and lacks two discrete marks (some *C. pulchellus*) on gular-chest region and two spots ventrally at the base of the arm. *Colostethus jacobuspetersi* is distinguished from *C. pulchellus* by lacking expanded discs on fingers and toes.

Description and variation.—Rivero's (1991b) description is appropriate.

A recently metamorphosed juvenile (MHNG 18926.1) has a SVL of 13.0 mm.

Color in life: QCAZ 1349: dorsum pale brown with greenish tint and diffuse reddish-brown marks; white oblique lateral stripe; white stripe on the upper lip; abdomen reddish orange; throat and chest with scattered white flecks on pale orange ground color; ventral surfaces of thighs, anal region and forelimbs pale red (L. A. Coloma, field notes, 28 May 1989).

Calls.—Two recordings are available. One is from 5 km W Aloag, 2945 m, Provincia Pichincha, recorded at 14°C; the other (Fig. 8A) is from Bosque Protector Cashca Totoras, ca. 3000 m, Provincia Bolívar. No specimen is associated directly with either of the recordings, but *Colostethus jacobuspetersi* is the only species of the genus known from these localities. Both recordings consist of single notes 0.23–0.31 sec long with intervals of 5.4–12.6 sec between notes. One animal emitted 16 calls in 2 min. The fundamental frequency lies between 1300 and 1500 Hz; the dominant frequency is between 2900 and 3400 Hz. Frequency rises towards the end of the call. There are two harmonics above the dominant frequency.

Distribution and ecology.—*Colostethus jacobuspetersi* is known from the inter-Andean valleys of Guayllabamba, Toachi, Chimbo, and Cañar, and on the western slopes on the Andes in northern and central Ecuador, where it occupies areas between 1500 and 3800 m (Fig. 13). The distribution lies mainly within Low Humid Montane Forest, and Humid Montane Forest life zones. Annual mean precipitation is 1000–2000 mm, and 500–1000 mm respectively; annual mean temperature is 12–18°C in Low Humid Montane Forest and 7–12°C in Humid Montane Forest.

Colostethus jacobuspetersi lives in the montane and cloud forests and prefers small streams. Tadpoles presumably of this species have been found in these streams and in pools near the margins of the stream.

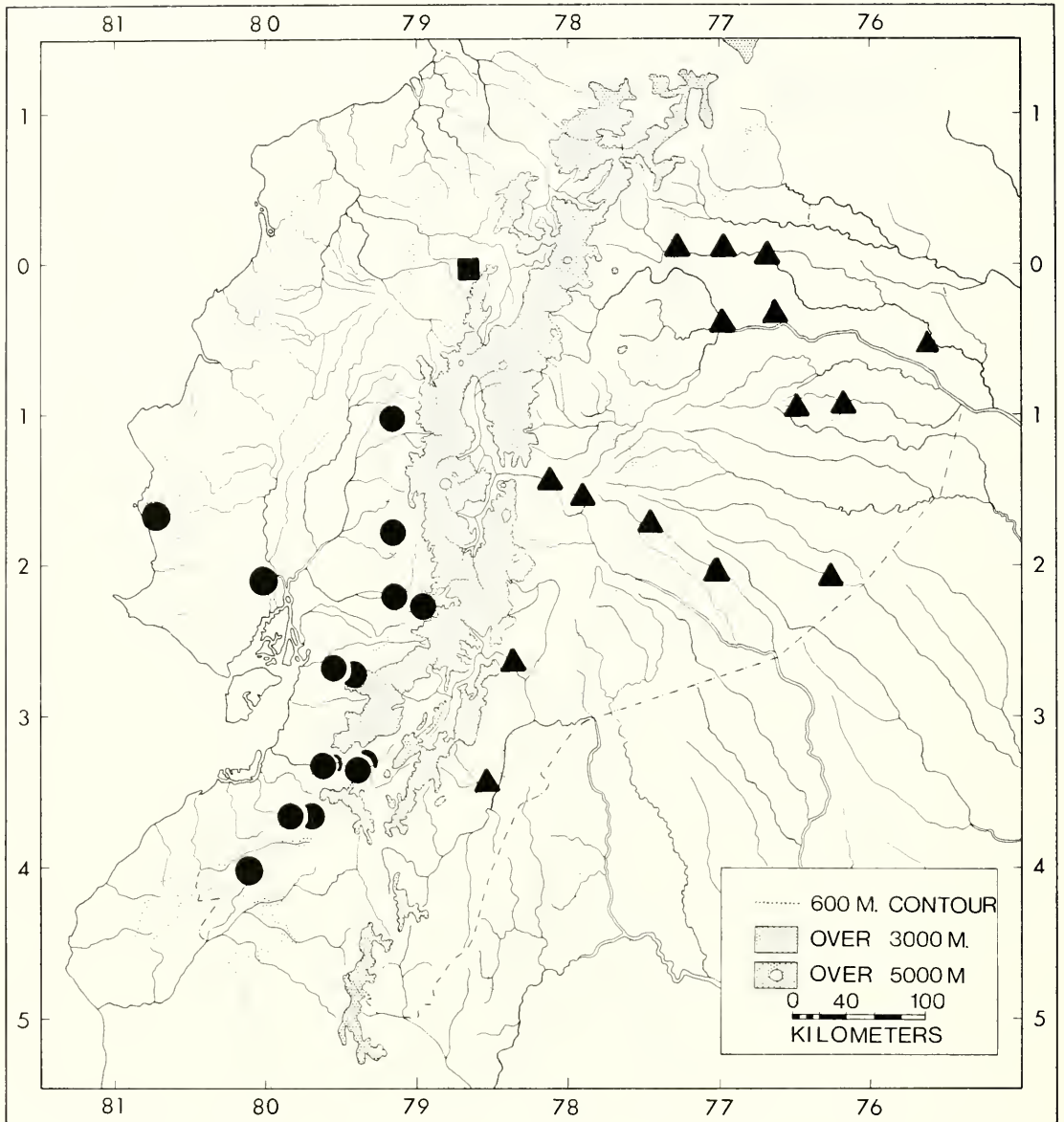


Fig. 12. Distributions of *Colostethus infraguttatus* (●), *C. maquipucuna* (■), and *C. marchesianus* (▲).

Colostethus jacobuspetersi has not been found sympatrically with any other dendrobatids, but in the vicinity of Pallatanga, it occurs near *C. infraguttatus*. In the Páramos de Guamaní on the western slopes of the Cordillera Oriental, it occurs near *C. pulchellus*.

Patzelt (1978) published a photograph of a *C. jacobuspetersi* carrying four tadpoles.

Comments.—Rivero (1991b) described *C.*

torrenticola and *C. jacobuspetersi* in the same paper. He noticed the similarity of both species and distinguished them by the different ventral coloration, smaller size and shorter snout of *C. torrenticola*. Rivero (1991b) compared specimens from the Guaranda-Pilaló region (an area between the type localities of *C. jacobuspetersi* and *C. torrenticola*) with *C. torrenticola* and *C. jacobuspetersi* and he suggested (Rivero, 1991b:6) that *C. torrenticola*

and the Guaranda-Pilaló populations “may qualify as subspecies of each other”; also he suggested that *C. jacobuspetersi*, the Guaranda-Pilaló populations and *C. torrenticola* “may be found to belong to the same artencreis.” Examination of type material and many specimens from a large geographic area shows that the characters used by Rivero to distinguish *C. torrenticola* from *C. jacobuspetersi* and the Guaranda-Pilaló populations either vary continuously or they are an artifact of preservation. For example, the color of the venter, used to contrast *C. torrenticola* from the Guaranda-Pilaló populations (see Rivero, 1991b:figs. 3–4), is similar in both samples when well-preserved material is compared. The SVL range of *C. torrenticola* falls within the SVL range of *C. jacobuspetersi*. The continuous variation recorded precludes the recognition of more than one species at this time; therefore, I consider *C. torrenticola* (Rivero 1991b) to be a junior synonym of *C. jacobuspetersi* (Rivero, 1991b).

Colostethus kingsburyi (Boulenger)

Plate 1C

Phyllobates kingsburyi Boulenger, 1918:427–428.—
Lectotype: BM 1947.2.14.5, (designated by
Silverstone, 1971:7) from El Topo, Río Pastaza,
1280 m, Provincia Pastaza, Ecuador.

Phyllobates intermedius Andersson, 1945:5.—Ho-
lotype: NHMG 1903 from the Río Pastaza,
Provincia Pastaza, Ecuador. New Synonymy.

Phyllobates intermedius—Andersson, 1945:5. Syn-
onymy fide Cochran, 1955.

Colostethus intermedius—Edwards, 1971:148.

Colostethus kingsburyi—Edwards, 1971:148.

Colostethus intermedius—Edwards, 1974b:5.

Diagnosis.—(1) SVL, males, 22.3–24.5, $n = 6$; females, 22.7–26.2 ($\bar{x} = 24.8$; $n = 6$); (2) disc on Finger III expanded; (3) Finger I longer than Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe present or keel-like on Toe IV; (7) outer tarsal fold present, not well developed; (8) webbing absent; (9) dorsolateral stripe present; (10) short oblique lateral stripe present; (11) ventrolateral stripe present; (12) discrete markings absent on chest-gular region; (13) abdomen white in females, reticulated or black spotted with white in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus kingsburyi is compared with those species that have white or cream dorsolateral and ventrolateral stripes (*C. marchesianus* and *C. talamancae*). *Colostethus kingsburyi* is larger than *C. marchesianus* and lacks basal webbing. It is distinguished from *C. talamancae* by having an inguinal stripe.

Description and variation.—The original description is adequate for the lectotype which has the following measurements (mm): SVL 24.6, tibia length 2.2, foot length 10.4, head length 9.5, head width 8.9, eye diameter 3.9, eye-nostril distance 2.5, tympanum diameter 2.0.

Edwards (1974) provided data for specimens (under the name *Colostethus intermedius*) from S slope Cordillera del Dué.

Ventral coloration is sexually dimorphic. Females have uniform white venters in contrast to males in which the chest and abdomen are black reticulated or spotted with white and the gular region is pale gray. Some specimens have two white bands across the base of the thigh. A short oblique lateral stripe sometimes is present. Juveniles have a wider dorsolateral line than adults.

Color in life: KU 122293: dorsum brown; dorsolateral stripe cream, paler at the border of snout; flanks black; tympanic region brown; oblique lateral stripe cream; ventrolateral stripe white, extending anteriorly to lower border of eye, where it contrasts with cream-yellow upper lip; dorsal surfaces of forelimbs pale brown with short, dark, longitudinal stripe on anterior surface; dorsum of hind limbs pale brown with scattered dark marks; digital scutes cream; lateral aspects of abdomen cream-yellow; iris black with golden flecks (KU Color Transparency 2911).

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus kingsburyi* is known from a narrow altitudinal zone (1140–1300 m) on the eastern slopes of the Andes in the vicinity of Volcán Reventador and in the Río Pastaza Trench (Fig. 10). The distribution lies within the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 18–24°C.

Colostethus kingsburyi occurs in sympatry with *C. bocagei*, *C. fuliginosus*, *C. pulchellus*, *C. shuar*, and *Minyobates abditus* in the vicinity of Volcán

Reventador and with *C. bocagei*, *C. marchesianus*, *C. marmoreoventris*, and *C. pulchellus* in the Río Pastaza Trench.

Comments.—Andersson's (1945) description of *Phyllobates intermedius* was based on a single specimen from the Río Pastaza. Edwards (1974b) re-described *Colostethus intermedius* from specimens from Provincia Napo; however, he failed to compare it to the type material of *Phyllobates kingsburyi* described by Boulenger in 1918 from Río Pastaza. Andersson (1945) contrasted the nominal taxa and noted several differences between *P. kingsburyi* and *P. intermedius* (characters for *P. intermedius* in parentheses)—e.g., throat and chest mottled with grayish brown (white); hind limbs shorter (longer); disc of Toe I as large as that of Toe II (disc of Toe I about two thirds that of Toe II); and tubercles absent on posterior part of dorsum and on hind limbs (present). I compared the type material of both nominal taxa and additional material from near the type locality and found that the characters used by Andersson to distinguish the two taxa vary intraspecifically. Therefore, I consider *Phyllobates intermedius* (Andersson 1945), to be a junior synonym of *P. kingsburyi* (Boulenger, 1918).

Colostethus lehmanni Silverstone
Plate 2H

Colostethus lehmanni Silverstone, 1971:3.—Holotype: LACM 44156, from Santa Rita near Río Nare, 1890–1910 m, Departamento Antioquia, Colombia.

Diagnosis.—(1) SVL, males, 15.4–20.0, $n=24$; females, 17.0–22.8 ($\bar{x}=20.0$; $n=40$); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorso-lateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) two discrete markings absent on gular-chest region; (13) abdomen black in males, white or gray in females; (14) Finger III not swollen in males; (15) testes white.

Colostethus lehmanni is compared with those species that have a complete oblique lateral stripe, lack discrete markings on gular-chest region, and

lack a marbled, spotted, or reticulated venter, but have black suffusion ventrally (*C. anthracinus* and *C. toachi*). It is distinguished from *C. anthracinus* by having expanded digital discs on the toes and from *C. toachi* by lacking brown testes and having transverse bars on the thighs.

Description and variation.—Silverstone's description (1971) is appropriate.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus lehmanni* occurs in a wide latitudinal range on the western slopes of the Andes from Colombia to Ecuador. In Ecuador, it is known from elevations of 1460–2120 m (Fig. 11). The distribution lies within the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 18–24°C.

Colostethus lehmanni occurs in sympatry with *C. chocoensis*, *C. awa* and *Epipedobates spinosai*, and possibly *C. whymperi*. Its lower distributional limit is near the upper limit known for *Colostethus toachi*.

Comments.—The range extension of *C. lehmanni* is surprising because the type locality is located in the northern part of the Cordillera Central in Colombia at about 850 km airline from the nearest record of this species in Ecuador. I compared type material of *C. lehmanni* with the specimens herein assigned to this nominal taxon, and I have not found any character to distinguish the Ecuadorian material from the type material. The enormous geographic gap, between the type locality and the Ecuadorian specimens localities, where no *C. lehmanni* have been reported, suggests that the Ecuadorian populations represent another species; however, morphological evidence to support this speculation is lacking.

Colostethus machalilla new species
Plate 2D

Holotype.—QCAZ 1414, an adult female, from a series from Río Ayampe, 25 km N Montañita, 1°40' S, 80°47' W, 70 m, boundary of Provincia Manabí and Provincia Guayas, Ecuador, collected on 5 April 1990 by Felipe Campos, Stella de la Torre, John J. Wiens, and Luis A. Coloma.

Paratypes.—KU 220645–59, QCAZ 1415–28 same data as holotype; EPN 3975–77, from Sector

Guale (S Río Ayampe), 70 m, Provincia Guayas; QCAZ 1405, 1412–13, KU 220634–44, from the Río Cuaque, 68 km NW El Carmen, near Pedernales, 100 m, Provincia Manabí; KU 220631–33, QCAZ 1401, from 38 km NW El Carmen on road to Pedernales, 330 m, Provincia Manabí, Ecuador.

Diagnosis.—(1) SVL, males, 14.4–16.0, $n=22$; females, 15.0–17.6 ($\bar{x} = 15.8$; $n = 28$); (2) disc on Finger III slightly expanded; (3) Finger I usually longer than Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing formula $12-3\frac{1}{2}II2-3\frac{1}{2}III3-4IV4\frac{1}{2}-3V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe present; (12) discrete markings absent on chest; (13) abdomen white in both sexes; (14) Finger III swollen in males; (15) testes brown.

Colostethus machalilla is compared with those species that have a complete oblique lateral stripe and immaculate venter, and have rudimentary or no webbing on the toes (*C. breviquartus*, *C. fugax*, and *C. cevallosi*). It is distinguished from *C. breviquartus* and *C. cevallosi* by males having Finger III swollen. *Colostethus machalilla* differs from *C. fugax* in being slightly larger and by usually having an “X”-shaped mark in the scapular region. *Colostethus machalilla* resembles *C. toachi* in having brown testes and immaculate venters in females; however, males of *C. toachi* lack a swollen Finger III and have black suffusion on the throat. Females can be distinguished by the dorsal pattern (“X”-shaped mark in *C. machalilla*).

Description of holotype.—Adult female, 15.6 mm in SVL; body slender; head slightly longer than wide; head length 36.5% SVL; head width 32.6% SVL; snout bluntly rounded in dorsal view, protruding in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance about two thirds diameter of eye; supratympanic fold diffuse, obscuring posterodorsal part of barely visible tympanum; diameter of tympanum 31.8% diameter of eye. Forelimbs moderately long; Finger I slightly longer than Finger II; fingers unwebbed, lacking lateral fringes; terminal discs slightly expanded; subarticular tubercles large, elevated, round; palmar tubercle large, rounded, barely elevated; thenar tubercle moderately rounded, smaller than palmar tubercle. Hind limbs moderately robust,

long; tibia length 45.5% SVL; foot length 41.0% SVL; outer tarsal fold absent; inner tarsal fold sigmoid, on distal two thirds of tarsus; outer metatarsal tubercle round, about half size of elliptical inner metatarsal tubercle; webbing vestigial between Toes III and IV; toes lacking lateral fringes; terminal discs slightly expanded; subarticular tubercles small, round; supernumerary tubercles absent.

Skin on dorsum of body, limbs, flanks, and venter smooth; anal opening directed posteroventrally at one-fourth upper level of thighs; anal sheath short; tongue elongately elliptical, widest posteriorly, free posteriorly for about two thirds of its length.

Color in preservative. Dorsum of body gray with dark brown marks consisting of “X”-shaped mark in scapular region, and dark dorsolateral stripe extending from anal region to scapular region. White oblique lateral stripe, diffuse behind the eye; dorsum of snout uniform gray; flanks with black band extending from tip of snout to groin; upper lip white; dorsal surfaces of forearms gray with pale spots; anterior surfaces of upper arm tan with brown longitudinal stripe; dorsal surfaces of hind limbs gray with two white stripes on thighs, one longitudinal on anterior surface and other transverse proximally and longitudinal distally; two or three transverse bars brown on thigh; interrupted brown stripe on anterior surface of thigh; posterior surface of thigh brown with small white spots; dorsal surfaces of fingers and toes with transverse brown bars; white scutes on tips of digits; throat, chest, groin, and ventral surfaces of limbs white; palmar and plantar surfaces gray.

Measurements of holotype (mm): SVL 15.6, tibia length 7.1, foot length 6.4, head length 5.7, head width 5.1, eye diameter 2.2, eye-nostril distance 1.5, tympanum diameter 0.7.

Variation.—No noteworthy geographic variation was noted in the specimens examined. Dorsal patterns vary from an almost uniform brown dorsum to irregularly distributed spots and a well-defined “X”-shaped mark (Fig. 2C). Some specimens have a narrow middorsal black stripe. Also, in some specimens the white ventrolateral stripe is barely visible. Some individuals have small, scattered marks on the throat, others have two marks in the mental region (Fig. 3A). A juvenile (9.4 mm SVL) has stippling regularly distributed on throat. Other juveniles have two dark marks in the mental region.

Color in life: The dorsum pale olive-tan with dark brown markings forming an "X" in the scapular region; canthus and flanks dark brown to black; upper lip creamy yellow with pinkish tones; oblique lateral stripe creamy yellow or white with pale pink suffusion anteriorly; arms pale orange; dorsal surfaces of legs pale brown with faint, narrow, darker brown bars; posterior surfaces of thighs with yellowish orange bar just below level of vent; orange, diffuse marks in axilla and shank, discrete orange mark in groin; venter cream; iris gold; scutes on fingers white (L. A. Coloma, field notes, 31 December 1989, 5 April 1990).

Tadpoles.—The following description is based on an individual in Stage 25 (Fig. 6F) from a series of 15 back-riding tadpoles (KU 142833).

Total length 7.6 mm; body moderately depressed, about two thirds as deep as wide; about equal width along the body; snout bluntly rounded in dorsal and lateral profiles; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.4 mm; spiracle sinistral; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; ventral fin slightly higher than dorsal fin; tail length 63% total length, tail height 15% total length, dorsal fin height 0.2 mm at midlength of tail, not extending onto body; ventral fin height 0.3 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform; oral disc width 0.7 mm; tooth row formula 2/3; second upper row narrowly interrupted medially; first and second lower rows subequal in length to upper rows; third lower row interrupted, weakly developed, shorter than other rows; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by one row of marginal papillae.

Dorsum and sides of body dark brown; abdomen transparent cream with scattered pigment anteriorly; caudal musculature cream with dark brown flecks proximally; fins translucent with scattered dark brown flecks on proximal part of dorsal fin.

Calls.—Unknown.

Distribution and ecology.—*Colostethus machalilla* occurs in the Pacific lowlands of Ecuador (Provincias El Oro, Los Ríos, Bolívar, Guayas, and Manabí) at elevations of 10–515 m (Fig. 13).

The distribution lies mainly within the Tropical Desertic Thicket, Tropical Thorny Scrub, and Very Dry Tropical Forest. Annual mean precipitation is 125–1000 mm, and annual mean temperature is 24–26°C.

Specimens have been found in great densities at the shore of the Río Ayampe.

Colostethus machalilla occurs in sympatry with *C. awa* at the Montañas de Chindul at the Coastal Cordillera, and with *C. infraguttatus* at about 600 m in the Río Chimbo Drainage, and in the Coastal Cordillera.

Colostethus machalilla releases tadpoles in small pools on the shores of rivers. Males transport the larvae.

Etymology.—The specific name is a noun in apposition and refers to the Parque Nacional Machalilla where the species occurs. This park includes relictual forests and is an important archeological site where native cultures, such as the Valdivia, Machalilla, Chorrera, Bahía, Guangala, and Manteña occurred successively during the past 5000 years.

Colostethus maquipucuna new species

Holotype.—KU 202882, an adult female, from 9.4 km SW of Tandayapa, 0°2' S, 78°42' W, 2390 m, Provincia Pichincha, Ecuador, obtained on 2 April 1984 by David M. Hillis.

Paratypes.—KU 202880–81, adult female and male, respectively, collected with the holotype.

Diagnosis.—(1) SVL, male, 21.2 mm; females, 23.5–24.1 mm (\bar{x} = 23.8; n = 2); (2) disc on Finger III expanded; (3) Finger I usually shorter than Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorso-lateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) discrete markings absent on gular-chest region, two small black spots ventrally at base of arm; (13) abdomen white in females, abdomen blackish with light spots in male; (14) Finger III not swollen in males; (15) testes white.

Colostethus maquipucuna is compared with those species that have a complete white oblique lateral stripe, lack two discrete marks on the gular-chest region, have a reticulate or spotted venter, and possess two small spots at base of arms ventrally (*C.*

delatorreae). *Colostethus maquipucuna* is distinguished from *C. delatorreae* by its larger size, a wider oblique lateral stripe and by lacking scattered dark marks on dorsal surfaces of thighs.

Description of holotype.—Adult female, 23.5 mm in SVL; body moderately robust; head longer than wide; head length 37.8% SVL; head width 34% SVL; snout bluntly rounded in dorsal view, and in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance half length of eye; supratympanic fold diffuse; diameter of tympanum 53% length of eye. Forelimbs moderately long; Finger I slightly shorter than second; fingers unwebbed, lacking lateral fringes; terminal discs expanded; subarticular tubercles small, low, round; palmar tubercle moderately large, rounded, barely elevated; thenar tubercle moderately small, elliptical. Hind limbs moderately robust; tibia length 53.2% SVL; foot length 48.9% SVL; outer tarsal fold absent; inner tarsal fold sigmoid on distal two thirds of tarsus; outer metatarsal tubercle small, oval, less than half size of elliptical inner metatarsal tubercle; toes unwebbed, lacking lateral fringes; terminal discs expanded, about twice width of digits; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum of body and limbs smooth except slightly pustular in pelvic region; skin on flanks and venter smooth; anal opening directed posteroventrally at midlevel of thighs; anal sheath moderately long; tongue narrowly triangular, free posteriorly for about two thirds of its length.

Color in preservative: Dorsum brown with dark brown marbling. Two black dorsolateral stripes extending from anterior borders of eyes to anal region; dorsum of snout uniform pale brown; black band extending entire length of flank; broad cream oblique lateral stripe from upper eyelid to groin; upper lip creamy white; narrow brown stripe along entire border of lower lip; dorsal surfaces of forearms cream with minute gray stippling; short brown stripe on anterior surface of upper arm; brown stripe on posterior surface of upper arm extending to ventral surface of forearm; dorsal surfaces of hind limbs cream with minute gray spotting, brown stripes on anterolateral and dorsal surface of thighs; brown spots in anal region and one spot on posterolateral dorsal surface of thigh; brown spots on outer surface of shank, diffuse transverse bars on dorsal surfaces

of fingers, brown spots on dorsal surfaces of toes; throat, chest, abdomen, and groin cream; small gray spot at the base of forearms; ventral surfaces of arms, tarsi, and palmar and plantar surfaces brown; tips of digits brown; brown marks on outer surface of shank.

Measurements of holotype (mm): SVL 23.5, tibia length 12.1, foot length 11.5, head length 8.9, head width 8.0, eye diameter 3.2, eye-nostril diameter 1.6, tympanum diameter 1.7.

Variation.—Structurally, the three specimens are similar; the male (KU 202881) is smaller than the females and has vocal slits and a vocal sac. The male has diffuse dark reticulations on the abdomen, blackish marks on the throat, and an oval white mark on the dorsal surface of the forearm.

Color in life: Black dorsally and laterally, with a bright yellow dorsolateral stripe; legs orange, venter yellow (W. E. Duellman, field notes, 2 April 1984).

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus maquipucuna* is known only from the type locality (Fig. 12) within the Lower Very Humid Montane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 12–18°C.

Colostethus maquipucuna has not been found sympatrically with any other dendrobatids.

Etymology.—The specific name refers to the Reserva Maquipucuna in the vicinity of the type locality that contains unique western Andean cloud forest. Maquipucuna (“tender hands”) is a Quechua name referring to the steep valleys that resemble cupped hands.

Colostethus marchesianus (Melin)

Plate 1H

Phyllobates marchesianus Melin, 1941:64.—

Syntypes: NHMG 509 from Taracua, Rio Uaupes, Estado Amazonas, Brasil.

Colostethus marchesianus—Edwards, 1971:148

Diagnosis.—(1) SVL, males 15.5–18.5, $n = 20$; females, 16.5–18.7 ($\bar{x} = 17.4$; $n = 22$); (2) disc on Finger III expanded; (3) Finger I usually longer than Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present, but not well developed; (8) toe webbing formula $12-3\frac{1}{2}II2-3III3-4IV4\frac{1}{2}-$

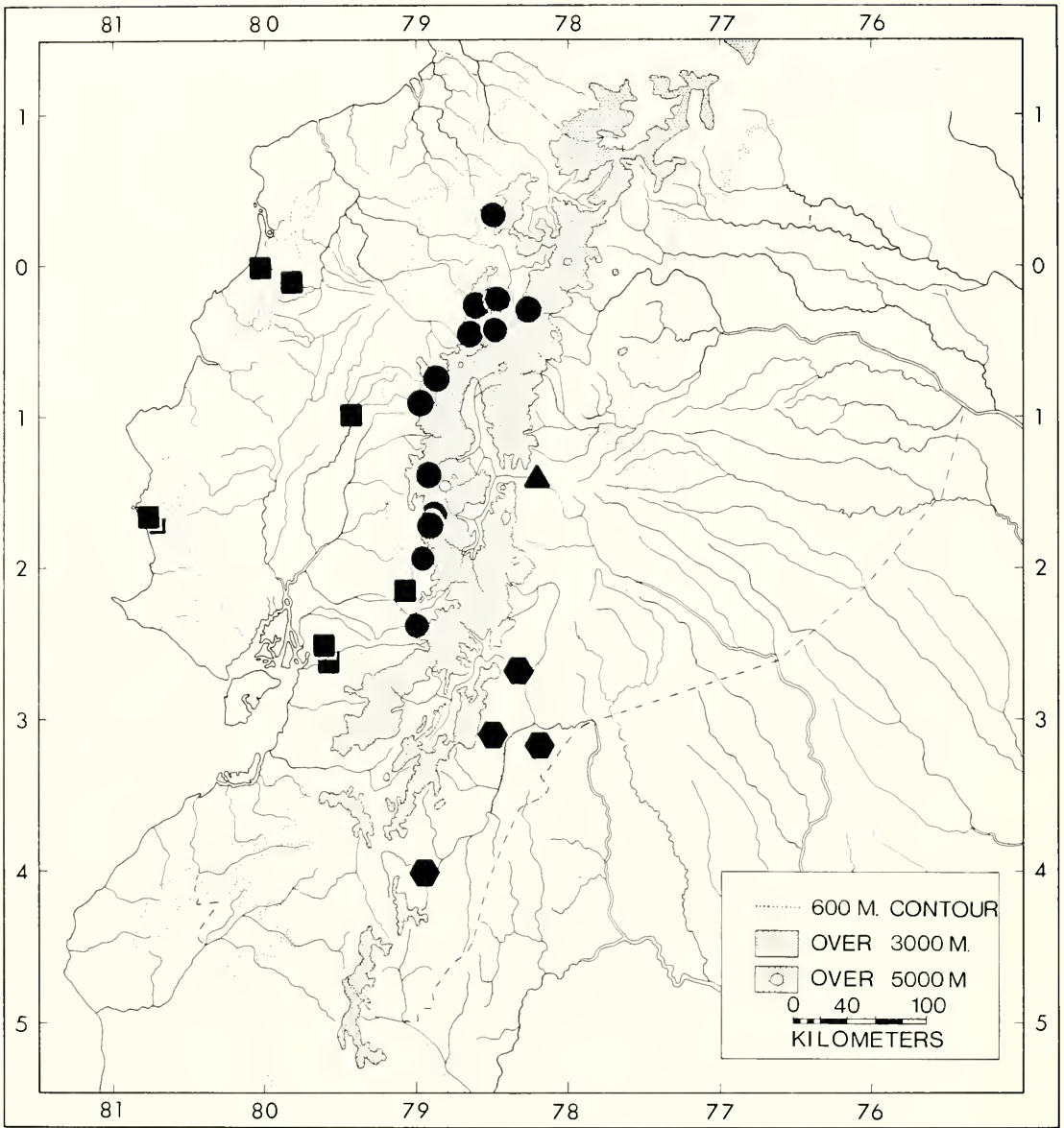


Fig. 13. Distributions of *Colostethus machalilla* (■), *C. jacobuspetersi* (●), *C. marmoreoventris* (▲), and *C. nexipus* (hexagons).

3V; (9) dorsolateral stripe present; (10) short oblique lateral stripe present or absent; (11) ventrolateral stripe present; (12) discrete markings absent on chest-gular region; (13) abdomen white in females, throat stippled with gray in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus marchesianus is compared with those species that have white dorsolateral and ventrolat-

eral stripes (*C. kingsburyi* and *C. talamancae*). It is distinguished from both by its smaller size.

Description and variation.—Edwards (1974b) provided a good redescription of the species. Additional descriptions were provided by Duellman (1978). In some of the specimens observed, however, the short oblique stripe is lacking. A recently metamorphosed juvenile (QCAZ 3356) has a SVL of 7.0 mm.

Tadpoles.—Free-swimming tadpoles in Stages 27–40 were described by Edwards (1974b) and tadpoles in Stage 30 were described by Duellman (1978).

Calls.—A male (KU 220660), SVL 16.2 mm was recorded at Méndez, 500 m, Provincia Morona Santiago, at 25°C, at approximately 11:00 h, with the microphone 2–3 m from the frog (Fig. 8). The call is a trill consisting of 22–33 notes. The shortest call of 22 notes lasted 5.32 sec and the longest lasted 8.10 sec. The frog emitted 5 calls in 5 min. Each note has a duration of 0.11 sec and intervals between notes are 0.11–0.24 sec, increasing gradually towards the end of the call. In three of the calls, intervals between the first and second notes were 0.40–0.65 sec, greater than those between the remaining notes. The fundamental frequency is at about 800–1300 Hz and the dominant frequency begins at about 2600 Hz and increases to 3800 Hz. There are two harmonics above the dominant frequency. Duellman (1978) described a call of specimens from Santa Cecilia as a soft single “peep.”

Distribution and ecology.—*Colostethus marchesianus* is known from the lowlands of the Amazon Basin and lower slopes of the eastern Andes. In Ecuador it occurs at elevations of 200–1140 m (Fig. 12). The distribution lies within Humid Tropical Forest, Very Humid Premontane Forest, and Humid Premontane Forest. The annual mean precipitation in the former two is 2000–4000 mm, and 1000–2000 mm in the later; annual mean temperature is 24–25°C in Tropical Humid Forest, 18–24°C in Humid Premontane Forest and Very Humid Premontane Forest.

Colostethus marchesianus was found breeding throughout the year at Santa Cecilia (Duellman, 1978) and at Montalvo and surrounding localities (Almendáriz, 1987). Mean ovarian complements of 13.4 were reported for *C. marchesianus* by Duellman (1978).

Specimens from Méndez were collected in a swampy area with abundant leaf litter in secondary forest. According to Duellman (1978), *Colostethus marchesianus* released tadpoles in a water-filled segment of a fallen bamboo.

Food items have been reported for *C. marchesianus* (Duellman 1978, Almendáriz, 1987). They found ants to be the most abundant prey.

Colostethus marchesianus occurs sympatrically

with *C. sauli* and *C. bocagei* at lower elevations of its range. At Mera, Provincia Pastaza it occurs with *C. kingsburyi*, and at Méndez it occurs with *C. nexipus*. The range of *C. marchesianus* overlaps the localities for *C. cevallosi* and *C. fugax* at Cabeceras del Río Bobonaza.

Comments.—Rivero and Almendáriz (1991) commented on the taxonomic status of *Colostethus marchesianus* and *C. brunneus* pointing out the fact that there are not records of the latter for Ecuador; however, they included *C. brunneus* within the Ecuadorian fauna. I choose not to include *C. brunneus* within the Ecuadorian *Colostethus* before its taxonomic status is clarified and reliable records are available. Recordings of calls of specimens from Reserva Cuzco Amazónico, Departamento Madre de Dios, Peru, reveal calls composed of two notes. These calls differ from the call of the individual from Méndez described previously. Populations currently assigned to *C. marchesianus* do not exhibit major morphological differences; however, the differences noted on the calls suggest that more than one species is involved within this nominal taxon, which requires further analysis.

Colostethus marmoreoventris Rivero

Colostethus marmoreoventris Rivero, 1991b:3–4.—
Holotype: USNM 282979, from Río Negro, 4100 ft [1225 m], Provincia Tungurahua, Ecuador.

Diagnosis.—(1) SVL, male, 21.7; (2) disc on Finger II expanded; (3) length of Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorso-lateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) two discrete markings absent on gular-chest region; (13) white spots in abdomen in male; (14) Finger III not swollen in male; (15) testes white.

Colostethus marmoreoventris is distinguished from *C. fallax*, which also lacks dorsal, oblique and ventrolateral stripes and webbing on the toes, by having a spotted venter.

Tadpoles.—Unknown.

Calls.—Unknown.

Description and variation.—Rivero’s description (1991b) is appropriate.

Distribution and ecology.—*Colostethus marmoreoventris* is only known from the type locality in the eastern slopes of the Ecuadorian Andes in Provincia Tungurahua (Fig. 13). The distribution lies within the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 18–24°C.

Colostethus marmoreoventris occurs sympatrically with *C. bocagei*, *C. kingsburyi*, and *C. pulchellus*.

Comments.—*Colostethus marmoreoventris* resembles some members of *Epipedobates* and *Dendrobates*; however, before additional material and data are gathered, it is not possible to associate the only specimen available to any of the putative monophyletic groups within “*Epipedobates*” or *Dendrobates*.

Colostethus mystax Duellman and Simmons

Colostethus mystax Duellman and Simmons, 1988:117.—Holotype: KU 147095, from the headwaters of the Río Piuntza, 1830 m (approx. 3°30' S, 78°20' W), western slope of the Cordillera del Cóndor, Provincia Morona Santiago, Ecuador.

Diagnosis.—(1) SVL, males, 19.5–21.5, $n=3$; females, 19.2–21.8 ($\bar{x}=20.6$; $n=3$); (2) disc on Finger III expanded; (3) length of Finger I = II; (4) fringe absent on Finger II, but weak keel present; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV, but weak keel present; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) discrete markings absent on chest-gular region; (13) scattered dark spots on abdomen; pronounced black stippling on throat in males; (14) Finger III not swollen in males; (15) testes brown.

Colostethus mystax is distinguishable from *C. pumilus*, which also lacks webbing on the toes and pale dorsolateral, oblique, and ventrolateral stripes, by the absence of ill-defined dorsolateral folds, and by its larger size.

Description and variation.—The original description (Duellman and Simmons 1988) is adequate, except in the following (data from original

description indicated in parenthesis): Finger I is equal to or barely shorter than Finger II (Finger I barely longer than Finger II); fringes on fingers and toes are not present, but weak keels are present (fringes on fingers and toes present); discrete markings are absent on the chest-gular region (discrete dark markings usually present on chest) as noted by Rivero and Almendáriz (1991). Males differ from females by having pronounced black stippling on the throat. The holotype is a female (not a male as originally stated by Duellman and Simmons, 1988) having a SVL of 22.8 mm.

Tadpoles.—Unknown.

Calls.—The call is a rapid series of chirps (Duellman and Simmons, 1988).

Distribution and ecology.—*Colostethus mystax* is known only from the type locality (Fig. 15). Ecological and natural history data were presented by Duellman and Simmons (1988).

Colostethus mystax occurs sympatrically with *C. exasperatus* and *C. shuar* in the Cordillera del Cóndor.

Comments.—See comments under *Colostethus pumilus*.

Colostethus nexipus Frost

Plate 3A

Colostethus nexipus Frost, 1986:214.—Holotype: BM 1983.1061, from Los Tayos, Provincia Morona Santiago, Ecuador. 3°10' S, 78°12' W.

Colostethus citreicola Rivero, 1991b:11–12.—Holotype: USNM 282687 from the immediate environs of Limón (General Plaza), 1097 m, Provincia Morona-Santiago, Ecuador. New synonymy.

Diagnosis.—(1) SVL, males, 20.0–23.9 ($n=4$); females, 18.8–23.0 ($\bar{x}=21.6$; $n=5$); (2) disc on Finger III expanded; (3) Finger I shorter than Finger II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present, not well developed; (8) toe webbing formula $11-211-1\frac{1}{2}111\frac{1}{2}-21V2-1V$; (9) dorsolateral stripe usually present; (10) oblique lateral stripe usually present extending to eye; (11) ventrolateral stripe absent; (12) discrete markings absent on chest-gular region; (13) black stippling on abdomen, males with darker throats than females; (14) Finger III not swollen in males; (15) testes white.

Colostethus nexipus is compared with those species that have a dorsolateral stripe and lack a ventrolateral stripe (*C. exasperatus* and *C. whymperi*). It is distinguished from both by having extensive webbing on the toes. In preservative, some specimens of *C. nexipus* are easily confused with *C. bocagei*, from which it can be distinguished by having Finger I shorter than Finger II. In life, *C. nexipus* differs from other Ecuadorian *Colostethus* by having pink stripes and a red eye.

Description and variation.—The original description (Frost, 1986) is appropriate. Specimens from Limón Indanza, Provincia Morona Santiago, have the dorsum mottled with dark marks and black stripes. Adult males have blacker throats than females, which have a white band on throat followed by a black band between the anterior legs. Juveniles have minute white spots on the dorsum in the sacral region and on the legs. One juvenile lacks a complete oblique lateral stripe; it has a pale (reddish-orange, in life) mark behind the eye and white spots in place of the oblique lateral stripe.

A recently metamorphosed juvenile (QCAZ 1432) has a SVL of 11.6 mm

Color in life: KU 220661, male: dorsum greenish black with small white spiculae in the anal region, orange dorsolateral stripe behind eye extending to midlateral part of body [stripe yellowish distally in a male KU (KU 220664)]; oblique lateral stripe irregular greenish or beige, extending from midflank to groin; upper lip bright green; venter white with greenish reflection; throat pale blue with greenish reflection anteriorly, palmar and plantar surfaces black; white scutes; iris reddish silver. A juvenile female (QCAZ 1433) differs in that the entire body has minute whitish spotting; the marks behind the eyes are yellowish, and white spots are in the flanks (J. J. Wiens, field notes, 24 April 1990).

Tadpoles.—Unknown.

Calls.—A male (KU 220664, SVL 21.5 mm) was recorded at Méndez, 500 m, Provincia Morona Santiago, at 11:15 h on 24 April 1990, at an air temperature of 23°C, with the microphone 1 m from the frog. Another was recorded, but not collected, at Limón, 1090 m, Provincia Morona Santiago, on 21 March 1990 at 09:30 h at an air temperature of 25°C, with the microphone about 1 m from the frog (Fig. 8). The first frog emitted 6 calls in 1 min, the second,

14 calls in 2 min. Each call consists of 20–29 notes. Duration of calls are 1.43 and 1.65 sec in the first recording and between 2.22–2.37 sec the second; intervals between calls is 8.08–9.6 sec in the first recording and 6.24–7.63 sec in the second. In both recordings duration of notes is 0.03–0.04 sec, and intervals between notes is 0.05–0.06 sec in both cases. It seems possible that there is a fundamental frequency below 2000 Hz; however background noise obscures the analysis. Two other frequencies are at about 2500 and 4700 Hz; but it is not clear which one is the dominant frequency. There is one harmonic above them.

Distribution and ecology.—In Ecuador, *Colostethus nexipus* occurs at elevations of 500–1550 m on the lower eastern slopes and foothills of the Andes (Fig. 13). The distribution lies within the Very Humid Premontane Forest and Humid Premontane Forest. Annual mean precipitation is 2000–4000 mm and 1000–2000 mm respectively; annual mean temperatures are 18–24°C in both zones.

KU 220661–63, and QCAZ 1433–34 were collected under pieces of wood close to a swampy area inside a house in the city of Limón (General Plaza Gutiérrez). KU 220664, and QCAZ 1431–32 were collected in a stream close to Méndez. KU 220664 was calling from a stone at the edge of a river bordered by second growth vegetation.

Colostethus nexipus occurs sympatrically with *C. marchesianus* at Méndez; however, microhabitat preferences differ in that *C. nexipus* was found in a stream, whereas *C. marchesianus* was found in a swampy area at the edge of a forest.

Comments.—Rivero (1991) described *Colostethus citreicola* based on specimens from the immediate environs of Limón, 1097 m, Provincia Morona Santiago, Ecuador. (Provincia Azuay that was originally indicated is an error.) I examined the paratype (USNM 282686) and do not find any character to distinguish *C. citreicola* from *C. nexipus* collected in the same locality. In the description of *C. citreicola*, it is stated that the species lacks a dorsolateral stripe; however, the paratype examined possess the stripe that is not clearly visible because the specimen is darkened; therefore, I consider *C. citreicola* (Rivero, 1991b) to be a junior synonym of *C. nexipus* (Frost, 1986).

Colostethus peculiaris Rivero

Colostethus peculiaris Rivero, 1991b:13–14.—Holotype: USNM 282664 from Pailas, a tambo between Sevilla de Oro and Méndez, on E or NE facing slope, 7200 ft (2195 m), Provincia Morona Santiago, Ecuador.

Diagnosis.—(1) SVL male, 26.5; SVL females, 29.0–29.8 (\bar{x} = 29.4; n = 2); (2) disc on Finger III expanded; (3) Finger I shorter than Finger II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold absent; (8) toes half webbed; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) two discrete markings present on chest-gular region; (13) brown marbling on abdomen and spotting on throat of both sexes; (14) Finger III not swollen in male; (15) testes color unknown (not indicated in original description).

Colostethus peculiaris is compared with those species that lack dorsal, oblique, and ventrolateral stripes and have webbing on the toes (*C. chocoensis*). It is distinguished from *C. chocoensis* by having a pair of pectoral spots.

Description and variation.—Rivero's description (1991b) is adequate.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus peculiaris* is known only from the type locality which is on the eastern slopes of the Andes in southern Ecuador (Fig. 14). The distribution lies within the Premontane Humid Forest, where annual mean precipitation is 1000–2000 mm, and annual mean temperature is 18–24°C.

Colostethus peculiaris occurs in parapatry with *C. anthracinus*. The range of *C. anthracinus* is close to the type locality of *C. peculiaris*, but they have not been collected sympatrically.

Colostethus pulchellus Jiménez de la Espada
Plate 1D

Phyllodromus pulchellum Jiménez de la Espada, 1875:lam 3.—KU 142976, an adult male from 2.5 km WNW Cuyuja, 2550 m, Provincia Napo, Ecuador, collected on 26 October 1971 by Will-

iam E. Duellman, Bruce MacBryde, and John E. Simmons, herein designated as neotype.

Phyllodromus pulchellus—Boulenger, 1882b:139.

Prostherapis pulchellus—Peracca, 1904:17.

Phyllobates taeniatus—Andersson, 1945:8 from Río Cosanga, near Archidona, 800 m, Provincia Napo, Ecuador. New synonymy.

Phyllobates riocosangae—Andersson, 1945:10. Synonymy fide Edwards, 1974.

Colostethus pulchellum—Edwards, 1971:148.

Colostethus taeniatus—Edwards, 1971:148.

Colostethus riocosangae—Edwards, 1971:148.

Colostethus taeniatus—Edwards, 1974b:1.

Colostethus pulchellus—Frost, 1985:93.

Colostethus tergogranularis—Rivero, 1991b:6–7.—Holotype: USNM 282638 from slopes S Sumaco, Provincia Napo, Ecuador. New synonymy.

Diagnosis.—(1) SVL, males 17.3–21.5, n = 44; females, 19.6–24.4, (\bar{x} = 21.4; n = 16); (2) disc on Finger III expanded; (3) Finger I shorter or about equal in length to Finger II; (4) fringe usually present on Finger II; (5) disc on Toe IV wider than diameter of toe; (6) fringe absent on Toe IV, keel present; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe sometimes present; (12) discrete markings present on chest-gular region in some populations; (13) white spots on abdomen; (14) Finger III not swollen in males; (15) testes white.

Colostethus pulchellus is compared with those species that have a complete oblique lateral stripe and have reticulations or marbling on the venter, but lack webbing among toes (*C. maquipucuna* and *C. delatorreae*). It is distinguished from *C. maquipucuna* by its smaller size and from *C. delatorreae* by lacking two small spots at the base of the arms.

Description and variation.—Edwards (1974) redescribed the species under the name of *C. taeniatus* and presented appropriate data on variation in specimens from the Papallacta-Cuyuja region (including the neotype, KU 147926). The specimens from Papallacta-Cuyuja differ from specimens (type material of *C. taeniatus* and *C. riocosangae* and specimens from the Río Azuela and south of Sumaco) of lower elevation in that the fringe on Toe IV is keel-like. Also, some specimens from Papallacta-Cuyuja have two discrete spots in chest-gular region; these

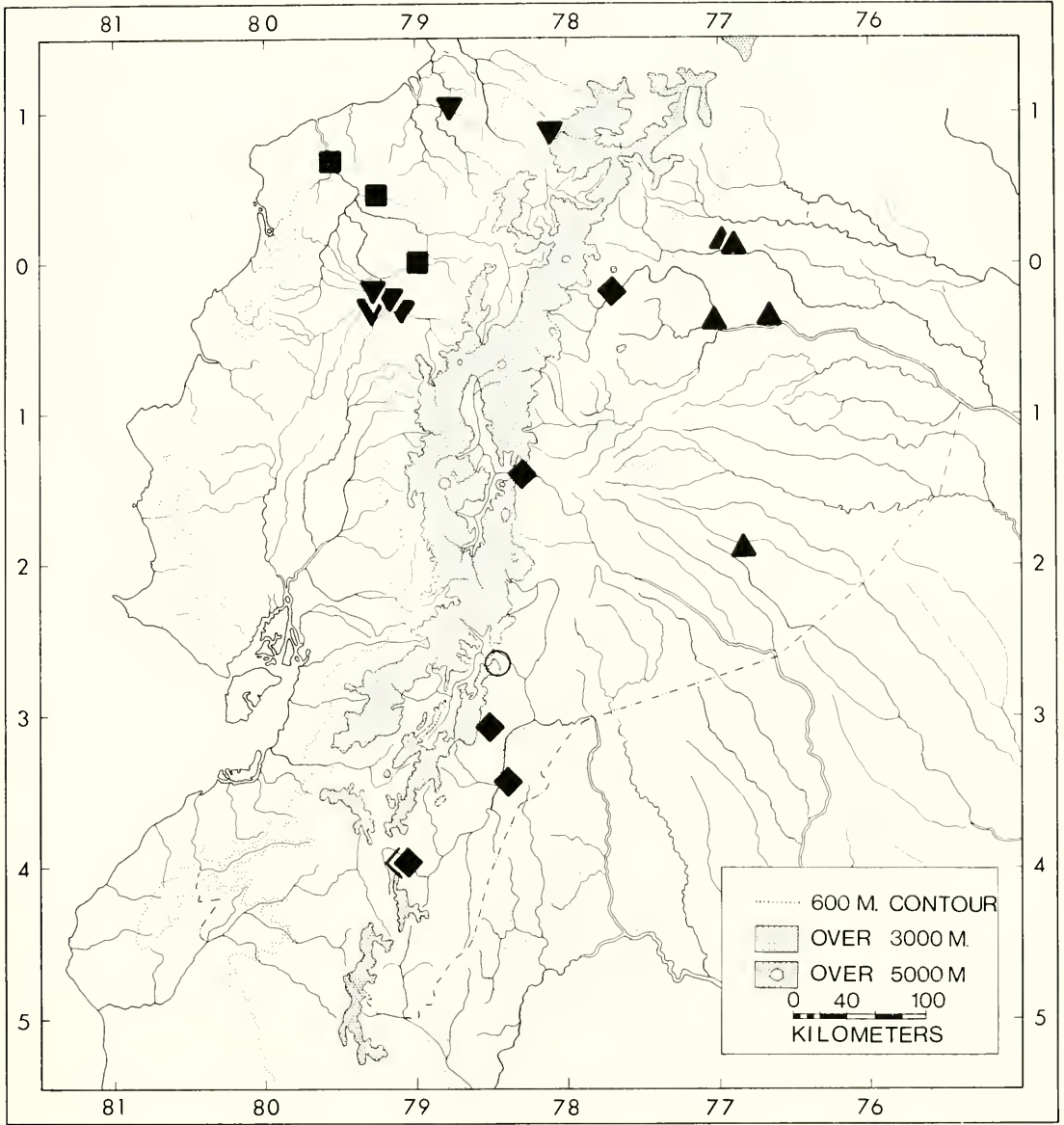


Fig. 14. Distributions of *Colostethus peculiaris* (●), *C. talamancae* (■), *C. sauli* (▲), *C. shuar* (◆), and *C. toachi* (▼).

are absent in individuals from the other populations.

Other populations assignable to this species occur in extreme northern Ecuador, in the Carchi Basin, and in headwaters of the Río Chota. These populations differ from the ones from Papallacta-Cuyuja in that a fringe is absent on Finger II, disc of Finger III is less expanded, two discrete markings on chest-gular region are replaced by scattered marks,

and the oblique lateral stripe is wider.

Specimens from the páramos to the east of Salcedo and near Baños have two discrete spots on chest-gular region. In some specimens from Tulcán, Monte Olivo, and the Río Azuela, the dorsum is gray with dark mottling; color of dorsum in other specimens are like the type color patterns illustrated by Edwards (1974b). Males have gray and white reticulations

ventrally with an interrupted white ventrolateral line, and the throat stippled with gray. Females have diffuse white spots ventrally. All specimens have a black stripe or series of marks on the edge of the lower lip.

A recently metamorphosed juvenile (RMNH 25237) is 11.4 mm in SVL.

Color in life: QCAZ 1324, from Monte Olivo, Provincia Carchi: dorsum dark brown with diffuse greenish tint; oblique lateral stripe cream with iridescent golden tint; inguinal region with greenish wash; groin, ventral surfaces of thighs and shanks yellow; throat yellowish cream; abdomen cream with greenish tint and diffuse, scattered brown marks; labial stripe cream; iris greenish yellow (L. A. Coloma, field notes, 4 June 1989). KU 117881–913 and KU 182144–63 from Tulcán, Provincia Carchi: oblique lateral stripe edged with brown or black; flanks black, spotted with yellow or not; venter pale yellowish white, spotted with black or not; throat dirty yellow; labial stripe bronze yellow; posterior surface of thighs reticulated with brown to black, spotted with orange-yellow; iris bronze above, brown below or greenish with black flecking (J. D. Lynch, field notes, 22, 24 February 1968 and 26 May 1977).

Measurements of the neotype (mm): SVL 20.4, tibia length 9.2, foot length 8.2, head length 6.9, head width 6.6, eye diameter 2.7, eye-nostril distance 1.9, tympanum diameter 1.7.

Tadpoles.—Edwards (1974b) described free-swimming tadpoles (Stages 28 and 37) and back-riding (Stages 25 and 26) tadpoles from the Papallacta region. The mouth of a back-riding tadpole (KU 127080) was illustrated.

The following description is based on an individual in Stage 25 (Fig. 6E) from a series of four back-riding tadpoles (KU 118113) from Tulcán. Total length 10.3 mm; body moderately depressed, about two thirds as deep as wide; snout rounded in dorsal view and in profile; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.3 mm; spiracle sinistral; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin low on anterior one fourth of tail, tail length 62% total length, tail height 15% total length, dorsal fin height 0.5 mm at midlength of tail fin, not extending onto body; ventral fin height 0.3 mm at midlength of tail; tip of fin rounded. Oral disc

directed ventrally, not umbelliform, 0.8 mm wide; denticles and beaks poorly developed; one upper and two lower rows of denticles barely visible; beaks slender, weakly keratinized; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; lateral folds present; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by one row of marginal papillae.

Dorsum and sides of body densely pigmented with dark brown; venter pigmented only in abdominal region; caudal musculature cream with dark brown flecks along entire length; fins translucent with scattered dark brown flecks on dorsal fin.

Calls.—One recording (Fig. 8) was obtained at Monte Olivo, 2450 m, Provincia Carchi, on 4 June 1989, 11:00–12:00 h, air temperature increasing from 24–30°C. No specimen is associated directly with the recording. Males were calling from under grass, thus making them difficult to locate; however, males were collected after removing the grass. The call is a buzz emitted 72 times during 4 min with intervals of 1.95–2.53 sec between calls, which are 0.37–0.63 sec long and consist of 4–6 notes having durations of 0.05 sec at intervals of 0.06–0.12 sec. The fundamental frequency is at about 1000–1100 Hz, and the dominant frequency is about 2700–3000 Hz with two harmonics above the dominant frequency.

Distribution and ecology.—*Colostethus pulchellus* occurs at elevations of 1590–2970 m in the inter-Andean páramos of northern Ecuador and on the eastern slopes of the Andes from northern Ecuador south to the headwaters of the Río Pastaza (Fig. 15). In northern Ecuador, it is distributed in the Low Montane Dry Forest and Low Humid Montane Forest. Annual mean precipitation is 500–1000 mm, and 1000–2000 mm respectively; annual mean temperature is 12–18°C in both zones. At one locality, Monte Olivo, mean annual temperature is 13°C, and mean annual precipitation is 750 mm (IGM, no date). The populations from the eastern slopes are distributed in Low Humid Montane Forest.

Specimens from Monte Olivo were found in a ditch about 50 cm wide (with almost no running water) in a swampy pasture near human habitations. Dead and living tadpoles were found in a swamp with little water. Other specimens have been found in seepages and marshy areas of the Río Carchi

Drainage. They have been found in abundance in a sewage ditch. Males call in and under grass. Others were found in moist situations on hillocks of grass with interconnected puddles on a hillside (J. D. Lynch, field notes, 22, 24 February 1968 and 26 May 1977). Males (KU 117920–21, 117881–82, and either 182149 or 182150) were carrying tadpoles.

Colostethus pulchellus occurs sympatrically with *C. bocagei*, *C. kingsburyi*, *C. fuliginosus*, and *C. shuar* at lower elevations of its range; however, at higher elevations and in the inter-Andean páramos, it has not been found with any other *Colostethus*.

Comments.—Jiménez de la Espada published the name *Phyllodromus pulchellum* in association with illustrations (1875, plate 3; figs. 3, 3a–c), but with no written description. Neither type specimens nor a type locality were mentioned. Boulenger (1882b) described the genus *Phyllodromus* and the species *P. pulchellus* based on material from “Intag” on the western slopes of the Ecuadorian Andes; he later (1898) assigned specimens from Cachabí, Provincia Esmeraldas, to this taxon. Peracca (1904) synonymized *Phyllodromus* with *Prostherapis* Cope, and assigned specimens from Valle Santiago, Valle del Río Peripa, Cuenca, Cañar, and Pun to *Prostherapis pulchellus*. Savage (1968) synonymized *Prostherapis* with *Colostethus*. Frost (1985) cited a personal communication by Stephen R. Edwards that *C. pulchellus* probably is an older name of *C. taeniatus* (Andersson, 1945). *Colostethus taeniatus*, as well as *C. shuar*, correspond to the original figure; they occur sympatrically in the Quijos Drainage on the eastern slopes of the Andes of Ecuador, a region visited by Jiménez de la Espada. They differ in size; *C. shuar* is larger than *C. taeniatus*. It is inferred from the figure that the species illustrated is not a large frog; thus, I associate the name *C. pulchellus* with *C. taeniatus*, which becomes a junior synonym of the former.

Rivero (1991b) described *Colostethus tergo-granularis* based on specimens from south of Volcán Sumaco. I compared these specimens with type specimens of *C. taeniatus* and *C. riosangae* (both synonyms of *C. pulchellus*) that were described from Río Cosanga in the vicinity of Volcán Sumaco, and I do not find differences to justify the recognition of *C. tergo-granularis*. Rivero (1991b) emphasized the presence of a granular and tubercular dorsum in *C. tergo-granularis*; however, this charac-

ter is present and varies intraspecifically in all populations herein assigned to *C. pulchellus*. Therefore, I consider *C. tergo-granularis* (Rivero, 1991b) to be a junior synonym of *C. pulchellum* (Jiménez de la Espada, 1875).

Some characters differing between the populations seem to be fixed, but until a detailed analysis is undertaken, it is not possible to determine if these few characters show clinal variation. I suspect that *C. pulchellus*, as presently recognized, is a complex of species; in particular the populations from the Carchi Basin may not be conspecific with *C. pulchellus*. (See variation section.)

Colostethus pumilus Rivero

Colostethus pumilus Rivero, 1991b: 10–11.—Holotype: USNM 282816, from 3 km W (by road) of San Vicente, slightly SW Limón, and ca. 35 km E (by road) of Gualaceo. 9800 ft (2987 m), Provincia Azuay, Ecuador.

Diagnosis.—(1) SVL, male 16.8; females, 12.4–18.1 (\bar{x} = 16.6; n = 4); (2) disc on Finger III not expanded; (3) Finger I < Finger II; (4) fringe absent on Finger II, but weak keel present; (5) disc on Toe IV not expanded; (6) fringe absent on Toe IV, but weak keel present; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe absent; (11) ventrolateral stripe usually absent; (12) two discrete marks absent on gular-chest region; (13) white venter in female; (14) Finger III not swollen in males; (15) testes color unknown (not examined).

Colostethus pumilus is compared with *C. mystax* that lacks a complete oblique lateral stripe and webbing on the toes. It is distinguished from *C. mystax* by having Finger I shorter than Finger II, and less expanded, smaller finger discs.

Description and variation.—Rivero’s description (1991b) is adequate.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus pumilus* is known only from the type locality in the Cordillera Oriental (Central or Real) in southern Ecuador (Fig. 15). The locality is in a transition zone between Very Humid Montane Forest and Lower Humid Montane Forest. Annual mean precipitation is 1000–

2000 mm in both life zones; annual mean temperature is 7–12°C in Very Humid Montane Forest, and 12–18°C in Lower Humid Montane Forest.

Comments.—*Colostethus pumilus* differs only slightly from *C. mystax*. The recognition of both nominal taxa draws attention to the differences among them; however, the differences in size, the expansion of the digits, and relative lengths of Fingers I and II may represent extremes of a continuous altitudinal variation within a single species.

Colostethus sauli Edwards

Plate 1A

Colostethus sauli Edwards, 1974b:10.—Holotype: KU 122217, from Santa Cecilia, 340 m, Provincia Sucumbíos, Ecuador.

Diagnosis.—(1) SVL, males, 19.5–22.8 ($n=9$); females, 21.9–25.2 ($\bar{x}=24.0$; $n=8$); (2) disc on Finger III expanded; (3) Finger I = II; (4) fringe present on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV; (7) outer tarsal fold present; (8) toe webbing formula $12-2\frac{1}{2}III(1\frac{1}{2})2-3III2\frac{1}{2}(3)-4IV(4)4\frac{1}{2}-3V$; (9) dorsolateral stripe absent; (10) oblique lateral stripe present; (11) ventrolateral stripe absent; (12) discrete markings absent on gular-chest region; (13) venter white in females, gray in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus sauli is compared with those species having an immaculate white venter and a complete oblique lateral stripe, and lacking discrete marks on the gular-chest region (*C. breviquartus*, *C. cevallosi*, and *C. machalilla*). It is distinguished from all of them by having basal webbing on the toes.

Description and variation.—The original description (Edwards, 1974b) is appropriate, except that Fingers I and II are about equal in length, whereas Edwards reported Finger I longer than Finger II; the oblique tarsal fold extends to the margin of toe and is continuous with a lateral fringe (oblique tarsal fold not extending from the inner metatarsal tubercle according to Edwards, 1974b). The dorsum was described as having distinct black blotches (Edwards, 1974b) or irregular, but usually transverse, black markings (Duellman, 1978). Usually the dorsum pattern consists of an interorbital square mark, a “V”-shaped mark on the anterior

body, and a transverse mark on the posterior part of the body; also a black dorsolateral stripe extends from the anal region to the scapular region. A narrow middorsal gray line occurs in one specimen. A single specimen from the southernmost locality NE Montalvo, in Locación Petrolera Garza 1, Provincia Pastaza, has slightly less webbing than topotypic material.

Tadpoles.—Edwards (1974b) described free-swimming tadpoles of Stages 27–36. Duellman (1978) described tadpoles in Stage 36.

Calls.—Duellman (1978) described the call as a series of two or three quickly repeated peeps.

Distribution and ecology.—*Colostethus sauli* is known from elevations of 250–340 m in the Tropical Humid Forest of Amazonian Ecuador (Fig. 14). The distribution lies within the Tropical Humid Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 24–25°C.

A mean ovarian complement of 11.3 was reported for *C. sauli* by Duellman (1978). *Colostethus sauli* tadpoles were found amidst detritus in shallow streams issuing from springs (Duellman, 1978). Duellman (1978) reported ants to be the most abundant prey for this species.

Colostethus sauli occurs sympatrically with *C. marchesianus* and *C. bocagei* at some localities.

Colostethus shuar Duellman and Simmons

Plate 1F

Colostethus shuar Duellman and Simmons, 1988:120.—Holotype: KU 147091, from the headwaters of the Río Piuntza, 1830 m (approx. 3°30' S, 78°20' W), western slope of the Cordillera del Cóndor, Provincia Morona Santiago, Ecuador.

Diagnosis.—A species characterized by (1) SVL, males, 24.2–30.8, $n=12$; females, 25.0–31.5 ($\bar{x}=27.4$; $n=10$); (2) disc on Finger III expanded; (3) Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe present on Toe IV, sometimes only keel present; (7) outer tarsal fold absent; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) discrete markings present on chest-gular region; (13) abdomen marbled or spotted in both

sexes; uniform gray throat in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus shuar is compared with those species having a complete oblique lateral stripe and discrete marks on gular-chest region, but lacking toe webbing (*C. pulchellus* and *C. vertebralis*). It is distinguished from *C. pulchellus* and *C. vertebralis* by its larger size.

Description and variation.—Duellman and Simmons' description (1988) is adequate; except in the following (data from original description indicated in parenthesis): the paratype is a male (female); fringe is absent on Finger II (fringe present on Finger II). Topotypic specimens have a keel on Toe IV and the abdomen has some black stippling.

Other specimens from other localities differ in having better-developed toe fringes. Also males and females have conspicuous spotted or reticulated patterns in abdomen, but the pattern usually is less conspicuous in females than in males.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus shuar* occurs at elevations between 1272–2370 m on the eastern slopes of the Ecuadorian Andes in Provincias Napo, Tungurahua, Morona Santiago, and Zamora Chinchipe (Fig. 14). The distribution mainly lies within the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm and annual mean temperature is 18–24°C. Ecological and natural history data for the type specimens and type locality were presented by Duellman and Simmons (1988).

In northeastern Ecuador *Colostethus shuar* occurs in sympatry with *C. bocagei*, *C. fuliginosus*, *C. kingsburyi*, *C. pulchellus*, and *Minyobates abditus* near Volcán Reventador. In southeastern Ecuador, the species occurs with *C. bocagei*, *C. kingsburyi*, and *C. pulchellus* at the Pastaza trench, and further south with *C. exasperatus*, *C. mystax*, and *C. peculiaris*.

Colostethus talamancae (Cope)

Plate 3E

Dendrobates talamancae Cope, 1875:102.—Holotype: ANSP (lost fide Dunn, 1931) from Provincia

Limón, Puerto Viejo (Old Harbour), 10 m, Costa Rica.

Hylaplesia talamancae—Brocchi, 1882:88.

Phyllobates talamancae—Barbour and Dunn, 1921:159.

Colostethus talamancae—Savage, 1968:758.

Diagnosis.—(1) SVL, male, 20.4; females, 23.8–24.1 (\bar{x} = 23.9; n = 2); (2) disc on Finger III expanded; (3) Finger I > Finger II; (4) fringe present on Finger II; (5) disc on Toe IV wider than diameter of toe; (6) fringe present on Toe IV; (7) outer tarsal fold present; (8) toe webbing formula I2—3½II2—3III3—4IV4½—3V; (9) dorsolateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe present; (12) discrete markings absent on chest-gular region; (13) abdomen white in females, throat and chest black in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus talamancae is compared with *C. kingsburyi* and *C. marchesianus* that have dorsolateral and ventrolateral stripes. It is distinguished from *C. marchesianus* by having larger size and from *C. kingsburyi* by having a fringe on Toe IV.

Description and variation.—Ecuadorian specimens agree with the description of *C. talamancae* provided by Savage (1968), except that they have basal webbing between Toes II, III and IV; also, one specimen (MHNG 18787) has a poorly defined black band bordering the medial edge of the pale dorsolateral line, and a narrow, diffuse, black mid-dorsal line.

Tadpoles.—Savage (1968) presented data on tadpoles in Stages 25–28.

Calls.—Zimmermann (1991) presented data on calls.

Distribution and ecology.—*Colostethus talamancae* ranges through the lowlands of the western side of the Andes from Costa Rica to northern Ecuador. In Ecuador, it occurs at elevations of 200–800 m (Fig. 14). The distribution lies within the Humid Tropical Forest and the Very Humid Premontane Forest. The annual mean precipitation is 2000–4000 mm in both zones, and the annual mean temperatures are 24–25°C and 18–24°C, respectively.

In Ecuador, *Colostethus talamancae* occurs within the range of *Colostethus awa*, *Dendrobates histrionicus* and *Epipedobates boulengeri*.

Colostethus toachi new species

Plate 3C

Holotype.—QCAZ 1437, a male, from Finca Gloria, 15 km NW Alluriquín (5 km NW of La Florida), 0°15' S, 79°01' W, 950 m, Provincia Pichincha, Ecuador, collected on 3 July 1989 by Luis Eduardo López and Luis A. Coloma.

Paratypes.—RMNH 25248–50, QCAZ 1438, from the type locality; KU 109333 from Rancho Brahman, 10 km NW Santo Domingo de los Colorados, 400 m, Provincia Pichincha; KU 202891 from Tinalandia, 15.5 km SE Santo Domingo de los Colorados, 700 m, Provincia Pichincha; CAS 10590–96 from Hacienda Espinosa, 9 km W Santo Domingo de los Colorados on road to Chone, Provincia Pichincha; UMMZ 132933 (2 specimens) from Hacienda Delta, 8 km SE Santo Domingo de los Colorados, Provincia Pichincha.

Diagnosis.—(1) SVL, males, 18.1–23.1, $n = 6$; females, 24.6–28.2 ($\bar{x} = 26.2$; $n = 3$); (2) disc on Finger III expanded; (3) Finger I > Finger II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV, but toe slightly keeled; (7) outer tarsal fold weak; (8) basal webbing present, toe webbing formula I2—3½II3—4III4—3IV4½—3V; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe present; (12) two discrete markings absent on gular-chest region; (13) venter white in females, throat gray in males; (14) Finger III not swollen in males; (15) testes brown.

Colostethus toachi differs from *C. lehmanni* and *C. anthracinus*, which have a complete oblique lateral stripe and gray ventral suffusions in males, in lacking marbling or spots on the abdomen and by having brown testes. *Colostethus toachi* differs from *C. lehmanni* by lacking stripes on anterodorsal surfaces of thighs and from *C. anthracinus* by having more expanded discs on the fingers and no marks on the dorsum. *Colostethus toachi* differs from *C. fugax* and *C. machalilla* by males lacking Finger III swollen.

Description of holotype.—Male, 18.1 mm in SVL; body slender; head slightly wider than long; head length 33.1% SVL; head width 35.4% SVL; snout bluntly rounded in dorsal view, protruding beyond lower jaw in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-

nostril distance more than half the diameter of eye; supratympanic fold weak, diffuse, obscuring posterodorsal part of tympanum; diameter of tympanum 44.4% diameter of eye. Forelimbs moderately long; first finger longer than second; fingers unwebbed, lacking lateral fringes; Finger III not swollen; terminal discs expanded; subarticular tubercles large, oval; palmar tubercle large, rounded; thenar tubercle moderately elliptical; nuptial excrescences absent. Hind limbs moderately slender; tibia length 50.3% SVL; outer tarsal fold present, not well developed; inner tarsal fold sigmoid on distal two thirds of tarsus, not connected with the inner metatarsal tubercle; outer metatarsal tubercle elliptical, about half size of elliptical inner metatarsal tubercle; toes basally webbed lacking lateral fringes, slightly keeled; terminal discs expanded, about twice width of digits; subarticular tubercles small, round; supernumerary tubercles absent.

Skin of dorsum with scattered, low granules in pelvic region; flanks and venter smooth; anal opening directed posteroventrally at upper level of thighs; anal sheath short; tongue elongately elliptical, indented posteriorly; free posteriorly for about two thirds of its length. Vocal slits and vocal sac not developed.

Color in preservative: Dorsum gray with pale snout; dark mark between eyes; small “V”-shaped mark in scapular region, scattered dark spots in pelvic region. Dark brown dorsolateral stripe extending from behind the eye to anal region, diffuse behind the eye; flanks with dark brown band, stippled with minute white spots posteriorly; oblique lateral stripe white, shaded with brown from behind eye to shoulder; tympanic region white with minute brown stippling; upper lip pale brown with white spots; ventrolateral stripe white, extending below dark band along entire length of body, straight anteriorly, sinuous posteriorly. Dorsal surfaces of forearm brown with small diffuse white spots; anterior and posterior surfaces of upper arm lacking stripes replaced by gray shading; dorsum of fingers dark brown with white transverse marks; dorsal surfaces of hind limbs pale brown with scattered diffuse dark brown spots; dark brown longitudinal stripe on dorsal surface of thigh bordering a posterior diffuse white band; anterior thigh lacking stripe; dorsum of toes dark brown with white transverse marks. Throat, chest, and abdomen white; ventral surfaces of upper

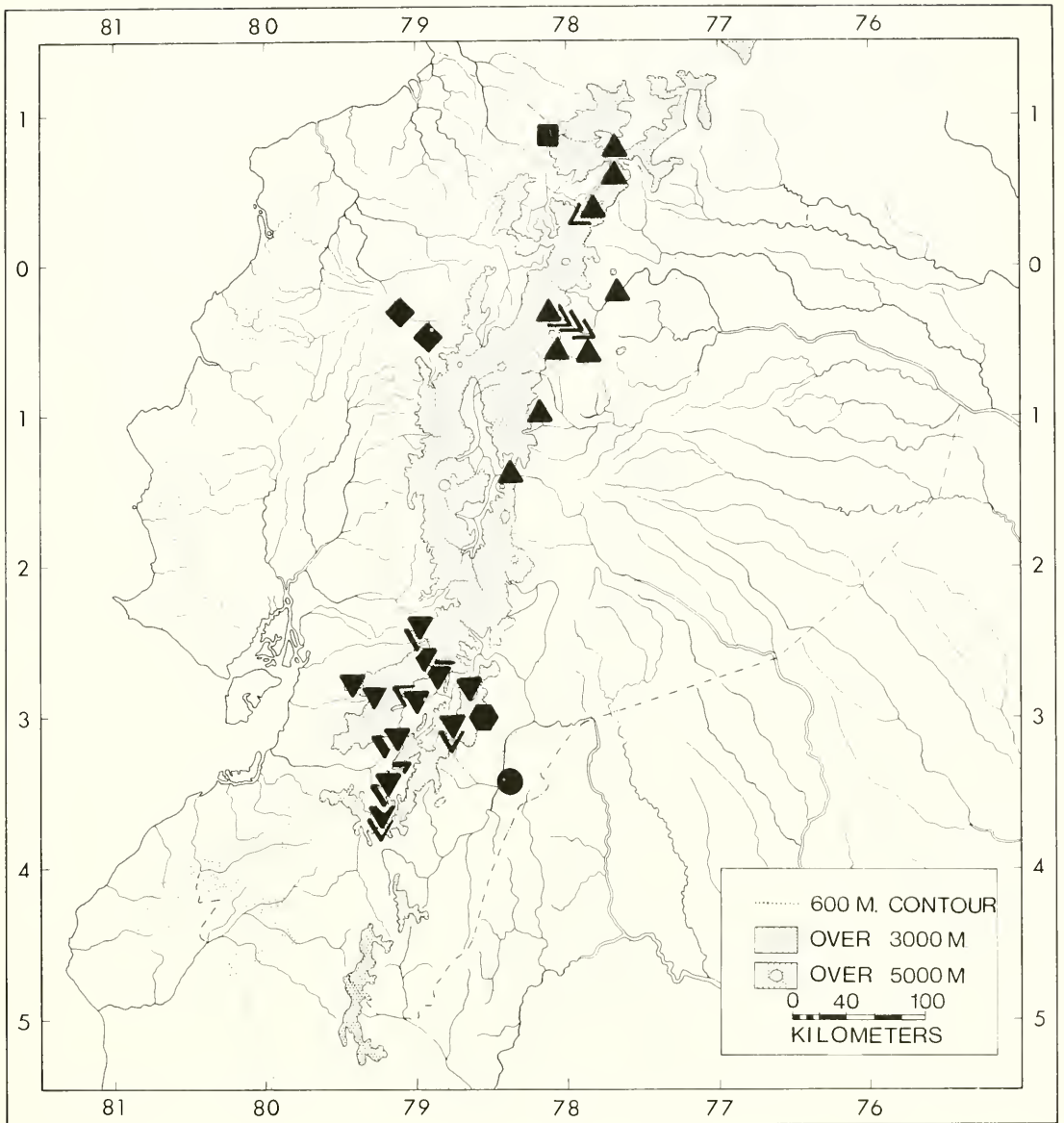


Fig. 15. Distributions of *Colostethus mystax* (●), *C. pulchellus* (▲), *C. pumilus* (hexagon), *C. delatorrae* (■), *C. vertebralis* (▼), and *C. whymeri* (◆).

arm and hind limbs white, except gray on lower arm, palmar and plantar surfaces.

Measurements of holotype (mm): SVL 18.1, tibia length 9.1, head length 6.0, head width 6.4, eye diameter 2.7, eye-nostril distance 1.9, tympanum diameter 1.2.

Variation.—Male (RMNH 25248) has a gray throat in contrast to females and the holotype (sub-

adult male) that have immaculate white throats. Color patterns in other specimens are like the holotype except some specimens that have fewer white stipples on the posterior part of the flank. Some specimens lack webbing on the toes.

A recently metamorphosed juvenile (CAS 10591) has a SVL of 9.5 mm and basal webbing. The dorsum is uniform brown and the throat is stippled with black.

Color in life: KU 202891—Venter white; thighs orange (W. E. Duellman, field notes, 20 March 1984). KU 109333—dorsum brown; tip of snout, canthal stripe, and lateral stripe dark gray; legs tan with dark transverse bars dorsally; venter except legs, white; iris pale bronze reticulated with black (W. E. Duellman, field notes, 31 March 1967). KU 182196—brown above with black-edged cream stripe; canthus rostralis bronze-cream; iris copper with brown horizontal streak; throat flesh-colored; venter off white; undersides of legs with orange cast (J. D. Lynch, field notes, 29 May 1977).

Tadpoles.—The following description is based on an individual in Stage 25 (Fig. 6) from a series of 16 back-riding tadpoles (RMNH 25248).

Total length 10.6 mm; body moderately depressed, about two thirds as deep as wide; snout rounded in dorsal view and in profile; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.56 mm; spiracle sinistral; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin low on anterior one fourth of tail, tail length 65% total length; tail height 15% total length, dorsal fin height 0.34 mm at midlength of tail, slightly extending onto body; ventral fin height 0.3 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform: 1.3 mm wide; denticles and beaks well developed; tooth row formula 2/3; second upper row narrowly interrupted medially; beaks slender, keratinized; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; lateral folds present; median part of upper lip bare; papillae at proximal margin of upper lip; papillae at proximal margin of upper lip; posterior lip bordered by one row of low marginal papillae.

Dorsum and sides of body heavily pigmented with dark brown; venter unpigmented anteriorly, scarcely pigmented on abdomen; caudal musculature cream with dark brown flecks along entire length; fins translucent with scattered dark brown flecks on dorsal fin.

Calls.—Unknown.

Distribution and ecology.—*Colostethustoachi* is known from elevations of 200–1410 m in north-western Ecuador (Fig. 14). It occurs in the Humid Tropical Forest and the Very Humid Premontane Forest. Annual mean temperatures are 24–25°C and 18–24°C respectively; annual mean precipitation is

2000–4000 mm in both zones.

The holotype was collected amidst leaf litter close to a water tank located in a creek surrounded by natural vegetation. Most of the natural vegetation in adjacent areas had been cut and replaced by pastures. Other individuals were collected on the forest floor by day and under a log above a waterfall in a creek (W. E. Duellman, field notes, 31 March 1967 and 20 March 1984; J. D. Lynch, field notes, 29 May 1977). Male RMNH 25248, was carrying 16 tadpoles (RMNH 25248).

Colostethus toachi occurs sympatrically with *C. awa*, *C. choocoensis*, and *Epipedobates spinosai* at 5 km NW La Florida in the type locality.

Etymology.—The specific name refers to Toachi, a native name of the basin and river system where this species occurs. This region possess the greatest diversity in the world of several groups of anurans; unfortunately only few remnants of forest remain and these are not effectively protected. The Toachi River Basin requires enhanced conservation efforts.

Colostethus vertebralis (Boulenger)

Plate 2A

Phyllodromus vertebralis Boulenger, 1899:456.—

Syntypes: Several specimens from Cañar, 2554 m, Provincia Cañar, Ecuador.

Prostherapis vertebralis—Peracca, 1904:17.

Phyllobates vertebralis—Barbour and Noble, 1920:401.

Colostethus vertebralis—Edwards, 1971:149.

Diagnosis.—(1)SVL, males, 14.1–17.5, $n=21$; females, 17.0–20.2 ($\bar{x}=18.5$; $n=20$); (2) disc on Finger III not expanded; (3) Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV not expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold present, poorly developed; (8) toe webbing absent; (9) dorsolateral stripe absent; (10) oblique lateral stripe present, extending to eye; (11) ventrolateral stripe absent; (12) discrete markings usually present on chest; (13) dark stippling on abdomen in females, darker in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus vertebralis is compared with those species that have a complete oblique lateral stripe and two discrete marks on gular-chest region, and lack toe webbing (*C. shuar* and *C. pulchellus*). *Colostethus vertebralis* is distinguished from *C.*

shuar by its smaller size and from *C. pulchellus* by having a cream middorsal stripe.

Description and variation.—Edwards' (1971) redescription of this species is appropriate. A recently metamorphosed juvenile is 9.4 mm in SVL. Juveniles have black pigment concentrated on the chest-gular region where barely discernible spots are present.

Tadpoles.—The following description is based on an individual in Stage 25 (Fig. 6) from a series of two back-riding tadpoles (QCAZ 1447). Total length 11.7 mm; body moderately depressed, about two thirds as deep as wide, widest at about three fourths of body; snout rounded in dorsal view and in lateral profile; nostrils about midway between eyes and tip of snout; eyes directed dorsolaterally, diameter 0.5 mm; spiracle sinistral, no opening visible; vent tube short, conical, dextral to ventral fin. Caudal musculature robust, gradually tapering to near tip of tail; dorsal fin low on anterior one fourth of tail, fins subequal in height; tail length 62% total length, tail height 16% total length, dorsal fin height 0.5 mm at midlength of tail, not extending onto body; ventral fin height 0.5 mm at midlength of tail; tip of fin rounded. Oral disc directed ventrally, not umbelliform; 1.3 mm wide; tooth row formula 2/3; second upper row narrowly interrupted medially; first and second lower rows subequal in length to upper rows; third lower row barely visible, shorter than other rows; beaks slender, serrate; upper beak broadly arch-shaped with long lateral processes; lower beak "V"-shaped; median part of upper lip bare; papillae at proximal margin of upper lip; posterior lip bordered by one row of marginal papillae.

Dorsum and sides heavily pigmented with dark brown; ventral pigmentation concentrated anteriorly with no pigment posteriorly. Caudal musculature cream with dark brown flecks along entire length; fins translucent with scattered dark brown flecks on dorsal fin.

Calls.—A male (QCAZ 1456) was recorded at Sigsig, 2480 m, Provincia Azuay, on 24 July 1989 at 16:30 h; air temperature 14°C, with the microphone 0.5 m from the frog (Fig. 8). It emitted 93 calls in 1 min. Each call consists of a single note with a duration of 0.07 sec; intervals between notes are 0.5–0.83 sec. The fundamental frequency is at about 1100–1200 Hz, and the dominant frequency begins at about 2700 Hz and increases to 3100 Hz with two harmonics above the dominant frequency.

Distribution and ecology.—*Colostethus vertebralis* occurs at elevations of 1770–3500 m in the inter-Andean valleys (at higher elevations) and on the Andean western slopes in southern Ecuador (Fig. 15). The distribution lies mainly within the Very Humid Montane Forest and Lower Humid Montane Forest. Annual mean temperatures are 7–12°C and 12–18°C, respectively; annual mean precipitation is 1000–2000 mm in both zones.

Colostethus vertebralis occupies open habitats in páramos, as well as disturbed areas, in contrast to *C. anthracinus*, which seems to be restricted to forested areas. Males transport the larvae. Read (1986) provided additional data on natural history; he reported clutches of 5–12 eggs 3mm in diameter under stones or moss.

Colostethus vertebralis occurs sympatrically with *C. anthracinus* in the cordilleras of Cordoncillo and Boliche in the Cordillera Oriental, and in the Mazán River, west of Cuenca. The distribution of *C. vertebralis* is parapatric to the range of *C. elachyhistus* near the southern extreme of Cordillera Cordoncillo and to the range of *C. infraguttatus* in the Molleturo region (Luz María).

Comments.—See comments under *Colostethus elachyhistus*.

Colostethus whymperi (Boulenger)

Prostherapis whymperi Boulenger, 1882:462.—

Holotype: BM 1947.2.14.25 male from Tanti, 607 m, Provincia Pichincha, Ecuador.

Colostethus whymperi—Edwards, 1971:149.

Diagnosis.—(1) SVL, males, 20.8–22.6, $n = 3$; adult females, unknown; (2) disc on Finger III expanded; (3) Finger I = II; (4) fringe absent on Finger II; (5) disc on Toe IV expanded; (6) fringe absent on Toe IV; (7) outer tarsal fold absent; (8) webbing absent; (9) dorsolateral stripe present; (10) oblique lateral stripe absent; (11) ventrolateral stripe absent; (12) discrete markings absent on chest; (13) black darkening on abdomen with white spots in males; (14) Finger III not swollen in males; (15) testes white.

Colostethus whymperi is compared with *C. exasperatus* that lacks oblique and ventrolateral stripes, and webbing on the toes. They differ because *C. whymperi* has a solid dark darkening in abdomen of males rather than diffuse dark and white

spots in abdomen of males of *C. exasperatus*. *Colostethus whymperei* closely resembles *Epipedobates erythromos* from which it differs by having solid black darkening on venter in contrast to the marbled patterns of *E. erythromos*.

Description.—The holotype is a male 22.6 mm in SVL (24 mm according to Boulenger, 1882). It is in poor condition, and few characters can be described precisely. No color patterns are visible.

Comparison of the type specimen with material from localities in the vicinity of the type locality revealed that three specimens from San Francisco de Las Pampas, can be assigned to this species. Herein, I describe a male [MHNG (GO 43)] from this series and indicate (in parentheses) any differences from the original description.

Male, 20.8 mm in SVL; body moderately robust; head about as long as wide; head length 37% SVL; head width 36.5% SVL; snout bluntly rounded in dorsal view, distinctly protruding beyond lower jaw in profile; loreal region barely concave; nostrils slightly protuberant laterally; eye-nostril distance half diameter of eye; supratympanic fold obscuring posterodorsal part of tympanum (tympanum entirely distinct); diameter of tympanum 36.4% diameter of eye; forelimbs moderately long; Fingers I and II about equal in length; fingers unwebbed, lacking lateral fringes; Finger III not swollen; terminal discs expanded; subarticular tubercles large, rounded (indistinct); palmar tubercle large, rounded, elevated; thenar tubercle elliptical; nuptial excrescences absent. Hind limbs robust; tibia length 50.5% SVL; outer tarsal fold absent; inner tarsal fold sigmoid on distal two thirds of tarsus; outer metatarsal tubercle round, about half size of elliptical inner metatarsal tubercle (outer metatarsal tubercle absent; inner metatarsal tubercle indistinct); toes unwebbed, without narrow lateral fringes, with slight hint of lateral keels; terminal discs expanded, about twice width of digits (discs of fingers and toes small); subarticular tubercles small, oval; supernumerary tubercles absent.

Skin on all surfaces smooth; three small tubercles posteroventral to tympanum; anal opening extended posteroventrally at midlevel of thighs by anal sheath; tongue narrowly triangular, indented posteriorly, free posteriorly for about two thirds of its length; vocal slits present; vocal sac single, median, subgular.

Color in preservative: Dorsum and flanks uniformly black; short pale oblique lateral stripe in groin; narrow dorsolateral stripe from tip of snout

along canthus rostralis and margin of upper eyelid to anal region; tympanic region dark brown; upper lip black; dorsal and anterior surfaces of forearms black; posterior surfaces of upper arm black proximally, white distally; dorsal surfaces of hind limbs black with some diffuse pale white proximally on thighs; throat and chest black, gray in gular region, abdomen black with white spots (throat and abdomen marbled with gray); white flecks in groin; ventral surfaces of limbs cream; palmar, ventral surfaces of tarsi, and plantar surfaces black; inner three digits of hands and feet gray with white transverse bands; other digits with diffuse transverse bands.

Variation.—A juvenile female MHNG (GO 41) has black bars across the thigh; venter is uniform gray.

Tadpoles.—Unknown.

Calls.—Unknown.

Distribution and ecology.—*Colostethus whymperei* is known only from Tanti, and the vicinities of San Francisco de Las Pampas at about 600–1800 m in west-central Ecuador (Fig. 15). These localities are in the Very Humid Premontane Forest, where annual mean precipitation is 2000–4000 mm, and annual mean temperature is 18–24°C.

Colostethus whymperei occurs in the same general area where *C. toachi*, *C. lehmanni*, *C. chocoensis*, *C. awa*, and *Epipedobates spinosai* occur.

Comments.—The type locality, Tanti, is a farm on the highway midway between Santo Domingo de los Colorados and Alluriquín.

Assignment of the specimens from San Francisco de Las Pampas to *Colostethus whymperei* is tentative, but is justified by the absence of significant differences between the original description of *C. whymperei* and the specimens from San Francisco de Las Pampas.

Epipedobates erythromos (Vigle and Miyata, 1980) is similar to *C. whymperei* and may be conspecific. However, comparison of *Epipedobates erythromos* and the type of *C. whymperei* is complicated owing to the poor preservation of the holotype of *C. whymperei*; differences in ventral color patterns may be a preservation artifact. Comparison of *Epipedobates erythromos* and the specimens from San Francisco de Las Pampas reveals that they are not conspecific. A more exhaustive comparison, or fresh specimens from the type locality of *C. whymperei* are needed to assess the taxonomic status of *Epipedobates erythromos*, *C. whymperei*, and the specimens from San Francisco de Las Pampas.

TAXONOMIC ADDENDUM

Colostethus festae Peracca

Prostherapis festae Peracca, 1904:16.—Syntypes: (3 males), MZU AN87(1–2) have been located, from Valle del Río Santiago, about 500–600 m, Provincia Morona Santiago, Ecuador.
Colostethus festae—Edwards, 1971:148.

I examined two syntypes of *Colostethus festae*.

They are well preserved and Peracca's (1904) description is rather detailed and corresponds with a red-backed granulated dendrobatid frog, *Epipedobates parvulus*; therefore, I consider *Colostethus festae* (Peracca, 1904) to be a junior synonym of *Epipedobates parvulus* (Boulenger 1882a).

SYSTEMATIC RELATIONSHIPS

The family Dendrobatidae contains 161 species grouped in nine genera: *Allobates*, *Aromobates*, *Colostethus*, *Dendrobates*, *Epipedobates*, *Mannophryne*, *Minyobates*, *Phobobates*, and *Phyllobates*. The family occurs from Nicaragua and the Lesser Antilles to southeastern Brazil and Bolivia. According to Griffiths (1963), Duellman and Trueb (1986), and Ford (1993), the sister group of poison-dart frogs (Dendrobatidae) is within the ranoids—viz., the Arthroleptidae (Ford, 1993). However, an alternate hypothesis is that of Lynch (1971), who considered dendrobatids to be more closely related to the leptodactylid subfamily Elosiinae. Ford (1993) evaluated the evidence for both the dendrobatid-ranoid and dendrobatid-elosiinae hypotheses and found the dendrobatid-ranoid hypothesis to be the most parsimonious explanation of the morphological data that she analyzed. Also, Ford (1993) presented evidence for the monophyly of Dendrobatidae. According to Myers et al. (1991), characters unique to the family are: (1) tympanum posterodorsally tilted under anterior edge of the massive superficial slip of the m. depressor mandibulae; and (2) alary processes of premaxillae projected anterodorsally. Additional evidence of the monophyly of Dendrobatidae is afforded by their unique life history (Myers and Daly, 1983; Weygoldt, 1987) characterized by complex social and breeding behavior that usually involves territoriality, egg attendance and tadpole transport.

The phylogenetic relationships within the Dendrobatidae are poorly resolved; however, they are being investigated by Myers, Daly, Ford (Myers, 1987), and Summers (pers. comm.). Preliminary assessments of relationships at supraspecific levels

based on a suite of characters (Myers, 1987) support the monophyly of a clade characterized by having lipophilic alkaloids in the skin; this clade is composed of *Epipedobates*, *Phyllobates*, *Dendrobates*, and *Minyobates* (including *Allobates* and *Phobobates*, both separated from *Epipedobates* and *Dendrobates*, respectively, by Zimmermann and Zimmermann, [1988]). A less inclusive monophyletic group is composed of *Phyllobates*, *Dendrobates*, *Phobobates*, and *Minyobates*, which are considered the most derived genera on the basis of larval and adult morphology, color patterns, behavior and skin toxins (Myers, 1987). *Epipedobates* may or may not be a natural group (Myers, 1987). No synapomorphies have been proposed to unite the species of *Colostethus* and it is considered to be a basal grade within the Dendrobatidae (Lynch, 1982). Myers et al. (1991) described *Aromobates* and considered it to be the sister taxon of all other dendrobatids. La Marca (1992) proposed the genus *Mannophryne* to include eight species of collared *Colostethus*.

Myers et al. (1991) were reluctant to recognize *Allobates* and *Phobobates* (Zimmermann and Zimmermann, 1988) because "they add to problems of paraphyly." *Aromobates* erected by Myers et al. (1991) and *Mannophryne* proposed by La Marca (1992), suffer similar problems that are discussed below (under *Colostethus*). The status of these four recently proposed genera warrants further attention.

Colostethus, the largest dendrobatid genus, contains at least 92 recognized species. It is diagnosed by a mosaic of attributes that include toe discs and pads, premaxillary and maxillary dentition, and cryptic coloration sometimes involving pale dorso-lateral, oblique lateral, and ventrolateral stripes, and

the absence of skin alkaloids. Several attempts have been made to clarify the systematics of dendrobatid frogs included within *Colostethus*. Savage (1968) proposed a generic arrangement for the inconspicuous and apparently nontoxic dendrobatid forms, and he synonymized *Prostherapis* (Cope 1868) and *Hyloxalus* (Jiménez de la Espada, 1871) with *Colostethus* Cope 1866. Edwards (1971) followed Savages' proposal (1968) and referred 43 nominal species to the genus *Colostethus*. He allocated species previously placed in other genera (e. g., *Phyllodromus*) to the genus *Colostethus*. Most of the work has been at the alpha level; however, in recent years, the systematics of the members included in this genus has begun to be addressed at supraspecific levels using phenetic and phylogenetic principles. Edwards (1974a) performed a phenetic analysis of *Colostethus* and created groups based on overall similarity. Some natural (monophyletic) groups have been proposed by Rivero (1979), Lynch (1982), La Marca (1985, 1992), and Myers et al. (1991). Rivero ("1988") reviewed previous groupings; he proposed eight putatively monophyletic groups and discussed intergroup relationships. Rivero and Serna ("1988") later added one other group to the eight previously recognized. Myers et al. (1991) discussed ingroup and outgroup hypotheses of relationships of *Colostethus*, and recognized *Aromobates* as the sister taxon of all other dendrobatids. They diagnosed *Colostethus* sensu stricto to include the species of the *C. inguinalis* group of Rivero ("1988") and suggested that *Hyloxalus* should be resurrected for the remaining *Colostethus* (sensu lato).

Myers et al. (1991) compared *Aromobates* with the collared species of *Colostethus* (*C. trinitatis* group of Rivero, "1988"; *Mannophryne* of La Marca, 1992) and argued that their resemblances may reflect symplesiomorphy, but cautioned that "some character reinterpretation may be necessary" when appropriate outgroups for the Dendrobatidae are available. In the absence of comparative outgroup data for the characters presented as evidence of the monophyly of a clade composed of *Colostethus* sensu lato plus dendrobatids that produce lipophilic alkaloids, the recognition of *Aromobates* as the sister taxon of all other dendrobatids will obscure subsequent analyses of ingroup relationships. As stated by Myers et al. (1991), the unique character states—i.e., nocturnal, aquatic, presence of M. ad-

ductor mandibulae external superficialis, large size (to 62 mm SVL)—of *Aromobates* might represent special apomorphies that are uninformative of relationships. Donoso-Barros ("1964") description of *C. riveroi* as large and nocturnal suggests that it may be related to *Aromobates*. Myers et al. (1991) discussed Donoso-Barros' description of *C. riveroi*, and based their discussion on specimens collected at the type locality; they suggested that *C. riveroi* is primarily diurnal. Additional observations of natural history of *C. riveroi* are required; however, the possibility that *C. riveroi* is nocturnal or facultatively nocturnal is strengthened by my observations that captives of species such as *C. nexipus*, *C. bocagei* and *C. awa* are facultatively nocturnal.

Despite Rivero's claim that his groupings were primarily based on apomorphic characteristics and geographic distribution as evidence of relationships (Rivero, "1988":4, 27), most of the character states given by Rivero ("1988") and Rivero and Serna ("1988") seem to be plesiomorphic at the level used; thus, no evidence (here understood as unique-shared derived characters) other than phenetic similarity and geographic proximity justify most of their groupings. Rivero ("1988") discussed the pitfalls of his hypotheses and stated his concern about the weakness of the evidence supporting his groups and the proposed relationships. The monophyly of each of these groups is questionable because there is conflicting evidence. Many of the hypothesized synapomorphic characters may represent symplesiomorphies or homoplasies. The species groups and intergroup relationships proposed by Rivero ("1988"), Rivero and Serna (1989), Myers et al. (1991), and La Marca (1992) are discussed below.

The *Colostethus inguinalis* group (Group IV of Rivero "1988") or *Colostethus* sensu stricto (Myers et al., 1991) is poorly supported, because the only synapomorphy, swollen third finger of males, is present in species such as *C. pratti* and *C. latinasus* (currently within the *C. inguinalis* group) for which, as discussed by Rivero ("1988") placement in either the *C. inguinalis* or *C. brunneus* groups is equivocal. It is possible that *C. pratti* and *C. latinasus* are more closely related to members of the *C. brunneus* group (sensu Rivero, "1988"), which is diagnosed by pale dorsolateral and short inguinal stripes (e.g., *C. marchesianus*, *C. kingsburyi*, and *C. brunneus*), than they are to members of the *C. inguinalis* group.

Colostethus talamancae, which has not been placed in any group, also may be allied to members of the *C. brunneus* group. The diagnosis of the *C. inguinalis* group is complicated further because there are some species of *Epipedobates* (e.g., *E. boulengeri*, *E. spinosai*, and *E. tricolor*) that possess a third swollen finger in males. Two possible explanations are that (1) these *Epipedobates* belong to the *C. inguinalis* group, or (2) the third swollen finger evolved independently in that lineage of *Epipedobates*.

The *Colostethus brunneus* group (Group II of Rivero, "1988") is characterized by a unique combination of dorsolateral and short oblique lateral (sometimes referred as inguinal) stripes. According to Rivero ("1988"), these characters are shared between members of the *C. brunneus* and *C. alagoanus* groups, thereby suggesting that one of the groups may be paraphyletic with respect to the other. Rivero ("1988") suggested that the *C. brunneus* group may be the ancestral group of all other *Colostethus*; he based his hypothesis on the group's wide distribution in the Amazonian region. However, as suggested by Rivero ("1988") and emphasized here, the *C. brunneus* group may be paraphyletic; as such, it may not have a unique history exclusive of other *Colostethus*. Furthermore, I do not consider wide distributions to be evidence of primitiveness.

The *Colostethus alagoanus* and *C. albuguttatus* groups (Groups III and VIII of Rivero, "1988," respectively) were characterized by a unique combination of features (most of them absences) of uncertain polarity. No reliable evidence of their monophyly exists. According to Rivero ("1988"), the *C. albuguttatus* group may be derived from an ancestor shared with members of the *C. fuliginosus* group.

Rivero and Serna ("1988") split the *Colostethus fuliginosus* group (VI of Rivero "1988") into two groups, the *C. fuliginosus* and *C. subpunctatus* groups (Group IX), and restricted the *C. fuliginosus* group to those species that either possess an incomplete oblique lateral stripe or lack a stripe, possess well-developed toe webbing, and have the first finger shorter than the second. The *C. subpunctatus* group was characterized by possession of a complete oblique lateral stripe, reduced or absent toe webbing, and the first finger longer than the second. The characters diagnosing both groups are of unknown polarity and, in addition, appear in several of the other groups.

Based on the absence of a dorsolateral stripe and similar geographic distributions in the Andes, Rivero ("1988") hypothesized that the *Colostethus fuliginosus* group is the stem-group of the *C. inguinalis* group. Again, I do not think that geographic distribution provides evidence of relationship; and the absence of dorsolateral stripe is probably plesiomorphic at that level; thus, there is no evidence for the monophyly of the group.

The *Colostethus vertebralis* group (Group I of Rivero, "1988") is diagnosed by the presence of two discrete spots on gular-chest region (unique character shared by all the members of the *C. vertebralis* group). The presence of a black collar is a suggested synapomorphy of *Mannophryne* (*C. trinitatis* group, Group VII of Rivero "1988"). A yellow throat, complex courtship and aggressive behavior, and other characters used by La Marca (1992) to diagnose *Mannophryne* either are not unique, or are absent in some of the species; their polarities are uncertain. The monophyly of each of these groups is questionable. Myers et al. (1991) discussed the problems in determining homology based on collarlike markings alone and they suggested that "symplesiomorphy seems likely if all collars are judged homologous." Because the band of members of *Mannophryne* are similar with the marks on members of the *C. vertebralis* group, only a single group is tentatively diagnosed by the presence of gular-chest marks or bands. Furthermore, the group must be expanded to include species such as *C. bocagei* (formerly not assigned to a group), that also possesses a diffuse mark on chest-gular region.

Also, Rivero (1979; "1988") stated that some members of the *Colostethus vertebralis* group may be related more closely to those of *C. trinitatis* group (= *Mannophryne*). He hypothesized ("1988") that the *C. fuliginosus* and *subpunctatus* groups are the stem-groups of the *C. trinitatis* and *C. vertebralis* groups. There is much character conflict among these four groups and no compelling reason to recognize any of the four groups. To do so would introduce bias to a phylogenetic analysis. A noteworthy character of members of the *C. trinitatis*, and *C. fuliginosus* groups is the presence of a neopalatine which is a primitive character within the Dendrobatidae; it is absent in most *Colostethus*, but retained in *Aromobates nocturnus* (Myers et al. 1991), *C. collaris*, *C. haydecae*, *C. mayorgai*, *C.*

olmonae, *C. trinitatis*, *C. riveroi*, *C. herminae*, *C. chocoensis*, and *C. bocagei* (pers. obs.). The monophyly and relationships among members of these four groups warrants testing by means of a phylogenetic analysis.

The *Colostethus edwardsi* group (Group V of Rivero, "1988") is characterized by the presence of an anal sheath unique to dendrobatids and shared by two hypothesized sister-species, *C. edwardsi* and *C. ruizi* (Lynch 1982). Rivero ("1988") suggested a close relationship between this group and the *C. fuliginosus* group.

In summary, the phylogenetic relationships within "*Colostethus*" (sensu lato) constitute an enormous polytomy that involves 101 species (*Aromobates* and *Mannophryne* included). Limited evidence suggests the following: (1) some members of *Colostethus*

sensu stricto may be closely related to some *Epipedobates* with which they share a third swollen finger in males; (2) members within the *Aromobates*, *Mannophryne* and *C. vertebralis-fuliginosus* polytomy may represent basal taxa within "*Colostethus*"; (3) the recognition of a sister-taxa relationship within the *C. edwardsi* group; (4) *C. awa*, *C. bocagei* and *C. nexipus*, which are secretive (facultatively nocturnal under captive conditions), may be derived from an ancestor shared with nocturnal species such as *Aromobates nocturnus* and *C. riveroi*. Owing to their putative position as a basal grade, a phylogenetic analysis of *Colostethus* is pivotal to any further understanding of patterns of morphological, behavioral, and molecular evolution within the family Dendrobatidae.

BIOGEOGRAPHY

No discussion of the historical biogeography of Ecuadorian *Colostethus* is possible because of the lack of fossils and the largely unsolved phylogenetic history of the group. However, a summary of the geographical and ecological distributions of the species is pertinent. Rivero and Almendáriz (1991) presented a geographic summary of the Ecuadorian *Colostethus*; however, owing to the numerous taxonomic changes, the geographic information must be updated.

Ecuadorian *Colostethus* occur from near sea level (*C. machalilla*) to about 3800 m (*C. jacobuspetersi*) in the Andes. A cross-sectional summary of their altitudinal and ecological distributions is presented in Figure 16. Most of the species occupy narrow altitudinal zones; however, some species, such as *C. elachyhistus* and *C. jacobuspetersi* in western Ecuador and *C. bocagei* from east of the Andes, have relatively wide altitudinal ranges.

To date, 24 (77%) of the species are endemic. Some species included in this study are only known from the type locality (*C. maquipucuna*, *C. marmoreoventris*, *C. mystax*, *C. peculiaris* and *C. pumilus*). Others have restricted ranges; in some cases, these ranges may be real, whereas in others, they are the result of the paucity of locality data (e.g., *C. cevallosi*, *C. delatorrae*, *C. exasperatus*, *C. fallax*, *C. fugax*, *C. fuliginosus*, and *C.*

whymperi). However, there are some widely distributed species, such as *C. bocagei*, *C. marchesianus*, and *C. sauli* in the Amazon Basin of Ecuador, and *C. breviquartus*, *C. chocoensis*, *C. lehmanni*, and *C. talamancae* on the Pacific versant of the Andes and adjacent lowlands of Central America and/or Colombia and Ecuador. Fifteen species occur on the Pacific side of the Andes and 16 on the Amazonian side of the Andes; all species are either on the western or eastern side of the Andes except *C. vertebralis*, which occurs on the western slopes of the Andes as well as in the inter-Andean valleys of Azogues-Cuenca and toward the east in the Gualaceo-Sigsig valleys. Some populations of two other species occupy inter-Andean valleys—*C. pulchellus* in northern Ecuador in the Carchi Valley and *C. jacobuspetersi* in the Guayllabamba, Toachi, Chimbo and Cañar valleys; *C. elachyhistus* occupies the Catamayo and several western valleys within the orographically intricate Huancabamba Depression in southern Ecuador.

The ecological distributions of the species are described in the species accounts. For analytical purposes, I used Cañadas' (1983) classification of life zones of Ecuador, which is based on the Holdridge (1947) system. The number of species is low in dry life-zones, increases in Humid Tropical and Premontane Forests (Fig. 16), and de-

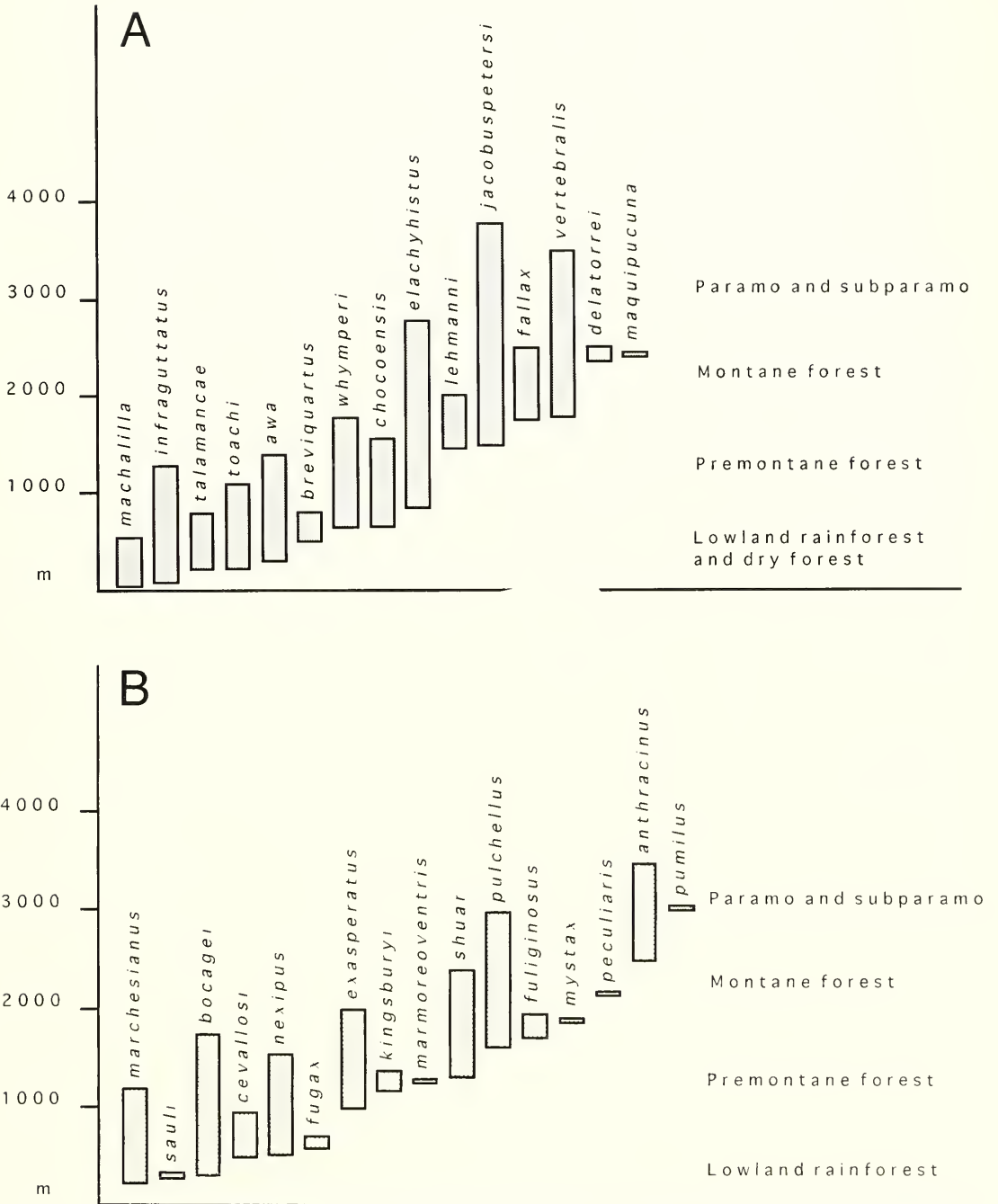


Fig. 16. Altitudinal and ecological distribution of Ecuadorian *Colostethus*: (A) species from the western side of the Andes and inter-Andean valleys, and (B) species from the eastern side of the Andes.

creases in montane forest and páramo environments.

Two species, *Colostethus machalilla* and *C. elachyhistus*, mostly inhabit dry life-zones characterized by pronounced seasonality and low precipitation. Also, populations of *C. awa* and *C. infraguttatus* occupy the dry-tropical life zones, but the former species mostly occupies wet and cloudy environments in the northern part of the coastal cordillera in that zone. *Colostethus machalilla* and *C. infraguttatus* occur in sympatry throughout their ranges; the former is sympatric with *Epipedobates tricolor* in southern Ecuador.

Most species inhabit wet life-zones characterized by high humidity and precipitation; in the Humid Tropical Forest and Humid Premontane Forest of the lowlands of northwestern Ecuador three species occur (*C. awa*, *C. toachi*, and *C. talamancae*), and they are sympatric with two other dendrobatids, *Dendrobates histrionicus* and *Epipedobates boulengeri*. In the Humid Tropical Forest of the lowlands of the Amazon Basin three species occur (*C. bocagei*, *C. marchesianus* and *C. sauli*) and they are sympatric with four other dendrobatids—*Allobates femoralis*, *Dendrobates ventrimaculatus*, *Epipedobates pictus* and one of the following: *E. bilinguis*, *E. parvulus*, or *E. zaparo*. The greatest diversity of *Colostethus* is in Humid Premontane Forest on both sides of the Andes where as many as five species of frogs can be found in sympatry on each side. For example, five species (*C. chocoensis*, *C. lehmanni*, *C. awa*, *C. toachi*, and *C. whymperi*) have been recorded from the Santo Domingo de los Colorados–Tandapi

area on the Pacific slopes; they are sympatric with one other dendrobatid, *Epipedobates spinosai*; in cloud forest around Volcán Reventador on the Amazonian slopes, five other species (*C. bocagei*, *C. fuliginosus*, *C. kingsburyi*, *C. pulchellus*, and *C. shuar*) have been found and they occur sympatrically with *Minyobates abditus*.

Most species of *Colostethus* in Humid Premontane Forest coexist in an anuran community that includes other diverse taxa such as Centrolenidae and *Eleutherodactylus*. A comparison of the diversity of these three groups reveals a general, shared distribution pattern with the greatest diversity of the three groups occurring in Humid Premontane Forest at the same sites (Tandapi and Río Azuela in the western and eastern slopes, respectively) in Ecuador. For example, Duellman and Burrowes (1989) recorded seven sympatric species of Centrolenidae at Tandapi; at the Río Azuela (near Volcán Reventador), Lynch and Duellman (1973; 1980) recorded five sympatric centrolenids and 11 sympatric *Eleutherodactylus*. It is clear from these examples that the highest diversities of *Colostethus*, Centrolenidae, and *Eleutherodactylus* occur in the Humid Premontane Forest; however, the abundance of species of the three taxa at the same sites may be biased by the intensive collecting efforts made at these localities compared to other Humid Premontane Forest sites.

The general distribution pattern discussed above suggests that these anuran communities may have a common biogeographic history; however, a phylogenetic analysis of these groups is necessary as a basis for further analysis.

NATURAL HISTORY

Life history data for the Ecuadorian *Colostethus* are extremely limited. Most species are primarily diurnal and some of them are secretive. Myers (1991) reported *C. chocoensis* to be a secretive frog and I have observed *C. awa*, *C. bocagei*, and *C. nexipus* to be diurnal, secretive frogs as well. It is interesting to note that these three species are sometimes active at night under captive conditions.

Few observations of territorial behavior have been made. Some limited knowledge, based on play-back recordings, suggests that male territo-

rial behavior exists in *Colostethus awa*, *C. marchesianus*, and *C. nexipus*. In these species, males responded by attacking the potential intruder simulated by the recorder. Amplexant position has not been observed. Reproductive cycles are unknown except for *C. marchesianus* that was found breeding throughout the year at Santa Cecilia (Duellman, 1978) and at Montalvo and surrounding localities (Almendáriz, 1987). Mean ovarian complements of 13.4 and 11.3 were reported for *C. marchesianus* and *C. sauli*, respectively, by Duellman (1978). The oviposition site and clutch

size is known for *C. awa*, *C. elachyhistus*, and *C. vertebralis*. Edwards (1971) reported a male *C. elachyhistus* guarding a clutch of 19 eggs beneath a rock; a captive *C. awa* deposited a clutch of 21 eggs on a dead leaf; Read (1986) reported clutches of *C. vertebralis* with 5–12 eggs 3 mm in diameter under stones or moss and did not observe parental care of the eggs. Adults of seven species have been observed transporting larvae. In all recorded species, males carried 1–16 tadpoles. Tadpole-releasing sites vary depending on the life zones where the species live and, apparently, are species specific. However, the association of free-swimming tadpoles with adults is complicated unless actually observed or inferred when only a single species is known at a given locality. Thus, observations are tentative. According to Duellman (1978), *C. marchesianus* released tadpoles in a water-filled segment of a fallen bamboo and *C. sauli* tadpoles were found amidst detritus in shallow streams issuing from springs. *Colostethus machalilla* releases tadpoles in small pools on the shores of rivers. Other species, such as *C. awa*, *C. vertebralis*, *C. pulchellus*, and *C. delatorreae*, release tadpoles in swampy areas, small ponds, and road rivulets. *Colostethus anthracinus* and *C. jacobuspetersi* live in the upper montane forests and páramos; they prefer small, cold-water rivers where tadpoles have been found in these streams and in stream-margin pools.

Food items have been reported for *C. marchesianus* (Duellman 1978, Almendáriz, 1987) and *C. sauli* (Duellman, 1978). They found ants to be the most abundant prey for both species. Predation has not been reported, except for *Eleutherodactylus crenunguis* feeding on recently metamorphosed juveniles of *C. awa*.

As mentioned above, there are several localities where at least six species of dendrobatids have been reported from the same general area. However, microhabitat preferences are poorly known. Duellman (1978) found that *C. marchesianus* is equally abundant in primary and secondary forest; he reported that the species is not necessarily associated with streams, but widely dispersed in the forest in contrast to the sympatric *C. sauli*, which seemed to be more restricted to vicinities of small streams. Most of the other species also seem to be restricted to streams, except *C. vertebralis*,

C. pulchellus, *C. delatorreae*, and *C. jacobuspetersi*, which also occur in swampy areas.

EXTINCTION TRENDS

Despite absence of data on population numbers and status for any of the Ecuadorian *Colostethus*, it has become increasingly obvious that population sizes have declined dramatically in the last decades. The disappearance of species is correlated with the same time frame during which global amphibian declines and extinctions have been reported (Blaustein and Wake, 1990). In several cases, the cause of these disappearances is habitat destruction; in others, the cause or causes are unknown, and may represent a complex of factors. Because of our lack of understanding of the apparent disappearances and declines in population sizes of these anurans, I consider it appropriate to present anecdotal data that may enhance conservation efforts.

Through 1982, species such as *Colostethus jacobuspetersi* were common in the creeks in the suburban neighborhoods of the city of Quito and extremely abundant on the western slopes of the Andes around San Juan in the Cordillera Occidental in Provincia Pichincha. However, none of these anurans has been collected from the environs of Quito since 1982; creeks around Quito are polluted and vegetation along them is disturbed. In contrast, there have been no apparent, major habitat modifications on the slopes of the Cordillera Occidental since 1982; nonetheless, only one individual was found on 28 May 1989 and no additional specimens have been collected since, despite efforts to locate this frog. The same phenomenon has been noticed for the species in the protected forest of Cashca Totoras, Provincia Bolívar, in the southern part of its range.

Colostethus pulchellus was very common along rivulets at sides of the road between Papallacta, Baeza, and Cosanga in Provincia Napo. In this area, the habitat has been severely altered as a result of increased vehicular traffic and construction of a water reservoir around the lake at Papallacta. A few individuals can still be found in relictual patches of forest near Baeza and in the protected forest of Aragón near Cosanga.

Colostethus vertebralis, which once was com-

mon in Provincia Azuay, is now rare. Read (1986) reported this species to be the most abundant and widespread frog at Mazán in August–September 1986; however, recent visits to these protected forests revealed no specimens of this species. Relictual populations of *C. vertebralis* are found in the Páramos de Matanga in the eastern Cordillera and in the Molleturo area on the western slopes of the Cordillera Occidental.

The vicinity of Volcán Reventador, which is one of the sites of the greatest diversity of dendrobatid frogs, was visited in different months during 1988–1993; however, only *Colostethus bocagei* was found. A similar trend has been noted throughout the Quijos-Topo Depression on the central-eastern slopes of the Ecuadorian Andes. Severe population decreases have been observed for *C. elachyhistus*, *C. awa*, and the species in premontane and montane forest habitats. Repeated efforts (since 1987) to find *C. maquipucuma* and *C. lehmanni* have been unsuccessful.

The lowland populations of *Colostethus* on the western side of the Andes have patchy distributions owing to the effects of deforestation. Dodson and Gentry (1991) estimated that less than 4.4% of primary forest remained in western lowlands of Ecuador. Since 1991, deforestation has accelerated in the small forest remnants; thus, massive extinctions of the *Colostethus* species in the area may be occurring. In contrast, eastern lowland populations of species such as *C. marchesianus* seem to be more stable in the protected areas such as Reserva Faunística Cuyabeno and Parque Nacional Yasuní.

Global warming, habitat modification, and a host of other factors may be affecting the populations of *Colostethus*. Given the accelerating rates of observed extinctions, I consider it imperative conservation priority to monitor extant populations and breed captives of as many species as possible.

RESUMEN

Se resume el conocimiento sobre las ranas dendrobátidas del género *Colostethus* en Ecuador. Se presenta la historia taxonómica del grupo y se describen caracteres taxonómicamente útiles (ej. morfología externa, gónadas, renacuajos y cantos). Se reconocen treinta y un especies entre las cuales se incluyen cinco nuevas para la ciencia que son descritas en este trabajo. Ocho especies nominales son sinonimizadas; estas son: *Colostethus citreicola* (*C. nexipus*), *C. festae* (*Epipedobates parvulus*), *C. intermedius* (*C. kingsburyi*), *C. maculosus* (*C. bocagei*), *C. parvus* (*C. exasperatus*), *C. taeniatus* (*C. pulchellus*), *C. tergoangularis* (*C. pulchellus*), y *C. torrenticola* (*C. jacobuspetersi*). Se designan lectotipos para *C. bocagei* y *C. infraguttatus*, y se propone un neotipo

para *C. pulchellus*. Varias especies son redescritas y además se presentan sumarios taxonómicos para cada especie, los cuales incluyen información adicional sobre variación. Se extienden hacia Ecuador los rangos de especies conocidas previamente de otros países (*C. breviartus*, *C. lehmanni*, y *C. talamancae*). Se proveen nuevos registros geográficos con mapas de distribución, nuevos datos ecológicos, descripciones de los renacuajos de ocho especies y los cantos de seis especies. Se presenta una clave dicotómica para facilitar la identificación de especímenes. Se resume y discute la información sobre la sistemática, distribución, historia natural y patrones de extinción.

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APPENDIX

SPECIMENS EXAMINED

Frogs are preserved in alcohol, and larvae in formalin; C&S = cleared-and-stained skeletal preparations.

Colostethus anthracinus

ECUADOR: *Provincia Azuay*: 9 km S Cumbe, 3300 m, KU 132129; Río Mazán, 3150 m, KU 207512–13; Río Mazán, between 3000–3500 m, EPN 2378–79; 11.5 km SE Gualaceo, 2940 m, KU 202827; 17.6 km SE Gualaceo, 3150 m, KU 202813; Páramos de Matanga, borderline of *Provincia Zamora Chinchipe*, QCAZ 2697

(tadpoles): *Provincia Loja*: Abra de Zamora 13–14 km E Loja, 2850 m, KU 120637–8; 166118–20, 182210–11, 141563; *Provincia Morona Santiago*: Páramo de Raranga, 12 km S Cutchil, 3400 m, KU 120639 (holotype), 120640–55, 121031; *Provincia Zamora Chinchipe*: Abra de Zamora, 15 km E Loja, 2710 m, KU 142544, 142545 (C&S), 142546–47.

Colostethus awa

ECUADOR: *Provincia Esmeraldas*: 7 km E San José de Bilsa, 00°37' N, 79°51' W, 265 m, EPN 3964–72;

Provincia Imbabura: Lita, 570 m, MECN 737–44, 745 (C&S), 746–54, 755 (C&S), 756. MHNG 18595: Lita 520 m, KU 133285–95, 133296 (C&S), 13297–99, 133301–05, NMW 32158:1–2; Río Intag, 12 km N García Moreno, 1220 m, QCAZ 1325; *Provincia Pichincha*: 9 km N Nanegal Chico, along Río Alambi, UMMZ 132930 (4223–24); Mindo, UMMZ 55521; San Miguel de los Bancos, MHNG (GO 40), Puerto Quito, MHNG 18879.1–3; Tandapi, MHNG [GO 28, 29 (C&S), 35 (C&S), 47], 18829; 3.7 km E Dos Ríos, 1190 m, KU 142460–62; 4 km NE Dos Ríos, 1140 m, KU 166078–85, 166086 (C&S), 166087–90; Río Toachi, 12 km E Alluriquín, 920 m, KU 142860; 15 km NW Alluriquín (5 km NW La Florida), Finca Gloria, 79°01' W, 0°15' S, 920–950 m, MHNG 18781.1–2, RMNH 25224–32, QCAZ 1326, 1327 (holotype), 1328–29, 3206 (tadpoles), 3251–54, 3350 (tadpole), KU 220602–07; approx. 15 km SE Santo Domingo de los Colorados, at Tinalandia, 800 m, AMNH 111541–44; 5 km E La Palma, 900 m, KU 166076–77; banks of the rivers Pupusa and Quila, Santo Domingo de los Colorados, CAS 10376–78; Hacienda Espinosa, 9 km W Santo Domingo de los Colorados, road to Chone, CAS 10587–90; hills by Río Posta, 10 km W Santo Domingo de los Colorados on road to Chone, CAS 10379; Hacienda Delta, 8 km SE Santo Domingo de Los Colorados, UMMZ 132935 (4399); *Provincia Cotopaxi*: vicinity of San Francisco de Las Pampas, MHNG 18923.1–4, 18923.1–3; approx. 18 km W Pilaló, 940 m, QCAZ 1330; 18.6 km W Pilaló, 930 m, KU 142463; 20.3 km W Pilaló, 830 m, KU 142464, 166159, 202892; *Provincia Manabí*: 38 km W El Carmen, Road to Pedernales, 330 m, QCAZ 1331–39, KU 220608–14.

Colostethus bocagei

ECUADOR: *Provincia Sucumbíos*: Bermejo # 4, 77°22' W, 00°11' N, 15 km ENE Lumbaquí, 720 m, KU 122211, 122222–24; *Provincia Napo*: San José de Moti (Cantón Quijos), MNCN 1583 (lectotype), 1584 (paralectotype); Río Oyacachi at Quito–Lago Agrio Road, 1550 m, AMNH 89570–1; Río Azuela, 1740 m, KU 166100–05; 2 km SSW Río Reventador, 1490 m, KU 166106–10; 20.8 km SE Cosanga bridge on Baeza–Tena Road, 1950 m, KU 189935–38; Río Coca, 300 m, tributary of Río Napo, UMMZ 90381; 75 km E Coca, Hostería La Selva, QCAZ 5032; Río Suno, tributary Río Napo, 300 m, UMMZ 90379 (2); Río Cotapino, UMMZ 90372 (1 of 2); Río Bununo, S Venecia 1°7' S, 77°42' W, UMMZ 182474; Río Huaguayacu, S Venecia 1°7' S, 77°42' W, UMMZ 182475–76; Río Nachiyacu, UMMZ 182482–84; *Provincia Tungurahua*: Río Negro, 1260 m, KU 120511–12, KU 120513 (C&S); 37.4 km E Baños, 1370 m, KU 141527–28; 23.2 km E Baños, 1470

m, KU 141529; *Provincia Pastaza*: 38 km NNE Puyo, 740 m, KU 146219–28, 146271–72; 25 km NNE Puyo, 1040 m, KU 146218; Mera, KU 120487–92; 120504–10, 132942–46, 132947 (C&S), 132948–78, 132979 (C&S), 182118–20; Mera, 1140 m, RMNH 25239–47; Hills N Mera, 78°8' W, 1°26' S, UMMZ 182465–68, 182470; Abitagua, 1100 m, CAS–SU 5064, 5076; Abitagua, 1200 m, UMMZ 90380 (7); 3.5 km W Mera, 1180 m, KU 146239; 4.5 km W Mera, KU 146238; 5 km E Veracruz, 970 m, KU 146229–37, Chontoa, 780 m, KU 120496–97; Río Pastaza, 500 m, CAS–SU 5086; Sarayacu, 400 m, KU 120498–503; Locación Petrolera Garza 1, NE Montalvo, 300 m, KU 220615–17, QCAZ 1318–19; Río Pastaza watershed, RMNH 1910 (13); *Oriente*: San José, AMNH 22167, 22170–71, 22173, 22186; *Oriente*: UMMZ 90378.

Colostethus breviquartus

ECUADOR: *Provincia Carchi*: Cabeceras del Río Baboso, NE Lita, 600–900 m, MECN 734–36; Chical, approx. 900 m, NMW 32008:2.

Colostethus cevallosi

ECUADOR: *Provincia Pastaza*: El Triunfo, 27 km NE Puyo, RMNH 25223; 5 km E Veracruz, 970 m, KU 146237; Canelos, Bobonaza R. 1°35' S, 77°45' W, 480 m, CAS 10327; Palanda, E Sarayacu, Río Bobonaza, about 700 m, USNM 282648 (holotype).

Colostethus chocoensis

ECUADOR: *Provincia Carchi*: Cabeceras del Río Baboso, NE Lita, 600–900 m, MECN 757; *Provincia Pichincha*: Finca Gloria, 15 km NW Alluriquín (5 km NW La Florida), 950 m, RMNH 25233–34; 3.5 km NE Mindo, 1540 m, KU 166157–58; Tandapi, 1460 m, MHNG 18454.1 (C&S), 18454.2, MHNG [GO 30–34, 36 (C&S), 47]; *Provincia Cotopaxi*: vicinity of San Francisco de Las Pampas, MHNG 18370–2, 18852, 19107, 19110 (C&S).

Colostethus delatorreae

ECUADOR: *Provincia Carchi*: approx. 5 km W El Laurel, 2340 m, approx. 25 km E Maldonado, KU 202825 (holotype), 202826, 202977 (back-riding tadpole); Maldonado–Tulcán Road, 18.5 km E Maldonado, 2420 m, KU 220618–20, 26.9–27.3 km E Maldonado, 2420 m, KU 220621, QCAZ 1436; 14 km (airline) SE Maldonado, 2500 m, KU 182197–99, 182200 (C&S), 182202.

Colostethus elachyhistus

ECUADOR: *Provincia Loja*: 2 km NE Sabiango, 850 m, KU 142531; 17 km NE Macará, 1240 m, KU 142518–30; Gonzanamá, QCAZ 945–47; 5 km NE Cariamanga, 1870 m, KU 142532–43, KU 142509–17; 14.4 km S Loja, 2260 m, KU 202820–21; 12 km S Loja, 2250 m, KU 166091–98; 7.6 km S Loja, 2210 m, KU 142350; 4 km S Loja, 2180 m, KU 142344–49; 2 km S Loja, CAS 21849, 21850, 93895–96; 166091–98; Loja, KU 202814–15; Loja, 2150 m, KU 120515–20, 120522–39, 120540 (holotype), 120542 (C&S); 2 km N Loja, 2100 m, KU 142351–76; 3 km W Loja, 2150 m, KU 138800–808; 5 km W Loja, UMMZ 177958; 5.2 km W Loja, 2130 m, KU 202816–17, 202818–19 (C&S); 8 km W Loja, Cerro Uillonaco, UMMZ 177959, 10 km W Loja, 2500 m, KU 138810; 2 km N Loja, 2100 m, KU 142351–76; 2.7 km N San Lucas, 2620 m, KU 182110–11, 182112 (C&S), 182113–17; 6 km N San Lucas, 2760 m, KU 166099.

Colostethus exasperatus

ECUADOR: *Provincia Pastaza*: 5 km E Veracruz, 970 m, KU 146240–41, 146776 (back-riding tadpoles); *Provincia Morona Santiago*: tambo on the trail between Limón and Gualaceo, 10 km SSW Limón, 1707 m, USNM 282532–34; Camp 2, “Yapitya,” 1700 m on the trail from Logroño to Yaupi, west slope of the Cordillera de Cutucú, KU 209648, ANSP 29219; Río Piuntza, 1830 m, Cordillera del Cóndor, KU 147100.

Colostethus fallax

ECUADOR: *Provincia Bolívar*: El Tornado, 2430 m, EPN 3620.

Colostethus fuliginosus

ECUADOR: *Provincia Napo*: Río Azuela, 1740 m, KU 143086–89, KU 166072–75, 166156; 3.2 km NNE Oritoyacu, 1910 m, KU 182104 (C&S), 182105–06; 8.9 km NE Santa Rosa, KU 189934; Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, 146214–17; San José de Moti, (Cantón de Quijos), MNCN 1585 (lectotype), 1586 (paralectotype).

Colostethus infraguttatus

ECUADOR: *Provincia Manabí*: 2.5 km E Puerto Rico, QCAZ 3224–26; Río Ayampe, 70 m, QCAZ 4222–23, 3937–48; Cerro San Sebastián, Parque Nacional Machalilla, 550 m, EPN 3956–63; *Provincia Guayas*:

Cerro Blanco, QCAZ 2635; Cerro Azul Bosque Protector Cerro Blanco, EPN 3949–55; *Bolívar*: Balsapamba, 800 m, KU 132130 (C&S), 132131–36, 132137 (C&S), 132138–41; 6 km ESE Balsapamba, 1270 m, KU 142382–86; *Provincia Chimborazo*: “Puente del Chimbo, the railway terminus about 112 km from Guayaquil, at an elevation of about 304 m,” BM 1947.2.14.7 (lectotype), 1947.2.14.8 (paralectotype); camp at junction of Chiguancay (Chihuancay) and Chanchán rivers, ANSP 18180, 18183–4, 18186, 18189, 18194, 18199; Pallatanga, 1500 m, EPN 2496–2507, 3618; *Provincia Azuay*: 13.5 km W Luz María, 740 m, QCAZ 1200 (tadpoles), 1340, 1341 (back-riding tadpoles), KU 220622–23; 12.9 km W Luz María, 780 m, KU 220624–30, QCAZ 1342–47; W Luz María, 1040 m, QCAZ 1348; 55.4 km E Pasaje, ca. 1000 m, KU 152062–64; *Provincia Guayas*: Río Pescado, AMNH 17511; approx. 16 km (air) W Santa Isabel, 1000m, AMNH 89563–5, 91824, 104346–48, 104841–45; 10 km (air) W Santa Isabel, 1490 m, AMNH 104846–48; Río Minas, 8 km (air) W Santa Isabel, 1440 m, AMNH 104849; *Provincia El Oro*: Uzhcurrumi, MHNG 2383.53–79; ca. 20 km (air) E Pasaje, 240 m, AMNH 91823, 104838–40; 29.2 km E Pasaje, ca. 280 m, KU 152061; 3 km SE Piñas, KU 142408–11; 12.6 km W Piñas, 880 m, KU 142400, 142403–05; 18 km W Piñas, 780 m, KU 166113–16; 18.5 km W Piñas, 620 m, KU 142389, 142392, 142394, 142396, 142398; *Provincia Loja*: Alamor, AMNH 16349–61, 16363–78, 16380–410, 16519–46, 16548–56, 16558–66.

Colostethus jacobuspetersi

ECUADOR: *Provincia Imbabura*: Intag, UMMZ 83688.90; *Provincia Pichincha*: 34 km W of Papallacta on Quito-Baeza Road, 3280 m, KU 189939; 1.5 km E Km-197 marker on Quito-Baeza Road, KU 189940; Barrio Villa Flora, Quito, approx. 2800 m, UMMZ 132929 (3); Quito, EPN 1610; La Chorrera, Monte Pichincha, EPN 1652–55; 6–7 km W Chillogallo, approx. 3000 m, UMMZ 132931 (5); Cotogyacu, Lloa, EPN 1645–48; 6–7 mi W Chillogallo, UMMZ 152791 (C&S); 1.5 km E & 3.5 km S San Juan, 3600 m, KU 182195; 2 km E San Juan, old road Quito–Santo Domingo, UMMZ 132932 (2); 19.8 km W Chillogallo (by road Quito–Chiriboga), 2810 m, QCAZ 1349; Otongoro, W San Juan, on Quito–Chiriboga Road, MHNG 18756.1 (C&S), 18756.2, 18788; 14.8 km (by road) E Chiriboga, 2410 m, KU 182126–28, 182129 (C&S), 182130–33; Hacienda Garzón to Monte Pichincha, 3192 m, ANSP 18241; Antisanilla (SE Pintag), AMNH 20110, 20112–13, 20116–17, 20119, 20122; Hacienda El Beaterio, KU 182134–40; on Aloag–Santo Domingo Road, MHNG 18724; 16 km E Aloag, 2810 m, KU 111572–73; 5 km

W Aloag, N slope Cerro Corazón, 2945 m, KU 109324–25; 7 km W Aloag, N slope Cerro Corazón, 2810 m, KU 109326–27; Salto Dos Novias, N slope Cerro Corazón, 2635 m, KU 109328–32; 20 km W of Aloag, Los Alpes, 2600 m, KU 117933–34, 117937–45, 117949–52; *Provincia Cotopaxi*: Isinlivi, MHNG (GO 45–46), 18926.1–2; 17.6 km E Pilaló, 3440 m, KU 142479; 14.5 km E Pilaló, 3160 m, KU 142465–78; 8 km E Pilaló, Guilo, Páramo de Apagua, 3500 m, KU 132272–78, 5 km E Pilaló, W slope Apagua, 3200 m, KU 132279–98; 3 km E Pilaló, 2900 m, KU 132299–301, 132302 (C&S), 132303–06; Pilaló, 2700 m, KU 120660; Pilaló, 2580 m, KU 132232–71, 132529; Pilaló, 2400 m, KU 182192–94, Pilaló, 2320 m, KU 202893; *Provincia Bolívar*: 6 km SE Chimborazo-Bolívar border on Ambato-Guaranda Road, 3800 m, KU 132314–17; 24.8 km (by road) N Guaranda, 3800 m, KU 182108–09; borderline between Bolívar-Chimborazo provinces on Riobamba-Guaranda Road, 3700 m, KU 132307–13; Bosque Protector Cashca Totoras, 10 km E Santiago, 2700–3400 m, QCAZ 908–11, 1201 (C&S), 1350–55, 1356 (C&S), 1357–61, 1362 (C&S), 1363–91, 1392 (C&S), 1393–1400; *Provincia Chimborazo*: 5 km N Pallatanga, at waterfall at Saint Mary Sanctuary, USNM 282604–16; vicinities of Pallatanga, approx. 1500 m, EPN 3613–14; *Provincia Cañar*: 15 km NW El Tambo, 2840 m, KU 166117.

Colostethus kingsburyi

ECUADOR: *Provincia Napo*: South slope Cordillera del Dué, above Río Coca, 1150 m, KU 122293; *Provincia Tungurahua*: 700 m W Río Negro, Río Pastaza, 1250 m, RMNH 25256; El Topo, Río Pastaza, 1276 m, BM 1947.2.14.5 (lectotype); Hacienda Mapoto, on route between Baños and Mera, 1300 m, UMMZ 89063–64; *Provincia Pastaza*: Abitagua, mountains NW of Puyo, 1200 m, UMMZ 90373–5; Mera, 1000 m, UMMZ 90376; near Mera, UMMZ 90377; Mera, 1140 m, RMNH 25258; Río Pastaza, RMNH 1903 (holotype *Phylllobates intermedius*).

Colostethus lehmanni

COLOMBIA: *Antioquia*: Santa Rita (near Río Nare), 1890–1910 m, LACM 44154–55, 44157–61.

ECUADOR: *Provincia Imbabura*: “Intag,” BM, 78.1.25.17; *Provincia Pichincha*: 4 km W Chiriboga, 2120 m, KU 142428–43, 142444 (C&S), 142445–47, 142448 (C&S), 142449–58; 14 km W Chiriboga, 1960 m, KU 166152–54; Tandapi, 1500 m, KU 138017–29, 138030 (C&S), 138031–42; Tandapi, 1460 m, KU 111574–97, 111598–99, 111603–07, 111610–12, 120662–63, 182188–89; Tandapi, MHNG 18449.1–2,

[GO 13–24, 25–26 (C&S), 27]; 1–2 km NW Tandapi, 1500 m, AMNH 91825–7; vicinity of Santo Domingo de los Colorados, MHNG (GO 1–12, 37–39), 18398.1–4, 18398.6–10, 18398.12–17, 18828.1–5; *Provincia Cotopaxi*: vicinity of San Francisco de Las Pampas, MHNG 18363, 18852, 18294, 18364 (2), 18280.1–2, 18334–1.

Colostethus machalilla

ECUADOR: *Provincia Manabí*: 38 km NW El Carmen, on El Carmen-Pedernales Road, 330 m, KU 220631–33, QCAZ 1401–03; 68 km NW El Carmen, Río Cuaque, on El Carmen-Pedernales Road, 100 m, QCAZ 1404–13, KU 220634–44; *Provincia Guayas*: Manabí-Guayas Border, Río Ayampe, 25 km N Montañita, 1°40' S, 80°47' W, 70 m, KU 220645–59, QCAZ 1414 (holotype) 1415–28; Sector Guale, S Río Ayampe, 70 m, EPN 3973–79; 29.5 km SW Troncal, KU 152067–80, 152081 (C&S), 152082; 17 km NE Naranjal, 10 m, KU 142480–508, 142833 (back-riding tadpoles); Naranjal, MHNG 18982, 18988–9, 18991 (C&S), 18992, QCAZ 912–913; *Provincia Los Ríos*: 4 km N Quevedo, 140 m, KU 132318–38, 132533 (back-riding tadpoles), 138080–82; *Provincia Bolívar*: 10–12 km above Bucay, 515 m, CAS 9436–49.

Colostethus maquipucuna

ECUADOR: *Provincia Pichincha*: 9.4 km SW Tandayapa, 78°42' W, 0°2' S, 2390 m, KU 202880–81, 202882 (holotype).

Colostethus marchesianus

ECUADOR: *Provincia Sucumbios*: Santa Cecilia, 340 m, QCAZ 161, KU 106956–57, 109299–310, 11156270, 122204–10, 139133, 146203–13, 149663–90, 149691 (C&S), 149692–707, UMMZ 129337 (2); Bermejo # 4, 15 km ENE Lumbaqui, 720 m, KU 122211; Puerto Libre, Río Aguarico, 570 m, KU 122212 (C&S), 122213; Limoncocha, KU 182124–25, 183529, QCAZ 3648–50; Limoncocha-Pompeya, QCAZ 1595–97; San Pablo de Kantesiya, QCAZ 2320; Reserva Faunística Cuyabeno, approx. 250 m, QCAZ 2029, 2040, 2060, 2076, 2095, 2118, 2129, 2142, 2163, 2166, 2235, 2250–51, 3356, 3394; Zancudococha, approx. 200 m, QCAZ 2273–74; *Provincia Napo*: Río Yasuní, 150 km upstream Río Napo, KU 175165–66; Río Yasuní, 200 km upstream Río Napo, KU 175167–70; Dureno, 320 m, KU 175485; Francisco Orellana (= Coca), KU 158615, 175486–87, MHNG 2382.53–58, 2382.59 (C&S), 2382.60, QCAZ 450–51, 488; *Provincia Pastaza*: Mera, 1140 m, RMNH 25259; Mera, 1100 m, KU 182203

(C&S), 182204–06; 12 km E Veracruz, El Siguín, 1000 m, KU 120659; Sarayacu, 400 m, KU 120544; 85 km E Montalvo, Pozo Huito, 220 m, RMNH 25251; Montalvo, 350 m, RMNH 25252–5, 25257; *Provincia Morona-Santiago*: Misión Bomboiza, 840 m, KU 147112; Méndez, 500 m, KU 220660, QCAZ 1429–30; *Eastern Ecuador*, AMNH 79993.

Colostethus marmoreiventris

ECUADOR: *Provincia Tungurahua*: Río Negro, 1225 m, USNM 282979 (holotype).

Colostethus mystax

ECUADOR: *Provincia Morona Santiago*: Río Piuntza, 1830 m, KU 147094, 147095 (holotype), 147096–98, 147105.

Colostethus nexipus

ECUADOR: *Provincia Morona Santiago*: 5.3 km NE Plan de Milagro, 1550 m, KU 202822–24; Méndez, 500 m, QCAZ 1431–32, KU 220664; Limón-Indanza, 1200 m, MECN 758–60; Limón (General Plaza Gutiérrez), 1090 m, KU 220661–63, QCAZ 1433–34; immediate environs of Limón, 1097 m, USNM 282686; Los Tayos, from bottom (50 m) of main cave shaft, on walls, KU 194164.

PERU: *San Martín*: 14 km ESE Shapaja, 360 m, KU 211818 (C&S), 211822 (C&S).

Colostethus pulchellus

ECUADOR: *Provincia Carchi*: Tulcán, 3000 m, KU 117881–117913, 117915–16 (C&S), 117918–19 (C&S), 117920–32, 118113 (back-riding tadpoles); Tulcán, 2770 m, KU 182144–57; 182158 (C&S), 182159–62, 182163 (C&S); CAS 9480–84; Atal, near San Gabriel, Montúfar, UMMZ 83687 (10); Monte Olivo, 2450 m, 0°23'33" N, 77°51'39" W, KU 220665–68, QCAZ 1320–24; *Provincia Imbabura*: La Delicia, 2700 m, KU 182190–91; *Provincia Napo*: Chalpi, 2950 m, EPN 2420–26; 0–2.5 km E Papallacta, 10250–10500 ft, UMMZ 167052–53; 3 km ESE Papallacta, 2900 m, KU 117953–58, 117962–63, 117967–77; 3.2 km E Papallacta, 2970 m, KU 143047–53; 4.6 km E Papallacta, Río Papallacta, KU 143046; 5.7 km E Papallacta, 2910 m, KU 143035–45, 143054–56; 8.3 km E Papallacta, 2750 m, KU 182164–65; 11 km E Papallacta, 2660 m, KU 166121–26, 166128–36; 12 km E Papallacta, 2630 m, KU 166137–38; 13.1 km ESE Papallacta, 2610 m, KU 182166; 15 km E Papallacta, 2600 m, KU 127058–79;

22 km W Baeza, AMNH 114709–10; 7.8 km WNW Cuyuja, 2750 m, KU 143023–34; Cuyuja, EPN 1658; 5.0 km WNW Cuyuja, KU 143020–22; 2.5 km WNW Cuyuja, 2550 m, KU 142974–75, 142976 (neotype), 142977–3019; 10 km SE Cuyuja, 2160 m, KU 166139; on Cuyuja-Baeza Road, MHNG 18733.1, 18733.2 (C&S), 18733.3–5, 18733.6 (C&S), 18733.7; 2 km W Baeza, 1910 m, RMNH 25235–38; 3.2 km NNE Oritoyacu, 1910 m, KU 182167–72; Río Azuela, 1740 m, KU 143058–73, 143075–80, 143082–85, 166140–43; Río Azuela, eastern base Volcán Reventador, 1700 m, AMNH 89538–39 (C&S), 89540–49; 60 km E San Miguel de Salcedo, 2550 m, KU 202828–34; faldas S Sumaco, USNM 282637, 282639–41; Sierra Azul, Bosque Aragón, QCAZ 4144 (back-riding tadpoles), 4507–13; Río Cosanga, near Archidona, 800 m, RMNH 1904 (holotype *Phyllobates taeniatus*), RMNH 1906 (2 syntypes *Phyllobates riososangae*); *Provincia Tungurahua*: 8.4 km E Baños, 1590 m, KU 182207–09.

Colostethus pumilus

ECUADOR: *Provincia Azuay*: 3 km W San Vicente, slightly SW of Limón and ca. 35 km E of Gualaceo, 2987 m, USNM 282812–13.

Colostethus sauli

ECUADOR: *Provincia Sucumbíos*: Santa Cecilia, 340 m, KU 109315–20, 109322, 122214–16, 122217 (holotype), 122218–20, 149708–10, 175479–82, 175483 (C&S), 175484; 2 km N Santa Cecilia, Río Conejo, KU 111571; Lago Agrío, 330 m, KU 126289–90, 126291 (C&S); Limoncocha, 300 m, KU 99121, 183530; *Provincia Napo*: Puerto Francisco Orellana (= Coca), 250 m, QCAZ 485–86, MHNG 2382.52; Río Huagra-yacu, S Venecia 1°7' S, 77°42' W, UMMZ 182477–79; Río Cotapino, UMMZ 90372 (1 of 2 specimens); *Provincia Pastaza*: Locación Petrolera Garza 1, NE Montalvo, 300 m, QCAZ 1435.

Colostethus shuar

ECUADOR: *Provincia Napo*: Río Azuela, 1740 m, KU 143057, 143074, 143081, 166143, 166155; Río Azuela, 1700 m, eastern base Volcán Reventador, AMNH 89572–3; 11.1 km NE Santa Rosa on Lago Agrío Road, KU 189941; 8.9 km NE Santa Rosa on Lago Agrío Road, KU 189942; *Provincia Tungurahua*: El Topo, Río Pastaza, 1272 m, BM 1947.2.14.3 (Syntype *C. kingsburyi*); 1.3 km W Río Verde, 1570 m, KU 142558–63, 142564–65 (C&S), 142566–72; 18.5 km E Baños, 1600 m; *Provincia Morona Santiago*: 2 km WSW Plan

de Milagro, 1980 m, KU 202883; 5.2 km WSW Plan de Milagro, 2160 m, KU 202884–88; 8.8 km WSW Plan de Milagro, 2370 m, KU 202889–90; Río Piuntza, 1830 m, KU 147091 (holotype), 147092; *Provincia Zamora Chinchipe*: 19 km W Zamora, 1630 m, KU 142548–49; 21.5 km W Zamora, 1620 m, KU 142550–55; 22.6 km W Zamora, 1700 m, KU 142556–57; Quebrada Zurita, Loma Trigal, Loja-Zamora Road, 03°58'06" S, 79°6'42" W, EPN 2492–95.

Colostethus talamancae

ECUADOR: *Provincia Esmeraldas*: La Sexta, (near Quinindé), approx. 500 m, MHNG 18571; Viche, 200m, QCAZ 5033; *Provincia Pichincha*: Reserva Forestal Endesa, km 113 on Quito–Puerto Quito Road (E Pedro Vicente Maldonado), 800 m, MHNG 18787.

Colostethus toachi

ECUADOR: *Provincia Esmeraldas*: "Cachabe" (Cachabí) BM 98.3.1.10–11; *Provincia Carchi*: Maldonado, 1410 m, KU 182196; *Provincia Pichincha*: Rancho Brahman, 10 km NW Santo Domingo de los Colorados, 400 m, KU 109333; Tinalandia, 15.5 km SE Santo Domingo de los Colorados, 700 m, KU 202891; Finca Gloria, 15 km NW Alluriquín (5 km NW La Florida), 0°15' S, 79°01' W, 950 m, RMNH 25248–50, QCAZ 1437 (holotype), 1438; Hacienda Espinosa, 9 km W Santo Domingo de los Colorados, road to Chone, CAS 10590–96; Hacienda Delta, 8 km SE Santo Domingo de los Colorados, UMMZ 132933 (4431, 4436), 55506; Río Baba, 5–10 km SSW Santo Domingo de los Colorados, 500 m, AMNH 89550–62.

Colostethus vertebralis

ECUADOR: *Provincia Chimborazo*: 30 mi S Alausí, CAS 85179; *Provincia Cañar*: 20 km N Gun (junction Road), 2918 m, Chunchi–El Tambo Road, UMMZ 132934 (15); 7.6 km N Zhud, 2880 m, QCAZ 1439; Río Cebadas, Cebadas, EPN 2487; Alpachaca, sector Silante Alto, EPN 2490–91; 8 km SE Cañar, 3000 m, AMNH 89569; 15 km SSE Cañar road to Azogues, UMMZ 138596 (7); 8 km NW Biblián, 3420 m, KU 132211–31; 5.6 km NNW Biblián, 2920 m, KU 202867–72; 4.5 km NW Biblián, 2085 m; 3 km S Azogues, 2500 m, KU 137991–138005; *Provincia Azuay*: Simincay, 8300 ft, AMNH 17458, 17604–8; 3 km NW Girón, 2100 m, AMNH 89566–68; Laguna de Zurucuchu (= Llaviuco in recent maps), 16 km NW Cuenca, KU 120612–31,

202836–47; Río Mazán, 3150 m, KU 202714–15; Río Mazán, 3000–3500 m, EPN 2376–77; Cuenca, 2540 m, KU 120603–11; NW edge of Cuenca, 2650 m, KU 182181–87; 8 km N Cuenca from tributary stream to Río Matadera, Quinta of J. S. Strobel, 79° W, 28° S, 2500 m, CAS 94095–99; 10–15 km E Luz María, approx. 2500 m, KU 220675–81, QCAZ 1440–45; 0.9 km W Luz María, 1770 m, QCAZ 1446–47 (back-riding tadpoles), KU 220674; vicinity Lake Zurucuchu (= Llaviuco in recent maps), 28 km SW Cuenca, CAS 94106; 10 km SW Victoria del Portete, 2700 m, KU 132142–210; 10 km NE Girón, 2750 m, KU 202835; 11 mi W Cuenca, CAS 85162; 4 km E Cuenca, 2540 m, KU 137925–90; 11.5 km SE Gualaceo, 2940 m, KU 202848–58; 14.3 km SE Gualaceo, 3090 m, KU 202859; 17.6 km SE Gualaceo, 3150 m, KU 202860–63; 12.9 km SW La Paz, 2720 m, KU 202864–65; 5.7 km SW La Paz, 3000 m, KU 202866; Sevilla de Oro, 82 km E Cuenca, CAS 94103; 0.8 km S Cutchil, 2535 m, KU 141545–46; 3.5 km S Cutchil, 2785 m, KU 141533–35; 6.2 km S Cutchil, 2800 m, KU 220682, QCAZ 1448; 7 km E Sigsig, 2890 m, QCAZ 1449–51, KU 220669–73; Sigsig, 2450 m, QCAZ 1205 (C&S), 1452–53, 56; Río Ayllón (Santa Bárbara), Sigsig, 2940 m, QCAZ 1454 (C&S), 1455; km 79, along Pan-American Highway Cuenca–Loja, CAS 94104, CAS-SU 22953–54; Laguna Busa, Cantón San Fernando, 2830 m, EPN 2464, 2466, 2468, 2474–75, 2480, 2488; Shila, Parroquia Oña, 2250 m, EPN 2447; Río Shio, Parroquia Principal, EPN 2473; *Provincia Loja*: 87 km N Loja, San Antonio de Cumbe, 3020 m, EPN 2427–32, 2434–38, 2441–46, 2449–57; 12 km NE Urdaneta, 3000 m, KU 182179–80; 11 km NE Urdaneta, 2970 m, KU 142325–35, 142337–43; 10 km NE Urdaneta, 2850 m, KU 166150, 51; 9.9 km NE Urdaneta, 2910 m, KU 202874–75; 2 km SSW Urdaneta, 2250 m, KU 166070–71; Saraguro, Barrio Lagunas, EPN 2433, 2439–40, 2448, 2458, 2462; Saraguro, 2500–2510 m, KU 138006–16, 141547–61, 142412–24; 2 km S Saraguro, 2680 m, KU 142425–27; 2 km SSW Saraguro, 2560 m, KU 182178; 3.7 km S Saraguro, 2800 m, KU 202873; 8–9 km N San Lucas, 3000–3100 m, KU 120545–69; 10 km S Saraguro, 3050 m, KU 166144–49; *Provincia Morona Santiago*: 8 km S Cutchil, KU 120570–602; 11.5 km S Cutchil, 2820 m, KU 141536–44; 28 km WSW Plan de Milagro, KU 202876–79.

Colostethus whymperi

ECUADOR: *Provincia Pichincha*: Tanti, 608 m (2000 ft), BM 1942.2.14.25 (holotype); *Provincia Cotopaxi*: vicinity of San Francisco de Las Pampas, between 600–1800 m, MHNG (GO 41–43).

PLATE 1



A. *Colostethus sauli*, KU 122217.



B. *Colostethus exasperatus*, KU 146241.



C. *Colostethus kingsburyi*, KU 122293.



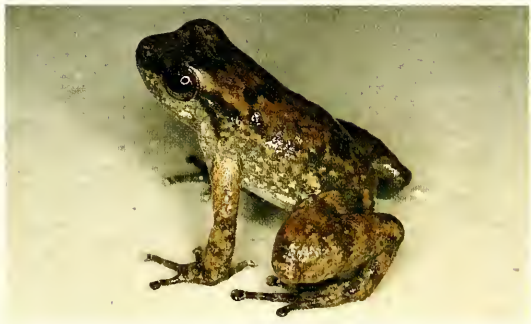
D. *Colostethus pulchellus*, KU 143023.



E. *Colostethus fuliginosus*, KU 166072.



F. *Colostethus shuar*, KU 166155.



G. *Colostethus bocagei*, KU 122211.



H. *Colostethus marchesianus*, KU 122205.

PLATE 2



A. *Colostethus vertebralis*, KU 120545.



B. *Colostethus elachyhistus*, KU 120515.



C. *Colostethus awa*, QCAZ 1327.



D. *Colostethus machalilla*, Río Ayampe, Manabí, Ecuador.



E. *Colostethus anthracinus*, KU 1206636.



F. *Colostethus infraguttatus*, KU 166113.



G. *Colostethus jacobuspetersi*, KU 166117.



H. *Colostethus lehmanni*, KU 166152.

PLATE 3



A. *Colostethus nexipus*, Santiago, Morona Santiago, Ecuador.



B. *Colostethus breviquarum*, MECN (LAC 1256–58).



C. *Colostethus toachi*, LAC 738.



D. *Colostethus delatorreae*, KU (LA 507).



E. *Colostethus talamancae*, QCAZ 5033.

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