

NUMBER 268  
JULY 12, 1975

TWO NEW SPECIES OF *COLOSTETHUS*  
(AMPHIBIA: ANURA: DENDROBATIDAE) FROM COLOMBIA

By PHILIP A. SILVERSTONE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE



Published by the NATURAL HISTORY MUSEUM  
OF LOS ANGELES COUNTY  
900 Exposition Boulevard, Los Angeles, California 90007

SERIAL PUBLICATIONS OF THE  
NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

Prior to November 30, 1973, publications of the Natural History Museum have appeared under various formats—*Leaflet Series, Museum Graphic, Science Series, Study Guides, Contributions in Science, Contributions in History, Science Bulletins*, unnumbered catalogs of exhibitions, and other miscellaneous publications. The Museum now publishes the following serials at irregular intervals as CONTRIBUTIONS IN SCIENCE, HISTORY BULLETINS, SCIENCE BULLETINS, EDUCATION SERIES, HISTORY SERIES, and SCIENCE SERIES. The Contributions are short papers of octavo size. The Bulletins are longer, comprehensive papers of quarto size. The Series are papers of variable lengths of quarto or larger size. Papers in each serial are numbered separately and consecutively.

CONTRIBUTIONS IN SCIENCE contain articles in the earth and life sciences, presenting results of original research. Emphasis is intended principally for papers allied to biosystematic research, but other subjects and review-oriented ones will be considered. Number 1 was issued on January 23, 1957. Contributions must be not less than 8 nor exceed 72 printed pages.

INSTRUCTIONS FOR AUTHORS

Acceptance of manuscripts will be determined by the significance of new information. Priority will be given to manuscripts by staff members. All manuscripts must be recommended by the curator in charge of each discipline or by the Editorial Board. *Manuscripts must conform to the specifications listed below.* They will be examined for suitability by the Editorial Board and will include review by specialists outside the Museum.

Authors must adhere to the International Code of Nomenclature of Bacteria and Viruses, International Code of Botanical Nomenclature, and International Code of Zoological Nomenclature, including their respective recommendations. Further, authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that all primary types have been deposited in an appropriate scientific institution of their choice and must cite that institution by name.

MANUSCRIPT FORM.—(1) In preparation of copy follow the 1972 CBE Style Manual, third edition (AIBS), Chapters 5 and 6. (2) Footnotes should be avoided; acknowledgments as footnotes will not be accepted. (3) An informative abstract must be included for all papers. (4) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. (5) A differential diagnosis must accompany any newly proposed taxon. (6) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in proper proportions for reduction to CONTRIBUTIONS page size. In preparing illustrations and legends consult the 1972 CBE Style Manual, third edition (AIBS), Chapter 5. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Submit duplicate copies of all illustrations. Original illustrations will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. No changes or alterations, other than typesetting corrections, will be allowed unless paid by author. Requests for reprints may be placed through the Editor.

*Editor*

All communications concerning CONTRIBUTIONS IN SCIENCE should be sent to the Editor, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007

TWO NEW SPECIES OF *COLOSTETHUS*  
(AMPHIBIA: ANURA: DENDROBATIDAE) FROM COLOMBIA<sup>1</sup>

By PHILIP A. SILVERSTONE<sup>2</sup>

ABSTRACT: Two new species of dendrobatid frogs are described from Colombia: *Colostethus abditaurantius* from Bello, Departamento de Antioquia, and *C. imbricolus* from the Alto del Buey, Departamento del Chocó. *C. abditaurantius* has extensively webbed toes, an orange calf-spot, and lacks a pale lateral stripe. *C. imbricolus* has basally webbed toes, an orange calf-spot, and an incomplete pale lateral stripe.

INTRODUCTION

During field studies in Colombia in 1971, I collected specimens of two undescribed species of dendrobatid frogs belonging to the genus *Colostethus*. The two species are described in this paper.

ACKNOWLEDGMENTS

Field work was supported by the Natural History Museum of Los Angeles County Foundation. Collections were made under a scientific hunting license issued by INDERENA, for which I thank S. M. Franky V. and J. Hernández C. I thank J. W. Wright, R. L. Bezy, and F. Truxal, Natural History Museum of Los Angeles County (LACM), Reverendo Hermano Nicéforo María and Reverendo Hermano Daniel, Instituto de La Salle, Bogotá, and C. J. Marinkelle, Universidad de los Andes, Bogotá, for their aid. The photographs are by the photographic staff of the Natural History Museum of Los Angeles County.

*Colostethus abditaurantius* new species

Figures 1 and 2

*Holotype*.— LACM 72000, collected at the Quebrada Altagracia, Bello, Departamento de Antioquia, Colombia, about 1450 m elevation, 28 August 1971, by P. A. Silverstone.

*Topoparatypes*.—Two specimens, LACM 71999 and PAS 1003.71 (deposited with INDERENA), same data.

*Definition*.—Snout-vent length (SVL) moderate (27-30 mm in known adult specimens); skin slightly granular on dorsum, smooth on venter; first finger

<sup>1</sup>REVIEW COMMITTEE FOR THIS CONTRIBUTION

Robert L. Bezy  
John R. Meyer  
Norman J. Scott  
John W. Wright

<sup>2</sup>Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

slightly shorter than second; third finger of adult male not swollen; toes three-fourths webbed; pale ventrolateral, lateral, dorsolateral, and vertebral stripes absent; ventral spotting and marbling absent; throat of male not uniformly dark, not contrasting with color of belly; pale spot (orange in life, indistinguishable from white ground color in preservative) on proximoventral surface of calf.

*Diagnosis.*—*Colostethus abditaurantius* differs from all described species of *Colostethus* in having a combination of two characteristics: a pale proximoventral calf-spot in life and extensively webbed toes. *C. imbricolus* and some specimens of *C. subpunctatus* also have a pale proximoventral calf-spot. *C. abditaurantius* differs from *C. imbricolus* in having extensively webbed toes, in lacking a pale lateral stripe, and in having an immaculate white venter (*C. imbricolus* has basally webbed toes, an incomplete pale lateral stripe, and a dark venter with pale spots that



FIGURE 1. *Colostethus abditaurantius*, dorsal aspect. Left: holotype, LACM 72000, female, 30.0 mm snout-vent length. Right: paratype, LACM 71999, male, 27.0 mm snout-vent length.

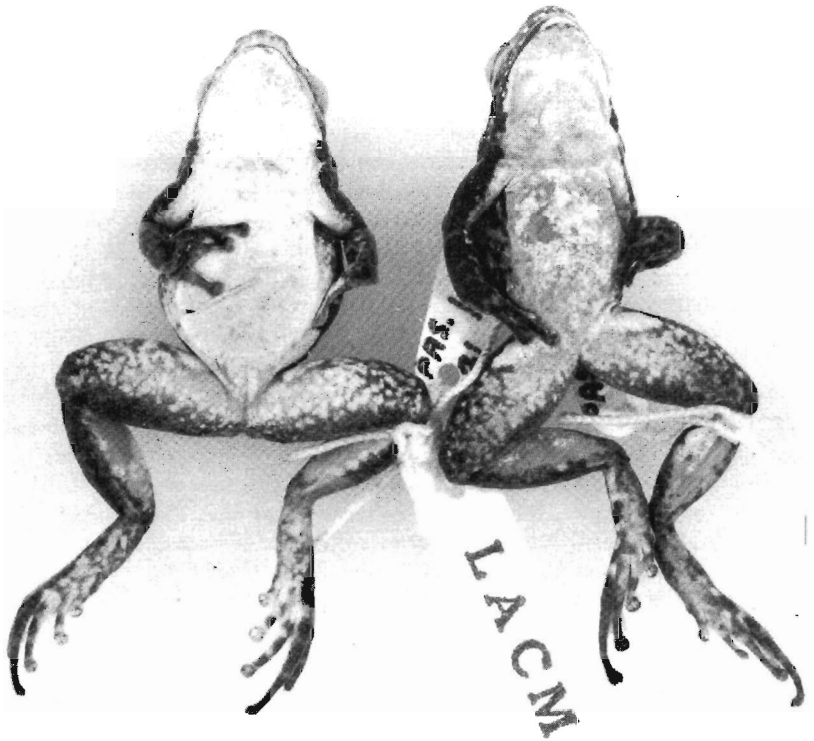


FIGURE 2. *Colostethus abditaurantius*, ventral aspect. Left: holotype, LACM 72000. Right: paratype, LACM 71999.

are blue in life). *C. abditaurantius* differs from *C. subpunctatus* in having extensively webbed toes, and in lacking pale lateral and vertebral stripes (*C. subpunctatus* has basally webbed toes, has a complete pale lateral stripe, and often has a pale vertebral stripe). *C. bocagei*, *C. chocoensis*, *C. collaris*, *C. dunnii*, *C. fuliginosus*, *C. palmatus*, *C. riveroi*, *C. shrevei*, and *C. vergeli* also have extensively webbed toes. *C. abditaurantius* differs from them in having a pale proximoventral calf-spot in life. It further differs from *C. collaris* and *C. riveroi* in lacking a dark breast-band, from *C. palmatus* in having a smooth belly, and from *C. collaris*, *C. dunnii*, *C. palmatus*, *C. shrevei*, and *C. vergeli* in lacking a pale lateral stripe. *C. abditaurantius* differs from *Phyllobates pictus* (which also has a pale proximoventral calf-spot) in having teeth, in having toe webbing, in lacking a pale lateral stripe, and in lacking ventral marbling (*P. pictus* usually lacks teeth, lacks toe webbing, has a complete pale lateral stripe, and has dark or pale ventral marbling).

*Description of holotype and LACM paratype.*—The characteristics of the holotype are given first, followed in parentheses by the characteristics of the paratype, when they differ. The holotype is an adult female, 30.0 mm SVL (the paratype is an adult male, 27.0 mm SVL). The width of the body between the axillae is 35 percent (31 percent) of SVL. The length of the calf is 47 percent (50 percent) of SVL. The skin of the dorsum is slightly granular; the skin of the venter is smooth. A few ill-defined tubercles occur on the posterior portion of the upper sides of the body; a large, ill-defined tubercle occurs just back of the corner of the mouth. A longitudinal swelling extends from the posterior corner of the eye to the shoulder, concealing the posterodorsal portion of the tympanum. Maxillary and premaxillary teeth are present; vomerine teeth are absent. The end of the snout is rounded in dorsal and lateral aspects. The canthus rostralis is rounded on the left side of the snout and angular on the right side. The loreal region is slightly concave. The interorbital distance is a little greater than the width of the upper eyelid. The diameter of the eye is almost twice the distance from the eye to the nostril and 2.3 times the diameter of the tympanum. The tympanum is round and somewhat indistinct; its posterodorsal portion is concealed. The finger disks are small relative to those of *Dendrobates*; they are about 1.5 times the width of the fingers. The first finger is slightly shorter than the second. The fingers are fringed but not webbed. A subarticular tubercle juts from the ventral surface of each phalangeal joint. An oblong inner and round outer tubercle protrude from the ventral surface of both the metacarpus and metatarsus. The tarsal fold is flaplike and slightly curved at its proximal extremity; it extends along the distal two-fifths of the distance between the inner metatarsal tubercle and the heel fold. The tarsal tubercle is absent. The toes are fringed and about three-fourths webbed (Fig. 3). The webbing formula (Savage and Heyer 1967) is:

$$\begin{array}{l} \text{I } 1^{-}2 \text{ II } 1-2.5 \text{ III } 2^{-}3 \text{ IV } 3^{-}1 \text{ V} \\ (\text{I } 1-2^{-} \text{ II } 1^{+}2.5 \text{ III } 2-3 \text{ IV } 3-1.5 \text{ V}). \end{array}$$

Color and color pattern: In life, the head and back were dark gray. Stripes were absent. White spots adorned the side of the head and body and the ventral surface of the thigh. There was an orange spot in the axilla, another in the groin, and another on the proximoventral surface of the calf. The throat, breast, and belly were white.

In preservative, the head and back are immaculate dark brown (the head and back are pale brown, with the following dark brown areas: three spots on the dorsal surface of the snout; an interorbital band, connecting posteriorly with a short median stripe; an undulating chevron on the back, with its apex posterior; the lateral borders of the mid-back; and extensive irregularly shaped areas on the posterior back). There are no pale ventrolateral, lateral, dorsolateral, or vertebral stripes. The upper lip is bordered with white, above which, to the level of the nostril, it is dark brown with a few small whitish spots (the upper lip is entirely dark brown, except for a whitish area on the tip of the snout); the side of the snout above the level of the nostril is immaculate dark brown, except for a short whitish stripe running from the eye almost to the nostril. The lower lip is white

with dark brown mottling, except at its posterior end, where it is brown with a few small white spots. The tympanum is white. The upper portion of the side of the body is dark brown, not contrasting strongly with the dark brown ground color of the dorsum (contrasting strongly with the light brown ground color of the dorsum); each side bears more than 25 small white spots. A white spot lies in the axilla. Four or five white spots decorate the side of the body on the border between the brown dorsal and white ventral ground colors; the most posterior of these spots lies in the groin. The dorsal surface of the forelimb is light brown, with a dark brown transverse band at the midpoint of the lower arm. The dorsal surface of the first and second fingers is much paler than that of the third and fourth fingers. The anterior surface of the upper arm is dark brown; that of the lower arm is mostly white. The ventral surface of the forelimb is white. The dorsal surface of the hind limb is light brown, with a dark brown transverse band on the thigh at a point one-third of the distance from the groin to the knee, another at the midpoint of the calf, and two more on the plantar surface of the tarsus (the

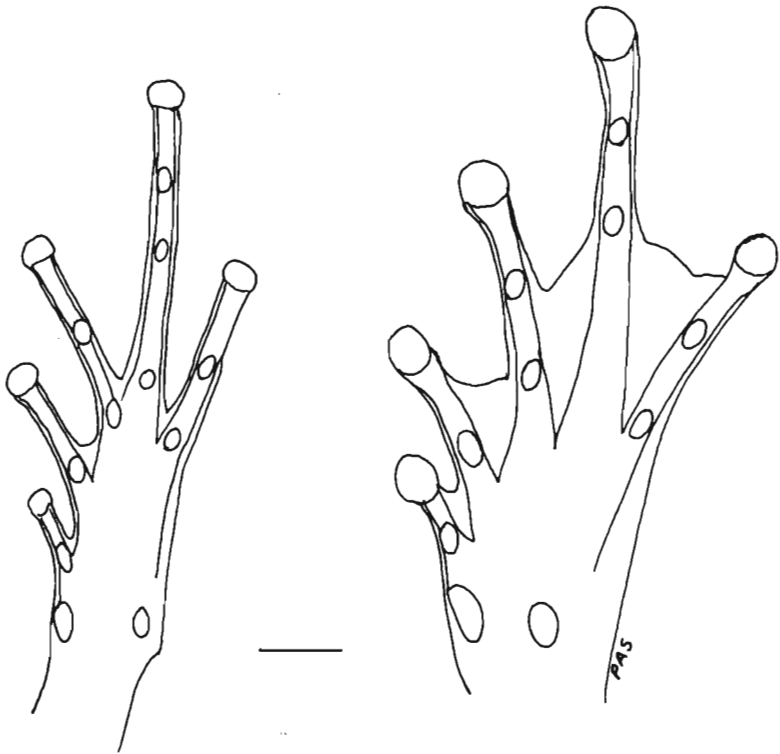


FIGURE 3. Left foot, ventral aspect. Left: *Colostethus imbricolus*, holotype, LACM 71998. Right: *Colostethus abditaurantius*, paratype, LACM 71999. Line equals one millimeter.

transverse bands are darker and better defined, and the band on the thigh is slightly more distal). There is no light hook-shaped mark on the thigh. The dorsal surface of the first, second, and third toes is much paler than that of the fourth and fifth toes. The toe webbing is white. The proximal half of the anterior surface of the thigh bears a dark brown longitudinal stripe and three white spots (the spots are confluent and blend into the ventral ground color). The posterior surface of the thigh is dark brown with small oblong white spots. The median portion of the ventral surface of the thigh is white; this white area is surrounded by light brown (dark brown) borders, broken by extensive white mottling. The ventral surface of the calf is white. The throat, breast, and belly are immaculate white, except for a small amount of dark brown on the chin and lower lips.

The surfaces of the muscles are pale flesh color with flecks of brown pigment; the flecks are sparse on the dorsum and absent on the venter.

*Type locality*.—Bello is a town in the Cordillera Central, in the Departamento de Antioquia, Colombia, 10 km north of Medellín. It has an elevation of 1450 m and a mean annual temperature of 22° C (data from the Oficina Departamental de Estadística de Antioquia).

*Etymology*.—The name *abditaurantius* (from Latin: *abditus* = hidden, and *aurantius* = orange color) refers to the orange spots, which are concealed when the frog is in a sitting position.

### *Colostethus imbricolus* new species

#### Figure 4

*Holotype*.—LACM 71998, collected at the upper Quebrada Mutatá, Alto del Buey, Departamento del Chocó, Colombia, about 200 to 300 m elevation, 22 August 1971, by Philip A. Silverstone.

*Topoparatypes*.—Sixteen specimens, LACM 71983-97 and PAS 924.71 (deposited with Inderena), same data.

*Definition*.—Snout-vent length moderate (28.5 mm in only known adult specimen); skin smooth except for few tubercles on posterior back; first finger slightly shorter than second; toes basally webbed; pale ventrolateral and vertebral stripes absent; incomplete pale lateral stripe present; pale dorsolateral stripe present (but ill defined) in life, absent in preservative; venter dark with numerous small pale (blue in life) spots; throat of male not uniformly dark, but contrasting with color of belly; pale spot (orange in life, pink or white in preservative) on proximoventral surface of calf.

*Diagnosis*.—*Colostethus imbricolus* differs from all described species of *Colostethus* in having a combination of three characteristics: a pale proximoventral calf-spot, basally webbed toes, and an incomplete pale lateral stripe. *C. abditaurantius* and some specimens of *C. subpunctatus* also have a pale proximoventral calf-spot. *C. imbricolus* differs from *C. abditaurantius* in having basally webbed toes, an incomplete pale lateral stripe, and a dark venter with small pale spots that are blue in life (*C. abditaurantius* has extensively webbed toes, lacks a pale lateral stripe, and has an immaculate white venter). *C. imbricolus* dif-



fers from *C. subpunctatus* in having an incomplete pale lateral stripe and in lacking a pale vertebral stripe (*C. subpunctatus* has a complete pale lateral stripe and often has a pale vertebral stripe). *C. imbricolus* further differs from some or all of the other Chocoan species of *Colostethus* in having basally webbed toes (the toes are extensively webbed in *C. chocoensis* and webless in *C. nubicola*, *C. pratti*, and *C. talamancae*), in having an incomplete pale lateral stripe (the stripe is complete in *C. nubicola* and absent in *C. chocoensis* and *C. talamancae*), in having a dark venter with small pale spots that are blue in life (the venter is not so patterned and lacks blue in *C. inguinalis*, *C. latinasus*, *C. nubicola*, *C. pratti*, and *C. talamancae*), and in lacking a contrasting dark throat and pale belly in males (males have this pattern in *C. inguinalis*, some populations of *C. nubicola*, and *C. talamancae*). *Colostethus imbricolus* resembles *Phyllobates pictus* in having a pale spot on the proximoventral surface of the calf, but differs from *P. pictus* in the following respects: (1) the maxillary and premaxillary teeth are present (the teeth usually are absent in *P. pictus*); (2) the toes are basally webbed (the toes are webless in *P. pictus*); (3) the muscles are more sparsely pigmented than in *P. pictus*; (4) the first finger is shorter than the second (the first finger is equal to or longer than the second in *P. pictus*); (5) the pale lateral stripe is incomplete (the pale lateral stripe is complete in *P. pictus*); (6) the skin of the dorsum is smooth, except for a few posterior tubercles (the skin of the dorsum is granular in *P. pictus*).

*Description of holotype.*—The holotype is an adult female, 28.5 mm SVL. The width of the body between the axillae is 23 percent of SVL. The length of the calf is 40 percent of SVL. The skin is smooth, except for a few low tubercles on the extreme posterior back and a few wrinkles on the posterior belly. Maxillary and premaxillary teeth are present; vomerine teeth are absent. The end of the

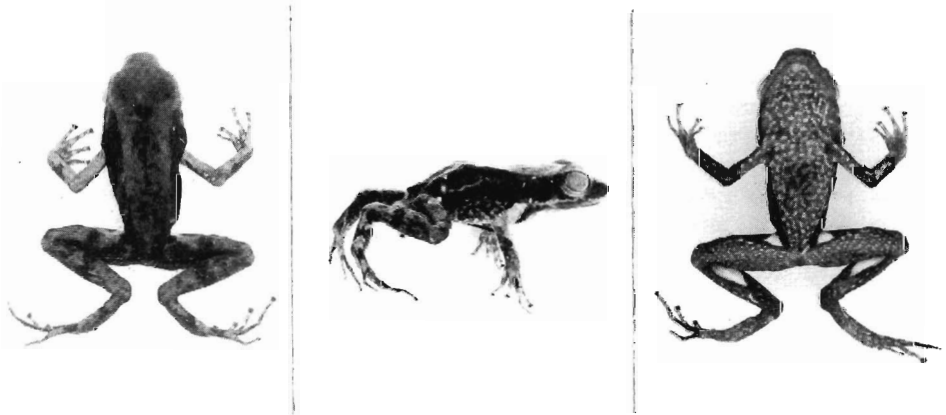


FIGURE 4. *Colostethus imbricolus*, holotype, LACM 71998, female, 28.5 mm snout-vent length. Left: dorsal aspect; center: lateral aspect; right: ventral aspect.

snout is truncate in dorsal aspect and rounded in lateral aspect. The canthus rostralis is angular. The loreal region is slightly concave. The interorbital distance is a little greater than the width of the upper eyelid. The diameter of the eye is 1.4 times the distance from the eye to the nostril and almost three times the diameter of the tympanum. The tympanum is round; its posterodorsal portion is concealed. The finger disks are small relative to those of *Dendrobates*; they are about 1.5 times the width of the fingers. The first finger is slightly shorter than the second. The fingers lack fringes and webbing. A subarticular tubercle juts from the ventral surface of each phalangeal joint. An oblong inner and round outer tubercle protrude from the ventral surface of both the metacarpus and metatarsus. The tarsal fold is ridgelike and slightly curved. The tarsal tubercle is ill defined. The toes are fringed and basally webbed (Fig. 3). The webbing formula (Savage and Heyer 1967) is:

$$I \ 2^-2.5 \ II \ 2^-3 \ III \ 3^-4 \ IV \ 4^+3^- \ V.$$

Color and color pattern: In life, the head and back were dark brown with a pair of dull gold dorsolateral stripes, which were broad and ill defined on the back and narrow and well defined on the snout. The iris was black. The upper lip bore a gold stripe. The side of the body was black; it bore an incomplete gold lateral stripe. The dorsal surface of the hind limb was light brown with black transverse bands. There was a bright orange spot in the axilla, another on the proximoanterior surface of the thigh, and another on the proximoventral surface of the calf. The throat, breast, belly, and most of the ventral surface of the limbs were black with many small light blue spots.

In preservative, the head and back are light brown with scattered dark brown mottling. There are no pale ventrolateral or vertebral stripes. The dorsolateral stripes have disappeared. An undulating white stripe extends from the arm insertion to a point beneath the anterior corner of the eye. Ventral to this, another white stripe begins at the posterior corner of the mouth and continues along the edge of the upper lip and around the tip of the snout. The side of the head and body is dark brown, except for white spots on the lower portion of the side of the body. A large white spot lies in the axilla. An incomplete undulating white lateral stripe extends from the groin to a point about three-fourths of the horizontal distance from the groin to the axilla, and three-fourths of the vertical distance from the belly to the back. The anterior portion of the stripe is ill defined. On the right side, the stripe bears a small break midway between the groin and axilla. The dorsal surface of the forelimb is tan. The anterior, posterior, and ventral surfaces of the forelimb are light brown with small white spots, except the anterior surface of the upper arm, which bears an elongate, dark brown, diagonal triangle, whose apex is distal. The dorsal surface of the hind limb is tan, with a dark brown transverse band at mid-thigh, another at mid-calf, and another at mid-tarsus, a dark brown proximal area on the thigh (surrounding an indistinct light brown hook-shaped mark), and irregular dark brown proximal areas on the calf. The anterior and posterior surfaces of the thigh are dark brown with a few small white

spots; a large white spot adorns the proximoanterior surface of the thigh. The ventral surface of the hind limb is light brown with many small white spots, except the proximal half of the calf, which bears a large, oblong white spot. The throat, breast, and belly are light brown, covered with numerous, small, close-set, elongate, sometimes curved white spots.

The surfaces of the muscles are pale flesh color with flecks of brown pigment; the flecks are fairly numerous on the dorsum and sparse on the venter.

*Description of paratypes.*—The 15 LACM paratypes, measured to the nearest one-half millimeter, vary from 16.0 to 20.5 mm SVL, with a mean of 18.4 mm (the mean for all 16 LACM specimens, including the 28.5 mm holotype, is 20.9 mm). All the paratypes are juveniles. They resemble the holotype. In some paratypes, the posterior belly is slightly granular. The end of the snout is vertical to rounded in lateral aspect. In some paratypes, the tarsal tubercle is well defined; in others, it is absent. Some specimens lack toe fringes, but this may be an artifact of preservation.

*Color and color pattern:* In life, the colors resembled those of the holotype, except that the ventral surface of the thigh was entirely light brown in some paratypes (it was black with blue spots, as in the holotype, in the others).

In preservative, the dorsolateral stripes have disappeared. The pale lateral stripe extends only half-way along the side of the body; in a few specimens, the stripe is broken into three white spots. In the four smallest paratypes, the dark brown limb-bands contrast more strongly with the pale ground color than in the holotype; in these specimens, the dorsal surface of the thigh bears a white proximal hook-shaped mark (surrounded by dark brown) and three dark brown transverse bands. The most distal band meets a longitudinal dark brown stripe on the anterior surface of the thigh. The calf and the tarsus each have two dark brown transverse dorsal bands. In some of the larger paratypes (e.g., LACM 71995), the dark brown transverse bands cover most of the dorsal surface of the hind limb. In those specimens where the ventral surface of the thigh was uniform light brown in life, the light brown has become white in preservative. The white spot on the proximoventral surface of the calf covers from one-half to three-fourths of the length of the calf. In LACM 71992, the distal portion of the calf-spot narrows into an undulating stripe. The throat, breast, and belly are light gray or brown; they bear white markings, varying from tiny discrete white spots, to spots partially coalescing into marbling, to close-set marbling without discrete spots.

*Type locality.*—The Alto del Buey is a mountain in the Serranía de Baudó, in the Departamento del Chocó, Colombia. It lies in Holdridge's (1967) lowland tropical rain forest zone, near the Pacific coast, on the divide between the Pacific drainage (the Río del Valle to the west and the Río Baudó to the south) and the Caribbean drainage (the Río Atrato to the east and northeast). The American Geographic Society map NB-18 (scale 1:1,000,000) incorrectly shows the elevation of the summit of the Alto del Buey as 1810 m; the actual elevation (shown on a summit marker and corroborated by my altimeter) is 1070 m. The type series of *C. imbricolus* was collected in the daytime, at the base of the Alto del Buey, on the

bank of the upper Quebrada Mutatá (a tributary of the Río del Valle), at an elevation of about 200 to 300 m. The quebrada flows through virgin forest.

*Etymology.*—The name *imbricolus* (from Latin: *imber* = rain, and *colus* = inhabiting) refers to the climate of the type locality.

*Generic allocation.*—The discovery of *C. imbricolus* further narrows the distinction between the genera *Phyllobates* and *Colostethus* (see Silverstone 1975). *C. imbricolus* is allocated to the genus *Colostethus* because: (1) the first finger is shorter than the second finger (this characteristic varies in *Colostethus*, but in all species of *Phyllobates*, the first finger is equal to or longer than the second finger); (2) the color of the muscles is pale, as in *Colostethus* (Savage 1968); (3) the dorsal and lateral coloration resembles that of many species of *Colostethus*.

#### RESUMEN

En esta obra se describen dos nuevas especies de *Colostethus* (Amphibia: Anura: Dendrobatidae) procedentes de Colombia: *C. abditaurantius* de Bello, Departamento de Antioquia, y *C. imbricolus* del Alto del Buey, Departamento del Chocó. Ambas especies tienen una pinta anaranjada en la pantorrilla. *C. abditaurantius* carece de una lista lateral y tiene la membrana interdigital bien desarrollada. *C. imbricolus* tiene una lista lateral parcial y tiene la membrana interdigital escasamente desarrollada.

#### LITERATURE CITED

- HOLDRIDGE, L. R. 1967. Life zone ecology. Revised ed. Tropical Science Center, San José, Costa Rica. 206 pp.
- SAVAGE, J. M. 1968. The dendrobatid frogs of Central America. *Copeia* 1968:745-776.
- SAVAGE, J. M., AND W. R. HEYER. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. *Beitr. Neotrop. Fauna* 5:111-131.
- SILVERSTONE, P. A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Nat. Hist. Mus. Los Angeles Co., Sci. Bull.* 21:1-55.