

Two new species of *Colostethus* (Anura: Dendrobatidae) from the Venezuelan Guayana

CÉSAR L. BARRIO-AMORÓS, OSWALDO FUENTES & GILSON RIVAS

Abstract

Two new species of *Colostethus* are described from Venezuelan Guayana. Both inhabit low tepuis or lowlands at the base of tepuis (350-700 m above sea level in Cerro Santa Rosa and 150 m above sea level in the Cuao-Sipapo massif) and are small species (up to 22 mm adult SVL). They share an oblique lateral stripe, lack dorsolateral and ventrolateral stripes and the finger III is not expanded in males. Including these new taxa, the number of known *Colostethus* species from Venezuelan Guayana increases to 17.

Key words: Amphibia: Dendrobatidae: *Colostethus triunfo* sp. n., *C. wothuja* sp. n.; Guayanan Venezuela; systematics.

1 Introduction

The dendrobatid fauna of the Venezuelan Guayana (the Venezuelan part of the Guiana Shield after HOOGMOED 1979) has received increasing attention during recent years. Dealing with non-aposematic dendrobatids, until 1992, only four species of the genus *Colostethus* COPE, 1866 were reported from the Venezuelan Guayana, *C. brunneus* (COPE, 1887), *C. fuliginosus* (JIMÉNEZ DE LA ESPADA, 1871), *C. sanmartini* RIVERO, LANGONE & PRIGIONI, 1986 and *C. shrevei* (RIVERO, 1961) (LA MARCA 1992, McDIARMID & PAOLILLO 1988). McDIARMID & PAOLILLO (1988) reported two undescribed species from Estado Amazonas. MORALES (1994) reported *C. marchesianus* (MELIN, 1941), whereas in 1996 eight new species were described, *C. ayarzaguenai* LA MARCA, 1996, *C. guanayensis* LA MARCA, 1996, *C. murisipanensis* LA MARCA, 1996, *C. parimae* LA MARCA, 1996, *C. parkerae* MEINHARDT & PARMELEE, 1996, *C. praderioi* LA MARCA, 1996, *C. roraima* LA MARCA, 1996, and *C. tepuyensis* LA MARCA, 1996. Two additional species were named *C. tamacuarensis* MYERS & DONNELLY, 1997 and *C. undulatus* MYERS & DONNELLY, 2001 by MYERS & DONNELLY (1997, 2001). BARRIO-AMORÓS (1998) and BARRIO-AMORÓS & FUENTES (1999) provide the most recent checklist of Venezuelan dendrobatids. Beyond this, CALDWELL et al. (2002) pointed out that the Venezuelan *C. marchesianus* reported by MORALES (1994) does not refer to this species, which may remain unnamed. Summarising these data, until today, the number of *Colostethus* from Venezuelan Guayana is 15 (including the *marchesianus*-like one).

In recent years, during field surveys in Venezuelan Guayana, material of two unnamed species has become available. The purpose of this paper is to describe these.

2 Material and Methods

The specimens of the two new and of additional species (for comparison) are hosted in the following collections: Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG); Colección de Herpetología del Museo de Biología de la Universidad Central de Venezuela, Caracas (MBUCV); Museo de Historia Natural La Salle, Caracas (MHNLS).

The diagnosis scheme follows DUELLMAN & SIMMONS (1988) plus the character presence/absence of a median lingual process (GRANT et al. 1997), whereas the

description scheme follows that of MYERS & DONNELLY (1997, 2001). Comparative data were taken from RIVERO (1961), RIVERO et al. (1986), LA MARCA (1996), MEINHARDT & PARMELEE (1996), LESCURE & MARTY (2000) and MYERS & DONNELLY (1997, 2001). The toe webbing formula follows the system of MYERS & DUELLMAN (1982). A mammography was arranged in order to see the palatine bones without damaging the few specimens of both species; the machine used was a Lorad 3- 8 MAS mammography (AGFA Industriales), of 1000 ampers/sec in 22 kv. The criterion for sex determination was the presence or absence of vocal slits, sexual dimorphism in colouration, and sexual maturity by the presence of circumvolute oviducts and mature testes. Measurements (in mm) were taken with a Mitutoyo® Digital Caliper to the nearest 0.1. Measurements of adult frogs are: SVL: snout-vent length; TL: tibia length; FeL: femur length; FL: foot length; HeL: head length; HW: head width; InD: inter-narial distance; UEW: upper eyelid width; IOD: inter-orbital distance; EN: anterior edge of eye to nostril; ED: horizontal eye diameter; TD: horizontal tympanum diameter; FD: disc width of Finger III; T4D: disc width of Toe IV; ETS: distance between the anterior edge of the eye to the tip of snout; 1FiL: length of Finger I; 2FiL: length of Finger II. Terminology and characters used in the tadpole description follows ALTIG & McDIARMID (1999) and CALDWELL et al. (2002). All measurements are in mm. Larval stages are those of GOSNER (1960). Measurements (in mm) of tadpoles are: TL: total length; BL: body length; BW: body width; BD: body depth; TAL: tail length; TD: tail depth; ODW: oral disc width; EN: anterior edge of eye to nostril. Geographic position and elevation were obtained with a GPS Garmin® II Plus. Illustrations were made using a stereo-microscope Leica Wild M5-A, with camera lucida.

3 Results

Colostethus triunfo sp. n. (Fig 1)

Holotype: EBRG 4756, an adult male from the summit of Cerro Santa Rosa, Serranía del Supamo, 685 m above sea level. 6°40'39''N, 62°24'26''W, Estado Bolívar, Venezuela, obtained by OSWALDO FUENTES on 7 April 1999.

Paratypes: EBRG 4757, an adult and EBRG 4759, a subadult female; EBRG 4758, an adult male; CVULA 6521-2, subadult females, obtained at the slopes of the Cerro Santa Rosa, Serranía del Supamo, Estado Bolívar, Venezuela, by FREDY MENDOZA on June 1997.

Referred specimens: CVULA 6523-6, a lot of four recently metamorphosed specimens from the slopes of Cerro Santa Rosa; MBUCV 6585, 6667, two recently metamorphosed specimens, same data as holotype.

Diagnosis: (1) A small *Colostethus* (up to 20 mm SVL), (2) disc on Finger III wider than diameter of finger; (3) Finger I distinctly longer than Finger II; (4) fringes on fingers absent; (5) disc on Toe IV distinctly wider than diameter of toe; (6) fringes on toes present; (7) outer tarsal fold present; (8) toe webbing formula I 1½-2 II 1¾-3 III 2¾-4 IV 4-2 V; (9) dorsolateral stripe absent; (10) oblique lateral stripe short, whitish; (11) ventrolateral stripe absent; (12) chest without markings; (13) venter white in males, pale brown in females; (14) sexual dimorphism in ventral pattern present: venter white in males, brownish in females; (15) Finger III of males not expanded; (16) dorsal skin smooth, ventral skin smooth; (17) tympanum indistinct, only visible in preserved animals after a while outside of the liquid; (18) median lingual process present.



Fig. 1. *Colostethus triunfo* sp. n. in life/im Leben. Photo: C.L. BARRIO-AMORÓS.

Colostethus triunfo is similar to *C. parkerae*, *C. shrevei*, *C. tamacuarensis* and *C. tepuyensis*, which are the only species from the Venezuelan Guayana known to have a median lingual process. *Colostethus triunfo* can be easily distinguished from those species having scanty toe webbing (*C. beebei* (NOBLE, 1923), *C. brunneus* (COPE, 1887), *C. praderioi* and *C. roraima*) by having moderately webbed toes. In addition, it is distinguished from other Guianan species by the following characters (those of *C. triunfo* in parentheses). *Colostethus ayarzaguenai* has dorsally a rounded snout (nearly truncate) and a protruding profile (rounded), Finger I shorter than II (longer); fingers with lateral fringes (absent) and an uniform pattern without dorsal spots (consistent pattern). *Colostethus brunneus* (northern populations not considered) is smaller, up to 16.8 mm (up to 20), dorsal skin with tubercles (smooth), fingers with lateral fringes (absent), short tarsal fold (longer), toe webbing almost inconspicuous (webbed, see formula above), no oblique lateral stripe (present). *Colostethus beebei* (from the Guianas) has a granular dorsum (smooth), scanty toe webbing (webbed, see formula above), ventrolateral stripe present (absent), oblique lateral stripe absent (present). *Colostethus degranvillei* LESCURE, 1975 (from French Guiana) has a granular dorsum (smooth), Finger I shorter than II (longer), oblique lateral stripe absent (present), a post tympanic white bar (absent) and ventral surfaces brown with white spots (whitish or pale brownish). *Colostethus guanayensis* has dorsal skin with flat tubercles (smooth), Finger I shorter than II (longer), fingers with lateral fringes (absent), dark ventral colouration (pale white to pale brown). *Colostethus marchesianus* has white dorsolateral and ventrolateral stripes (absent). *Colostethus murisipanensis* has a Finger I shorter than II (longer), no oblique lateral stripe (present), dark ventral colours (pale white to pale brown). *Colostethus parimae* has tubercular dorsal skin (smooth), non consistent pattern (consistent), a dorsally rounded snout (nearly truncate), Finger I shorter than II (longer), fingers with lateral fringes (absent). *Colostethus parkerae* has a rounded snout in dorsal view (round to truncate), fingers with lateral fringes (absent), oblique lateral stripe absent (present). *Colostethus praderioi* has small tubercles on posterior part of the dorsum (skin smooth), Finger I equal than II (I longer than II), weak lateral fringes on fingers (absent), oblique lateral stripe absent (present), scanty toe webbing (see formula above). *Colostethus roraima* has tubercular skin on the dorsum (smooth), rounded snout in dorsal view (round to truncate), almost no toe webbing (moderately webbed, see formula above), oblique lateral stripe absent

(present). *Colostethus sanmartini* has a dorsum with flat tubercles and small spicules (smooth), tympanum large, 57 % of eye diameter (indistinct), pale dorsolateral stripes (absent). *Colostethus shrevei* has a larger size up to 36 mm (up to 20), Finger I shorter than II (longer), fingers with lateral fringes (absent). *Colostethus tamacuarensis* has granular skin (smooth), anal tubercles present (absent), Finger III slightly expanded (not expanded), fringes on fingers (absent). *Colostethus tepuyensis* has a rounded snout in dorsal view (round to truncate), Finger I shorter than II (longer), lateral fringes on Fingers II and III (absent), oblique lateral stripe absent (present). *Colostethus undulatus* lacks a median lingual process (present), usually has an wavy-edged dorsal marking (absent), lacks pale oblique lateral stripe (present), has scanty toe webbing (moderately webbed, see formula above). The listing of *Colostethus fuliginosus* for Venezuela (McDIARMID & PAOLILLO 1988) is probably in error (L.A. COLOMA, pers. com.). *Colostethus fuliginosus* has a Finger I slightly shorter or equal than Finger II (longer), fringes present on Finger II (absent), throat dark in males (pale white). Comparisons with the other new species described in this publication are provided below. Usually the shape and distinctness of the tympanum is a useful taxonomic character. No other *Colostethus* have the tympanum indistinct, except *C. tamacuarensis*, *C. undulatus* and *C. beebei*, which are easily distinguished from *C. triunfo* by other characters given above. In *C. ayarzaguenai*, *C. brunneus*, *C. degranvillei*, *C. parkerae*, *C. praderioi*, *C. roraima*, the tympanum is visible but not conspicuous. In the remaining species, the tympanum is distinct, although usually only the lower part, concealed above by the supratympanic fold.

Description: Males and females up to 20 mm SVL. Dorsal and ventral skin smooth in all specimens except EBRG 4758, which is finely shagreened. Dorsal skin usually forming a well-defined rounded, posteriorly projecting flap well above vent, which opens at upper level of thighs; no anal tubercles. In holotype, EBRG 4759, CVULA 6521 and CVULA 6522 there is a small anal flap clearly visible (ill-defined in EBRG 4757 and EBRG 4758), but no as well developed as in the *C. edwardsi* group (LYNCH 1982).

Head (Fig. 2) longer than wide, greatest head width (between angles of jaws) 34 % of SVL. Snout rounded in profile, nearly truncate in dorsal and ventral views (except in the holotype, in which it is rounded). Nares situated near tip of snout and directed slightly posterolaterally; nares visible from front, barely or not visible from above, but well visible from below. Canthus rostralis straight, indistinct; loreal region almost flat. Interorbital region wider than upper eyelid. Snout longer than eye diameter. Tympanic membrane concealed (except in EBRG 4758, which is barely distinct because the specimen is somewhat desiccated, with the upper half obscured by a very diffuse supratympanic fold). Tympanum positioned close behind eye and low, almost touching angle of jaws. Palatine bones absent.

Hand moderate, its length 26 % of SVL. Relative lengths of adpressed fingers: III>IV>I>II; tip of Finger II reaching the proximal end of disc in Finger I. Discs of all fingers moderately expanded; disc of Finger III 1.4 times the width of distal end of adjacent phalanx. Base of palm with moderately large median metacarpal tubercle, triangular; elliptical inner metacarpal tubercle on base of Finger I; one subarticular tubercle each on Fingers I and II, and two subarticular tubercles each on Fingers III and IV, distal ones each smaller, almost indistinct; all tubercles low, with rounded surfaces. No keel-like fringes on fingers, except in EBRG 4758, probably through the desiccation. No ulnar tubercles or fold.



Fig. 2. Lateral and dorsal views of head of *Colostethus triunfo* sp. n. (EBRG 4757). Scale equals 5 mm.

Lateral- und Dorsalansicht des Kopfes von *Colostethus triunfo* sp. n. (EBRG 4757). Die Linie entspricht 5 mm.

Hind limbs of moderate length, with heel of adpressed limb extending beyond the eye and reaching the tip of snout in EBRG 4757; tibia 47-52 % of SVL. Relative lengths of adpressed toes: IV>III>V>II>I; first toe reaching to base, or distal edge, of subarticular tubercle of Toe II. Toe discs moderately expanded. Feet moderately

Character/ Merkmal	Males/Männchen (n = 2)	Females/Weibchen (n = 4)
SVL	19.7 ± 0.42 (19.4-20.0)	15.8 ± 2.83 (14.0-20.0)
TL	9.65 ± 0.49 (9.3-10.0)	8.4 ± 1.49 (7.0-10.5)
FeL	9.5 ± 0.70 (9.0-10.0)	8.0 ± 1.38 (7.2-9.6)
FL	9.45 ± 0.63 (9.0-9.9)	7.5 ± 1.67 (6.2-10.0)
HeL	7.35 ± 0.07 (7.3-7.4)	7.5 ± 1.67 (6.2-10.0)
HW	6.55 ± 0.07 (6.5-6.6)	5.3 ± 0.81 (4.7-6.5)
InD	2.75 ± 0.07 (6.5-6.6)	2.2 ± 0.28 (2.0-2.6)
UEW	1.8 ± 0.28 (1.6-2.0)	1.8 ± 0.21 (1.5-2.0)
IOD	2.15 ± 0.07 (2.1-2.2)	8.2 ± 0.31 (1.8-2.5)
EN	1.55 ± 0.49 (1.2-1.9)	1.55 ± 0.49 (1.2-1.9)
ED	2.6 ± 0.14 (2.5-2.7)	2.2 ± 0.45 (1.8-2.8)
TD-	—	—
F3D	0.75 ± 0.07 (0.7-0.8)	0.5 ± 0.1 (0.4-0.6)
T4D	0.85 ± 0.07 (0.8-0.9)	0.6 ± 0.12 (0.5-0.8)
ETS	3.1 ± 0.14 (3.0-3.2)	2.6 ± 0.58 (2.2-3.5)
1FiL	2.8 ± 0.28 (2.6-3.0)	2.2 ± 0.54 (1.8-3.0)
2FiL	3.1 ± 0.14 (3.0-3.2)	2.6 ± 0.58 (2.2-3.5)

Tab. 1. Measurements (in mm) of *Colostethus triunfo* sp. n. Values include means ± standard deviation (range in parentheses). For abbreviations see text.

Maßangaben (in mm) von *Colostethus triunfo* sp. n. Werte schließen den Mittelwert ± Standardabweichung sowie die Spannweite in Klammern ein. Für die Bedeutung der Abkürzungen siehe Text.



Fig. 3. View of Cerro Santa Rosa from Triunfo camp site. Photo: C.L. BARRIO-AMORÓS.
Ansicht des Cerro Santa Rosa vom Triunfo camp.



Fig. 4. Stream on the Cerro Santa Rosa summit; type locality of *Colostethus triunfo* sp. n. Photo: O. FUENTES.

Bachlauf auf dem Gipfel des Cerro Santa Rosa; Typuslokalität von *Colostethus triunfo* sp. n.

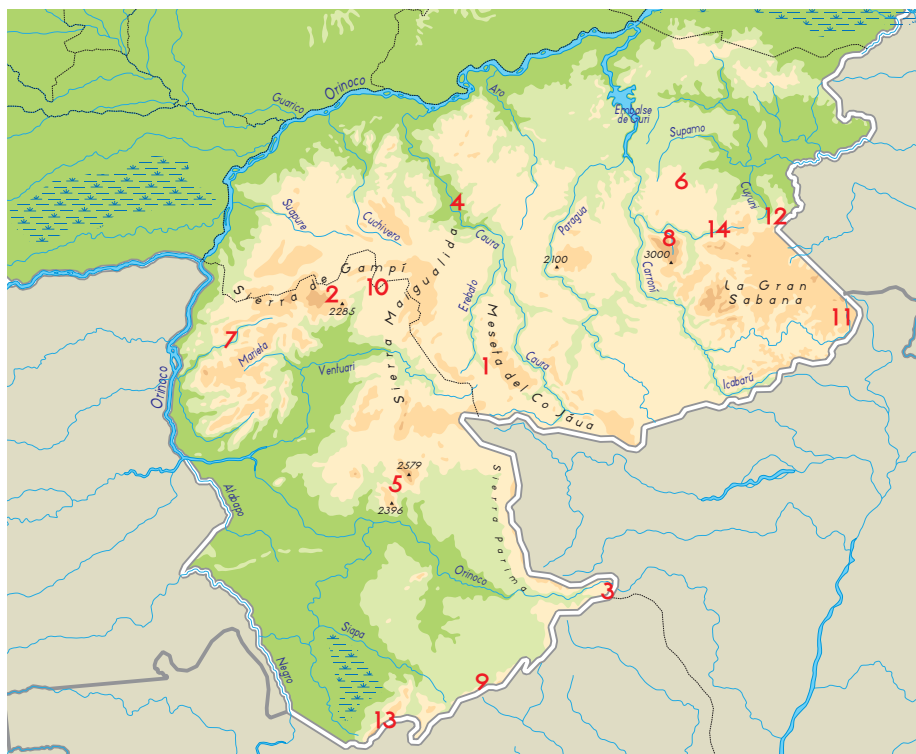


Fig. 5. Distributional map of the genus *Colostethus* in southern Venezuela:

Verbreitungskarte der Gattung *Colostethus* im südlichen Venezuela:

1. *Colostethus ayarzaguenai*; 2. *C. guanayensis*; 3. *C. parimae*; 4. *C. sanmartini*; 5. *C. shrevei*, *C. brunneus* and *C. aff. marchesianus*; 6. *C. triunfo* sp. n.; 7. *C. wothuja* sp. n.; 8. *C. tepuyensis*; 9. *C. tamacuarensis*; 10. *C. undulatus*; 11. *C. praderioi* and *C. roraima*; 12. *C. parkerae*; 13. *C. "fuliginosus"* (see text); 14. *C. murisipanensis*.

webbed, the web distally continuous with narrow fringes on Toes II-V. Webbing formula I 1½-2 II 1¾-3 III 2¾-4 IV 4-2 V. Well developed fringes on all toes in the holotype and EBRG 4758, fringes ill defined in EBRG 4757, EBRG 4759, CVULA 6521 and CVULA 6522. One to three non-protuberant subarticular tubercles on toes (each one on Toes I and II, two on Toes III and V and three on Toe IV, but distal tubercle ill defined). Two metatarsal tubercles, including a small round outer metatarsal tubercle, a slightly larger elliptical inner metatarsal tubercle, only EBRG 4758 shows an almost indistinct median metatarsal tubercle on the left foot. A narrow tarsal fold or keel, straight, maximum length one third of tarsus, continuous with the narrow fringes on free edge of Toe I; no tubercle at proximal end of distinctly raised tarsal keel.

Maxillary teeth present. Tongue longer than wide, rounded or cordiform, posteriorly free for one half to one third; median lingual process longer than wide (in holotype and in EBRG 4759) or as wide as long (EBRG 4757, CVULA 6521, CVULA 6522), or wider than long as in EBRG 4758. Vocal slits of males short, extending from near

tongue insertion to nearly the end of tongue. For measurements of the type series see Table 1.

Measurements of holotype (mm): SVL: 19.4; TL: 9.3; FeL: 9; FL: 9.9; HeL: 7.4; HW: 6.6; Ind: 2.8; UEW: 2; IOD: 2.2; EN: 1.9; ED: 2.7; TD: 1.3; F3D: 0.8; T4D: 0.8; ETS: 3.2; 1FiL: 3; 2FiL: 2.8.

Colouration: In preserve, dorsally dark to pale brown with a consistent pattern in all specimens of the type series. The pattern consists of a dark brown interorbital bar, straight, usually without apex at anterior margin, a large V shaped mark between shoulders, two symmetrical paravertebral spots at midbody, and a single small and median posterior spot near the end of body. This pattern, although present in all animals, is most distinct in the holotype and the three subadult females (EBRG 4759, CVULA 6521 and CVULA 6522). A pale whitish oblique lateral stripe is present in some specimens, although varying in shape (always short), and never well defined. It is better defined in EBRG 4757 and EBRG 4759, and less well defined in the holotype and CVULA 6522; it is almost indistinct in EBRG 4758 and CVULA 6521.

Canthal and supratympanic stripes dark brown and very distinct. In the holotype the upper lip is whitish with marks consisting of an irregular profusion of melanophores. Upper lips whitish in EBRG 4757, EBRG 4759, CVULA 6521 and CVULA 6522, with some brown scattered melanophores. EBRG 4758 has dark bars between the lip and the eye. Supratympanic stripe is continuous to the arm in EBRG 4758, interrupted although well defined in EBRG 4757, and ill defined in the holotype. Flanks are darker than dorsum in EBRG 4757 and EBRG 4758, but without definite borders. In the holotype and subadult females, the flanks are not dark, but have the same colour as the dorsum.

Arms and forearms pale grey to pale brown, the latter with dark crossbars; black band on forearm (as defined by GRANT & CASTRO 1998) absent. The holotype has two symmetrical whitish bars on the posterior surface of the thighs, surrounding the anal opening. They are also apparent in the rest of the animals (except EBRG 4759 and CVULA 6521), but less definite. The thighs have ill defined darker crossbars.

Males (holotype and EBRG 4758) have a completely white throat (a few melanophores become visible by microscope view on the lower lip of the holotype, and more melanophores especially on the lower lip but also on the rest of the venter in EBRG 4758). Lower distal portion of the thighs, tibia and tarsi brown, and feet soles dark brown. The females have a brownish throat, venter and lower legs.

In life (Fig. 1, based on slides of one unidentified specimen, probably EBRG 4757 or EBRG 4758) *C. triunfo* is brown dorsally, with described pattern visible in the photograph; upper lip whitish, iris bronze.

Distribution: The new species is only known from two localities at Cerro Santa Rosa both at the base, 350 m above sea level (Fig. 3), and the summit, 685 m a.s.l. (Fig. 4), at Supamo massif (Fig. 5). Both localities fall into medium to tall, evergreen, basimontane and lower montane forests (HUBER & ALARCÓN 1988).

Natural history: This species is a fast moving frog, living in both forest floor litter along creeks and at quiet pools along small streams in rainforest. It has only been seen along streams originating from the summit and slopes of Cerro Santa Rosa. The call (not recorded) is a long "trill" repeated continuously during the day. *Colostethus triunfo* is only found in streams without large fishes, and often in syntopy with *Pipa arrabali* IZECKSON, 1976. The semi-aquatic lizard *Neusticurus rudis* BOULENGER, 1900 was also observed in the same habitat. The tadpoles of the new species are unknown.

Etymology: Triunfo is a location where the senior author spent three months in different seasons conducting a survey of the herpetofauna of the Supamo area (northern Estado Bolívar). It is part of an open-pit gold mine. The specific name is used as a noun in nominative singular, in apposition to the generic name.

***Colostethus wothuja* sp. n.** (Fig. 6)

Holotype: MBUCV 6689, an adult female from base of Cerro Sipapo, Tobogán del Cuaio, 150 m above sea level, 5°05'09''N, 67°27'07''W, Estado Amazonas, Venezuela, obtained by ELDA SÁNCHEZ and JOHN PÉREZ on 19 May 2000.

Paratypes: EBRG 4760-61 (two females), MBUCV 6690 (male), same data as holotype.

Referred material: A lot of eight larvae (MHNLS 15794), a tadpole in Stage 31 (MHNLS 16720) and other in Stage 40 (MHNLS 16659) with the same data as the holotype.

Diagnosis: (1) A small *Colostethus* (up to 22 mm SVL); (2) disc on Finger III slightly wider than diameter of finger; (3) Finger I slightly longer than Finger II; (4) fringes on fingers present; (5) disc on Toe IV slightly wider than diameter of toe; (6) fringes present on toes; (7) outer tarsal fold present; (8) toe webbing formula I 1½-2 II 1⅔-3 III 3-3½ IV 4-2 V; (9) dorsolateral stripe absent; (10) oblique white lateral stripe from the groin to the halfway point of the flank, complete or broken; (11) ventrolateral stripe absent; (12) chest without markings; (13) venter light brownish in males, immaculate white in females; (14) sexual dimorphism in ventral pattern present; (15) Finger III of males not expanded; (16) dorsal skin granular, ventral skin smooth; (17) tympanum distinct, postero-superior half concealed by a supratympanic fold; (18) median lingual process present.

Comparisons: *Colostethus wothuja* is similar to *C. parkerae*, *C. shrevei*, *C. tamaquarensis*, *C. tepuyensis* and *C. triunfo*, which are the only ones known to have a median lingual process. *Colostethus wothuja*, which has a short oblique lateral stripe, is easily distinguishable from Guianan species lacking a short oblique lateral stripe as *C. beebei*, *C. brunneus*, *C. guanayensis*, *C. murisipanensis*, *C. parkerae*, *C. praderioi*, *C. roraima* and *C. tepuyensis*. *Colostethus wothuja* has relative extension of toe webbing (see formula below) that distinguishes it from species with scanty toe webbing (*C. beebei*, *C. brunneus*, *C. praderioi* and *C. roraima*). Moreover, *C. wothuja* is distinguishable from Guianan species by the following characters (those of *C. wothuja* in parentheses). *Colostethus ayarzaguenai* has smooth dorsum (granular), snout rounded in dorsal view (nearly truncate), a sole tubercle at the mouth commissure (absent), Finger I shorter than Finger II (longer), more extension of toe webbing (according to LA MARCA 1996: I 1-2 II 1⅓-2½ III 2-2½ IV 2⅔-1½ V versus I 1½-2 II 1⅔-3 III 3-3½ IV 4-2 V in the new species). *Colostethus brunneus* (northern populations not considered) has a smaller size, up to 16.8 mm (up to 22) and a short tarsal fold (longer). *Colostethus guanayensis* has Finger I shorter than II (longer), dark ventral colouration (immaculate white to light brownish), more extensive toe webbing (I 1-2 II 1⅓-2½ III 2½-3⅔ IV 3⅔-2½ V versus I 1½-2 II 1⅔-3 III 3-3½ IV 4-2 V in the new species). *Colostethus murisipanensis* has a Finger I shorter than Finger II (longer), no oblique lateral stripe (present), dark ventral colouration (immaculate white to light brownish). *Colostethus parimae* has a Finger I shorter than Finger II (longer), a rounded snout in dorsal view (nearly truncate), ventral parts with a great profusion of melano-



Fig. 6. *Colostethus wothuja* sp. n. in life/
im Leben. Photo: P.
VELA.

phores, including females (females immaculate white). *Colostethus parkerae* has a rounded snout in dorsal view (nearly truncate), an oblique lateral stripe absent (present), I shorter than II (longer). *Colostethus praderioi* has Finger I equal than Finger II (longer), belly and inferior part of thighs in life orange-reddish in life (white). *Colostethus roraima* has a rounded snout in dorsal view (nearly truncate) and Finger I shorter than Finger II (longer). *Colostethus sanmartini* has tympanum large, 57 % of eye diameter (less than the half of the eye diameter), pale dorsolateral stripes (absent), fingers without fringes (fringes present). *Colostethus shrevei* has a smooth dorsal skin (granular), larger SVL up to 36 mm (up to 22 mm), Finger I shorter than Finger II (longer). *Colostethus tepuyensis* has a rounded snout in dorsal view (nearly truncate), Finger I shorter than Finger II (longer), lateral fringes on Fingers II and III (on all fingers), oblique lateral stripe absent (present). *Colostethus tamacuarensis* has an inconspicuous tympanum (conspicuous inferiorly), Finger III slightly expanded in males (not expanded), conspicuous dorsal pattern and cross bars on limbs (neither dorsal pattern nor bars on limbs). *Colostethus undulatus* lacks a median lingual process (present), has usually a wavy-edged dorsal marking (absent), lacking pale oblique lateral stripe (present), and scanty toe webbing (webbed, see formula above). *Colostethus marchesianus* has white dorsolateral and ventrolateral stripes (absent). *Colostethus fuliginosus* has a Finger I slightly shorter than or equal to Finger II (longer), fringes present on Finger II (fringes on all fingers), fringes present on Toe IV (fringes on all toes), throat dark in males (light brownish). *Colostethus beebei* (from the Guianas) has a ventrolateral stripe (absent). *Colostethus degranvillei* (from French Guiana) has a Finger I shorter than Finger II (longer), oblique lateral stripe absent (present), and the ventral surfaces brown with white spots (white or light pale brownish). *Colostethus triunfo* has smooth dorsal skin (granular), no fringes on fingers (fringes present), conspicuous dorsal pattern and cross bars on limbs (no dorsal pattern nor bars on limbs) and tympanum indistinct (conspicuous inferiorly).

Description: Females up to 22 mm of SVL; males up to 20 mm of SVL. Dorsal skin granular in holotype and EBRG 4760; smooth anteriorly but granular posteriorly in



Fig. 7. Lateral and dorsal views of head of *Colostethus wothuja* sp. n. (EBRG 4760). Scale equals 5 mm.

Lateral- und Dorsalansicht des Kopfes von *Colostethus wothuja* sp. n. (EBRG 4760). Die Linie entspricht 5 mm.

EBRG 4758 and MBUCV 6690. Dorsal skin forming a well-defined rounded, posteriorly projecting flap well above vent, which opens at upper level of thighs; a prominent tubercle on each thigh lateral to and slightly above vent opening.

Head slightly longer than wide (Fig. 7), greatest head width (between angles of jaws) 34 % of SVL. Snout sloping, pointed in profile, nearly truncate in dorsal and ventral views. Nares situated near tip of snout and directed posterolaterally; nares barely visible from front, barely or not visible from above and below. Canthus rostralis straight but indistinct; loreal region almost flat. Interorbital region wider than upper eyelid. Snout longer than eye diameter. Tympanum distinct, surrounded by an ossified annulus, a portion (usually half) concealed posterodorsally by supratympanic fold. Tympanum more than one third and less than half of eye diameter; tympanum positioned close behind eye and low, almost touching angle of jaws. Palatine bones absent.

Hand moderate, its length 26 % of SVL. Relative lengths of adpressed fingers III>IV>I>II; tip of Finger II reaching half disc of Finger I. Discs of all fingers small, not too expanded; disc of Finger III 1.4 times wider than distal end of adjacent phalanx. Base of palm with large median metacarpal tubercle, rounded; elliptical inner metacarpal tubercle on base of Finger I; one subarticular tubercle each on Fingers I and II, and two subarticular tubercles each on Fingers III and IV, distal ones smaller, almost indistinct; all tubercles low, with rounded surfaces. Keel-like fringes on sides of fingers. No ulnar tubercles or fold. No black arm band.

Hind limbs of moderate length, with heel of appressed limb extending beyond the eye; tibia 46-50 % of SVL. Relative lengths of appressed toes IV>III>V>II>I; Toe I reaching half of subarticular tubercle of Toe II. Feet webbed; webbing formula I 1½-2 II 1⅔-3 III 3-3½ IV 4-2 V. All toes with fringes. One to three nonprotuberant subarticular tubercles on toes: one on Toes I and II, two on Toes III and V and three on Toe IV, the distal tubercle ill defined. A large round outer metatarsal tubercle, and a slightly smaller elliptical inner metatarsal tubercle; only EBRG 4760 shows an almost indistinct median metatarsal tubercle on the left foot. A well defined tarsal fold or keel, reaching distal half of tarsus, continuous with the narrow fringes on outer edge

Character/ Merkmal	Male/Männchen (n = 1)	Females/Weibchen (n = 3)
SVL	20.0	21.4 ± 0.66 (20.7-22.0)
TL	9.5	10.3 ± 0.64 (9.8-11.0)
FeL	9.0	9.7 ± 0.11 (9.6-9.8)
FL	9.0	9.6 ± 0.81 (9.2-10.5)
HeL	7.0	7.8 ± 0.21 (7.6-8.0)
HW	6.0	7.2 ± 0.34 (7.0-7.6)
InD	2.4	2.6 ± 0.11 (2.5-2.7)
UEW	1.7	2.0 ± 0.05 (2.0-2.1)
IOD	2.0	2.3 ± 0.05 (2.2-2.3)
EN	2.0	2.0 ± 0.05 (1.9-2.0)
ED	2.5	2.9 ± 0.11 (2.8-3.0)
TD	1.1	1.2 ± 0.1 (1.1-1.3)
F3D	0.7	0.7 ± 0.05 (0.7-0.8)
T4D	0.8	0.8 ± 0.05 (0.7-0.8)
ETS	3.0	3.2 ± 0.05 (3.1-3.2)
1FiL	3.0	3.1 ± 0.11 (3.0-3.2)
2FiL	2.6	2.8 ± 0.05 (2.7- 2.8)

Tab. 2. Measurements (in mm) of *Colostethus wothuja* sp. n. Values include means ± standard deviation (range in parentheses). For abbreviations see text.

Maßangaben (in mm) von *Colostethus wothuja* sp. n. Werte schließen den Mittelwert ± Standardabweichung sowie die Spannweite in Klammern ein. Für die Bedeutung der Abkürzungen siehe Text.

of Toe I; no tubercle at proximal end of distinctly raised tarsal keel, which in all specimens curves laterally at along its proximal end.

Maxillary teeth present. Tongue longer than wide; free posteriorly; median lingual process almost indistinct (except in MBUCV 6690, the only male). Vocal slits large, extending from near tongue insertion nearly to angle of jaw. For measurements of the type series see Table 2.

Measurements of holotype (mm): SVL: 22; TL: 11; FeL: 9.8; FL: 10.5; HeL: 7.7; HW: 7.6; Ind: 2.7; UEW: 2.2; IOD: 2.8; EN: 1.9; ED: 2.8; TD: 1.2; F3D: 0.8; T4D: 0.8; ETS: 3.2; 1FiL: 3.2; 2FiL: 2.8.

Colouration: In preserve, dorsally dark brown with no distinct pattern. A more or less distinct interorbital bar present, darker than the rest of the dorsum. The head, anterior to the interorbital bar is light brown; in the only male (MBUCV 6690), there is a small dark blotch on the top of the snout. Flanks blackish, without dorsolateral pale stripe. A white oblique lateral stripe is present in all specimens, reaching the halfway point of the body, but only continuous in MBUCV 6690; in the females, this stripe consists of white irregular spots, and is not well defined. Flanks well demarcated inferiorly, without ventrolateral pale stripe, but with a definite contrast between the flank and belly.

The dark brown canthal and supratympanic stripes separate the dorsal background colour from the upper lips, which are whitish with a profusion of brown melanophores.

Upper arms dark brown, lower arms white. Traces of cross bars on forearms of EBRG 4760 and MBUCV 6690; black or dark band on forearm absent.

Fore limbs dark brown, not crossed by darker bars. Two symmetrical whitish narrow transverse bars on the posterior surface of the thighs, surrounding the anal opening,

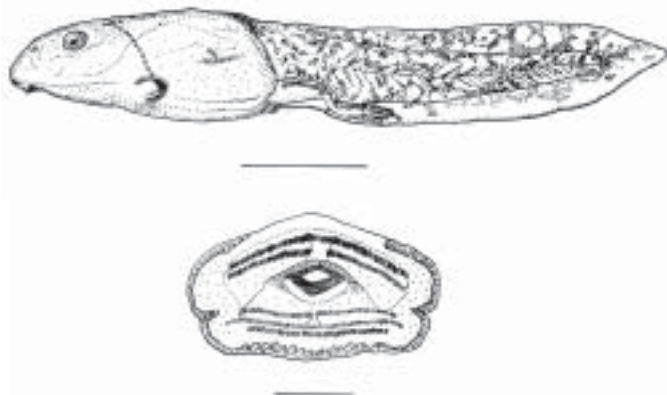


Fig. 8. Lateral view of tadpole of *Colostethus wothuja* sp. n. (above; MHNLS 16659; scale equals 3 mm) and ventral view of its oral disc (MHNLS 16720; scale equals 1 mm).

Lateralansicht der Larven von *Colostethus wothuja* sp. n. (oben; MHNLS 16659; die Linie entspricht 3 mm) und Ventralansicht des Mundfelds (MHNLS 16720; die Linie entspricht 1 mm).

most apparent in EBRG 4760 and MBUCV 6690. Ventrally, all specimens (both sexes) are immaculate white, with just a few melanophores on the chin. The male (MBUCV 6690) also has melanophores (visible only by microscope) on throat and chest. Soles dark brown.

In life (based on slides of one unidentified specimen; Fig. 6): *C. wothuja* is dorsally dark brown, with black flanks and a white oblique lateral stripe. A bright white spot is present below tympanic area. The axilla is white. Throat, chest and belly yellowish, lower arms, and hind limbs are greyish. Some finger discs are white. The upper lip is dirty white, the iris bronze.

Tadpole description: A series of nine exotrophic tadpoles was collected (seven are in the same lot MHNLS 15794), two of them were on the back of the male MBUCV 6690; the remaining were in a small pool beside a stream. The series include two larvae in Stage 25 (those from the back of the male); two in Stage 31; one in each Stage 36 and 40; and three in Stage 38. The tadpole in Stage 40 (MHNLS 16659) was chosen for a detailed description (Fig. 8), except for mouth parts, which are based on MHNLS 16720 in Stage 31 (measurements are in mm): body depressed, TL: 28, BL: 10.7, BD: 4.2; BW: 7.5. Snout round from above, subacuminate in profile; InD: 2.05; nares very small, opening anterodorsally, EN: 0.92. Eyes dorsal, directed dorsolaterally, ED: 1.2; IOD: 1.2.

Spiracle sinistral, in shape of short, tube of 1.3 long, projected posterodorsally; opening of spiracle 0.8. Distance from snout to spiracular opening 5.94. Vent tube short, dextral, free posteriorly.

Caudal musculature robust, gradually narrower to the tip of the tail; tail 59.7% of the total length and relatively high, TD: 4.2 at midtail and tapering gradually. Upper fin deeper than lower fin; upper fin originates 2 mm posterior to junction of body and tail. Both fins less deep than caudal musculature; ending of tail semieliptic and acute; notochord ends from narrowly rounded tail tip. Two lateral lines present, one is indistinct, from the anterior edge of the eye to the nare, without reaching it; the other

originates posterodorsal to the eye to the ventral side, growing in size, and forming a semi-arch, ending near the spiracle (Fig. 8). Developing hind limb bud 5.11 in length.

The oral disc Stage 31 (MHNLS 16720) is located ventrally and emarginated, 2.1 mm in transverse width, 38.9 % of maximum body width (Fig. 8). Margin of disc surrounded by irregular papillae of differing lengths; papillae present on upper lip, submarginal papillae absent. Marginal papillae conic-pointed, simple from lateral edges of upper lip to lower lip, they are arranged in a weak double row at the centre of lower lip; marginal papillae alternate, in a single row, surrounding the oral disc, except for a gap superiorly. Labial tooth row formula 2(2)/3(1). Tooth row A-1 complete, equal in length than A-2, extended near the marginal papillae, 1.95; A-2 consist in two rows, separated by a diastema (0.92 and 0.93) (gap 0.38), extended above of upper jaw sheath. Upper jaw partially keratinised, as wide as high, arched, convex medially, with minute serrations; with short, lateral processes; jaw sheath broadly V-shaped, partially keratinised. Both upper and lower sheaths finely serrated; serrations extend entire length of sheaths, including lateral processes. Row P-1 with a short gap (0.82 and 0.83) (gap 0.06); row P-2 longer than P-1, 2.15 mm; P-3 the shortest, 1.82 mm.



Fig. 9. View of Serranía del Cuao with the stream from where the type series of *Colostethus wothuja* sp. n. was collected. Photo: O. FUENTES.

Ansicht der Serranía del Cuao mit dem Bachlauf, an dem die Typuserie von *Colostethus wothuja* sp. n. gesammelt wurde.

In preserve, body dark brown, with some indistinct melanophores sparced through the body. Some cartilages are visible through the skin and are cream-coloured or light ivory. Oral parts keratinised, black. Eyes dark brown. Caudal musculature almost translucent, cream-coloured, with huge density of dark grey and brown points and spots. Upper and lower fins translucent with same density of points and spots. Life colour is the same as in preserve.

Distribution: The new species is known only from the type locality at 150 m above sea level (Fig. 5). The whole area falls into medium to tall, evergreen, lower montane and montane forests (HUBER & ALARCÓN 1988).

Natural History: *Colostethus wothuja* is a diurnal frog, being found in primary rainforest at the base of the Cuao-Sipapo massif from 150 to 200 m above sea level. All specimens were on the bank of a small stream (Tobogan del Cuao; Fig. 9), on a slab of pink sandstone. Only one male was obtained, which carried two larvae on the dorsum (see above).

Etymology: The name *wothuja* (*wóthujä*) is the proper denominative for the Piaroa or Dearuwa people, who live in the area of Cuao-Sipapo massif, northern Amazonas state. It is used as a noun in nominative singular, in apposition to the generic name.

4 Discussion

RIVERO (1988 “1990”) defined phenetic groups among *Colostethus*, mainly reinforcing EDWARDS’ (1974) effort. This grouping is highly artificial and we do not use it here.

The presence of median lingual process (GRANT et al. 1997) in almost all Guayanan species reviewed recently, could be of taxonomic importance, but until today no one has concluded anything about this character. Also, the presence or absence of palatine (or neopalatine) bones has been mentioned as possibly important for systematic relationships (KAPLAN 1997). Both, *Colostethus triunfo* and *C. wothuja*, lack palatine bones. MYERS (1991) and COLOMA (1995) suggested that the absence of palatines could be synapomorphic within the family Dendrobatidae. Although KAPLAN (1997) reviewed some dendrobatids searching for palatine bones, no one was from the Venezuelan Guayana. MYERS & DONNELLY (2001) found no palatine bones in *Colostethus undulatus*, but this species lacks also a median lingual process, which distinguishes it from most of the Venezuelan Guayana forms.

Recent molecular phylogenetic arrangements (e. g. VENCES et al. 2003; SANTOS et al. 2003) do not include any Guianan species, and thus, relationships among them are yet unknown. So far, at this time we cannot conclude with confidence any relationship among Guayanan species of *Colostethus*. We include the new species in the genus *Colostethus* provisionally, until a phylogenetic arrangement can clear the panorama.

Fig. 5 shows the distribution of some species of Venezuelan Guayana *Colostethus*, including the type localities of *C. triunfo* and *C. wothuja*.

Acknowledgements

We appreciate the help offered by CHARLES MYERS (AMNH, New York), ROGER PÉREZ, CARMEN FERREIRA, RICARDO GUERRERO, and MERCEDES SALAZAR (Museo de Biología, Universidad Central de Venezuela, Caracas), RAMÓN RIVERO and FRANCISCO BISBAL (Museo de la Estación Biológica de Rancho Grande, Maracay). Also we are indebted to the Piaroa (Wóthujä) community of Raudal del Danto, in Cuao river, especially to their capitan JULIO CAMICO and the guide PRÓSPERO PÉREZ. Dr. ALEXIS RODRÍGUEZ, LUIS FERNANDO NAVARRETE, JOHN PÉREZ, ELDA SANCHEZ, LUIS GONZÁLEZ, DENIS and PATTY VELA were the best companions during the expedition, organised by Dr. ALEXIS RODRÍGUEZ to the Cuao river. Thanks to the interest of CHARLES BREWER-CARÍAS, the senior author

could spend long times at the Triunfo forest. FREDDY MENDOZA and other residents were very helpful in providing some specimens. RICHARD WASSERSUG commented an early version of the tadpole description. We thank deeply the revision of the manuscript by ROSS MACCULLOCH (Royal Ontario Museum, Canada). This work is part of the herpetological results of the expedition Cuao-Sipapo-Autana by CHARLES BREWER-CARÍAS and the FUNDACIÓN CISNEROS.

Resumen

Dos nuevas especies de Colostethus (Anura: Dendrobatidae) de la Guayana venezolana.

Se describen dos nuevos *Colostethus* de la Guayana venezolana. Ambas especies habitan en zonas bajas de tepuis (350 a 700 m sobre el nivel del mar en Cerro Santa Rosa, y a 150 m sobre el nivel del mar en la base de la Serranía Cuao-Sipapo). Ambas son especies de pequeño tamaño (máximo 22 mm LCC) que comparten caracteres como presencia de banda oblicua lateral, ausencia de bandas dorsolaterales y ventrolaterales, y Dedo III de la mano no engrosado. Hasta la fecha, incluidas las nuevas especies, se conocen 17 *Colostethus* en la Guayana venezolana.

Palabras clave: Amphibia: Dendrobatidae: *Colostethus triunfo* sp. n., *C. wothuja* sp. n.; Guayana venezolana; sistemática.

Zwei neue *Colostethus*-Arten (Anura: Dendrobatidae) aus dem venezolanischen Guayana

Zwei neue *Colostethus* aus dem venezolanischen Guayana werden beschrieben. Beide Arten bewohnen niedrige Tafelberge oder Niederungen am Fuße der Tafelberge (350-700 m ü.NN in Cerro Santa Rosa und 150 m ü.NN im Cuao-Sipapo-Massiv). Beide Arten sind relativ klein (bis 22 mm). Sie haben laterale Querstreifen gemein, ihnen fehlen Dorso- und Ventrolateralstreifen und Finger III bei den Männchen ist nicht geschwollen. Mit diesen beiden neuen Arten erhöht sich die Anzahl der aus dem venezolanischen Guyana bekannten *Colostethus*-Arten auf 17.

Schlagwörter: Amphibia: Dendrobatidae: *Colostethus triunfo* sp. n., *C. wothuja* sp. n.; venezolanisches Guayana; Systematik.

References

- ALTIG, R. & R.W. McDIARMID (1999): Body plan: development and morphology. – pp: 24-51 in R.W. McDIARMID & R. ALTIG (Eds.): Tadpoles: The Biology of Anuran Larvae. – University of Chicago Press, Illinois, U.S.A.
- BARRIO-AMORÓS, C.L. (1998): Sistemática y Biogeografía de los anfibios (Amphibia) de Venezuela. – Acta Biologica Venezuelica, **18**(2): 1-93.
- & O. FUENTES (1999): Sinopsis de la familia Dendrobatidae (Amphibia: Anura) de Venezuela. – Acta Biologica Venezuelica, **19**(3): 1-10.
- CALDWELL, J.P., A.P. LIMA & C. KELLER (2002): Redescription of *Colostethus marchesianus* (MELIN, 1941) from its type locality. – Copeia, Lawrence, **2002**: 157-165.
- , — & G.M. BIAVATI (2002): Descriptions of tadpoles of *Colostethus marchesianus* and *Colostethus caeruleodactylus* (Anura: Dendrobatidae) from their type localities. – Copeia, Lawrence, **2002**: 166-172.
- COLOMA, L. (1995): Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). – Univ. Kansas Nat. Hist. Mus. Misc. Publ. **87**: 1-72.
- DUELLMAN, W.E. & J.E. SIMMONS. (1988): Two new species of Dendrobatid frogs, genus *Colostethus*, from the Cordillera del Cóndor, Ecuador. – Proc. Acad. Nat. Sci. Philadelphia, **140**(2): 115-124.
- EDWARDS, S.R. (1974): A phenetic analysis of the Genus *Colostethus* (Anura: Dendrobatidae). – Unpublished Ph. D. Dissertation, University of Kansas.
- GOSNER, K.L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. – Herpetologica. **16**:183-190.

- GRANT, T., E.C. HUMPHREY & C.W. MYERS (1997): The median lingual process of frogs: a bizarre character of old world ranoids discovered in South American dendrobatids. – *Am. Mus. Novitates*, **3212**: 1-40.
- HOOGMOED, M.S. (1979): The Herpetofauna of the Guianan Region. – pp. 241-279 in DUELLMAN, W.E. (ed.): *The South American Herpetofauna: its origin, evolution and dispersal*. – *Mus. Nat. Hist. Univ. Kansas Monogr.*, **7**.
- HUBER, O. & C. ALARCON (1988): *Vegetation map of Venezuela*. – MARNR and The Nature Conservancy, Caracas.
- KAPLAN, M. (1997): A new species of *Colostethus* from the Sierra Nevada de Santa Marta (Colombia) with comments on intergeneric relationships within the Dendrobatidae. – *J. Herpetol.* **31**(3): 369-375.
- LA MARCA, E. (1992): Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. – *Cuadernos Geográficos U. L.A., Mérida*, **9**, 197 pp.
- (1996 “1997”): Ranas del género *Colostethus* (Amphibia: Anura: Dendrobatidae) de la Guayana Venezolana con la descripción de siete especies nuevas. – *Publ. Asoc. Amigos de Doñana*, **9**: 1-64.
- LESCURE, J. & C. MARTY (2000): *Atlas des Amphibiens de Guyane*. – *Muséum National d’Histoire Naturelle. Patrimoines Naturels*, **45**, Paris, 388 pp.
- LYNCH, J.D. (1982): Two new species of poison-dart frogs (*Colostethus*) from Colombia. – *Herpetologica*, **38**(3): 366-374.
- MCDIARMID, R.W. & A. PAOLILLO. (1988): Herpetological collections: Cerro de la Neblina. – in BREWER-CARIAS (ed.): *Cerro de la Neblina. Resultados de la expedición 1983-1987*. – Fudeci, Caracas, 922 pp.
- MEINHARDT, D.J. & J.R. PARMELEE (1996): A new species of *Colostethus* (Anura: Dendrobatidae) from Venezuela. – *Herpetologica*, **52**(1): 70-77.
- MORALES, V.R. (1994): Taxonomía de algunos *Colostethus* (Anura: Dendrobatidae) de Sudamérica, con descripción de dos especies nuevas. – *Rev. Esp. Herp.*, **8**: 95-103.
- MYERS, C.W. (1991): Distribution of the dendrobatid frog *Colostethus chocoensis* and description of a related species occurring macrosympatrically. – *Amer. Mus. Novitates*, **3010**: 1-15.
- & M.A. DONNELLY (1997): A Tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil: Report from the Phelps Tapirapecó Expedition. – *Amer. Mus. Novitates*, **3213**: 1-71.
- & — (2001): Herpetofauna of the Yutajé-Corocoro Massif, Venezuela: Second report from the ROBERT G. GOELET American Museum-Terramar Expedition to the northwestern Tepuis. – *Bull. Am. Mus. Nat. Hist.* **261**: 1-85.
- & W.E. DUELLMAN (1982): A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. – *Amer. Mus. Novitates*, **2752**: 1-32.
- RIVERO (1961): Saliencia de Venezuela. – *Bull. Mus. Comp. Zool. Harvard*, **126**(1): 1-207.
- (1988 “1990”): Sobre las relaciones de las especies del género *Colostethus* (Amphibia, Dendrobatidae). – *Mem. Soc. Cien. Nat. La Salle*, **48**(129):3-32.
- , J.A. LANGONE & C.M. PRIGIONI (1986): Anfíbios Anuros colectados por la Expedición del Museo Nacional de Historia Natural de Montevideo al Río Caura, Estado Bolívar, Venezuela; con la descripción de una nueva especie de *Colostethus* (Dendrobatidae). – *Com. Zool. Mus. Hist. Nat. Montevideo*, **11**(157): 1-15.
- SANTOS, J.C., L.A. COLOMA & D. CANNATELLA (2003) Multiple, recurring origins of aposematism and diet speciation in poison frogs. – *PNAS* **100**(22): 12792-12797.
- VENCES, M., J. KOSUCH, R. BOISTEL, C.F.B. HADDAD, E. LA MARCA, S. LÖTTERS & M. VEITH (2003). Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. – *Org. Divers. Evol.* **3**: 215-226.

Appendix: Specimens examined

Colostethus parkerae: from Salto El Danto, La Escalera, Sierra de Lema, estado Bolívar, Venezuela: MBUCV 6642 (3 specimens). *Colostethus shrevei*: Cerro Duida, 1000 m, estado Amazonas, Venezuela: MBUCV 6687-8. *Colostethus tepuyensis*: Auyan tepuy, camp 4., 5°58'N-62°33'W, 1600 m, estado Bolívar, Venezuela: EBRG 2694, EBRG 2701-2. *Colostethus triunfo*: see type series and referred specimens. *Colostethus undulatus*: Cerro Yutajé, 1750 m., 5°46'N-66°08'W. EBRG 3040-2 (paratypes). *Colostethus wothuja*: see type series.

Manuscript received: 9 May 2003

Authors: CÉSAR L. BARRIO-AMORÓS, Fundación Andígen A., Apartado postal 210, 5101-A Mérida, Venezuela, E-Mail: cesarlba@yahoo.com; OSWALDO FUENTES, Colección de Herpetología, Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela; GILSON RIVAS, Museo de Historia Natural La Salle, Apartado postal 1930, Caracas 1010-A, Venezuela.