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SYSTEMATIC STATUS OF AN ENIGMATIC AND POSSIBLY ENDANGERED DENDROBATID FROG (*COLOSTETHUS DUNNI*) FROM THE VALLEY OF CARACAS, NORTHERN VENEZUELA

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Abstract: A redescription of *Colostethus dunni,* a poorly known dendrobatid frog from the central part of the Venezuelan Coastal Range, is provided. The paper presents a definition and diagnosis as well as a more detailed description of the species, accompanied with an extensive list of name usages (chresonymy), data on musculature, coloration in life and in ethanol, morphometry, geographic and ecological distribution, and discussion of relationships. Although usually associated with collared frogs (*Mannophryne*) it now appears that the species is not closely related to any members of this genus, nor to *Nephelobates* or other dendrobatid frogs. Its phylogenetic relationships remain enigmatic. This species is considered to be endangered and suggested to be elevated to some formal category of conservation.

Key words: Systematics, Amphibia, Dendrobatidae, *Colostethus dunni*, *Mannophryne*, *Nephelobates*, *Colostethus*, Venezuela.

Resumen: **"Status sistemático de una rana dendrobatida enigmática y posiblemente amenazada (*Colostethus dunni*) del Valle de Caracas, Norte de Venezuela".** En este trabajo se provee una redescripción de *Colostethus dunni*, una rana poco conocida proveniente de la porción central de la Cordillera de la Costa, en el norte de Venezuela. Se presenta una definición y diagnosis, así como una descripción detallada de la especie, acompañada con una lista extensa de nombres usados en la literatura (cresonimia), datos sobre musculatura, coloración en vida y en alcohol etílico, morfometría, distribución geográfica y ecológica, y una discusión de relaciones de parentesco. Aunque generalmente asociada con ranas acollaradas (*Mannophryne*), parece que la especie no está estrechamente relacionada con ningún miembro en este género, ni con *Nephelobates* ni otras ranas dendrobátidas. Sus relaciones filogenéticas permanecen enigmáticas. Esta especie se considera en peligro y se sugiere que sea elevada a alguna categoría formal de protección.

Palabras clave: Sistemática, Amphibia, Dendrobatidae, *Colostethus dunni*, *Mannophryne*, *Nephelobates*, *Colostethus*, Venezuela.

Colostethus dunni is a poorly known dendrobatid frog inhabiting the central part of the Cordillera de la Costa, in the vicinities of Caracas, northern Venezuela. Originally described as a *Prostherapis*, it was transferred by Edwards (1971) to the genus *Colostethus*, where it still stands. In contrast to its relatively stable taxonomic history, its phylogenetic relationships have been shifting and unclear through time. Nonetheless, ever since the *Colostethus* revision by Edwards (1971, 1974a,b), the species has been more clearly associated or mistaken with collared frogs (genus *Mannophryne*).

The main purpose of this paper is to provide a more detailed description of *Colostethus dunni*, and to comment on the relationships of this taxon, to counteract misapplication of names as well as the short original description.

MATERIALS AND METHODS

Specimens employed for comparative purposes and examined in association with this study are indicated in Appendix I. Morphological measurements were taken under a dissecting stereomicroscope, using a dial caliper with a precision of 0.1 mm. Drawings were done with a camera lucida attachment. Detailed measurements are given only for adult specimens. Adults are defined as follows: males having vocal slits and enlarged testes, and females having deeply convoluted oviducts and/or mature ova. Muscle terminology follows Ecker (1889) and Tyler (1971). The system to record the amount of webbing is a variant of Edwards (1974) method, as stated and employed in La Marca (e.g. 1984, 1985, 1996). Terminology follows La Marca (1996).

Museum abbreviations are as follows: American Museum of Natural History (AMNH); British Museum of Natural History (BM); Colección de Vertebrados de la Universidad de Los Andes, Mérida (CVULA); Field Museum of Natural History (FMNH); Museum of Natural History, University of Kansas (KU); Museo de Biología, Universidad Central de Venezuela (MBUCV); Museo de Ciencias Naturales Guanare, Venezuela (MCNG); Museo de Historia Natural La Salle, Caracas (MHNLS); Texas A&M University, Texas Cooperative Wildlife Collection (TCWC); Colección de Enrique Yústiz, Universidad Centro Occidental Lisandro Alvarado (UCLA); Colección de Anfibios y Reptiles, Laboratorio de Biogeografía, Universidad de Los Andes, Mérida (ULABG); Museum of Zoology of the University of Michigan (UMMZ), Herpetological Collection at University of Puerto Pico in Mayagüez (UPRM), and United States National Museum (USNM).

Colostethus dunni (Rivero), 1961

Prostherapis dunni (Rivero 1961:157; 1964:311; Solano 1968:288; Tello 1968:247; La Marca 1994b:39).
Colostethus (*Prostherapis*) *dunni* (Edwards 1971:148).
Colostethus dunni (Edwards 1974b:2; Gorham 1974:115; Marx 1976:33; Rivero 1978:331; Lynch 1979:214; Duellman 1979:443; Harding 1983:79; La Marca 1984:130; La Marca 1985:4; Rivero 1990:158; Myers *et al.* 1991:20; La Marca 1992:25; La Marca 1995:61; Duellman 1993:55; La Marca 1993:11; Frank and Ramus 1995:48; La Marca 1997:114; Barrio 1998:17; Duellman 1999:302.

Taxonomic remark: "Eight" paratypes were cited in the original description, but only six specimens were explicitly listed (FMNH 67379-67384). I regard that two other frogs, listed as "paratypes" in the FMNH herpetological collection (67378 and 67385), should also be considered paratypes of the species, agreeing with a sequential series and the original count of eight.

Definition and Diagnosis: A medium sized Colostethus (x SVL; males: 19.9 mm, females: 24.5 mm) distinguished from other *Colostethus* by the following combination of characters: (1) skin of dorsum smooth; (2) tympanum small, distinct in its lower part, its length less than 1/3 that of eye, (3) snout bluntly pointed in dorsal view, rounded to truncate in lateral profile; (4) *canthus rostralis* not well defined, slightly curved; loreal region almost flat to slightly convex, abruptly descending to lips; (5) first finger shorter than second; (6) pad on third finger almost twice as wide as preceding phalanx; (7) fingers bearing lateral fringes; (8) cloacal sheath absent; (9) slight tarsal fold not ending in tubercle; (10) toes extensively webbed, web formula: **I**(2.0-3.0) 1.0**II**2.0-(1.5-2.0)**III**(3.0-4.0) 2.0**IV**2.0 (2.0-3.0)**V**; (11) toes with lateral fringes; third toe bearing flap-like lateral fringes; (12) dorsolateral stripe absent; (13) discs on fourth toe wider than adjacent phalanx; (14) pale, short oblique inguinal stripe; (15) discrete dark markings absent on chest (throat mottled, with melanophores sometimes occupying only borders of lips and middle part of throat); (16) ventrolateral stripe absent; (17) pale venter, without conspicuous markings; (18) third finger not swollen in males; (19) long, fang-like teeth.

Colostethus dunni is unique among Venezuelan dendrobatids by the combination of its peculiar dorsal pattern (Fig. 1), extensive webbing (Fig. 2), and characteristic dentition (Fig. 3). Absence of a collar in *C. dunni* provides no information to evaluate phylogenetic relationships between this species and members of the genus *Mannophryne*, but the presence of at least two characters (dentition and throat pattern) is suggestive of a closer relationship between *C. dunni* and members of the genus *Nephelobates*. The extensive webbing of *C. dunni* is in sharp contrast with the brief webbing of the members of *Nephelobates* (but see discussion).

Colostethus dunni was previously known only from the type specimens. The following description is based on the type series and on previously unreported UMMZ material identified as "*Colostethus alboguttatus*".

Description: Females slightly larger than males [x SVL in males = 19.9±1.5 mm (range = 18.0-22.4; N=5), x SVL, in females = 24.5±0.7 mm (range = 24.1-25.5; N=4); head width about 36% SVL (N=8)]; head almost as wide as long; frontoparietals somewhat elevated, but not prominent; interorbital distance about 1.8 times wider than upper eyelid width; *canthus rostralis* not well defined, slightly curved; nostrils scarcely elevated, directed laterally and closer to tip of snout than to eye (Fig. 4); nostril openings not visible from above; loreal region almost flat to slightly convex, abruptly descending to lips; snout bluntly pointed in dorsal view; tip of snout broadly pointed in dorsal view, rounded in lateral profile; length of eye about 2.2 times greater than eye-to-nostril distance (N=6); internostril distance about 1.6 times larger than eye-to-nostril distance (N=6); tympanum small, about 1/3 length of eye, distinct in its inferior part, slanted with anterior part slightly elevated; tympanum separated from eye by about its own horizontal length (Fig. 4); thick supratympanic ridge; one small tubercle at corner of mouth.

Tongue longer than wide, oval, not notched behind; posterior half of tongue not adherent to floor of mouth; choanae rounded, concealed by maxillary arch of palatal shelf; maxilla and premaxilla toothed; teeth pedicelate at the base, fang-like (Figs. 3, 5).

FIG. 1. *Colostethus dunni*. Dorsal view of UMMZ 167133, female, SVL= 25.5 mm.

Colostethus dunni. Vista dorsal de UMMZ 167133, hembra, SVL= 25.5 mm.

Dorsum and flanks smooth; throat, chest and venter smooth; upper arm and forearm smooth; hand length 29.9 ± 2.1% SVL (N=7); palmar tubercle single, rounded; thenar tubercle elongated, not well-defined, about 2 times longer than wide; no supernumerary palmar tubercles; subarticular palmar tubercles single, rounded to oval, not elevated; large discs on fingers; largest disc on third finger, about same size or slightly larger than tympanum; discs on fingers wider than long, disc on second finger about 1.8 times wider than adjacent phalanx; widely separated pale scutes; fingers free, bearing lateral keels; first finger shorter than second (Fig. 2); third finger not swollen in males.

Cloacal opening well above midlevel of thighs, directed straight backwards; no cloacal sheath; thighs and shanks smooth, dorsally and ventrally; slight tarsal fold not ending in tubercle; tibia length 52.8 ± 2.7% SVL (N=8); foot length 50.1 ± 2.7% SVL (N=8); outer metatarsal tubercle small, rounded; inner metatarsal tubercle oval, twice longer than wide, about twice as large as outer; no supernumerary plantar tubercles; subarticular tubercles flattened, round to oval; toes extensively webbed, foot web formula: **I**(2.0-3.0) 1.0 **II** 2.0 (1.5-2.0)**III**(3.0-4.0) 2.0**IV**2.0 (2.0-3.0)**V** (Fig. 2); phalanges free from web, bearing lateral fringes; antepenultimate and penultimate phalanx on third toe, bearing flap like lateral fringes; fringe along fifth toe not extending beyond base of digit; discs large, wider than long; largest disc on fourth toe, smaller than disc on third finger; largest disc about 1.5 times wider than adjacent phalanx (Fig. 2); heels do not overlap when thighs are held at right angles to body axis, reaching to anterior corner of eye when legs adpressed forward (this later condition was not checked in the holotype and paratypes, due to the brittle condition of these type specimens).

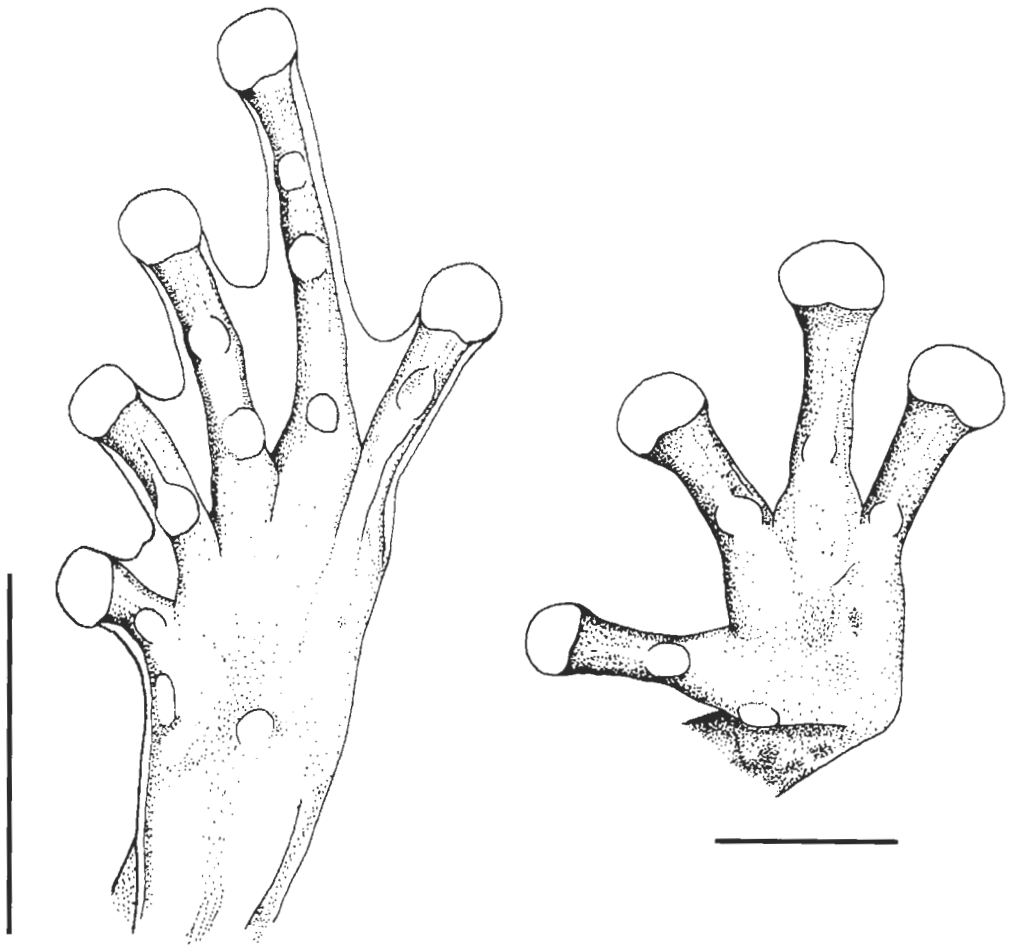

FIG. 2. Left foot (scale = 5 mm) and left hand (scale = 2.5 mm) of *Colostethus dunni* (FMNH 67385, paratype).
Pata izquierda (escala = 5 mm) y mano izquierda (escala = 2.5 mm) de *Colostethus dunni* (FMNH 67385, paratipo).

Musculature (based on UMMZ 167133): Intermandibular musculature: the *m. submentalis* is a moderate-size, araphic, thin sheet of muscle with lateral attachments from the posterior end of jaws to the *m. submentalis*. The *m. geniohyioideii* are visible through a reduced median aponeurosis of the *m. intermandibularis*. Hind leg musculature: *m. biceps* almost completely concealed by *m. triceps femoris; The m. pyriformis* is narrow, inserting deeply below *m. vastus externus* and *m. biceps*. Depressor musculature: the *m. adductor mandibulae externus superficialis* is absent.

Morphological remarks: The type series is in a precarious state of preservation. The holotype is missing the 4th finger on the left hand; the paratypes are in different degrees of deterioration, especially concerning fingers, toes, hands and arms (detached or almost detached). FMNH 67384, a female paratype, is the specimen that is in relatively better condition. The largest specimen ever recorded (in spite that larger specimens were sometimes apparently seen; cf. Solano 1968, who referred maximum size of 30 mm) is UMMZ 167133, an adult female now cleared and stained. From the recorded museum specimens, only the female holotype reaches close to this value, with 24.2 mm (but see original description for a different value of maximum size for FMNH 67384, which we measured as 24.1 mm SVL).

Coloration in preservative: Dorsum brown, with small pale flecks (cf. Rivero 1964:318) or large pale spots on mid-dorsum that may or may not be conspicuous (Fig. 1); a very short dark brown band originating at the posterior border of eye and fusing with dark background of dorsum is present in the holotype, but not so well defined in some of the paratypes; pale line from anterior border of eye to nostril (almost imperceptible in holotype), not continuous around tip of snout, but rather reaching the nostril and then fusing with irregular dark blotches that makes it loose its previous well-defined form (for a different opinion, cf. Rivero 1960: 158); loreal region brown; lips dusky, paler than elsewhere on head; dark supratympanic band (tympanum pale-colored, encompassed by dark brown in holotype); pale line descending along inferior part of tympanum and posterior to it; upper eyelid dark with pale brown borders; a short, pale, oblique line from inguinal region to mid-body; dark brown crossbars, with pale flecks and spots (sometimes inconspicuous) on thighs, shank and tarsi; dark bars separated by narrower cream bands; shanks cream below, dusky towards dorsal surfaces; two dark bands from cloacal opening to interior part of knee, along midline of thighs; throat paler than venter; some isolated minute melanophores on chest (slightly resembling, but not making a collar), mid-throat (along *m. geniohyioideii*), and along borders of maxillae; venter cream, without pattern (holotype with dark gray melanophores on venter); palms and soles specked with brown.

Coloration in life: Notes of coloration provided in the original description indicated that the species has whitish and yellowish spots on dorsum; posterior part of thighs with "an irregularly margined, longitudinal, yellow band"; and yellow areas that separate brown cross bars on top of thighs. In some paratypes, there was more yellow and less brown on the thighs than the holotype. Throat was described originally as "yellowish, with some slight infuscation on the margins of the jaw"; the belly was described as white, and the hind limbs as yellow (Rivero 1961:158). Solano (1968:288-289) provided a coloration that does not differ substantially from the original description.

Measurements (in mm): Holotype (adult female with deeply convoluted oviducts and mature ova 1.7 mm in diameter; FMNH 35987): snout to vent length (SVL) 24.2; head width (HW) 8.7; Head length 8.6; tibia length (TL) 12.6; eye to nostril distance (EN) 1.8; internostril distance (IN) 2.9; hand length (Hand) 7.2; foot length (Foot) 10.8

Adults males (vocal slits; testes 1.2-3.6 mm in diameter; FMNH 67378-67380, UMMZ 167131-167132): SVL 18.0-22.4; HW 6.9-7.8; TL 10.2-11.3; horizontal length of eye (Eye): 3.1; EN 1.5-1.8; IN 2.9-3.1; IO 2.6-3.1; upper eyelid width (UEW) 1.6-1.8; Hand 6.1-6.3; Foot 9.8-10.8.

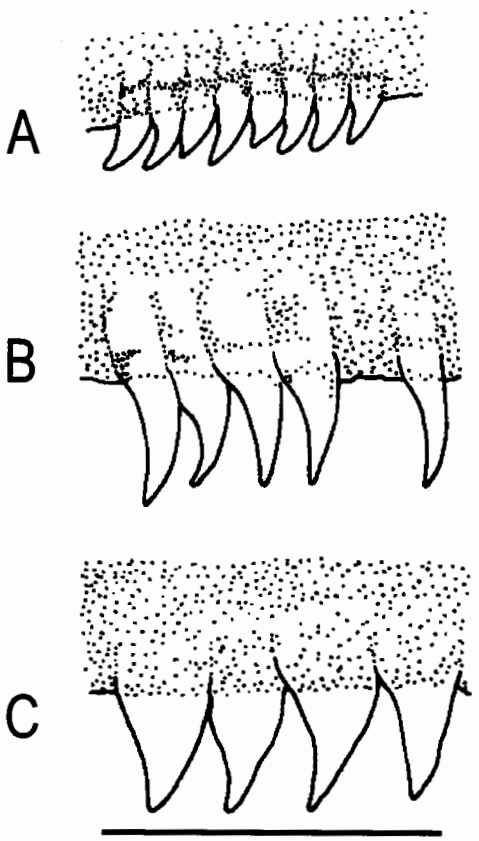

FIG. 3. Maxillary section view (at middle part of *pars palatina*) showing dentition of (A) *Mannophryne neblina* (UMMZ 113018; SVL= 28.3 mm), (B) *Colostethus dunni* (UMMZ 167133; SVL= 25.5 mm), and (C) *Colostethus leopardalis* (KU 132924; SVL= 27.9 mm). Scale = 0.5 mm.

Vista de sección maxilar (en la parte media del *pars palatina*) mostrando la dentición de (A) *Mannophryne neblina* (UMMZ 113018; SVL= 28.3 mm), (B) *Colostethus dunni* (UMMZ 167133; SVL= 25.5 mm), y (C) *Colostethus leopardalis* (KU 132924; SVL= 27.9 mm). Escala = 0.5 mm.

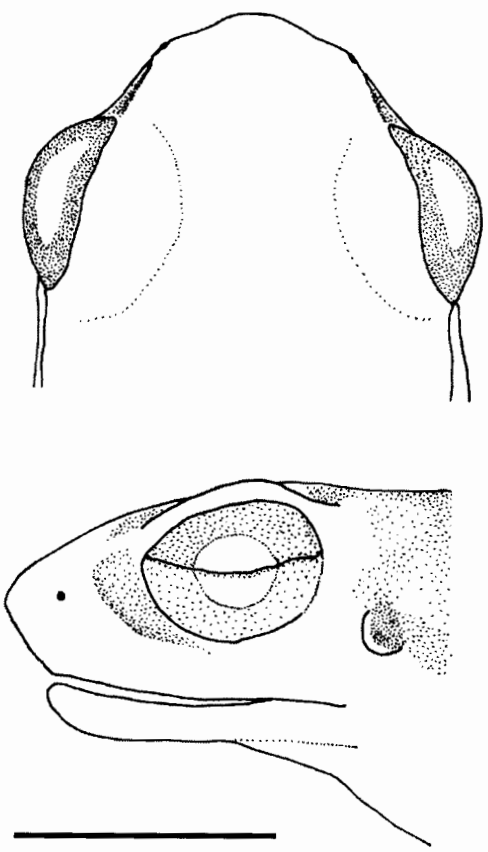

FIG. 4. Diagramatic dorsal (top) and lateral (bottom) views of head of *Colostethus dunni* (FMNH 67385, paratype). Scale = 5 mm
Vista diagramática dorsal (arriba) y lateral (abajo) de la cabeza de *Colostethus dunni* (FMNH 67385, paratipo). Escala = 5 mm

Adult females (deeply convoluted oviducts; mature ova 1.5-2.2 mm in diameter; FMNH 67384-67385; UMMZ 167133): SVL 24.1-25.5; HW 8.2-9.2; TL 12.4-12.5; Eye: 3.6-3.8; EN 2.0-2.2; IN 3.2-3.4; IO 2.9-3.0; UEW 2.0-2.2; Hand 7.0-7.2; Foot 11.7-12.3.

Juveniles females (non convoluted oviducts; eggs absent or just present as minute ovarian eggs; FMNH 67381-67383, UMMZ 167134): SVL 20.1-21.9; TL 10.9-11.4.

Geographic and ecological distribution: The most recent account (Frost 2004) gives the distribution of *Colostethus dunni* as the "Central portion of the Coastal Range of Venezuela, 500-1520 m", as it was previously considered by Frost (1985:89) and La Marca (1992:25). In an earlier statement, Duellman (1977:443) indicated the distribution range as the Cordillera de la Costa, at elevations between 370 and 1650 m. I suspect this consideration could have been based on frogs identified as *Colostethus dunni* in KU and collected at localities ranging from 370 to 1610m in the central part of the Venezuelan coastal range in the state of Aragua and in the Distrito Federal. Those frogs were later identified by La Marca (1994a) as *Mannophryne herminae*.

On these grounds, Aragua state, as was given by Duellman (*op. cit.*) and later by Barrio (1998:17) should be deleted from the distribution of the species. I could not find support to the contention that the species altitudinal range is as low as 500 m, since, apparently, the only actual recorded datum is that of 1520 m. So far as it is known, the species occurs in the Distrito Federal, as documented by the types and the additional material referred herein, and in Miranda state, judging from an apparently unvouchered record, accredited to Solano, coming from Quebrada de Caurimare (Barrio *op. cit.*). This place is close to the type locality and it comes not to a surprise, since Solano (1968) already had indicated that the species was also found in other mountain streams of the Caracas valley. To my knowledge, apparently there is only one additional record from Miranda state, not examined by me, listed in the UPRM herpetological holdings as *C. dunni* and coming from the road from Santa Teresa to Higuerote.

Data on the natural history of *Colostethus dunni* are lacking. There is an audiospectrogram attributed by Edwards (1974b) as belonging to to *Colostethus dunni*, and based on a recording made at the same region as the calls considered by Edwards (1974a; cf. La Marca 1994) as belonging to *Mannophryne herminae*. When these audiospectrograms are superimposed, they agree in the amplitude of the three harmonics. There is a minor difference in the intensity and amplitude of pulses in the main harmonic. In *M. herminae*, the pulses are, although not well-defined, of equal amplitude, with the exception of two pulses higher than the others. In the audiospectrogram attributed to *C. dunni*, there is a slight increase in frequency from pulse to pulse as the note is uttered, but all pulses have equal amplitude (La Marca 1984a). Lack of voucher specimens prevents taxonomic comparisons, but I am convinced that these calls are not attributable to *C. dunni* as understood here, but rather are associated with some population of *M. herminae*; this suspicion is corroborated by my assignment (La Marca 1992) of the frogs considered by Edwards (1974a) as *C. dunni* to the Rancho Grande collared frog, *M. herminae*.

The type locality of Los Venados is an old coffee finca now within El Avila National Park, about halfway up inland slope of the Cordillera de la Costa, overlooking Caracas (Handley 1976). I suspect the species to be found in either the lower limits of the "lower montane humid forest" (cf. Ewel *et al.* 1976, map), thus agreeing with the assessment of Handley (op. cit.), or else in a transition zone of the later and the life zone of "premontane dry forest" prevailing in the Caracas valley. Lack of precise local climatic data precludes a more detailed assessment, but it is worth noting that both units share the same general limits of mean annual precipitation (1000-2000 mm) and amount of water lost by evapotranspiration, that vary from half to equal the precipitation (Ewel *et al.* 1976:178); the later indicating a favorable water balance. The transition zones are about in the isotherm of 18 °C. These values of precipitation and temperature may be useful indicators of where to search for the species. Additionallly to the above indicated life zones, most "premontane humid forests" near the type locality seems also adequate for searching these frogs, especially near their upper range (1500 m). Duellman (1977:443) considered the habitat for the species to be rain forest and cloud forest. This is perhaps about right, since the type locality of *Colostethus dunni*, at 1520 m,

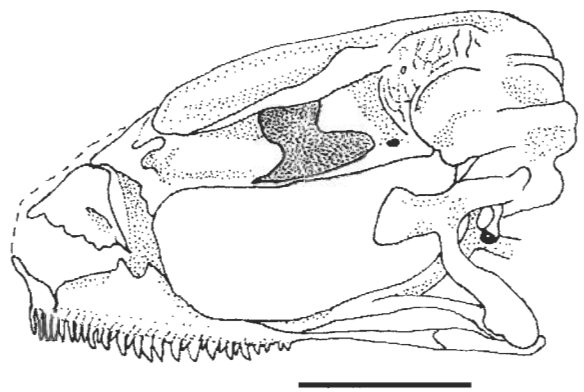

FIG. 5. Lateral view of skull of *Colostethus dunni* (UMMZ 167133). Note shape of teeth. Scale = 2 mm
Vista lateral del cráneo de *Colostethus dunni* (UMMZ 167133). Note la forma de los dientes. Escala = 2 mm

could be considered to be at a transitional zone between cloud forest and a lower montane humid forest. In the terminology of Huber and Alarcón (1988), this would be a Montane ombrophilous evergreen forest ("bosque ombrófilo Montano, siempreverde"). Huber (1997) indicated that the southern slopes of the central Coastal Range are dryer than the northern ones facing the humid trade winds; this perhaps could translate in cloud formation at higher elevations than 1500 m. Handley (1976) noted that Los Venados is located in a place with mostly gentle slopes, with numerous small, rocky, swift-flowing streams (e.g. Quebrada Anauco and Quebrada Guayabal). According to Gilson Rivas (pers. comm.), the locality has been highly modified by human intervention, with introduced *Eucalyptus* trees, although some original vegetation remains by the streams. Apparently, it is not a cloud forest, but rather a semi-deciduous ("seasonal") forest. Some frog species, like *Mannophryne herminae* and *Gastrotheca walkeri* have been seen in the place in searches conducted by J. Celsa Señaris and G. Rivas (pers. comm.) from 1992-1993, and in 2004. There is no reason to believe that the frog *Eleutherodactylus terraebolivaris*, reported by Solano (1968) from the close Quebrada Anauco, could not be found also at the same place.

Conservation: *Colostethus dunni* was considered one of the common species of the Caracas valley (Solano 1968). Recent intensive searches (G. Rivas pers. comm.), in 1992-1993 and 2004, have failed to document the presence of this taxon in the places it was formerly common. There is not information in collections to gather an idea of when the popupations of this species begun to decline. Manzanilla and La Marca (2004) documented the declines of *Atelopus cruciger*, a formerly common frog in most of the streams of the same region inhabited by *C. dunni*. It is most likely that similar declines were experienced by *C. dunni*. Lack of recent collected specimens supports the idea that the species be considered as endangered (EN). A detailed field study is needed to determine a more proper conservation status. Measures need to be taken to ensure the conservation of the species.

DISCUSSION

For a long time, *Colostethus dunni* has been associated, intentionally or not, with collared frogs (*Mannophryne*). Examination of the frogs upon which Edwards (1974a) based his descriptions of *C. dunni* revealed that these specimens actually do not belong to this species (La Marca 1994a), but rather represent a different taxon belonging to the genus *Mannophryne*. That *C. dunni* may be a species related to collared frogs can be inferred from some other works (e.g. Rivero 1978; Duellman 1986; Myers *et al.* 1991). Some misapplications of the name are also part of the taxonomic history of the taxon. For example, Hardy (1982) referred to *C. dunni* specimens he later described as *C. olmonae* (Hardy 1983). His new species was deemed to be similar to *C. dunni*. I have not examined Hardy (1983) "*C. dunni*" specimens, but another study based on specimens collected at the same places and time as the ones studied by Edwards (cf. La Marca 1994a) leaves no doubt about their identity. I am now convinced that Hardy´s name "*C. dunni*" was based on misidentified specimens. They are, as well as the frog without museum number depicted in his figure 3 (Hardy 1983:50), collared frogs of the genus *Mannophryne*. Other works complete the history of misapplication of the name; for example, the "*Colostethus dunni*" found by Duellman (1986) on the Maracay-Ocumare de la Costa road (estado Aragua) are most probably *Mannophryne herminae*. Since all the frogs identified as *Colostethus dunni* by Edwards (1974a) have revealed to be co-specific with *Mannophryne herminae*, some of the statements about *C. dunni* made by later authors relying on this work may be simply wrong. One of these characters is the presence of a dark collar. Although the pattern of melanophores on the chest of *C. dunni* may be suggestive of a collar, I consider this resemblance to be either a homoplasy or a convergent character; therefore, not a valid indication of close relationship to *Mannophryne* frogs.

The presence of extensive foot webbing in *C. dunni* is shared with some *Mannophryne* frogs (e.g. *M. collaris* and *M. oblitterata*), but it is not exclusive to them. Other geographically close Venezuelan Andean dendrobatids (e.g. *Colostethus leopardalis* and *Aromobates nocturnus*) also show this condition. The presence of lateral fringes along the second and third fingers of *C. dunni* is shared with *C. leopardalis* and *C. mandelorum*, both frogs also of unclear relationships.

La Marca (1985) considered *C. dunni* as a member of his "*C. alboguttatus*" group, based on the presence of a dental condition (long maxillary and premaxillary teeth) also shared with some members of this assemblage of frogs. However, when he erected the genus *Nephelobates* for them (La Marca 1994b), he excluded *C. dunni*, as well as he excluded *Colostethus leopardalis*. The appearance of the combination "*N. leopardalis*" in La Marca (1994b:40) is an error; the species was not listed in the formal diagnosis of *Nephelobates* in the same paper. Long teeth are also exhibited by *C. leopardalis* (Fig. 3) and *Aromobates nocturnus*. The presence of this condition in the later, and the lack of knowledge of its occurrence among *Nephelobates* and other dendrobatid frogs, precludes ascertain its phylogenetic significance at present. Cloacal sheath, considered diagnostic of *Nephelobates* by La Marca (1994b), is absent in *C. dunni*.

Rivero (1961) stated that *C. dunni* does not have any close relative in Venezuela, and later (Rivero 1990) placed it as a doubtful species not assignable to any of his eight *Colostethus* species groups. Its phylogenetic relationships remain enigmatic.

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APPENDIX I (SPECIMENS EXAMINED)

Colostethus ayarzaguenai La Marca. MHNLS 12949 (holotype), sector central de Cerro Jaua, Bolívar state.

Colostethus bromelicola Test. UMMZ 113027, Rancho Grande, Aragua state.

Colostethus brunneus Cope. ULABG 4202-4211, Parque Nacional Duida-Marahuaka, alrededor del centro recreacional Duida-Culebra, rio Cunucunuma, NW Cerro Duida, Amazonas state.

Colostethus dunni (Rivero). FMNH 35987 (holotype), 67378 67385 (paratypes), above Caracas, Distrito Federal; UMMZ 167131-167132, 167133 (cleared and stained), Coffee Finca "Los Venados", in Avila Range above and N. of Caracas, 1520 m, Distrito Federal.

Colostethus guanayensis La Marca. MHNLS 10708 (holotype), Alto Rio Parguaza, Serranía de Guanay, Amazonas state.

Colostethus humilis Rivero. UPRM 3526 (holotype), Boconó, Laguneta artificial M.A.C., 1470 m, Trujillo state.

Colostethus leopardalis Rivero, MCNG 700-701, La Corcovada, Páramo de Mucubaji, Distrito Rangel, Merida state.

Colostethus mandelorum (Schmidt). FMNH 17789 (holotype), Mount Turumiquire, 8000 ft., Sucre state.

Colostethus murisipanensis La Marca. MHNLS 11385 (holotype), Murisipan-Tepui, 2350m, Bolívar state.

Colostethus parimae La Marca. ULABG 4221 (holotype), Pista Constitución, nr. Cerro Delgado Chalbaud, Amazonas state.

Colostethus parkerae Meinhardt and Parmelee 1996. ULABG 4198-4201. Km 112 on road El Dorado- Santa Elena de Uairén, 860m, Bolívar state.

Colostethus praderioi La Marca. ULABG 4196 (holotype), Monte Roraima, tercera quebrada a partir de la base, 1950m, Canaima National Park, Bolívar state.

Colostethus roraima La Marca. ULABG 4197 (holotype), Paso de la Muerte, 2700m, Monte Roraima, Bolívar state.

Colostethus saltuensis Rivero. UPRM 5147 (holotype), de la Fria a Michelena, 830 m, Táchira state.

Colostethus shrevei Rivero. ULABG 4067 (holotype), base of Mt. Duida, 350 m, Culebra-Jukudi Jidi trail, Amazonas state.

Colostethus tepuyensis La Marca. ULABG 2557 (holotype), Danto-Piñón trail, on the way from Kamarata to Auyantepui, 1650m, Bolívar state.

Colostethus sp. (undescribed species to be dedicated to Henri Pittier; taxon usually stated as "*C. brunneus*" in the literature for northern Venezuelan amphibians). La Trilla, 170 m, Municipio Mario Briceño Iragorry, Aragua State.

Mannophryne collaris (Boulenger). BM 1947.2.14.40, 1947.2.14.42, (syntypes), Mérida, 5200 feet, Mérida state.

Mannophryne cordilleriana La Marca. ULABG 763 (holotype), Presa hidráulica José Antonio Páez, 1600m, near La Mitisús, Mérida state.

Mannophryne herminae (Boettger). KU 167275-167316, Km 13-34, Maracay-Ocumare de La Costa Rd.; 167317, 16 Km NNW Petaquire, 1610 m; 167621, 167810-167812 (tadpoles), Km 29-34, Maracay Ocumare de La Costa Rd., 270-370 m; Aragua state (identified as *Colostethus dunni* in Edwards, 1974a).

Mannophryne larandina (Yústiz). ULABG 4800 (Holotype of *Colostethus larandinus*; formerly UCLA 0087), Hato Arriba, Distrito Morán, Sierra de Barbarcoas, 1800 m. s. n. m., Estado Lara

Mannophryne neblina (Test). KU 154403; UMMZ 113002-113003, 113005-113026 (paratypes), Portachuelo Pass, Rancho Grande, Aragua state.

Mannophryne oblitterata (Rivero). TCWC 61386 (holotype of *Colostethus guatopoensis*), Quebrada Guatopo, Serranía del Interior, W Altagracia de Orituco, 736m, Guárico state.

Mannophryne riveroi (Donoso-Barros). USNM 165603 (paratype), Cerro Azul, Macuro, Sucre state.

Mannophryne trinitatis (Garman). KU 154442-154455, Maracas Falls, St. George, Trinidad Island.

Mannophryne yustizi La Marca. CVULA 2842 (holotype) 14 Km SSE Sanare, 1475m, Lara state.

Nephelobates alboguttatus (Boulenger).-- AMNH 639-641, 644, 646-648, 3147, Merida, 10502-10506, Rio Albirregas [=Albarregas?], nr. Mérida; 51266, 58904 (5, identified by Boulenger), Merida state.

Nephelobates duranti Péfaur. CVULA 1608 (holotype), Páramo de La Culata, 2880m, Distrito Libertador, Mérida state.

Nephelobates haydeeae Rivero. UPRM 4706 (holotype), El Vivero después del Páramo del Zumbador, hacia Mesa de Aura, Táchira state.

Nephelobates mayorgai Rivero. UPRM 5160 (holotype), El Chorotal (El Sineral), carretera Mérida La Azulita, 1800 m, Mérida state

Nephelobates meridensis Dole and Durant. MBUCV 6168 (holotype), Chorotal, 15 km south east of Azulita, 1880 m, Mérida State.

Nephelobates molinarii La Marca. CVULA 2820 (holotype), Las Playitas, 2270m, near Bailadores, Mérida state.

Nephelobates orostoma Rivero. UPRM 4509 (holotype), Boca de Monte, Camino de Pregonero, 2615 m, Táchira state.

Nephelobates serranus Péfaur. CVULA 2847 (holotype), vía El Morro, 2300m, Distrito Libertador, Mérida state.