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 new usages (crosyonymy), data on musculature, coloration in life and in ethanol, morphometry, geographic and ecological distribution, and discussion of relationships. Although usually associated with collared frogs (Marmoriphinae) it now appears that the species is not closely related to any members of this genus, nor to Neophylax or other dendrobatids frogs. Its phylogenetic relationships remain enigmatic. This species is considered to be endangered and suggested to be elevated to some formal category of conservation.

Keywords: Systenatik, Amphibia, Dendrobatidae, Colostethus dunni, Marmoriphinae, Neophylax, Colostethus, Venezuela.

Resumen: “Género sistemático de una rana dendrobatida enigmática y posiblemente amenazada (Colostethus dunni) del Valle de Caracas, Norte de Venezuela”. En este trabajo se provee una redescritpción 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 diagnóstico, así como una descripción detallada de la especie, acompañada con una lista extensa de nombres usados en la literatura (crosyonymy), 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 aculíadas (Marmoriphinae), parece que la especie no está estrechamente relacionada con ningún miembro en este género, ni con Neophylax o otras ranas dendrobatidas. Sus relaciones filogenéticas permanecen enigmáticas. Esta especie se considera en peligro y se sugiere que sea elevado a alguna categoría formal de protección.

Palabras clave: Sistematización, Amphibia, Dendrobatidae, Colostethus dunni, Marmoriphinae, Neophylax, Colostethus, Caracas, Venezuela.

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

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 tarsi, and females having deeply constricted ovaries and/or mature eggs. Muscle terminology follows Esch (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, 1992). Terminology follows La Marca (1996).

Museum abbreviations are as follows: American Museum of Natural History (AMNH), British Museum of Natural History (BM), Colección de Vértidos de la Universidad de Los Andes, Mérida (CVULA); Field Museum of Natural History (FMNH), Museum of Natural History, University of Kansas (MUS), Museo de Biología, Universidad Central de Venezuela (MUBCV), Museo de Ciencias Naturales Guanare, Venezuela (MCGN), Museo de Historia Natural La Salle, Caracas (MHNSL), Texas AM University, Texas Cooperative Wildlife Collection (TCWC), Colección de Enrique Ystást, Universidad Centro Occidental Lázaro Alvarado (UCLA), Colección de Anfibios y Reptiles, Laboratorio de Biogeografía, Universidad de Los Andes, Mérida (ULARD); Museum of Zoology of the University of Michigan (UMZC); herpetological Collection at University of Puerto Rico in Mayaguez (UPRM), and United States National Museum (USNM).
Colostethus dunnii (Rivero), 1961


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 eggs.

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 lip; (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 1(2-0-3-0) 1.082-0(1-5-2-0)1.042-0(1-4-0) 2.002-0(2-3-0)1W (11) toes with lateral fringes; third toe bearing flap-like lateral fringes; (12) dorsolateral stripe absent; (13) disc on fourth toe widest 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 ventral, without conspicuous markings; (18) third finger not swollen in males; (19) long, fang-like teeth.

Colostethus dunnii 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. dunnii provides no information to evaluate phylogenetic relationships between this species and members of the genus Mannophrynus, but the presence of at least two characters (dentition and throat pattern) is suggestive of a closer relationship between C. dunnii and members of the genus Nephelobates. The extensive webbing of C. dunnii is in sharp contrast with the brief webbing of the members of Nephelobates (but see discussion).

Colostethus dunnii was previously known only from the type specimens. The following description is based on the type series and on previously unreported USMZ material identified as "Colostethus albocephalus."
Tarsus and flanks smooth; throat, chest and venter smooth; upper arm and forearms smooth; hand length 30.8 ± 2.1% SVL (N=7); palmar tubercle single, rounded; mental tubercle elongated, not well-defined; about 2 times larger 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 phalax; widely separated pale scutum; 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 shield; thighs and shanks smooth, dorsally and ventrally; slight tarsal fold not ending in tuberect; 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: 1:1:0-3:3, 1:0:0:2:0 (1:1:0:3:3, 1:0:0:2:0) 2:0:0:2:0 (2:0:0:2:0:2) (Fig. 2); phalanges free from web, bearing lateral fringes; antepenultimate and penultimate phalax 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 toe; largest disc about 1.5 times wider than adjacent phalax (Fig. 2); heels do not overlap when thighs are held at right angles to body axis, reaching to anterior corner of eye when legs addressed 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 Clandesthus duvii (FMNH 47385, paratype). Par a izquierda (escala = 5 mm) y mano izquierda (escala = 2.5 mm) de Clandesthus duvii (FMNH 47385, paratipo).
Musculature: based on UMMZ 167133; jaw-mandibular musculature: the m. submentalis is a moderate-fat, arrophic, thin sheet of muscle with lateral attachments from the posterior end of the jaw to the m. submentalis; the m. geniobradyi is visible through a reduced median area of the m. intemamentalis. Hind leg musculature: m. bigem almost completely concealed by m. sartor femoris. The m. pyriformis is narrow, inserting deeply below m. vastus externus and m. biceps. Depressor musculature: 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 skin 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 matches 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 SLV).

Coloration in preservative: Dorsum brown, with small pale flecks (cf. Rivero 1964-319) or large pale spots on mid-dorsal rift 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 indiscernible in holotype), not continuous around tip of snout, but rather reaching the nostril and then fusing with irregular dark blotches that make it lose its previous well-defined form (for a different opinion, cf. Rivero 1960: 158); lateral region brown; lips dusky, paler than elsewhere on head; dark supratympanic band (tymanum 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 inner eye 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; Shirley cream below, dusky towards dorsal surfaces; two dark bands from clavical opening to posterior part of knee, along midline of thighs; throat paler than ventrum; some isolated minute melanophores on chest (slightly resembling, but not making a collar), mid-throat (along m. geniobradyi), and along borders of maxilla; venter cream, without pattern (holotype with dark grey melanophores on venter); palins and soles streaked 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 iridescence on the margins of the jaw", the belly was described as white, and the hind limbs as yellow (Rivero 1961-158). Solano (1968: 288-298) provided a coloration that does not differ substantially from the original description.

Measurements (in mm): Holotype (adult female with deeply convoluted ovicculus and narinii ova: 1.7 mm in diameter; FMNH 30987) snout to vent length (SVL): 24.2; head width (HW): 6.7; Head length 8.6; snout length (TL): 12.6; eye to nostril distance (EN): 1.8; internasal distance (IN): 2.6; hand length (Hand): 7.2; foot length (Foot): 10.9.

Adults males (trivial slits, testes: 1.2 x 0.6 mm in diameter; FMNH 67378-67380; UMMZ 167131-167132); SVL: 18.5-22.4; HW: 6.9-7.6; TL: 12-13; horizontal length of eye (Eye): 3.1; EN: 1.5-1.6; IN: 2.5-3.1; IO: 2.6-3.1; upper eyelid with (UEW): 1.6-1.8; Hand: 6.1-6.3; Foot: 9.8-10.8.

**Fig. 1.** Mandible view (at middle part of parietal palatine) showing division of (A) Maxillotympanic (UMMZ 132018; SVL = 28.3 mm), (B) Caleostomus dani (UMMZ 167132; SVL = 25.5 mm), and (C) Caleostomus lepidopterus (KU 132924; SVL = 21.9 mm). Scale = 0.5 mm.

**Fig. 2.** View of maxillary (in the area media des pares palatine) mostrando la dentición (a) Maxillotympanic (UMMZ 132018; SVL = 28.3 mm), (B) Caleostomus dani (UMMZ 167132; SVL = 25.5 mm), y (C) Caleostomus lepidopterus (KU 132924; SVL = 21.9 mm). Escala = 0.5 mm.
On these grounds, Aragua state, as was given by Durrell (op. cit.) and later by Barro (1968:17) 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 520 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 type and the additional material referred herein; and in Miranda state, judging from an apparently unverified record, according to Solano, coming from Guadalupe de Caracas (Barro, op. cit.). This place is close to the type locality and it comes near 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 LPRN 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 (1974a) as belonging 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 in the note is uttered, but all pulses have equal amplitude (La Marca 1984a). Lack of voucher specimens prevents taxonomic comparison, but I am convinced that these vocalizations are not attributable to C. dunni as understood here, but rather are associated with some population of M. herminae; this supposition is corroborated by my assignment (La Marca 1992) of the frogs considered by Edwards (1974a) as C. dunni to the Rancho Grands colonel-fig. M. herminae.

The type locality of Los Venados is an old coffee finca now within El Avila National Park, about halfway up inland slopes of the Cordillera de la Costa, overlooking Caracas (Handley 1979). I suspect the species to be found in either the lower limit of the "lower montane humid forest" (see, e.g., Ewel et al. 1974), thus agreeing with the assessment of Handley (op. cit.), or else in a transition zone of the latter and the life zone of "premontane dry forest" prevailing in the Caracas valley. Lack of precise local climatic data provides a more detailed assessment, but it is worth noting that all units share the same general limits of mean annual precipitation (1500-2000 mm) and amount of waterlost by evapotranspiration, that vary from half to equal the precipitation (Ewel et al. 1974:178), the latter inducing a favorable water balance. The transition zones are zoned in the iso-hem of 18 °C. These values of precipitation and temperature may be useful indications of where to search for the species. Additionally, to the above indicated life zones, most "premontane humid forest" is considered the type locality seems also adequate for surviving these frogs, especially near their upper range (1550 m). Durrell (1974) 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,
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 ombrophilo Montano, siempreverde"). Huber (1957) 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. Inanley (1976) noted that Los Venados is located in a place with mostly gentle slopes, with numerous small, rocky, swiftly-flowing streams (e.g. Quebrada Arcano and Quebrada Guayabal). According to Gilson Rivers (pers. comm.), the locality has been highly modified by human intervention, with introduced Eucalyptus species, 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 Maniophrynus herminae and Gastrotheca walwichi have been seen in the place in searches conducted by J. Caja (unpubl.) and G. Rivers (pers. comm.) from 1992-1993, and in 2004. There is no reason to believe that the frog Neoteresitrus terricolorviviparus, reported by Solano (1989), from the close Quebrada Arcano, could not be found also at the same place.

Conservation: Colostethus dunnii was considered one of the common species of the Caracas valley (Solano 1986). Recent intensive searches (G. Rivers 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 no information in collections to gather an idea of when the populations of this species began to decline. Mascareñas 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. dunnii. It is most likely that similar declines were experienced by C. dunnii. 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 dunnii has been associated, informally or not, with collared frogs (Maniophrynidae). Examination of the frogs upon which Edwards (1974a) based his descriptions of C. dunnii revealed that these specimens actually do not belong to this species (La Marca 1994a), but rather represent a different taxon belonging to the genus Maniophrynus. That C. dunnii may be a species related to collared frogs can be inferred from some other works (e.g. Rivero 1980; 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. dunnii specimens he later described as C. omojaro (Hardy 1983). His new species was deemed to be similar to C. dunnii. I have not examined Hardy (1983) "C. dunnii" 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. dunnii" 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 Maniophrynus. Other works complete the history of misapplication of the name, for example, the "Colostethus dunnii" found by Duellman (1986) on the Maracaibo-Occunare de la Costa road (estado Aragua) are most probably Maniophrynus herdmani. Since all the frogs identified as Colostethus dunnii by Edwards (1974a) have revealed to be co-specific with Maniophrynus herdmani, some of the statements about C. dunnii 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 maniophrynids on the chest of C. dunnii may be suggestive of a collar, I consider this resemblance to be either a homoplasious or a convergent character; therefore, not a valid indicator of relationship to Maniophrynus.

The presence of extensive foot webbing in C. dunnii is shared with some Maniophrynus frogs (e.g. M. collaris and M. oliviverrucatus), but it is not exclusive. One morphologically close Venezuelan Andean dendrobatids (e.g. Colostethus ioponidus and Aromobates nocturnus) also show this condition. The presence of lateral fringes along the second and third fingers of C. dunnii is shared with C. ioponidus and C. mandoniadum, both frogs also of similar coloration. La Marca (1985) considered C. dunnii as a member of his "C. abogotatulis" group, based on the presence of a dental condition (long mandible and maxilla), which is shared with some members of this assemblage of frogs. However, when he erected the genus Nephelobates for them (La Marca 1994a), he excluded C. dunnii, as well as he excluded Colostethus leopoldantis. The appearance of the combination "N. ioponidus" in La Marca (1994a: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. leopoldantis (Fig. 3) and Aromobates nocturnus. In the presence of this condition in the later, and the lack of knowledge of its occurrence among Nephelobates and other dendrobatids frogs, predaceous ascertain its phylogenetic significance at present. Cecal shear, considered diagnostic of Nephelobates by La Marca (1994a), is absent in C. dunnii.

Rivero (1961) stated that C. dunnii does not have any close relative in Venezuela, and later (Rivero 1980) stated it as a doubtful species not assignable to any of his eight Colostethus species groups. Its phylogenetic relationships remain enigmatic.
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LITERATURE CITED


APPENDIX I (SPECIMENS EXAMINED)

Colostethus ayacuchoensis La Marca, MNHS 12949 (holotype), sector central de Cerro Jauja, Buvík state.

Colostethus brometicola 2r. UMMZ 113027, Rancho Grande, Aragua state.


Colostethus dunnii (Rivero). FMNH 35855 (holotype), 67378 (paratype), arroyo Caracas, Distrito Federal, UMMZ 161134-161135, 161138 (collected and stained). Coffee Finca "Los Verados", in Avila Range above and of Caracas, 1520 m, Distrito Federal.

Colostethus guayanesis La Marca, MNHS 10708 (holotype), Alto Pío Parguaza, SE of Guayana, Amazonas state.
Colostethus humilis Rivero, UPRM 3526 (holotiplo), Boconó, Laguna artificial M.A.C., 1470 m., Trujillo state.

Colostethus isaspardalis Rivero, MCNG 700-701, La Corvadilla, Parque de Mucubají, Distrito Rangel, Mérida state.

Colostethus mandolusorum (Schmidt), FMNH 17789 (holotiplo), Mount Tumuripí, 8900 ft., Sucre state.

Colostethus muriathanesi La Marca, MNHN 11385 (holotiplo), Muisipan-del-Canaima, Amazonas state.

Colostethus parimae La Marca ULAB 4221 (holotiplo), Pista Constitución, nr. Cerro Délégac-Chalbaut, Amazonas state.

Colostethus navae Meinhardt and Parmelee 1996, ULABG 4195-4201. Km. 112 on road El Curoado-Santa Elena de Uairén, 800 m., Bolivar state.

Colostethus praderoi La Marca. ULABG 4196 (holotiplo), Monte Roraima, litoral quebrada a partit de la base, 1950 m., Canaima National Park, Bolivar state.

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

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

Colostethus asvevi Rivero. ULABG 4057 (holotiplo), base of Mt. Duida, 350 m., Culebra-Juduí Jidi trail, Amazonas state.

Colostethus tepuyensis La Marca. ULABG 2657 (holotiplo), Dantio-Píton trail, on the way from Kamarana to Auyan tepui, 1650 m., Bolivar state.

Colostethus sp. (underscribed species) to be dedicated to Henk Pitter: taxon usually stated as "C. brommei" in the literature for northern Venezuelan amphibians), La Triba, 170 m., Municipio Mario Briceño Iragorry, Aragua State.


Manophrynus cordillerae La Marca. ULABG 763 (holotiplo), Presa hidroeléctrica José Antonio Páez, 1600 m., near La Milus, Mérida state.

Manophrynus herminae (Boettger), KU 16727/167316, Km 33-34, Maracay-Ocumare de La Costa Rd.; 97317, 16 Km NWH Petaquere, 1610 m., 167321, 167810-167812 (paratiplos), Km 29-34, Maracay Ocumare de La Costa Rd., 270-370 m.; Aragua state (identified as Colostethus dunni in Edwards, 1974a).

Manophrynus larandina (Yáñez). ULABG 4800 (holotiplo de Colostethus larandina; formerly ULA 0087), Hato Ambu, Distrito Morán, Sierra de Barinasocas, 1800 m. s. n. m., Estado Lara


Manophrynus obliteratus (Rivero). TCWC 61386 (holotiplo of Colostethus gutupoaenensis), Quebrada Guatapo, Sierra del Interior, W Alturagea de Orinoco, 730m., Guárico state.

Manophrynus rivera (Donoso-Barros). USNM 165603 (paratiplo), Cerro Azul, Mucuro, Sucre state.

Manophrynus trinitatis (Gaimard). KU 154442-154455, Maracas Falls, St. George, Trinidad Island.

Manophrynus yustzi La Marca. CVLA 2842 (holotiplo) 11 Km SSE Sanara, 1475 m., Lara state.

Nephelobates alboguttatus (Boulenger).—AMNH 639-641, 644, 645-648, 3147, Mérida, 1053-1055, Río Albamarra (Juliana Regal), nr. Mérida; 51296, 58904 (9, identified by Boulenger), Mérida state.

Nephelobates durandi Pfeiffer. CVLA 1608 (holotiplo), Parámar de La Culata, 2885 m., Distrito Libertador, Mérida state.

Nephelobates haydweae Rivero. UPRM 4706 (holotiplo), El Ríosito después del Páramo del Zambador, hacia Mesa de Aura, Táchira state.

Nephelobates mayorgai Rivero. UPRM 5160 (holotiplo), El Chorrol (El Seral), carretera Mérida-La Azulita, 1909 m., Mérida state.

Nephelobates mardensis Dodge and Durant. MBUCV 6168 (holotiplo), Chorotal, 15 km south east of Azulita, 1880 m., Mérida State.

Nephelobates molinari La Marca. CVLA 2820 (holotiplo), Las Playitas, 2270m., near Villaflor, Mérida state.

Nephelobates oceotona Rivero. UPRM 4609 (holotiplo), Boca de Monte, Carrancito de Preguine, 2815 m., Táchira state.

Nephelobates serruos Pfeiffer. CVLA 2947 (holotiplo), via El Marco, 2300m., Distrito Libertador, Mérida state.