

A new *Phyllomedusa* from southwestern Amazonia (Amphibia: Anura: Hylidae)

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Abstract: A new species of *Phyllomedusa* is described, and data on its ecology and reproductive behavior are provided. The new species was mistaken in the past for *P. boliviana*, a fact that generated considerable taxonomic confusion. The new species occurs in southwestern Amazonia (Brazil, Peru and Bolivia). In some areas of Bolivia, it is sympatric with *P. boliviana*.

Keywords: Hylidae, *Phyllomedusa*, new species, South America

Resumen: Una nueva *Phyllomedusa* del suroeste de Amazonia (Amphibia: Anura: Hylidae).- Se describe una nueva especie de *Phyllomedusa* y se dan datos sobre su ecología y comportamiento reproductor. Dicha especie ha generado considerable confusión durante años al haber sido erróneamente identificada como *P. boliviana*. Su distribución comprende el sudoeste de la Cuenca Amazónica en Brasil, Perú y Bolivia, país en el que, en algunas zonas, es simpátrica con *P. boliviana*.

Palabras clave: Hylidae, *Phyllomedusa*, especie nueva, Sudamérica

INTRODUCTION

The subfamily Phyllomedusinae, distributed from Mexico to Argentina, consists of six genera: *Agalychnis* Cope, *Hylomantis* Peters, *Pachymedusa* Duellman, *Phasmahyla* Cruz, *Phrynomedusa* Miranda-Ribeiro, and *Phyllomedusa* Wagler. The most speciose genus is *Phyllomedusa*, which ranges from Costa Rica to Argentina. Whereas some species of *Phyllomedusa* remain without assignment to any particular group of species, others have been included in more or less well-defined species groups as, for example, the *buckleyi*, *burmeisteri*, *hypochondrialis*, *perinesos*, and *tarsius* groups (FROST, 1985). The poorly defined *tarsius* group consists of six species that occur in Panama (*P. venusta* Duellman & Trueb), Trinidad and coastal Venezuela (*P. trinitatis* Mertens), Upper Amazon basin [*P. tarsius* (Cope) and *P. coelestis* (Cope)], semiarid lowlands and valleys of Bolivia and adjacent parts of Brazil and Argentina (*P. boliviana* Boulenger), and the Chaco of Bolivia, Argentina and Paraguay, and surrounding areas of southwestern Brazil [*P. sauvagii* Boulenger; the latter

species is one of the most distinctive *Phyllomedusa* (CANNATELLA, 1980), and probably it would deserve its own species group].

FUNKHOUSER (1957) provided the only available review of the genus *Phyllomedusa* (then comprising all the present-day Phyllomedusinae), which is now clearly out of date. CANNATELLA (1983) pointed out that FUNKHOUSER (1957), in her account of *P. boliviana*, relied on BOULENGER's (1902) description of the species to identify a sample of specimens from different localities, but did not examine the syntypes. The comparison of six specimens of *Phyllomedusa* from El Pailón (Santa Cruz, Bolivia) with those specimens used by Funkhouser, led SHREVE (1959) to describe a new species, *P. pailona*. LAURENT (1967) reported *P. pailona* in Argentina (as *Pithecopus pailonus*) and compared it with some of the specimens examined by Funkhouser, pointing out remarkable differences between the two species. HEYER (1977) commented on some specimens of *Phyllomedusa* from Restauração (Amazonas, Brazil), which he identified as *P. nr. boliviana* based on specimens identified as such at the USNM. Upon comparison of Funkhou-

ser's material and the syntypes of *P. boliviana*, CANNATELLA (1983) concluded that: 1) none of the specimens used by Funkhouser represented *P. boliviana* but an undescribed species; 2) *P. pailona* is a junior synonym of *P. boliviana*; and 3) Heyer's specimens belong to the undescribed species.

This new species has turned out to be quite common and widespread. As a result, comments on it (often as *Phyllomedusa* sp.) have appeared in numerous herpetological papers dealing with frogs of Bolivia and Peru in the recent years (e. g., DUELLMAN *et al.*, 1988; DE LA RIVA, 1990; RODRIGUEZ & CADLE, 1990; RODRIGUEZ, 1992; DUELLMAN & SALAS, 1991; DE LA RIVA, 1993; DUELLMAN, 1995; DUELLMAN & MENDELSON, 1995; DUELLMAN & THOMAS, 1996; MORALES & MC-DIARMID, 1996; KÖHLER & LÖTTERS, 1999). The new species is similar to, but clearly distinguishable from, *P. boliviana* and, albeit mostly parapatric, both species occur in microsympatry in some parts of the Bolivian lowlands. The aim of this paper is to describe this well known, but long-time neglected, *Phyllomedusa* and compile the available information about its natural history and distribution.

MATERIAL AND METHODS

Measurements were taken with digital calipers to the nearest 0.1 mm. Recordings were obtained and analyzed as explained in DE LA RIVA *et al.* (1995). To facilitate comparisons, the diagnosis and description follow CANNATELLA's (1983) redescription of *P. boliviana*, with some modifications. Museum acronyms are as follows: CET, Centro de Estudios Tropicales (Sevilla, Spain); KU, Natural History Museum, The University of Kansas (Lawrence, U.S.A.); NKA, Museo de Historia Natural "Noel Kempff Mercado" (Santa Cruz, Bolivia); UMMZ, University of Michigan, Museum of Zoology (Ann Arbor, U.S.A.); USNM, National Museum of Natural History,

Smithsonian Institution (Washington, U.S.A.); ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn, Germany).

SYSTEMATICS

Phyllomedusa camba, sp. nov.

(Figures 1 and 2).

Holotype: NKA 0084, an adult male from Puerto Almacén, Provincia Ñuflo de Chávez, Departamento de Santa Cruz, Bolivia (15°46'S/62°15'W), collected on 27 December 1987 by I. De la Riva.

Paratypes: KU 215408, from Cuzco Amazónico, 15 E of Puerto Maldonado, Departamento de Madre de Dios, Peru (12°33'S/69°03'W), collected on 27 January 1990 by F. M. Cuadros; KU 215409, from Cuzco Amazónico, collected on 29 January 1990 by J. J. Wiens; KU 215410-11, from Cuzco Amazónico, collected on 31 January 1990 by W. E. Duellman; NKA 0293, 0322-3, and 0325, adult males from Puerto Almacén, Bolivia, collected by I. De la Riva; NKA 1497, an adult male from Villa Tunari, Provincia Chapare, Departamento de Cochabamba, Bolivia (16°57'S/65°24'W); NKA 2886 from Caranda, Provincia Ichilo, Departamento de Santa Cruz, Bolivia (17°32'S/63°31'W); NKA 3068, an adult male from Lago Caimán, Parque Nacional Noel Kempff Mercado, Provincia Velasco, Departamento de Santa Cruz, Bolivia (13°35'S/60°54'W), collected by G. Scrocchi; NKA 3821-2, adult male and female respectively, from Arroyo Agua Clara, Reserva de la Biosfera Pilón-Lajas, Provincia Ballivián, Departamento de Beni, Bolivia (15°17'S/67°04'W), collected by L. Gonzáles; USNM 336142 from Moira Camp, Alto Madidi, Provincia Iturrealde, Departamento de La Paz, Bolivia (13°35'S/68°46'W); USNM 336143, from Río Satariapo, ca. 13 km SW of Ixiamas, Provincia Iturrealde, Departamento de La Paz, Bolivia (13°53'S/68°15'W); USNM 281889, from Puerto Linares, Provincia Nor Yungas, Depar-

tamento de La Paz, Bolivia (15°29'S/67°30'W); USNM 336157, from El Encanto Camp, Parque Nacional Noel Kempff Mercado, Provincia Velasco, Departamento de Santa Cruz, Bolivia (14°38'S/60°42'W); USNM 118699-70, from Buenavista, Provincia Ichilo, Departamento de Santa Cruz, Bolivia (17°27'S/63°40'W); USNM 332462, from Colpa de Guacamayos, Tambopata, Departamento de Madre de Dios, Peru; USNM 304285, from extreme W bank of Lago Valencia, Río Madre de Dios, Departamento de Madre de Dios, Peru; USNM 304284, from Pakitza, Parque Nacional Manu, Departamento de Madre de Dios, Peru (11°56'S/71°17'W); USNM 266142-3, from Cachoeira Nazaré, W Bank of Río Jiparaná, Rondônia, Brazil; ZFMK 66781, an adult male from Cobija, Provincia Nicolás Suárez, Departamento de Pando, Bolivia (11°01'S/68°45'W), collected on 19 January 1998 by J. Köhler and S. Lötters; ZFMK 62819, an adult male from the Estación Biológica Beni, Provincia Ballivián, Departamento de Beni, Bolivia (14°51'S/62°21'W), collected by S. Reichle.

Referred specimens: CET A448-449; CET A1302-20; CET A1389-94; CET A1562, from several Bolivian localities (see section on Distribution below).

Diagnosis

A member of the genus *Phyllomedusa* (*sensu stricto*; CRUZ, 1990), allied to *P. tarsius* and *P. boliviana*, with the following combination of characters: (1) first toe longer than, and opposable to, the second; (2) moderately developed parotoid glands; (3) vomerine teeth present in adults; (4) no calcar or dermal appendages; (5) palpebral membrane nonreticulated; (6) in life, iris dark brown with small black flecks; (7) in life, upper eyelid edged with yellowish-cream; concealed surfaces of hindlimbs pale purple, with no markings.

Phyllomedusa camba is closely related and similar to *P. boliviana* (both species share the unique character of having a very dark brown

iris), with which it occurs in sympatry in a large area of Bolivia. From *P. boliviana*, *P. camba* differs by (*P. boliviana* in parentheses) having the border of the upper eyelid yellowish-cream (red), flanks with irregular pinkish-cream markings in the zone of contact of the green dorsum and the cream venter (a more or less straight line between both zones, often with small, flat cream tubercles, tipped with red), parotoid glands moderately developed (well developed), a white gular blotch (gular blotch absent), two white spots on the inferior surface of the thighs, near the cloacal opening always present (sometimes absent).

The distribution of *P. camba* might contact that of *P. tarsius* in the upper Amazon basin and, less likely, that of *P. sauvagii* in some parts of southeastern Bolivia. From both species, it differs, among other features, by having dark brown, almost black iris (bright orange-red with black flecks in *P. tarsius*; pale gray in *P. sauvagii*). Additionally, *P. sauvagii* has well developed parotoid glands, and rugose skin.

Description

A medium-sized *Phyllomedusa*. Head wider than body; snout short, rounded in dorsal view, truncate and inclined in lateral view; canthus rostralis slightly rounded, distinct; loreal region concave; lips thin and not flared; nostrils not protuberant, directed laterally; internarial region flat; eyes slightly protuberant; pupil vertically elliptical; palpebral membrane nonreticulated; parotoid glands moderately developed, extending from eyelid to approximately a point level where the elbow touches the body when the forelimb is adpressed backwards; supratympanic fold moderately developed, barely obscuring a small portion of tympanum; tympanum distinct, oval, its anterior edge separated from eye by distance of 1-2 mm.

Axillary membrane absent; upper arm slender, forearm moderately robust; ulnar fold low; relative length of fingers from shortest



Figure 1.- *Phyllomedusa camba* sp. nov., male, from Puerto Almacén, Bolivia.

Figura 1.- *Phyllomedusa camba* sp. nov., macho, de Puerto Almacén, Bolivia.

to longest I-II-IV-III; finger tips about half diameter of tympanum; subarticular tubercles large, round to conical; supernumerary tubercles poorly distinct; palmar tubercle oval, moderately distinct; prepollex elliptical, bearing horny, dark brown nuptial excrescence; palmar webbing absent.

Hind limb slender, moderately long, without calcar or dermal ornamentation; inner tarsal fold absent; outer tarsal fold low, poorly distinct; relative length of toes from shortest to longest II-III-I-V-IV; toe disks slightly smaller than those of fingers; inner metatarsal tubercle elliptical, low, flattened; no outer metatarsal tubercle; subarticular tubercles large, round to conical; no supernumerary tubercles on toes; plantar webbing absent.

Cloacal opening directed posteriorly at midlevel of thighs, unornamented; supra-cloacal fold present; skin of dorsal surfaces smooth, tubercles absent; skin of belly, flanks, and inferior surfaces of thighs tubercular; tongue large, suboval, posterior two thirds free; vo-

merine teeth present; dentigerous processes of vomers small, separated medially by distance equal to two thirds width of one process; processes directed posteromedially at midlevel of elliptical choanae; vocal slits short; vocal sac single, median, subgular, not distinct.

Measurements

Measurements of the holotype (in mm): SVL (snout-vent length) 64.4; TL (tibia length) 29.1; FL (footh length) 22.0; HL (head length) 19.4; HW (head width) 23.0; IOD (interorbital distance) 7.3; IND (internarial distance) 5.4; EW (eyelid width) 6.1; EL (eye length) 6.9; TD (tympanum diameter) 4.2; END (eye-nostril distance) 5.6. There is considerable sexual dimorphism in size (see Table 1).

Coloration

Live specimens are leaf green above (dorsum, head, tympanum, and upper parts of limbs). The border of the upper eyelid is yellowish-cream. The throat is grayish-cream to

Table 1: Measurements (in mm) of *Phyllomedusa camba*. See text for abbreviations.**Tabla 1:** Medidas (en mm) de *Phyllomedusa camba*. Para las abreviaturas, ver texto.

	Males (n=10)			Females (n=7)		
	Mean	SD	Range	Mean	SD	Range
SVL	65.83	3.16	60.8-69.6	81.46	1.94	78.0-84.0
TL	29.16	1.80	25.6-31.8	35.23	0.78	33.9-36.3
FL	22.24	1.35	20.3-24.1	25.51	0.68	24.5-26.6
HL	19.00	0.69	17.3-19.9	21.98	0.47	21.3-22.7
HW	22.45	0.96	20.7-24.0	27.29	0.59	26.2-27.9
IOD	6.72	0.52	6.0-7.7	8.00	0.50	7.2-8.7
IND	5.36	0.26	4.9-5.8	6.24	0.18	6.0-6.4
EW	5.35	0.40	4.8-6.0	6.23	0.51	6.0-6.9
EL	6.85	0.44	5.9-7.4	7.70	0.45	7.2-8.2
TD	4.13	0.22	3.7-4.4	5.03	0.32	4.6-5.4
END	4.80	0.45	4.2-5.6	5.47	0.47	5.0-6.4

pale brown; an elongate, irregular white spot is always present at a point level near the insertion of the upper arms. Other smaller similar spots may be present around the large one, extending onto the chest. The belly and ventral parts of limbs are grayish-cream. A series of small, white spots may be present along the inferior surface of each thigh, and there is always a larger spot on the proximal part, near the cloacal opening. The flanks have pinkish-cream blotches and reticulations separating the dorsal parts from the ventral parts of the flanks [see FUNKHOUSER (1957: 80)]. On the outer surface of limbs, the boundary between the dorsal and ventral color is straight and well marked by a cream line extending from the elbow to the disk of Finger IV, and from the heel to the disk of Toe V. The groin and the hidden surfaces of the thighs are pale purple. The lower lip is cream and a line of the same color extends from the corner of the mouth to the insertion of the upper arm. Although the iris color has been often reported as black, it is actually very dark brown with black flecks.

In preservative, the green color of dorsal parts becomes grayish-blue and the yellowish-cream line bordering the eyelid becomes cream.

Variation

No remarkable variation has been detected. The degree and extension of the reticulation of the flanks is variable, as well as the degree of throat pigmentation. Some specimens from the Madre de Dios drainage (Cuzco Amazónico, Pando), have a yellowish coloration in the groin and on the posterior part of flanks; this has not been observed in specimens from other Bolivian localities. For variation in measurements see Table 1.

Etymology

The specific name is a noun in apposition from the Bolivian word "camba", which designates the indigenous people from the lowlands (or the "oriente", mostly in Santa Cruz, Beni, and Pando), as opposite to the people from the Andean highlands and valleys, which are called "collas".

Distribution

Phyllomedusa camba has a moderately large area of distribution in the SW Amazon Basin, from SE Peru (departments of Madre de Dios and Ucayali) and W Brazil (states of Amazonas, Acre, and Rondônia) to E Bolivia (departments of Pando, Beni, Cochabamba,

La Paz, and Santa Cruz). There is a distance of about 1200 km between the most separated localities. Besides the localities of the holotype and paratypes given above, in Bolivia, the species has been found at the following localities: Rurrenabaque, Provincia Ballivián, Departamento de Beni (14°28'S/67°34'W) (UMMZ 58597 and 58955-56); Valle de Sajta, Provincia Chapare, Departamento de Cochabamba (17°00'S/64°50'W); Puerto Rico, Río Orthon, Provincia Manuripi, Departamento de Pando (11°05'S/67°32'W); Parque Nacional Amboró, Provincia Ichilo, Departamento de Santa Cruz (17°35'S/63°41'W) (with *P. boliviana*); and 20 km NE of Concepción, Provincia Ñuflo de Chávez, Departamento de Santa Cruz (15°50'S/62°05'W) (with *P. boliviana*) (voucher specimens at the CET). The altitudinal range of the species in Bolivia lies between 280 and ca. 1000 m.

A Colombian specimen of *Phyllomedusa* identified by Shreve as *P. boliviana* was reported by COCHRAN & GOIN (1970) from La Providencia, Departamento Caquetá, Colombia, but this specimen was identified as *P. coelestis* by DUELLMAN & MENDELSON (1995). FUNKHOUSER's (1957) records of *P. boliviana* from Abitagua, Río Pastaza, Ecuador, led DUELLMAN & SALAS (1991) to include southern Ecuador in the distribution of *P. camba* (as *Phyllomedusa* sp.). The specific identity of these Ecuadorian specimens remains to be investigated; it is plausible that they are *P. coelestis*.

Phyllomedusa camba and *P. boliviana* are sympatric in the region of the Andean foothills of La Paz and Cochabamba and in some parts of the lowlands of Santa Cruz. However, *P. camba* apparently is not as generalist as *P. boliviana*, which occurs in different habitats, such as montane forest, Chacoan vegetation, cerrado, and rainforest, from the montane region of the Yungas de La Paz to the lowlands of N Argentina and W Brazil, at elevations of 280-2000 m (CANNATELLA, 1983; DE LA RIVA, 1990).

Life history and ecology

Data on the reproductive biology and ecology are taken from DE LA RIVA (1993), who studied the species during two rainy seasons (October 1987 - April 1988 and November 1988 - April 1999, plus some shorter visits) at the type locality, Puerto Almacén. This locality lies in the "life zone" of "Humid Subtropical Forest" (TOSI *et al.*, 1975), although open cerrado formations are present about 50 km southwards. Puerto Almacén is a small ranch on the left bank of Río Negro. There are a few hectares of cleared areas for cattle pastures, and a moderate extension of secondary forest. The entire zone is surrounded by primary forest. The mean precipitation during the two rainy seasons was 1113 mm.

At Puerto Almacén, *P. camba* was found mostly in primary forest (60.8% of the observations; n = 51), followed by secondary forest (37.1%) and open areas (1.8%). The study of microhabitat use revealed that at its reproductive sites, *P. camba* is found mostly on trees, palms, and vines (85.7%; n = 56), and secondarily on bushes and *Heliconia* plants (14.3%). Individuals perch mostly on branches of variable diameter (66%; n = 56), leaves (21.4%) and trunks (12.5%) at an average height of 2.1 m above the ground. However, they can be observed much higher, even in the canopy, especially when not breeding. Individuals were observed 10 m above the ground at Cuzco Amazónico (De la Riva, pers. obs.), and DUELLMAN & THOMAS (1996) reported specimens above 27 m at Balta, Peru. At Pakitza, Peru, MORALES & MCDIARMID (1996) reported the species in upland forest on old alluvial terraces and in flooded forest on upper flood plain. In both macrohabitats, the species is found on branches, high in the trees.

As other species of *Phyllomedusa*, *P. camba* is exclusively nocturnal. At Puerto Almacén, calling and breeding activity started with the first heavy rains of the season, and lasted from November to March. Males do not form structured choruses, but they sometimes con-

gregate in a high number around reproductive sites, and their isolated calls make up a constant, low, background noise at these sites. The call of *P. camba* was described (as *Phyllomedusa* sp.) and illustrated by DE LA RIVA *et al.* (1995). The call is a short (mean, 48 ms), low, pulsed note repeated at uneven intervals (mean, 11.7 calls/minute), sometimes forming a sequence of several notes. The dominant frequency is at 800-900 Hz.

For reproductive purposes, the species seems to prefer swamps in primary forest, but inundated places on roadsides in disturbed habitat also are used. RODRIGUEZ (1992) reported water-filled holes in trees as a place of reproduction for this species. At Amboró National Park, the entire process of amplexus and oviposition was observed on 22 November 1989 at a small pond in a house garden. A lemon tree whose branches overhanging the pond was used for oviposition by both *P. camba* and *P. boliviana*.

Several amplexant pairs were found on or near the ground, close to the water, from where they climbed to the surrounding trees. PYBURN (1970), studied two species in the Phyllomedusinae genus *Agalychnis*, and suggested that this behavior is because of the necessity of the female to enter the water to hydrate its body and fill its bladder in order to hydrate the gelatinous capsules that protect the eggs as they are laid. At Amboró, an amplexant pair, after leaving the ground, climbed to the lemon tree and, for about an hour, moved through the tree's peripheral twigs and leaves, presumably in search of a suitable place to lay the clutch. Finally, at a point 2.5 m above the water, they chose a group of six leaves from which they positioned hanging upside down. Male and female kept their cloacal openings close to each other, but the male was a little ahead the female, on the leaves, which he grasped near their bases with his feet. The leaves partially encircled the female,



Figure 2.- Amplexant pair of *Phyllomedusa camba* sp. nov. at the moment of oviposition. Amboró National Park, Bolivia.

Figura 2.- Pareja de *Phyllomedusa camba* sp. nov. en amplexus, en el momento de la ovoposición. Parque Nacional Amboró, Bolivia.

and she grasped them near their tips. The act of laying eggs was fast, and progressed from the tips to the bases of the leaves; a slit between them formed a channel across which the sperm of the male flowed onto the eggs. A third male tried to mate with the female, but was unsuccessful and left. During all this time, the amplexant male called intermittently. The entire process took 75 minutes, and finished when the male released the female. Then, she remained with the eggs for an hour, gluing the clutch and the leaves. To do this, she embraced and pressed the set of leaves with her tarsi, keeping the heels in contact. (Figure 2). The result was a compact, well protected package. A similar clutch was observed on the same tree at 3.5 m above the water.

At Puerto Almacén, gravid females were found from December to March. Four females whose oviducts were examined had 250-375 (mean: 311) mature, cream eggs, 2.5 mm in diameter. They also contained ovarian, vitellogenic eggs, indicating that more than a clutch is laid per season. The tadpole and juveniles are unknown.

A stomach examined contained an orthopteran (Tettigonoidea) larger than 21 mm. Parasitic worms were observed under the skin, and trematodes (probably of the genus *Polystoma*) were found in the bladder of some specimens.

The abundance and presence of *P. camba* seems to vary locally. For example, at Cuzco Amazónico and Pakitza (Peru) it seems to be uncommon (DUELLMAN & SALAS, 1991; MORALES & MCDIARMID, 1996). DUELLMAN (1995) found a total number of 13 specimens during six sampling periods covering five rainy seasons, and all of them were found in the same sampling period. Contrarily, in Puerto Almacén the species was fairly abundant during the two rainy seasons studied (DE LA RIVA, 1993).

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REFERENCES

- BOULENGER, G. A. (1902): Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia. *Ann. Mag. Nat. Hist.*, 7 (10): 394-402.
- CANNATELLA, D. C. (1980): A review of the *Phyllomedusa buckleyi* group (Anura: Hylidae). *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, 87: 1-40.
- CANNATELLA, D. C. (1983): Synonymy and distribution of *Phyllomedusa boliviana* Boulenger (Anura: Hylidae). *Proc. Biol. Soc. Wash.*, 96 (1): 59-66.
- COCHRAN, D. M. & GOIN, C. J. (1970): Frogs of Colombia. *Bull. U. S. Natl. Mus.* 288: 1-655.
- CRUZ, C. A. G. DA. (1990): Sobre as relações intergenéricas de Phyllomedusinae da floresta Atlântica (Amphibia, Anura, Hylidae). *Rev. Bras. Biol.*, 50: 719-726.
- DE LA RIVA, I. (1990): Lista preliminar comentada de los anfibios de Bolivia con datos sobre su distribución. *Boll. Mus. reg. Sci. Nat. Torino* 8 (1): 261-319.
- DE LA RIVA, I. (1993): *Ecología de una comunidad neotropical de anfibios durante la estación lluviosa*. Ph. D. Thesis, Universidad Complutense, Madrid. 365 pp.
- DE LA RIVA, I., MÁRQUEZ, R. & BOSCH, J. (1995): Advertisement calls of eight Bolivian hylids (Amphibia, Anura). *J. Herpetol.*, 29 (1): 113-118.
- DUELLMAN, W. (1995): Temporal fluctuations in abundances of anuran amphibians in a seasonal amazonian rainforest. *J. Herpetol.*, 29 (1): 13-21.
- DUELLMAN, W. E., CADLE, J. E. & CANNATE-

- LLA, D. C. (1988): A new species of terrestrial *Phyllomedusa* (Anura: Hylidae) from southern Peru. *Herpetologica*, 44 (1): 91-95.
- DUELLMAN, W. E. & MENDELSON, J. R. (1995): Amphibians and Reptiles from Northern Departamento Loreto, Peru: Taxonomy and Biogeography. *Univ. Kansas Sci. Bull.*, 55 (10): 329-376.
- DUELLMAN, W. E. & SALAS, A. W. (1991): Annotated checklist of the amphibians and reptiles of Cuzco Amazónico, Perú. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, 143: 1-13.
- DUELLMAN, W. E. & THOMAS, R. (1996): Anuran Amphibians from a seasonally dry forest in southeastern Peru and comparisons of the anurans among sites in the Upper Amazon basin. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, 180: 1-34.
- FROST, D. R. (ed.) (1985): *Amphibian species of the world. A taxonomic and geographical reference*. Allen Press & ASC, Lawrence, Kansas, USA. 732 pp.
- FUNKHOUSER, A. (1957): A review of the neotropical tree-frogs of the genus *Phyllomedusa*. *Occ. Pap. Nat. Hist. Mus. Univ. Stanford*, 5: 1-90.
- HEYER, W. R. (1977): Taxonomic notes on frogs from the Madeira and Purus rivers, Brazil. *Papeis Avulsos Zool., S. Paulo*, 31 (8): 141-162.
- KÖHLER, J. & LÖTTERS, S. (1999): Annotated list of amphibian records from the Departamento Pando, Bolivia, with description of some advertisement calls. *Bonn. zool. Beitr.* 48 3/4: 259-273.
- LAURENT, R. F. (1967): Redescubrimiento de *Pithecopus pailonus* (Shreve) en Argentina. *Acta zool. Lilloana* 22: 231-247.
- MORALES, V. R. & MCDIARMID, R. W. (1996): Annotated checklist of the amphibians and reptiles of Pakitza, Manu National Park Reserve Zone, with comments on the herpetofauna of Madre de Dios, Perú, pp. 503-522, in D. E. Wilson and A. Sandoval (eds.), *Manu. The biodiversity of southeastern Peru*, Smithsonian Institution, Washington.
- PYBURN, W. F. (1970): Breeding behavior of the leaf-frogs *Phyllomedusa callidryas* and *Phyllomedusa dacnicolor* in Mexico. *Copeia*, 1970 (2): 209-218.
- RODRÍGUEZ, L. O. (1992): Structure et organisation du peuplement d'anoures de Cocha Cashu, Parc National Manu, Amazonie péruvienne. *Rev. Ecol. (Terre Vie)*, 47: 151-197.
- RODRÍGUEZ, L. B. & CADLE, J. E. (1990): A Preliminary Overview of the Herpetofauna of Cocha Cashu, Manu National Park, Peru, pp. 410-425, in A. H. Gentry (eds.), *Four Neotropical Rainforests*, Yale University, New Haven.
- SHREVE, B. (1959): A new *Phyllomedusa* from Bolivia (Salientia, Hylidae). *Breviora*, 113: 1-4.
- TOSI, J. A., UNZUETA, O., HOLDRIDGE, L. R. & GONZÁLEZ, A. (1975): Mapa Ecológico de Bolivia. MACA, La Paz.

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