

Notes on the distribution of the genus *Pseudopaludicola* Miranda-Ribeiro, 1926 (Anura: Leptodactylidae) in Paraguay

Esteban O. Lavilla¹, Andrea Caballero-Gini^{2*}, Diego Bueno-Villafañe² and Darío Cardoso³

1 Unidad Ejecutora Lillo (UEL) Fundación Miguel Lillo, CONICET, Miguel Lillo 251, 4000, San Miguel de Tucumán, Argentina

2 Instituto de Investigación Biológica del Paraguay (IIBP), Del Escudo 1607 casi Avenida Brasilia, Asunción, Paraguay

3 Instituto de Biología Subtropical (IBS UNaM/CONICET), Laboratorio de Genética Evolutiva, Félix de Azara 1552, Posadas, Misiones, Argentina

* Corresponding author. E-mail: ancgini@gmail.com

Abstract: Four species of *Pseudopaludicola*, *Pseudopaludicola boliviana*, *P. falcipes*, *P. mystacalis* and *P. ternetzi*, are usually cited for Paraguay. However, after analyzing 407 specimens assigned to this genus in herpetological collections of the country, we conclude that there are no specimens of *P. falcipes* in Paraguayan collections or vouchers cited in the literature, and almost all individuals referred to *P. ternetzi* are most probably *P. ameghini*. At the same time, a recently described species, *P. motorzinho*, is recorded for the first time in the country. Information on the distribution of these and the remaining species of *Pseudopaludicola* in Paraguay (*P. boliviana* and *P. mystacalis*) is provided.

Key words: Amphibia; Leiuperinae; dwarf swamp frogs; distribution assessment

INTRODUCTION

Pseudopaludicola Miranda Ribeiro, 1926 currently contains 21 species, which occur mainly in the lowlands of Argentina, Bolivia, Brazil, Colombia, Guyana, Suriname, Peru, Paraguay, Uruguay and Venezuela (Frost 2016). The genus includes very small (<30 mm snout-vent length), cryptic and highly polychromatic species (Lynch 1971; Haddad and Cardoso 1987; Pansonato et al. 2013; Carvalho et al. 2015a, 2015b). The genus is diagnosed by the presence of a hypertrophied antebrachial tubercle, epicoracoid cartilages slightly (or not) superposed, posterolateral process of the hyoid outlined or absent (Lynch 1989; Lobo 1995), and by ribosomal RNA sequences (Veiga-Menoncello et al. 2014). The conservative morphology of the taxa leads to the use of acoustic, chromosomal and molecular data to address taxonomic studies (Veiga-Menoncello et al. 2014; Carvalho et al. 2015a, 2015b).

In Paraguay, four species of *Pseudopaludicola* are

usually reported: *P. falcipes* (Hensel, 1867), *P. mystacalis* (Cope, 1887), *P. boliviana* Parker, 1927 and *P. ternetzi* Miranda-Ribeiro, 1937 (see Weiler et al. 2013 and references therein). The occurrence of *P. falcipes* in Paraguay is widely cited in the literature (Freiberg 1942; Cei 1980; Gallardo 1987; Langone 1994; Aquino et al. 1996; Brusquetti and Lavilla 2006; Lavilla and Brusquetti 2010; Weiler et al. 2013 and Motte et al. 2015). More recently, the distribution of this species in Paraguay was challenged by Langone et al. (2015), based on the absence of material of this species from Paraguay in some collections of Argentina, Brazil and Uruguay. However, these authors did not analyze material from Paraguayan collections. In turn, *Pseudopaludicola ternetzi* was cited by Lobo (1995) from the departments of Amambay, Concepción, Misiones, Caaguazú, Central, and San Pedro, including under this name the putative sample cited by McDiarmid and Foster (1987) as *P. ameghini*. Brusquetti and Lavilla (2006), extended the distribution of *P. ternetzi* to the departments of Boquerón and Presidente Hayes. However, the revalidation of *Pseudopaludicola ameghini* (Cope, 1887) from the synonymy of *P. ternetzi* by Pansonato et al. (2013) generates doubts about the identification of these Paraguayan populations. Of the remaining two species cited for the country, *Pseudopaludicola mystacalis* was reported only from Itapúa Department by Lobo (1995), and *Pseudopaludicola boliviana* was first cited for Asunción (capital district) by Parker (1935). Later, Lobo (1994b) extended its range to the departments of Alto Paraguay (but stated coordinates indicate a locality in Presidente Hayes near Pozo Colorado), Amambay, Caaguazú, Central, Concepción, Cordillera, Presidente Hayes and San Pedro, and Brusquetti and Lavilla (2006) extended its distribution to Paraguari Department. Finally, in a recent contribution, Pansonato et al. (2016) described two new *Pseudopaludicola* species,

one of them, *Pseudopaludicola motorzinho* Pansonato, Veiga-Menoncello, Mudrek, Jansen, Recco-Pimentel, Martins & Strüssmann, 2016, with distribution records in the states of Mato Grosso and Mato Grosso do Sul (Brazil), and in the department Santa Cruz (Bolivia), near the Paraguay border, so we consider its presence possible in Paraguay. Faced with these expectations (the absence of *P. falcipes* and the presence of *P. motorzinho* in the Paraguayan batrachofauna), the main goals of this contribution are to provide an update of the distribution of the genus *Pseudopaludicola* in Paraguay, to investigate the presence or absence of *P. falcipes* in the country, and to reanalyze all the available material assigned to *Pseudopaludicola* in Paraguayan collections.

MATERIALS AND METHODS

We analyzed all the specimens of the genus *Pseudopaludicola* housed at Museo Nacional de Historia Natural del Paraguay (MNHNP, San Lorenzo), in the herpetological collection of the Instituto de Investigación Biológica del Paraguay (IIBP-H, Asunción) and in the Colección Zoológica of the Facultad de Ciencias Exactas y Naturales (FACEN), Universidad Nacional de Asunción (CZCEN, San Lorenzo). The identifications were corroborated following the descriptions, diagnoses and redescrptions of each species (Hensel 1867; Cope 1887; Parker 1927; Miranda-Ribeiro 1937; Lobo 1994a, 1995, 1996; Pansonato et al. 2013, 2016). Localities contained in museum catalogs were georeferenced using gazetteers (Paynter 1989; Anonymous 1992), GPS records from collectors, estimations from maps and the information in Brusquetti and Lavilla (2006). We generated the map showing the distribution of *Pseudopaludicola* species in Paraguay using ArcGIS version 10.4. For ecoregions, we follow Dinerstein et al. (1995).

RESULTS

The examination of 407 specimens of *Pseudopaludicola* from 56 localities inside Paraguay (Table 1) resulted in the identification of four *Pseudopaludicola* species in the country, *P. motorzinho* being a new record for the country, and the reassignments of all *P. falcipes* records to the four abovementioned species.

Pseudopaludicola ameghini (Cope, 1887):

Figures 1G and H

Paludicola ameghini Cope (1887): 24.

Pseudopaludicola ameghini — Parker (1927): 20.

Body aspect robust, larger (SVL 16–22 mm) than *P. mystacalis* (Pansonato et al. 2013). Head subtriangular in ventral view. When hind leg is adpressed, heel reaches the posterior margin of the eye. Dorsal surface of the body with planar warts, specimens lack a vertebral line, which validates the identity of the vouchers as *P. ameghini* (see Discussion). Dorsal coloration in preserved specimens uniformly brown; a few individuals with two bright dorsolateral lines (Lobo 1996), ventral coloration white, immaculate. The Paraguayan specimens attributed to this species have $2n = 20$ chromosomes (Cardozo et al. 2016, as *P. ternetzi*).

Pseudopaludicola boliviana Parker, 1927:

Figures 1A and B, 2A and 2B

Pseudopaludicola boliviana — Parker (1927): 20.

Pseudopaludicola mirandae — Mercadal de Barrio and Barrio (1994): 16.

Tongue with small pigments at the base. Slender body, antibrachial tubercle developed; small, conical tubercle on the outer edge of heels. Toes slightly dilated distally, with T-shaped finger tips (Parker 1927; Lobo 1995, Cardozo and Suarez 2012). In addition, the presence of minute tubercles on upper eyelids (suggested by Lynch 1989) is variable (Figure 2). $2n = 20$ chromosomes (Cardozo et al. 2016).

Table 1. Examined specimens of *Pseudopaludicola* (all localities from Paraguay).

Current identification	Previous identification	Catalogue numbers	Locality	Department
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 3953	Estancia Apa-mí, 8 km SW from Bella Vista	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1173-1184, 1208, 1210-1212, 6285	Estancia San Juan, 20 km S from Bella Vista	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1336-1375, 1384-1385, 3480	Estancia Félix Ocariz, 2 km W from Bella Vista	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1196-1198, 1201-1207, 1334, 1376, 1378-1379, 1381, 4501, 5711, 7607	Parque Nacional Cerro Corá, admin.	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1195-1198, 4514, 5386	Parque Nacional Cerro Corá, 2 km S from admin.	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 4428, 5689-5690	Parque Nacional Cerro Corá, 3 km E from admin.	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 4392, 4425, 4495, 4508, 8973	Parque Nacional Cerro Corá, 4.5 km N from the command	Amambay
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1185-1194, 1199, 1218-1219, 1335, 1380	Capitigo stream, 85 km NE from Concepción	Concepción
<i>P. ameghini</i>	<i>P. ternetzi</i>	IIBP-H 815-831, 856, 867, 878-880, 898	Estancia Estancia Garay Cué S.A., Cerrados del Tagatiyá	Concepción
<i>P. ameghini</i>	<i>P. mystacalis</i>	CZCEN 255	Estancia Garay Cué S.A., Cerro Ministro	Concepción
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 1377, 1382-1383	Horqueta	Concepción
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 11120	Ministro Hill	Concepción
<i>P. ameghini</i>	<i>P. ternetzi</i>	IIBP-H 2528-2530, 2556-2569, 2571, 2581-2582	San Alfredo district, Cerrados del Tagatiyá Natural Reserve	Concepción
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 6982, 7021-7022, 7034, 7039, 7042-7043	Rancho Z	Concepción
<i>P. ameghini</i>	<i>P. mystacalis</i>	MNHNP 5368	19 km NE de Concepción, on the route to Loreto	Concepción

Continued

Table 1. Continued.

Current identification	Previous identification	Catalogue numbers	Locality	Department
<i>P. ameghini</i>	<i>P. falcipes</i>	MNHNP 1209	Cabaña Guavyray in San Ignacio	Misiones
<i>P. ameghini</i>	<i>P. ternetzi</i>	IIBP-H 743	Unspecified location	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 1386-1397	24 km N Coronel Oviedo	Caaguazú
<i>P. boliviana</i>	<i>P. sp</i>	MNHNP 1390	24 km N Coronel Oviedo	Caaguazú
<i>P. boliviana</i>	<i>P. falcipes</i>	CZCEN 677	Bahía de Asunción	Central
<i>P. boliviana</i>	<i>P. boliviana</i>	CZCEN 234, 369, 528-531, IIBP-H 1432	Surubi'i	Central
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 1399, 4504	Villeta	Central
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4460	19 km NE de Concepción, on the route to Loreto	Concepción
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 1398, 3819-3820, 4423, 6616	85 km NE Concepción, stream Capitigo	Concepción
<i>P. boliviana</i>	<i>P. boliviana</i>	IIBP-H 1029	Vallemí, beaches of the Apa river, in a lagoon	Concepción
<i>P. boliviana</i>	<i>P. boliviana</i>	IIBP-H 419, 1956-1958	Emboscada district, Cabaña Las Marías, Cerro Vy	Cordillera
<i>P. boliviana</i>	<i>P. boliviana</i>	IIBP-H 1267-1272	Natalicio Talavera	Guairá
<i>P. boliviana</i>	<i>P. boliviana</i>	IIBP-H 678	Estancia San José	Ñeembucú
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4468, 4490	Parque Nacional Ybycuí, Fundación La Rosada	Paraguari
<i>P. boliviana</i>	<i>P. boliviana</i>	IIBP-H 2422-2423, 2444-2460, 2471-2472	Estancia Fortín Salazar, Irala Fernandez district	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 3336, 6629-6630, 8296-8298, 8316-8320	Estancia Juan de Salazar	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 2125, 3322-3335, 3824, 3832, 8583	Estancia La Golondrina	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4432, 6613-6615, 6617	Estancia La Golondrina, 25 km NW from Villa Hayes	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4457	Estancia La Golondrina, 30 km NW from Villa Hayes	Presidente Hayes
<i>P. boliviana</i>	<i>P. falcipes</i>	MNHNP 4527	30 km NW to Villa Hayes	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 7543	Road to Falcón	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	CZCEN 391, 545-555, MNHNP 7136-7138, 7760	Estancia Karanda	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 3823, 5663-5669, 8203, 11476-11479	Estancia La Victoria	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 6596-6597, 8119, 8185, 8191, 8520	Estancia Palo Santo	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 10382	Estancia Santa María de la Doce, Fundación La Piedad, Retiro San Juan, km 61.5 Route Transchaco, 5 km W from the house	Presidente Hayes
<i>P. boliviana</i>	<i>P. falcipes</i>	MNHNP 7358, 7377, 7384, 7520-7523, 9083	Estancia Santa Catalina, km 330 Transchaco route; General Bruguez	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 9240-9241	Montelindo river	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4512, 5691-5694	Rio Negro Hotel, Transchaco route, km 174	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 3831	Transchaco route km 344, 21 km NW from Rio Verde	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4507	Transchaco route km 223	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 6620-6628	Transchaco route km 93	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 5688, 5815	Transchaco route km 86	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 7695, 7758-7763	Transchaco route km 65	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 3825, 3828, 4412, 4525, 6618	Riacho Negro, 44 km W to Concepción	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4511, 8543	Aguaray Guazú river, 73.9 km NW Benjamín Aceval, Ruta Transchaco	Presidente Hayes
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4491	Aguaray Guazú river, 2 km NW from Lima	San Pedro
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 4431, 6612, 6619	Lima	San Pedro
<i>P. boliviana</i>	<i>P. boliviana</i>	MNHNP 1400-1402	Villa del Rosario, Compañía Mbocayá	San Pedro
<i>P. motorzinho</i>	<i>P. boliviana</i>	IIBP-H 1087-1088, 1097-1108	Estancia Pirá Potrero (Vierci), Arroyo Guasú punto 22	Amambay
<i>P. cf. motorzinho</i>	<i>P. boliviana</i>	MNHNP 1182, 1213-1214	Estancia San Juan, 20 km S Bella Vista	Amambay
<i>P. cf. motorzinho</i>	<i>P. falcipes</i>	MNHNP 3319-3321	Colonia Potrerito	Alto Paraguay
<i>P. cf. motorzinho</i>	<i>P. boliviana</i>	MNHNP 3826-3827, 8217	Laguna General Díaz	Alto Paraguay
<i>P. mystacalis</i>	<i>P. falcipes</i>	MNHNP 5000, 5032-5034	Isla Yacyretá, Estancia Melgarejo	Itapúa
<i>P. mystacalis</i>	<i>P. mystacalis</i>	IIBP-H 1241-1244	Route Mariscal López, 11 km W from General Delgado	Itapúa
<i>P. mystacalis</i>	<i>P. falcipes</i>	MNHNP 67	Alcaráz Cué colony, 5 km NW from San Patricio	Misiones
<i>P. mystacalis</i>	<i>P. falcipes</i>	MNHNP 1200	Isla Yacyretá, 15 km SE from Ayolas, Base Aeronaval	Misiones
<i>P. mystacalis</i>	<i>P. boliviana</i>	MNHNP 3821	San Ignacio, Cabaña Guaviray	Misiones
<i>P. mystacalis</i>	<i>P. falcipes</i>	MNHNP 3822, 5670-5687, 8209	San Ignacio, Cabaña Guaviray	Misiones
<i>P. mystacalis</i>	<i>P. mystacalis</i>	IIBP-H 273, 282, 289, 303, 346, 676-677, 832-833	Estancia San José	Ñeembucú
<i>P. mystacalis</i>	<i>P. sp.</i>	MNHNP 10048	Pilar, 19.8 km SW	Ñeembucú
<i>Physalaemus sp.</i> (juvenile)	<i>P. falcipes</i>	MNHNP 7146	Parque Nacional Defensores del Chaco road to Cerro León	Alto Paraguay
<i>Physalaemus sp.</i> (juvenile)	<i>P. falcipes</i>	MNHNP 6603, 6605	37.6 km S de Platanillo, on route to Pirizal (Línea 1)	Boquerón
<i>Physalaemus sp.</i> (juvenile)	<i>P. falcipes</i>	MNHNP 3830	Km 695, Transchaco route	Boquerón
<i>Physalaemus sp.</i> (juvenile)	<i>P. ternetzi</i>	MNHNP 3829, 6602	Km 695, Transchaco route	Boquerón

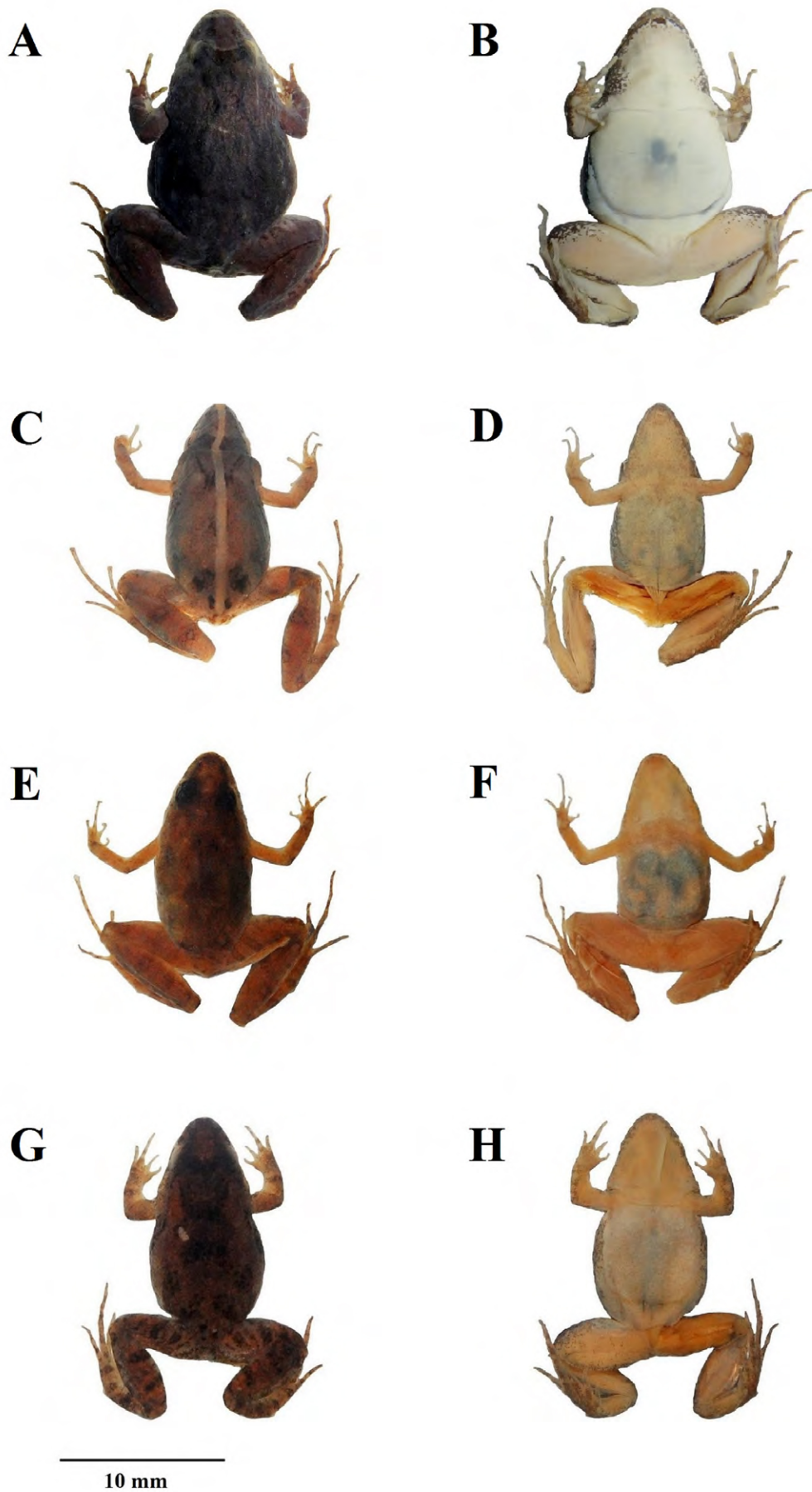


Figure 1. *Pseudopaludicola* species examined in Paraguayan collections. Dorsal (A) and ventral (B) views of *P. ameghini* (IIBP-H 2571). Dorsal (C) and ventral (D) views of *P. boliviana* (IIBP-H 1270). Dorsal (E) and ventral (F) views of *P. motorzinho* (IIBP-H 1087). Dorsal (G) and ventral (H) views of *P. mystacalis* (IIBP-H 289).

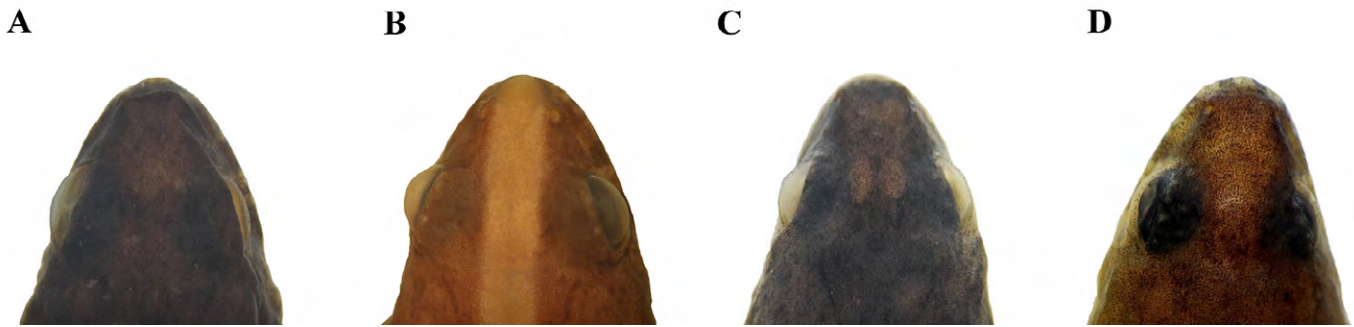


Figure 2. Detail of the upper eyelid of *Pseudopaludicola boliviana* and *P. motorzinho*. Smooth upper eyelids (A) and presence of tubercles (B) in *P. boliviana* (IIBP-H 2444, LGE 3019). Smooth upper eyelids (C) and presence of tubercles (D) in *P. motorzinho* (IIBP-H 1088, IIBP-H 1087).

Pseudopaludicola motorzinho Pansonato, Veiga-Menoncello, Mudrek, Jansen, Recco-Pimentel, Martins & Strüssmann, 2016

Figures 1C and D, 2C and 2D

Pseudopaludicola boliviana (in part) — Parker (1927): 20; Lobo (1994b): 231; Valdujo et al. (2012): 77.

Pseudopaludicola falcipes (in part) — Hensel (1867): 33; Souza et al. (2010): 473.

Pseudopaludicola sp. — Valério-Brun et al. (2010): 124; Pansonato et al. (2011): 81; Santos et al. (2011): 456. Pansonato et al. (2014): 258; Veiga-Menoncello et al. (2014): 263.

Pseudopaludicola sp. A — Jansen et al. (2011): 572.

Pseudopaludicola sp. 1 — Fávero et al. (2011): 828; Santos et al. (2015): 1497.

Pseudopaludicola motorzinho is morphologically cryptic in relation to *P. boliviana*, and the difference suggested by Pansonato et al. (2016) (absence of tubercles on upper eyelid) is not diagnostic (Figure 2). The identification of *P. motorzinho* from Estancia Pirá Potrero in Amambay Department was based on 13 specimens with $2n = 22$ chromosomes, distinguishable from *P. boliviana*, whose karyotype is $2n = 20$ chromosomes (Fávero et al. 2011, as *Pseudopaludicola* sp.; Cardozo et al. 2016).

Pseudopaludicola mystacalis (Cope, 1887):

Figures 1E and F

Paludicola mystacalis — Cope (1887): 24; Milstead (1963): 1963; Malnate (1971): 123.

Physalaemus mystacalis — Nieden (1923): 46; Parker (1927): 20.

Pseudopaludicola mystacalis — Haddad and Cardoso (1987): 36.

Slender body, smaller (SVL 10 to 17 mm) than *P. ternetzi* (Lobo 1996). Fingertips knobbed, head slightly elongated in ventral view. When hind leg is adpressed, heel goes beyond the eye, near the nostril. Dorsal coloration in preserved specimens brown, with few darker spots; some specimens with a vertebral line and two pale dorsolateral lines (Cope 1887; Lobo 1996), ventral coloration variable from immaculate to densely spotted. $2n = 16$ chromosomes (Cardozo et al. 2016).

DISCUSSION

Although *Pseudopaludicola falcipes* has been the most cited species for the country, as noted above,

no specimen of *Pseudopaludicola* with an absent or incomplete abdominal fold was recorded in any of the Paraguayan collections, which supports the suggestion of Langone et al. (2015) that this species does not occur in Paraguay. Furthermore, the specimen of *P. falcipes* from Bahía Negra (Motte et al. 2015), previously identified as *P. boliviana* by Brusquetti and Lavilla (2006) and Langone et al. (2015), was tentatively re-identified as *P. motorzinho*, while those referred by Brusquetti and Lavilla (2006) were re-identified mostly as *P. mystacalis*, plus nine specimens as *P. boliviana* and one as *P. ameghini*; three individuals from Boquerón and one from Alto Paraguay were re-identified as juveniles of a species of *Physalaemus*.

Pseudopaludicola ameghini was found in the departments of Amambay, Concepción, Misiones and Presidente Hayes, in transitional areas between Humid Chaco, Cerrado and Atlantic Forest ecoregions (Figure 3B). The only record from Misiones (MNHNP 1209), isolated from the main distribution of the species, is doubtful and probably is a curatorial error in the transcription of collection data. The species is also distributed in Chapada dos Guimarães and Vila Bela da Santíssima Trindade, Mato Grosso, Brazil (Pansonato et al. 2013) and probably is in adjacent Bolivia (Frost 2016).

Based on the absence of a vertebral line in the examined specimens, we assigned the Paraguayan specimens, previously *Pseudopaludicola ternetzi*, to *P. ameghini*. In fact, the line, which might be present in specimens of *P. ternetzi*, is the only externally visible character suggested by Pansonato et al. (2013) to distinguish *P. ameghini* from *P. ternetzi*. However, as *P. ameghini* and *P. ternetzi* share similar external morphologies, advertisement calls with overlapping ranges (Pansonato et al. 2013; Cardozo and Toledo 2013), and chromosome number $2n=20$ (Fávero et al. 2011; Cardozo et al. 2016, as *P. ternetzi*), we cannot discard the possibility that some of these specimens could be in fact *P. ternetzi*.

Pseudopaludicola boliviana is the most widely distributed species of the genus in the country (Figure 3B), mainly in the Humid Chaco ecoregion, but is also

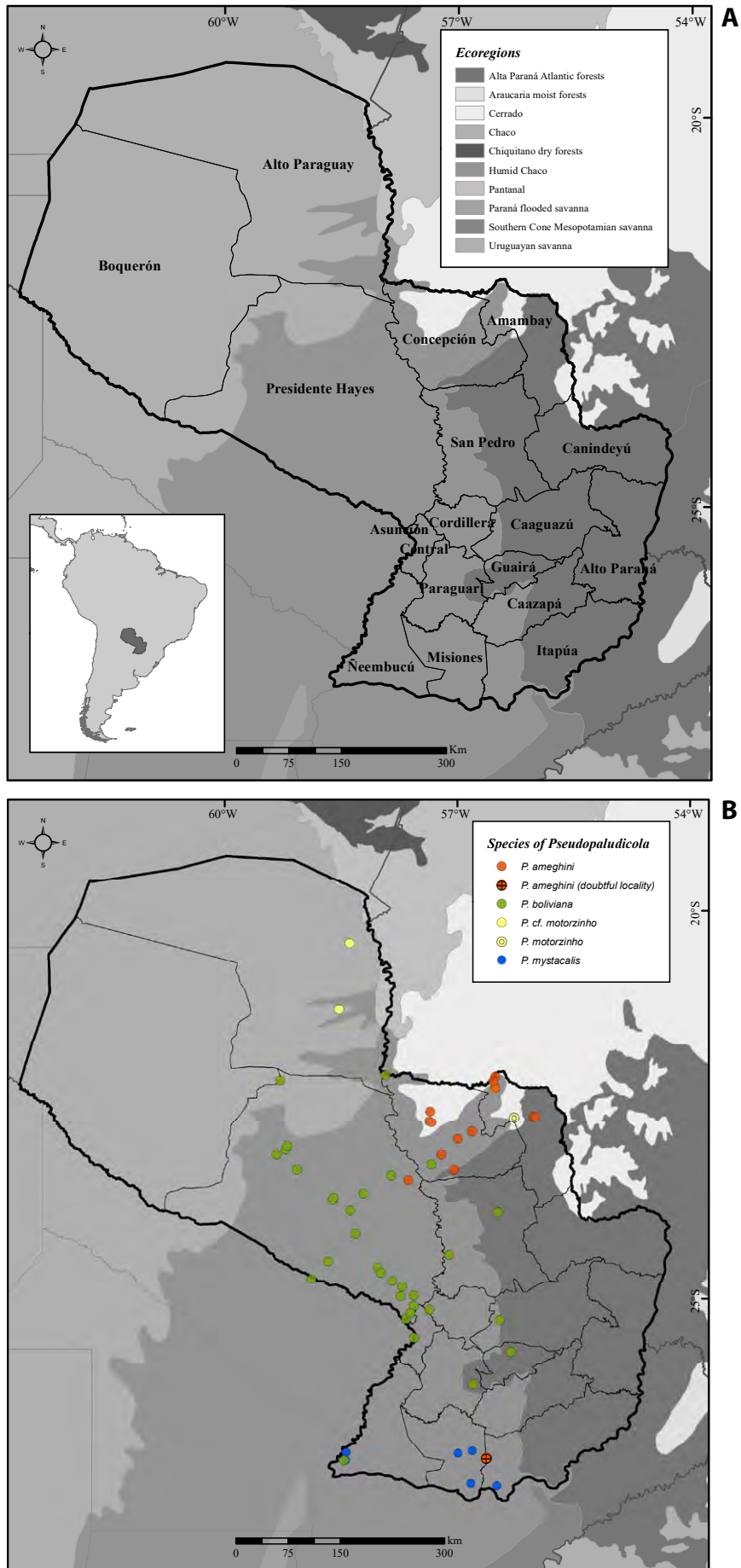


Figure 3. Distribution of *Pseudopaludicola* species in Paraguay. Map of Paraguay and ecoregions (A) according to Dinerstein et al. (1995); and current distribution of species in the country (B).

present in some localities of the Atlantic Forest. The specimens from Cerrado and Dry Chaco ecoregions are probably *P. motorzinho*, although the absence of diagnostic characters in external morphology does not allow us to an accurate identification, which is also hampered by the absence of acoustic information, DNA samples or chromosomal data. Our results confirm, in part, the distribution of *P. boliviana* in Paraguay, which was previously reported by Lobo (1994b) and Brusquetti and Lavilla (2006), with the inclusion of one new departmental record in southern Ñeembucú (Estancia San José, IIBP-H 678). In South America, *P. boliviana* is distributed in two discontinuous areas (De la Riva et al. 2000), while *Pseudopaludicola motorzinho* has unquestionable records (IIBP-H 1087 and IIBP-H 1088, IIBP-H 1097 to IIBP-H 1108) from the Department of Amambay. Besides, we consider that the specimens referred as *P. falcipes* in Motte et al. (2015) and those from Laguna General Díaz (MNHNP 3826–3827, 8217) are assignable to this species. *Pseudopaludicola boliviana* and *P. motorzinho* probably inhabit in syntopy in a wide area of their distribution, and using only the morphological features mentioned by Pansonato et al. (2016), it is almost impossible to assign specimens to either species. In Paraguay, *P. motorzinho* is probably associated with Chaco Seco and Cerrado ecoregions.

Pseudopaludicola mystacalis is distributed in southern Paraguay (Humid Chaco), in the departments of Misiones and Ñeembucú, and western Itapúa (Figure 3B). The species was first cited for Paraguay by Lobo (1995), based on individuals in the National Museum of Natural History, Smithsonian Institution (USNM 253526 to USNM 253528), this reference followed by Brusquetti and Lavilla (2006) (not included in Figure 3, because we were unable to examine the specimens). The general distribution of *P. mystacalis* also includes Argentina (Santa Fé and Entre Ríos provinces; Alcalde and Williams 2004), Bolivia (Beni and Santa Cruz departments; De la Riva et al. 2002) and Brazil (São Paulo, Goiás, Mato Grosso, Mato Grosso do Sul, Piauí, Maranhão and Pará states; Pansonato et al. 2014).

ACKNOWLEDGEMENTS

The authors are grateful to the curators and personnel of the collections studied: Humberto Sánchez, Flavia Netto and Francisco Brusquetti (IIBP); Frederick Bauer and Nicolás Martínez (MNHNP); and Andrea Weiler and Katia Airdi (CZCEN). We thank Diego Baldo for comments that improved the work, Guyra Paraguay for the ArcGis 10.4 license for map preparation. We also wish to thank Silvia de Oliveira-Lagoa, and the support of CONICET Argentina through PIP No. 0875, FONCYT PICT 2014-1343, and PRONII-CONACYT Paraguay. We take this opportunity to thank the reviewers and academic editor for suggestions and comments that improved the work.

LITERATURE CITED

- Alcalde, L. and J. Williams. 2004. Nuevas localidades para *Pseudopaludicola boliviana* y *P. mystacalis* en Argentina. Cuadernos de Herpetología 18: 75–76. <http://www.aha.org.ar/es/cuadherpetol/nuevas-localidades-para-pseudopaludicola-boliviana-y-p-mystacalis-en-argentina.html>
- Anonymous. 1992. Gazetteer of Paraguay. Names approved by the United States Board on Geographic Names. Washington, DC: Defense Mapping Agency. 117 pp.
- Aquino, A.L., N. Scott and M. Motte. 1996. Lista de los anfibios y reptiles del Museo Nacional de Historia Natural del Paraguay; pp. 331–400, in: O. Romero, (ed.). Colecciones de Fauna y Flora del Museo Nacional de Historia Natural del Paraguay. MNHNP: Asunción.
- Bokermann, W.C.A. 1966. Lista anotada das localidades tipo de anfibios brasileiros. São Paulo: Serviço de Documentação, Universidade Rural São Paulo. 183 pp.
- Brusquetti, F. and E.O. Lavilla. 2006. Lista comentada de los anfibios de Paraguay. Cuadernos de Herpetología 20: 3–79. <http://www.aha.org.ar/es/cuadherpetol/pdf/lista-comentada-de-los-anfibios-de-paraguay.html>
- Caramaschi, U. and J.P. Pombal Jr. 2011. The type series of *Pseudopaludicola ternetzi* Miranda-Ribeiro, 1937 (Anura, Leiuperidae) with designation of a lectotype. Zootaxa 3051: 62–64.
- Cardozo, D. and D. Baldo. 2012. *Pseudopaludicola ternetzi*: two lectotypes for the same taxon. Zootaxa 3192: 67–68. <http://www.mapress.com/jzt/article/view/12940/0>
- Cardozo, D. and P. Suárez. 2012. Osteological description of *Pseudopaludicola canga* with implications for the taxonomic position of this taxon. Zootaxa 3515: 75–82. doi: 10.15468/dsanxx
- Cardozo, D. and L.F. Toledo. 2013. Taxonomic status of *Pseudopaludicola riopiedadensis* Mercadal de Barrio and Barrio, 1994 (Anura, Leptodactylidae, Leiuperinae). Zootaxa 3734: 571–582. doi: 10.11646/zootaxa.3734.5.6.
- Cardozo, D., J.M. Boeris, J.M. Ferro, C. Borteiro, F. Kolenc, P. Suárez, F. Netto, F. Brusquetti and D. Baldo. 2016. Evidence for independent instances of chromosome number reduction in the genus *Pseudopaludicola* (Anura: Leptodactylidae). Salamandra 52 (1): 11–22. http://www.salamandra-journal.com/index.php?option=com_docman&Itemid=80.
- Carvalho, T.R., B.F.V. Teixeira, L.B. Martins and A.A. Giaretta. 2015a. Intraspecific variation and new distributional records for *Pseudopaludicola* species (Anura, Leptodactylidae, Leiuperinae) with trilled advertisement call pattern: diagnostic characters revisited and taxonomic implications. North-Western Journal of Zoology 11(2): 262–273. http://biozoojournals.ro/nwjz/content/v11n2/nwjz_151504_Carvalho.pdf
- Carvalho, T.R., L.B. Martins, B.F.V. Teixeira, L.B. Godinho and A.A. Giaretta. 2015b. Intraspecific variation in acoustic traits and body size, and new distributional records for *Pseudopaludicola giarettai* Carvalho, 2012 (Anura, Leptodactylidae, Leiuperinae): implications for its congeneric diagnosis. Papéis Avulsos de Zoologia 55(17): 245–254 doi: 10.1590/0031-1049.2015.55.17
- Cei, J.M. 1980. Amphibians of Argentina. Florencia: Monitore Zoologico Italiano (New Series) Monografía 2: 609 pp.
- Cope, E.D. 1887. Synopsis of the Batrachia and Reptilia obtained by H.H. Smith in the province of Mato Grosso, Brazil. Proceedings of American Philosophical Society 24: 44–60. <http://www.biodiversitylibrary.org/page/7106587#page/54/mode/1up>
- De la Riva, I., J. Köhler, S. Lötters and S. Reichle. 2000. Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. Revista Española de Herpetología 14: 19–164.
- De la Riva, I., A.B. Hennessey, J. Köhler, S. Lötters and S. Reichle. 2002. Guía Sonora de las ranas y sapos de Bolivia, in: R. Marquez,

- I. De la Riva, J. Bosch and E. Matheu (eds). Sounds of the Frogs and Toads of Bolivia. Alosa and Museo Nacional de Ciencias Naturales, Fonoteca Zoológica. Spain.
- Dinerstein, E., D.M. Olson, D.J. Graham, A.L. Webster, S.A. Primm, M.P. Bookbinder and G. Ledec. 1995. Una evaluación del estado de conservación de las ecorregiones terrestres de América Latina y el Caribe. Washington D.C.: WWF Banco Mundial. 176 pp. <http://documentos.bancomundial.org/curated/es/1995/12/6602177/conservation-assessment-terrestrial-ecoregions-latin-america-caribbean-una-evaluacion-del-estado-de-conservacion-de-las-ecoregiones-terrestres-de-america-latina-y-el-caribe>
- Fávero, E.R., A.C.P. Veiga-Menoncello, D.C. Rossa-Feres, C. Strüssmann, A.A. Giaretta, G.V. Andrade, P. Colombo and S.M. Recco-Pimentel. 2011. Intrageneric karyotypic variation in *Pseudopaludicola* (Anura: Leiuperidae) and its taxonomic relatedness. *Zoological Studies* 50: 826–836. <http://zoolstud.sinica.edu.tw/Journals/50.6/826.pdf>
- Freiberg M.A. 1942. Enumeración sistemática y distribución geográfica de los batracios argentinos. *Physis* 19: 219–240.
- Frost, D.R. [2016]. Amphibian species of the world: an online reference. Version 6.0. Accessed at: <http://research.amnh.org/herpetology/amphibia/index.html>, 15 August 2016.
- Gallardo, J.M. 1987. Anfibios Argentinos. Biblioteca Mosaico. Buenos Aires: Librería Agropecuaria S.A. 98 pp.
- Haddad, C.F.B. and A.J. Cardoso. 1987. Taxonomia de três espécies de *Pseudopaludicola* (Anura, Leptodactylidae). *Papéis Avulsos de Zoologia* 36: 287–300.
- Hensel, R. 1867. Beitrage zur Kenntniss der Wirbelthiere Südbrasilens. *Archiv für Naturgeschichte* 33(1): 120–162. <http://biodiversitylibrary.org/page/7058833>
- Jansen, M., R. Bloch, A. Schulze and M. Pfenninger. 2011. Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. *Zoologica Scripta* 40: 567–583. doi: [10.1111/j.1463-6409.2011.00498.x](https://doi.org/10.1111/j.1463-6409.2011.00498.x)
- Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimiento y aspectos biológicos). Montevideo: Museo Damaso Antonio Larrañaga. 123 pp.
- Langone, J.A., E.O. Lavilla, D. Cardozo and R. De Sá. 2015. Comments on the type locality, type series, and geographic distribution of *Pseudopaludicola falcipes* (Hensel, 1867) (Amphibia, Anura). *Zootaxa* 4058(1): 145–150. doi: [10.11646/zootaxa.4058.1.12](https://doi.org/10.11646/zootaxa.4058.1.12)
- Lavilla, E.O. and F.A. Brusquetti. 2010. Status of amphibian conservation and decline in Paraguay; 1–19 pp, in: H. Heatwole and C.L. Barrio-Amorós (eds.). *Amphibian biology*, Vol. 9. Australia: Surrey Beatty & Sons.
- Lobo, F. 1994a. Descripción de una nueva especie de *Pseudopaludicola* (Anura: Leptodactylidae), redescrpción de *P. falcipes* (Hensel, 1867) y *P. saltica* (Cope, 1887) y osteología de las tres especies. *Cuadernos de Herpetología* 8(2): 177–199. <http://www.aha.org.ar/es/cuadherpetol/pdf/descripcion-de-una-nueva-especie-de-pseudopaludicola-anura-leptodactylidae-redescripcion-de-p-falcipes-hensel-1867-y-p-saltica-cope-1887-y-osteologia-de-las-tres-especies.html>
- Lobo, F. 1994b. Primera cita de *Pseudopaludicola boliviana* Parker, 1927, para el Brasil y nuevos registros para el Paraguay. *Cuadernos de Herpetología* 8(2): 231–232. <http://www.aha.org.ar/es/cuadherpetol/pdf/primera-cita-de-pseudopaludicola-boliviana-parker-1927-para-el-brasil-y-nuevos-registros-para-el-paraguay.html>
- Lobo, F. 1995. Análisis filogenético del género *Pseudopaludicola* (Anura: Leptodactylidae). *Cuadernos de Herpetología* 9: 21–43. <http://www.aha.org.ar/es/cuadherpetol/pdf/analisis-filogenetico-del-genero-pseudopaludicola-anura-leptodactylidae.html>
- Lobo, F. 1996. Evaluación del status taxonómico de *Pseudopaludicola ternetzi* Miranda Ribeiro, 1937; *P. mystacalis* y *P. ameghini* (Cope, 1887). Osteología y distribución de las especies estudiadas. *Acta Zoológica Lilloana* 43: 327–346.
- Lynch, J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. *Miscellaneous Publication, Museum of Natural History, University of Kansas* 53: 1–238. <http://www.biodiversitylibrary.org/page/3662221>
- Lynch, J.D. 1989. A review of the leptodactylid frogs of the genus *Pseudopaludicola* in northern South America. *Copeia* 577–588.
- Malnate, E.V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Philadelphia (ANSP). *Proceedings of the Academy of Natural Sciences of Philadelphia* 123: 345–375.
- McDiarmid, R.W. and M.S. Foster. 1987. Additions to the reptile fauna of Paraguay with notes on a small herpetological collection from Amambay. *Studies on Neo-tropical Fauna and Environment* 22(1): 1–9. doi: [10.1080/01650528709360714](https://doi.org/10.1080/01650528709360714)
- Mercadal de Barrio, I.T. and A. Barrio. 1994. Reconsideración del género *Pseudopaludicola* de Argentina y descripción de dos nuevas especies *P. mirandae* y *P. riopiedadensis* (Amphibia, Anura). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, *Zoologia* 16: 65–80.
- Milstead, W.W. 1963. Notes on Brazilian frogs of the genera *Physalaemus* and *Pseudopaludicola*. *Copeia* 1963: 565–566.
- Miranda-Ribeiro, A.D. 1937. Alguns batrachios novos das colleções do Museo Nacional. *O Campo*. Rio de Janeiro 8: 66–69.
- Motte, M., M.E. Tedesco, J.A. Céspedes, N. Martínez, V. Zaracho and A. Yanosky. 2015. Contribución al conocimiento de la herpetofauna de Bahía Negra y sus alrededores, Departamento Alto Paraguay, Paraguay. *Boletín de la Sociedad Zoológica del Uruguay* (2ª época) 24 (1): 11–21. <http://szu.org.uy/node/70>
- Nieden, F. 1923. Anura I. Subordo Aglossa und Phaneroglossa, Sectio 1. ArCIFera. *Das Tierreich* 46: xxxii + 584.
- Pansonato, A., T. Mott and C. Strüssmann. 2011. Anuran amphibians' diversity in a northwestern area of the Brazilian Pantanal. *Biota Neotropica* 11: 77–86. doi: [10.1590/S1676-06032011000400008](https://doi.org/10.1590/S1676-06032011000400008)
- Pansonato, A., C. Strüssmann, J.R. Mudrek and I.A. Martins. 2013. Morphometric and bioacoustic data on three species of *Pseudopaludicola* Miranda-Ribeiro, 1926 (Anura: Leptodactylidae: Leiuperinae) described from Chapada dos Guimarães, Mato Grosso, Brazil, with the revalidation of *Pseudopaludicola ameghini* (Cope, 1887). *Zootaxa* 3620(1): 147–162. doi: [10.11646/zootaxa.3620.1.7](https://doi.org/10.11646/zootaxa.3620.1.7)
- Pansonato, A., J.R. Mudrek, A.C.P. Veiga-Menoncello, D.C. Rossa-Feres, I.A. Martins and C. Strüssmann. 2014. A new species of *Pseudopaludicola* Miranda-Ribeiro, 1926 (Anura: Leptodactylidae: Leiuperinae) from northwestern state of São Paulo, Brazil. *Zootaxa* 3861: 249–264. doi: [10.11646/zootaxa.3861.3.3](https://doi.org/10.11646/zootaxa.3861.3.3)
- Pansonato, A.C., P. Veiga-Menoncello, J.R. Mudrek, M. Jansen, S.M. Recco-Pimentel, I.A. Martins and C. Strüssmann. 2016. Two new species of *Pseudopaludicola* (Anura: Leptodactylidae: Leiuperinae) from eastern Bolivia and western Brazil. *Herpetologica* 72(3): 235–255. doi: [10.1655/Herpetologica-D-14-00047.1](https://doi.org/10.1655/Herpetologica-D-14-00047.1)
- Parker, H.W. 1927. A revision of the frogs of the genera *Pseudopaludicola*, *Physalaemus* and *Pleurodema*. *Annals and Magazine of Natural History* 6: 450–478. doi: [10.1080/00222932708655471](https://doi.org/10.1080/00222932708655471)
- Parker, H.W. 1935. The frogs, lizards and snakes of British Guiana. *Proceedings of the Zoological Society of London* 3: 505–530. <http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.1935.tb01678.x/abstract>
- Paynter, R.A. 1989. *Ornithological gazetteer of Paraguay*. 2nd ed. Cambridge, Mass.: Museum of Comparative Zoology. 59 pp. <http://biodiversitylibrary.org/item/50588>
- Santos, M.M., R.W. Ávila and R.A. Kawashita-Ribeiro. 2011. Checklist of the amphibians and reptiles in Nobres municipality, Mato Grosso state, central Brazil. *Herpetology Notes* 4: 455–461. http://www.herpetologynotes.seh-herpetology.org/Volume4_PDFs/Meireles_et_al_Herpetology_Notes_volume4_pages_455-461.pdf

- Santos, J.S., G.O. Intróini, A.C.P. Veiga-Menoncello and S.M. Recco-Pimentel. 2015. Ultrastructure variation in the spermatozoa of *Pseudopaludicola* frogs (Amphibia, Anura, Leptodactylidae), with brief comments on its phylogenetic relevance. *Journal of Morphology* 276: 1495–1504. doi: [10.1002/jmor.20438](https://doi.org/10.1002/jmor.20438)
- Valdujo, P.H., D.L. Silvano, G. Colli and M. Martins. 2012. Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. *South American Journal of Herpetology* 7: 63–78. doi: [10.2994/057.007.0209](https://doi.org/10.2994/057.007.0209).
- Valério-Brun, L.M., A. Pansonato, L.A. Solino-Carvalho, C. Strüssmann, T. Mott and R.M.L. Silveira. 2010. Sapos, rãs e pererecas; pp. 119–136, in: I.M. Fernandes, C. Signor and J.M. Penha (eds.). *Biodiversidade no Pantanal de Poconé*. Áttema, Brazil.
- Veiga-Menoncello, A.C.P., L.B. Lourenço, C. Strüssmann, D.C. Rossa-Feres, G.V. Andrade, A.A. Giarretta and S.M. Recco-Pimentel. 2014. A phylogenetic analysis of *Pseudopaludicola* (Anura) providing evidence of progressive chromosome reduction. *Zoologica Scripta* 43: 261–272. doi: [10.1111/zsc.12048](https://doi.org/10.1111/zsc.12048)
- Weiler, A., K. Núñez, K. Airaldi, E.O. Lavilla, S. Peris, S. and D. Baldo. 2013. *Anfibios del Paraguay*. San Lorenzo: Facultad de Ciencias Exactas y Naturales. 134 pp.

Author contributions: EOL is responsible for the idea and wrote the earlier version of the manuscript; DBV, ACG and DC collected the data and collaborated with the writing. DBV elaborated the maps and ACG took the photographs.

Received: 17 April 2016

Accepted: 1 December 2016

Academic editor: Thiago Ribeiro de Carvalho