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

Esteban O. Lavilla¹, Andrea Caballero-Gini²*, Diego Bueno-Villafañe¹ and Dario Cardozo³

1 Unidad Ejecutiva 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. motorzi-noho*, 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 antebrahial 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; Cej 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 McDiamid 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,
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**
- *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, antebrachial 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 in preserved specimens (see Discussion). *P. ternetzi* (Parker, 1927):

  1. 2n = 20 chromosomes (Cardozo et al. 2016, as *P. motorzinho*).

---

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

| Current identification | Previous identification | Catalogue numbers | Locality | Department |
|------------------------|-------------------------|-------------------|----------|------------|
| *P. ameghini* | *P. mystacalis* | MNHNHP 1173-1184, 1208, 1210-1212, 6285 | Estancia San Juan, 20 km S from Bella Vista | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 1336-1375, 1384-1385, 3480 | Estancia Felix Ocáriz, 2 km W from Bella Vista | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 1196-1198, 1201-1207, 1334, 1376, 1378-1379, 1381, 4501, 5711, 7607 | Parque Nacional Cerrito Corá, administración | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 1195-1198, 4514, 5386 | Parque Nacional Cerrito Corá, 2 km S from admin. | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 4428, 5689-5690 | Parque Nacional Cerrito Corá, 3 km E from admin. | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 4392, 4425, 4495, 4508, 8973 | Parque Nacional Cerrito Corá, 4.5 km N from the command | Amambay |
| *P. ameghini* | *P. mystacalis* | MNHNHP 1185-1194, 1199, 1218-1219, 1335, 1380 | Cabritgos stream, 8 km NE from Concepción | Concepción |
| *P. ameghini* | *P. ternetzi* | IIBP-H 815-831, 856, 867, 878-880, 898 | Estancia Estancia Garay Cué S.A., Cerrados del Tagatiyá | Concepción |
| *P. ameghini* | *P. mystacalis* | CZCEN 255 | Estancia Estancia Garay Cué S.A., Cerrados del Tagatiyá | Concepción |
| *P. ameghini* | *P. mystacalis* | MNHNHP 1377, 1382-1383 | Horqueta | Concepción |
| *P. ameghini* | *P. mystacalis* | MNHNHP 11120 | Ministro Hill | Concepción |
| *P. ameghini* | *P. ternetzi* | IIBP-H 2528-2530, 2556-2569, 2571, 2581-2582 | San Alfredo district, Cerrados del Tagatiyá Natural Reserve | Concepción |
| *P. ameghini* | *P. mystacalis* | MNHNHP 6982, 7021-7022, 7034, 7039, 7042-7043 | Rancho Z | Concepción |
| *P. ameghini* | *P. mystacalis* | MNHNHP 5368 | 19 km NE de Concepción, on the route to Loreto | Concepción |
Continued
Table 1. Continued.

| Current identification | Previous identification | Catalogue numbers | Locality | Department |
|-------------------------|--------------------------|-------------------|----------|------------|
| *P. ameghini* | *P. falcipes* | MNHNP 1209 | Cabaña Guayruy in San Ignacio | Misiones |
| *P. ameghini* | *R. ternetzi* | IIBP-H 743 | Unspecified location | Presidente Hayes |
| *P. boliviana* | *P. boliviana* | MNHNP 1386-1397 | 24 km N Coronel Oviedo | Caaguazú |
| *P. boliviana* | *P. sp.* | MNHNP 1390 | 24 km N Coronel Oviedo | Caaguazú |
| *P. boliviana* | *P. falcipes* | CZCEN 677 | Bahía de Asunción | Central |
| *P. boliviana* | *P. falcipes* | MNHNP 3821, 369, 528-531, IIBP-H 1432 | San Ignacio, Cabaña Guaviray Misiones | Misiones |
| *P. boliviana* | *P. falcipes* | MNHNP 1200 | Isla Yacyretá, 15 km SE from Ayolas, Base Aeronaval Misiones | Misiones |
| *P. boliviana* | *P. falcipes* | MNHNP 67 | Alcaráz Cué colony, 5 km NW from San Patricio Misiones | Misiones |
| *P. cf. motorzinho* | *P. falcipes* | MNHNP 1182, 1213-1214 | Estancia San Juan, 20 km S Bella Vista Amambay | Misiones |
| *P. boliviana* | *P. falcipes* | MNHNP 1399, 4504 | Isla Yacyretá, 15 km SE from Ayolas, Base Aeronaval Misiones | Misiones |
| *P. boliviana* | *P. falcipes* | MNHNP 4640 | 19 km NE of Concepción, on the route to Loreto | Concepción |
| *P. boliviana* | *P. falcipes* | MNHNP 1398, 3819-3820, 4423, 6616 | 85 km NE of Concepción, stream Capitigo | Concepción |
| *P. boliviana* | *IIBP-H 1029* | Vallení, beaches of the Apa river, in a lagoon | Concepción | Concepción |
| *P. boliviana* | *IIBP-H 419, 1956-1958* | Emboscada district, Cabaña Las Marias, Cerro Vy | Cordillera | Cordillera |
| *P. boliviana* | *IIBP-H 1267-1272* | Natalicio Talavera | Guaira | Guaira |
| *P. boliviana* | *IIBP-H 678* | Estancia San José | Neembucú | Neembucú |
| *P. boliviana* | *IIBP-H 4646, 4490* | Parque Nacional Ybycui, Fundición La Rosada | Paraguari | Paraguari |
| *P. boliviana* | *IIBP-H 2422-2423, 2444-2460, 2471-2472* | Estancia Fortin Salazar, Irala Fernandez district | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 3336, 6629-6630, 8296-8298, 8316-8320* | Estancia Juan de Salazar | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 2125, 3322-3335, 3824, 3832, 5853* | Estancia Lado Londerdina | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 4432, 6613-6615, 6617* | Estancia Lado Londerdina, 25 km NW from Villa Hayes | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 4457* | Estancia Lado Londerdina, 30 km NW from Villa Hayes | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 4527* | 30 km NW to Villa Hayes | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *IIBP-H 7543* | Road to Falcón | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 391, 545-555, MNHNP 7136-7138, 7760* | Estancia Karanda | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 3823, 5663-5669, 8203, 11476-11479* | Estancia La Victoria | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 6596-6597, 8119, 8185, 8191, 8520* | Estancia Palo Santo | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 10382* | Estancia Santa María de la Piedad, Retiro San Juan, km 61.5 Route Transchaco, 5 km W from the house | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 7358, 7377, 7384* | Estancia Santa Catalina, km 330 Transchaco route; General Bruguez | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 7380* | Estancia Santa Catalina, km 330 Transchaco route; General Bruguez | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 7380,* 4501* | Estancia Santa Catalina, km 330 Transchaco route; General Bruguez | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 3825, 3828, 4412, 4525, 6618* | Riohaco Negro, 44 km W to Concepción | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 4511, 8543* | Auaray Guazú river, 73.9 km NW Benjamin Aceval, Ruta Transchaco | Presidente Hayes | Presidente Hayes |
| *P. boliviana* | *CZCEN 4491* | Auaray Guazú river, 2 km NW from Lima | San Pedro | San Pedro |
| *P. boliviana* | *CZCEN 4431, 6612, 6619* | Lima | San Pedro | San Pedro |
| *P. boliviana* | *CZCEN 1400-1402* | Villa del Rosario, Compañía Mboycayá | San Pedro | San Pedro |
| *P. motorzinho* | *IIBP-H 1087-1088, 1097-1108* | Estancia Pirá Potro (Vierci), Arroyo Guasú puntu 22 | Amambay | Amambay |
| *P. cf. motorzinho* | *IIBP-H 1182, 1213-1214* | Estancia San Juan, 20 km S Bella Vista | Amambay | Amambay |
| *P. cf. motorzinho* | *IIBP-H 3319-3321* | Colonia Potriti | Alto Paraguay | Alto Paraguay |
| *P. mystacalis* | *P. mystacalis* | MNHNP 3826-3827, 8217 | Laguna General Díaz | Alto Paraguay |
| *P. mystacalis* | *P. mystacalis* | MNHNP 5000, 5032-5034 | Isla Yacryetá, Estancia Melgarejo | Itapúa |
| *P. mystacalis* | *P. mystacalis* | IIBP-H 1241-1244 | Route Mariscal López, 11 km W from General Delgado | Itapúa |
| *P. mystacalis* | *P. mystacalis* | MNHNP 67 | Alcaráz Cué colonia, 5 km NW from San Patricio | Misiones |
| *P. mystacalis* | *P. mystacalis* | MNHNP 1200 | Isla Yacryetá, 15 km SE from Ayolas, Base Aeronaval | Misiones |
| *P. mystacalis* | *P. mystacalis* | MNHNP 3821 | San Ignacio, Cabaña Guayvar | Misiones |
| *P. mystacalis* | *P. mystacalis* | MNHNP 3822, 5670-5678, 8209 | San Ignacio, Cabaña Guayvar | Misiones |
| *P. mystacalis* | *P. mystacalis* | IIBP-H 273, 282, 289, 303, 346, 676-677, 832-833 | Estancia San José | Neembucú |
| *P. mystacalis* | *P. sp.* | MNHNP 10048 | Pilar, 19.8 km SW | Neembucú |
| *Physalaemus sp.* (juvenile) | *P. falcipes* | MNHNP 7146 | Parque Nacional Defensores del Chaco road to Cerro León | Alto Paraguay |
| *Physalaemus sp.* (juvenile) | *P. falcipes* | MNHNP 6603, 6605 | 37.6 km S de Platanillo, on route to Pirizal (Línea 1) | Boquerón |
| *Physalaemus sp.* (juvenile) | *P. falcipes* | MNHNP 3830 | Km 695, Transchaco route | Boquerón |
| *Physalaemus sp.* (juvenile) | *P. ternetzi* | 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 mysticalis* — 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 Bahia 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 (MNHN 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 \textit{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 \textit{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, \textit{P. boliviana} is distributed in two discontinuous areas (De la Riva et al. 2000), while \textit{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 \textit{P. falcipes} in Motte et al. (2015) and those from Laguna General Díaz (MNHN 3826–3827, 8217) are assignable to this species. \textit{Pseudopaludicola boliviana} and \textit{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, \textit{P. motorzinho} is probably associated with Chaco Seco and Cerrado ecoregions.

\textit{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 \textit{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).

\section*{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 (MNHN); and Andrea Weiler and Katia Airaldi (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.

\section*{Literature Cited}

Alcalde, L. and J. Williams. 2004. Nuevas localidades para \textit{Pseudopaludicola boliviana} y \textit{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. MNHN: Asunción.

Bokermann, W.C.A. 1996. Lista anotada das localidades tipo de anfibios brasileiros. São Paulo: Servicio 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 \textit{Pseudopaludicola ternetzi} Miranda-Ribeiro, 1937 (Anura, Leiuperidae) with designation of a lectotype. Zootaxa 3051: 62–64.

Cardozo, D. and D. Baldo. 2012. \textit{Pseudopaludicola ternetzi}: two lectotypes for the same taxon. Zootaxa 3192: 67–68. http://www.mapress.com/j/zt/article/view/12940/0

Cardozo, D. and P. Suárez. 2012. Osteological description of \textit{Pseudopaludicola canga} with implications for the taxonomic position of this taxon. Zootaxa 3515: 75–82. doi: 10.15468/dsanxx

Cardozo, D. and I.F. Toledo. 2013. Taxonomic status of \textit{Pseudopaludicola riopiedadensis} Mercadal de Barrio and Barrio, 1994 (Anura, Leptodactylidae, Liuperinae). 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 \textit{Pseudopaludicola} (Anura: Leptodactylidae). Salamandra 52 (1): 11–22. http://www.salamandra-journal.com/index.php?option=com_docman&view=item&id=80.

Carvalho, T.R., B.F.V. Teixeira, L.B. Martins and A.A. Giaretta. 2015a. Intraspecific variation and new distributional records for \textit{Pseudopaludicola} species (Anura, Leptodactylidae, Liuperinae) 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 and new distributional records for \textit{Pseudopaludicola giarettaei} Carvalho, 2012 (Anura, Leptodactylidae, Liuperinae): implications for its congenic differentiation. Papéis Avulsos de Zoológia 55(17): 265–254 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=lup

De la Riva, I., J. Kohler, 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,
Lobo, F. 1996. Evaluación del status taxonómico de *Pseudopaludicola*

Dinerstein, E., D.M. Olson, D.J. Graham, A.L. Webster, SA. 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-ecorregiones-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: Leptodactylidae). Zootaxa 306: 826–836. http://zoostud.sinica.edu.tw/Journals/50/6/826.pdf

Freiberg M.A. 1942. Enumeración sistemática y distribución geográfica de los baterios argentinos. Physia 19: 219–240.

Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimiento y aspectos biológicos). Montevideo: Museo Damaso Antonio Larrañaga. 123 pp.

Hensel, R. 1867. Beitrage zur Kenntniss der Wirbeltiere Sud-Brasilien. Archiv fur Naturgeschichte 33(1): 120–162. http://biodiversitylibrary.org/page/7058833

Jansen, M., R. Bloch, A. Schulze and M. Pfenninger. 2011. Anuran amphibians’ diversity in a northwestern area of the Brazilian Pantanal. Biota Neotropica 11: 77–86. doi: 10.1590/S1666-06032011000400008

Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimiento y aspectos biológicos). Montevideo: Museo Damaso Antonio Larrañaga. 123 pp.

Haddad, C.F.B. and A.J. Cardoso. 1987. Taxonomía de tres especies de *Pseudopaludicola* (Anura, Leptodactylidae). Papéis Avulsos de Zoologia 36: 287–300.

Hensel, R. 1867. Beitrage zur Kenntniss der Wirbeltiere Sud-Brasilien. Archiv fur 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

Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimiento y aspectos biológicos). Montevideo: Museo Damaso Antonio Larrañaga. 123 pp.

Haddad, C.F.B. and A.J. Cardoso. 1987. Taxonomía de tres especies de *Pseudopaludicola* (Anura, Leptodactylidae). Papéis Avulsos de Zoologia 36: 287–300.

Hensel, R. 1867. Beitrage zur Kenntniss der Wirbeltiere Sud-Brasilien. Archiv fur 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

Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimiento y aspectos biológicos). Montevideo: Museo Damaso Antonio Larrañaga. 123 pp.

Haddad, C.F.B. and A.J. Cardoso. 1987. Taxonomía de tres especies de *Pseudopaludicola* (Anura, Leptodactylidae). Papéis Avulsos de Zoologia 36: 287–300.

Lynch, J.D. 1991. 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

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. riopiedraeensis* (Amphibia, Anura). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Zoología 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 batarhinos novos das colheções do Museu Nacional. O Campo. Rio de Janeiro 8: 66–69.

Motte, M., M.E. Tedesco, J.A. Céspedes, N. Martínez, V. Zaracho and A. Yanovsky. 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. Subordbo Aglossa und Phaneroglossa, Sectio 1. Arcifera. Das Tierreich 46: xxxi + 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/S1666-06032011000400008

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

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

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

Parker, H.W. 1927. A revision of the frogs of the genus *Pseudopaludicola*, *Physalaemus* and *Pleurodema*. Annals and Magazine of Natural History 6: 450–478. doi: 10.1002/00229370655471

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_pages455-461.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

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.

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. Giaretta 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

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