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Osteological description of *Pseudopaludicola canga* with implications for the taxonomic position of this taxon

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Abstract

Pseudopaludicola canga was described by Giaretta & Kokubum (2003) based on 74 individuals previously assigned to *P. mystacalis* by Lobo (1995). In the diagnosis of *P. canga*, the original authors assigned the presence of terminal T-shaped phalanges as a character state for this taxon. However, the osteology of *P. canga* is not described and the presence of toe tips not expanded laterally is a characteristic share with all members of *Pseudopaludicola* unassigned to any group. In this work is describe for first time the osteology of *P. canga*, re-examining the external morphology providing a new diagnosis and establishing the taxonomic position of *P. canga* in the framework of phylogenetic hypothesis proposed by Lobo (1995). Additionally, is compared the toe tip digit IV, between *P. falcipes* and all the species included in the *P. pusilla* group and updated the type locality of *P. canga*. The osteology reveals that *P. canga* has the toe tips not T-shaped as mentioned by the original authors and this characteristic has important consequences for the diagnosis of the species. Additionally, the erroneous inclusion of *P. canga* in the *P. pusilla* group is confirmed by the phylogenetic analysis.

Key words: *Pseudopaludicola pusilla* group, osteology, external morphology, taxonomy

Introduction

Pseudopaludicola is a genus of small-bodied frogs diagnosed by the presence of at least one tubercle on each forearm (Miranda-Ribeiro 1926; Lynch 1989; Lobo 1995). Members of this genus are widely distributed over northern and central South America, from northern Colombia to the south of Buenos Aires province in Argentina. This natural group is composed of 14 species: *P. boliviana*, *P. canga*, *P. ceratophyes*, *P. falcipes*, *P. giarettai*, *P. llanera*, *P. mineira*, *P. murundu*, *P. mystacalis*, *P. pusilla*, *P. riopiedadensis*, *P. saltica*, *P. serrana*, and *P. ternetzi* (Frost 2011; Carvalho 2012).

Lynch (1989) made the first attempt to assess the taxonomic structure of the group. In this work *Pseudopaludicola llanera* was described, *P. pusilla* and *P. boliviana* were considered as a valid species, correcting the previous synonymy proposed in Lynch (1971). Additionally, Lynch (1989) performed a cluster analysis of overall similarity, recognizing the *P. pusilla* group composed by *P. boliviana*, *P. ceratophyes*, *P. llanera*, and *P. pusilla*, grouped by the presence of toes tips T-shaped.

Lobo (1995), based on external morphology and osteological characters, proposed the first phylogenetic hypothesis for *Pseudopaludicola*, using the cladistic methodology. This work supported the genus as a natural group with three synapomorphies: presence of antebrachial tubercles; antero- and posterolateral processes of the hyoids vestigials or absents; and epicoracoids cartilages slightly overlapping each other or not overlapped. Additionally, the *P. pusilla* group proposed in the phenetic revision of Lynch (1989) was recovered as monophyletic in Lobo (1995) and supported by the presence of T-shaped phalanges, while the rest of the species of *Pseudopaludicola* remained unassigned to any group. In this sense, the shape of toe tips is an important character that allowed the diagnosis of the *P. pusilla* group (Lynch 1989; Lobo 1995). The bone expansion at the end of the

phalanges is reflected as an increased finger width in the external morphology. However, the grade of expansion is not the same for all species and could be misunderstood. On the other hand, all the species unassigned to any group have the end of the phalanges knobbed with a central groove, with no lateral expansion at the tips of the fingers visible in the external morphology.

Pseudopaludicola canga was described by Giaretta and Kokubum (2003) based on 74 individuals previously assigned to *P. mystacalis* by Lobo (1995). In the diagnosis of *P. canga*, the original authors assigned the presence of terminal T-shaped phalanges as a character state for this taxon. However, the osteology of *P. canga* was not described and the presence of toe tips not expanded laterally was mentioned in the diagnosis as a characteristic of the external morphology. However, this character state is shared with all the species unassigned to any group (Lobo 1995). The study of *P. canga* osteology reveals that the toe tips are not T-shaped as was mentioned in the original description, which has consequences for the diagnosis and taxonomic position of this taxon.

The aim of this work is to describe for first time the osteology of *P. canga*, re-examining the external morphology and establishing the taxonomic position of *P. canga* in the framework of the phylogenetic hypothesis of Lobo (1995). Additionally, we compare the toe tip digit IV, between *P. falcipes* and all the species included in the *P. pusilla* group.

Material and methods

External morphology was based on 41 voucher specimens (including the holotype ZUEC 6088 and eight paratypes, see Appendix I) under a Nikon SMZ 445 Stereomicroscope following Savage and Heyer (1967) and Duellman (1970). Sex was determined by visual inspection of secondary sexual characters, such as nuptial pads or extended vocal sacs in males and presence of ovarian follicles in females. Five adults, from both sexes of *P. canga* (three males; two females) were cleared and stained using the technique of Taylor and Van Dyke (1985). For general osteological description, we follow Trueb (1973); cranial osteology (Jurgens 1971), hyoid and larynx (Trewavas 1933), phalangeal formula (Alberch & Gale 1985); carpal and tarsal morphology (Fabrezi 1992, 1993; Fabrezi & Alberch 1996).

Additionally, we examined 20 cleared and stained specimens of *P. boliviana*, *P. ceratophyes*, *P. falcipes*, *P. llanera*, and *P. pusilla* to evaluate the morphology of the toe tips digit IV (Appendix I).

To evaluate the taxonomic position of *P. canga*, we scored the same characters used by Lobo (1995), including them in Lobo´s matrix. The phylogenetic analysis was performed using TNT (Goloboff *et al*. 2008) under the same conditions as Lobo (1995): using eight species of *Physalaemus*, *Eupemphix nattereri*, *Leptodactylus podicipinus*, and *L. mystacinus* as outgroups, with the latter used to root the tree. All the characters were treated as non-additive and the analyses were made using TBR branch swapping (10 addition sequences, saving 10 trees per replicate).

Pseudopaludicola canga osteology
(Figure 1)

Description based on MPEG 34368–72 (three males; two females, Appendix I).

Skull wider than longer. Complete maxillary arch. Alary processes of premaxillae directed dorsally, parallel to each other (frontal view). Premaxilae bearing 7–10 teeth and maxillae with 23–28 curved and pedicellated teeth. Nasal narrow and ovoid, with irregular inner margin and posterior end pointed. The nasals are separated from each other and do not overlap the maxillary. In dorsal view, the nasal bone slightly overlaps the sphenethmoid (but does not overlap the sphenethmoid in MPEG 34368). Anterior margin of the sphenethmoid not reaching the middle of the choana, posterior margin W-shaped. In dorsal view, the sphenethmoid is short with a thin internasal septum. Frontoparietals with irregular inner margins that leave the frontoparietal fontanelle almost hidden (Fig. 1A). Exooccipitals separated by a wide mineralized stripe. Optic foramen large sized, ovoid and placed on the junction between the prootics and the sphenethmoid (in MPEG 34368, the trochlear nerve exits from the neurocranium by an independent hole, placed anterodorsal to the optic foramen); Oculomotor foramen of narrow diameter, located posterior to the optic foramen (exit of cranial nerve III). Prootic foramen oval, placed posterior to the optic capsule (cranial nerve V). Jugular foramen with two holes (cranial nerves IX y X). Triradiate pterygoid. The posterior ramus of the pterigoid is longer than medium and is separated from the quadrate, while the medium is away from

the wings of the parasphenoid and supported by cartilage on the otic region of the skull. Anterior ramus separated from the palatine. Quadratojugal with maxillary process reduced (Fig. 1C). Triradiate parasphenoid with the tip of the cultriform process of irregular shape (rounded in MPEG 34368, 34370). Parasphenoid wings slightly laid back. Septomaxilary half-ring shaped (sickle-shaped in MPEG 34369, 34372). Neopalatines poorly developed, not overlapping the maxillae. Prevomers irregularly shaped, wider in middle region and without teeth. Squamosal with the ventral ramus wider at ventral end, zygomatic ramus shorter than otic with a descendent process well-developed (Fig. 1D). Tympanic annuli cartilaginous incomplete, dorsally open with the posterior end parallel to the otic ramus of the squamosal. Plectrum with uniform width. Cartilaginous operculum, rounded.

Hyoid plate cartilaginous, mineralized at the center. Anteromedial processes short and divergent (parallel in MPEG 34370–1). Postero- and anterolateral processes absent. Posteromedial processes short with cartilaginous ends.

The mandible has a thin dentary covering the lateral margins of the Meckels cartilage. The inner part of this cartilage is covered by the angular, which is thin and without coronoid process evident. The articular region of the mandible is cartilaginous and the dentary plain, without any serrate structures such as denticles.

The larynx has the arytenoid as two small oblong shells and the cricoid forming a complete ring. Esophageal process long and thin. Muscular processes thin. Cardiac processes poorly developed. In the females (MPEG 34370–1), the cricoid is thinner and the arytenoids smaller.

Arciferal pectoral girdle, with the left epicoracoid cartilage slightly superimposing the right one. Clavicle thin, posterior margin concave, separated from the acromial region of the scapula by an anterior projection of the procoracoid. Scapula with *pars acromialis* and *glenoidalis* poorly developed. Anterior process of the suprascapula developed. Omosternum cartilaginous, without distal expansion (expanded in MPEG 34369–70). Sternum simple, not bifurcated, with osseous mesosternum and cartilaginous xiphisternum expanded.

Humerus with deltoid crest developed. Radius-Ulna fused, leaving a groove between them, which begins at the union of the carpal elements and extends to two thirds of the length of both bones. Carpal composed by five elements: radial, ulnar, Y element, distal carpal V–IV–III and distal carpal II. Prepollex with osseous base and one mineralized long segment. Phalangeal formula: 2–2–3–3. Terminal phalanges knobbed, with central groove (Fig. 1E).

Vertebral column with eight procoelous presacral non-imbricate vertebrae (Fig. 1F). Cotilar facets of the atlas separated (Type I of Lynch 1971). The atlas body is the widest of the vertebrae. In dorsal view; the anterior margin of the atlas makes contact with the presacral II through a narrow neural process. Sacral diapophysis narrow, not expanded. Urostile with dorsal spine well-developed and exit of the spinal nerve X not visible. Urostilar articulation bicondylar. Anterior portion of the illium articulate with the ventral surface of the sacral diapophysis. Pubis cartilaginous. The hind limbs have the tibio-fibula fused at the distal end. Tarsal composed by: central, distal tarsal I, and distal tarsal II–III. Prehallux comprises an osseous base and one cartilaginous segment. Phalangeal formula: 2–2–3–4–3. Toe tips knobbed with central groove (Fig. 1G).

Additionally, all the specimens examined present the same combination of sesamoid bones and osseous lateral projections:

At the anterior extremities the metacarpal epiphysis and some phalanges have small lateral projections. In the forelimbs, in dorsal view, there is a small rounded sesamoid bone over the distal carpal V–IV–III, in the tendon of the muscle *extensor carpi ulnaris*. In ventral view, the palmar sesamoid (embedded in the *m. digitorum longus*) has an irregular quadrangular shape. Also present are glide sesamoids on the flexor tendons of the hands, at the junction of the proximal and medial phalanges in all the fingers.

The hind limbs have lateral projections at the epiphysis of some metatarsals and phalanges and a constant sesamoid bones distribution: S. graciella (at the union between femur-tibia fibula, embedded at the tendon of the *m. gracilis major*); sesamoid cartilage (in the tendon of the *m. plantaris profundus*) and two plantar sesamoids with ovoid shape and similar size, placed at the tendons that form the *aponeurosis plantaris*.

Additionally, near the distal end of the sacral diapophyses there are a couple of sesamoids (S. of the sacral vertebrae) with elongated shape and similar width to the diapophyses.

Comments about toe tip digit IV. As previously mentioned by Lynch (1989), *P. boliviana* and *P. ceratophyes* have additional pads or cutaneous expansion at the end of the digits, reflected in the external morphology as wider T-shaped phalange (Fig. 2E–F). On one hand, the T-shaped phalanges of *P. llanera* are the narrowest, but maintain a clear lateral expansion of the bone (Fig. 2D), while in *P. pusilla* the toe tips are expanded forming a "robust T"

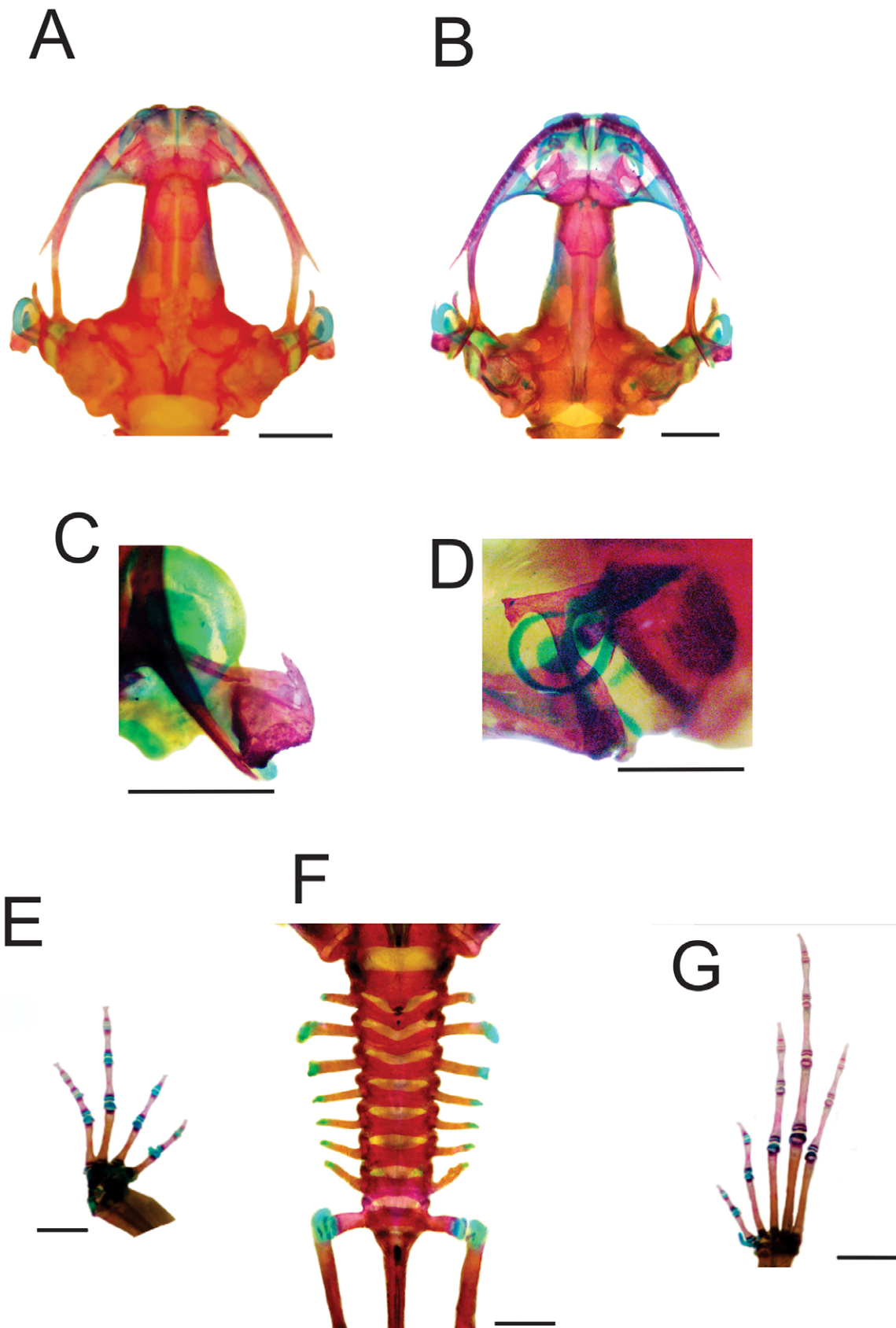**FIGURE 1.** *Pseudopaludicola canga* osteology. Skull: A) dorsal view; B) ventral view. C) Maxilar process of the quadratojugal; D) Descendant process of the squamosal. E) palmar view of hand; F) vertebral column; G) plantar view of foot. Scale bar 500 µm (C–D) and 1 mm (A–B; E–G).
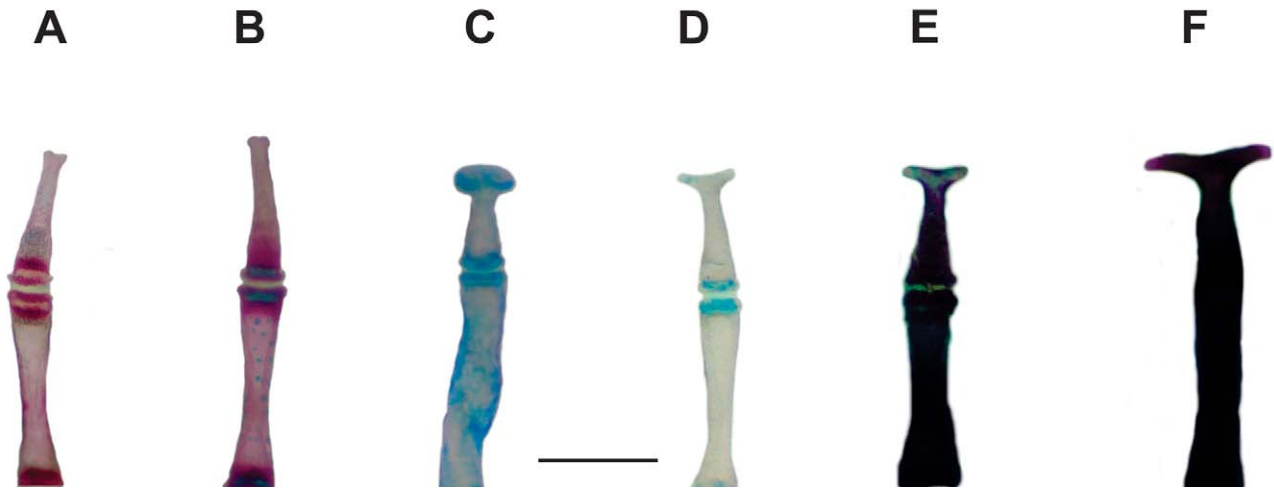
FIGURE 2. The IV digit toe tip in *Pseudopaludicola* species. A) *P. canga* (MPEG 34369) 14700); B) *P. falcipes* (LGE 3125); C) *P. pusilla* (ICN 14700); D) *P. llanera* (ICN 14025); E) *P. boliviana* (LGE 3027); F) *P. ceratophyes* (INPA 3540). Scale bar 1 mm.

(Fig. 2C). In both cases, the width of the bone is not visible in the external morphology, so the end of the fingers is not expanded laterally (see Lynch 1971). However, all the species included in the *P. pusilla* group have the terminal phalanges T-shaped without a central groove, with the toe tips wider than the base of the last phalange. On the other hand, all the species unassigned to any group have the tip of the phalanges knobbed, with a central groove with the fingertips narrower than the base of the last phalange (Lynch 1989; Lobo 1995), as is shown for *P. falcipes* (Fig. 2B). In *P. canga* the toe tips are not T-shaped as mentioned by the original authors (Fig. 2A) and this characteristic has important consequences for the diagnosis of the species.

　　***Pseudopaludicola canga* external morphology.** Giaretta and Kokubum (2003) provided a detailed description of the holotype (ZUEC 6088). In our study we agreed with the previous description, adding some features of interest for the diagnosis of the species. We disagreed with the authors about the presence of dorsal folds. The holotype and remaining vouchers examined in this study have no dorsal folds. Additionally the vocal sac has a central fold (the vocal sac is more developed than other taxa (except *P. serrana* and *P. murundu*), and in preservative forms a fold in the middle of the vocal sac). The toe tips in hands and feet are not expanded laterally, and are very similar to all species of *Pseudopaludicola* unassigned to any group. The absence of T-shaped phalanges is reflected in the fingertips being narrower than the base of the phalanges. Additionally, the inner thighs have a light brown background finely spotted with black.

　　Taxonomy of *P. canga*. The phylogenetic analysis obtained 16 maximum parsimony trees (length: 51 steps, consistency index 0.471; retention index 0.690). The strict consensus of this analysis is shown in Figure 3. Using the same character state and analysis methodology as Lobo (1995), *P. canga* has basal position in the clade formed by *P. mystacalis* (*P. pusilla* (*P. boliviana* (*P. llanera* + *P. ceratophyes*))) in all most parsimonious trees as shown in the consensus tree (Figure 3, black arrow). The unique monophyletic group recovered is the *P. pusilla* group, including *P. pusilla* (*P. boliviana* (*P. llanera* + *P. ceratophyes*)), supported by the presence of T-shaped toe tips. The remaining species are unassigned to any group (Fig. 3).

Discussion

The inclusion of *P. canga* in the matrix published by Lobo (1995) resulted in 16 maximum parsimony trees, while in Lobo (1995) only three hypotheses were obtained. However, the relationship between the ingroups was very similar to the results obtained in Lobo (1995), with *P. mystacalis* being the basal taxon in the *P. pusilla* group, supported by the same synapomorphy as in Lobo (1995) and included the same species. *P. mineira* became the basal taxon in the entire genus or basal in the clade formed by *P. canga* (*P. mystacalis* (*P. pusilla* (*P. boliviana* (*P. llanera* + *P. ceratophyes*)))). *P. ternetzi* was always related to the sister species *P. falcipes* + *P. saltica*. Further

phylogenetic analysis including the recently described species (*P. giarettai*, *P. murundu,* and *P. serrana*) could be useful to evaluate such relationships. The major changes were related to outgroups, mostly *Physalaemus* species (including *Eupemphix nattereri*) were floating terminals.
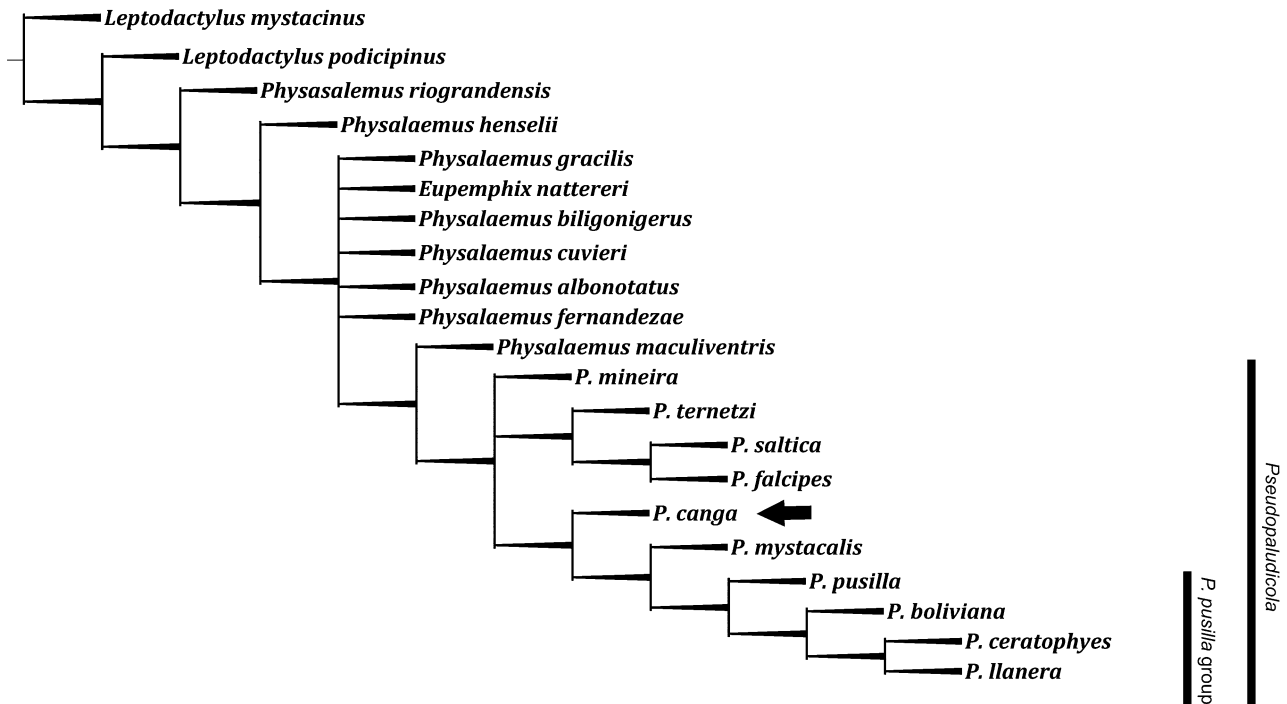

FIGURE 3. Strict consensus of 16 maximum parsimony trees obtained using the same characters and analytical parameters as in Lobo (1995). The black arrow indicates the taxonomic position of *P. canga*.

The erroneous inclusion of *P. canga* in the *P. pusilla* group was confirmed by the phylogenetic analysis and the osteology described in this study. The exclusion of *P. canga* from the *P. pusilla* group has important consequences on the diagnosis of this species, and is relevant to future descriptions. Therefore a new diagnosis is proposed for this taxon. *Pseudopaludicola canga* is similar to *P. mystacalis* and can be distinguished from these and all other recognized *Pseudopaludicola* species by a combination of external morphology, osteological, cytogenetic, and bioacustical characters.

As was previously mentioned by the original authors, the advertisement call of *P. canga* composed by notes with 1–9 pulses separate this taxon from all *Pseudopaludicola* species with advertisement call described (see Giaretta & Kokubum 2003).

Pseudopaludicola canga has a diploid number 2n=18, being the unique *Pseudopaludicola* species recognized with such karyotype (Duarte *et al.* 2010). The Brazilian populations assigned to *P.* aff. *canga* by Duarte *et al.* (2010) have taxonomic status unresolved, and further studies are needed to determine the identity of these specimens.

The toe tips knobbed with central groove separate *P. canga* from the species of *P. pusilla* group (*P. boliviana*, *P. ceratophyes*, *P. llanera*, and *P. pusilla*), which have toe tips T-shaped (Lynch 1989; Lobo 1995).

The smooth dorsal skin and the slender body with stylish aspect of *P. canga* differ from *P. ternetzi,* and *P. riopiedadensis* (robust body aspect with immaculate ventral surface and flattened dispersed warts (Lobo 1995, 1996, this work), and also from *P. mineira* which has a more globular body aspect (Lobo 1994, 1995).

The presence of a complete abdominal fold differentiates *P. canga* from *P. falcipes,* in which the abdominal fold is incomplete or absent (Lobo 1994, 1995).

The tibio-tarsal articulation reaching the eye, separates *P. canga* from *P. saltica*, *P. murundu*, and *P. serrana*, where the tibio-tarsal articulation extending beyond the tips of the snout (Lobo 1994, 1995; Toledo 2010; Toledo *et al.* 2010).

The prepollex composed of one element distinguishes *P. canga* from *P. falcipes*, *P. saltica*, and *P. ternetzi*

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(prepollex with base and two elements; Lobo 1995; this work). The prehallux formed by the base and one cartilaginous segment separates *P. canga* from *P. boliviana, P. llanera, P. mystacalis, P. pusilla*, and *P. ternetzi* (prehallux with base and two mineralized segments; Lobo 1995; this work).

Pseudopaludicola canga was proposed as an endemic species from the Serra dos Carajas, however the presence of this species in several localities of the Pará State (Appendix I) indicates that *P. canga* is a poorly known species, probably often confused with other taxa. The type locality is defined in the original article as "*Serra dos Carajás (approx. 6°S; 50°W; 700 m), municipality of Marabá*", was imprecise and made on the basis of outdated maps of Cunha *et al.* (1985), this region belongs to the municipality of Parauapebas since 1988, when it was separated from Marabá (Pará State law Nº 5.443/88). Future surveys and proper determination of the species are needed for the establishment of the correct distribution and conservation state of this taxon.

Acknowledgments

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APPENDIX. Material examined.

Institutional abbreviations make reference to: Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN); Instituto Nacional de Pesquisas da Amazonia, Brazil (INPA); Laboratorio de Genética Evolutiva, Universidad Nacional de Misiones, Argentina (LGE); Museu Nacional do Rio de Janeiro, Brazil (MNRJ); Museu Paraenese Emilio Goeldi, Brazil (MPEG); Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP) and Coleção Zoológica da Universidade Estadual de Campinas, Brazil (ZUEC).

Pseudopaludicola boliviana.—ARGENTINA:CHACO: Depto. Bermejo: Ruta Prov. 63 Antequera, Camino a Isla del Cerrito, LGE 2968 (♂), 3026 (♀), 3027 (♂). CORRIENTES: Depto. Gral. Paz: Itá Ibaté, LGE 2970 (♀). FORMOSA: Depto. Laishi: Ruta Prov. 1 Camino a Herradura, LGE 3083 (♂).

Pseudopaludicola canga.—BRAZIL: PARÁ: Conceição do Araguaia Municipality: Conceição do Araguaia, MZUSP 85906–911 (4 ♂, 2♀). Marabá Municipality: Marabá, MPEG 34371 (♀), MPEG 34372 (♂); Piçarreira, MPEG 28108 (♀); Projeto ALPA, 18 Km. de Amorin, MPEG 28290–292 (Juv, ♂, ♀); Projeto ALPA, Influênncia Ramal, Marabá MPEG 28293–94 (2 ♂). Parauapebas Municipality: Carajás: Acampamentos N1, MNRJ 57812–815 (2 Juv, ♂, ♀); Lago NL, MZUSP 61061–64 (4 ♂), MZUSP 61052–57 (6 ♂); Lago N4, ZUEC 6086 (♀), ZUEC 6088 (♂), ZUEC 6089 (♀), ZUEC 9991 (♀); ZUEC 9998 (♀). Canaã dos Carajas Municipality: Base do Niquel do Vermelho, MPEG 21277–278 (♂, ♀), MPEG 21281–282 (♂, ♀), MPEG 21284 (♀); Serra da Bocaína, MPEG 34368 (♂), MPEG 34369(♂), MPEG 34370 (♀).

Pseudopaludicola ceratophyes.—BRAZIL: AMAZONAS: Rio Juruá, INPA 2284 (♂), INPA 3482 (♂), INPA 3539–40 (♂, ♀).

Pseudopaludicola falcipes.— ARGENTINA: CORRIENTES: Depto. Curuzú Cuatiá: Estancia El Oscuro, Curuzú Cuatiá: LGE 3105 (♂). Depto. Ituzaingó: Estancia Santo Domingo: LGE 3125 (♂). Depto. Santo Tomé: Gdor. Virasoro, Arroyo Aguapeí: LGE 3164 (♂). ENTRE RÍOS: Depto. Federación: Arroyo Chajarí, Chajarí: LGE 3178 (♀). MISIONES: Depto. San Justo: LGE 3297; Depto. Candelaria: Ñu Pajú, Ruta Prov. 3 a 3,5 km. De Ruta Nac. 12: LGE 3112 (♀), 3312 (♀).

Pseudopaludicola llanera.—COLOMBIA: META: Ciudad de Puerto Gaitán: ICN 14021, ICN 14024; ICN 14025.

Pseudopaludicola pusilla.—COLOMBIA: SANTANDER: Puerto Wilches: ICN 14700, ICN 14712, ICN 14778; ICN 14779.