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Taxonomic characterization of Paradoxical frogs (Anura, Hylidae, Pseudae): geographic distribution, external morphology, and morphometry

ADRIAN ANTONIO GARDA[1,3,4], DIEGO JOSÉ SANTANA[2] & VINÍCIUS DE AVELAR SÃO-PEDRO[3]

[1]*Departamento de Botânica, Ecologia e Zoologia, Universidade Federal do Rio Grande do Norte, Campus Universitário – Lagoa Nova, Natal, RN, Brasil*

[2]*Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, PB, Brasil*

[3]*Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN, Brasil*

[4]*Corresponding author. E-mail: garda@cb.ufrn.br*

Abstract

Paradoxical frogs (Pseudae) have been difficult to characterize morphologically, and their phylogenetic affinities have long remained elusive despite several taxonomic revisions of the group. Based on the analysis of 1388 specimens we evaluate morphological characters used to identify and group species throughout their distributions. We also suggest other, previously unreported phylogenetically informative morphological characters and evaluate morphometric differences among species. The geographic distribution of Pseudae in Brazil confirms, to a certain degree, their association with hydrographic basins. Geographic variation in morphology is extensive in some species. Some characters traditionally used to identify species (e.g. stripes on the ventral surface of the thigh) vary extensively among populations, and in most cases do not distinguish among species. Body shape differences, skin texture, size and number of carpal and metatarsal tubercles, supernumerary tubercles, vocal sac structure, dorsal coloration, ventral stripes on the thigh, and geographic distribution need to be considered together to correctly identify species. Size of reproductive *Pseudis* varies considerably, most likely as a response to local conditions altering larval size at metamorphosis, given that post-metamorphic growth is reduced or absent in *Pseudis*. The previously suggested suite of ecological characters that allow disproportionate larval growth are therefore substantiated, while the paradox of a conserved body plan coupled with extensive character variation is implicated as the cause for confusion in the taxonomy of paradoxical frogs.

Key words: distribution, *Lysapsus*, Morphology, Morphometry, *Podonectes*, Pseudae, *Pseudis*, taxonomy

Resumo

Historicamente a caracterização morfológica das rãs paradoxais tem sido difícil e suas afinidades filogenéticas permaneceram incertas a despeito de diversas revisões taxonômicas do grupo. Com base na análise de 1388 espécimes nós avaliamos os caracteres da morfologia externa utilizados para identificar e agrupar as espécies de Pseudae ao longo de sua distribuição geográfica. Nós também sugerimos novos caracteres e avaliamos diferenças morfométricas entre as espécies utilizando uma análise de funções discriminantes. A distribuição geográfica de Pseudae no Brasil confirma sua associação com as bacias hidrográficas. A variabilidade geográfica na morfologia de algumas espécies é extensa. Alguns caracteres (p. ex. faixas longitudinais na superfície ventral das coxas) diagnosticam algumas espécies mas variam entre populações e, na maioria dos casos, são inúteis para distinguir espécies. Diferenças na forma do corpo, textura da pele, tamanho e número de tubérculos carpais e metatarsais, tubérculos supranumerários, número de sacos vocais, coloração dorsal, faixas na superfície ventral das coxas e distribuição geográfica tem de ser considerados para corretamente identificar as espécies de Pseudae. O tamanho de indivíduos reprodutivos varia consideravelmente, provavelmente como resposta a condições locais que modificam o tamanho da larva na metamorfose pois o crescimento pós-metamórfico é mínimo em *Pseudis*. O conjunto de caracteres sugeridos em outros trabalhos

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que permitem o crescimento larval desproporcional é, portanto, substanciado, enquanto o paradoxo de um plano corporal conservado associado a uma extensa variabilidade em diversos caracteres é implicado como a causa da confusão na taxonomia das rãs paradoxais.

Introduction

Since the first reports on the giant tadpoles of *Pseudis paradoxa*, where a reversed development from an amphibian to a fish was suggested (Pizzaro, 1876), paradoxical frogs (Pseudae) have been the source of curiosity and taxonomic confusion. Although support for the monophyly of the group has been unequivocal in both morphological and molecular studies, the phylogenetic position within Anura has been difficult to ascertain. They have been included within Ranidae (Günther, 1858), Leptodactylidae (Noble, 1922), Hylidae (Duellman & Trueb, 1986; Parker, 1935), and in their own family, Pseudidae (Savage & de Carvalho, 1953). It was not until a thorough analysis of morphological characters (da Silva, 1998) that the placement of Pseudae within Hylidae was accepted and this placement was later corroborated by molecular studies (Darst & Cannatella, 2004; Faivovich *et al*., 2005; Hoegg *et al*., 2004; Wiens *et al*., 2005).

The taxonomy of paradoxical frogs has also been highly variable with different authors recognizing between nine and eleven species in one to three genera (Aguiar *et al*., 2007; Garda & Cannatella, 2007 ; Wiens *et al*., 2010, Appendix I). Despite these recent phylogenetic assessments and their proposed taxonomic changes, a large gap remains on basic morphological variation within and among Pseudae species. Anatomical characters from larvae and adults, calls, geographic distribution, and external morphological data are incomplete and scattered in the literature. To be sure, the last complete review of Pseudae is almost 50 years old (Gallardo, 1961).

Rana paradoxa Linnaeus 1758 was recognized as a distinct genus by Wagler (1830), who proposed the name *Pseudis* for these aquatic frogs. *Pseudis minuta* was described 18 years later (Günther, 1858), shortly before the description of the genus *Lysapsus* (Cope, 1862b) and of *P. mantidactyla* (Cope, 1862a). A series of taxonomic suggestions and species descriptions was published subsequently, but was controversial mostly due to the unclear boundaries between genera (Savage & de Carvalho, 1953). *Pseudis minuta*, for example, has been placed in three genera and received four names (*Lysapsus mantidactylus*, *Pseudis meridionalis*, *Pseudis minutus*, and *Podonectes palmatus*, Appendix I).

Savage and de Caravalho (1953) outlined distinguishing characters of Pseudae genera and gave the group a family status (Pseudidae). They recognized two species of *Lysapsus* (*L. laevis* and *L. limellum*), and synonymized three *Pseudis* (*P. bolbodactyla*, *P. fusca*, and *P. mantidactyla*) with *P. paradoxa*. Their work was based mostly on osteological and external morphological characters. Gallardo (1961;1964), based on geographic distribution and external morphology, recognized two species of *Lysapsus*, *L. mantidactylus* and *L. limellum* (with four subspecies), and one of *Pseudis* (with six subspecies). *Pseudis meridionalis* (1926), omitted in Gallardo's publications on the group, was synonymized with *L. mantidactylus* by Bokermann (1966), and Cochran and Goin (1970) described a seventh subspecies of *P. paradoxa* from Colombia (*P. p. nicefori*). Fifteen years later, Klappenbach (1985) synonymized *L. mantidactylus* with *P. minuta*, and elevated *L. limellum*, *L. caraya*, *L. bolivianus*, and *L. laevis* to species, with the last two being closely related. The species status of some of the subspecies of *Pseudis* (*P. fusca* and *P. bolbodactyla*) proposed by Gallardo (1961) was recognized 14 years later, along with the description of *P. tocantins* (Caramaschi & Cruz, 1998). The last taxonomic addition to the group was the description of *P. cardosoi* from Serra Geral, a high altitude Plateau in southern Brazil (Kwet, 2000).

Garda and Cannatella (2007), in the first phylogenetic analysis including all members of the group, showed that *P. minuta* + *P. cardosoi* required recognition of a third genus to avoid nonmonophyly of *Pseudis*, leading them to resurrect the genus *Podonectes*. The authors also suggested the unranked name Pseudae Fitzinger 1843 for the group because of several distinguishing morphological and ecological characteristics. In their work, three *Pseudis paradoxa* subspecies (*P. p. paradoxa*, *P. p. platensis*, and *P. p. occidentalis*) showed little divergence, with *P. p. paradoxa* being the sister to a group in which *P. p. occidentalis* was nested

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within *P. p. platensis*. The authors recognized that both *L. limellum* and *P. paradoxa* were likely composed of multiple species, but concluded that insufficient data were available to substantiate their separation into additional species. Concomitantly, Aguiar *et al*. (2007) published a phylogenetic analysis with similar taxon and gene sampling to Garda and Cannatella (2007). Despite the virtually identical tree topology, a different (but equally valid) solution to avoid a paraphyletic *Pseudis* was chosen: *Lysapsus* was placed as a junior synonym of *Pseudis* and two subspecies were recognized as distinct species, *Lysapsus bolivianus* and *Pseudis platensis*. A recent analysis of the dataset used by Garda and Cannatella (2007) along with the most comprehensive dataset for hylids revisited the changes proposed in these two papers (Wiens *et al*., 2010). The authors found strong support for the monophyly of *Lysapsus* and recovered a monophyletic *Pseudis*, concluding therefore that neither the synonymization of *Lysapsus* and *Pseudis* nor the resurrection of *Podonectes* were substantiated (Wiens *et al*., 2010). We follow Wiens *et al*. (2010) throughout this paper and recognize two genera, *Lysapsus* and *Pseudis*. We also maintain and endorse the use of the unranked name Pseudae proposed by Garda and Cannatella (2007) for these two genera because of the ecological and morphological peculiarities of the group.

The above taxonomic propositions were based solely on the tree topology recovered in phylogenetic analyses of molecular data. The current lack of a thorough morphological assessment of Pseudae precluded the use of additional (and possibly diagnostic) characters in these phylogenetic analyses and in the decision-making process to lump or split genera and species. Here, we analyze morphometric, external morphology, and coloration characters from all species of Pseudae throughout their range in South America. We also produced updated georeferenced maps to interpret the distribution of the group in Brazil and provide a taxonomic key to identify currently recognized species in the group. Our specific goals were to 1) Evaluate external morphology characters used to diagnose species in the group; and 2) check for morphometric differences among species. By addressing such points we expected to make species identification easier, to provide a set of characters to discriminate among all species in the group in the field, and to facilitate the identification of potentially undescribed species.

Material and methods

Specimens used. We collected frogs of all species of Pseudae during field trips in Brazil between 2000 and 2007. Frogs were killed by rubbing 5% xylocaine cream onto their abdomens, fixed in 10% formalin, tagged with individual field numbers, and permanently stored in 70% ethanol. All specimens were deposited at the Coleção Herpetológica da Universidade de Brasília (CHUNB). In addition, we measured frogs deposited in museum and herpetology collections from ten institutions (see Appendix II for voucher numbers and localities). In total, 1388 individuals were measured (475 *Lysapsus* and 913 *Pseudis*). Museum acronyms used are those given in Leviton *et al*. (1985). All statistical analyses were conducted in SYSTAT® 11 for windows.

For morphometric analyses, specimens belonging to the same hydrographic basin were considered to represent the same species. This assumption, originally raised by Gallardo (1961), was mostly substantiated by recent molecular phylogenies (Aguiar *et al*., 2007; Garda & Cannatella, 2007). External morphology and coloration were used to refine this identification, and helped recognize that specimens found east of the Espinhaço mountain range all represent *P. fusca* (expanding its range and restricting *P. bolbodactyla* west of this range, contrary to Caramaschi & Cruz, 1998). Also, frogs in the Paranã River basin (an affluent of the Tocantins) were actually *P. bolbodactyla* and not *P. tocantins*. No syntopic distributions have been reported for Pseudae species.

Geographic distribution. We compiled geographic distribution data for all Pseudae species in Brazil. Several localities lacked associated coordinates, so we combined physical maps and electronic databases available from Google Earth to infer the best approximation of geographic coordinates from the information available in museum collections. This information was used to produce georeferenced maps for *Lysapsus* and *Pseudis* in Brazil with ArcView® GIS 3.2 for Windows.

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External morphology. *Color in life*.—We photographed a sample of live frogs from every locality surveyed to evaluate intra- and interspecific color variation. When pertinent, specific notes on dorsal and ventral color patterns were taken.

Ventral pattern and longitudinal stripes.—We photographed the ventral pattern of longitudinal stripes on the thigh and spots on the abdomen in samples of freshly caught individuals and museum collections vouchers. For *Pseudis,* we counted the number of individual stripes that spanned 80% or more of the length of the left thigh and measured the width of the thickest stripe with a digital caliper to the nearest 0.01 mm. Stripes that extended less than 80% of the length of the thigh, that were interrupted several times, or that were interwoven with other stripes were not considered. One commonly present stripe merged with the color pattern surrounding the cloaca on the posterior region of the thigh and was not considered in the counts. Individuals without stripes were excluded from the analysis. Spots on the abdomen were coded as follows: 0, no spots: 1, few spots (1–10): and 2, large number of spots (>10). We compared species (*P. fusca* was excluded because of small sample size) using MANCOVA, with SVL as a covariate, because stripe width and number are likely to be influenced by frog size.

Other characters.—We examined each individual frog for supernumerary tubercles on the hand and foot, skin texture, feet webbing, and any previously unreported morphological structures of potential diagnostic use. We also noted whether other characters suggested in previous taxonomic works on the group were consistent and therefore diagnostic of each species. These characters included: metacarpal and metatarsal tubercles, supratympanic folds, shape of the metatarsal tubercle, longitudinal dorsal stripes, and terminal discs on the hand and foot.

Morphometry. We recorded the following morphometric variables for each individual of all species (N = 1388): snout-vent length (SVL); head width (at the middle of the tympanum); commissure-snout length (from the commissure of the mouth to the tip of the snout); tympanum and eye diameter; eye–nostril and eye–snout distances; elbow-finger III length (from the elbow to the tip of finger III); hand length (from the proximal part of the insertion of finger I on the hand— near the wrist — to the tip of finger III); tibia length; and foot length (from heel to the tip of toe IV). Foot length demanded that a small force be applied to the articulation to straighten the foot and have heel and toes on the same plane. Hand digit numbers follow Duellman and Trueb (1986). We took all measurements with electronic calipers to the nearest 0.01 mm. In *Pseudis* species we also measured the diameter of the palmar tubercle and the length of the thenar and inner metatarsal tubercles.

Size at maturity.—We sexed individuals by directly examining gonads and external morphology characters. Males with large, developed testes and secondary sexual characters (i.e., developed vocal sacs), and females with convoluted oviducts and/or developed eggs were considered reproductive. Because of museum restrictions on specimen dissection, not all individuals were scored for reproductive condition. All individuals with SVL larger than the smallest reproductive male or female found for a particular species were considered sexually mature. Only sexually mature individuals were used in morphometric analyses.

We $\log_{10}$-transformed all morphometric variables prior to analyses to meet the requirements of normality (Zar, 1999). Univariate and multivariate outliers were either excluded from the analyses or corrected for a specific value, if the deviation could be identified and confidently judged as wrong. We corrected wrong values or missing data using a regression formula for the character against the SVL of the species. Differences in morphometric variables were investigated between genera, among *Lysapsus* species, and among *Pseudis* species combined. Because *P. minuta* was included in a different genus (*Podonectes* sensu Garda & Cannatella, 2007), we separated them from other *Pseudis* in the Discriminant Analysis comparing genera. Also, because only a few *P. cardosoi* were available, this species was excluded from the analyses. To evaluate differences in shape, we compared species and genera using the above mentioned morphometric variables (11 for *Lysapsus* and 14 for *Pseudis*) as predictors in a Sequential Discriminant Function Analysis (Tabachnick & Fidell, 2001). In this type of discriminant analysis one or more predictor variables are forced to enter the model first, and the analysis becomes a sequence of ANCOVAs (Tabachnick & Fidell, 2001). Hence, to account for the influence of body size on shape, we forced SVL to enter the model first, such that all other comparisons were body-size adjusted. Sequential discriminant analysis is also useful to provide a reduced set of predictor variables and, therefore, to diminish the number of measurements/observations needed to classify a specimen.

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Results

Geographic distribution

In Brazil, *L. limellum* is found in the Paraná and Amazon River basins, *L. laevis* is restricted to Amazon savannas in Roraima, and *L. caraya* is restricted to the Araguaia River floodplain (Fig. 1A). Species of *Pseudis* are present throughout most of Brazil, with the exception of some regions in the semi-arid Caatinga Biome (Fig. 1B). *Pseudis bolbodactyla* is found in the upper São Francisco, Paraná, and Tocantins River basins, while *P. fusca* is restricted to rivers east of the Espinhaço Mountain Range in Southern Bahia, Minas Gerais, and Espírito Santo states. *Pseudis tocantins* is found in the Tocantins-Araguaia River Basin, but also in regions of the upper Xingu River. *Pseudis paradoxa*, like *L. limellum*, occurs in the Paraná and Amazon River Basins, but also in the Mearim River Basin in Maranhão State (Fig. 1B).

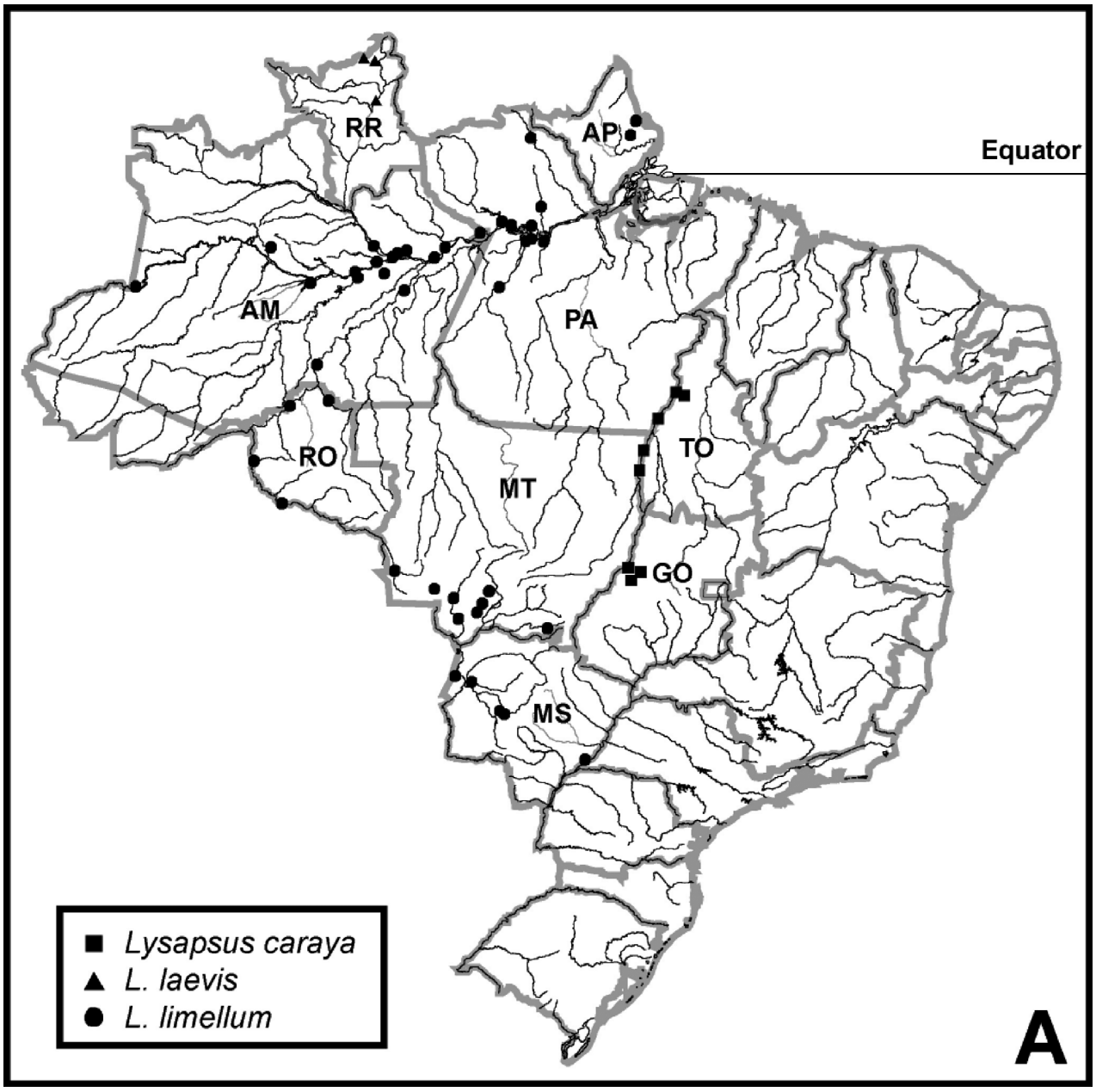

FIGURE 1A. Geographic distribution of *Lysapsus* species in Brazil. Data points correspond to the localities listed in Appendix II. Brazilian political units: AM, Amazonas; AP, Amapá; BA, Bahia; ES, Espírito Santo; GO, Goiás; MA, Maranhão; MG, Minas Gerais; MT, Mato Grosso; MS, Mato Grosso do Sul; PA, Pará; PR, Paraná; RO, Rondônia; RS, Rio Grande do Sul; RR, Roraima; SC, Santa Catarina; SP, São Paulo; TO, Tocantins.

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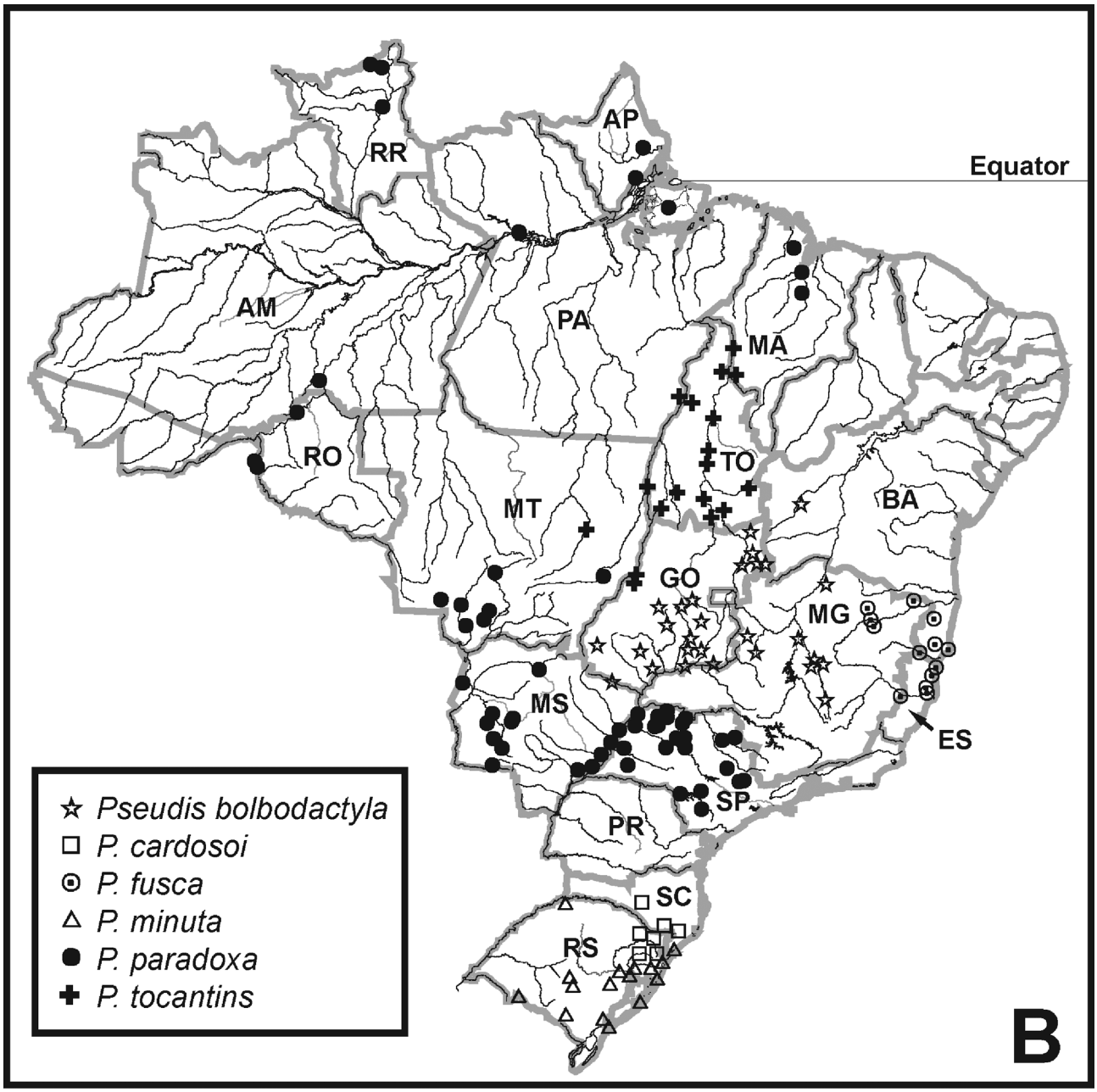

FIGURE 1B. Geographic distribution of *Pseudis* species in Brazil. Data points correspond to the localities listed in Appendix II. Brazilian political units: AM, Amazonas; AP, Amapá; BA, Bahia; ES, Espírito Santo; GO, Goiás; MA, Maranhão; MG, Minas Gerais; MT, Mato Grosso; MS, Mato Grosso do Sul; PA, Pará; PR, Paraná; RO, Rondônia; RS, Rio Grande do Sul; RR, Roraima; SC, Santa Catarina; SP, São Paulo; TO, Tocantins.

External morphology characters

Color in life—All species of Pseudae from 26 municipalities in 11 Brazilian states were used in the live color comparisons (Table 1). Color patterns varied considerably among and within species (Fig. 2). In some cases, geographic variation within one species was greater than between species. This is the case of *P. paradoxa* and *P. bolbodactyla* (Fig. 2, A–G). No distinct pattern was observed in *P. minuta* and *P. cardosoi* or within *Lysapsus* species. The only species with a distinct and consistent dorsal color pattern is *P. tocantins*, in which spots of varying sizes are seen flanking a midorsal stripe (Fig. 3, H–I). Within-population variation is smaller, but still present. *Pseudis paradoxa* from Maranhão show variable amounts of white warts and a distinct brown

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blotch on the back in some individuals (Fig. 2A), but these warts are reduced and even absent in other individuals from the same population, causing individuals to resemble specimens from Amapá (Fig. 2B).

TABLE 1. Brazilian municipalities where live specimens were photographed and/or annotated for color pattern. Brazilian political unities: AM—Amazonas, AP—Amapá, GO—Goiás, MA—Maranhão, MG, Minas Gerais, MS—Mato Grosso do Sul, MT—Mato Grosso, PA—Pará, RS—Rio Grande do Sul, RR—Roraima, and TO—Tocantins.

Species	Locality
Lysapsus caraya	GO: Aruanã, Britânia; TO: Couto Magalhães, PA: Conceição do Araguaia.
L. laevis	RR: Boa Vista
L. limellum	AM: Humaitá; AP: Tartarugalzinho; MS: Corumbá.
Pseudis cardosoi	RS: Jaquirana.
P. minuta	RS: Porto Alegre.
P. bolbodactyla	GO: Alvorada do Norte, Iaciara, Pirenópolis, Aporé, Itumbiara; MG: Lagoa Grande, Buritizeiro, Itacarambi.
P. fusca	MG: Araçuaí.
P. tocantins	GO: Aruanã, Britânia; TO: Couto Magalhães, Formoso do Araguaia, Palmas, Pedro Afonso, Sandolândia; PA: Conceição do Araguaia;
P. paradoxa	AP: Tartarugalzinho; MA: Pinheiro; MS: Corumbá; MT: Poconé; RR: Boa Vista

Ventral pattern and longitudinal stripes.—Longitudinal stripes on the thigh varied among and within populations (Fig. 3). Number and width of longitudinal stripes also varied considerably among species (Table 2). Variation in abdominal spots and number and thickness of longitudinal stripes on the thigh was significant among species (Wilk's Lambda = 0.767, $p < 0.001$). *Pseudis minuta* is characterized by a small number (usually one) of thin stripes on the thigh, *P. bolbodactyla* and *P. paradoxa* by larger numbers of thick stripes, and *P. tocantins* by large numbers of thin stripes.

TABLE 2. Number and width (in millimeters) of stripes on the ventral surface of the thigh in *Pseudis* species. Ranges are within parentheses. N = sample size.

Species	Number of Stripes	Stripe Width
P. minuta (N = 99)	1.1 ± 0.3 (1–3)	0.9 ± 0.3 0.2–1.9
P. bolbodactyla (N = 242)	2.6 ± 0.6 (1–3)	1.2 ± 0.4 0.5–2.8
P. fusca (N = 10)	1.9 ± 0.9 (1–3)	0.9 ± 0.3 0.4–1.3
P. paradoxa (N = 196)	2.3 ± 0.8 (1–4)	1.6 ± 0.7 0.5–5.9
P. tocantins (N = 83)	2.4 ± 0.9 (1–4)	0.5 ± 0.3 0.2–1.3

Individuals excluded from the analysis for different reasons. Some lacked any pattern on the thighs, such as some individuals of *P. paradoxa* from Roraima (Fig. 3E). Frogs from eastern Amazonia (*P. p. paradoxa*, and *P. p. caribensis*) commonly showed a reticulated pattern on the thighs, with no distinct stripe (some frogs in Fig. 3A). Several *P. minuta* lacked a pattern altogether, and a reticulated pattern of broken stripes was observed in some individuals of *P. tocantins*.

Other characters.—*Pseudis bolbodactyla* has granulated skin that readily distinguishes it from other species of *Pseudis* (Fig. 2, E–F). *Lysapsus caraya* and *L. limellum* have the ventral and dorsal portions of the body covered with small pointed tubercles, contrasting with the smooth skin of *L. laevis* (Fig. 2, K–M).

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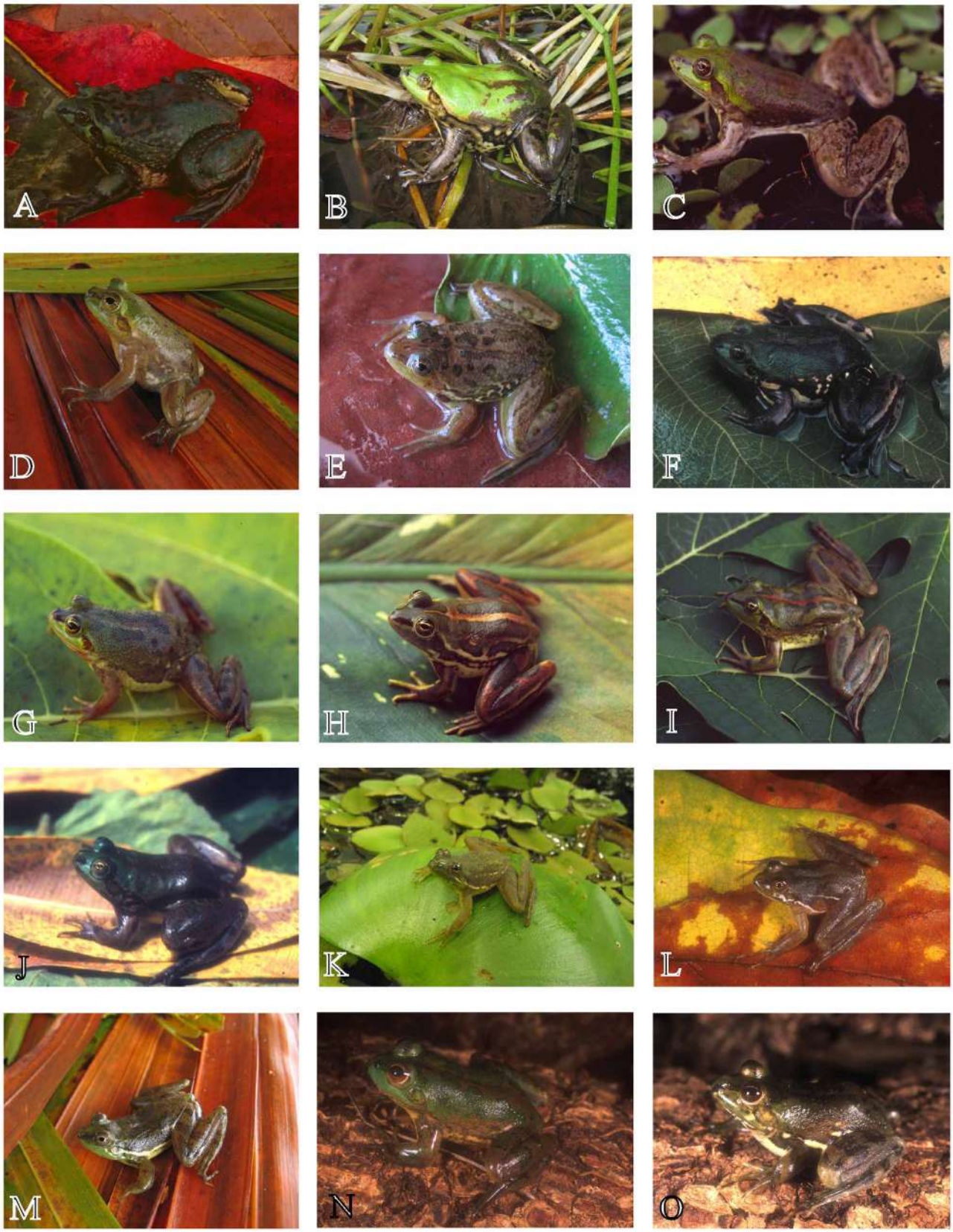

FIGURE 2. Live color patterns in Pseudae species in Brazil. *Pseudis paradoxa*: A—Pinheiro, Maranhão; B—Tartarugalzinho, Amapá; C—Corumbá, Mato Grosso do Sul; D—Boa Vista, Roraima. *Pseudis bolbodactyla*: E—Aporé, Goiás; F—Buritizeiro, Minas Gerais; G—Iaciara, Goiás. *Pseudis tocantins*: H— Britânia, Goiás; I—Formoso do Araguaia, Tocantins. J—*P. fusca*: Araçuaí, Minas Gerais. K—*Lysapsus limellum*, Corumbá, Mato Grosso do Sul. L—*L. caraya*, Britânia, Goiás. M—*L. laevis*, Boa Vista, Roraima. N—*Pseudis cardosoi*, Jaquirana, Rio Grande do Sul. M—*Pseudis minuta*, Porto Alegre, Rio Grande do Sul.

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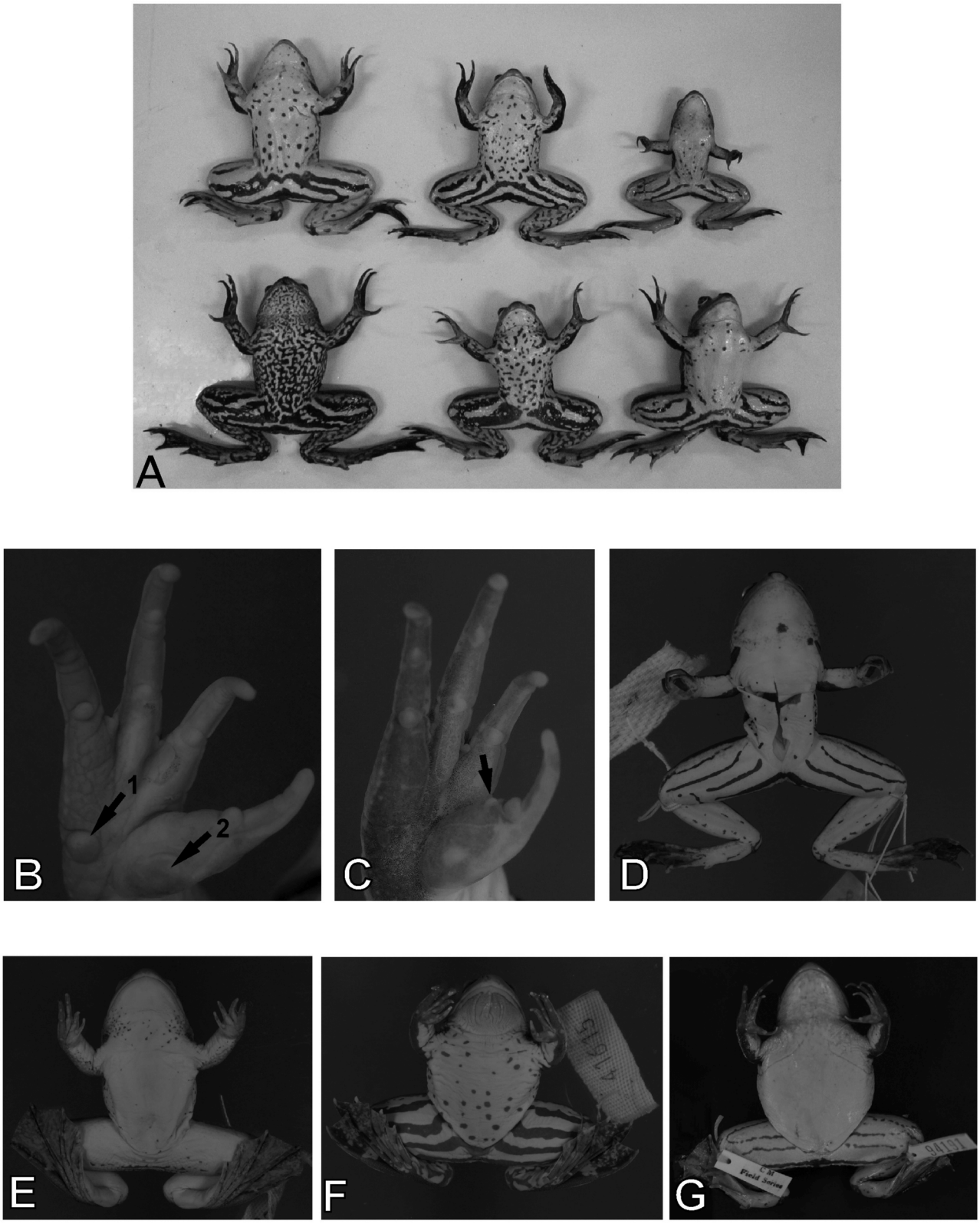

FIGURE 3. Ventral patterns of longitudinal stripes on the thigh and tubercles used in the present study. A—Ventral pattern variation in frogs collected in the same pond in Corumbá, Mato Grosso do Sul, Brazil; B—Hand of *P. paradoxa* from Presidente Hayes, Paraguay, showing the palmar tubercle (1) and the thenar tubercle (2); C—Hand of *P. fusca* from Linhares (Espírito Santo, Brazil) showing the supernumerary tubercle on the thumb characteristic of this species; D—three longitudinal stripes on the thigh of *P. bolbodactyla* from Quirinópolis (Goiás, Brazil). E–G—Ventral pattern variation in *P. paradoxa* from Pacaraima (Roraima, Brazil), Humaitá (Amazonas, Brazil), and Boqueron (Filadelfia, Paraguay).

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Pointed tubercles are also present in both *P. minuta* and *P. cardosoi*, especially in larger individuals. Skin texture was sometimes absent from museum specimens, but this was usually associated with inappropriate fixation (too much or not enough formalin). Supernumerary tubercles on the thumb were characteristic of *P. fusca*, *P. minuta*, and *P. cardosoi*. Two swollen areas, usually white in coloration, were observed flanking the cloaca in large, reproductive *P. minuta* and *P. cardosoi* females.

Morphometry

Minimum and maximum size of reproductive individuals varied considerably among and within species. *Lysapsus* species reach maturity at similar sizes, regardless of the population or the species under consideration, although *L. laevis* has a tendency to be larger and *L. caraya* to be smaller (Table 3). In contrast, reproductive *P. paradoxa* are larger, on average, than any other species (Table 3) but vary depending on the population considered (Fig. 2). Reproductive male *P. paradoxa* SVL averaged 39.11 ± 3.34 mm (range 34.03–45.57, N = 10) in Boa Vista (Roraima, Brazil), 59.03 ± 5.74 mm (range 49.10–71.86, N = 25) in Tartarugalzinho (Amapá, Brazil), and 63.91 ± 4.47 mm (range 55.83–71.74, N = 14) in Pinheiro (Maranhão, Brazil). In contrast, males averaged 49.99 ± 3.76 mm (range 41.29–57.28, N = 16) SVL in Corumbá (Mato Grosso do Sul, Brazil), but showed no sign of reproductive maturity, either externally or internally. A similar pattern of size variation was observed in *P. bolbodactyla* and *P. tocantins*. Reproductive male *P. tocantins* averaged 43.60 ± 1.51 mm (range 40.11–45.76, N = 14) in Britânia, (Goiás, Brazil), while one reproductive male collected in Formoso do Araguaia (Tocantins, Brazil) had a SVL of 61.24 mm. In Alvorada do Norte (Goiás, Brazil), male *P. bolbodactyla* averaged 33.82 ± 3.09 (range 30.11–39.52, N = 23), while in Buritizeiro (Minas Gerais, Brazil) males averaged 43.80 ± 2.66 mm (range 39.04–49.63, N = 19). Similar size discrepancies were also observed in *P. minuta* and *P. cardosoi*. Populations of *P. minuta* in Caçapava do Sul (Rio Grande do Sul, Brazil) are much larger than those in the vicinities of Porto Alegre (Rio Grande do Sul, Brazil). Likewise, populations of *P. cardosoi* in São Francisco de Paula (Rio Grande do Sul, Brazil) are larger than those in Jaquirana (Rio Grande do Sul, Brazil).

TABLE 3. Summary of morphometric measurements of sexually mature Pseudae species. Means are in millimeters followed by their corresponding standard deviations and ranges. Abbreviations: SVL–snout-vent length; CS–Commissure-snout length; HW—head width; TD—tympanum diameter; ED—eye diameter; EN—eye-nostril distance; SL—snout length; EIII—elbow-finger III length; HaL—hand length; TL—tibia length; FL—foot length; SW—thigh stripe width; ThL—thenar tubercle length; PD—palmar tubercle diameter; TaL—tarsal tubercle length.

Species/Sex (**N**)	SVL	CS	HW	TD	ED	EN	SL
L. caraya ♀ (**9**)	19.6 ± 1.2 18.0–21.9	6.6 ± 0.3 6.1–7.0	7.1 ± 0.3 6.7–7.6	1.7 ± 0.2 1.5–2.0	2.7 ± 0.17 2.5–2.9	1.5 ± 0.1 1.5–1.6	2.7 ± 0.2 2.4–2.8
L. caraya ♂ (**11**)	17.4 ± 0.7 16.1–19.1	5.8 ± 0.4 5.2–6.7	6.3 ± 0.3 6.0–7.0	1.5 ± 0.1 1.4–1.7	2.4 ± 0.1 2.2–2.6	1.4 ± 0.1 1.3–1.6	2.5 ± 0.1 2.3–2.6
L. laevis ♀ (**31**)	20.4 ± 1.5 17.2–23.9	7.0 ± 0.5 6.4–8.0	7.3 ± 0.5 6.4–8.2	1.8 ± 0.2 1.5–2.3	2.9 ± 0.2 2.5–3.4	1.6 ± 0.1 1.4–2.0	2.9 ± 0.2 2.5–3.4
L. laevis ♂ (**36**)	18.9 ± 1.1 16.6–21.0	6.6 ± 0.4 5.9–7.4	6.9 ± 0.4 6.1–8.06	1.7 ± 0.2 1.3–2.1	2.8 ± 0.2 2.5–3.2	1.5 ± 0.1 1.3–1.7	2.7 ± 0.2 2.3–3.1
L. limellum ♀ (**172**)	19.7 ± 1.7 16.2–24.8	6.8 ± 0.5 5.4–8.9	7.2 ± 0.6 5.6–9.3	1.8 ± 0.2 1.3–2.4	2.8 ± 0.23 2.2–3.4	1.7 ± 0.2 1.2–2.2	2.8 ± 0.3 2.3–3.4
L. limellum ♂ (**141**)	17.9 ± 1.1 15.2–21.0	6.3 ± 0.4 5.1–7.5	6.5 ± 0.4 5.4–7.7	1.7 ± 0.2 1.2–2.2	2.6 ± 0.2 2.1–3.2	1.5 ± 0.1 1–1.8	2.6 ± 0.2 2.0–3.4
P. cardosoi ♀ (**9**)	45.4 ± 7.2 34.9–54.7	15.0 ± 2.1 11.6–17.7	16.6 ± 2.3 13.3–19.3	3.8 ± 0.6 2.9–4.5	5.5 ± 0.7 4.3–6.8	3.0 ± 0.6 2.2–3.9	5.9 ± 0.9 4.5–7.0
P. cardosoi ♂ (**8**)	41.4 ± 3.6 34.0–45.4	14.1 ± 1.0 12.0–15.	15.3 ± 1.0 13.1–16.2	3.2 ± 0.4 2.6–3.7	5.4 ± 0.4 4.7–5.9	2.6 ± 0.3 2.1–2.9	5.5 ± 0.5 4.5–6.1

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TABLE 3. (continued)

Species/Sex (**N**)	SVL	CS	HW	TD	ED	EN	SL
P. minuta ♀ (**23**)	43.0 ± 5.1 35.0–51.6	14.1 ± 1.7 11.2–17.0	15.8 ± 2.0 12.6–19.3	3.9 ± 0.6 2.5–5.1	5.2 ± 0.5 4.4–6.2	2.8 ± 0.3 2.4–3.6	5.6 ± 0. 6 4.7–6.6
P. minuta ♂ (**73**)	32.7 ± 4.4 20.0–41.0	10.9 ± 1.3 7.6–13.8	12.4 ± 1.5 8.6–16.7	3.0 ± 0.4 2.0–4.3	4.6 ± 0.5 3.5–5.5	2.3 ± 0.3 1.6–3.0	4.5 ± 0.5 3.1–6.0
P. bolbodactyla ♀ (**59**)	44.6 ± 3.2 40.1–52.9	14.5 ± 0.9 13.0–17.6	16.2 ± 1.0 14.6–19.3	3.4 ± 0.5 2.3–4.1	5.7 ± 0.5 4.5–6.7	3.1 ± 0.35 2.5–3.9	5.7 ± 0.5 4.8–6.8
P. bolbodactyla ♂ (**107**)	38.0 ± 4.2 32.3–49.6	12.8 ± 1.1 10.8–15.8	14.2 ± 1.3 11.8–17.5	3.0 ± 0.5 1.9–4.2	5.2 ± 0.5 4.0–6.7	2.6 ± 0.3 2.0–3.7	5.0 ± 0.5 3.7–6.3
P. fusca ♀ (**14**)	40.8 ± 3.7 33.7–48.3	14.5 ± 1.6 11.2–17.6	16.1 ± 1.7 13.2–19.7	3.0 ± 0.5 1.9–3.7	5.5 ± 0.6 4.4–6.3	2.8 ± 0.4 2.2–3.8	5.3 ± 0.6 4.1–6.5
P. fusca ♂ (**20**)	38.5 ± 3.5 33.9–48.0	13.0 ± 1.4 11.2–16.5	14.5 ± 1.41 12.9–18.5	2.8 ± 0.5 2.0–3.9	5.1 ± 0.6 3.8–6.0	2.7 ± 0.4 2.0–4.0	4.9 ± 0.5 4.2–6.3
P. paradoxa ♀ (**128**)	52.6 ± 8.8 38.2–76.4	17.5 ± 2.7 11.4 –24.8	19.6 ± 3.2 13.9–28.6	3.9 ± 0.7 2.2–5.4, **126***	6.6 ± 0.8 4.9–8.6	3.9 ± 0.7 2.6–5.7	7.2 ± 1.3 4.8–10.2
P. paradoxa ♂ (**157**)	51.9 ± 8.0 34.0–71.9	17.2 ± 2.4 11.8–23.7	19.4 ± 3.0 12.7–27.0	3.9 ± 0.6 2.3–6.4	6.5 ± 0.7 4.7–8.1	3.7 ± 0.6 2.5–5.6	7.0 ± 1.2 4.5–10.8
P. tocantins ♀ (**17**)	55.3 ± 7.0 54.4–65.9	19.1 ± 2.2 15.5–22.8	20.9 ± 2.7 17.2–25.4	4.2 ± 0.5 3.1–4.8	7.1 ± 0.9 5.8–8.7	4.4 ± 0.5 3.5–5.2	7.8 ± 1.0 6.5–9.3
P. tocantins ♂ (**24**)	46.1 ± 4.9 37.9–61.3	16.0 ± 1.4 13.5–19.4	17.2 ± 1.9 14.6–22.1	3.6 ± 0.5 5.0–3.6	6.1 ± 0.5 5.3–7.1	3.6 ± 0.5 3.0–4.9	6.4 ± 0.7 5.4–8.3

Continued.

Species	EIII	HaL	TL	FL	SW	ThL	PD	TaL
L. caraya ♀ (**9**)	11.5 ± 0.5 10.6–12.1	7.3 ± 0.5 6.7–8.2	12.9 ± 0.9 11.6–14.2	17.5 ± 1.0 15.9–18.7	—	—	—	—
L. caraya ♂ (**11**)	10.2 ± 0.8 9.2–11.8	6.4 ± 0.4 5.7–7.0	11.8 ± 1.0 10.3–13.2	15.8 ± 1.4 13.6–17.7	—	—	—	—
L. laevis ♀ (**31**)	0.9 ± 0.7 9.5–12.5	6.9 ± 0.5 6.3–8.2	12.0 ± 0.7 10.9–13.4	16.4 ± 1.1 14.5–18.6	—	—	—	—
L. laevis ♂ (**36**)	10.1 ± 0.6 9.1–11.1	6.5 ± 0.5 5.4–7.4	11.2 ± 0.7 9.4–12.3	15.1 ± 1.0 12.9–17.0	—	—	—	—
L. limellum ♀ (**172**)	10.9 ± 1.0 8.6–13.5	6.9 ± 0.7 5.4–8.9	12.8 ± 1.0 10.7–15.9	16.7 ± 1.5 13.9–20.9	—	—	—	—
L. limellum ♂ (**141**)	9.8 ± 0.7 7.8–11.1	6.2 ± 0.5 4.7–7.9	11.5 ± 0.7 9.8–13.4	15.1 ± 1.1 12.5–18.5	—	—	—	—
P. cardosoi ♀ (**9**)	22.1 ± 2.9 17.1–25.7 8	13.3 ± 1. 9 10.0–16.1 8	21.7 ± 2.8 16.8–24.4	32.9 ± 3.7 25.6–37.4	0.5 ± 0.14 0.3–0.6, **3**	2.5 ± 0.4 1.7–3.1	—	1.6 ± 0.3 1.0 –1.8
P. cardosoi ♂ (**8**)	21.2 ± 1.8 18.4–22.7 6	13.3 ± 1.2 11.1–14.3 6	21.5 ± 1.5 18.1–22.8	32.3 ± 2.1 27.8–34.2	0.3 1	2.7 ± 0.5 1.8–3.2	—	1.6 ± 0.3 1.3–2.0
P. minuta ♀ (**23**)	21.4 ± 2.4 17.6–25.4 22	13.8 ± 1.5 11.6–16.7 22	23.6 ± 2.9 17.0–28.8	34.2 ± 3.7 27.1–40.8	0.9 ± 0.4 0.4–1.7 15	1.7 ± 0.6 0.8–2.8	0.5 ± 0.1 0.3–0.8 22	1.1 ± 0.3 0.5–1.8
P. minuta ♂ (**73**)	17.2 ± 2.0 12.0–20.9 72	11.1 ± 1.3 7.1–13.7 72	18.4 ± 2.3 12.5–23.0	27.2 ± 3.1 19.0–33.3	1.0 ± 0.3 0.2–1.9 65	1.8 ± 0.5 0.5–2.9 72	0.6 ± 0.2 0.3–1.3 69	1 .1 6 ± 0.31 0.5–1.8
P. bolbodactyla ♀ (**59**)	22.4 ± 1.4 19.2–25.9 54	14.2 ± 1.0 12.1–16.7 55	24.9 ± 2.0 21.4–29.5	35.7 ± 2.4 31.8–41.0	1.2 ± 0.5 0.5–2.8	2.2 ± 0.4 0.8–3.0 55	0.8 ± 0.3 0.4–1.9 56	2.4 ± 0.5 1.0–3.4

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TABLE 3. (continued)

Species	EIII	HaL	TL	FL	SW	ThL	PD	TaL
P. bolbodactyla ♂ (**107**)	19.9 ± 1.8 16.1–24.5 105	12.7 ± 1.2 9.9–15.8 105	21.8 ± 2.3 17.4–28.3	31.6 ± 3.3 25.0–40.1	1.2 ± 0.4 0.7–2.3 59	1.9 ± 0.5 0.9–2.9 54	0.8 ± 0.2 0.4–1.4 52	2.4 ± 0.4 1.4–3.3 60
P. fusca ♀ (**14**)	21.6 ± 1.9 19.2–24.7	13.6 ± 1.4 11.7–16.0	23.6 ± 2.0 20.9–26.8	32.6 ± 2.8 28.0–37.0	0.8 ± 0.3 0.4–1.2 4	2.4 ± 0.4 1.6–2.9	0.7 ± 0.2 0.6–1.2	2.3 ± 0.4 1.8–3.2
P. fusca ♂ (**20**)	19.6 ± 1.9 16.9–24.4	12.3 ± 1.3 10.9–15.7	21.7 ± 2.1 18.9–27.2	29.7 ± 2.97 25.9–36.7	0.9 ± 0.3 0.6–1.3, **5**	2.3 ± 0.4 1.5–3.0	0.7 ± 0.1 0.5–1.0	2.2 ± 0.3 1.5–2.8
P. paradoxa ♀ (**128**)	26.9 ± 4.8 19.2–40.6 97	17.2 ± 2.9 12. 5–24.7 107	29.0 ± 5.0 19.5–41.9 127	40.9 ± 7.8 26.1–59.51, **127**	1.4 ± 0.3 0.9–2.0	2.9 ± 0.7 1.1–4.7 127	1.4 ± 0.4 0.15–2.35 125	4.2 ± 1.2 1.5–6.8
P. paradoxa ♂ (**165**)	27.8 ± 5.1 17.7–39.7 138	17.5 ± 3.1 11.2–26.3 141	28.3 ± 5.1 16.4–40.9	40.4 ± 8.6 23.9–61.4	2.6 ± 0.7 2.0–6.0 40	3.0 ± 0.5 1.7–4.7 156	1.5 ± 0.4 0.7–2.7 156	4.2 ± 1.0 2.1–6.5
P. tocantins ♀ (**17**)	29.0 ± 3.7 23.3–34.6	14.0 ± 2.3 14.0–22.3	39.6 ± 5.7 27.0–38.0	49.13 ± 5.65 39.6–57.0	0.8 ± 0.3 0.4–1.3	3.2 ± 0.5 2.32 –4.0	0.9 ± 0.3 0.5–1.4	3.1 ± 0.4 2.4–3.9
P. tocantins ♂ (**24**)	24.1 ± 2.8 20.5–32.7 21	15.3 ± 1.9 15.7–20.7 21	27.0 ± 3.3 22.4–37.7	39.1 ± 4.7 31.3–52.7	0.6 ± 0.2 0.3–0.2 22	2.6 ± 0.4 1.7–3.7	0.8 ± 0.2 0.5–1.5	2.7 ± 0.4 2.0–3.8

* Bold numbers after ranges indicate sample sizes different from the values listed after the species name.

TABLE 4. Discriminant function analysis of $\log_{10}$-transformed morphometric variables among genera of Pseudae.

	Canonical statistics			
Function	Eigenvalue	Cumulative proportions	C	P
1	10.95	0.96	13.57	<0.0001
2	0.40	1.00	4.02	<0.0001

	Raw canonical coefficients	
Variable	Function 1	Function 2
Snout-vent length	8.66	1.26
Commissure-snout length	-8.20	-19.55
Head width	-19.94	21.20
Tympanum diameter	3.33	9.10
Eye diameter	-12.26	-2.63
Eye-nostril distance	4.14	-15.66
Snout length	8.07	12.12
Elbow-Finger III length	-2.08	-17.26
Hand length	3.16	8.13
Tibia length	27.94	-21.43
Foot length	-21.72	19.50
	Canonical scores of group means	
Genus	Canonical variable 1	Canonical variable 2
Lysapsus	4.11	-0.11
P. minuta	-1.33	1.73
Pseudis	-2.89	-0.31

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TABLE 5. Classification matrices based on the discriminant functions described in Table 4, using full and jackknifed datasets.

	Lysapsus	*minuta*	*Pseudis*	%correct
Lysapsus	432	2	0	100
Pseudis minuta	1	113	15	88
Pseudis	0	68	489	88
Total	433	183	504	92
Jackknifed classification matrix				
Lysapsus	432	2	0	100
Pseudis minuta	1	112	16	87
Pseudis	0	73	484	87
Total	433	187	500	92

TABLE 6. Discriminant function analysis of $\log_{10}$-transformed morphometric variables among the three species of *Lysapsus*.

	Canonical statistics			
Function	Eigen-value	Cumulative proportions	C	*P*
1	0.68	0.70	6.24	<0.0001
2	0.29	1.00	-12.89	<0.0001
		Raw canonical coefficients		
Variable		Function 1	Function 2	
Snout-vent length		8.74	6.13	
Commissure-snout length		12.83	-18.05	
Head width		.	.	
Tympanum diameter		.	.	
Eye diameter		12.05	-8.69	
Eye-nostril distance		-5.04	-15.52	
Snout length		12.52	1.55	
Elbow-finger III length		2.46	31.99	
Hand length		9.01	4.34	
Tibia length		-48.70	-39.97	
Foot length		4.48	27.52	
		Canonical scores of group means		
Species		Canonical variable 1	Canonical variable 2	
caraya		-1.23	1.98	
laevis		1.82	0.34	
limellum		-0.28	-0.22	

The discriminant function based on the 11 variables measured in all specimens efficiently separated *Lysapsus* from *Pseudis* (Tables 4,5; Figs. 5A). The separation produced by the first discriminant function is explained mostly by a contrast between tibia length and a combination of foot length and head width. The group mean for *Lysapsus* is positive, characterizing it as having larger tibias, shorter feet, and narrower heads (relative to SVL) compared to *Pseudis* (Table 4). The second discriminant function, which accounted for the separation between *P. minuta* and *Pseudis*, is an interaction between four variables, foot length and head width contrasting with commissure-snout length and tibia length (Table 4). A DFA involving only *Lysapsus* species

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TABLE 7. Classification matrices based on the discriminant functions described in Table 6, using full and jackknifed datasets.

	caraya	*laevis*	*limellum*	%correct
caraya	25	1	0	96
laevis	1	62	6	90
limellum	46	41	252	74
Total	72	104	258	78
Jackknifed Classification Matrix				
caraya	23	2	1	88
laevis	1	9	9	86
limellum	47	45	247	73
Total	71	106	257	76

TABLE 8. Discriminant function analysis of $\log_{10}$-transformed morphometric variables among species of *Pseudis*.

	Canonical statistics			
Function	Eigen-value	Cumulative proportions	C	P
1	5.57	0.76	-10.02	<0.001
2	0.87	0.88	-7.24	<0.001
		Raw canonical coefficients		
Variable		Function 1		Function 2
Snout-vent length		0.40		2.67
Commissure-snout length		-0.56		-1.88
Head width		0.69		0.14
Tympanum diameter		-0.11		-0.02
Eye diameter		-0.32		-0.44
Eye-nostril distance		-0.58		-0.26
Snout length		0.51		-0.76
Elbow-finger III length		-1.32		0.01
Hand length		0.59		-0.73
Tibia length		0.41		0.63
Foot length		0.88		0.01
Thenar tubercle length		0.18		-0.63
Palmar tubercle length		-0.10		0.33
Metatarsal tubercle		-1.43		0.62
		Canonical scores of group means		
Species		Variable 1		Variable 2
bolbodactyla		0.10		0.83
fusca		0.47		0.21
minuta		4.18		-0.00
paradoxa		-2.68		0.05
tocantins		-0.03		-2.22

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did not produce consistent results (Tables 6,7; Fig. 5B), as evidenced by the fluctuations in the classification success in the jackknifed data set (Table 7). The DFA considered the contributions of head width and tympanum diameter not significant, so these variables were dropped from the analysis (Table 6). Tibia length exerts the most influence on the first discriminant function, characterizing *L. laevis* as having a shorter tibia compared to *L. caraya* and *L. limellum* (Table 6). The second discriminant function represents a contrast between tibia length and a combination of foot and elbow-finger III length, and indicates that *L. caraya* has larger arms and feet compared to *L. limellum*.

The DFA involving only *Pseudis* and including the 14 variables measured for these species consistently separated *P. minuta* from other species (Tables 8,9, Fig. 5C). Results were also consistent for *P. tocantins* and *P. paradoxa*, but considerably weak for *P. bolbodactyla*, and especially problematic for *P. fusca* (Table 9). The two first discriminant functions accounted for 88% of the total morphological variation (Table 8). The first discriminant function represented the combined effect of size of the metatarsal tubercle and elbow-finger III length, characterizing *P. minuta* as having small values for both variables. *Pseudis bolbodactyla*, *P. fusca*, and *P. tocantins* had intermediate values for this function, whereas *P. paradoxa* had large values indicating a large elbow-finger III length and large tubercles (Table 8). Longer heads relative to overall body size (SVL) separated *P. tocantins* from the other species in the second discriminant function (Table 8).

TABLE 9. Classification matrices based on the discriminant functions described in Table 8, using full and jackknifed datasets.

	bolbodactyla	*fusca*	*minuta*	*paradoxa*	*tocantins*	%correct
bolbodactyla	182	18	2	2	13	84
fusca	5	31	0	0	1	84
minuta	2	0	126	0	0	98
paradoxa	10	4	0	191	9	89
tocantins	7	1	0	1	80	90
Total	206	54	128	194	103	89
Jackknifed classification matrix						
bolbodactyla	179	19	3	3	13	82
fusca	6	28	1	0	2	76
minuta	3	0	125	0	0	98
paradoxa	12	5	0	188	9	88
tocantins	7	1	0	1	80	90
Total	207	53	129	192	104	88

Discussion

Geographic distribution. Current knowledge of the geographic distribution of Pseudae species is substantially better than when Gallardo (1961) first suggested their close association with South American river basins. Amphibian faunal surveys and species lists for several countries are now available, such as those recently published Bolivia (de la Riva, 2000), Venezuela (Barrio-Amorós, 2004), and Uruguay (Núñez *et al.*, 2004). Because of its larger geographic area, a similar publication is not yet available for Brazil. This is especially relevant for Pseudae, because five of its species (*L. caraya*, *P. cardosoi*, *P. bolbodactyla*, *P. fusca*, and *P. tocantins*) are endemic to this country (Fig. 1).

Some common aspects of Pseudae species distributions are evident. All species occur in flooded areas where medium to long-lasting ponds are available for reproduction. Most species are tropical (except *P. cardosoi* and *P. minuta* in Southern Brazil, Uruguay, and northern Argentina) and do not occur in altitudes above 800 m (the exception is *P. cardosoi* in Rio Grande do Sul and Santa Catarina States, reaching altitudes

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above 1000 m). Because of the need for large ponds, species most likely do not occur inside closed-canopy forests. *Lysapsus limellum*, however, is sometimes found in ponds within forested areas, but usually the canopy over such ponds is open. Most populations of *Pseudis* in central Brazil are found along the floodplains of large rivers. Areas where rivers change direction abruptly or where tributaries join large rivers tend to have several lakes, which commonly harbor *Pseudis* populations. Smaller populations are found upstream in smaller tributaries (in regions of southern Goiás, for example, *P. bolbodactyla* is easily found in man-made ponds) creating a typical metapopulation structure where the source is along major rivers and flood plains.

Another common pattern throughout South America, is the co-occurrence of *Lysapsus* and *Pseudis*. Species of these two genera co-occur in the Pantanal (Mato Grosso and Mato Grosso do Sul States, Brazil), in floodplains along the Pilcomayo River, in the Rupununi Savanna in Guyana and Brazil, in the Araguaia River, and in Amapá State (Brazil). Nevertheless, most localities currently have only one species of each of these genera (Fig. 1A,B). *Lysapsus* seems to be closely associated with regions where large, long-lasting floodplains are available (Garda *et al*., 2007). In fact, this genus is absent from most of central Brazil, where *Pseudis* are widespread and large floodplains are lacking. In this region it is only found along the Araguaia River, where the second largest wetland in Brazil is found. *Pseudis*, on the other hand, is present at east and west Amazon River sites, but is absent from intervening sites, where *L. limellum* is abundant (Garda *et al*., 2007).

The one basin–one species hypothesis of Gallardo (1961) is an oversimplification, resulting from the few localities for which samples were available at the time he reviewed the group. *Pseudis paradoxa*, for example, clearly does not follow this pattern, even if we consider only one of the subspecies he proposed, *P. p. paradoxa*. This taxon occurs from Guyana through Maranhão (Brazil) in Eastern South America to central Bolivia and central Brazil (Fig. 1). It is therefore widespread and not restricted to one hydrographic basin. *Pseudis bolbodactyla*, *P. fusca*, and *L. limellum* also occur in more than one river basin, not corroborating Gallardo's (1961) generalization. *Pseudis tocantins* occurs in the Tocantins-Araguaia basin and in the upper Xingu River Basin. The southern limit of its distribution on the Tocantins River is the Brazilian Central Plateau and the Paranã River Valley (where *P. bolbodactyla* occurs). *Pseudis fusca*, formerly considered to be restricted to the vicinities of the type locality in Araçuaí, Minas Gerais State (Caramaschi & Cruz, 1998), is widespread from southern Bahia to Southern Espírito Santo in rivers east of the Espinhaço Range (Jequitinhonha, Mucuri, and Doce).

In Brazil, the lack of Pseudae from the northeast region is most likely due to the semi-arid climate in the region (Fig. 1A,B). Also, for some reason, these species are absent from the Paraíba do Sul River. Along the Amazon Basin, large river basins with Terra Firme forests also commonly lack Pseudae species. Hence, historical, geological, and phylogenetic constraints should be considered to fully understand the distribution of these frogs. The best-surveyed area in Brazil for Pseudae is the state of São Paulo, where the species is becoming increasingly rare because of habitat destruction, river damming, and mechanized agriculture (Denise Rossa-Feres, pers. comm.). *Pseudis bolbodactyla* has an interesting distribution, occurring in three large hydrographic basins. It is the only *Pseudis* in the São Francisco River Basin, while sharing (although not syntopically) the Tocantins River Basin (Paranã valley) with *P. tocantins* and the Paraná River basin (Paranaíba River) with *P. paradoxa*. The northeast distribution of *P. paradoxa* seems limited by the Grande River, on the border of São Paulo and Minas Gerais states (Fig. 1B), separating it from *P. bolbodactyla* to the North.

External morphology characters. Extensive variation in color pattern in Pseudae frogs renders such characters almost useless for identification purposes. With the exception of *P. tocantins*, most populations of *Pseudis* showed patterns that were more representative of the local population than of the species. The ventral pattern of longitudinal stripes on the thigh was the main character used by Gallardo (1961) to divide the group into multiple subspecies of *P. paradoxa*. Why he regarded these taxa as subspecies rather than species is not clear, but the differences he described are not consistent even within the subspecies he designated. Ventral patterns of longitudinal stripes are known to vary within populations to such a degree that individual identification is possible (Miranda *et al*., 2005). Nevertheless, some species are characterized by specific and geographically consistent patterns, as is the case with *P. tocantins*, *P. bolbodactyla*, and *P. minuta* (Table 2).

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The number of stripes in *P. bolbodactyla* is more invariable than in *P. paradoxa*, for example, while stripes in *P. tocantins* are thinner than in any other species (Caramaschi & Cruz, 1998). The lack of stripes in *P. fusca*, however, is due to sampling bias because until this paper only a few frogs from the middle Jequitinhonha basin were considered as *P. fusca* (Caramaschi & Cruz, 1998). Other populations from the middle Jequitinhonha and other populations east of the Espinhaço range have stripes on the thighs.

In total, 21 external morphology characters have been used among the nine papers dealing with species descriptions and taxonomy of Pseudae (Appendix I). Some characters used in previous publications vary with body condition, size, and state of formalin fixation. Supratympanic folds, suggested by Gallardo (1961), were present in some individuals, especially large ones (*P. paradoxa* and *P. tocantins* in Fig. 3A,I, for example), but were not consistently found in any species (Fig. 3C,H, same species but lack the fold). Klappenbach (1985) also noted that this character occurred intermittently and was of little use for species diagnosis. The shape of the metatarsal tubercle, suggested by Gallardo (1961) to distinguish *Pseudis* subspecies, was influenced by the position of the foot when the specimen was fixed (well-fixed specimens usually have the metatarsal tubercle compressed under the foot), and also body size.

Terminal discs on the hands and feet also varied intraspecifically. This character was used in several species descriptions and revisions of the group (Klappenbach, 1985; Kwet, 2000; Miranda-Ribeiro, 1926; Savage & de Carvalho, 1953), but an interpopulation-level assessment of its variation was never conducted. *Pseudis minuta*, for example, was reported as lacking expanded discs (Miranda-Ribeiro, 1926), as well as having them (Kwet, 2000). *Lysapsus* has well developed discs (Cope, 1862b; Savage & de Carvalho, 1953), but conspicuous discs are usually observable only in large individuals. In *Pseudis,* discs are absent, but some specimens have considerably expanded discs. Similar to the supratympanic fold, the sizes of lines on the ventral surface of the thighs seem to vary with body size to such a degree that interespecific comparisons are difficult.

Supernumerary tubercles on the thumb were depicted by Kwet (2000) as representative of *P. minuta* and *P. cardosoi*, but were overlooked in the resurrection of *P. fusca* (Caramaschi & Cruz, 1998). Caramaschi and da Cruz (1998) considered *P. fusca* restricted to the upper Jequitinhonha River and referred to populations in southeast Bahia, Espírito Santo, and along the Doce River in Minas Gerais and Espírito Santo as *P. bolbodactyla* based on the presence of longitudinal stripes on the thighs (such stripes were absent in populations along the Jequitinhonha). Supernumerary tubercles are present in all *Pseudis* east of the Serra do Espinhaço (Minas Gerais, Brazil). This suggests that these populations constitute one or more closely related species, distinct from *P. bolbodactyla*, given the general variability of stripes on the thighs in most species and its constancy in *P. bolbodactyla*. We therefore consider populations east of the Espinhaço as *P. fusca*. Other characters used in previous works are also useful and corroborated by the present assessment. These include skin texture (distinguishes *P. bolbodactyla* from *P. paradoxa* and *L. limellum* and *L. caraya* from *L. laevis*), number of metatarsal tubercles (distinguishes *Pseudis*, with one, from *Lysapsus*, with two), and size of carpal tubercles(distinguishes *P. paradoxa* from other *Pseudis*).

Size at maturity, geographic size variation, and tadpole gigantism. The highly variable size at maturity in *Pseudis* can be due to tadpole size at metamorphosis, post-metamorphic growth, or an interaction of these factors (Alford & Harris, 1988). Because post-metamorphic growth in *Pseudis* was recently shown to be nil or very limited (Downie *et al*., 2009; Fabrezi *et al*., 2009), the variability in size at maturity reported herein can be attributed primarily to differences in larval size at metamorphosis. Several ecological factors affect amphibian life histories by directly influencing neurohormonal processes that initiate the onset of metamorphosis (Wilbur & Collins, 1973). Variation in amphibian body size at metamorphosis is due to individual variation in growth rates in time and/or space within a given species or population (Wilbur & Collins, 1973). Constrains must exist that define minimum and maximum larval size at metamorphosis, especially in individuals that reproduce in ephemeral environments such as ponds (Collins, 1979).

For Pseudae, Roček *et al*. (2006) postulated that specific local ecological factors allowed larvae to grow to gigantic proportions, most notably the presence of very large temporary ponds with low densities of predators. For Roček *et al*. (2006) this suite of characters could account for the gigantic larvae found in the Chaco region (Dixon *et al*., 1995). In agreement with these expectations, all populations of *Pseudis* with large adult

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individuals collected by the authors of the present work were found in areas that fit the description of Roček *et al*. (2006). Large *P. paradoxa* were collected in Pinheiro (Maranhão, Brazil) along large floodplains of the Pericumã River, in the Brazilian Pantanal, and in Amapá (Brazil), which currently holds the record for the largest *Pseudis* tadpole collected (Bokermann, 1967). The habitat of large *P. tocantins* collected in Formoso do Araguaia (Tocantins, Brazil, Fig. 3I) is a rice field near Bananal Island, which is flooded during most of the year. Large flooded areas under the bridge that crosses the São Francisco River between the cities of Pirapora and Buritizeiro (Minas Gerais, Brazil) were the collection sites of the largest *P. bolbodactyla* (Fig. 3F). In contrast, the smallest *P. paradoxa* were collected in ponds near the city of Boa Vista (Roraima, Brazil, Fig. 3D), characterized by the poor sandy soils of the local savannas (Lavrados) and extremely ephemeral, small ponds. Likewise, small *P. bolbodactyla* were collected in small temporary ponds over sandy soils in Iaciara (Goiás, Brazil).

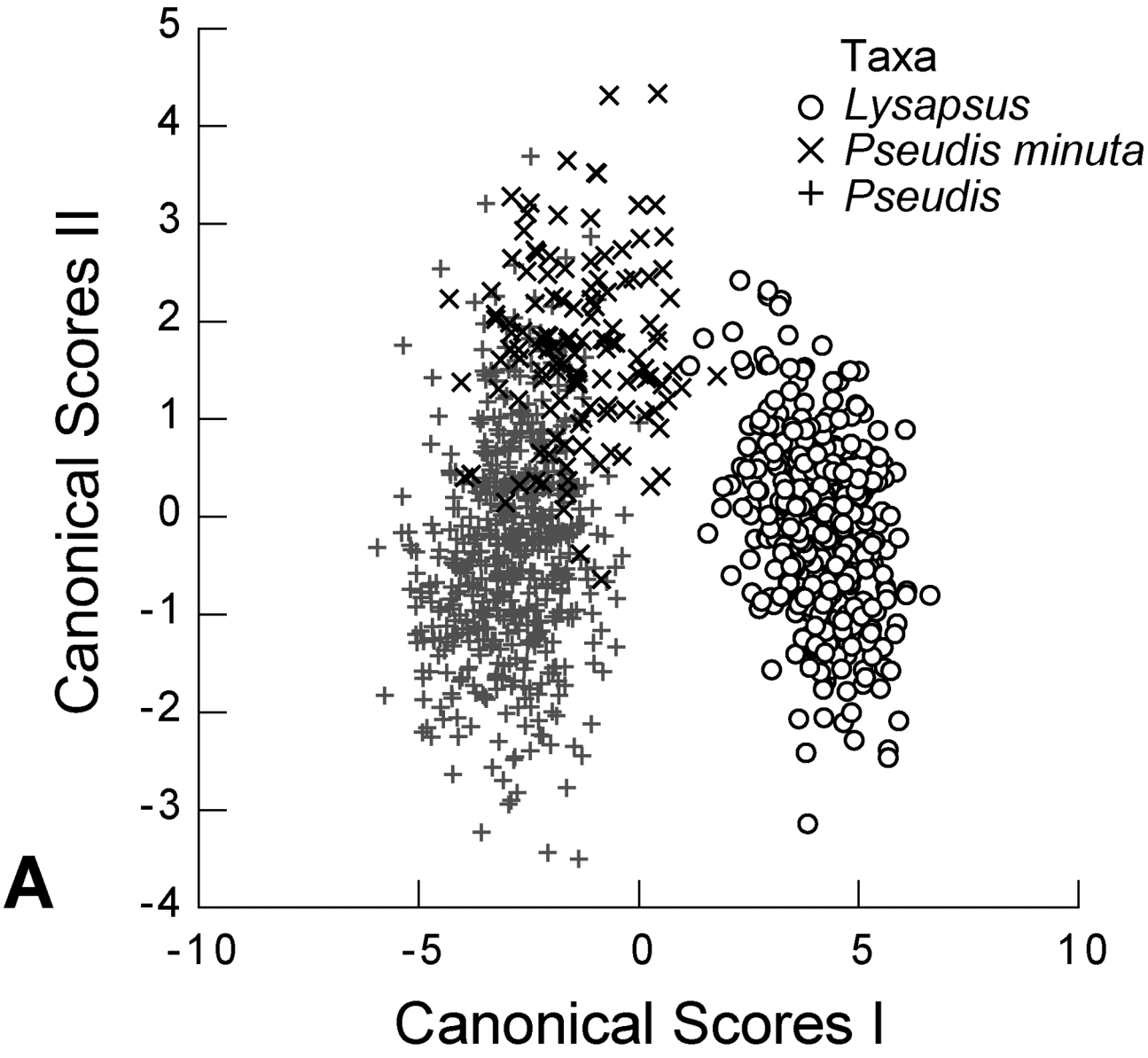

FIGURE 4A. Canonical plots of individual values for Discriminant Functions I and II for the two genera combined with *P. minuta* appart (A), for *Lysapsus* species (B), and for *Pseudis* species combined (C). Each dot represents one individual plotted according to its specific values for each discriminant function.

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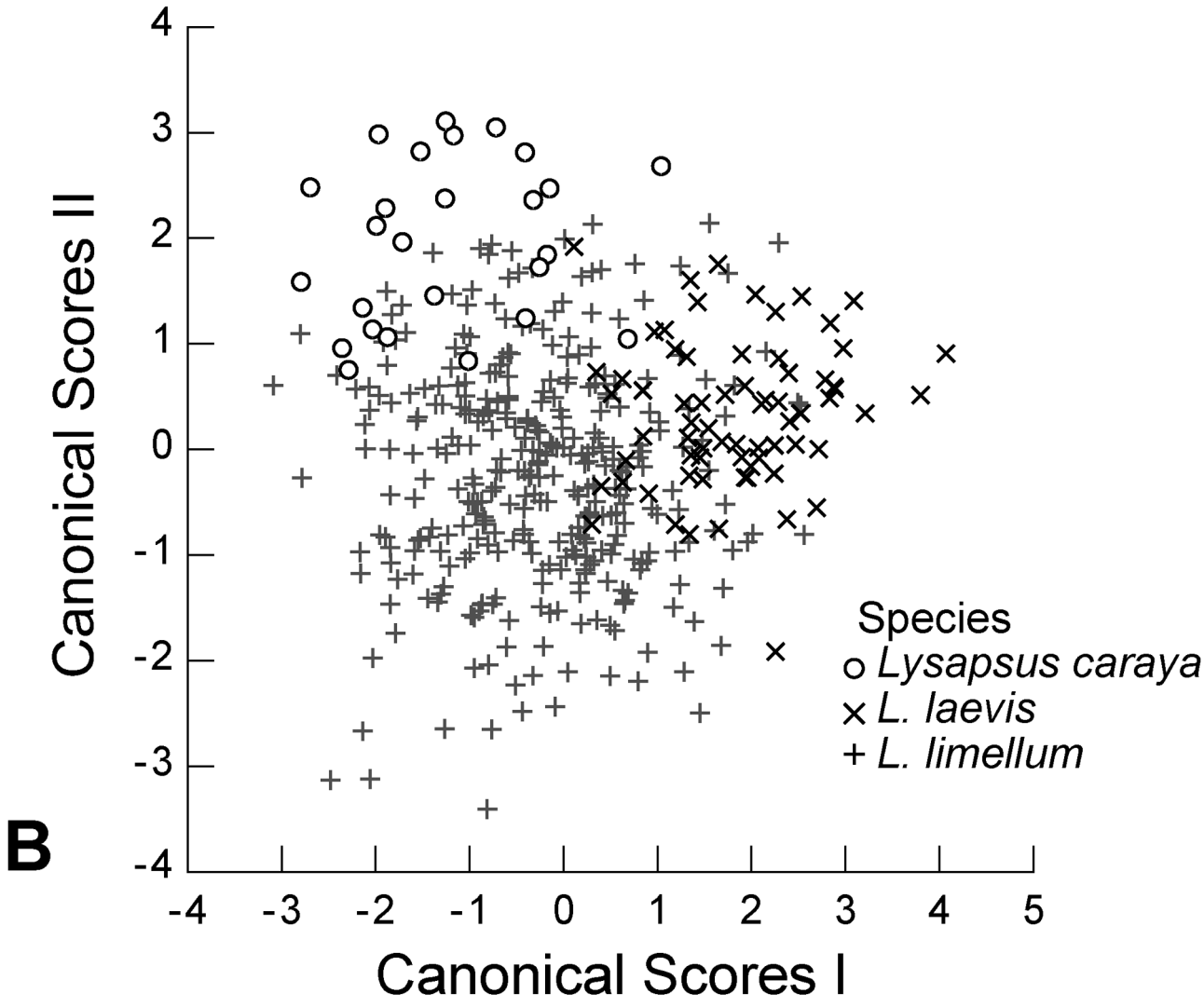

FIGURE 4B. Canonical plots of individual values for Discriminant Functions I and II for the two genera combined with *Lysapsus* species. Each dot represents one individual plotted according to its specific values for each discriminant function.

Although the above observations represent only circumstantial evidence that ecological factors are involved in larval gigantism, they do provide a foundation for future work. Controlled experiments focusing on factors that influence larval development in *Pseudis* would help to determine the proximate and ultimate causes of larval gigantism. The smaller larval sizes reported for *Pseudis* are within the upper limits reported for other species (Roček *et al*., 2006); however, the larger sizes far exceed sizes of other anurans (Emerson, 1988).

Morphometry and taxonomic implications. Several previously unreported shape differences among species were found with the morphometric analyses. Large elbow-finger III lengths and metatarsal tubercles characterize *P. paradoxa*, while *P. minuta* has small values for these measurements. *A proportionally larger tibia than Pseudis, as well as a narrower head and shorter feet characterize Lysapsus*. Along with other previous morphological differences differentiation *Pseudis* and *Lysapsus*, such as differences in the structure of the autopodia (Goldberg & Fabrezi, 2008), these morphometric variables further substantiate the recognition of both genera. *Pseudis tocantins* has a longer head than the remaining *Pseudis*, as already reported in its original description (Caramaschi & Cruz, 1998). *Pseudis fusca* and *P. bolbodactyla* are difficult to distinguish morphometrically, at least with the present small sample size for *P. fusca*, but head width does not seem to separate them, as was previously suggested (Caramaschi & Cruz, 1998). *Pseudis bolbodactyla*, *P.*

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fusca, and *P. tocantins* were grouped together based on the small or nearly absent palmar tubercle (Caramaschi & Cruz, 1998). Given the average measurement of this character for each species (Table 3), this is clearly not the case. The character can be useful, though, to separate some species. *Pseudis cardosoi* lacks this tubercle, at least in the small sample size we analyzed. *Pseudis paradoxa* has a significantly larger palmar tubercle than *P. bolbodactyla* (ANCOVA with SVL as a covariate, $p < 0.001$), which can help in its identification given their proximate distributions along the border of São Paulo and Minas Gerais states in Brazil (Fig. 1B). Nevertheless, a separate discriminant analyses with these two species (results not shown) still reveals elbow-finger III length and metatarsal tubercle as the best discriminators. Other previously reported morphometric characters used in species descriptions and comparisons were not significant in the present analysis. These include head size, body size (within genera), and size of tympanum. We did not measure the shape of foot and hand digits, but the difference seems to be related to robustness of larger frogs, as mentioned above.

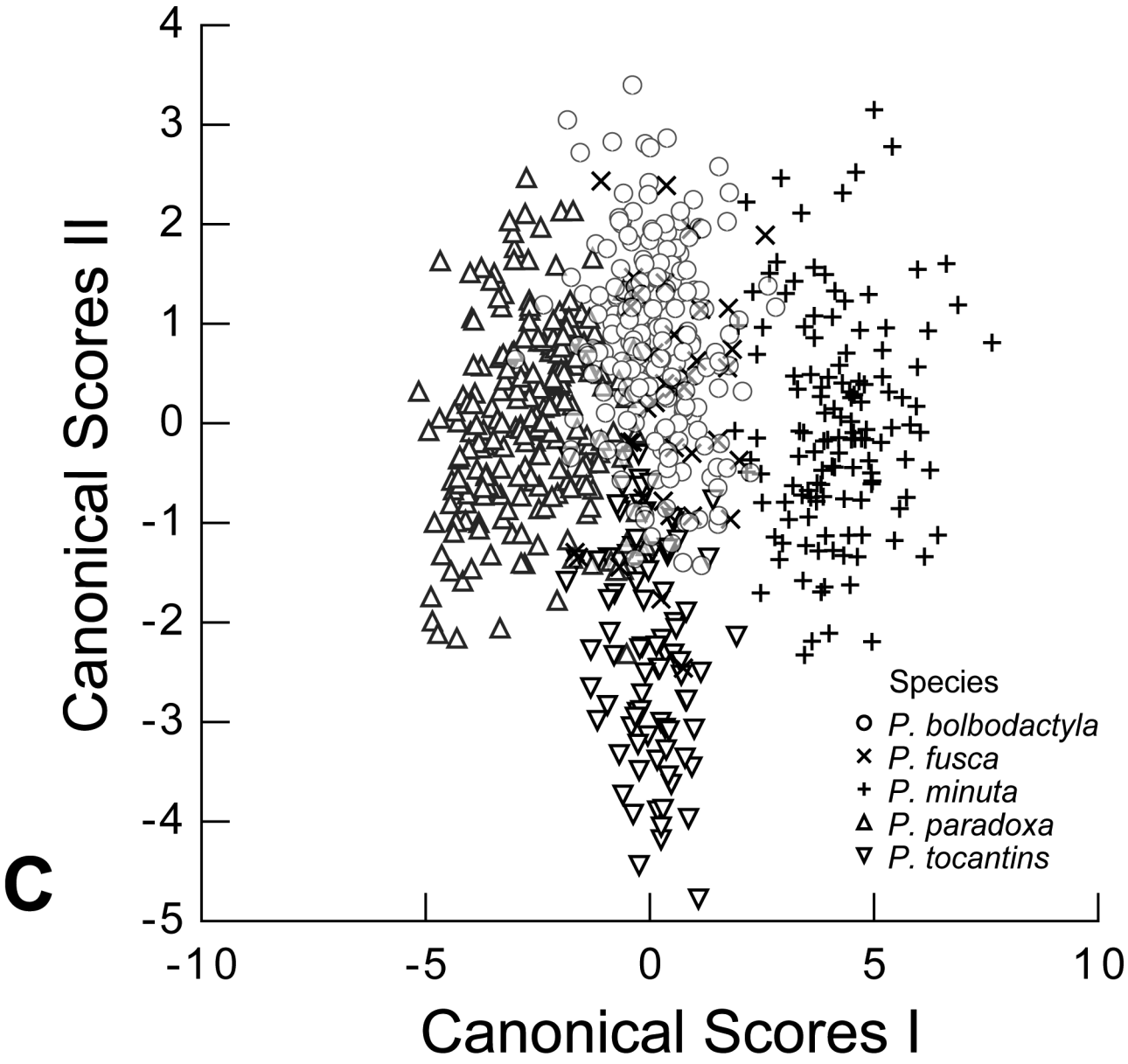

FIGURE 4C. Canonical plots of individual values for Discriminant Functions I and II for the two genera combined with *Pseudis* species. Each dot represents one individual plotted according to its specific values for each discriminant function.

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External morphology, coloration, and morphometric analyses did not provide diagnostic characters to separate the subspecies of *L. limellum* and *P. paradoxa*, which were recognized as full species by Aguiar *et al.* (2007). Although these taxa were not considered in the analyses presented herein, we ran several independent analyses using all subspecies available for these two species. Results were not consistent (resolutions and classification matrix stability were lower than the ones we present) and no distinguishing coloration or external morphology character was identified. To be sure, there is currently no character to substantiate the separation of these species. Cytogenetic analysis of *P. paradoxa paradoxa* and *P. paradoxa platensis* recovered identical karyotypes for these species (Busin *et al.*, 2008). Likewise, karyotypes of *L. limellum limellum* and *L. limellum bolivianus* were described as very similar (Busin *et al.*, 2006). Advertisement calls also do not vary among these subspecies pairs (Garda, unpublished data). Aguiar *et al.* (2007) mentioned some morphological differences noted by anuran specialists to substantiate the recognition of *L. bolivianus* and *P. platensis*, but unfortunately did not specify these characters. Gallardo (1961) based the subdivision of *P. paradoxa* mostly on the ventral coloration of the thighs, size, and supratympanic folds, which, as discussed above, are affected by body size. Likewise, most of the characters he proposed to diagnose *L. limellum bolivianus* (discs of feet, interdigital membrane, and black lines on ventral thigh) do not discriminate among frogs from different river basins (Gallardo, 1961).

Nevertheless, populations of *Pseudis* and *Lysapsus* from the Paraná and Amazon River Basins form reciprocally monophyletic mitochondrial DNA lineages (Aguiar *et al.*, 2007; Garda & Cannatella, 2007). Given the seemingly allopatric distributions of lineages, it is tempting to raise these subspecies to species. However, gender-biased patterns of migration are present in many frogs and inferences of population connectivity may be biased when using only mitochondrial markers (Austin *et al.*, 2003; Lampert *et al.*, 2003; Palo *et al.*, 2004). Therefore, a phylogeographic analysis employing nuclear markers with additional population sampling is needed to test if these populations represent different species. The headwaters of both river basins are only 100 km apart in western Brazil and western Bolivia, and likely a suitable route for migration, at least for *Pseudis*.

A similar situation exists for *P. minuta* and *P. cardosoi*. As discussed above, several of the characters used to describe *P. cardosoi* are affected by body size. *Pseudis cardosoi* occurs on top of the Serra Geral, in Rio Grande do Sul and Santa Catarina states in Brazil. Some areas of this plateau reach more than 1700 m above sea level, but in Rio Grande do Sul the plateau tappers south and west to lower altitudes, so the connection among populations of *Pseudis minuta* and *P. cardosoi* is possible. Furthermore, there is a low degree of genetic variation, as evidenced by the low support for these species and shallow branches recovered by Garda and Cannatella (2007). Karyotypical differences among these species are substantial, however (Busin *et al.*, 2000), and the present morphological assessment indicated one character that clearly distinguishes them (palmar tubercle presence/absence). Species boundaries among these groups are clearly difficult to establish, and further work should concentrate on sampling strategies designed to systematically test species limits using adequate taxon, gene, and morphology sampling. Additionally, geographic variation in advertisement call parameters, tadpole descriptions, and fine-scale osteological analysis will likely be needed to clearly delimit all species in Pseudae.

Conclusions

The long-lasting confusion on Pseudae species delimitation is due mostly to restricted geographic sampling of a phenotypically variable group with a conserved overall body shape. Pseudae species resulted from a habitat shift, where an ancestral hylid treefrog colonized aquatic habitats. While the body plan of these aquatic hylids is remarkably constant, coloration and body size are extremely variable within some species. Not only are the species of *Pseudis* morphologically similar, but also the smaller *Lysapsus* is essentially a miniature version (Yeh, 2002). Frogs of a particular species vary intra- and inter-populationally with respect to dorsal coloration, body size, and number and size of stripes on the thigh, which previously have been some of the characters commonly used to differentiate species. In addition to poor geographic sampling, this morphological variation

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has led taxonomists to synonymize species incorrectly, describe species based on local population characteristics, and even describe valid species using inappropriate characters.

The present work is the most comprehensive examination of Pseudae frogs to date, and includes use of live specimens, color patterns, geographic distribution, external morphology, and morphometric characters. While several characters were surprisingly consistent given the small sample sizes available to previous taxonomists and the variability among individuals and populations in this group, others showed inconsistencies that negate their use in species identification. Nevertheless, basic information on Pseudae species is lacking. Advertisement calls and tadpoles are not described for all species, nor is there any information on osteology or chondrocranium, which renders the most common set of characters used for anuran taxonomy still incomplete. This analysis has shown that some structures vary both geographically and with body size while clarifying those morphological characters that differentiate genera and species in the group. Nevertheless, caution should always be exercised in future work with this group, heeding Garman's (1877) 133-year-old advice: "…the reputation of *Pseudis* as a deceiver is too well established."

Key to the species of Pseudae

1 Presence of inner and outer metatarsal tubercles ..... 2 (*Lysapsus*)
- Only the inner tubercle is present ..... 4 (*Pseudis*)
2 Granulated skin on the dorsum ..... *L. laevis*
- Smooth skin on the dorsum 3
3 Distributed in the Araguaia River basin ..... *L. caraya*
- Distributed in the Amazon Basin ..... *L. limellum*
4 Supernumerary tubercles on the thumb 5
- Only carpal tubercle on the thumb present 7
5 Double lateral vocal sacs in males, distributed from southern Paraná state in Brazil to Rio Grande do Sul, Uruguay and Northeast Argentina 6
- Single vocal sac in males, distributed east of the Serra do Espinhaço in southeast Bahia, east Minas Gerais, and Espírito Santo States in Brazil ..... *P. fusca*
6 Palmar tubercle absent, 2n = 28 ..... *P. cardosoi*
- Palmar tubercle present, 2n = 24 ..... *P. minuta*
7 Thin stripes (0.25 – 0.75 mm) in the ventral portion of the thighs. ..... *P. tocantins*
- Thicker stripes (0.48 – 2.79 mm) in the ventral portion of the thighs 8
8 Granulated skin on the dorsum ..... *P. bolbodactyla*
- Smooth skin on the dorsum ..... *P. paradoxa*

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APPENDIX I. Major taxonomic papers on Pseudae, Characters used, and their respective contributions.

Publication	Taxonomic and Phylogenetic Implications
Linnaeus (1758)	Described *Rana paradoxa*
Wagler (1830)	Proposed the genus *Pseudis* (*paradoxa*)
Günther (1858)	Described *P. minuta*
Cope (1862b)	Described the genus *Lysapsus* (*L. limellum*)
Cope (1862a)	Described *L. mantidactylus*
Steindachner (1864)	Created a new genus and species by citing Fitzinger's *Podonectes palmatus*
Boulenger (1882)	Considered *Lysapsus* synonym of *Pseudis*
Garman (1883)	Described *P. fusca*
Lutz (1925)	Described *P. bolbodactyla*
Miranda-Ribeiro (1926)	Described *P. meridionalis*
Parker (1935)	Describes *P. laevis*
Savage and de Carvalho (1953)	1) Suggested the Family Pseudidae including: *Lysapsus* (*limellum*, *laevis*), *Pseudis* (*paradoxa*, *meridionalis*, and *minuta*) 2) Considered *bolbodactyla*, *fusca*, and *mantidactylus* synonyms of *paradoxa*
Gallardo (1961)	1) Two genera within two species and their subspecies: *Lysapsus limellum* (*bolivianus, limellum* and *laevis*) and *Pseudis paradoxa* (*paradoxa*, *caribensis*, *bolbodactyla*, *fusca*, *platensis*, and *occidentalis*) 2) *P. mantidactyla* revalidated as *Lysapsus mantidactylus*
Gallardo (1964)	1) Described *L. limellum caraya*
Bokermann (1966)	1) Considered *meridionalis* a synonym of *mantidactylus*
Cochran and Goin (1970)	1) Described *P. paradoxa nicefori*
Klappenbach (1985)	1) Considered *mantidactylus* synonym of *minuta* 2) Clarified generic limits of *Pseudis* and *Lysapsus* 3) Elevation of *Lysapsus* subspecies; proposes a close relationship between *L. limellum bolivianus* and *L. laevis*
Caramaschi and da Cruz (1998)	1) Revalidated *P. fusca* and *P. bolbodactyla* 2) Described of *P. tocantins* 3) Proposed grouping based on palmar tubercles
da Silva (1998), Darst and Cannatella (2004), Hoegg *et al*. (2004)	1) Placed Pseudae in Hylidae based on novel morphological, mitochondrial, and nuclear DNA evidences, respectively
Kwet (2000)	1) Described *Pseudis cardosoi*
Garda and Cannatella (2007)	1) Included *cardosoi* and *minuta* in a third genus, *Podonectes* 2) Renamed the group using Pseudae from Fitzinger 1843 3) Presented low support for some *P. paradoxa* subspecies (*occidentalis* and *platensis*) and for the recognition of *L. limellum limellum* and *L. limellum bolivianus* as distinct species
Aguiar *et al*. (2007)	1) Synonymized *Lysapsus* and *Pseudis* 2) Elevated subespecies of *L. limellum limellum, L. limellum bolivianus,* and *P. paradoxa platensis* to full species
Wiens *et al*. (2010)	1) Suggested that neither the allocation of *minuta* and *cardosoi* in *Podonectes* nor the synonymization of *Lysapsus* and *Pseudis* were necessary 2) Endorsed the recognition of two genera, *Pseudis* and *Lysapsus*.

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Characters used to diagnose Pseudae species in the literature.

Character	1	2	3	4	5	6	7	8	9	10
External morphology										
Body size	X	X	X	X	X		X	X	X	X
Chantus rostralis	X			X						
Coloration	X	X	X	X		X		X	X	X
Foot interdigital membranes				X	X		X			X
Head proportions				X				X		X
Number and shape of vocal sacs		X	X	X			X		X	X
Number of carpal tubercles							X	X		X
Number of dark bands on the back				X		X			X	X
Number of tarsal tubercles							X			X
Shape of foot digits		X	X	X	X		X		X	X
Shape of hand digits				X			X		X	X
Internal metatarsal tubercle shape	X					X				X
Snout shape	X								X	
Tongue shape	X			X						
Size and shape of nostrils	X			X						
Size and shape of tarsal fold							X			
Digit size	X				X					
Limb size	X			X					X	X
Tympanum size	X	X		X		X				X
Eye size				X						
Skin texture	X	X		X	X			X		X
Supratympanic fold						X	X			X
Osteology										
Fore feet terminal phalanx shape					X		X			
Hind feet terminal phalanx shape					X		X			
Location of prevomerine teeth					X		X			
Premaxillary and maxillary teeth shape					X					
Location of premaxillary and maxillary teeth					X					
Choana opening							X			
Palatines					X		X			
Parasphenoid shape							X			
Transverse process of vertebra III							X			
Sacral diapophysis shape		X					X			
Pectoral girdle shape					X		X			
Prevomer shape							X			
Size of vomerine teeth	X			X		X				
Sternum bones				X						
Total	12	7	4	17	12	6	19	5	8	15

1. Cope (1862a); 2. Cope (1862b); 3. Garman (1883); 4. Miranda-Ribeiro (1926); 5. Savage & de Carvalho (1953); 6. Gallardo (1961); 7. Klappenbach (1985); 8. Caramaschi & Cruz (1998); 9. Kwet (2000); 10. this paper.

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APPENDIX II. Specimens examined.

Lysapsus caraya. **BRAZIL**. **Goiás**: Britânia: CHUNB 30361, 42738, 42739; **Pará**: Conceição do Araguaia: CHUNB 43134–36, 43138–39, 43143–44; **Tocantins**: Caseara: CHUNB 45935–45; CHUNB 43129–32, 43137–38, 43140–41, 43143, 45932–33; Couto Magalhães: CHUNB 43129–32, 43137, 43140–41.

Lysapsus laevis. **BRAZIL**. **Roraima**: Pacaraima: MNRJ 37481, 37489, 37495, 37506, 37516, 37552, 37554, 37611, 37624, 37651, 37664, 37678, 37694, 37708, 37727, 37746, 37749, 37794, 37808, 37821, 40073, 4091016, 40918–19, 40921–22, 40924, 40926, 40931–32, 40935, 40939, 40944, 40946, 40975–77, 40991, 40995, 40998, 41004, 41020, 41044, 41095, 41131, 41151, 41176, 41201–02, 41303, 41305, 41307, 41309, 41313–14, 41321, 41323, 41327, 41334, 41339, 41340, 41342, 41344–45.

Lysapsus limellum. **BRAZIL**. **Amapá**: Amapá: CHUNB 02282, 02284, 14104–135; Tartarugalzinho: CHUNB 02283, 02279–81. **Amazonas**: Borba: MNRJ 1377, 2448, 7617–18, 7623–25, 7643, 7646, 7648, 11309; Humaitá: MNRJ 13984–88; CHUNB 32357–65, 32367, 32369–71, 32373–75, 32377–91, 32393–439, 32479, 34587; Manaus: MNRJ 30405–07, 33907, 33909–20, 33922–29, 33931–41; Rio Solimões: MNRJ 41406–09. **Mato Grosso**: Nossa Senhora do Livramento: MNRJ 15922–21 34071–75, 34077–82; **Mato Grosso do Sul**: Nhecolândia: MNRJ 14307–09, 14311, 14313, 14316, 14319–20, 14326–28; Mato Grosso do Sul (Corumbá): MNRJ 41423–24, 41426, 41428–29, 41432, 41435–36, 41441, 41449. **Pará**: Alter do Chão: MNRJ 1255–57; Monte Alegre: CHUNB 31365–430, 35171; Oriximiná: MCZ A-10076, A-90722– 59, A-91054–64, A-10077; MNRJ 38226, 38236–38, 38243, 38248; Santarém: MNRJ 33822, 33860, 33864–66, 33870, 33873–74, 33879, 33880, 33885, 33887, 33889, 33894, 33896, 33902–06, 15932, 15926, 15928. **Rondônia**: Guajará-Mirim: MNRJ 33948, 33954, 33955, 33960, 33963, 33966, 33971; Porto Velho: MNRJ 1087577. **PARAGUAY**. **Assunción**: MNRJ 4908, 4909; **Hotel Kay**: MNRJ 13991, 4993.

Pseudis cardosoi: **BRAZIL**: **Rio Grande do Sul**: São Francisco de Paula: MCP 1793, 1809, 1848, 3371, 3373, 3378, 3726–27, 6163, 7927–29, 7940, 3347–48; Vacaria: MCP 3774; **Santa Catarina**: Lebon Régis: MCP 8607.

Pseudis minuta. **ARGENTINA**. **Buenos Aires**: MCP 3491, 3492; **La Plata**: FMNH 9698. **BRAZIL**. **Rio Grande do Sul**: KU 176175, 176176, 93208, 93209, 93210, 93212, 93213; Balneário Pinhal: MCP 4241 4869, 4871, 4872, 4873, 5480, 5481; Caçapava do Sul: MCP 2578, 2582, 2583, 2584, 2585, 2586, 2587, 2589, 3368, 3369, 3370, 3372, 3376, 3377, 3440; Candiota: MCP 4099, 4143, 4146, , 4714, 4775, 4779, 4795, 5000, 5043, 5063, 5065, 5098, 5116, 5122, 5358, 5363, 5366, 5370, 5371, 5400, 5409, 5503, 5505, 5510, 5514, 5826, 5830, 5833, 5846, 5848, 5886, 6004, 6016; Capão da Canoa: FMNH 80574, 80575, 80577; Mostardas: MCP 1123; Osório: FMNH 80554, 80565, 80568; Pelotas: MCP 8047; Porto Alegre: FMNH 80569, 80571, 80572, 80573, 80578, 80580, 80593, 80594, 80596, 80597, 80598, 80599, 80600, 80601, 80602, 80603; MCP 8351, 8352, 8353, 8356; Santana do Livramento: MCP 5774, 5776; Santo Antonio da Patrulha: MCP, 1606, 1607; Viamão: MCP 1002. **URUGUAY**. **Lavalleja**: FMNH 10381, 10382, 10383, 10384, 10385, 10394; **Maldonado**: FMNH 10205, 10207, 9628, 9629, 9630, 9631, 9632, 9633, 9642; **Mossoler**: MCP 6136; **Rivera**: MCP 5674, 5675, 5680, 5681, 5682; **Rocha**: FMNH 10210, 10250, 10295; **Salto**: MCP6472; **Soriano**: FMNH 10778, 10779; **Treinta y Tres**: FMNH 10428, 10429, 10430, 10431, 10432, 10433, 10434, 10468, 10498, 10522, 10523, 10524, 10525, 10526, 10527, 10528, 10529.

Pseudis bolbodactyla. **BRAZIL**. **Bahia**: MNRJ 2698; **Goiás**: Alvorada do Norte: CHUNB 33124, 33229, 33241–67, 33269–79, 33281–98, 33300–01, 33628, 36984–85, 38513, 38515–29; Aporé: CHUNB 42678, 42764–67, 42769–75; MNRJ 40851–56; Flores de Goiás: CHUNB 38378–95; Iaciara: CHUNB 42910; Mossâmedes: MNRJ 21808–12); Pirenópolis: CHUNB 8319–21, 24677–78, 24681–92, 24963; Quirinópolis: MNRJ 19792, 34031–55; São Domingos: CHUNB 33280, 35290, 35382–89, 35391–94, 36967, 36969–83; **Minas Gerais**: Buritizeiro: CHUNB 42871–85, 44548; GRCOLLI 17201–05, 17224–36; MNRJ 14124–26; Corinto: MCZ 25729; Jaíba: MNRJ 21315–22, 14036–38, 14040–41, 14043, 14046–50, 14052–56, 14062–70, 14072, 14074–76, 14078–80, 14083, 14085–86, 14088–93, 14098, 14100–01, 14105, 14118, 14121, 14392.

Pseudis fusca. **BRAZIL**. **Bahia**: Guaratinga: MNRJ 29973; Teixeira de Freitas: MNRJ 29974; **Espírito Santo**: Linhares: MNRJ 39865, 30372–73; São Mateus: MNJR 18793; Sooretama: MNRJ 2692, 12390; **Minas Gerais** Araçuaí: CHUNB 42607–25; MNRJ 17020–21; Coronel Murta: MNRJ 35459, 35460, 35461; Diamantina: MCN-AM 556–557; Marliéria: MNRJ 15899; Salinas: MNRJ 14127–28.

Pseudis paradoxa. **ARGENTINA**. **Formosa**: CAS 100509; KU 128900–904; LACM 73454–58, 74007–74013; **Salta**: MCZ A-136472–73. **BOLIVIA**. **Santa Cruz**: MCZ 29958–59; CAS 85290; CM 36218, 36220–23; KU 183283–97, 209762, 215536. **BRAZIL**. **Amapá**: Tartarugalzinho: CHUNB 42913–32, 42934, 42936–40, 43030; Macapá: MNRJ 32577; **Amazonas**: Humaitá: 14123, 41615; **Maranhão**: Pinheiro: CHUNB 43016, 43019–23, 43025–29, 43031–37; Arari: MNRJ 14034; Bacabal: MNRJ 33857–59; **Mato Grosso**: Poconé: CHUNB 13857–58; Rosário d'Oeste: KU 93214–18; **Mato Grosso do Sul**: Aquidauana: CHUNB 30525; Corumbá: CHUNB 42846–70; MNRJ 41616; **Roraima**: Boa Vista: CHUNB 42990–43011, 43013–15, 43017–18, 43024; Pacaraima: MNRJ 27265–86; **São Paulo**: Álvares Florence: DZSJRP 1516; Avanhandava: DZSJRP 1517; Cardoso: 1514; Dracena: DZSJRP1926–29, 1931–36; Fernandópolis: DZSJRP 1518; General Salgado: DZSJRP 1504; Ibirá: DZSJRP 1497–98, 1505, 1520; Icém: DZSJRP 1478, 1480, 1484, 1488, 1494–96, 1521–24, 2259, 2261–63; Nova Aliança: DZSJRP 1507, 1820,

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1822–23, 351, 6617-19, 6918, 7006, 7235, 7439, 7530, 8491–92; Nova Granada: DZSJRP 1501; Novo Horizonte: DZSJRP 3435–36, 3438–49; Pereira Barreto: DZSJRP 1500; Piraju: MNRJ 31319; Ribeirão Preto: DZSJRP 5516, 5518–22, 5524–26, 5528–31; Rubinéia: DZSJRP 1502. **Guiana**. CAS 85295; **Demerara**. MCZ 12135–36. **Paraguay**. **Boqueron**: Filadelfia: CM 94187–93, 94231–35; Presidente Hayes: MNRJ 15477-78; Bella Vista: MNRJ 41617-18. **Peru**: **Madre de Dios**: KU 209762, 215536. **Suriname**. **Wanica**: KU 154616, 221537; **Saramacca**: CM 49508–11, 49513–15, 55999, 44275–77, 50563–64, 50587. **Trinidad y Tobago**. CM 33787; FMNH 49706, 217113, 251227, 49705; MCZ 44934–36. **Venezuela**. **Apure**: KU 185770; **Bolivar**: KU 79178–79, 84179; **Guaraunos**: KU 125866–70, 150814–15, 167257–71.

Pseudis tocantins. **Brazil**. **Goiás**: Aruanã: CHUNB 42686; Britânia: CHUNB 30355–57, 42605, 42681–82, 42684–85, 42687–91, 42693–97; **Mato Grosso**: Santa Terezinha: CHUNB 10369–70; **Pará**: Conceição do Araguaia: CHUNB 42753–62, 42952; **Tocantins**: Formoso do Araguaia: CHUNB 43038; Palmas: CHUNB 11236–38, 11277–78, 14703, 16122, 16124, 21947, 24256–59; Pedro Afonso: CHUNB 42890–912; Porto Nacional: MNRJ 35456–58; Sandolândia: CHUNB 42935, 42941–53, 42954.