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Taxonomic revision of *Rhinella granulosa* species group (Amphibia, Anura, Bufonidae), with a description of a new species

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ABSTRACT

An extensive review of Rhinella granulosa *species group was conducted based on external morphological and morphometrical characteristics. Data set included 8700 specimens deposited in 35 collections, representing 865 localities, from South and Central America. Twelve species were recognized for the group, one described as new; they are:* Rhinella granulosa *(Northeastern Brazil),* R. pygmaea *(Rio de Janeiro State, Brazil),* R. bergi *(Paraguay, Northwestern Argentina, and Mato Grosso State, Brazil),* R. major *(Argentina, Bolivia, Paraguay, and North and Western Brazil),* R. mirandaribeiroi *(Central Brazil and Bolivia),* R. azarai *(Provincia de Misiones, Argentina, Paraguay, and Mato Grosso do Sul State, Brazil),* R. nattereri *(Venezuela, Guiana, Roraima State, Brazil),* R. fernandezae *(Argentina, Uruguay, Paraguay, and Rio Grande do Sul State, Brazil),* R. dorbignyi *(Provincia de Buenos Aires, Argentina, Uruguay, and Rio Grande do Sul State, Brazil),* R. merianae *(Venezuela, Surinam, Guiana, and Brazilian States of Amazonas and Roraima),* R. humboldti *(Colombia, Venezuela, Surinam, Guiana, Trinidad),* R. centralis *sp. n. (Panama). External morphological characters, such as head and snout shape, type of cephalic crests, size of tympanum, size and shape of parotoid gland, and skin granulation, are some of the traits used to identify the species. For each species, comparative diagnosis, description, and summaries of distribution are provided. An artificial key to species is also presented. The geographic distributions of species of* Rhinella *are largely associated with the open habitats of South America and Panama.*

Keywords: Bufonidae; *Rhinella granulosa* group; Taxonomic revision; Geographic distribution; South and Central America.

INTRODUCTION

Rhinella granulosa group assembles common, moderate-sized, and wide-ranging South American toads, occurring also in Panama. Species are characterized by having a small parotoid gland, wart skin, and well-developed and keratinized cranial crests.

The first two species of the group were described in the 19th century: *Rhinella granulosa* (Spix, 1824) from Bahia, Brazil, and *Rhinella dorbignyi* (Duméril &

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Bibron, 1841), from Montevideo, Uruguay. In subsequent years, these names were randomly used on the attempt to identify specimens found between the type localities of the two species (Gallardo, 1957). In 1936, Müller & Hellmich described a subspecies for *Rhinella granulosa* (*Rhinella granulosa major*) from San José de Chiquitos, Bolivia. *Rhinella pygmaea* was described by Myers & Carvalho in 1952, from Rio de Janeiro, Brazil, and another subspecies (*Rhinella granulosa fernandezae*) was described by Gallardo in 1957 from Argentina.

Distribution and taxonomy of the forms of the group were first assigned by Gallardo (1965), who recognized 14 subspecies of *Rhinella granulosa* (*R. g. major, R. g. fernandezae, R. g. dorbignyi, R. g. granulosa, R. g. pygmaea, R. g. azarai, R. g. beebei, R. g. humboldti, R. g. merianae, R. g. mirandaribeiroi, R. g. mini, R. g. lutzi, R. g. goeldii,* and *R. g. barbouri*). The author presented a hypothesis to explain the distribution of the subspecies based on their fidelity to the South American hydrographic systems. After his work, two other forms were described for the group: *Rhinella granulosa nattereri* (Bokermann, 1967), and *Rhinella bergi* (Cespedez, 2002). A few of the subspecies (*Rhinella fernandezae, Rhinella dorbignyi, Rhinella pygmaea*) were elevated to specific rank by Cei (1968, 1972), a decision followed by other authors (Achaval & Olmos, 1997; Carvalho e Silva & Carvalho e Silva, 1994; Duellman, 1999; Langone, 1999; Lavilla *et al.,* 1992; Maneyro *et al.,* 1995). In 1986, Rivero *et al.* considered *Rhinella beebei* a valid species based on information available in the literature and on indications of sympatry among the subspecies described by Gallardo. Besides the absence of a thoroughly revision, this decision was followed by Frost (2008), who recognized six species for the group (*Rhinella granulosa, Rhinella dorbignyi, Rhinella fernandezae, Rhinella pygmaea, Rhinella bergi,* and *Rhinella beebei*).

Nevertheless, the diagnosis and descriptions made available by Gallardo and subsequent authors were inadequate to recognize taxonomic variation in the group, and *Rhinella granulosa* remain as a convenience name for this complex. The amount of material accumulated in collections over the past 40 years provides a new perspective in this scenario, allowing an extensive taxonomic revision of the group, stated as needed by several authors (Klappenbach & Langone, 1992; Langone, 1994; Prigioni & Achaval, 1992).

The purpose of this study is to provide, based on museum specimens, an analysis of geographic variation of the forms of *Rhinella granulosa* species group in South and Central America and to determine their taxonomic status. Detailed diagnoses and descriptions, an artificial key to identification, and a summary of the known distributions are provided for all recognized taxa, including a description of a new species. The geographic distribution of the species is discussed hereinafter.

MATERIAL AND METHODS

External morphology

Up to 8700 specimens deposited in 35 collections were studied representing 865 localities in South and Central America. Specimens examined are in Appendix 1. The following external morphological characters were examined.

Head shape

Three categories of head shape were recognized in dorsal view: rounded (Fig. 1A), elongated (Fig. 1B) or subtriangular (Fig. 1C). The rounded head is semicircular with a short snout (tip of snout not surpassing anterior margin of maxilla in ventral and dorsal views (Figs. 2A and 2C), or with a slightly protruding snout. The head shape exhibited in Fig. 2D occur in only one species of the group and it is also considered in the rounded category; although it is not perfectly rounded in profile due to the presence of a long snout; nevertheless, the circumference of the head is considerably perceptible. The subtriangular head is wide with a long snout (Fig. 2F). The elongated head is narrow with a long snout (Fig. 2E).

Snout shape

In dorsal view, the snout can be rounded or squared (Fig. 2D); in lateral view, it can be rounded (Figs. 3A and 3C) or straight (Figs. 3D and 3F). In lateral and dorsal view, the snout can be short (tip of snout not surpassing anterior margin of maxilla or surpassing it only slightly); or long (tip of snout highly surpassing anterior margin of maxilla).

Dorsal body granulation

Dorsal granulation can vary in intensity but tubercles are always keratinized, partially or totally. Tubercles can be conical, rounded or elongated; flattened or fleshy. Pungent conical tubercles can be almost entirely keratinized or have one to several keratinized spicules.

Head granulation

Skin is always smooth; when present, keratinized granules, spicules or flecks are always spaced out, leaving portions of smooth skin visible between them. A few species present a more intense granulation on top of head (Fig. 2D) than others, where granulation is more spaced (Figs. 2C and 2F). Keratinization covering tubercles, granules, and crests may fade after long periods of storage and manipulation.

Color pattern

Dorsal colors vary from dark-brown to light olive-green, with dark spots. In dark-brown patterns, spots are nonexistent or not conspicuous. A labial stripe, lightly colored or spotted, may be present between upper maxilla and infraorbital crest, visible or not in dorsal view.

Longitudinal dorsal stripe

A mid-dorsal longitudinal stripe, white, yellow or lighter than the dorsal color pattern, extending from nostril or eye level to end of body, can be present (Figs. 2B, 2C and 2E) or absent. When present, it is better visualized if observed through the glass of a receptacle full of alcohol.

Cephalic crests

All species of *R. granulosa* group present cephalic crests with keratinized borders. Regarding height, crests can be high or low. In high crests, borders are usually continuous (Figs. 2A and 2C); in low crests, they are usually discontinuous, granulose (Figs. 2D and 2F). In some cases, crests with continuous borders may present gaps (Fig. 2B); and crests with granulose borders may present a few united granules (Fig. 2E). Cephalic crests may be bulky (Fig. 2C).

The following categories of cephalic crests were recognized:

Supraorbital crest

Supraorbital crest is situated dorsally to eye, between canthal and supratympanic crests. It can be straight, forming a continuous straight line with canthal and supra tympanic crests (Fig. 2C) or, as in most cases, rounded (Fig. 2E). Compared to other cephalic crests, supraorbital crest presents the highest variation related to height (high or low), thickness (thin or bulky), and type of keratinization (continuous or granular). When high and continuous, it can be laterally and posteriorly wrinkled, and gapped or serrate at the top (Fig. 2B). When granular, the granules can be well individualized or partially united. Interorbital portion of supraorbital crest can be strongly curved (Fig. 2E) or almost straight.

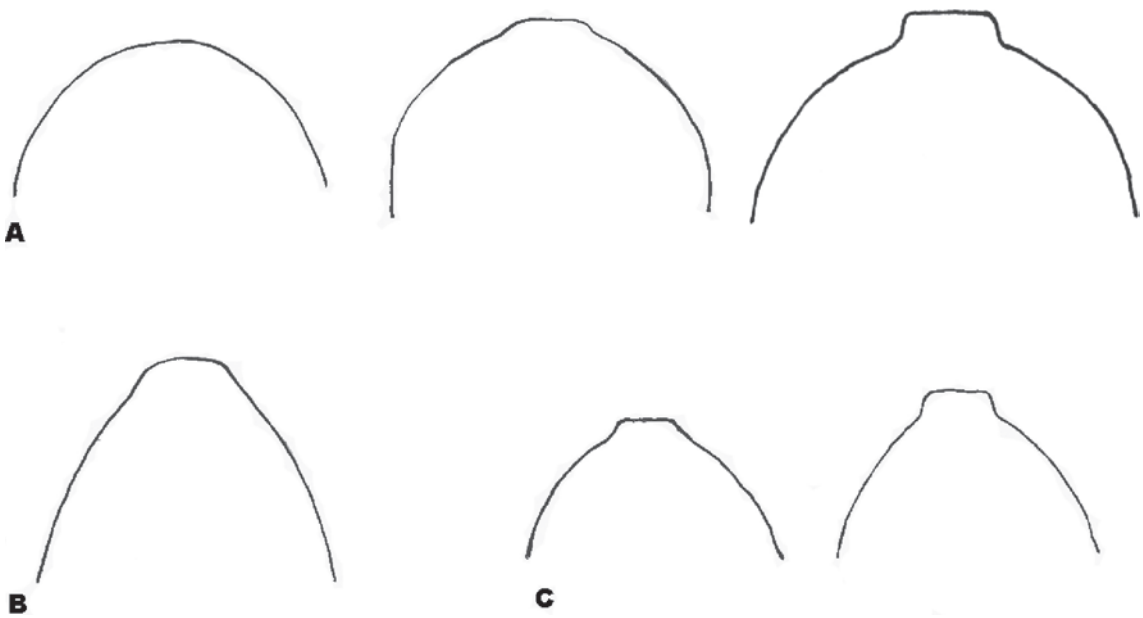

FIGURE 1: Dorsal outline of head: **A.** rounded; **B.** elongated; **C.** subtriangular.

Infraorbital crest

Infraorbital crest is situated ventrally to eye and can be present, reduced of absent (Fig. 3D). A lateral expansion, hiding part of maxillary crest in dorsal view can be present (Fig. 2b). Infraorbital crest can be short or long (posteriorly extending beyond post-orbital crest; Figs. 3A, 3E, and 3F). When granular, it can be difficult to verify if its extended portion is present or not, because granules of the crest may be

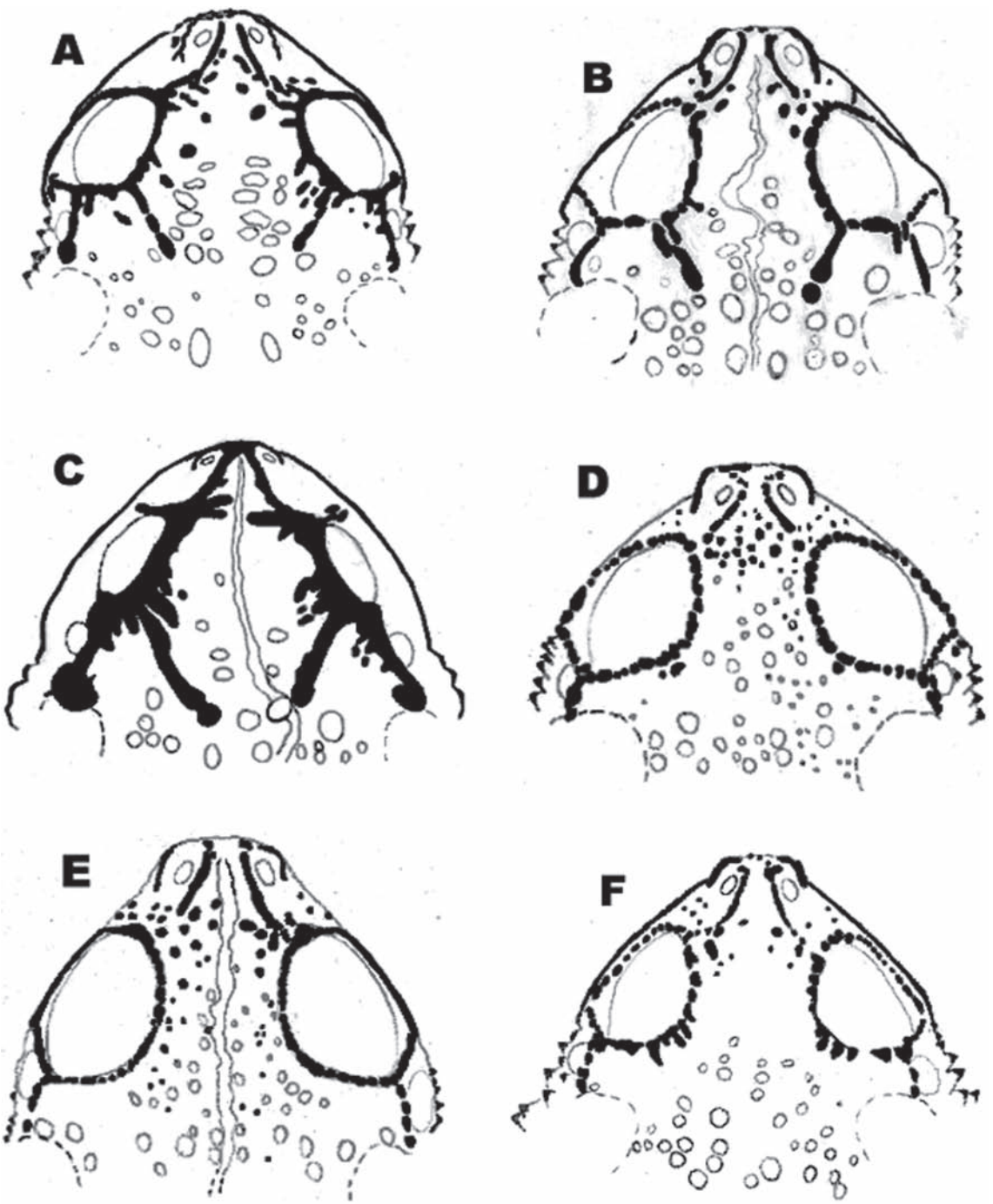

FIGURE 2: Schematic dorsal views of the head in *Rhinella granulosa* complex showing differences in shape of head, type of cephalic crests, and cutaneous granulation.

misidentified as granules from the side of the head. Granules of the head are usually conical with a keratinized spicule; those of the crest are not conical and present a broader keratinized portion. The crest can be straight (Fig. 3A) or slightly curved (Fig. 3E).

Preorbital crest

Preorbital crest is situated frontal to eye, anteriorly bordering the orbit. It can be continuous with supraorbital crest, and separated from infraorbital crest. This crest is the least subject to variation, being continuous or interrupted (granular).

Postorbital crest

Postorbital crest is situated posterior to eye. It can be continuous with supra orbital crest, and discontinuous with infraorbital crest. This crest can be conspicuous or reduced and non-keratinized (Fig. 3D), and it can vary from continuous to granular. Regarding shape, it can be straight (Fig. 3A), medially curved (concave) (Fig. 3D), or distally curved backwards (slightly convex). Small perpendicular branches towards tympanum may be present (Fig. 3E).

Supratympanic crest

Supratympanic crest is situated above tympanum, between eye and parotoid gland. It can be short or long, straight or curve, high or low. It can also present a dilated posterior portion (Fig. 3D). Keratinization of this crest may be smooth and continuous (Figs. 3D and 3E), or it may present rounded or elongated, usually fleshy, granules, which may be aligned in one or more irregular rows (Fig. 3C).

Parietal crest

Parietal crest may be present (Fig. 2C), indistinct, or absent (Figs. 2D and 2E). This crest begins at the posterior third of postorbital crest and converges to the central posterior portion of cranium, never contacting its symmetrical at midline. Kerati-

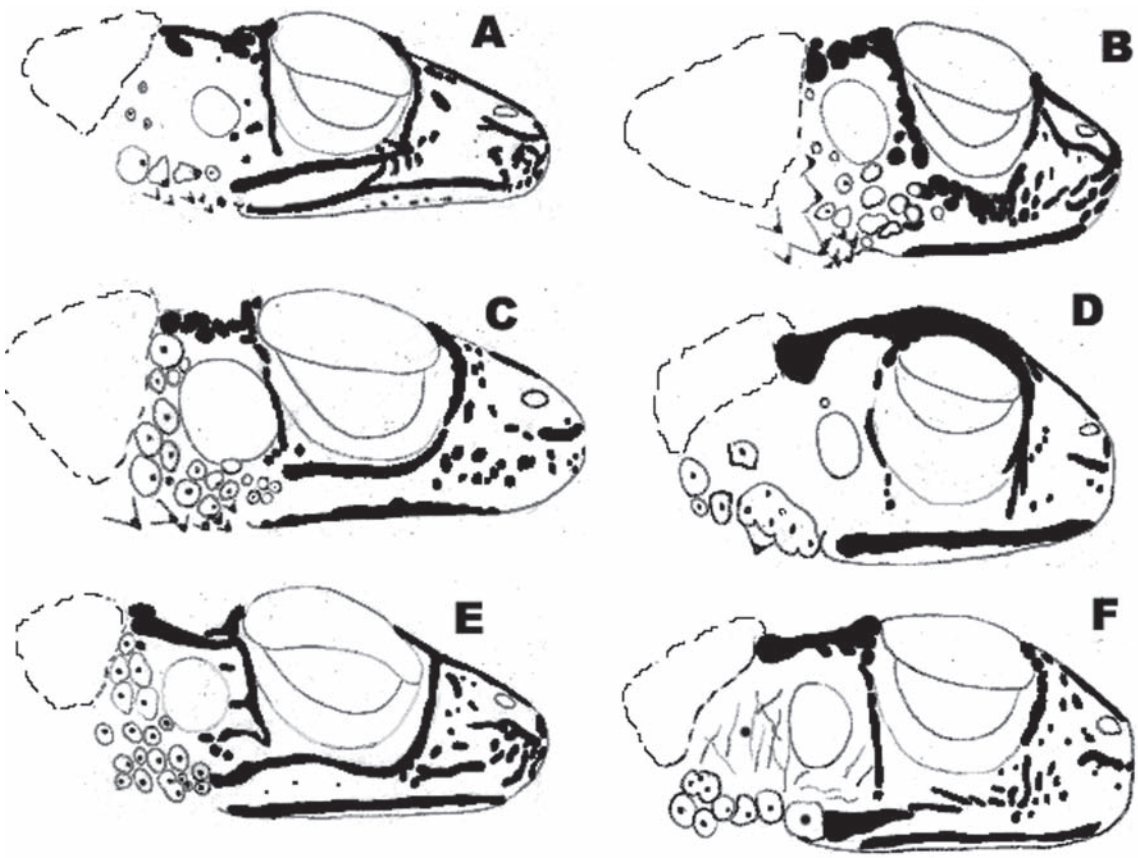

FIGURE 3: Schematic lateral views of the head in *Rhinella granulosa* complex, showing differences in shape of head, types of cephalic crests, shape, and relative size of tympanum and of parotoid gland, and cutaneous granulation.

nization of this crest can be continuous (Fig. 2C) or granular, and a few granules may be united (Figs. 2A and 2B).

Canthal (rostral) crest

Canthal crest is situated along *canthus rostralis,* usually reaching snout extremity. It can be continuous with preorbital crest (Fig. 2C); when it is not continuous, a few fleshy keratinized granules may be present between canthal and preorbital crests (Figs. 2D and 2E).

Subnasal crest

Subnasal crest is situated right below nostrils and can be short or long (extending beyond posterior border of nostrils; Fig. 3E), bulky or not. Rivero (1961) considered the subnasal crest as the semi-circular extension of canthal crest around nostrils. In *R. granulosa* group, canthal and subnasal crests are not continuous, separated by scattered keratinized granules.

Maxillary crest

The maxillary crest is a keratinization of the border of the maxilla. This keratinization is usually continuous and it can reach ventral surface of maxilla. In a few cases, part of this crest can be visible in dorsal view (Figs. 2A, 2B, 2C and 2F).

Upper lip (maxilla)

The superior lip can be flared, presenting an expanded horizontal flap, visible in ventral and dorsal views (Figs. 2A and 2C). In lateral view, the upper lip can present an angular (sharp) or rounded (slightly convex) border. In specimens with rounded lips, maxillary crest may not follow the superior border and it can curve upwards, allowing a visible portion of the lip in lateral view, below the maxillary crest (Fig. 3A).

Loreal region

In dorsal view, loreal region can be distinctly or scantly visible. The superior half may be concave or straight; the inferior portion may be straight, concave or oblique. The level of keratinized granules is highly variable. Granules may have a variety of shapes and sizes.

Tympanum

Tympanum is always visible in *R. granulosa* species group. Its borders, however, are not always conspicuous. Tympanum may vary in size (Figs. 3A, 3C, and 3D); and position: touching postorbital crest (Fig. 3C), or distinctively separated from it (Figs. 3A and 3F).

Parotoid glands

Parotoid glands are conspicuous in most cases. Its borders can be well delimited or with inconspicuous posterior or ventral limits. Parotoid glands can be elongated (Fig. 3D), rounded (Fig. 3E) or subtriangular (Fig. 3C) with vertex generally pointing down. Width of parotoid glands can vary from 9.8 to 24.3% of SVL; height of parotoid glands can vary from 7.3 to 21.1% of SVL. Parotoid glands have individualized keratinized tubercles, usually flattened on dorsal surfaces and conical on lateral surfaces of gland.

Nostrils

Nostrils are longer than wide and dorsolateral in position, but their openings can be slightly dorsal or slightly lateral. The longitudinal axis of nostrils can be obliquely directed, practically parallel, or almost perpendicular to the longitudinal axis of head.

Morphometric characters

Measurements of 23 morphometric characters were taken on 2267 specimens (1510 males, 757 females) and were used in a multivariate statistical analysis along with nine body ratios. The measurements were obtained to the nearest 0,01 mm with a digital caliper (Mitutoyo) under a stereoscope. They were: snout-vent length (SVL), from tip of snout to cloacal opening, firmly holding the toad as straight as possible; head width (HW), between median portion of tympani; head length (HL), perpendicularly from posterior margin of tympanum to tip of snout; internarial distance (IND), between inner edge of nostrils; snout width (SW), between external edges of snout at nostrils' level; eye-nostril distance (END), from anterior corner of eye to inner edge of nostril; eye-snout distance (ESD), from anterior margin of eye to tip of snout; interorbital distance (IOD), between inner edges of eyelids (IOD_1), in the point of

contact between canthal and preorbital crests (IOD_2), and in the point of contact of supraorbital and parietal crests (IOD_3); IOD_3, however, were not used in the statistical analysis because the parietal crest is not present in all taxa; eye diameter (ED), from posterior to anterior corners of the eye using upper part or caliper; tympanum diameter (TD), from posterior to anterior edges of tympanum; tympanum height (TH), from superior to inferior edges of tympanum; eyelid width (EW), between internal and external edges of eyelid; parotoid gland width (PGW), from anterior to posterior borders of parotoid; parotoid gland height (PGH), from superior to inferior borders of parotoid; supratympanic crest length (STCL), from anterior to posterior edge of crest; postorbital space (POS), from postorbital crest to anterior margin of parotoid gland, at the level of median region of tympanum; hand length (HAL), ventrally from posterior edge of palmar tubercle to tip of finger III; thigh length (THL), from middle of cloacal opening to outer edge of flexed and ad-pressed knee; tibia length (TIL), from outer edge of flexed knee to heel; tarsus length (TAL), from heel to tarsus-metatarsal articulation; foot length (FOL), from posterior edge of metatarsal tubercle to tip of toe IV. In addition, four other measures were chosen in the end of the work to help describe the species and were not included in the statistical analysis (N varying from 7 to 23): distance from tympanum to postorbital crest (DTP), from anterior border of tympanum at the level of median region, to anterior border of postorbital crest; distance from tympanum to supra tympanic crest (DTS), from superior edge of tympanum to supra tympanic crest; distance from tympanum to parotoid gland (DTG), from posterior edge of tympanum, at the middle, to anterior margin of parotoid gland; head height (HH), from ventral face of inferior maxilla, at eye level, to the highest point of supra orbital crest. The body ratios used in addition to raw measurements were: HL/HW; IND/SW; END/ESD; ED/IOD_1; IOD_1/IOD_2; TW/TH; PGL/PGH; TIL/THL; STC/POS.

Statistical analysis

Statistical analyses were performed using SPSS 8.0 for Windows; a 5% significant level was adopted for all tests. Analysis were performed with adult males and females tested separately. Adult males were recognized by secondary sexual characters, such as presence of vocal sac or nuptial pads on fingers I and II; adult females were recognized by extended abdomen or lack of nuptial pads and vocal sac. Statistical analysis was not used to identify species but otherwise as a resource to test the species previously defined by morphological analysis, and to help describe them. The 12 species, recognized with external morphological analysis, were used as OTU (operation taxonomic unit) and were numbered from OTU-1 to OTU-12 as follow: *Rhinella granulosa* (OTU-1); *Rhinella pygmaea* (OTU-2); *Rhinella bergi* (OTU-3); *Rhinella major* (OTU-4); *Rhinella mirandaribeiroi* (OTU-5); *Rhinella azarai* (OTU-6); *Rhinella nattereri* (OTU-7); *Rhinella fernandezae* (OTU-8); *Rhinella dorbignyi* (OTU-9); *Rhinella merianae* (OTU-10); *Rhinella humboldti* (OTU-11); *Rhinella centralis* sp. n. (OTU-12).

A descriptive analysis was conducted obtaining values for mean, standard deviation, variance, and range for all variables. Kolmogorov-Smirnof ($N > 50$) and Shapiro-Wilk ($N < 50$) tests were used to verify normality of variables, and Levene test was used to test homogeneity of variances. Box plot graphs were constructed to visualize range of variables, to allow the exclusion of outliers, and to identify possible measurement errors. All outliers observed on box plot graphs were twice removed from original data set (231 specimens were removed), and the matrix analyzed included 1367 males for 12 OTUs, and 669 females for 11 OTUs.

A Canonical Discriminant Analysis (CDA) was conducted (Albrecht, 1980; Cavalcanti & Lopes, 1993) and scores were projected in the space of canonical axis, allowing a graphical differentiation of the species analyzed. The variables which most counted for the discriminant analysis were tested with an analysis of variance (ANOVA) to compare means, and Turkey multiple comparisons test was used when means were considered not homogeneous. Analyses were performed using raw values, ratios, and logarithmic standardized data. However, only results for raw values are presented here because tests did not differ markedly.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; CAS, California Academy of Sciences, San Francisco, USA; CFBH, Célio F. B. Haddad collection, Departamento de Biologia da Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil; CHUNB, Coleção Herpetológica da Universidade de Brasília, DF, Brazil; EI, Eugenio Izecksohn collection, Universidade Federal Rural do Rio de Janeiro, RJ, Brazil; FML, Fundação Miguel

Lillo, Tucumán, Argentina; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil; JJ, Jorge Jim collection, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Botucatu, SP, Brazil (currently in Museu Nacional, Rio de Janeiro); KU, University of Kansas, Natural History Museum, USA; MACN, Museu Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MACN-CENAI, Adolpho Barrio collection, Museu Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MBML, Museu de Biologia Mello Leitão, Santa Teresa, ES, Brazil; MCN-FZB, Museu de Ciências Naturais da Fundação Zoobotânica, Porto Alegre, RS, Brazil; MCN-PUC, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, MG, Brazil; MCT-PUC, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MHNM, Museo de Historia Natural de Montevideo, Uruguay; MNHNP, Museo Nacional de Historia Natural del Paraguay; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, RJ, Brazil; MPEG, Museu Paraense Emílio Goeldi, Belém, PA, Brazil; MUFAL, Museu da Universidade Federal de Alagoas, Maceió, AL, Brazil; MZUM, Museum of Zoology, University of Michigan, USA; MZUSP, Museu de Zoologia da Universidade de São Paulo, SP, Brazil (currently including the WCAB, Werner Bokermann collection); NHM, The Natural History Museum, London, England; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; UEFS, Universidade Estadual de Feira de Santana, BA, Brazil; UFMA, Universidade Federal do Maranhão, São Luís, MA, Brazil; TNHC, Texas Natural History Collection, University of Texas, USA; UFC, Universidade Federal do Ceará, Fortaleza, CE, Brazil; UFPB, Universidade Federal da Paraíba, João Pessoa, PB, Brazil; UFV, Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa, MG, Brazil; UNC, Universidad Nacional de Colombia, Bogota, Colombia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, USA; UTA, University of Texas at Arlington, USA; ZUEC, Museu de História Natural do Instituto de Biologia da Universidade Estadual de Campinas (UNICAMP), Campinas, SP, Brazil; ZSM, Zoologische Staatssammlung München, Germany; ZVCB, Colección de la Faculdad de Ciencias de la Universidad de la República del Uruguay, Montevideo, Uruguay.

RESULTS

Statistical analysis

The first CDA conducted with 12 OTUs for males and 11 OTUs for females showed a clear separation between OUTs 8 and 9 and the remaining OTUs, for males and females (Figs. 4 and 5). Supratympanic crest length (STCL) is the variable that accounts for the first discriminant function (Table 13 and 14). The average length of supratympanic crest is significantly higher for OTUs 8 and 9 (ANOVA: males: $F = 270$. $p = 0.000$; females: $F = 78$, $p = 0.000$). The second discriminant function separates OTUs 8 and 9 with a slight overlap in the case of the males. The variables with the higher values for this function are SW for males and IOD_2 for females. Because of the morphological conspicuousness of the two species (specially the short snout), OTU 8 (*R. fernandezae*) and OUT 9 (*R. dorbignyi*) were subsequently removed from the data set tested.

A subsequent analysis was conducted with smaller groups of OTUs, in order to maximize the differences among species. Groups were chosen according to geographical proximity and morphological similarities among species. Species were grouped as follow: *R. granulosa, R. major,* and *R. mirandaribeiroi* (OTUs 1, 4, 5); *R. pygmaea, R. bergi,* and *R. azarai* (OTUs 2, 3, 6); *R. merianae, R. humboldti,* and *R. centralis* sp. n (OTUs 10, 11, 12). *Rhinella nattereri* (OUT-7) was removed from the analysis because of a small number of specimens (n = 7 adult males and no adult female).

Rhinella granulosa, R. major, and *R. mirandaribeiroi* showed a slight overlap for males and females (Figs. 6 and 7). For males, POS and STCL are the variables with higher values for the first discriminant function, and IOD_2 and IOD_1 are the variables with the higher values for the second discriminant function (Table 15); variables STCL, POS, IOD_2, and IOD_1 are, in average, significantly different for *R. granulosa, R. major,* and *R. mirandaribeiroi* (Tukey, ANOVA; $p < 0.05$). For females, SW and ESD are the variables with higher values for the first discriminant function, and IOD_2 and POS account for the second function (Table 15). In average, SW is significantly different among the three species (Tukey, ANOVA; $p < 0.05$), ESD differs significantly between *R. granulosa* and *R. mirandaribeiroi,* and between *R. major* and *R. mirandaribeiroi* (Tukey, ANOVA; $p < 0.01$), and POS and IOD_2 differ significantly between *R. granulosa* and *R. major* (Tukey, ANOVA; $p < 0.01$).

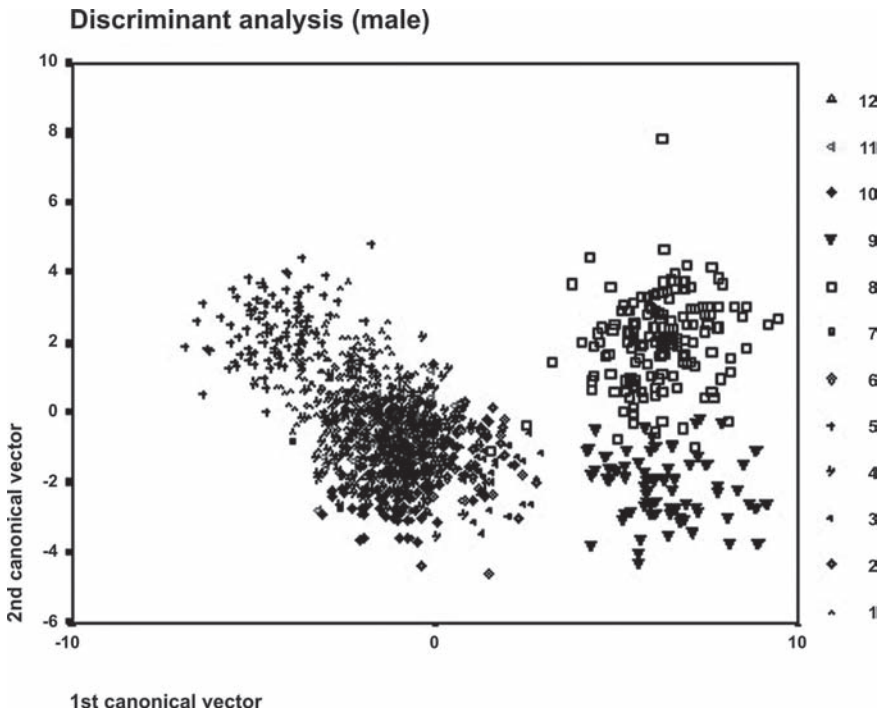

FIGURE 4: Projection of the individual scores of the 12 combined OTUs in the reduced space of the 1st and 2nd canonical variables, for males. *Rhinella granulosa* (1); *R. pygmaea* (2); *R. bergi* (3); *R. major* (4); *R. mirandaribeiroi* (5); *R. azarai* (6); *R. nattereri* (7); *R. fernandezae* (8); *R. dorbignyi* (9); *R. merianae* (10); *R. humboldti* (11); *R. centralis* sp. n. (12).

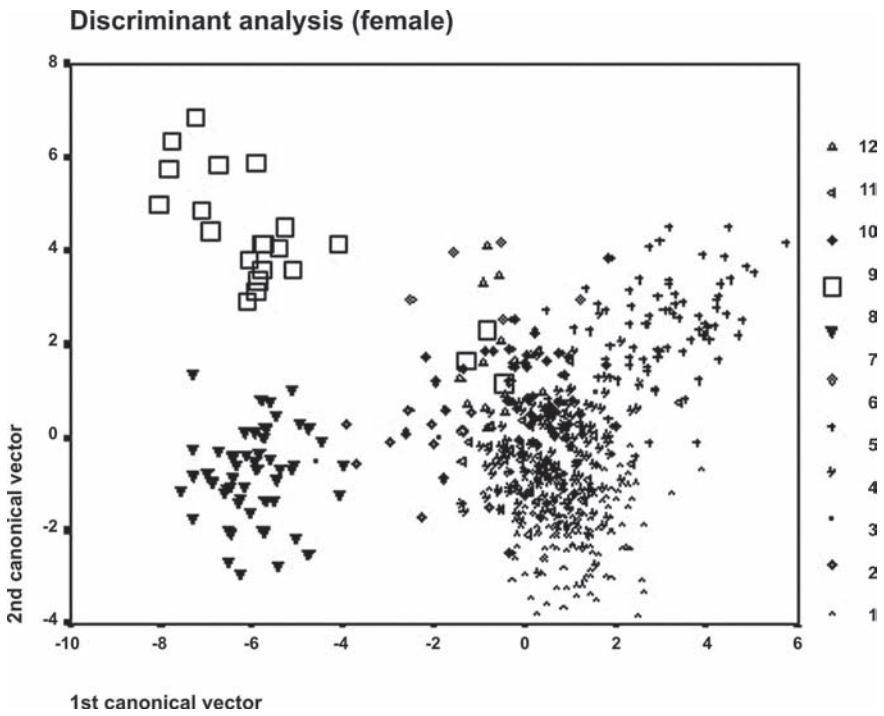

FIGURE 5: Projection of the individual scores of the 11 combined OTUs in the reduced space of the 1st and 2nd canonical variables, for females. *Rhinella granulose* (1); *R. pygmaea* (2); *R. bergi* (3); *R. major* (4); *R. mirandaribeiroi* (5); *R. azarai* (6); *R. fernandezae* (8); *R. dorbignyi* (9); *R. merianae* (10); *R. humboldti* (11); *R. centralis* sp. n. (12).

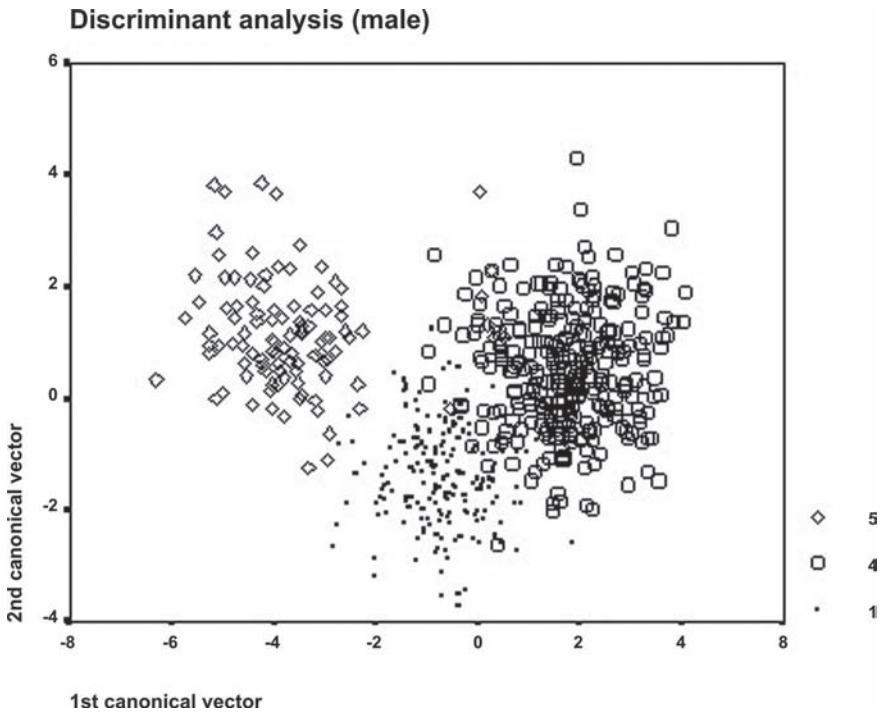

FIGURE 6: Projection of the individual scores of the combined samples for *Rhinella granulose* (1), *R. major* (4), and *R. mirandaribeiroi* (5), in the reduced space of the 1st and 2nd canonical variables, for males.

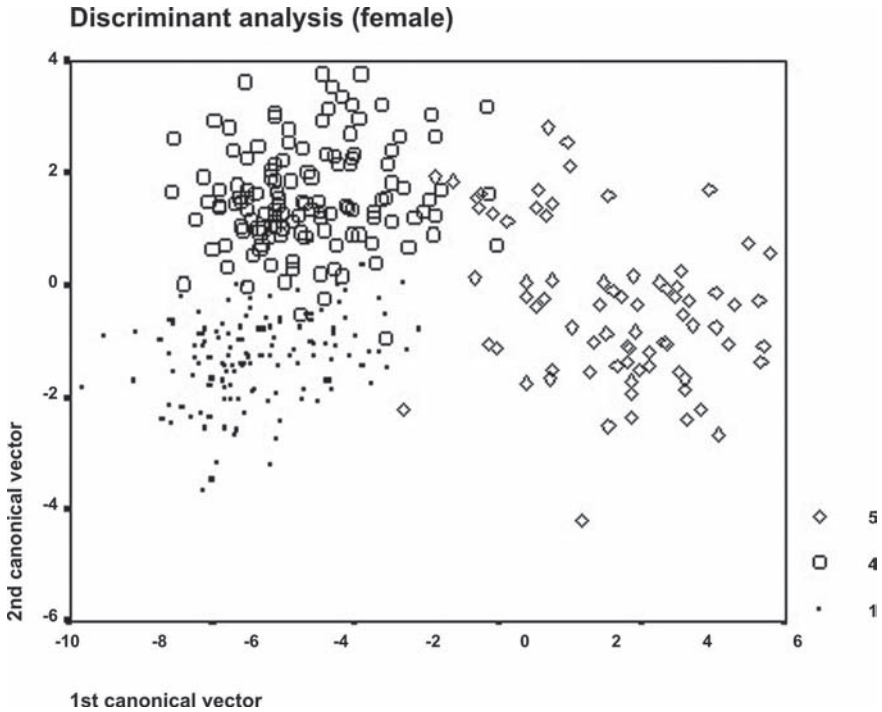

FIGURE 7: Projection of the individual scores of the combined samples for *Rhinella granulose* (1), *R. major* (4), and *R. mirandaribeiroi* (5), in the reduced space of the 1st and 2nd canonical variables, for females.

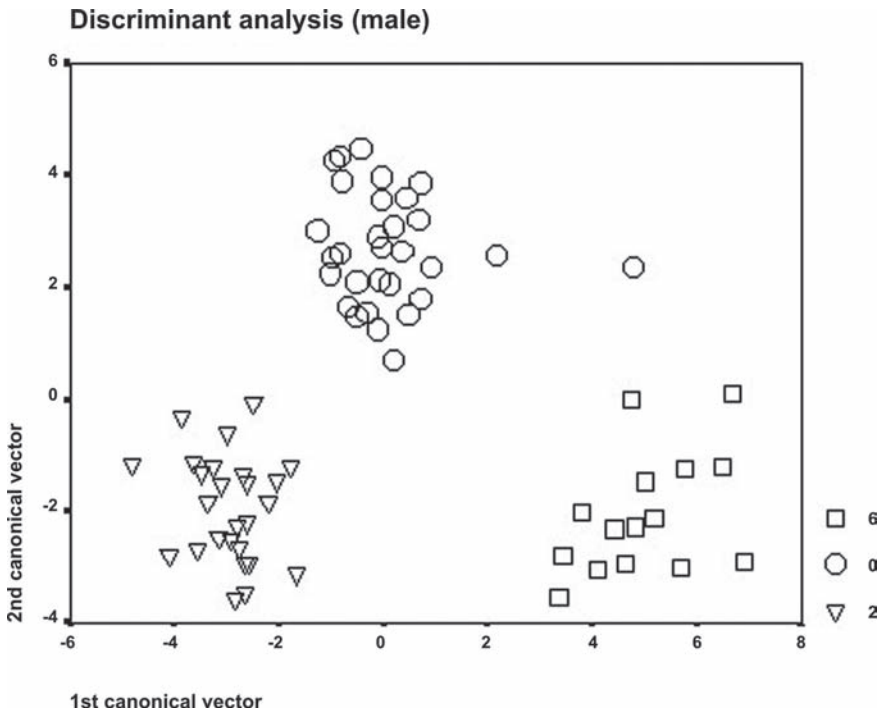

FIGURE 8: Projection of the individual scores of the combined samples for *Rhinella pygmaea* (2), *R. bergi* (3), and *R. azarai* (6), in the reduced space of the 1st and 2nd canonical variables, for males.

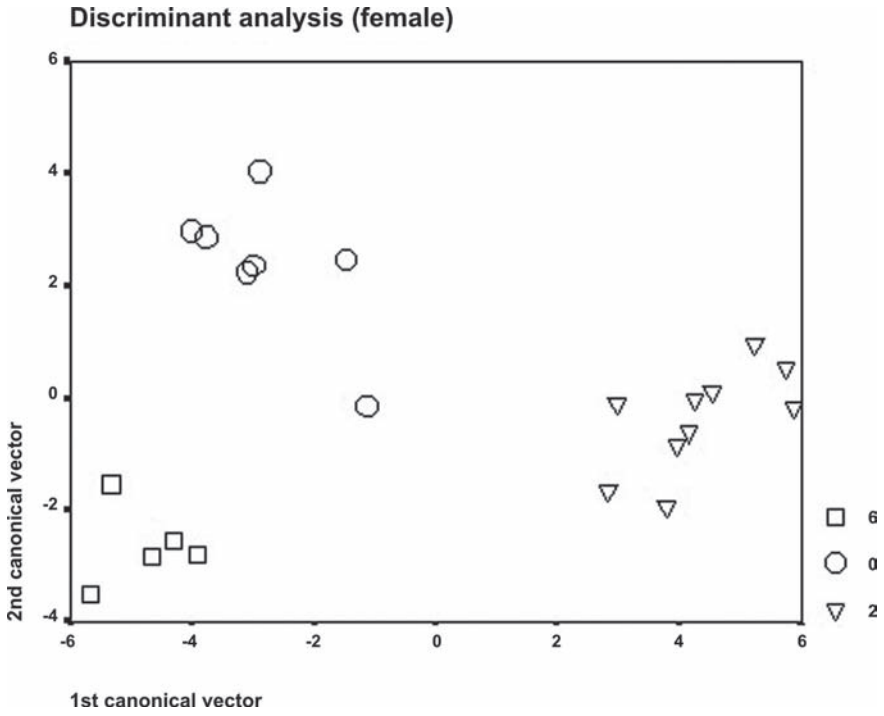

FIGURE 9: Projection of the individual scores of the combined samples for *Rhinella pygmaea* (2), *R. bergi* (3), and *R. azarai* (6), in the reduced space of the 1st and 2nd canonical variables, for females.

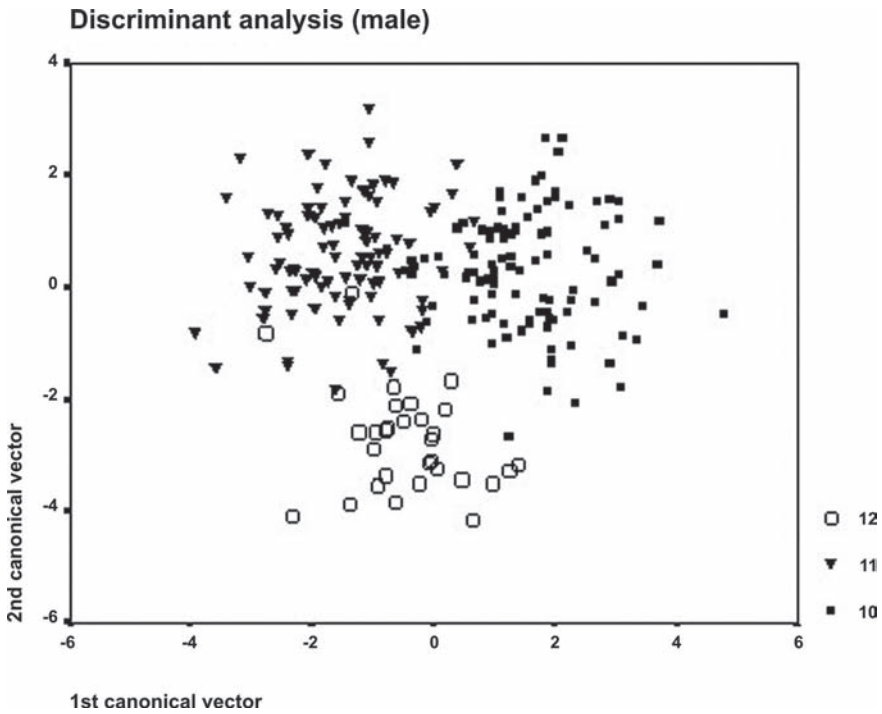

FIGURE 10: Projection of the individual scores of the combined samples for *Rhinella merianae* (**10**), *R. humboldti* (**11**) and *R. centralis* sp. n. (**12**), in the reduced space of the 1st and 2nd canonical variables, for males.

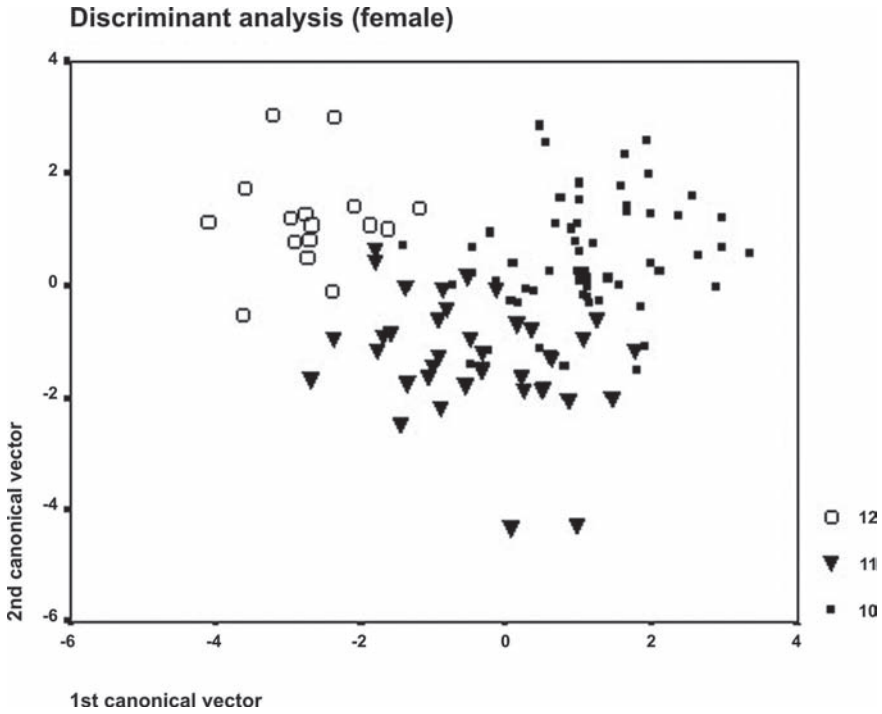

FIGURE 11: Projection of the individual scores of the combined samples for *Rhinella merianae* (**10**), *R. humboldti* (**11**), and *R. centralis* sp. n. (**12**), in the reduced space of the 1st and 2nd canonical variables, for females.

Rhinella pygmaea, R. bergi, and *R. azarai* showed a neat separation between taxa, for males and females (Figs. 8 and 9). For males, IOD_2 and IOD_1 account for the first discriminant function, and PGW and PGH account for the second (Table 16). For females, PGW is the variable that accounts for the first discriminant function, and ED accounts for the second function (Table 16). For males, IOD_2 and IOD_1 are significantly different among the three species (Tukey, ANOVA; $p < 0.01$); and PGW and PGH are significantly different between *R. pygmaea* and *R. bergi,* and between *R. pygmaea* and *R. azarai* (Tukey, ANOVA; $p < 0.001$). For females, PGW differs significantly among OTUs 2, 3, and 6 (Tukey, ANOVA; $p < 0.001$), and ED differs significantly between OTUs 3 and 6 (Tukey, ANOVA; $p < 0.001$).

Rhinella merianae, R. humboldti, and *R. centralis* sp. n. present a slight overlapping, as showed in Figs. 10 and 11. The values of the discriminant functions are in Table 17. The variable PGH accounts for the first function, for males and females; variables END and STCL account for the second function, respectively, for males and females. For males, END is significantly different between *R. merianae* and *R. centralis* sp. n., and between *R. humboldti* and *R. centralis* sp. n. (Tukey, ANOVA; $p < 0.001$). For females, PGH and STCL are significantly different between *R. merianae* and *R. humboldti,* and between *R. merianae* and *R. centralis* sp. n.

Results of the statistical analysis presented here corroborate the taxonomic groups that were assigned based on morphological external characters.

Species accounts

1. *Rhinella granulosa* (Figure 12)

Bufo (*Oxyrhynchus*) *granulosus* Spix, 1824
Bufo globulosus Spix, 1824
Chaunus marmoratus Wagler, 1828
Bufo (*Rhinella*) *granulosus* – Cuvier, 1829
Chaunus globulosus – Wagler, 1830
Bufo inutulus Wiegmann, 1833
Phrynoidis granulosus – Cope, 1863
Bufo granulosus granulosus – Müller & Hellmich, 1936
Chaunus granulosus – Frost *et al.,* 2006
Rhinella granulosa – Chaparro *et al.,* 2007
Rhinella granulosus – Pramuk *et al.,* 2008

Holotype: ZSM 40/0; according to Gallardo (1965) and Hoogmoed & Gruber (1983); the holotype was destroyed during World War II.

Type locality: Provincia Bahiae.

Comments: The usual concept of type locality as we know today did not exist in the 19th century, and species were registered for the common area where they occur (Vanzolini, 1981). On Spix's books we can find different ways of registering a type locality: from the name of the country or the state, to better defined localities. Spix & Martius extensively traveled in the State of Bahia, which limits were smaller than the actual size of the state, and they collected in all possible environments, from Caatinga to Atlantic Forest (Vanzolini, 1981).

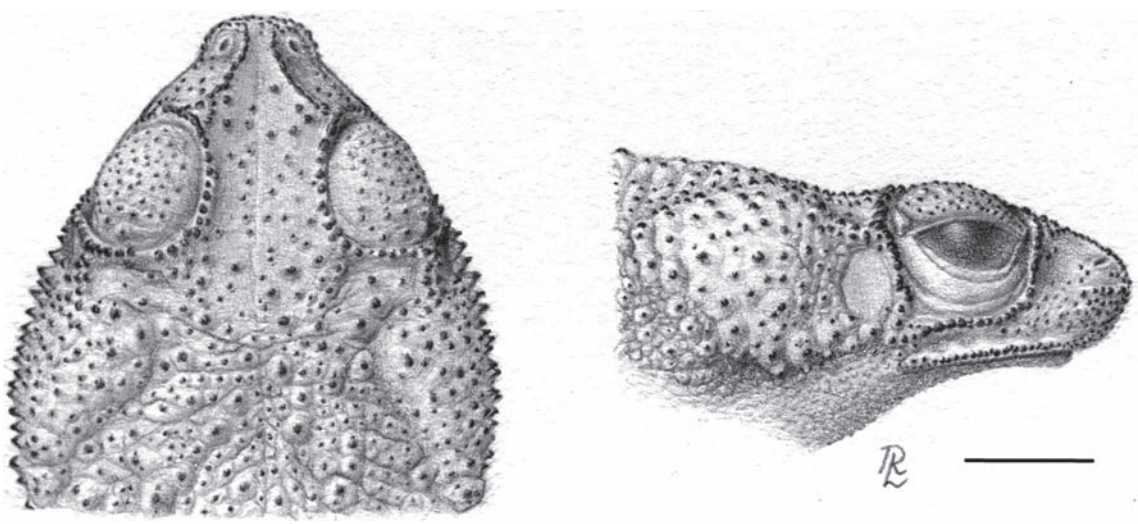

FIGURE 12: *Rhinella granulosa,* MZUSP 38800 (Campo Formoso, Bahia), dorsal and lateral views of head. (Scale bar = 5 mm).

Taxonomic nomenclatural comment: Rhinella granulosa was described by Spix (1824:51), based on a specimen from Bahia. In the same book (1824:49), Spix described *Rhinella globulosa* from Itapicuru River. In 1872, Peters re-examined the types and, disregarding page priority, synonymized the two species choosing *R. granulosa* as a senior name. Both types were destroyed during World War II (Hoogmoed & Gruber 1983), and Peters' decision is sanctioned by the International Code of Zoological Nomenclature as the first reviser (Myers & Carvalho 1952). Nevertheless, because of the non-accurate recordings of the type localities in the 19th century publications, there is still a remaining question regarding the type locality of *Rhinella globulosa* (Vanzolini, 1981). The type locality (*ad flumen Itapicuru*) is uncertain because there are two rivers in Brazil named Itapicuru: one in the State of Bahia and another in the State of Maranhão, both within the Morfoclimatic Domain of the Caatinga (Ab'Saber, 1977), and both in the itinerary of Spix & Martius. In the Bahia State, the Itapicuru River was crossed near Queimadas (previously named Arraial do Santo Antonio das Queimadas); in the Maranhão State they traveled the Itapicuru River from Caxias to Arraial (Spix & Martius, 1981; Bokermann, 1966; Vanzolini, 1981). Bokernann (1966) suggested that the type locality of *Rhinella globulosa* should be Queimadas, contrarily to Vanzolini (1981) who claimed that it should be between Caxias and Arraial. According to Martius' description of the trip, the region of Queimadas was under an intense drought as it had not rained for three years, and the Itapicuru River was dry, formed by a series of small ponds (Spix & Martius, 1981). On the other hand, the trip throughout the Itapicuru River in Maranhão took 13 days, and several stops were made at small villages along the river. *Rhinella crucifer, Iguana iguana,* and *Kentropyx calcarata,* also described under the type locality *"ad flumen Itapicuru",* occur both in Bahia and Maranhão. The fact that Martius cited specimens of *Iguana iguana* (described as *Iguana viridis* by Spix) observed on the riverside of the Itapicuru River in Maranhão may indicate that *Iguana iguana* was then collected in Maranhão. This may be an indication that all the other specimens, in which the type locality is cited as *ad flumen Itapicuru,* were collected in Maranhão. As far as we presently know, if *Rhinella globulosa* was collected in Bahia, it is certainly a synonym of *Rhinella granulosa.* On the contrary, if it was collected in Maranhão, it may be referred to another species and the name *R. globulosa* should be valid. Unfortunately, we do not have any further information on that subject, and *Rhinella globulosa* is so far been kept in the synonymy of *Rhinella granulosa.*

Diagnosis: Adult males ranging from 31.4 to 62.4 mm (SVL x = 48.1 mm, n = 255), and adult females ranging from 31.5 to 76.6 mm (SVL x = 52.9 mm, n = 150); cephalic crests predominantly granulose; supraorbital crest rounded, low; infraorbital crest short (not extending posteriorly beyond pos-orbital crest); supratympanic crest granulose, short (STCL 3.1-7.7% SVL); parietal crest absent or inconspicuous; maxillary crest reduced, not visible in dorsal view; snout rounded in dorsal and lateral views, long, posterior margin of nostrils surpasses anterior margin of mandible; longitudinal dorsal stripe usually present; belly usually not pigmented; interorbital distance short (IOD_2 7.2-11.3% SVL).

Comparison between species: Rhinella pygmaea, R. bergi, and *R. azarai* present a smaller adult medium size (males 32.1 mm, 40.4 mm, 42.1 mm; females 40.8 mm, 49.9 mm, 45.4 mm, respectively), cephalic crests predominantly continuous, parietal crest present, a high supraorbital crest, and a long infraorbital crest; *R. major* presents a straight snout in lateral view and squared in dorsal view, and a maxillary crest highly developed and visible in dorsal view; *R. dorbignyi* and *R. fernandezae* present a straight snout in lateral view and squared in dorsal view, smaller parotoid glands, and a longer distance between tympanum and postorbital crest, continuous keratinized crests, and a high supraorbital crest; *R. mirandaribeiroi* presents a longitudinal dorsal stripe, an elongated head, snout wider and flattened dorsoventrally, and loreal region distinctly visible in dorsal view; *R. nattereri* presents a rounded head with a long snout, snout straight in lateral view and squared in dorsal view, a high supraorbital crest, and larger parotoid glands; *R. merianae* and *R. centralis* sp. n. present larger parotoid glands, a high supraorbital crest, head extensively warted, snout narrower in lateral view and sloping dorsoventrally; *R. humboldti* presents larger parotoid glands, crest predominantly continuous, and a high supraorbital crest.

Description: Head subtriangular, wider than long (width 29.1-37.5% SVL, length 22-30% SVL), and low (height 12.7-15.5% SVL). Snout rounded in dorsal and lateral views, long in dorsal and lateral views; maxilla projecting over mandible anteriorly; in lateral view, posterior margin of the nostril surpassing anterior margin of mandible. Eye lateral, encapsulated, its diameter approximately equal to interorbital distance and larger than eye-nostril distance. Nostrils subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely

disposed in relation to longitudinal axis of head. *Canthus rostralis* distinctly angulated, highlighted by keratinized canthal crest. Loreal region scantly visible in dorsal view, slightly concave near the eye. Upper lip with a slightly sharp border highlighted by a keratinized maxillary crest, upper lip not flared. Tympanum oval, higher than wider, near the postorbital crest (DTP 0.6-1.3% SVL), with inconspicuous borders. Parotoid gland dorsolateral, conspicuous, borders well delimited, subtriangular, vertex pointing down, wider than higher (width 11.7-22.4% SVL; height 10.1-21.1% SVL).

Cephalic crests with conspicuous borders and keratinized granules. Supraorbital crest rounded, low, with small irregularly shaped and usually spaced granules, separated by non-keratinized areas, its interorbital portion strongly curved (IOD_2/IOD_1 x = 0.82) not forming a straight line with supratympanic crest. Preorbital crest granulose, occasionally bulky, with partially fused granules; postorbital crest straight, with no branching toward tympanum, long, reaching lower margin of eye, reaching or not the infraorbital crest. Infraorbital crest granulose, slightly curved, short, with no lateral expansion. Supratympanic crest short and straight, with irregular shaped and sized granules, which may be fleshy and occasionally coalescent, aligned in one or two irregular rows, posterior portion not dilated. Parietal crest inconspicuous or absent. Canthal crest slightly curved, diverging posteriorly, usually continuous by the irregular coalescence of a few granules, not reaching preorbital crest, extending anteriorly to tip of snout or ending at the level of anterior margin of nostril. Subnasal crest long, its posterior portion extending beyond posterior margin of nostril, usually bulky and continuous by the coalescence of irregular granules. Maxillary crest reduced and with interrupted regions of keratin, its keratinization slightly invading the ventral surface of maxilla, usually not visible in dorsal view; posterior lateral portion of maxilla (between infraorbital and maxillary crests) flat or slightly concave.

Palmar and metatarsal tubercles, and tip of toes and fingers slightly cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, oval, salient, subconical in lateral view. Nuptial asperities present on dorsum of fingers I and II, and on part of inner palmar tubercle in males. Relative size of fingers: I ≥ II ≤ IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical, variable in size, smaller than subarticulars. Hindlimbs short, tibio-tarsal articulation reaches axilla, and only fourth toe surpasses the snout when the leg is stretched and adjoined to the body. Inner metatarsal tubercle oval, salient, subconical in lateral view, slightly larger than the outer one, rounded, salient, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½⁺-1 V; distal subarticular tubercle of fourth toe divided, one element larger than its symmetrical; supranumerary tubercles conical, variable in size, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable size, conical with keratinized apices; larger conical or fleshy tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, especially between parotoids. Belly with small granules, adjoined, conical or not. Upper eyelid with small, scattered granules, with or without keratinized spicules, external margin with dots of keratin, irregularly aligned. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized granules, not fleshy, usually with spicules; small points of keratin, slightly spiculated, on the tip of snout and below subnasal crest. Ventral surface of maxilla with minuscule keratinized spicules, aligned in irregular rows. Interorbital area with scattered, conical or flattened, keratinized granules, usually not fleshy; small, keratinized granules between tympanum and postorbital crest; smooth or slightly keratinized granules between tympanum and parotoid gland.

In preserved specimens, dorsum light or dark brown with large scattered darker spots, or with small, darker, closely placed spots forming a mosaic; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; mid-dorsal longitudinal stripe absent; labial stripe present, lightly colored, of variable width. Belly yellowish or light cream, usually scattered with small dark spots.

Variation: Although extremely rare, a few individuals may present a mid-dorsal longitudinal stripe. Certain individuals may present reduced nuptial asperities in the lateral sides of finger III; parotoid glands can be highlighted by having a conspicuous olive color or by having a color different from dorsum. The labial light stripe may be dotted with small dark spots.

Younger specimens present more spaced granules in the cephalic crests, with lower concentration of keratin; maxillary and subnasal crests not conspicuous, formed by a conglomeration of small spaced granules. For descriptive statistics, see Table 1.

Distribution: Northeastern Brazil, predominantly at Caatinga Domain, occurs in the States of Minas Gerais, Bahia, Espírito Santo, Alagoas, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe. See map at Figure 13.

Natural history: Rhinella granulosa is an explosive breeding toad, spawning in temporary ponds after heavy rains. It can form reproductive gatherings that do not last more than one or two days.

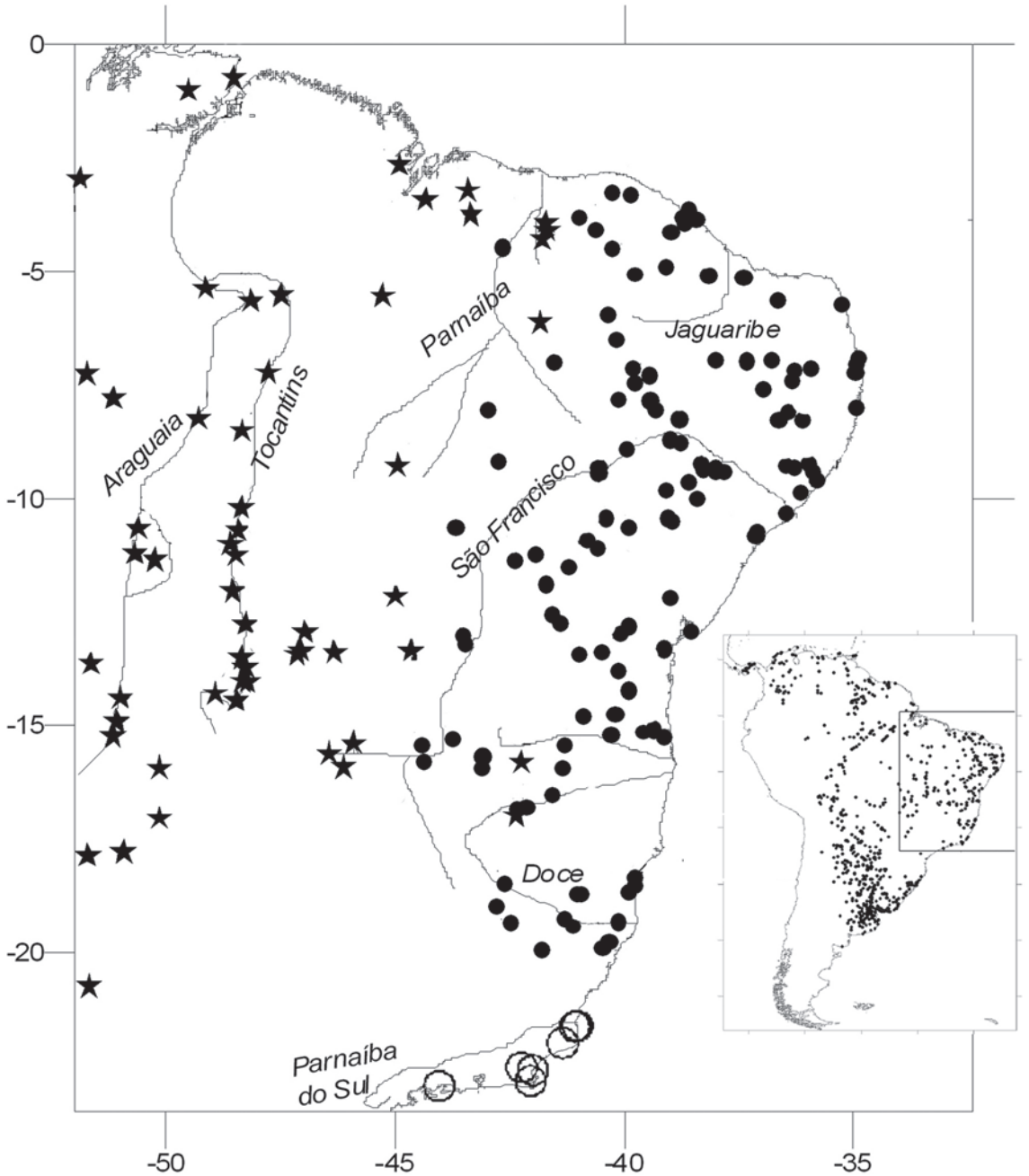

FIGURE 13: Geographic distribution of *Rhinella granulosa* (closed circles), *R. mirandaribeiroi* (black stars), and *R. pygmaea* (open circles).

TABLE 1: Descriptive statistics of measurements (in mm) of males (N = 255) and females (N = 150) of *Rhinella granulosa* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	48.10	52.89	31.4	31.5	62.4	76.6	6.28	10.11
HW	15.97	16.99	11.1	11.1	19.9	22.7	1.80	2.65
HL	12.72	13.24	8.6	8.5	16.7	17.3	1.37	2.07
IND	1.97	2.11	1.3	1.3	2.8	3.0	0.28	0.37
SW	5.11	5.46	3.6	3.5	6.6	7.3	0.59	0.87
END	3.34	3.49	2.2	2.3	4.3	4.8	0.38	0.51
ESD	5.24	5.57	3.7	3.5	6.9	7.8	0.60	0.91
IOD1	5.50	5.90	3.9	3.8	7.2	7.7	0.63	0.89
IOD2	4.49	4.85	3.2	3.0	6.2	6.7	0.57	0.82
ED	4.39	4.49	3.1	3.0	5.4	6.1	0.42	0.69
TD	2.36	2.32	1.3	1.2	3.3	3.5	0.36	0.50
TH	2.87	2.82	1.6	1.7	3.8	4.4	0.40	0.55
EW	3.91	4.10	2.8	2.6	5.3	5.6	0.42	0.59
PGW	8.45	9.33	4.1	4.9	13.2	16.1	1.61	2.12
PGH	6.58	7.28	3.8	4.2	11.0	11.8	1.22	1.53
STCL	2.42	2.61	1.5	1.2	3.7	4.6	0.40	0.54
POS	4.06	4.14	2.4	2.4	6.5	6.7	0.61	0.84
THL	10.83	11.73	7.3	7.2	14.5	17.0	1.47	2.20
TIL	17.51	18.40	10.8	10.8	24.3	28.3	2.67	3.82
TAL	16.31	16.90	10.5	10.0	22.3	25.4	2.51	3.45
HAL	10.96	11.45	7.0	6.7	14.9	17.2	1.68	2.32
FOL	17.41	17.99	10.6	10.6	29.8	26.4	2.64	3.53

2. *Rhinella pygmaea* (Figure 14)

Bufo pygmaeus Myers & Carvalho, 1952; Cei & Roig, 1964.

Bufo granulosus pygmaeus – Gallardo, 1965; Bokermann, 1966.

Chaunus pygmaeus – Frost *et al.,* 2006.

Rhinella pygmaea – Chaparro *et al.,* 2007, by implication.

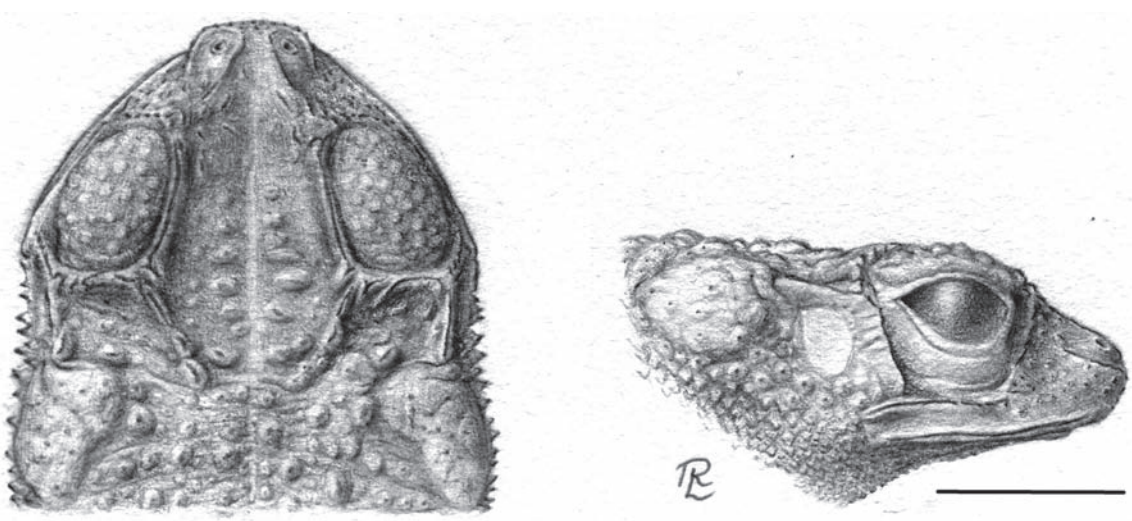

FIGURE 14: *Rhinella pygmaea,* MNRJ 2331 (Holotype), dorsal and lateral views of the head. (Scale bar = 5 mm).

Holotype: MNRJ 2331.

Type locality: São João da Barra, Rio de Janeiro, Brazil.

Diagnosis: Adult males ranging from 24.6 to 42.7 mm (SVL x = 32.1 mm, n = 28), and adult females ranging from 28.8 to 49.1 mm (SVL x = 40.8 mm, n = 15); cephalic crests continuous; infraorbital crest long, with posterior lateral expansion visible in dorsal view; parietal crest present; supratympanic crest long (STCL 5.9-9.1% SVL), slightly curved, sloping upwards posteriorly; interorbital portion of the supraorbital crest almost straight, parallel; snout rounded in lateral and dorsal views; belly pigmented; tympanum not close to postorbital crest (DTP 2.1-3.1% SVL); loreal region distinctly visible in dorsal view.

Comparison between species: Rhinella bergi presents a vertical snout in lateral view and squared in dorsal view, a larger parotoid gland, and a shorter supratympanic crest; *R. azarai* presents a flared upper lip, forming an extended horizontal flap, which lead to a rounded head and a short snout in dorsal profile, a smaller eye, and a longer interorbital distance; *R. granulosa* presents predominantly granulose cephalic crests, absence of parietal crest, and a short infraorbital crest; *R. major* presents a vertical snout in lateral view and squared in dorsal view, infraorbital crest not prolonged, and absence of parietal crest; *R. dorbignyi* and *R. fernandezae* present a short snout in lateral and dorsal views, postorbital space wider and extremely smooth; *R. mirandaribeiroi* presents granulose cephalic crests, supraorbital crest low and curved, snout wider and sloping dorsoventrally; *R. nattereri* presents rounded head, snout straight in lateral view and squared in dorsal view, interorbital area with numerous keratinized granules, and a larger parotoid gland; *R. merianae, R. humboldti,* and *R. centralis* sp. n. present cephalic crests predominantly granulose or serrate, larger parotoid glands, and parietal crest absent or inconspicuous.

Description: Head subtriangular, high (height 15.4-18.3% SVL), wider than long (width 32-40.5% SVL, length 25.5-32% SVL). Snout rounded and long in dorsal and lateral views; maxilla projecting ahead of mandible anteriorly in lateral view, posterior margin of nostril surpasses anterior margin of mandible. Eye lateral, encapsulated, its diameter approximately equal to interorbital distance and larger than eye-nostril distance. Nostrils subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region distinctly visible in dorsal view, its superior half concave, inferior half strongly oblique; upper lip not flared, with a slightly sharp border highlighted by keratinized maxillary crest. Tympanum oval, higher than wider, with inconspicuous borders, not close to postorbital crest (DTP 2.1-3.1% SVL). Parotoid glands dorsolateral, conspicuous, borders not well delimited, rounded or elongated, slightly wider than higher (width 9.8-15.3% SVL; height 7.3-14.8% SVL).

Cephalic crests predominantly continuous, with conspicuous and keratinized borders. Supraorbital crest high, continuous, serrate or not, with gaps and wrinkles, rounded, interorbital portion straight, almost parallel or diverging posteriorly (IOD_2/IOD_1 males x = 0.94; females x = 1.0), not forming a straight line with supratympanic crest, posterior portion usually wrinkled. Preorbital crest continuous, occasionally with gaps, not fleshy. Postorbital crest long, straight or medially curved, usually with perpendicular branches toward tympanum, reaching lower margin of eye, and reaching or not the infraorbital crest. Infraorbital crest predominantly continuous, long, posteriorly extending beyond postorbital crest, straight or slightly curved, occasionally with gaps and wrinkles, and with perpendicular branches toward maxillary crest and loreal region; a posterior lateral expansion may be present and it is visible in dorsal and ventral views. Supratympanic crest long, slightly curved and posteriorly inclined upwards, continuous, posterior portion occasionally dilated. Parietal crest present, continuous, occasionally with gaps. Canthal crest continuous, slightly curved, posteriorly diverging, occasionally reaching preorbital crest and extending beyond anterior margin of nostril. Subnasal crest long, its posterior portion extending beyond posterior margin of nostril, not fleshy, continuous. Maxillary crest developed and continuous, its keratinization reaches the ventral surface of maxilla, usually not visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) concave.

Palmar and metatarsal tubercles, and tip of toes and fingers slightly cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, oval, salient; nuptial asperities on dorsum of fingers I and II, and in part of the inner palmar tubercle in males. Relative size of fingers: I < II < IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of

fingers absent; distal subarticular tubercle of the third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than subarticulars. Hindlimbs short, tibiotarsal articulation reaches axilla and only fourth toe surpasses the snout when the leg is stretched and adjoined to the body. Inner metatarsal tubercle oval, high, subconical in lateral view, larger than the outer one, rounded, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½⁺-2 V; distal subarticular tubercle of fourth toe doubled, one element larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical, with keratinized apices; larger conical or fleshy tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, especially between parotoids. Belly with small adjoined granules, conical or rounded. Upper eyelid with granules of variable size, usually rounded, keratinized, external margin irregularly keratinized. Parotoids with individualized, fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized, usually elongated, and highly fleshy granules; small points of keratin, not fleshy, on tip of snout, larger ones below subnasal crest. Ventral surface of maxilla with minuscule keratinized spicules, aligned in regular or irregular rows, usually concentrated at the inner margin. Interorbital area with granules of variable sizes, conical or rounded, keratinized, usually fleshy; area between tympanum and postorbital crest with keratinized granules of variable sizes, elongated or rounded; area between tympanum and parotoid gland with small granules, conical, with keratinized apices.

In preserved specimens, dorsum brownish light with small, dark, and closely placed spots, forming a mosaic; extension of spots may vary rendering individuals more or less melanic; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; mid-dorsal longitudinal stripe present or absent; labial stripe present, light colored, of variable thickness. Belly light cream, with small dark spots.

Variation: The labial light stripe may be dotted with small dark spots.

Distribution: Apparently restricted to Restinga areas in the Rio de Janeiro State, Brazil. Probably associated with sandy lowlands (Izecksohn & Carvalho e Silva, 2001). The Northern limit of distribution reaches the city of São João da Barra, and the Southern, Mangaratiba. See map in Figure 13.

Natural history: According to Carvalho e Silva & Carvalho e Silva (1994), *R. pygmaea* lives in Restinga areas, and remains burrowed inside hollows, getting out only in order to eat. Reproduction occurs in temporary ponds, after heavy rains right after the dry season (Carvalho e Silva & Carvalho e Silva, 1994).

3. *Rhinella bergi* (**Figure 15**)

Bufo bergi Céspedez, 2000
Bufo pygmaeus Cei, 1956a, 1956b, 1972, 1980; Cei & Roig, 1964; Contreras & Contreras, 1982; Lavilla, 1992; Stetson, 1994; Yanosky *et al.,* 1993, 1997; Bridarolli & Di Tada, 1994; Céspedez *et al.,* 1995
Chaunus bergi – Frost *et al.,* 2006
Rhinella bergi – Chaparro *et al.,* 2007

Holotype: UNNEC 2790 (Colección Herpetológica de la Universidad Nacional del Nordeste, Corrientes, Argentina).

Type locality: Corrientes, Provincia Corrientes, Argentina.

Diagnosis: Adult males ranging from 34.6 to 49.8 mm (SVL x = 40.4 mm, n = 31), and adult females ranging from 36 to 59.3 mm (SVL x = 49.9 mm, n = 8); cephalic crests predominantly continuous; infraorbital crest long; lateroposterior expansion of infraorbital crest visible in dorsal view; snout squared in dorsal view, straight in lateral view; belly pigmented; longitudinal dorsal stripe usually present; parietal crest present; hindlimbs very short, tibio-tarsal articulation do not reach axilla, and fourth toe do not surpass the head when the leg is stretched and adjoined to the body.

Comparison between species: Rhinella pygmaea presents a rounded snout in dorsal and lateral views, a smaller parotoid gland, and a longer supratympanic crest; *R. azarai* presents a flared upper lip, forming an extended horizontal flap, which lead to a rounded head and a short snout in dorsal profile, a smaller eye, and a longer interorbital distance; *R. granulosa* presents cephalic crests predominantly granulose, in-

fraorbital crest short, and no parietal crest; *R. major* presents predominantly granulose crests, infraorbital crest short, parietal crest and longitudinal dorsal stripe absent; *R. dorbignyi* and *R. fernandezae* present snout squared in dorsal view and straight in lateral view, area between postorbital crest and tympanum larger and extremely smooth; *R. mirandaribeiroi* presents granulose crests, supraorbital crest low and curved, snout wider horizontally, and flattened dorsoventrally; *R. nattereri* presents a rounded head with a long snout, predominantly granulose crests, infraorbital crest short, and more developed parotoid glands; *R. merianae, R. humboldti,* and *R. centralis* sp. n. present predominantly granulose or serrate crests, more developed parotoid glands, and snout narrower horizontally and highly sloping dorsoventrally, parietal crest absent or inconspicuous, and longitudinal dorsal stripe absent.

Description: Head subtriangular, wider than long (width 30-39% SVL, length 23-29.5% SVL), high (height 14.5-17.1% SVL). Snout squared in dorsal view and straight in lateral view, long in dorsal and lateral views. Maxilla projecting ahead of the mandible anteriorly; in lateral view, posterior margin of nostril at the same level of anterior margin of the mandible. Eye lateral, encapsulated, its diameter smaller than interorbital distance and approximately equal to eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis almost parallel to the longitudinal axis of the head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region scantly visible in dorsal view, superior half slightly concave, inferior half almost straight. Upper lip with a slightly sharp border highlighted by keratinized maxillary crest, upper lip not flared. Tympanum oval, distinct, with conspicuous borders, higher than wider, not close to postorbital crest (DTP 1.4-2.4% SVL). Parotoid gland dorsolateral, conspicuous, borders well delimited, subtriangular, vertex pointing down, wider than higher (width 12.9-20.9% SVL; height 11.1-16.5% SVL).

Cephalic crests predominantly continuous, with pronounced and keratinized borders. Supraorbital crest high, continuous, frequently serrate, it can have gaps and wrinkles, rounded, not forming a straight line with supratympanic crest, interorbital portion almost parallel (IOD_2/IOD_1 x = 0.9), posterior portion usually wrinkled. Preorbital crest may be granulose or continuous, usually with gaps and irregularly wrinkled, usually bulky. Postorbital crest continuous or granulose, straight or slightly curved, occasionally with perpendicular branches toward tympanum, long, sometimes surpassing lower margin of the eye, not reaching infraorbital crest. Infraorbital crest almost straight, continuous, occasionally with gaps, long, posteriorly extending beyond postorbital crest; a posterior lateral expansion is visible in dorsal view, posterior portion occasionally bulky. Supratympanic crest long, straight or slightly inclined upwards posteriorly, continuous, occasionally with gaps, posterior portion occasionally dilated. Parietal crest present, continuous, sometimes with gaps, or formed by rounded tubercles more or less aligned. Canthal crest continuous, occasionally reaching preorbital crest,

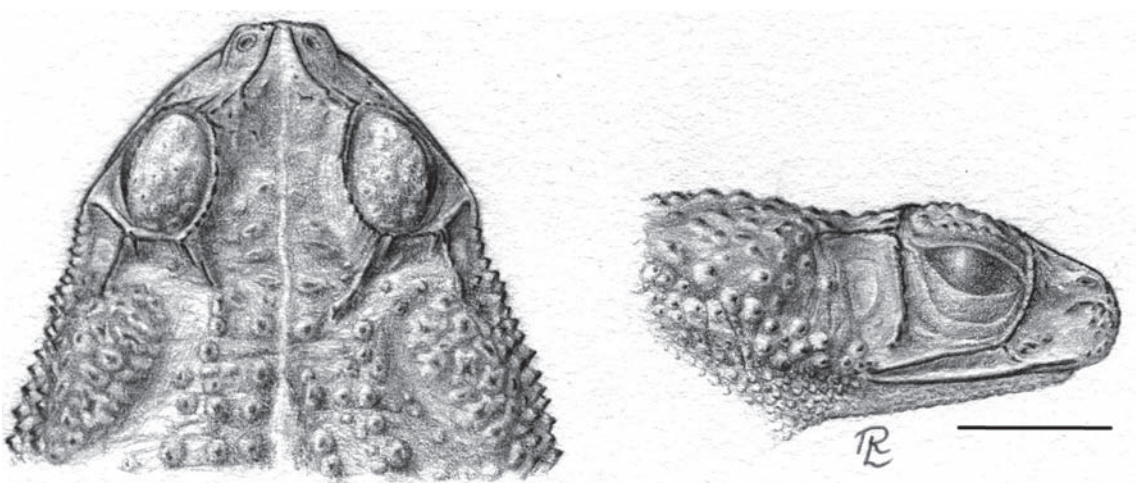

FIGURE 15: *Rhinella bergi,* MZUSP 125074 (Puerto Antequera, Chaco, Argentina), dorsal and lateral views of the head. (Scale bar = 5 mm).

extending to tip of snout beyond anterior margin of nostril, slightly curved, diverging posteriorly. Subnasal crest short, its posterior portion not extending beyond posterior margin of nostril or slightly surpassing it, highly bulky, continuous. Maxillary crest developed, continuous, its keratinization reaches the ventral surface of maxilla, visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) distinctly concave.

Palmar and metatarsal tubercles and tip of fingers and toes cornified. External palmar tubercle rounded or oval, salient, twice or three times larger than the inner one, oval, salient, rounded in lateral view. Males with nuptial asperities on dorsum of finger I, reduced or absent on finger II, and absent on inner palmar tubercle. Relative size of fingers: I = II < IV < III; fingers without fringes, their lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than subarticulars. Hindlimbs very short, tibio-tarsal articulation do not reach axilla and tip of fourth toe do not surpass the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval, high, subconical in lateral view, slightly larger than the outer one, rounded or subtriangular, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½-2 V; distal subarticular tubercle of fourth toe doubled, one element distinctly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical, with keratinized apices; larger and rounded tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, especially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with just a few granules of variable sizes, rounded or spiculated, keratinized, external margin with dots of keratin, occasionally coalescent. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized granules, usually elongated and narrow, highly fleshy; small points of keratin, rounded and not fleshy, on tip of snout, larger ones below subnasal crest. Ventral surface of the maxilla with a few minuscule keratinized spicules, aligned or not. Interorbital area with large granules, rounded and keratinized, usually highly fleshy, slightly aligned in two longitudinal and parallel rows; area between tympanum and postorbital crest smooth or with small granules, keratinized, elongated or rounded; area between tympanum and parotoid gland with small granules, conical with keratinized apices.

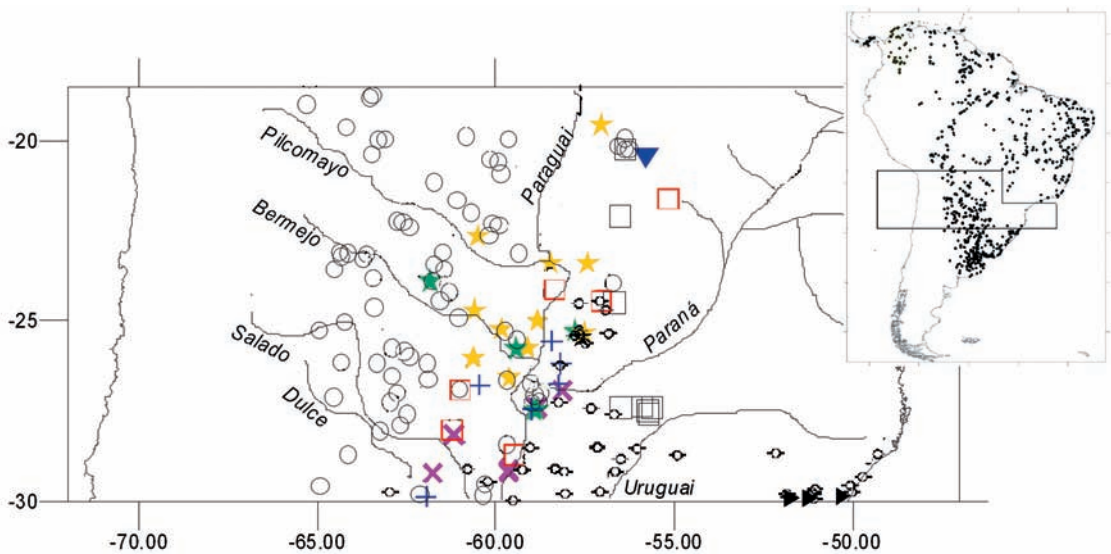

FIGURE 16: Geographic distribution of *Rhinella bergi* (red square), *R. azarai* (black square), partial distribution of *R. major* (large circle), *R. fernandezae* (small circle), and partial distribution of *R. dorbignyi* (black triangle). Sympatry of *R. major* and *R. mirandaribeiroi* (blue triangle); *R. bergi* and *R. major* (yellow star); *R. bergi* and *R. fernandezae* (red X); *R. major* and *R. fernandezae* (green star); *R. bergi, R. major,* and *R. fernandezae* (blue cross).

In preserved specimens, dorsum brownish or brownish light, with large and dark, closely placed spots, forming a mosaic; a lateral light stripe between parotoid and inguinal region, with irregular margins and occasionally with gaps, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe usually present; labial light stripe present, variable in width. Belly light cream, with high density of small dark spots.

Variation: The longitudinal dorsal stripe may be absent in some individuals. A few specimens present a dotted labial stripe. Larger individuals may present a flared upper lip (an expanded horizontal flap).

Distribution: The species occur in the Chaco region of Paraguay and Northwestern Argentina, where it is locally parapatric with *R. major* and *R. fernandezae;* and in Corumbá, in the Mato Grosso do Sul State, Brazil, where it is sintopic with *R. major* (C. Prado, *pers. comm.*). See maps in Figs. 16 and 25.

Natural history: According to Cei (1956a, b), the species is terrestrial and dig inclined hollows (cylindrical tunnels) in the ground near temporary pools in open areas. Vocalization is performed close to the entrance of the tunnel even during the day.

4. *Rhinella major*
(**Figure 17**)

Bufo granulosus major Müller & Helmich, 1936; Gallardo, 1965.

Bufo manicorensis Gallardo, 1961 – new synonym.

Bufo granulosus goeldii Gallardo, 1965 – new synonym.

Bufo granulosus minor Gallardo, 1965 – new synonym.

Bufo granulosus mini Gallardo, 1967 – new synonym.

Holotype: ZSM 153/1928. According to F. Glaw (*pers. comm.*), the holotype was probably destroyed during World War II.

Type locality: San José de Chiquitos, Santa Cruz, Bolivia.

Diagnosis: Adult males ranging from 35.8 to 72.8 mm (SVL x = 53.8 mm, n = 321), and adult females ranging from 33.9 to 81.1 mm (SVL x = 54.3 mm, n = 191); cephalic crests predominantly granulose; infraorbital crest short; parietal crest absent; interorbital portion of the supraorbital crest slightly curved; supratympanic crest short (STCL 3.5-7.4% SVL); snout squared in dorsal view and straight in lateral view; loreal region, maxillary crest, and labial light stripe visible in dorsal view; interorbital area and area between tympanum and parotoid gland usually smooth, without granules; belly not pigmented; longitudinal dorsal stripe absent.

Comparison between species: Rhinella pygmaea, R. bergi, and *R. azarai* present an average smaller size (males 32.1 mm, 40.4 mm, 42.1 mm; females 40.8 mm, 49.9 mm, 45.4 mm, respectively), cephalic crests predominantly continuous, parietal crest present and

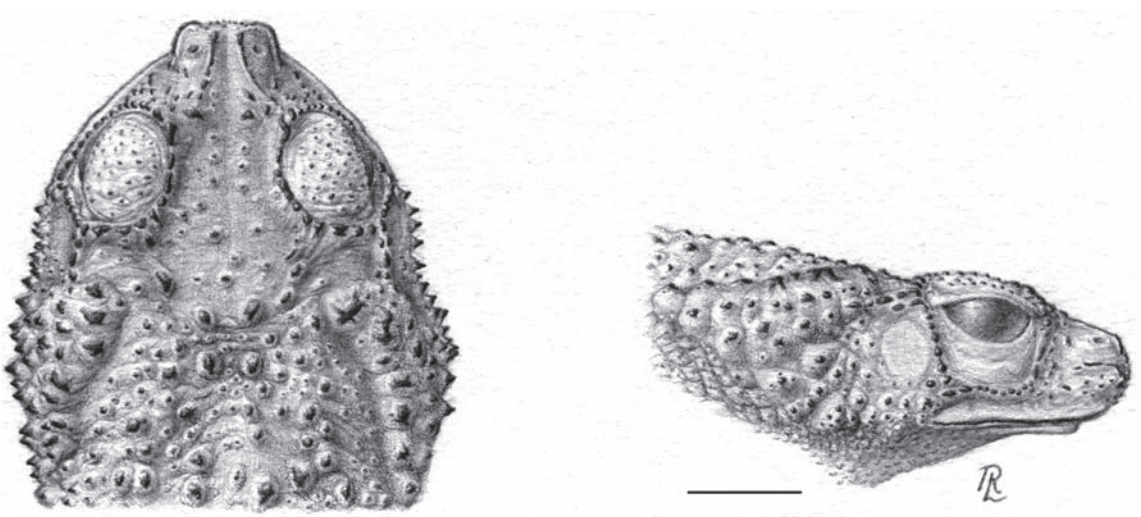

FIGURE 17: *Rhinella major,* MZUSP 21266 (San José de Chiquitos, Bolivia), dorsal and lateral views of the head. (Scale bar = 5 mm).

infraorbital crest long; *R. granulosa* presents rounded snout in dorsal and lateral views, and less developed maxillary crest; *R. dorbignyi* and *R. fernandezae* present snout squared in dorsal view and straight in lateral view, cephalic crests continuous and higher, postorbital space larger; *R. mirandaribeiroi* presents longitudinal dorsal stripe, snout wider in dorsal view and flattened dorsoventrally, less developed maxillary crest; *R. nattereri* presents rounded head with long snout, more developed parotoid glands, and interorbital area with numerous keratinized granules; *R. merianae, R. humboldti,* and *R. centralis* sp. n. present more developed parotoid glands, rounded snout in lateral view, snout narrower and sloping dorsoventrally.

Description: Head subtriangular, high (HH 13.6-16.5% SVL), wider than long (width 28-38% SVL, length 21-31% SVL). Snout squared in dorsal view and straight in lateral view, long in dorsal and lateral views, maxilla projecting ahead of mandible in lateral view, posterior margin of nostril at the level of anterior margin of mandible. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostrils subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis almost obliquely disposed in relation to longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest. Loreal region scantly visible in dorsal view, superior half slightly concave, inferior half barely straight. Upper lip with a slightly sharp border highlighted by keratinized maxillary crest, upper lip slightly flared laterally and labial light stripe visible in dorsal view. Tympanum oval, very close to postorbital crest (DTP 0.6-1.6% SVL), higher than wide, borders somewhat conspicuous. Parotoid glands dorsolateral, conspicuous, posterior and inferior borders not well delimited, subtriangular, vertex pointed down, wider than higher (width 11.8-22.8% SVL; height 9.1-17.6% SVL).

Cephalic crests predominantly granulose with conspicuous and keratinized borders. Supraorbital crest high, continuous and frequently serrate, occasionally with gaps and wrinkles, rounded, not forming a straight line with supratympanic and canthal crest, its interorbital portion slightly curved (IOD_2/IOD_1 x = 0.86), posterior portion usually wrinkled. Preorbital crest usually granulose, occasionally wrinkled, usually bulky. Postorbital crest usually granulose, straight, with no branching toward tympanum, long, reaching inferior margin of eye, usually not reaching infraorbital crest. Infraorbital crest usually curved and granulose, without lateral expansion, short, not posteriorly extending beyond postorbital crest, not posteriorly bulky. Supratympanic crest short, straight, continuous or granulose, posterior portion occasionally dilated. Parietal crest absent. Canthal crest continuous, straight or slightly curved, diverging posteriorly, usually not reaching preorbital crest, occasionally extending beyond anterior margin of nostril. Subnasal crest short, continuous, highly bulky, its posterior portion at the level of posterior margin of nostril. Maxillary crest developed and continuous, its keratinization reaches ventral surface of maxilla, part of which is visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) concave.

Palmar and metatarsal tubercles, and tip of toes and fingers cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, oval, salient. Nuptial asperities on dorsum of fingers I and II, and in part of the inner palmar tubercle in males. Relative size of fingers: I > II < IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than the subarticulars. Hindlimbs short, tibio-tarsal articulation reaches axilla and only fourth toe surpasses the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval or elongated, high, subconical in lateral view, larger than the outer one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized spicules; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½⁺ IV 3½⁺-2 V; distal subarticular tubercle of fourth toe doubled, one element distinctly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical with keratinized apices; larger rounded tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, specially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with a few small granules, keratinized, rounded or spiculated, external margin with dots of keratin, occasionally coalescent. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized granules, usually elongated, highly fleshy; small points of keratin, rounded and

TABLE 2: Descriptive statistics of measurements (in mm) of males (N = 28) and females (N = 15) of *Rhinella pygmaea* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	32.12	40.76	24.6	28.8	42.7	49.1	4.79	6.32
HW	11.58	13.84	8.9	10.1	14.7	17.1	1.72	2.16
HL	9.60	11.33	7.3	8.5	12.7	13.2	1.42	1.58
IND	1.26	1.43	1.1	1.0	1.6	1.8	0.14	0.23
SW	3.49	4.11	2.8	3.1	4.3	4.9	0.45	0.51
END	2.76	3.23	2.1	2.5	3.6	3.9	0.37	0.36
ESD	4.08	4.78	3.0	3.7	5.4	5.9	0.61	0.66
IOD1	3.76	4.40	3.0	3.5	4.8	5.3	0.48	0.57
IOD2	3.50	4.38	2.5	3.0	4.8	5.5	0.58	0.72
ED	3.22	3.77	2.4	2.6	4.2	4.4	0.50	0.57
TD	1.54	1.79	1.0	1.4	2.0	2.6	0.28	0.33
TH	1.80	2.13	0.9	1.3	2.4	2.9	0.40	0.39
EW	2.62	3.01	2.2	2.2	3.2	3.7	0.32	0.39
PGW	3.90	4.63	2.9	2.8	6.1	6.3	0.76	0.82
PGH	3.38	4.16	2.2	2.6	5.0	6.4	0.89	1.16
STCL	2.47	3.09	1.7	2.1	3.3	4.0	0.48	0.59
POS	3.37	3.98	2.4	2.8	4.8	5.5	0.57	0.75
THL	7.23	8.87	5.4	6.4	9.2	11.1	1.14	1.42
TIL	10.36	12.46	7.7	9.1	14.4	15.9	1.79	2.09
TAL	9.62	11.39	6.8	8.4	13.1	14.6	1.84	2.19
HAL	6.87	8.22	4.9	5.8	9.3	10.7	1.18	1.35
FOL	11.23	13.21	8.0	9.8	15.2	16.3	1.96	2.07

TABLE 3: Descriptive statistics of measurements (in mm) of males (N = 31) and females (N = 8) of *Rhinella bergi* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	40.37	49.93	34.6	36.0	49.8	59.3	3.85	6.94
HW	14.24	16.62	12.5	12.8	17.0	20.8	1.28	2.46
HL	10.47	12.38	9.1	9.3	12.3	14.1	0.88	1.50
IND	1.59	1.83	1.2	1.4	2.0	2.2	0.21	0.27
SW	4.09	4.69	3.5	3.7	5.0	5.4	0.39	0.54
END	3.10	3.60	2.6	2.7	3.6	4.1	0.27	0.46
ESD	4.46	5.25	3.8	3.9	5.2	5.9	0.38	0.68
IOD1	4.81	5.78	4.1	4.5	5.9	6.5	0.46	0.63
IOD2	4.35	5.28	3.6	4.1	5.9	6.2	0.52	0.64
ED	3.36	4.03	2.6	2.9	4.1	4.5	0.33	0.53
TD	1.65	2.01	1.3	1.2	2.1	2.7	0.21	0.42
TH	2.25	2.59	1.8	1.7	2.8	3.1	0.26	0.45
EW	3.00	3.65	2.6	2.6	3.6	4.2	0.25	0.52
PGW	6.34	8.78	4.9	5.0	8.0	10.4	0.87	1.89
PGH	5.34	6.57	4.4	4.6	6.7	7.9	0.69	1.11
STCL	2.63	2.99	2.1	2.5	3.4	4.0	0.30	0.54
POS	3.79	4.54	3.1	3.4	4.8	6.0	0.47	0.86
THL	8.87	10.52	7.5	7.5	10.5	13.4	0.84	1.78
TIL	13.36	16.39	10.8	10.9	16.5	19.6	1.57	2.78
TAL	12.61	14.99	10.4	9.7	15.9	17.7	1.41	2.65
HAL	8.46	10.05	7.2	6.9	10.4	11.9	0.87	1.66
FOL	13.21	15.70	10.7	11.1	16.4	18.4	1.36	2.36

TABLE 4: Descriptive statistics of measurements (in mm) of males (N = 321) and females (N = 191) of *Rhinella major* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	53.78	54.33	35.8	33.9	72.8	81.1	7.50	8.77
HW	18.05	17.92	12.0	12.1	25.2	34.4	2.21	2.68
HL	13.66	13.40	10.1	8.9	17.6	17.8	1.38	1.67
IND	2.06	2.04	1.4	1.3	3.0	3.4	0.30	0.32
SW	5.33	5.24	3.8	3.5	7.5	7.4	0.67	0.71
END	3.68	3.73	2.7	2.8	4.5	5.4	0.35	0.41
ESD	5.67	5.67	4.2	4.1	7.3	7.4	0.55	0.64
IOD1	6.34	6.37	4.7	4.7	8.4	8.9	0.79	0.86
IOD2	5.47	5.49	3.5	3.5	7.8	9.1	0.74	0.92
ED	4.73	4.56	3.5	3.2	6.4	6.7	0.53	0.61
TD	2.49	2.28	1.4	1.2	3.8	3.5	0.40	0.45
TH	3.18	3.00	1.9	2.1	4.5	4.6	0.45	0.47
EW	4.07	4.00	2.6	2.7	6.5	5.4	0.44	0.49
PGW	9.48	9.63	4.8	6.1	13.8	15.2	1.64	1.74
PGH	7.41	7.35	3.8	4.8	10.7	10.8	1.19	1.30
STCL	2.85	2.80	1.9	1.7	4.1	4.1	0.39	0.50
POS	4.81	4.65	3.3	3.0	6.8	6.9	0.65	0.73
THL	11.88	11.78	8.3	8.0	16.1	17.1	1.56	1.72
TIL	19.21	18.32	12.2	12.0	28.2	29.1	3.32	3.15
TAL	18.18	17.10	11.9	9.5	27.8	26.0	3.05	2.88
HAL	12.17	11.61	8.1	7.2	17.7	17.9	1.91	2.02
FOL	18.68	17.37	12.2	10.8	27.5	25.1	2.75	2.69

not fleshy, on tip of snout, larger ones below subnasal crest. Ventral surface of maxilla with a few minuscule keratinized spicules, aligned or not. Interorbital area smooth or with large and rounded or small and spiculated keratinized granules; area between tympanum and postorbital crest smooth, usually without granules; area between tympanum and parotoid gland with small conical granules with keratinized spicules.

In preserved specimens, dorsum brownish light with scattered or closely placed dark spots, forming a mosaic; a lateral light stripe between parotoids and inguinal region, with irregular margins and occasionally with gaps, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe absent; labial light stripe present, visible in dorsal view. Belly light cream, without pigmentation.

Variation: A few specimens may have numerous tiny spicules of keratin around the central apex of conical tubercles that cover dorsum, lateral portion of parotoids, and limbs. See descriptive statistics in Table 4.

Distribution: occurs in the chaco region, Argentina, Paraguay, and Bolivia, and in open formations along the rivers Beni, Madeira, Amazonas, Tapajós, and Xingú, and in the Amapá state, Brazil. See map in Figs. 16, 19, and 25.

Natural history: Reproduction occurs in temporary ponds in open areas, covered by grass (A. Lopez, *pers. comm.*).

5. *Rhinella mirandaribeiroi* (Figure 18)

Bufo granulosus mirandaribeiroi Gallardo, 1965.
Bufo granulosus lutzi Gallardo, 1965 – new synonym.

Holotype: NHM 1923.11.9.15.

Type locality: Ilha de Marajó, Pará, Brazil.

Diagnosis: Adult males ranging from 40.9 to 71.4 mm (SVL x = 51.2 mm, n = 152), and adult females ranging from 49.1 to 73 mm (SVL x = 60.3 mm, n = 105); cephalic crests predominantly granulose with occasionally coalescent granules; supraorbital crest low; infraorbital crest short, not extending beyond postor-

bital crest; maxillary crest reduced, usually discontinuous; snout sloping dorsoventrally, rounded in dorsal and lateral views; loreal region distinctly visible in dorsal view; tympanum very close to postorbital crest (DTP 0.4-1.0% SVL); upper lip with slightly convex borders; longitudinal dorsal stripe present.

Comparison between species: Rhinella bergi presents a straight snout in lateral view and squared in dorsal view, crests predominantly continuous, supraorbital crest high, tympanum not close to postorbital crest (DTP 1.4-2.4% SVL), supratympanic crest longer; *R. pygmaea* presents predominantly continuous crests, parietal crest, infraorbital crest long, tympanum widely separated from postorbital crest (DTP 2.1-3.1% SVL); *R. azarai* presents flared upper lip, forming an extended horizontal flap which lead to a rounded head and a short snout in dorsal profile, longer interorbital distance, parietal crest present, tympanum not close to postorbital crest (DTP 1.5-2.4% SVL); *R. granulosa* presents loreal region scantly visible in dorsal view, longitudinal dorsal stripe absent, snout narrower; *R. major* presents straight snout in lateral view and squared in dorsal view, maxillary crest highly developed and visible in dorsal view, longitudinal dorsal stripe absent; *R. dorbignyi* and *R. fernandezae* present squared snout in dorsal view and straight in lateral view, supraorbital crest high, a larger and extremely smooth postorbital space, head higher, tympanum not close to postorbital crest (*R. dorbignyi* DTP 1.5-2.3% SVL; *R. fernandezae* DTP 1.5-2.7% SVL); *R. nattereri* presents rounded head with a long snout, straight snout in lateral view and squared in dorsal view, supraorbital crest high, more developed parotoid glands; *R. merianae* and *R. centralis* sp. n. present more developed parotoid glands, snout narrow and sloping dorsoventrally, longitudinal dorsal stripe absent, tympanum not close to postorbital crest (*R. merianae* DTP 1.1-2.1% SVL; *R. centralis* sp. n. DTP 1.6-2.2% SVL), supraorbital crest high; *R. humboldti* presents more developed parotoid glands, supraorbital crest high, longitudinal dorsal stripe absent.

Description: Head low (height 11.3-14.9% SVL), elongated, wider than long (width 26-35.5% SVL, length 22-29.5% SVL). Snout rounded in dorsal and lateral views, long in dorsal and lateral views, maxilla projecting ahead of mandible anteriorly, posterior margin of nostril at the level of anterior margin the mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of the snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region distinctly visible in dorsal view, superior half concave, inferior half oblique. Upper lip not flared, rounded with slightly convex borders. Tympanum rounded, with conspicuous borders, very near the postorbital crest (DTP 0.4-1.0% SVL). Parotoid glands dorsolateral, conspicuous, borders not well delimited, subtriangular, vertex pointing down,

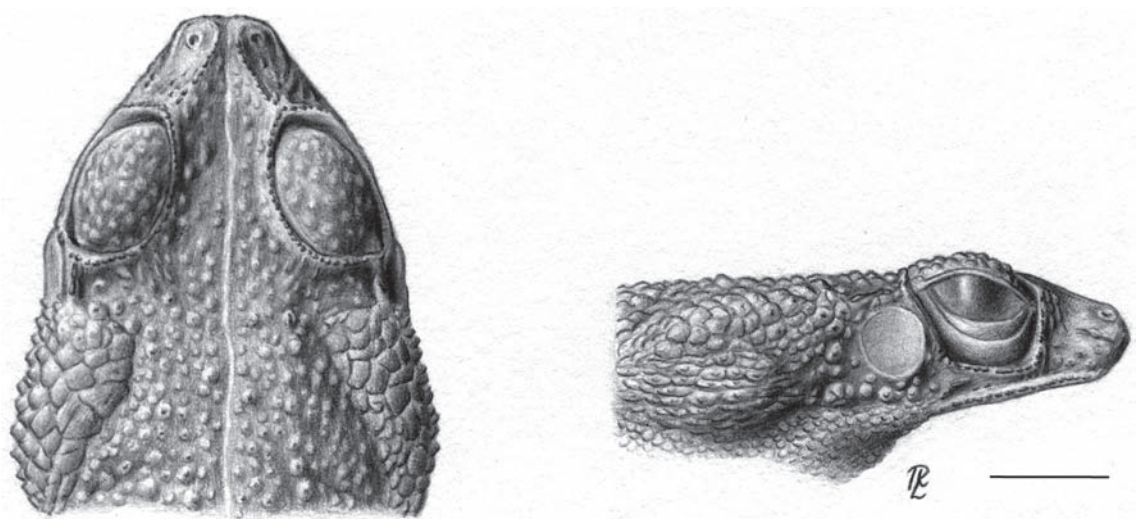

FIGURE 18: *Rhinella mirandaribeiroi,* NHM 1923.11.9.15 (Holotype of *Rhinella granulosa mirandaribeiroi*), dorsal and lateral views of the head. (Scale bar = 5 mm).

wider than higher (width 13.1-23% SVL; height 10.1-18.6% SVL).

Cephalic crests predominantly granulose, with conspicuous, keratinized borders. Supraorbital crest low, granulose, occasionally with a few coalescent granules, supraorbital crest rounded, not forming a straight line with supratympanic crest, interorbital portion highly curved (IOD_2/IOD_1 x = 0.81). Preorbital crest granulose, occasionally with a few coalescent granules, sometimes bulky. Postorbital crest granulose, occasionally with a few coalescent granules, straight, long, reaching lower margin of eye, reaching or not infraorbital crest. Infraorbital crest curved, granulose or continuous (coalescent granules may provide a continuous aspect), short, ending at the level of the maxillary crest, not flared, posterior portion not fleshy. Supratympanic crest short, straight, with granules of irregular size and form, bulky or not, occasionally coalescent, aligned in two or more irregular rows, posterior portion occasionally dilated. Parietal crest absent. Canthal crest granulose or continuous (coalescent granules may provide a continuous aspect), straight or slightly curved, diverging posteriorly, not reaching preorbital crest and occasionally extending beyond anterior margin of nostril. Subnasal crest variable in size (short or long), its posterior portion usually not extending beyond posterior margin of nostril, highly fleshy, granulose or continuous. Maxillary crest reduced, with gaps or rows of granules, not highlighted, not visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) flat or slightly concave.

Palmar and metatarsal tubercles, and tip of toes and fingers slightly cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, oval, high, rounded or subconical in lateral view. Nuptial asperities on dorsum of fingers I and II, and on inner palmar tubercle in males. Relative size of fingers: I > II < IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized apices; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than the subarticulars. Hindlimbs short, tibio-tarsal articulation reaches axilla and only fourth toe surpasses the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval or subtriangular, high, subconical in lateral view, slightly larger than the outer one, rounded or subtriangular, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3$^+$ IV 3½-1 V; distal subarticular tubercle of fourth toe doubled, one element occasionally highly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical with keratinized apices; larger rounded tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, especially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with small and scattered granules of variable sizes, spiculated or rounded, keratinized, external margin with dots of keratin, irregularly aligned. Parotoid with individualized and fleshy tubercles, flattened on dorsal and conical on lateral faces of gland. Loreal region with small keratinized granules, usually rounded, not fleshy; small points of keratin, spiculated or not, on tip of snout, larger granules below subnasal crest. Ventral surface of the maxilla with numerous minuscule keratinized spicules, aligned or not. Interorbital area with small scattered granules, rounded or spiculated, not fleshy; there is nearly no space between tympanum and postorbital crest; area between tympanum and parotoid gland with small, conical granules, with keratinized spicules.

In preserved specimens, dorsum brownish or olive, with large, dark, spaced spots or with small closely placed dark spots forming a mosaic; a lateral light stripe between parotoid and inguinal region, with irregular margins and occasionally with gaps, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe present; labial light stripe present, of variable width. Belly light cream or yellowish, usually without pigmentation.

Variation: A few specimens may present nuptial asperities on ventral surface of fingers I and II, and on lateral surface of finger III. Rarely, the longitudinal dorsal stripe is absent. In a few specimens, the lateral stripe is not conspicuous. Younger specimens present crests with highly scattered granules and with reduced amount of keratin; maxillary and subnasal crests not conspicuous, formed by a gathering of small and scattered granules. See descriptive statistics in Table 5.

Distribution: Occurs in Cerrado areas of Central Brazil, in the states of Bahia, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, and Piauí; in the Noel Kampf National Park, in Bolivia; and in enclaves of Cerrado in the Amazon Forest, in the states of Amazonas and Rondônia, Brazil. See maps in Figs. 13 and 19.

TABLE 5: Descriptive statistics of measurements (in mm) of males (N = 152) and females (N = 105) of *Rhinella mirandaribeiroi* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	51.23	60.34	40.9	49.1	71.4	73.0	4.77	4.92
HW	16.22	17.80	11.2	14.6	23.9	22.8	1.86	1.55
HL	13.46	14.61	11.5	12.3	18.3	18.2	1.13	1.05
IND	2.07	2.33	1.6	1.8	2.6	3.0	0.19	0.26
SW	5.72	6.35	4.6	5.2	7.5	7.6	0.45	0.53
END	3.55	3.97	2.9	3.1	4.8	4.8	0.36	0.37
ESD	5.69	6.32	4.6	5.0	7.8	7.6	0.57	0.53
IOD1	6.04	6.76	4.8	5.7	8.2	7.9	0.54	0.50
IOD2	4.85	5.55	3.8	4.2	7.1	7.4	0.62	0.65
ED	4.45	4.67	3.6	3.9	5.8	5.6	0.38	0.39
TD	2.69	2.76	2.0	2.0	3.4	3.6	0.30	0.32
TH	3.22	3.30	2.1	2.4	3.9	4.1	0.31	0.33
EW	4.01	4.34	3.0	3.7	5.4	5.3	0.32	0.32
PGW	9.60	11.04	7.1	7.1	12.5	14.6	1.19	1.44
PGH	7.12	8.29	4.8	5.2	10.3	11.4	1.15	1.11
STCL	2.45	2.76	1.6	1.5	4.2	4.3	0.52	0.55
POS	3.94	4.15	2.7	2.2	6.6	5.9	0.65	0.77
THL	10.46	11.50	8.4	9.4	15.6	14.8	1.31	1.13
TIL	17.66	18.94	12.8	13.3	24.8	25.9	2.25	2.24
TAL	16.80	17.59	12.5	13.2	23.6	22.3	1.96	1.85
HAL	11.40	12.24	8.3	9.2	15.5	16.0	1.39	1.41
FOL	17.22	17.93	9.5	14.4	25.1	22.8	2.19	1.72

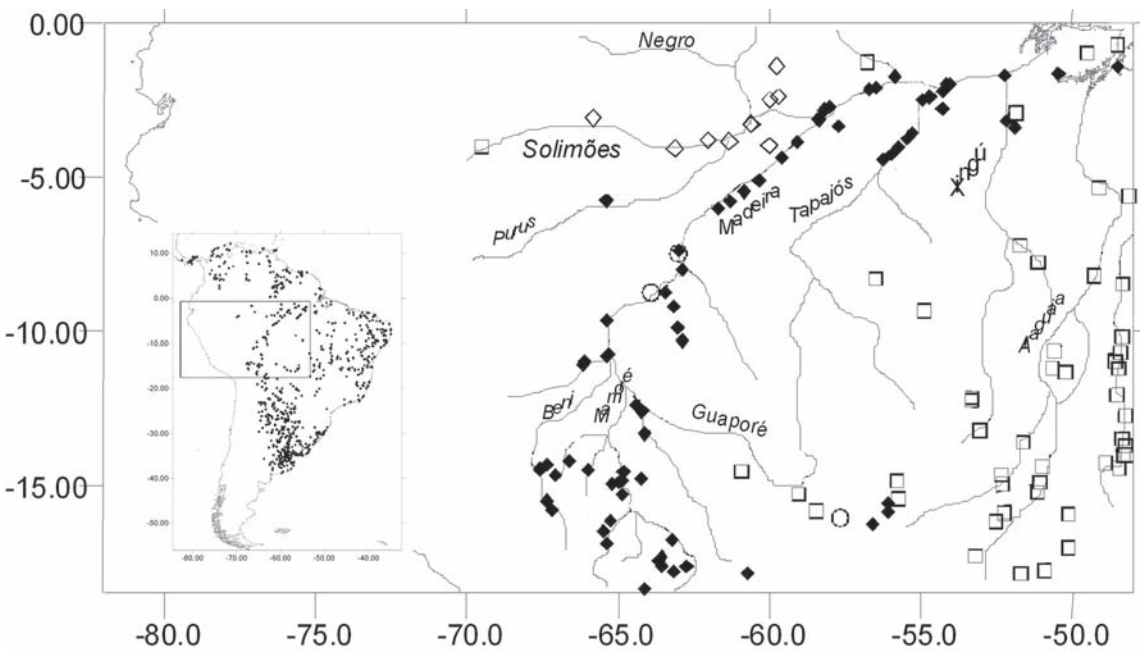

FIGURE 19: Partial geographic distributions of *Rhinella major* (closed diamond), of *R. mirandaribeiroi* (square), and of *R. merianae* (open diamond). Sympatry of *R. major* and *R. mirandaribeiroi* (open circles).

Natural history: Reproduction occurs on permanent or temporary ponds, in open areas, after heavy summer rains.

6. *Rhinella azarai*
(Figure 20)

Bufo granulosus azarai Gallardo, 1965.

Holotype: NHM 1955.15.47.

Type locality: Primavera, High Paraguay, Paraguay.

Diagnosis: Adult males ranging from 34.7 to 50.6 mm (SVL x = 42.1 mm, n = 16), and adult females ranging from 40.7 to 58.2 mm (SVL x = 45.4 mm, n = 7); cephalic crests predominantly continuous; interorbital portion of supraorbital crest straight; infraorbital crest long, extending beyond postorbital crest; supratympanic crest long, continuous; parietal crest present; maxillary crest visible in dorsal view, anteriorly inclined up in lateral view; snout rounded, highly elongated in lateral view and short in dorsal view; upper lip fleshy and rounded (convex border), part of ventral surface of maxilla visible in lateral view below maxillary crest; eye diameter twice smaller than interorbital distance and smaller than eye-nostril distance; a flared upper lip, forming an extended horizontal flap, which lead to a rounded head and short snout in dorsal profile; loreal region concave, distinctly visible in dorsal view; interorbital distance long (IOD_2 10.6-14.5% SVL); longitudinal dorsal stripe usually absent; belly pigmented.

Comparison between species: Rhinella dorbignyi and *R. fernandezae* present higher heads, snout short and straight in lateral view, smaller parotoid glands, interorbital area smooth or with just a few granules, postorbital distance longer; *R. pygmaea* and *R. bergi* present shorter interorbital distance, eye diameter larger than eye-nostril distance, upper lip sharp, longitudinal dorsal stripe usually present; *R. major* presents predominantly granulose crests, parietal crest absent, infraorbital crest short, straight snout in lateral view, and interorbital area with a few granules; *R. mirandaribeiroi* presents predominantly granulose crests, parietal crest absent, longitudinal dorsal stripe present, snout wider and flattened dorsoventrally; *R. nattereri* presents predominantly granulose crests, rounded head with long snout, snout straight in lateral view and squared in dorsal view; *R. merianae, R. humboldti,* and *R. centralis* sp. n. present predominantly granulose crests, parietal crest absent or inconspicuous, and more developed parotoid glands.

Description: Head low (height 13.9-15.6% SVL), rounded, wider than long (width 29-36.5% SVL, length 22-27% SVL). Snout rounded in lateral view, squared or rounded in dorsal view, long in lateral view and short (slightly protruding) in dorsal view, maxilla projecting ahead of the mandible in lateral view, posterior margin of nostril at level of anterior margin of mandible. Eye lateral, encapsulated, its diameter

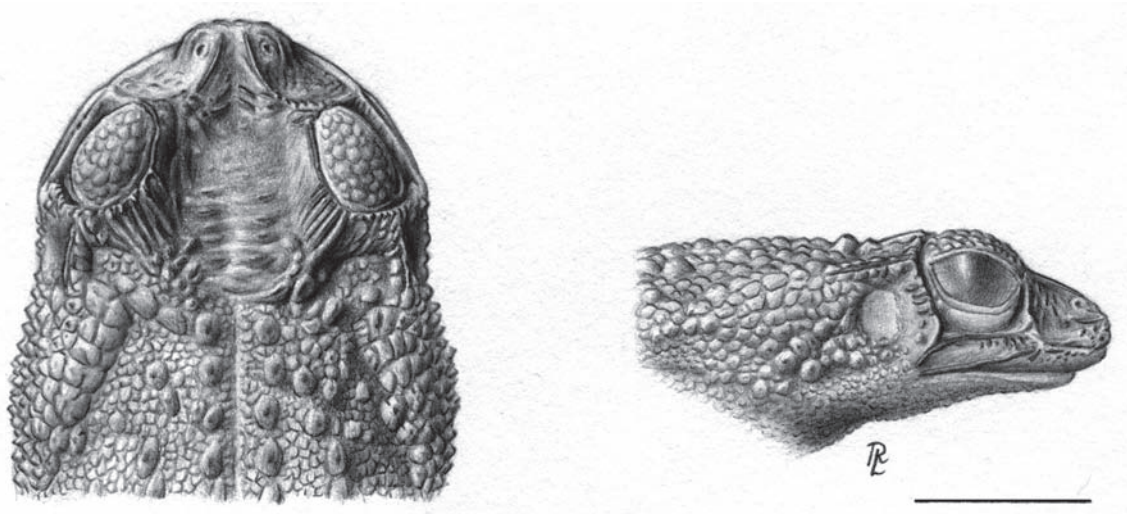

FIGURE 20: *Rhinella azarai,* NHM 1955.15.47 (Holotype of *Rhinella granulosa azarai*), dorsal and lateral views of the head. (Scale bar = 5 mm).

almost twice smaller than interorbital distance and smaller than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest. Loreal region distinctly visible in dorsal view, superior and inferior half distinctly concave. Upper lip rounded, with convex borders, maxillary crest anteriorly inclined up, ventral surface of maxilla visible in lateral view, upper lip flared, forming an extended horizontal flap, which lead to a rounded head and a short snout in dorsal profile. Tympanum oval, higher than wider, borders not well delimited, not close to postorbital crest (DTP 1.5-2.4% SVL). Parotoid gland dorsolateral, conspicuous, anterior and inferior borders not well delimited, subtriangular, vertex pointing down or back, wider than higher (width 14.2-24.3% SVL; height 10.2-16.8% SVL).

Cephalic crests predominantly continuous, with conspicuous and keratinized borders. Supraorbital crest high, continuous, occasionally with gaps and wrinkles, rounded, not aligned with supratympanic crest, interorbital portions straight, almost parallel (IOD_2/IOD_1 x = 1.0), usually wrinkled posteriorly. Preorbital crest continuous, occasionally gapped and wrinkled, portions of keratin arrayed perpendicularly toward loreal region, usually not fleshy. Postorbital crest long, reaching inferior margin of eye, reaching or not infraorbital crest, straight, usually with perpendicular branches toward tympanum. Infraorbital crest straight or curved, continuous, occasionally gapped and with perpendicular branches toward eye and maxillary crest, long, posteriorly extending beyond postorbital crest, a distinctive lateroposterior expansion, visible in ventral view is present. Supratympanic crest long and slightly inclined up posteriorly, continuous or aligned in two or three irregular rows of elongated granules, posterior portion not dilated. Parietal crest present, continuous, occasionally interrupted posteriorly. Canthal crest continuous, occasionally reaching preorbital crest, ending at the level of anterior margin of nostril, slightly curved, diverging posteriorly. Subnasal crest long, its posterior portion extending beyond posterior margin of nostril, not bulky, continuous or interrupted posteriorly. Maxillary crest developed, visible in dorsal view, its keratinization not reaching ventral surface of maxilla, crest inclined up anteriorly, occasional branches at medial portion of crest toward infraorbital crest; posterior portion of

TABLE 6: Descriptive statistics of measurements (in mm) of males (N = 16) and females (N = 7) of *Rhinella azarai* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	42.09	45.45	34.7	40.7	50.6	58.2	4.55	6.62
HW	13.64	13.87	11.3	12.4	15.9	17.2	1.30	1.73
HL	10.98	10.94	9.4	9.3	12.3	13.2	0.82	1.39
IND	1.51	1.60	1.2	1.3	1.8	2.1	0.17	0.30
SW	4.37	4.28	3.9	3.7	4.9	5.2	0.31	0.59
END	3.47	3.54	3.1	2.9	4.0	4.4	0.28	0.47
ESD	5.07	5.20	4.4	4.5	5.9	6.3	0.43	0.66
IOD1	5.37	5.43	4.3	4.9	6.5	6.3	0.53	0.51
IOD2	5.33	5.56	4.3	4.5	6.3	6.9	0.53	0.88
ED	3.04	2.99	2.5	2.5	3.6	3.3	0.25	0.30
TD	1.92	1.75	1.4	1.5	2.4	2.2	0.31	0.24
TH	2.39	2.13	1.8	1.8	2.9	2.6	0.35	0.31
EW	2.74	2.66	2.3	2.3	3.3	3.1	0.23	0.28
PGW	6.65	6.82	5.6	6.1	8.5	9.0	0.94	1.08
PGH	5.05	5.25	4.1	4.5	6.0	6.2	0.66	0.62
STCL	2.56	3.04	2.0	1.9	3.2	4.4	0.33	0.85
POS	4.12	4.13	3.4	3.4	5.1	5.1	0.47	0.57
THL	8.50	8.59	7.3	7.5	9.6	10.5	0.64	1.18
TIL	12.48	12.60	10.3	10.9	14.9	17.2	1.37	2.42
TAL	11.63	11.82	9.6	10.0	14.2	15.8	1.24	2.17
HAL	8.13	8.40	6.9	6.8	9.5	11.1	0.74	1.45
FOL	12.59	12.84	10.9	11.3	14.0	16.5	0.89	2.00

maxilla (between infraorbital and maxillary crests) flat or slightly concave.

Palmar and metatarsal tubercles, and tip of toes and fingers slightly cornified. External palmar tubercle salient, rounded or oval, three times larger than the inner one, oval, salient. Nuptial asperities on dorsum of finger I, reduced or absent on finger II, and reduced on the inner palmar tubercle in males. Relative size of fingers: I = II < IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than subarticulars. Hindlimbs very short, tibio-tarsal articulation do not reach axilla and fourth toe do not surpass the snout when the leg is stretched and adjoined to body; inner metatarsal tubercle oval, high, subconical in lateral view, smaller than the outer one, rounded, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½⁺-2 V; distal subarticular tubercle of the fourth toe doubled, one element occasionally highly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars; tarsal fold absent.

Dorsum with conical tubercles of variable sizes with keratinized apices; larger rounded tubercles, highly keratinized, arrayed on the dark spots of anterior third of body, especially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with a few large granules, rounded and keratinized, external margin with dots of keratin, irregularly aligned, occasionally coalescent. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small, usually elongated and not fleshy keratinized granules; large, rounded or elongated and not fleshy points of keratin, occasionally coalescent, forming a reticulated complex at the tip of snout and below subnasal crest. Ventral surface of maxilla with numerous tiny spicules of keratin, aligned or not, those external larger and visible in lateral view. Interorbital area with a few large granules, rounded and keratinized, usually highly fleshy, slightly aligned in two longitudinal and parallel rows; area between tympanum and postorbital crest with keratinized granules of variable sizes, elongated or rounded; area between tympanum and parotoid with small conical granules with keratinized apices.

In preserved specimens, dorsum brownish with small dark and very closely placed spots forming a mosaic of variable extension, which renders individuals more melanic than others. The highly melanic with an uniform dark-brown dorsum, without conspicuous spots; a lateral light stripe between parotoid and inguinal region, with irregular margins and occasionally with gaps, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe usually absent; labial light stripe usually present, of variable width. Belly light cream, with small dark spots.

Variation: Rarely, a longitudinal dorsal stripe may be present. See descriptive statistics in Table 6.

Distribution: Occurs at the lowlands of Posada, in Misiones, Argentina, in the Mato Grosso do Sul State, Brazil, and in Paraguay. See map in Fig. 16.

Natural history: Reproduction at temporary or permanent ponds, after heavy rains. Males vocalize inside water, near marginal vegetation.

7. *Rhinella nattereri*
(Figure 21)

Bufo granulosus nattereri Bokermann, 1967.

Holotype: MZUSP 73715.

Type locality: Cachoeira Uranduíque, Rio Maú, Roraima, Brazil.

Diagnosis: Adult males ranging from 49.8 to 55.4 mm (SVL x = 52.8 mm, n = 7, no adult females available); rounded head with long snout; crests predominantly granulose; supraorbital crest high; infraorbital crest short; parietal crest absent or inconspicuous; interorbital portion of supraorbital crest highly curved; supratympanic crest low; snout squared in dorsal view; interorbital area with several keratinized granules; belly usually pigmented; longitudinal dorsal stripe absent.

Comparison between species: Rhinella fernandezae, R. azarai, R. pygmaea, and *R. bergi* present predominantly continuous crests, parietal crest present; infraorbital crest long. *Rhinella dorbignyi* presents predominantly continuous crests, parietal crest present, postorbital crest reduced, and interorbital area extremely smooth. *Rhinella granulosa* presents rounded snout in dorsal view, supraorbital crest low, and less developed max-

illary crest; *R. mirandaribeiroi* presents longitudinal dorsal stripe, rounded snout in dorsal view and flattened dorsoventrally, and less developed maxillary crest; *R. major* presents smooth interorbital area or with only a few granules, loreal region, maxillary crest, and labial stripe visible in dorsal view; *R. humboldti* presents rounded snout in dorsal view, larger eye-nostril distance, and smaller parotoid gland; *R. merianae* and *R. centralis* sp. n. present snout squared in dorsal view and rounded in lateral view, narrower in lateral view and highly sloping dorsoventrally.

Description: Head low (height 13.8-15.7% SVL), rounded with a long snout, wider than long (width 33.5-36.5% SVL, length 24-27% SVL). Snout squared in dorsal view, rounded or vertical in lateral view, long in dorsal and lateral views, maxilla projecting ahead of mandible in lateral view, posterior margin of the nostril at level of anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region narrow, barely visible in dorsal view, superior half concave, inferior half almost straight. Upper lip with slightly convex borders, not flared. Tympanum oval, higher than wide, with inconspicuous borders, very close to postorbital crest (DTP 0.9-1.4% SVL). Parotoid gland dorsolateral, conspicuous, borders well delimited, subtriangular, vertex pointing down or back, wider than high (width 16-24% SVL; height 11.3-16.4% SVL).

Cephalic crests with marked keratinized borders, predominantly granulose. Supraorbital crest high, strongly serrate, granulose in aspect, rounded, not aligned with supratympanic crest, interorbital portion of supraorbital crest highly curved (IOD_2/IOD_1 x = 0.87), posterior portion occasionally wrinkled. Preorbital crest usually granulose, with a few coalescent granules, occasionally bulky and irregularly wrinkled. Postorbital crest long, reaching inferior margin of eye, usually reaching infraorbital crest, straight. Infraorbital crest usually curved, granulose, short, ending at the level of maxillary crest, usually without lateral expansion. Supratympanic crest short and straight, formed by fleshy granules aligned in one or two irregular rows, posterior portion not dilated. Parietal crest absent or inconspicuous. Canthal crest usually continuous, occasionally reaching preorbital crest and anterior margin of nostril, occasionally fused with granules of tip of snout, slightly curved, diverging posteriorly. Subnasal crest continuous or granulose, usually short, its posterior portion occasionally extending beyon posterior margin of nostril, usually bulky, what gives a squared aspect to the snout in dorsal view. Maxillary crest developed, occasionally with gaps, its keratinization reaches the ventral surface of maxilla, usually not visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) concave.

Palmar and metatarsal tubercles, and tip of toes and fingers cornified. External palmar tubercle salient, rounded or oval, twice or three times larger

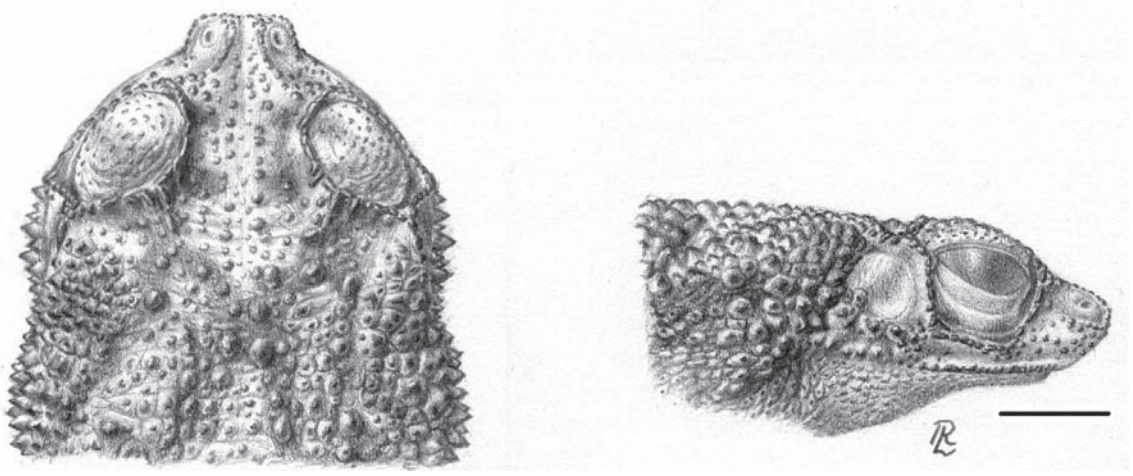

FIGURE 21: *Rhinella nattereri,* MZUSP 73715 (Holotype of *Rhinella granulosa nattereri*) dorsal and lateral views of the head. (Scale bar = 5 mm).

than the inner one, oval or elongated, high, rounded in lateral view. Nuptial asperities on dorsum of finger I, in part of the inner palmar tubercle, and reduced on finger II in males. Relative size of fingers: I > or = II < or = IV < III; fingers without fringes, lateral surface serrate, formed by conical tubercles, which may have keratinized apices; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars. Hindlimbs short, tibio-tarsal articulation reaching axilla and only fourth toe surpassing snout when leg is stretched and adjoined to the body. Inner metatarsal tubercle oval or elongated, very high, subconical in lateral view, slighly larger or equal to the external one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½-2 V; distal subarticular tubercle of fourth toe doubled, one element occasionally much larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical or rounded, keratinized; larger rounded tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, specially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with small granules, spiculated or rounded, keratinized, external margin with dots of keratin, irregularly aligned. Parotoids with individu-

TABLE 7: Descriptive statistics of measurements (in mm) of males (N = 7) of *Rhinella nattereri* (SD = standard deviation).

Characters	Average	Minimum	Maximum	SD
SVL	52.77	49.9	55.4	1.89
HW	18.80	17.8	19.5	0.62
HL	13.28	12.1	14.6	0.81
IND	1.95	1.8	2.1	0.09
SW	5.47	5.0	5.9	0.41
END	3.43	2.9	3.9	0.35
ESD	5.51	5.0	5.9	0.28
IOD1	6.34	5.7	7.3	0.49
IOD2	5.53	5.0	6.8	0.61
ED	4.63	4.0	5.8	0.57
TD	2.23	2.0	2.8	0.29
TH	2.96	2.7	3.1	0.15
EW	4.41	4.2	5.0	0.27
PGW	11.67	10.9	12.7	0.71
PGH	8.33	7.9	8.9	0.45
STCL	2.60	2.2	2.9	0.27
POS	3.89	3.1	4.4	0.44
THL	12.05	11.5	13.0	0.55
TIL	19.30	18.3	22.4	1.44
TAL	17.49	16.2	20.5	1.58
HAL	12.17	11.1	13.7	0.91
FOL	18.89	17.4	21.0	1.13

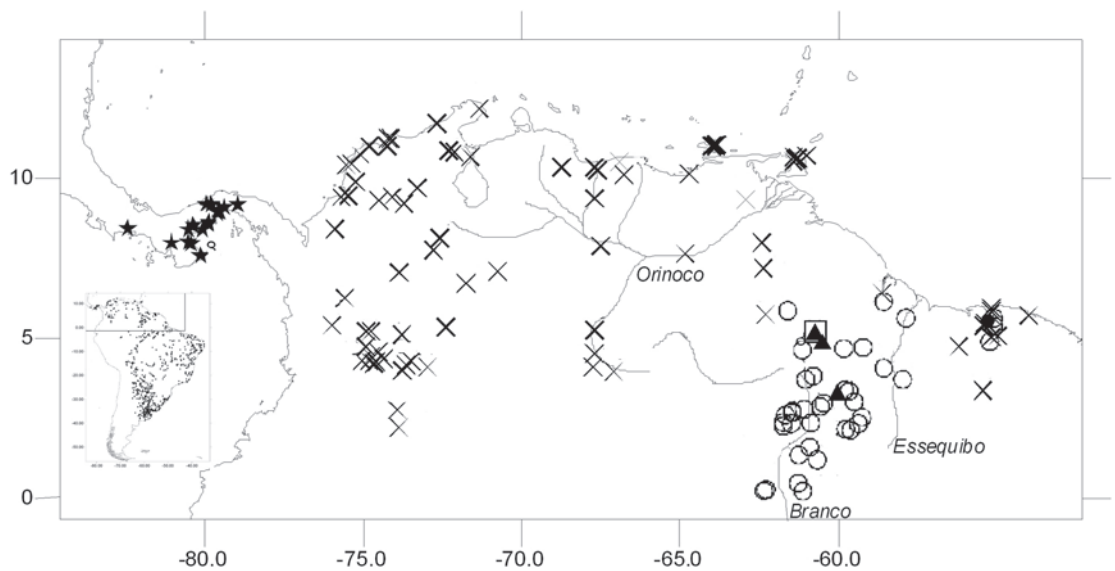

FIGURE 22: Geographic distribution of *Rhinella nattereri* (triangle), *R. merianae* (circles), *R. humboldti* (X), and *R. centralis* sp. n. (black star). Sympatry of *R. nattereri* and *R. merianae* (square).

alized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized granules, rounded or elongated, not fleshy; small rounded points of keratin not fleshy at tip of snout and larger points below subnasal crest. Ventral surface of the maxilla with minuscule keratinized spicules, slightly aligned in irregular rows. Interorbital area with numerous keratinized granules of variable sizes, rounded and not fleshy, scattered or slightly aligned in two longitudinal rows; area between tympanum and postorbital crest smooth; area between tympanum and parotoid gland with very few small keratinized granules, conical or rounded.

In preserved specimens, dorsum brownish light with large scattered dark spots or very closely placed, forming a mosaic, the extension of spots may vary and some individuals are more melanic than others; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe absent; labial light stripe present, of variable width. Belly light cream or yellowish, usually with small dark spots.

Variation: The parotoid gland may be highlighted by an olive or orange coloration and may present less defined granulation, providing a smoother and homogeneous aspect. A few specimens may not present pigmentation on the belly. A few individuals may have very reduced nuptial asperities on the lateral surface of finger III. See descriptive statistics in Table 7.

Distribution: Northeast of the State of Roraima, Brazil. The species is known only from three localities: Serra do Sol and Cachoeira Uranduíque, Rio Maú, in the State of Roraima, Venezuela (Bolivar, Mount Roraima), and Guyana (Cuyuni-Mazaruni, Mount Roraima). Ecological preferences are unknown. See map in Fig. 22.

Natural history: Unknown.

8. *Rhinella fernandezae* (**Figure 23**)

Bufo granulosus fernandezae Gallardo, 1965.
Bufo fernandezae – Cei, 1964.
Chaunus fernandezae – Frost *et al.,* 2006.
Rhinella fernandezae – Chaparro *et al.,* 2007 by implication.

Holotype: MACN 10.334.

Type locality: Bella Vista, Buenos Aires, Argentina.

Diagnosis: Adult males ranging from 38.2 to 67.3 mm (SVL x = 55.3 mm, n = 200), and adult females ranging from 40 to 76.4 mm (SVL x = 57.0 mm, n = 100); snout straight in lateral view, short, posterior margin of nostril do not surpass anterior margin of mandible in lateral view; head high (HH 14.5-18.8% SVL); supraorbital crest continuous, high and bulky; postorbital crest long; parietal crest present; infraorbital crest long; interorbital area, loreal region and tip of snout smooth or with just a few granules; tympanum with inconspicuous borders, widely separated from parotoid gland (DTG 4.4-6.8% SVL).

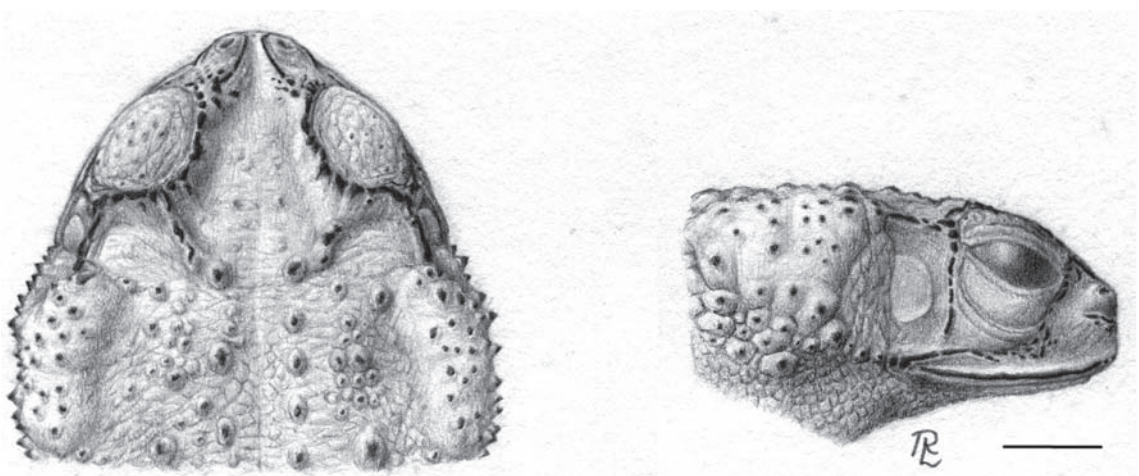

FIGURE 23: *Rhinella fernandezae,* MACN 10.334 (Holotype of *Rhinella granulosa fernandezae*), dorsal and lateral views of the head. (Scale bar = 5 mm).

Comparison between species: Rhinella dorbignyi presents reduced postorbital crest, supraorbital crest higher and bulker, forming a straight line with canthal and supratympanic crests, infraorbital crest absent or reduced and short; *R. granulosa, R. nattereri, R. centralis, R. humboldti, R. merianae, R. major,* and *R. mirandaribeiroi* present lower and predominantly granulose crests, snout long in dorsal and lateral views, parietal crest absent or inconspicuous; *R. pygmaea* presents smaller size (males x = 32.1 mm; females x = 40.8 mm), snout rounded and long in dorsal and lateral views, posterior margin of nostril at level of anterior margin of mandible in lateral view; *R. bergi* presents smaller size (males x = 40.4 mm; females x = 49.9 mm), snout protruding in dorsal and lateral views, posterior margin of the nostril at the level of anterior margin of the mandible in lateral view; *R. azarai* presents smaller size (males x = 42.1 mm; females x = 45.4 mm), long snout in lateral view, loreal region distinctly visible in dorsal view, concave.

Description: Head rounded or subtriangular, high (HH 14.4-18.8% SVL), wider than long (width 30-38.5% SVL, length 21-28% SVL). Snout squared or rounded in dorsal view, straight in lateral view, slightly long in dorsal and lateral views, maxilla slightly projecting ahead of the mandible anteriorly, posterior margin of nostril do not surpass anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and approximately equals to eye-nostril distance. Nostril subelliptic, dorsolateral with lateral openings, closer to tip of snout than to eye, its longitudinal axis almost perpendicularly disposed in relation to longitudinal axis of the head. *Canthus rostralis* angulated, highlighted by keratinized canthal crest; loreal region scantly visible in dorsal view, superior half straight or slightly concave, inferior half straight. Upper lip with sharp border, highlighted by keratinized maxillary crest, a slightly lateral expansion of the upper lip may occur. Tympanum oval, higher than wide, with inconspicuous borders, not close to postorbital crest (DTP 1.5-2.7% SVL). Parotoid gland dorsolateral, conspicuous, inferior borders not well delimited, elongated or subtriangular, vertex pointing down, wider than high (width 10.9-19.8% SVL; height 7.4-14.6% SVL).

Cephalic crests continuous, keratinized and with smooth borders. Supraorbital crest high and bulky, continuous, occasionally serrate and with gaps and wrinkles, posterior portion occasionally wrinkled, supraorbital crest rounded, not in a straight line with canthal and supratympanic crests, interorbital portion almost straight, diverging posteriorly (IOD_2/IOD_1 x = 0.98). Preorbital crest continuous, frequently gapped. Postorbital crest long, surpassing lower margin of the eye, reaching or not infraorbital crest, usually straight without ramifications, occasionally gapped. Infraorbital crest continuous, frequently gapped, long, posteriorly extending beyond postorbital and maxillary crests, posterior portion bulky with a slightly lateral expansion visible in dorsal view, posterior portion occasionally united to maxillary crest. Supratympanic crest long and straight, continuous, interrupted or not, bulky and ornamented with wrinkles and gaps, posterior portion occasionally dilated. Parietal crest present, high, usually continuous or formed by large rounded and aligned tubercles, posterior portion usually bulky. Canthal crest continuous, almost straight, diverging posteriorly, occasionally reaching preorbital crest, extending or not beyond anterior margin of nostril. Subnasal crest short, posterior portion at the level of posterior margin of nostril, usually bulky, continuous. Maxillary crest highly developed and continuous, its keratinization may reach the ventral surface of maxilla, posterior portion occasionally bulky, visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) concave.

Palms and metatarsal tubercles, and tip of fingers and toes cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, salient, oval. Nuptial asperities on dorsum of fingers I and II and in part of the inner palmar tubercle in males. Relative size of fingers: I < II < or = IV < III; fingers without fringes, lateral surface serrate, formed by conical or rounded tubercles, which may have keratinized apices; interdigital membrane reduced, present between the fingers II and III, conspicuous in larger specimens; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than the subarticulars. Hindlimbs short, tibio-tarsal articulation reaches axilla and only fourth toe surpasses the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval or elongated, high, subconical in lateral view, approximately the same size of external one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface extensively serrate, formed by conical tubercles, with keratinized apices and secondary points of keratin; interdigital membrane of toes with extensively serrate borders; webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½-2 V; distal subarticular tubercle of fourth toe doubled, one element much larger than

its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars; tarsal fold absent.

Dorsum with keratinized tubercles of variable sizes, conical or rounded; larger rounded tubercles, highly keratinized, arrayed longitudinally on the anterior half of body. Belly with small conical granules, adjoined. Upper eyelid with a few keratinized granules of variable size, rounded or spiculated, external margin extensively keratinized. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region, tip of snout, and area below subnasal crest smooth, with very few keratinized granules, rounded or elongated, not fleshy. Ventral surface of maxilla smooth or with minuscule keratinized spicules, aligned on the internal margin; interorbital area completely smooth or with very few rounded and keratinized granules, usually highly fleshy; area between tympanum and postorbital crest smooth or with a couple of small granules; area between tympanum and parotoid gland completely smooth or with very few small granules, conical with keratinized apices.

In preserved specimens, dorsum brownish light or grayish with dark spots, or dark-brownish without conspicuous spots; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe present or absent; labial light stripe present, variable in width. Belly cream, yellowish or dark gray, with or without small dark spots.

Variation: In some specimens, the nuptial asperities are reduced on lateral surface of finger III. A few specimens showed parotoid gland with reduced granulation, becoming smoother and homogeneous in aspect. Some specimens may have numerous tiny spicules of keratin around the apex of the conical tubercles covering dorsum, on the lateral face of parotoid glands and on the limbs. In a few specimens from Rio Grande do Sul and from Uruguay, the infraorbital crest is formed by elongated pieces of keratinization, occasionally scaled, arrayed horizontally or vertically (Fig. 24); the long infraorbital crest may occasionally be present in only one side of the head. See descriptive statistics in Table 8.

Distribution: Associated with the Litoral-Mesopotamic area (along the rivers Paraná-Paraguay and Uruguay) defined by Cei (1980). This area constitutes part of the Oriental Chaco (Ab'Sáber, 1977) and encloses the phytogeographic provinces of Espinal Chaqueño and Pampeana, Argentina. The species also occurs in Uruguay (frontier of Argentina and at the River Prata basin), and in the State of Rio Grande do Sul, Brazil. See map in Figs. 16 and 25.

Natural history: Specimens were found hiding inside hollows in the ground or above fallen logs, protecting against dryness (Vellard, 1948). Langone (1994) observed fragmosis in specimens of *Rhinella fernandezae,* and specimens building hollows with their hind legs using mud accumulated after heavy rains. Toads only leave their hollows in order to feed or to reproduce; toads have the ability to guide themselves back to their own hollow when taken very far from them. Reproductive period, according to the author, is from October through March, right after heavy rains. According to Norman (1994), the specimens that inhabit the region of Chaco in Argentina, stayed buried during the prolonged dry season.

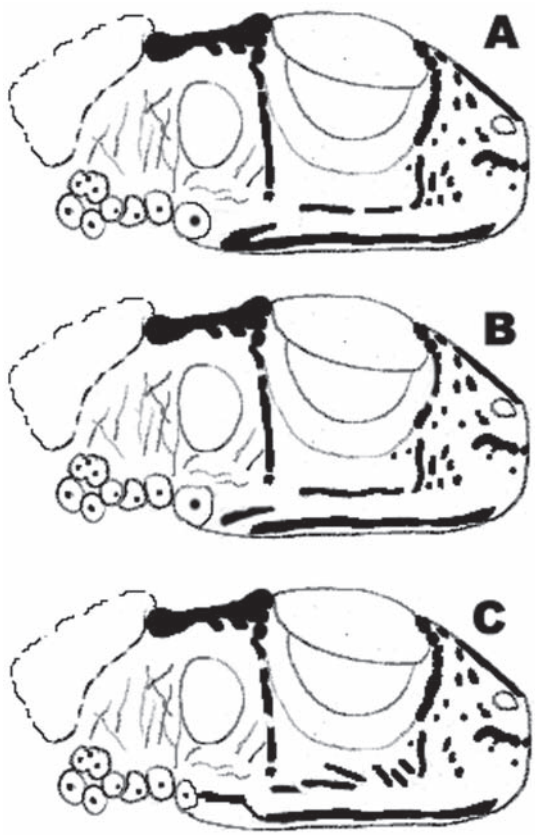

FIGURE 24: Schematic drawings showing some infraorbital crest variations observed in *Rhinella fernandezae.* **A.** Gapped crest, and gapped prolongation uniting to infraorbital and maxillary crests; **B.** Crest with gapped prolongation; **C.** Gapped crest with scaled parts, and gapped prolongation uniting infraorbital and maxillary crests.

TABLE 8: Descriptive statistics of measurements (in mm) of males (N = 200) and females (N = 100) of *Rhinella fernandezae* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	55.32	57.01	38.2	40.0	67.3	76.4	5.23	7.49
HW	19.06	19.03	13.7	14.1	30.0	25.3	1.84	2.24
HL	13.62	13.78	10.6	10.6	16.5	19.9	1.04	1.65
IND	2.18	2.24	1.5	1.6	3.1	3.2	0.28	0.36
SW	5.71	5.74	4.2	4.3	7.2	7.8	0.55	0.77
END	3.67	3.76	2.9	3.1	4.6	4.8	0.31	0.42
ESD	5.44	5.54	4.3	4.5	6.5	7.1	0.43	0.62
IOD1	5.88	5.99	4.4	4.7	7.3	7.9	0.71	0.70
IOD2	5.78	5.88	4.0	4.3	7.8	8.4	0.73	0.85
ED	4.18	4.29	2.9	3.2	5.6	9.7	0.42	0.79
TD	2.49	2.40	1.7	1.8	3.3	3.4	0.34	0.37
TH	3.15	3.07	2.2	2.1	4.3	4.4	0.38	0.49
EW	3.62	3.65	3.0	2.9	4.9	4.7	0.37	0.39
PGW	8.35	8.36	5.2	6.0	12.5	12.3	1.34	1.41
PGH	6.24	6.08	3.5	3.4	9.1	9.7	1.00	1.00
STCL	4.42	4.49	3.0	2.9	5.6	6.6	0.51	0.75
POS	6.38	6.50	4.6	4.4	8.4	9.5	0.78	0.98
THL	12.86	12.93	8.6	9.1	15.8	17.0	1.29	1.74
TIL	17.99	17.70	11.6	13.4	22.9	23.5	2.39	2.38
TAL	17.50	16.94	10.5	12.3	22.2	22.8	2.04	2.51
HAL	12.09	11.66	7.7	8.1	16.0	16.5	1.37	1.82
FOL	19.79	19.24	13.6	13.2	25.2	26.4	2.18	2.55

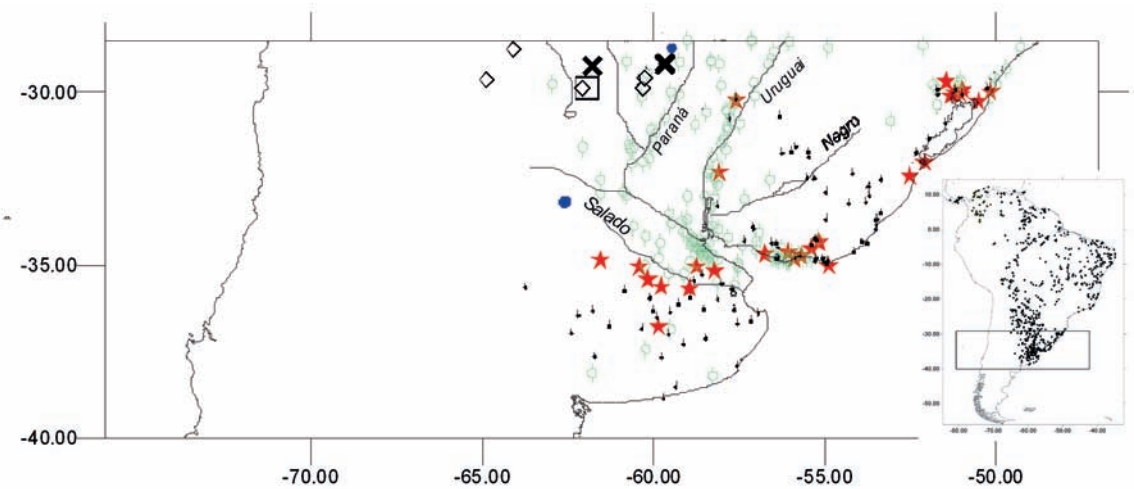

FIGURE 25: Geographic distribution of *Rhinella fernandezae* (green circle), *R. dorbignyi* (black dot), partial distributions of *R. bergi* (blue circle) and of *R. major* (diamond). Sympatry of *R. fernandezae* and *R. dorbignyi* (red star); *R. fernandezae* and *R. bergi* (cross); *R. fernandezae, R. bergi,* and *R. major* (square).

9. *Rhinella dorbignyi* (Figure 26)

Bufo d'Orbignyi Duméril & Bibron, 1841.
Chilophryne d'orbignyi – Fitzinger, 1843.
Bufo orbignyi Bibron *in* D'Orbignyi & Bibron, 1847.
Bufo d'orbignyi – Günther, 1859 "1858".
Phrynoidis d'orbignyi – Cope, 1863.
Bufo dorbignyi Cope, 1885 "1884".
Bufo globulosus d'orbignyi – Parker, 1935.

Bufo granulosus d'orbignyi – Müller & Hellmich, 1936.
Bufo granulosus dorbignyi – Gallardo, 1965.
Bufo d'orbignyi – Cei, 1972.
Chaunus dorbignyi – Frost *et al.,* 2006.
Rhinella dorbignyi – Chaparro *et al.,* 2007 by implication.

Holotype: MNHN 4960.

Type locality: Montevideo, Uruguay.

Comments: In 1847, Bibron presented a short description of *Rhinella dorbignyi* collected by D'Orbigny from holes in the ground near the city of Maldonado. This record was commented upon by Gallardo (1957) who, based on the information, considered Maldonado the type locality for the species. This action was contrarily to Duméril & Bibron (1841), who indicated Montevideo as the type locality for *R. dorbignyi.* Klappenbach & Langone (1992) did not agree with Gallardo arguments and followed Duméril & Bibron. Among the specimens analyzed in this work, only one specimen of *Rhinella fernandezae* was available from the city of Montevideo, and no specimen were attributed to the city of Maldonado. However, from the 28 specimens available for localities at the Departamento Montevideo, 21 were identified as *R. fernandezae* and seven as *R. dorbignyi.* Between the 36 specimens available for localities at the Departamento Maldonado, seven were identified as *R. fernandezae* and 29 as *R. dorbignyi.* Although we observed a higher frequency for the occurrence of *R. dorbignyi* in the Departamento Maldonado, and a higher frequency for the occurrence of *R. fernandezae* in the Departamento Montevideo, this data are not sufficient to propose the alteration of the type locality for *R. dorbignyi.*

Diagnosis: Adult males ranging from 36.1 to 63.7 mm (SVL x = 48.2 mm, n = 152), and adult females ranging from 42.1 to 68.5 mm (SVL x = 55.6 mm, n = 36); snout short, squared or rounded in dorsal view, and straight in lateral view, posterior margin of nostril do not surpass anterior margin of mandible in lateral view; head high (HH 16.5-19.6% SVL); supraorbital crest continuous, very high and thick; preorbital crest long, surpassing lower margin of eye; postorbital crest reduced; parietal crest present; infraorbital crest absent or reduced, never extending beyond postorbital crest; interorbital area, loreal region and tip of snout highly smooth or with just a few granules; tympanum scantly visible, widely separated from parotoid gland (DTG 3.7-7.5% SVL) and from supratympanic crest (DTS 3.7-6.5% SVL); longitudinal dorsal stripe present.

Comparison between species: Rhinella fernandezae presents more developed postorbital crest, supraorbital crest lower, infraorbital crest always present and extending beyond postorbital crest; *R. granulosa, R. major,* and *R. mirandaribeiroi* present a lower and predominantly granulose supraorbital crest, snout long, parietal crest absent or inconspicuous; *R. nattereri, R. centralis* sp. n., *R. humboldti,* and *R. merianae* present lower and frequently serrate supraorbital crests, snout long in lateral view, parietal crest absent or inconspicuous; *R. pygmaea* presents smaller size (males x = 32.1 mm; females x = 40.8 mm), snout long, rounded in dorsal and lateral views, posterior margin of the nostril at the level of anterior margin of mandible in lateral view;

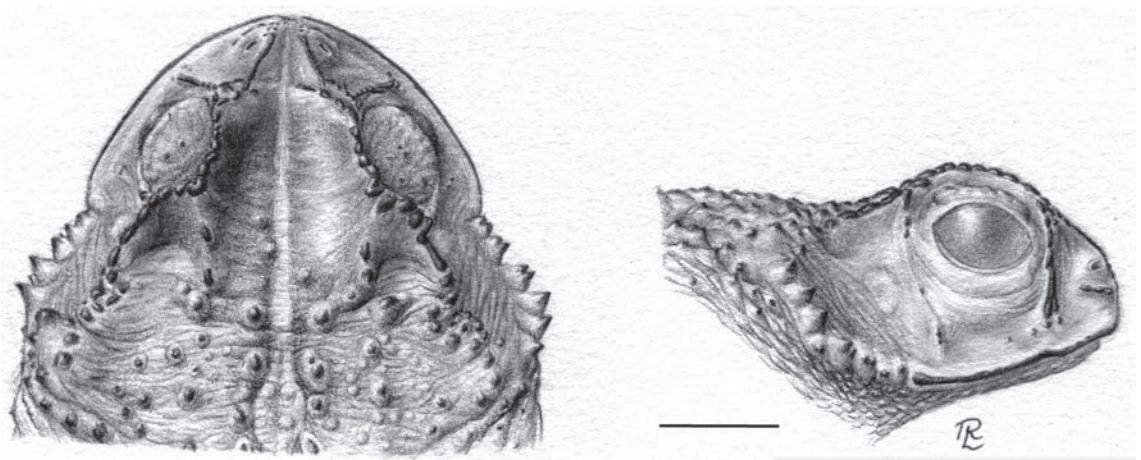

FIGURE 26: *Rhinella dorbignyi,* zvc 1711 (La Coronilla, Rocha, Uruguai), dorsal and lateral views of the head. (Scale bar = 5 mm).

R. bergi presents smaller size (males x = 40.4 mm; females x = 49.9 mm), snout long, posterior margin of the nostril at the level of anterior margin of mandible in lateral view; *R. azarai* presents smaller size (males x = 42.1 mm; females x = 45.4 mm), snout long in lateral view, loreal region distinctly concave.

Description: Head rounded, high (HH 16.5-19.6% SVL), wider than long (width 31-40% SVL, length 22.5-29% SVL). Snout rounded in dorsal view and straight in lateral view, slightly protruding in dorsal and lateral views, maxilla projecting anteriorly slightly ahead of mandible, posterior margin of nostril not surpassing anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and approximately equal to eye-nostril distance. Nostril subelliptic, dorsolateral with lateral opening closer to tip of snout than to eye, its longitudinal axis almost perpendicularly disposed in relation to the longitudinal axis of the head. *Canthus rostralis* angulated, highlighted by keratinized canthal crest; loreal region scantly visible in dorsal view, superior half straight or slightly concave, inferior half almost straight. Upper lip angulated, with slightly sharp borders, highlighted by keratinized maxillary crest, border of maxilla with a pronounced horizontal expansion. Tympanum oval, higher than wide, with inconspicuous borders, not close to postorbital crest (DTP 1.5-2.3% SVL). Parotoid gland dorsolateral, conspicuous, lower borders not well delimited, elongated or subtriangular, vertex pointing down, wider than high (width 11.8-21.5% SVL; height 8.9-15.7% SVL).

Cephalic crests continuous, with rounded and keratinized borders. Supraorbital crest very high and thick, continuous, occasionally serrate and ornamented with wrinkles and gaps, posterior portion occasionally wrinkled, supraorbital crest slightly rounded, continuous or not with canthal and suprapympanic crests, interorbital portion almost straight, diverging posteriorly (IOD_2/IOD_1 males x = 1.03; females x = 1.09). Preorbital crest very long, almost reaching maxillary crest, continuous, not bulky, branches/ramifications may be present at lower end, gaps occasionally create a granulose aspect. Postorbital crest reduced, very long, surpassing lower margin of eye, almost reaching maxillary crest, straight or slightly curved, without ramifications, usually gapped. Infraorbital crest absent or reduced, discontinuous, never extending beyond postorbital crest. Supratympanic crest long and inclined down posteriorly, usually simple and continuous, thick and ornamented, posterior portion dilated. Parietal crest present, high, usually continuous, it may be interrupted, posterior portion bulky. Canthal crest continuous, almost straight, diverging posteriorly, occasionally reaching preorbital crest, ending at the level of anterior margin of nostril. Subnasal crest short, its posterior portion barely reaches posterior margin of nostril, not bulky, continuous. Maxillary crest highly developed, continuous, visible in dorsal view, its keratinization occasionally reaching ventral surface of maxilla, posterior portion of crest bulky; posterior portion of the maxilla (between infraorbital and maxillary crests) flat.

Palmar and metatarsal tubercles, and tip of toes and fingers cornified. External palmar tubercle fleshy, rounded or oval, three times larger than the inner one, fleshy, oval. Nuptial asperities on dorsum of fingers I and II, and in part of the inner palmar tubercle in males. Relative size of fingers: I < or = II < or = IV < III; fingers without fringes, lateral surface serrate, formed by conical or rounded tubercles, which may have keratinized spicules; interdigital membrane reduced, present between fingers II and III, conspicuous in larger specimens; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than subarticulars. Hindlimbs very short, tibio-tarsal articulation reaches axilla and tip of fourth toe barely reaches the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval, high, subconical in lateral view, smaller than the outer one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles, with keratinized spicules and secondary points of keratin; interdigital membrane of toes with extensively serrate borders; webbing toes formula: I 1-2 II 1-3 III 2-3½ IV 3½-1½ V; distal subarticular tubercle of fourth toe doubled; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical or rounded, keratinized; larger rounded tubercles, highly keratinized, arrayed longitudinally on the anterior half of body, especially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with a few small granules, rounded and keratinized, external margin extensively keratinized. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region, tip of snout, and region below subnasal crest highly smooth, with just a few keratinized granules, rounded or elongated, not fleshy. Ventral surface of maxilla with minuscule keratinized spicules, usually aligned. Interorbital area highly smooth or with just a few rounded and keratinized granules, usually highly fleshy; area between tympanum and postorbital crest,

TABLE 9: Descriptive statistics of measurements (in mm) of males (N = 152) and females (N = 36) of *Rhinella dorbignyi* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	48.22	55.58	36.1	42.1	63.7	68.5	5.95	7.42
HW	17.28	19.15	12.8	15.2	23.0	30.4	1.92	2.82
HL	12.38	13.66	9.7	11.1	15.9	16.4	1.18	1.39
IND	2.51	2.76	1.8	1.7	3.3	3.8	0.28	0.49
SW	5.14	5.59	3.9	4.5	6.8	6.7	0.59	0.60
END	3.44	3.83	2.8	2.8	4.2	4.7	0.31	0.41
ESD	5.10	5.69	4.0	4.7	6.4	6.7	0.42	0.52
IOD1	6.05	6.85	4.5	4.9	8.9	8.4	0.68	0.81
IOD2	6.31	7.38	4.2	4.2	11.0	10.2	1.02	1.37
ED	3.88	4.32	1.9	3.5	5.2	5.4	0.46	0.47
TD	2.03	2.08	1.4	1.6	3.2	2.9	0.32	0.32
TH	2.72	2.92	1.7	2.2	3.9	3.8	0.40	0.41
EW	3.04	3.16	2.2	2.4	8.6	4.3	0.74	0.51
PGW	7.68	8.84	4.8	5.6	10.4	12.5	1.17	1.57
PGH	6.21	7.05	4.1	4.9	9.8	9.4	1.07	1.08
STCL	3.93	4.38	2.2	2.0	6.3	6.1	0.66	0.93
POS	5.39	5.70	3.9	3.5	7.6	8.5	0.75	1.11
THL	11.10	11.93	7.7	9.1	14.7	14.7	1.40	1.53
TIL	14.96	16.23	10.6	12.0	20.5	21.2	2.05	2.29
TAL	14.37	15.53	10.1	11.8	20.0	19.5	2.10	2.11
HAL	10.46	11.08	7.2	8.3	14.9	13.9	1.49	1.45
FOL	16.67	17.29	11.3	12.9	23.9	22.4	2.58	2.39

and between tympanum and parotoid gland highly smooth and without granules.

In preserved specimens, dorsum brown or grayish with light spots, or dark-brown without conspicuous spots; a lateral light stripe between parotoid and inguinal region, with irregular margins and occasionally with gaps, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe always present; labial light stripe present. Belly cream or dark-grey with small dark spots.

Variation: One specimen had the longitudinal dorsal stripe widely interrupted at sacral region. A few individuals present reduced nuptial asperities on the lateral of finger III, and parotoid glands may present a less conspicuous granulation creating a smoother and homogenous aspect. In some specimens, the labial light stripe is visible in dorsal view, above the lateral expansion border of the maxilla. Young specimens may present a dotted labial light stripe. Gallardo (1957) reported a specimen with 77 mm SVL. See descriptive statistics in Table 9.

Distribution: Occurs in Rio Grande do Sul, Brazil, in Uruguay and Argentina (Provincia Buenos Aires). The species seems to be more associated with dryer habitats than *R. fernandezae.* See map in Figs. 16 and 25.

Natural history: In Uruguay (Klappenbach, 1969), in Argentina (Milstead, 1956), and in State of Rio Grande do Sul, Brazil (Braun, 1978), the species was found inside small holes, in softy soil and grassy areas, where they remain with the head at the entrance of the hole, waiting for potential preys. They disappear inside the holes when disturbed. Maneyro *et al.* (1995) and Achával & Olmos (1997) also found the species in Uruguay under rocks or inside holes in the middle of grassy fields; and fragmosis was observed. Achával & Olmos (1997) described the hole as a vertical tunnel of 17 to 28 cm deep, dug with the posterior legs. Reproduction takes place at spring and summer, from October to March, after heavy rains (Braun, 1978; Maneyro *et al.,* 1995; Achával & Olmos 1997).

10. *Rhinella merianae* (**Figure 27**)

Bufo granulosus merianae Gallardo, 1965.

Holotype: AMNH 46531.

Type locality: Rio Essequibo, Guiana.

Diagnosis: Adult males ranging from 30.1 to 67.4 mm (SVL x = 48.4 mm, n = 110), and adult females ranging from 32.2 to 77.1 mm (SVL x = 55.1 mm, n = 61); cephalic crests predominantly continuous and frequently serrate; supratympanic crest long; parietal crest absent or inconspicuous; subnasal crest long, usually extending beyond posterior margin of nostril; rounded snout in lateral view and squared in dorsal view, highly sloping dorsoventrally; longitudinal dorsal stripe absent; belly usually pigmented.

Comparison between species: Rhinella granulosa presents rounded snout in dorsal view, lower supraorbital crest, and less developed maxillary crest; *R. pygmaea, R. bergi,* and *R. azarai* present smaller average size (males 32.1 mm, 40.4 mm, 42.1 mm; females 40.8 mm, 49.9 mm, 45.4 mm, respectively), cephalic crests predominantly continuous, parietal crest present and infraorbital crest long, posteriorly extending beyond postorbital crest; *R. major* presents interorbital area smooth or with just a few granules, loreal region, maxillary crest, and labial light stripe visible in dorsal view; *R. dorbignyi* and *R. fernandezae* present shorter snout in lateral and dorsal views, posterior margin of nostril do not surpass anterior margin of mandible in lateral view, smaller parotoid gland, larger postorbital space; *R. mirandaribeiroi* presents longitudinal dorsal stripe, head elongated, snout rounded in dorsal view and flattened dorsoventrally, less developed maxillary crest; *R. nattereri* presents rounded head and snout flattened and sloping dorsoventrally; *R. humboldti* presents head narrower and longer, snout rounded in dorsal view, flattened and sloping dorsoventrally; *R. centralis* sp. n. presents an extremely high concentration of keratinized granules on the head, smaller parotoid gland, maxillary crest visible in dorsal view.

Description: Head subtriangular, low (HH 14.0-17.8% SVL), wider than long (width 30-39% SVL, length 21.5-29% SVL). Snout squared in dorsal view, rounded in lateral view, long, maxilla projecting ahead of mandible in lateral view, posterior margin of nostril at the level of anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region narrow, visible in dorsal view, superior half slightly concave, inferior half oblique. Upper lip may be angulated or rounded, with slightly convex border, anterior portion of lip occasionally visible in lateral view below maxillary crest, upper lip not flared. Tympanum oval, higher than wide, borders occasionally inconspicuous, not close to postorbital crest (DTP 1.1-2.1% SVL). Parotoid gland dorsolateral, conspicuous, borders well delimited, subtriangular, vertex pointing down, slightly wider than higher (width 15-24.1% SVL; height 11.8-18.3% SVL).

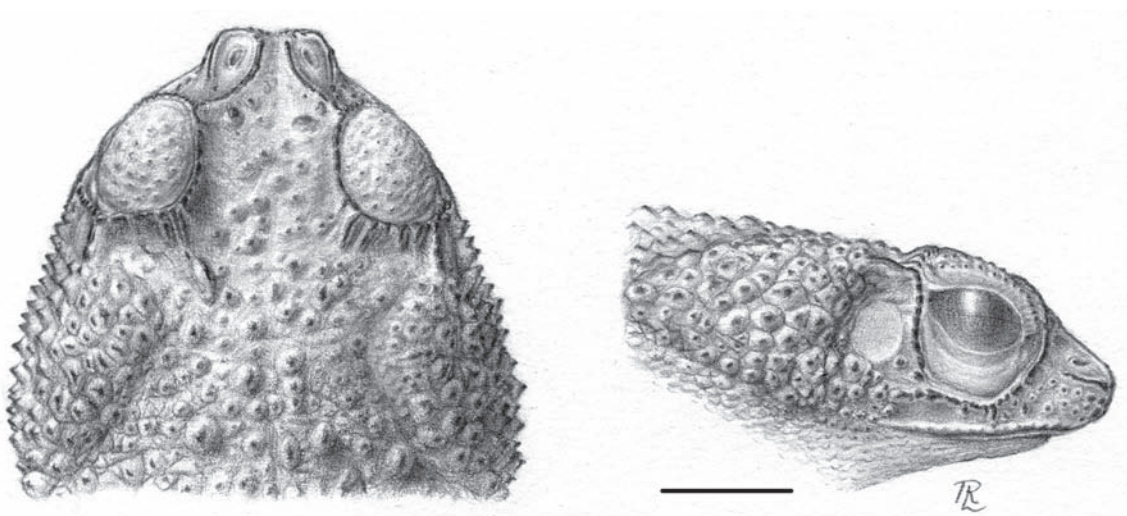

FIGURE 27: *Rhinella merianae,* MZUSP 65795 (Serra da Saracura, Roraima), dorsal and lateral views of the head. (Scale bar = 5 mm).

Cephalic crests with conspicuous borders, keratinized, predominantly continuous and frequently serrate. Supraorbital crest high, continuous or granulose; when continuous, it is frequently serrate, usually ornamented with wrinkles and gaps; when granulose, a few granules may be coalescent; supraorbital crest rounded, not forming a straight line with canthal and supratympanic crests, its interorbital portion curved (IOD_2/IOD_1 x = 0.9), posterior portion usually wrinkled. Preorbital crest usually granulose, occasionally with coalescent granules, bulky and irregularly wrinkled. Postorbital crest long, reaching the level of inferior margin of eye, usually not reaching infraorbital crest, straight, occasionally with ramifications/branches toward tympanum. Infraorbital crest granulose or continuous with posterior gaps, short or long, extending or not beyond postorbital crest and ending at the level of the maxillary crest, a slight lateral expansion, visible in dorsal and ventral views may be present. Supratympanic crest long and straight, continuous or formed by elongated granules, occasionally bulky and coalescent, arrayed in one or two irregular lines, posterior portion not dilated. Parietal crest absent or inconspicuous. Canthal crest usually continuous and occasionally reaching preorbital crest, diverging posteriorly, ending at the level of anterior margin of nostril and occasionally merged with granules the tip of snout, slightly curved. Subnasal crest long, its posterior portion usually extending beyond posterior margin of nostril, frequently continuous and occasionally bulky creating a squared profile of snout in dorsal view. Maxillary crest developed, discontinuous in a few specimens, with gaps, its keratinization reaches ventral surface of maxilla, usually not visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) distinctly concave.

Palmar and metatarsal tubercles, and tip of toes and fingers cornified. External palmar tubercle salient, rounded or oval, twice or three times larger than the inner one, salient, oval. Nuptial asperities on dorsum of fingers I and II, and in part of inner palmar tubercle in males. Relative size of fingers: I > II < IV < III; fingers without fringes, lateral surface serrate, formed by conical granules, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical, of variable sizes, smaller than subarticulars. Hindlimbs short, tibio-tarsal articulation reaches the axilla, and fourth toe surpasses the snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval or elongated, high, subconical in lateral view, smaller than the outer one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders, webbing toes formula: I 1-2 II 1-3 III 2-3½$^{++}$ IV 4^{-}-2 V; distal subarticular tubercle of fourth toe doubled, one element occasionally highly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, conical or rounded, keratinized; larger tubercles, rounded or conical, highly keratinized, arrayed on the dark spots of the anterior third of body, especially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with granules of variable sizes, spiculated or rounded, keratinized, external margin with dots of keratin, irregularly aligned. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with small keratinized granules, rounded or elongated, not fleshy; small dots or irregular spots of keratin, practically flatten, on tip of snout and below subnasal crest. Ventral surface of maxilla with minuscule keratinized spicules, slightly aligned, arrayed on irregular lines. Interorbital area with a few granules of variable sizes, conical or rounded, keratinized, usually highly fleshy, scattered of slightly arrayed in two longitudinal lines; area between tympanum and postorbital crest with small granules, conical, keratinized; area between tympanum and parotoid gland smooth or with small granules, keratinized.

In preserved specimens, dorsum brownish light with closely placed dark spots of variable size forming a mosaic, some individuals are more melanic; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe absent; labial light stripe present, of variable width. Belly light cream or yellowish, with small dark spots.

Variation: Parotoid gland may be highlighted by an olivaceous or orange coloration. A few specimens presented belly highly pigmented from inguinal to gular region, labial light stripe present, and dotted with small dark spots. See descriptive statistics in Table 10.

Distribution: Venezuela, Guiana, Suriname and French Guiana, and in the Brazilian States of Amazonas and Roraima, north of the Amazon River, at the rivers Solimões, Negro, and Branco. See map in Figs. 19 and 22.

TABLE 10: Descriptive statistics of measurements (in mm) of males (N = 110) and females (N = 61) of *Rhinella merianae* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	48.42	55.11	30.1	32.2	67.4	77.1	8.86	12.27
HW	17.12	18.49	11.2	11.6	22.5	26.1	2.80	3.52
HL	12.73	13.69	8.8	9.0	16.2	18.1	1.97	2.33
IND	1.86	2.05	1.2	1.3	2.5	2.7	0.31	0.35
SW	5.15	5.68	3.5	3.5	6.8	7.6	0.81	1.05
END	3.33	3.63	2.2	2.4	4.5	5.2	0.54	0.71
ESD	5.29	5.70	3.7	3.7	7.4	8.1	0.87	1.04
IOD1	6.01	6.49	4.0	1.7	8.3	9.1	1.01	1.37
IOD2	5.37	5.99	3.2	3.3	8.4	8.9	1.10	1.26
ED	4.18	4.44	2.9	3.0	5.3	6.0	0.57	0.71
TD	2.38	2.57	1.4	1.4	3.5	5.2	0.51	0.64
TH	2.89	3.09	1.9	1.9	4.2	4.7	0.54	0.66
EW	3.79	4.08	2.8	2.9	4.9	6.8	0.50	0.75
PGW	9.54	10.55	6.1	6.0	14.1	15.1	1.90	2.25
PGH	7.46	8.14	4.8	5.0	10.2	11.6	1.33	1.81
STCL	3.02	3.39	1.6	2.0	4.9	5.9	0.76	0.92
POS	3.99	4.41	2.4	2.8	6.2	7.2	0.89	1.09
THL	10.96	12.05	6.7	7.2	14.5	17.1	2.07	2.61
TIL	17.57	18.56	11.1	10.7	25.9	26.9	3.63	4.10
TAL	16.43	17.22	10.1	9.5	23.2	26.0	3.42	3.91
HAL	11.03	11.85	6.7	6.5	15.0	18.0	2.20	2.78
FOL	17.08	17.96	10.0	10.4	22.9	26.0	3.53	4.13

Natural history: In French Guiana, Lescure & Marty (2000) observed the species in savanna and rocky areas. Reproduction occurs in temporary ponds at the beginning of the rainy season. According to Hoogmoed & Gorzula (1979), in Venezuela the species is the first to reproduce at the beginning of the rainy season, especially in temporary ponds.

11. *Rhinella humboldti* (Figure 28)

Bufo granulosus humboldti Gallardo, 1965.
Bufo granulosus barbouri Gallardo, 1965 – new synonym.
Bufo granulosus beebei Gallardo, 1965 – new synonym.
Bufo beebei – Rivero, Langone & Prigioni, 1986 – new synonym.
Chaunus beebei – Frost *et al.,* 2006 – new synonym
Rhinella beebei – Chaparro *et al.,* 2007 – new synonym.
Rhinella humboldti – Pramuk *et al.,* 2008.

Holotype: MCZ 24882.

Type locality: Gualanday, Tolima, Colombia. The name *humboldti* was chosen preferably over *beebei* because it is associated with continental populations while *beebei* was named after insular specimens obtained at Trinidad and Tobago.

Diagnosis: Adult males ranging from 32.5 to 64.4 mm (SVL x = 46 mm, n = 188), and adult females ranging from 33.7 to 70.3 mm (SVL x = 52.2 mm, n = 61); snout rounded in lateral and dorsal views, long, posterior edge of the nostril at the level of anterior margin of mandible in lateral view; cephalic crests predominantly continuous and frequently serrate and wrinkled; supratympanic crest long and granulose; parietal crest absent or inconspicuous; subnasal crest very long, its posterior portion extending beyond posterior margin of nostril, occasionally reaching preorbital crest; longitudinal dorsal stripe absent, belly usually pigmented.

Comparison between species: Rhinella granulosa presents granulose cephalic crests, low supraorbital crest, less developed maxillary crest; *R. pygmaea, R. bergi,* and *R. azarai* present smaller average size (males 32.1 mm, 40.4 mm, 42.1 mm; females 40.8 mm, 49.9 mm,

45.4 mm, respectively), cephalic crests strictly continuous, parietal crest present; *R. major* presents snout straight in lateral and squared in dorsal view, interorbital area smooth or with just a few granules, loreal region, maxillary crest and labial light stripe visible in dorsal view; *R. dorbignyi* and *R. fernandezae* present snout shorter in lateral and dorsal views, smaller parotoid glands, larger postorbital space, posterior margin of nostril not surpassing anterior margin of mandible in lateral view; *R. mirandaribeiroi* presents longitudinal dorsal stripe, elongated head, snout flattened dorsoventrally, maxillary crest less developed; *R. nattereri* presents rounded head with long snout, squared snout in dorsal view, shorter subnasal crest, its posterior portion not extending beyond posterior margin of nostril; *R. merianae* presents wider and shorter head, snout squared in dorsal view, narrower and sloping dorsoventrally; *R. centralis* sp. n. presents an extremely high concentration of keratinized small granules on top of head, snout narrower and sloping dorsoventrally.

Description: Head subtriangular, low (height 13.4-15.6% SVL), wider than long (width 30-47% SVL, length 20-30% SVL). Snout rounded in dorsal and lateral views, long, maxilla projecting ahead of mandible in lateral view, posterior margin of nostril at the level of anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal openings, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region scantly visible in dorsal view, superior half slightly concave, inferior half almost straight. Upper lip angulated, with a slightly sharp border, or rounded with a slight convex border, highlighted by keratinized maxillary crest, anterior portion of lip occasionally visible in lateral view below maxillary crest, upper lip not flared. Tympanum oval, higher than wide, with conspicuous borders, close to postorbital crest (DTP 0.6-1.6% SVL). Parotoid gland dorsolateral, conspicuous, borders well delimited, subtriangular, vertex pointing down, wider than higher (width 12.3-21.7% SVL; height 10-17.8% SVL).

Cephalic crests with conspicuous borders, keratinized, predominantly continuous and serrate. Supraorbital crest high, continuous and frequently serrate, usually ornamented with gaps and wrinkles, or granulose with a few coalescent granules, supraorbital crest rounded, not forming a straight line with supratympanic crest, interorbital portion slightly curved (IOD_2/IOD_1 x = 0.88), posterior portion extensively wrinkled. Preorbital crest granulose with a few coalescent granules, occasionally bulky and irregularly wrinkled. Postorbital crest long, reaching lower margin of eye, it may also reach infraorbital crest, straight, occasionally with perpendicular branches toward tympanum. Infraorbital crest usually curved and continuous, occasionally with posterior gaps, usually short, occasionally with a lateral expansion. Supratympanic crest long and straight, with granules of irregular size and shape, which may be fleshy and occasionally coalesced, arrayed in one or two irregular lines, posterior

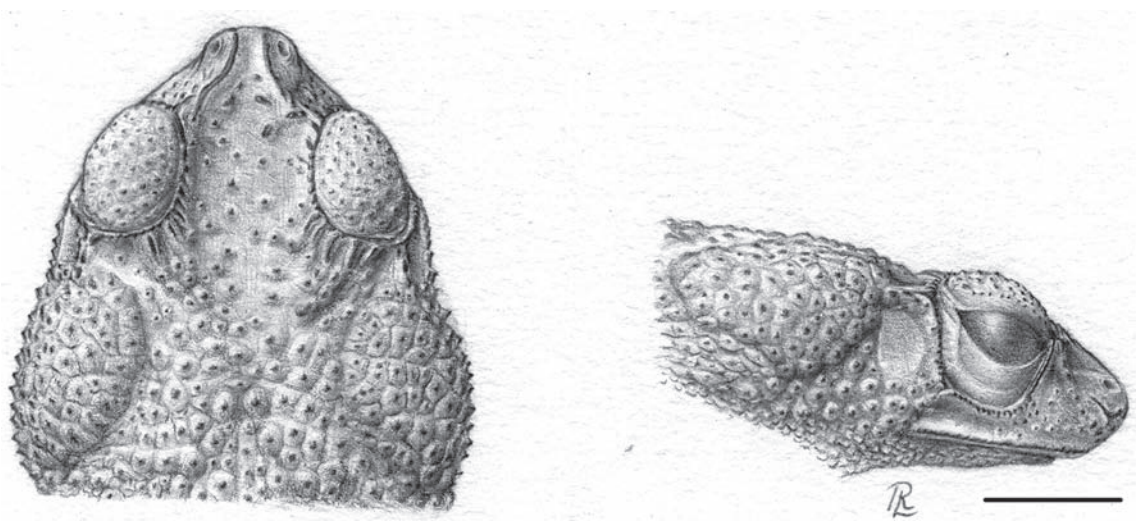

FIGURE 28: *Rhinella humboldti,* MZUSP 105889 (Villavicencio, Colombia), dorsal and lateral views of the head. (Scale bar = 5 mm).

portion not dilated. Parietal crest absent or inconspicuous. Canthal crest continuous, occasionally reaching preorbital crest, ending at the level of anterior margin of nostril, slightly curved, diverging posteriorly. Subnasal crest very long, its posterior portion extending beyond posterior margin of nostril, occasionally reaching preorbital crest, occasionally bulky, usually continuous, posterior portion occasionally with gaps. Maxillary crest developed, its keratinization reaches ventral surface of maxilla, usually not visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) concave.

Palmar and metatarsal tubercles, and tip of toes and fingers slightly cornified. External palmar tubercle salient, rounded or oval, twice larger than the inner one, elongated or oval, high, rounded in lateral view. Nuptial asperities on dorsum of fingers I and II and in part of the inner palmar tubercle in males. Relative size of fingers: I > II < IV < III; fingers without fringes, lateral surface serrate, formed by conical granules, which may have keratinized spicules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical, of variable sizes, smaller than subarticulars. Hindlimbs very short, tibio-tarsal articulation reaches axilla and tip of fourth toe barely reaching snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval, high, subconical in lateral view, smaller than outer one, rounded or oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles with keratinized apices; interdigital membrane of toes with serrate borders; webbing toes formula: I 1-2 II 1-3 III 2-3½⁺ IV 3½⁺-1⁺ V; distal subarticular tubercle of fourth toe doubled, one element occasionally distinctly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than the subarticulars; tarsal fold absent.

Dorsum with tubercles of variable sizes, rounded or conical, keratinized; larger rounded tubercles, highly keratinized, arrayed on the dark spots of the anterior third of body, specially between parotoids. Belly with small granules, adjoined, conical or rounded. Upper eyelid with granules of variable sizes, spiculated or rounded, keratinized, external margin with dots of keratin, irregularly aligned. Parotoids with individualized and fleshy tubercles, flattened on dorsal and conical on lateral surfaces of gland. Loreal region with a few small keratinized granules, rounded or

TABLE 11: Descriptive statistics of measurements (in mm) of males (N = 188) and females (N = 61) of *Rhinella humboldti* (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	46.01	52.16	32.5	33.7	64.4	70.4	6.27	8.55
HW	15.82	17.21	11.3	11.6	21.7	22.9	2.03	2.45
HL	12.31	13.08	8.8	9.2	15.9	16.6	1.42	1.69
IND	1.81	2.03	1.3	1.4	2.4	2.8	0.25	0.32
SW	4.98	5.42	3.7	3.8	6.6	7.3	0.56	0.81
END	3.36	3.70	2.3	2.8	4.5	5.1	0.41	0.51
ESD	5.12	5.64	3.7	3.6	6.7	8.4	0.60	0.86
IOD1	5.75	6.36	4.2	4.2	7.6	8.5	0.73	0.91
IOD2	5.04	5.61	3.6	3.7	7.0	7.6	0.71	0.94
ED	4.18	4.30	3.1	3.0	5.5	5.4	0.48	0.55
TD	2.29	2.30	1.2	1.4	3.4	3.3	0.41	0.47
TH	2.73	2.79	1.5	1.5	4.2	4.3	0.46	0.55
EW	3.63	3.84	2.5	2.9	4.6	4.8	0.41	0.49
PGW	8.34	9.50	4.8	5.4	12.5	13.4	1.41	1.71
PGH	6.26	7.07	3.2	4.1	10.2	9.6	1.09	1.20
STCL	2.85	3.13	1.6	1.8	5.2	5.1	0.57	0.59
POS	3.94	4.15	1.9	2.3	5.6	5.8	0.65	0.72
THL	10.27	11.58	7.0	8.0	14.5	15.3	1.52	1.81
TIL	16.47	17.97	10.7	11.1	26.0	23.4	2.76	2.97
TAL	15.51	16.92	10.0	10.9	24.0	22.5	2.71	2.99
HAL	10.36	11.28	7.1	7.5	15.1	15.1	1.64	1.86
FOL	16.20	17.58	10.6	11.9	23.6	23.3	2.43	2.92

elongated, not fleshy; small dots or irregular spots of keratin, almost flatten, on the tip of snout and below subnasal crest. Ventral surface of maxilla smooth or with minuscule keratinized spicules, slightly aligned, arrayed in irregular lines. Interorbital area with a few granules of variable sizes, conical or rounded, keratinized, usually highly fleshy, arrayed or not in two longitudinal lines; area between tympanum and parotoid gland smooth or with a few keratinized granules; area between tympanum and postorbital crest with small granules, conical and keratinized.

In preserved specimens, dorsum brownish light or dark-brown with scattered dark spots of variable sizes; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe absent; labial light stripe present, of variable width. Belly light cream or yellowish, usually with small dark spots.

Variation: A few individuals presented reduced nuptial asperities at the lateral surface of finger III; small points of keratinization on the tip of snout, arrayed between canthal and subnasal crests, giving the impression that the crests are continuous. Certain individuals presented an inconspicuously long infraorbital crest, extending beyond postorbital crest. In larger specimens, parietal crest may be conspicuous and continuous, and the supratympanic crest may be continuous. Specimens from Isla Margarita (Venezuela) usually present interorbital area extensively covered by keratinized branches from cephalic crests. Specimens from Trinidad and Tobago presented smaller size (males, x = 42.2 mm, n = 42; females, x = 51.5 mm, n = 6) compared to specimens from the continent (males, x = 46.6 mm, n = 127; females, x = 52.2 mm, n = 50). See descriptive statistics in Table 11.

Distribution: Colombia, Venezuela, Surinam, Guyana, and Trinidad. See map in Fig. 22.

Natural history: According to Kenny (1969), this species occurs in open areas and in plantation fields in Trinidad and Tobago, at low altitude. Renjifo & Lundberg (1999) observed the species in Colombia, hiding during the day under rocks, fallen logs or in small holes in the ground.

12. *Rhinella centralis* sp. n.
(Figure 29)

Bufo granulosus humboldti Gallardo, 1965 (part).

Holotype: USNM 203600; *Paratypes:* MZUSP 111002-111003, 110995; USNM 203595-203612.

Type locality: Chitre, Herrera, Panama.

Diagnosis: Adult males ranging from 38.1 to 58.4 mm (SVL x = 47.6 mm, n = 44), and adult females ranging from 41 to 61.8 mm (SVL x = 51.6 mm, n = 1 7); crests predominantly granulose, supraorbital crest high, continuous, frequently serrate; infraorbital crest short; supratympanic crest long formed by one or two lines of granules; subnasal crest long, its posterior portion extending beyond posterior margin of nostril; parietal crest absent or inconspicuous; upper lip an-

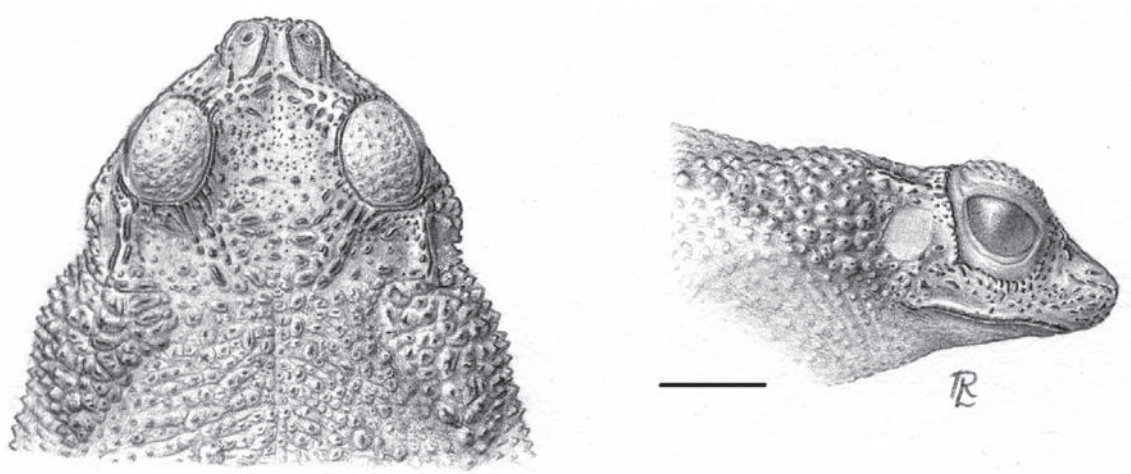

FIGURE 29: *Rhinella centralis* sp. n., USNM 203600 (Holotype), dorsal and lateral views of the head. (Scale bar = 5 mm).

gulated; snout distinctly narrow in dorsal profile and highly sloping dorsoventrally in lateral view; longitudinal dorsal stripe absent; belly pigmented; tympanum not close to postorbital crest (DTP 1.6-2.2% SVL).

Comparison between species: Rhinella granulosa presents lower supraorbital crest, less developed maxillary crest, tympanum very close to postorbital crest (DTP 0.6-1.3% SVL); *R. pygmaea, R. bergi,* and *R. azarai* present smaller average size (males 32.1 mm, 40.4 mm, 42.1 mm; females 40.8 mm, 49.9 mm, 45.4 mm, respectively), cephalic crests predominantly continuous, parietal crest present, infraorbital crest long, posteriorly extending beyond postorbital crest; *R. major* presents straight snout in lateral view, tympanum very close to postorbital crest (DTP 0.6-1.6% SVL), interorbital area smooth or with just a few granules, loreal region, maxillary crest, and labial light stripe are visible in dorsal view; *R. dorbignyi* and *R. fernandezae* present short snout in lateral and dorsal views, smaller parotoid glands, larger postorbital space, posterior end of nostril not surpassing anterior margin of mandible in lateral view; *R. mirandaribeiroi* presents longitudinal dorsal stripe, lower supraorbital crest, less developed maxillary crest, tympanum very close to postorbital crest (DTP 0.4-1.0% SVL); *R. nattereri* presents rounded head with a long snout, tympanum very close to postorbital crest (DTP 0.9-1.4% SVL), more developed parotoid glands, shorter subnasal crest, its posterior portion not extending beyond posterior margin of nostril; *R. merianae* presents more developed parotoid glands, belly more extensively pigmented; *R. humboldti* presents tympanum very close to postorbital crest (DTP 0.9-1.6% SVL), snout wider and less sloping dorsoventrally in lateral view, rounded in dorsal view, subnasal crest very long, its posterior portion extending beyond posterior margin of nostril.

Description of holotype: Head subtriangular, low (HH 14.6% SVL), wider than long (width 32.1% SVL, length 24.5% SVL). Snout squared in dorsal view, rounded in lateral view, long in dorsal and lateral views, maxilla projecting ahead of mandible in lateral view, posterior margin of nostril at the level of anterior margin of mandible in lateral view. Eye lateral, encapsulated, its diameter smaller than interorbital distance and larger than eye-nostril distance. Nostril subelliptic, dorsolateral with dorsal opening, closer to tip of snout than to eye, its longitudinal axis obliquely disposed in relation to the longitudinal axis of head. *Canthus rostralis* slightly angulated, highlighted by keratinized canthal crest; loreal region scantly visible in dorsal view, superior half slightly concave, inferior half oblique. Upper lip angulated, with a slightly sharp border highlighted by keratinized maxillary crest, upper lip not flared. Tympanum oval, higher than wide, with inconspicuous borders, not close to postorbital crest (DTP 2.2% SVL). Parotoid gland dorsolateral, conspicuous, inferior borders not well delimited, subtriangular, with vertex pointing backwards, wider than high (width 19.3% SVL; height 13.2% SVL).

Cephalic crests with conspicuous borders, keratinized, predominantly continuous and frequently serrate. Supraorbital crest high, continuous, rounded, not forming a straight line with supratympanic crest, interorbital portion of supraorbital crest curved (IOD_2/IOD_1 = 0.91), posterior portion wrinkled. Preorbital crest granulose, occasionally with a few coalescent granules, bulky and irregularly wrinkled. Postorbital crest straight, long, reaching inferior margin of eye and infraorbital crest. Infraorbital crest short, curved, granulose, occasionally with a few coalescent granules. Supratympanic crest long and inclined up posteriorly, highly bulky, in part continuous and in part formed by elongated granules arrayed in two lines, posterior portion dilated. Parietal crest inconspicuous. Canthal crest continuous, usually not reaching preorbital crest, extending beyond anterior border of nostril, slightly curved, diverging posteriorly. Subnasal crest long, its posterior portion extending beyond posterior margin of nostril, formed by elongated granules, bulky, providing a squared aspect to snout in dorsal view. Maxillary crest developed, its keratinization reaches ventral surface of maxilla, scantly visible in dorsal view; posterior portion of maxilla (between infraorbital and maxillary crests) distinctly concave.

Palmar and metatarsal tubercles, and tip of toes and fingers cornified. External palmar tubercle fleshy, rounded, three times larger than the inner one, oval, fleshy. Nuptial asperities on dorsum of fingers I and II, on part of the inner palmar tubercle, and reduced on the lateral surface of finger III in males. Relative size of fingers: I > II < IV < III; fingers without fringes, lateral surface serrate, formed by conical granules; interdigital membrane of fingers absent; distal subarticular tubercle of third finger doubled; supranumerary tubercles conical or rounded, of variable sizes, smaller than the subarticulars. Hindlimbs short, tibio-tarsal articulation reaches axilla and only fourth toe surpasses snout when the leg is stretched and adjoined to body. Inner metatarsal tubercle oval, high, subconical in lateral view, smaller than outer one, oval, high, subconical in lateral view. Relative size of toes: I < II < V < III < IV; toes without fringes, lateral surface serrate, formed by conical tubercles; in-

terdigital membrane of toes with serrate borders; webbing toes formula: I 1-2 II 1-3+ III 2-3½ IV 3½-2 V; distal subarticular tubercle of fourth toe doubled, one element distinctly larger than its symmetrical; supranumerary tubercles conical, of variable sizes, smaller than subarticulars; tarsal fold absent.

Dorsum with keratinized tubercles, larger and rounded at anterior half of dorsum, smaller and conical at posterior half; a few dorsal tubercles present tiny spicules of keratin around the central keratinization. Belly with small granules, adjoined, rounded. Upper eyelid with small granules, rounded and keratinized, external margin with dots of keratin, irregularly aligned. Parotoids with individualized tubercles, fleshy and with minuscule keratinized spicules around the central keratinization, tubercles flattened on dorsal and conical on lateral surfaces of gland. Loreal region covered by small or tiny keratinized granules, rounded or elongated, highly fleshy; numerous points or irregular spots of keratin, highly fleshy, at tip of snout and below subnasal crest. Ventral surface of maxilla with minuscule keratinized spicules, irregularly aligned. Interorbital area with granules of variable sizes, elongated or rounded, keratinized, highly fleshy, arrayed between numerous tiny spicules of keratin; area between tympanum and postorbital crest with small granules, keratinized, highly fleshy; area between tympanum and parotoid gland with small granules, conical and keratinized.

Color of the dorsum brownish light with dark spots of variable sizes, closely placed, forming a mosaic; a lateral light stripe between parotoid and inguinal region, with irregular margins, is delimited by the dorsal pattern of spots; longitudinal dorsal stripe absent; labial light stripe present, reaching tip of snout. Belly light cream with reduced pigmentation.

Measurements of holotype: SVL 52.8; HW 17.5; HL 13.4; IND 1.8; LFO 5.5; END 4.0; ESD 5.9; IOD_1 6.9; IOD_2 6.1; ED 4.1; TD 2.4; TH 2.7; EW 3.5; PGW 7.6; PGH 6.1; STCL 3.75; POS 4.4; HAL 11.2; THL 16.4; TIL 17.1; TAL 11.2; FOL 17.3.

Variation: In a few specimens, belly pigmentation is concentrated at the gular and/or pectoral region; labial light stripe may be absent or reduced; snout may present a rounded or squared profile in dorsal view. A few individuals presented an inconspicuously long infraorbital crest. Certain individuals do not present the tiny spicules of keratin on the interorbital area. See descriptive statistics in Table 12.

TABLE 12: Descriptive statistics of measurements (in mm) of males (N = 44) and females (N = 17) of *Rhinella centralis* sp. nov. (SD = standard deviation).

Characters	Average		Minimum		Maximum		SD	
	Male	Female	Male	Female	Male	Female	Male	Female
SVL	47.63	51.61	38.1	41.1	58.5	61.8	4.69	5.87
HW	16.07	16.84	13.1	13.8	18.9	20.5	1.27	1.76
HL	12.25	12.71	10.0	10.8	14.5	14.6	1.01	1.18
IND	1.79	1.85	1.4	1.6	2.3	2.1	0.19	0.17
SW	5.12	5.34	3.9	4.5	6.8	6.3	0.54	0.52
END	3.55	3.76	2.8	3.2	4.2	4.5	0.28	0.33
ESD	5.28	5.52	4.3	4.6	6.2	6.4	0.40	0.50
IOD1	5.76	6.02	4.6	5.0	7.2	7.0	0.51	0.64
IOD2	5.21	5.58	4.1	4.5	6.7	6.7	0.53	0.66
ED	3.86	3.89	3.2	3.4	4.7	4.4	0.38	0.30
TD	2.17	2.15	1.4	1.7	3.1	2.6	0.29	0.29
TH	2.50	2.47	1.8	2.1	3.4	3.0	0.31	0.25
EW	3.69	3.76	2.7	3.2	4.6	4.3	0.34	0.31
PGW	8.29	8.95	6.4	7.0	10.9	12.8	1.15	1.57
PGH	6.32	6.47	4.5	4.4	9.0	9.3	0.95	1.08
STCL	3.14	3.48	2.5	2.6	4.3	4.4	0.41	0.47
POS	3.97	4.01	3.3	3.0	5.1	4.7	0.43	0.44
THL	10.06	10.67	7.8	8.8	12.8	13.1	1.07	1.09
TIL	15.94	16.32	12.4	12.7	20.1	20.5	1.64	2.03
TAL	15.29	15.79	11.6	12.5	18.5	19.9	1.58	1.92
HAL	10.24	10.66	8.3	8.4	12.9	13.5	1.02	1.25
FOL	15.67	16.16	11.8	12.6	19.9	19.1	1.71	1.78

Distribution: Panama, in the lowlands toward the Pacific Ocean. See map in Fig. 22.

Natural history: According to Ibáñez *et al.* (1999), in Barro Colorado the species occurs in open grassy areas and reproduction starts during rainy season, specially on rainy nights. Eggs are laid in temporary ponds.

Etymology: The specific name was chosen after Central America because it is the only species of the *Rhinella granulosa* group occurring in Panama.

Artificial key for the species of *Rhinella granulosa* group

Although we examined a large series of specimens, some overlapping of diagnostic features is possible. For this reason, descriptions and plates should be consulted extensively to help identification. Metric measurements were included as additional help.

1a. Cephalic crests continuous, supraorbital crest very high and bulky; snout very short in dorsal and ventral views, straight in lateral view (Fig. 3F); interorbital distance, space between postorbital crest and tympanum, and space between tympanum and parotoid gland almost entirely smooth, eventually with a few granules; head height (HH) 14.5-19.6% SVL; distance between tympanum and postorbital crest (DTP) 1.5-2.7% SVL, and distance between tympanum and parotoid 3.6-7.5% SVL; postorbital space (POS) 7.4-15.1% SVL; supratympanic crest length (STCL) 5.2-10.6% SVL.....2

1b. Cephalic crests continuous or granulose, supraorbital crest high or low; snout long in lateral view; interorbital distance, space between postorbital crest and tympanum, and between tympanum and parotoid with granules; head height (HH) 11.3-18.3% SVL; distance between tympanum and postorbital crest (DTP) 0.4-3.1% SVL, and distance between tympanum and parotoid 1.2-6.1; postorbital space (POS) 4.8-13.2% SVL; supratympanic crest length (STCL) 2.5-9.1% SVL.....3

2a. Infraorbital crest always present, long, extending beyond postorbital crest; longitudinal dorsal stripe present or absent; no pronounced horizontal expansion of the border of maxilla; supraorbital crest not projecting over eyelid, which is entirely visible in dorsal view. (Figs. 23 and 30).....*Rhinella fernandezae*

2b. Infraorbital crest absent, or highly reduced, short, never extending beyond postorbital crest; longitudinal dorsal stripe always present; postorbital crest may be reduced; a pronounced horizontal expansion of the border of maxilla may be present; supraorbital crest may be very high, highly projecting over eyelid, which is not entirely visible in dorsal view (Figs. 26 and 31) ..... *Rhinella dorbignyi*

3a. Infraorbital crest continuous, long, extending beyond postorbital crest (Figs. 3A, 3E); parietal crest continuous and conspicuous; adult size (SVL) vary from 24.6 to 50.6 mm in males and from 28.8 to59.3 mm in females 4

3b. Infraorbital crest continuous, not long (Fig. 3C), or infraorbital crest granulose and discontinuous, long or not (Fig. 3B); parietal crest absent or inconspicuous; adult size (SVL) vary from 30.1 to 72.8 mm in males and from 31.5 to 84.9 mm in females 6

4a. Loreal region broad and distinctly visible, highly concave; snout short, not prominent in dorsal view duo to anterior-lateral expansion of the border of the maxilla (Fig. 2A), interorbital distance 1.5 to 2 times larger than the eye diameter; eye diameter smaller than eye-nostril distance; upper lip swollen with convex border (Figs. 20 and 32) .....*Rhinella azarai*

4b. Loreal region less visible, straight; snout long, prominent in dorsal view; interorbital distance 1.0 to 1.5 times larger than eye diameter; eye diameter longer than eye-nostril distance; upper lip angular in lateral view 5

5a. Cephalic crests continuous; snout rounded in dorsal and lateral views; space between postorbital crest and tympanum with granules and/or horizontal projections from the postorbital crest toward tympanum (Fig. 3E); distance from tympanum to postorbital crest (DTP) 2.1-3.1% SVL; hindlimbs short, tibiotarsal articulation reaches the axilla and the fourth toe surpasses the snout when the leg is stretched and adjoined to body (Fig. 14).....*Rhinella pygmaea*

5b. Cephalic crests predominantly continuous, frequently gaped; snout squared in dorsal view and straight in lateral view (Fig. 3F); area between postorbital crest and tympanum smooth; a lateral expansion of the suborbital crest may be present, visible in dorsal view; distance from tympanum to postorbital crest (DTP)

1.4-2.4% SVL; hindlimbs very short, tibio-tarsal articulation do not reach the axilla, and the fourth toe do not surpass the head when the leg is stretched and adjoined to body (Fig. 15) ..... *Rhinella bergi*

6a. Longitudinal dorsal stripe absent; head rounded or subtriangular; parietal crest absent or inconspicuous; distance from tympanum to postorbital crest (DTP) 0.6-2.2% SVL; distance from tympanum to parotoid (DTG) 1.2-4.6% SVL 7

6b. Longitudinal dorsal stripe present; large portion of loreal region visible in dorsal view; head elongated, narrow and long (Fig. 2E); parietal crest always absent; tympanum practically touching postorbital crest (DTP 0.4-1.0% SVL); distance from tympanum to parotoid 1.5-2.5% SVL (Figs. 18 and 33)..... ..... *Rhinella mirandaribeiroi*

7a. Interorbital space granulose; labial light stripe not visible in dorsal view; maxillary crest usually not visible in dorsal view; distance from tympanum to parotoid (DTG) 1.2-3.9% SVL; distance from tympanum to postorbital crest (DTP) 0.6-2.2% SVL; belly with or without pigmentation; parietal crest absent or inconspicuous 8

7b. Interorbital space smooth or with very few granules; maxillary crest, loreal region and labial light stripe visible in dorsal view; distance from tympanum to parotoid (DTG) 2.6-4.6% SVL; distance from tympanum to postorbital crest (DTP) 0.6-1.6% SVL; belly without pigmentation; parietal crest absent (Figs. 17 and 34)..... *Rhinella major*

8a. Supraorbital crest high; snout long in lateral and dorsal views, posterior border of nostrils at the same level of anterior margin of maxilla, snout rounded or squared in dorsal view; distance from tympanum to postorbital crest DTP 0.9-2,2% SVL; interorbital distances IOD_1 8.9-14.7% SVL, IOD_2 8.0-13.8% SVL; maxillary crest pronounced; belly without pigmentation 9

8b. Supraorbital crest low; snout very long (highly protruding) in lateral view, posterior border of nostrils surpasses anterior margin of maxilla, snout rounded in dorsal view; distance from tympanum to postorbital crest DTP 0.6-1.3% SVL; interorbital distances (IOD_1) 8.1-13.3% SVL, (IOD_2) 7.2-11.3% SVL; maxillary crest less developed; belly without pigmentation (Figs. 12 and 35)..... *Rhinella granulosa*

9a. Head subtriangular; subnasal crest usually long, surpassing posterior border of nostrils.....10

9b. Head rounded with a long snout (Fig. 2D); snout squared in dorsal view, high in lateral view; subnasal crest usually short, not extending beyond posterior border of nostrils, darker spots on dorsum highly outstanding (Fig. 21) .....*Rhinella nattereri*

10a. Snout squared in dorsal view, rounded in lateral view, narrow in lateral view, with a pronounced dorsoventral slope; belly extensively pigmented; distance tympanum postorbital crest (DTP) 1.1-2.1% SVL; head height 14.0-17.8% SVL; thigh length (THL) 18,1-23% SVL; parotoid gland width (PGW) 15-24.1% SVL; parotoid height (PGH) 11.8-18.3 (Fig. 27) ..... *Rhinella merianae*

10b. Snout rounded in dorsal and lateral views, wide in lateral view and slightly sloping dorsoventrally; subnasal crest very long, its posterior portion extending beyond posterior margin of nostril; distance tympanum postorbital crest (DTP) 0.9-1.6% SVL; distance tympanum supratympanic crest (DTS) 1.5-2.6% SVL; parotoid width (PGW) 12,3-21.7% SVL; parotoid height (PGH) 10-17.8% SVL; (Fig. 28) ....*Rhinella humboldti*

10c. Snout squared in dorsal view, rounded in lateral view, narrow in lateral view, with a pronounced dorsoventral slope; tip of snout, loreal region and interorbital distance extensively covered with highly fleshy keratinized granules; belly with reduced pigmentation; head height (HH) 13.8-15.7% SVL; thigh length (THL) 18.8-25.7% SVL; parotoid width (PGW) 13.7-21.8% SVL; parotoid height (PGH) 10.8-16.8% SVL; distance tympanum postorbital crest (DTP) 1.6-2.2% SVL (Fig. 29) ..... *Rhinella centralis* sp. n.

DISCUSSION

We recognize twelve species in the *Rhinella granulosa* species group: *R. granulosa, R. pygmaea, R. bergi, R. major, R. mirandaribeiroi, R. azarai, R. nattereri, R. fernandezae, R. dorbinyi, R. merianae, R. humboldti,* and *R. centralis* sp. n. The geographic distribution of the group is associated with open areas of South America and Panama (Fig. 36): Caatinga (*R. granulosa*), Cerrado (*R. mirandaribeiroi*), the so called "Restingas" or open vegetated sandy areas along the coast (*R. pygmaea*), Chaco (*R. bergi, R. major, R. azarai,* and *R. fernandezae*), Pampa (*R. fernandezae* and *R. dorbignyi*), Llanos (*R. humboldti*), Northern Savannas (*R. major, R. nattereri, R. merianae,* and *R. centralis* sp. n.).

Gallardo (1965) suggested that the majority of the subspecies of *R. granulosa* he described would be associated to the major hydrographic basins of South America. However, our study indicates that the species we recognize for this complex have their distributions predominantly associated with open formations and more congruent to the Morphoclimatic Domains defined by Ab'Sáber in 1977. *Rhinella mirandari-*

FIGURE 30: *Rhinella fernandezae* (photographed by Ariel Lopes, Argentina).

beiroi, R. granulosa, and *R. bergi* are allopatric and occur, respectively, in the Cerrado, Caatinga and Chaco Domains, known as the great diagonal belt of open formations from South America (Ab'Sáber, 1974; Vanzolini, 1974), and there is no overlapping in the distribution of the three species, each one showing high fidelity to one or another Domain. Similar distributional patterns associated with Domains comprising the great diagonal of open formations from South America have been reported for lizards of the *Tropidurus torquatus* group (Rodrigues, 1987) and snakes of the *Bothrops neuwiedi* complex (Silva, 2000; Silva & Rodrigues, 2008). This pattern was, until recently, largely unexpected for most species of anurans associated with open formations, usually presenting wide distribution through these Domains (for example, some species of *Physalaemus, Leptodactylus, Scinax* gr. *ruber,* see Frost, 2008). However, recent investigations are showing that, at least for some of these species complexes, these results might be due to insufficient taxonomic work, and species considered to have wider distributions were not, in fact, single taxonomic units as new species have been described (Heyer, 2005; Heyer *et al.,* 2005; Nascimento *et al.,* 2005; Caramaschi, 2006; Camargo *et al.,* 2006; Cruz *et al.,* 2007). In the genus *Rhinella, R. jimi* was described for the Caatingas (Stevaux, 2002), and two new species, *R. veredas* (Brandão *et al.,* 2007) and *R. cerradensis* (Maciel *et al.,* 2007) were recently described as endemic to the Brazilian Cerrado biome. We think that future taxonomic work with frogs from the Cerrado, Caatinga, and Chaco will broken the apparent general pattern of frogs widely distributed along the three main blocks of open formations and will result in the discovery of more species yet to be described, with specific habitat requirements. Further elucidative taxonomic studies of complex groups of anurans inhabiting open formations may bring to light new patterns of distribution.

Species distributions of the of *R. granulosa* group are predominantly allopatric, sympatry being limited to only 7% of the localities (64 out of 880 localities studied). Similar values were found for the *Tropidurus torquatus* group with 10% of sympatry and *Bothrops neuwiedi* complex with 7% of sympatry (Rodrigues, 1987; Silva, 2000; Silva & Rodrigues, 2008). However, for some species of the *Rhinella granulosa* group, the distributions are largely overlapping, specially at the humid Chaco (Argentina and Paraguay; *R. major, R. bergi, R. azarai,* and *R. fernandezae*) and the Pam-

FIGURE 31: *Rhinella dorbignyi* (photographed by Ariel Lopes, Argentina).

FIGURE 32: *Rhinella azarai* (photographed by Diego Baldo, Argentina).

FIGURE 33: *Rhinella mirandaribeiroi* (photographed by Gabriel Skuk, Tocantins).

FIGURE 34: *Rhinella major* (photographed by Ariel Lopes, Argentina).

FIGURE 35: *Rhinella granulosa* (photographed by Gabriel Skuk).

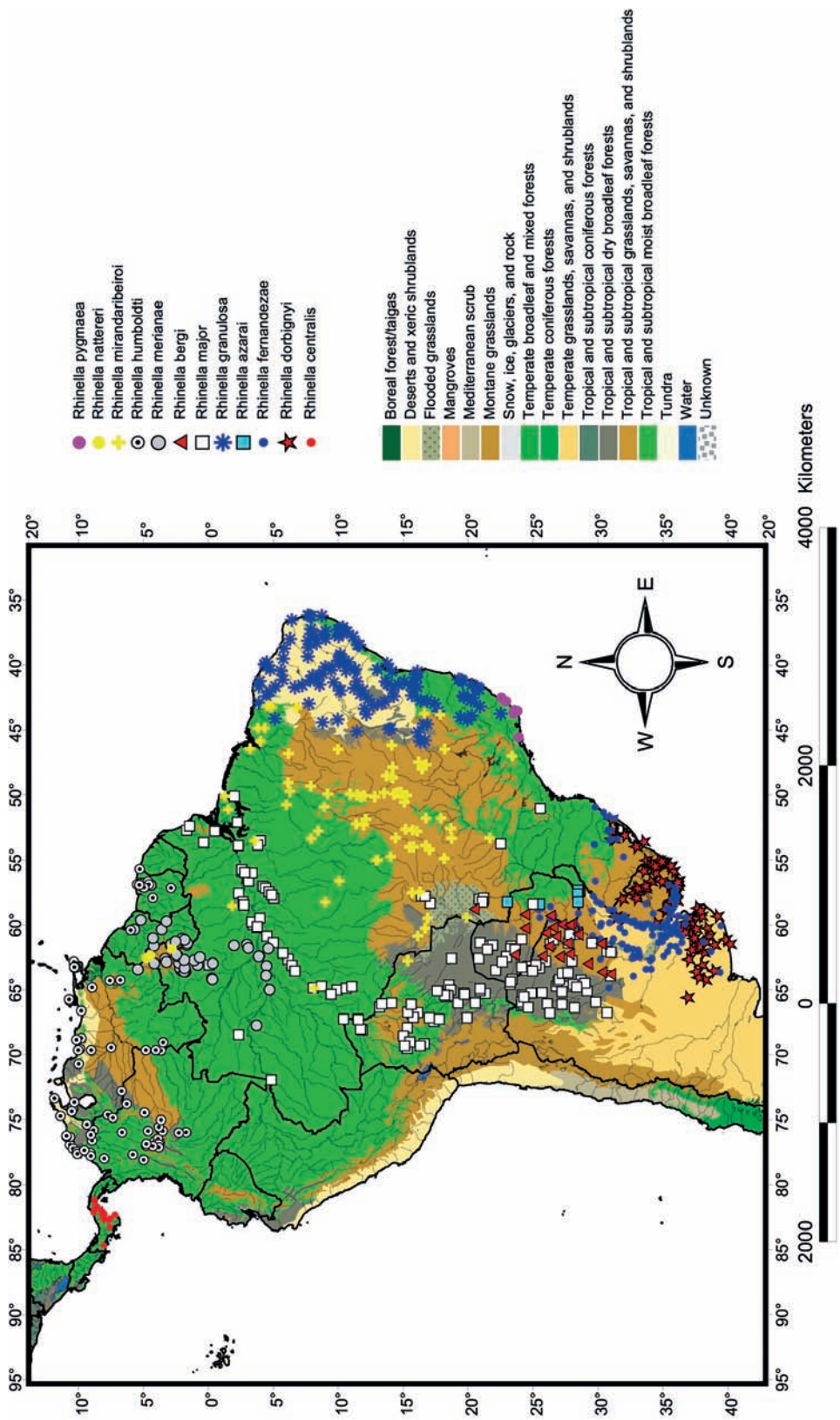

FIGURE 36: Geographic distribution of the 12 species of the *Rhinella granulosa* group in the context of the Morphoclimatic Domains of South and Central America.

TABLE 13: Standardized coefficients of the canonical analysis of the 22 morphometric characters of the 12 combined OTU's, for males.

	1	2	3	4	5	6	7	8	9	10	11
STCL	0.452*	0,191	0,214	-0,074	0,430	0,108	0,410	0,090	-0,136	-0,188	0,321
EW	-0,222	0,285	0.554*	0,125	0,447	0,110	0,250	-0,234	0,236	-0,213	0,235
HAL	0,106	0,236	0.542*	0,206	0,420	0,130	0,131	0,157	0,281	-0,078	0,339
TAL	-0,040	0,240	0.503*	0,165	0,459	0,036	0,263	0,087	0,098	0,038	0,366
TIL	-0,060	0,196	0.490*	0,166	0,398	0,080	0,180	0,106	0,176	-0,002	0,367
ED	-0,130	0,161	0.488*	0,387	0,323	0,096	0,393	0,164	-0,042	-0,245	0,053
FOL	0,033	0,296	0.483*	0,185	0,396	0,141	0,180	0,155	0,210	-0,124	0,277
POS	0,366	0,371	0.478*	0,242	0,350	-0,219	0,189	0,281	0,086	-0,164	0,132
IND	0,116	0,175	0,077	0.590*	0,409	0,288	0,222	-0,119	0,262	0,053	0,345
PGW	-0,108	0,120	0,329	0,160	0.689*	0,207	0,013	0,016	0,278	-0,043	-0,044
IOD1	-0,009	0,015	0,283	0,287	0.669*	-0,044	0,289	0,139	0,241	-0,031	0,225
PGH	-0,105	0,008	0,363	0,180	0.663*	0,157	-0,066	-0,086	0,025	0,027	0,308
IOD2	0,171	-0,084	0,190	0,225	0.622*	-0,064	0,265	0,226	0,296	-0,178	0,283
SW	0,004	0,391	0,205	0,177	0.618*	0,124	0,233	0,055	0,213	-0,067	0,182
TH	-0,044	0,321	0,340	0,284	0.574*	-0,013	-0,041	0,142	-0,103	-0,037	0,258
HW	0,108	0,155	0,500	0,202	0.561*	0,090	0,154	-0,049	0,159	-0,139	0,272
SVL	0,036	0,277	0,431	0,233	0.548*	-0,067	0,164	-0,034	0,213	-0,093	0,304
ESD	-0,044	0,168	0,255	0,236	0.511*	-0,128	0,197	0,029	0,193	-0,266	0,388
HL	-0,012	0,263	0,383	0,258	0.504*	0,021	0,237	0,134	0,127	-0,224	0,359
HAL	-0,010	0,235	0,455	0,217	0.468*	0,068	0,211	0,038	0,112	-0,144	0,310
END	0,032	0,138	0,255	0,195	0,392	-0,265	0,333	-0,020	0,347	-0,029	0,289
TD	-0,080	0,333	0,218	0,154	0,463	0,072	0,155	0,274	-0,001	-0,198	0,471

TABLE 14: Standardized coefficients of the canonical analysis for the 22 morphometric characters of the 11 combined OTU's, for females.

	1	2	3	4	5	6	7	8	9	10
STCL	0.428*	0,260	0,005	0,214	0,016	0,265	-0,103	0,362	0,190	0,192
IOD2	-0,130	0.376*	0,264	0,063	0,225	0,188	0,042	0,152	0,059	0,065
IND	-0,028	0,242	-0,048	-0,136	0,653	0,189	0,236	0,329	-0,111	0,031
TH	0,082	0,141	-0,025	-0,097	0,247	0.601*	-0,096	0,185	0,165	0,121
PGW	0,215	0,173	0,070	0,105	0,296	0.512*	0,226	0,105	-0,109	0,206
TD	0,128	0,098	-0,148	0,093	0,201	0.484*	-0,074	0,119	0,104	0,103
EW	0,241	-0,067	-0,084	0,034	0,174	0.482*	0,032	0,362	-0,269	0,099
PGH	0,210	0,163	0,089	0,103	0,350	0.444*	0,003	0,073	-0,079	0,166
HW	-0,040	0,093	0,097	0,020	0,202	0.444*	0,012	0,300	-0,043	0,104
POS	-0,335	0,040	0,007	-0,233	0,045	0.441*	0,079	0,091	0,152	0,172
SW	0,097	0,200	-0,217	0,118	0,375	0.425*	0,138	0,320	0,115	-0,038
SVL	0,050	0,159	-0,083	-0,033	0,208	0.418*	0,079	0,238	-0,055	0,094
TAL	0,086	0,000	0,035	0,048	0,210	0.385*	0,203	0,306	0,050	0,068
HL	0,064	0,133	-0,025	-0,016	0,222	0.373*	-0,020	0,315	0,068	0,126
HAL	-0,040	-0,031	0,057	0,016	0,264	0.367*	0,083	0,231	0,023	0,002
IOD1	0,092	0,268	0,178	-0,022	0,253	0.366*	0,242	0,247	0,138	-0,019
HAL	0,077	0,046	0,005	0,024	0,226	0.365*	0,051	0,278	0,020	-0,022
TIL	0,107	-0,037	0,028	0,062	0,237	0.347*	0,155	0,233	0,087	0,221
FOL	-0,003	-0,039	-0,039	0,049	0,277	0.341*	0,120	0,225	0,037	0,071
ESD	0,129	0,207	-0,065	-0,045	0,143	0.263*	0,049	0,239	0,100	0,077
ED	0,134	-0,005	0,069	-0,127	0,257	0,257	-0,187	0,486	0,153	0,209
END	0,043	0,235	-0,029	-0,110	0,000	0,261	0,164	0,359	-0,010	0,158

TABLE 15: Discriminant scores among *Rhinella granulosa, R. major,* and *R. mirandaribeiroi.*

(males)	1	2	(females)	1	2
POS	0.372	0.214	SW	0.326	-0.227
STCL	0.314	0.248	ESD	0.288	0.007
HW	0.292	0.234	END	0.274	0.158
HAL	0.277	0.050	PGW	0.257	-0.019
ED	0.180	0.154	IOD1	0.249	0.181
FOL	0.163	0.059	TD	0.245	-0.119
TIL	0.160	0.091	TH	0.240	0.078
IOD2	0.311	0.475	PGH	0.240	-0.043
IOD1	0.181	0.447	SVL	0.231	-0.008
TH	0.017	0.376	HL	0.212	-0.016
ESD	0.073	0.369	IND	0.190	-0.146
PGH	0.127	0.332	EW	0.143	-0.120
END	0.156	0.305	HAL	0.113	-0.019
SW	-0.097	0.304	TAL	0.074	-0.012
PGW	0.043	0.293	ED	0.073	0.035
SVL	0.152	0.284	HAL	-0.025	0.008
HL	0.111	0.269	IOD2	0.185	0.281
TD	-0.090	0.245	POS	-0.061	0.273
HAL	0.152	0.182	STCL	0.056	0.183
TAL	0.165	0.168	HW	0.076	0.119
IND	0.012	0.164	FOL	0.017	-0.099
EW	0.065	0.107	TIL	0.052	-0.061

TABLE 16: Discriminant scores among *Rhinella pygmaea, R. bergi,* and *R. azarai.*

(males)	1	2	(females)	1	2
IOD2	0.318	0.156	PGW	-0.453	0.868
IOD1	0.291	0.257	ED	0.190	0.770
END	0.224	0.140	TH	0.135	0.757
SW	0.202	0.192	HL	-0.002	0.743
ESD	0.194	0.081	HAL	0.118	0.699
POS	0.142	0.123	HAL	0.133	0.663
TD	0.137	0.027	SVL	-0.044	0.655
HL	0.120	0.118	EW	0.003	0.652
PGW	0.283	0.417	PGH	-0.123	0.639
PGH	0.166	0.371	IOD1	-0.039	0.619
TAL	0.091	0.304	ESD	0.041	0.616
TIL	0.090	0.280	FOL	-0.069	0.615
HW	0.103	0.276	HW	0.136	0.608
HAL	0.103	0.274	TAL	0.010	0.599
SVL	0.198	0.269	TIL	0.047	0.593
IND	0.089	0.259	IOD2	-0.129	0.501
HAL	0.096	0.247	TD	-0.098	0.492
EW	0.017	0.235	IND	-0.118	0.489
FOL	0.071	0.217	SW	0.050	0.432
TH	0.144	0.183	STCL	-0.040	0.331
ED	-0.040	0.109	END	0.178	0.320
STCL	0.016	0.086	POS	-0.017	0.275

TABLE 17: Discriminant scores among *Rhinella merianae, R. humboldti,* and *R. centralis* sp. n.

(males)	1	2	3	(females)	1	2
PGH	0.488	0.045	0.021	PGH	0.348	0.236
PGW	0.402	0.065	-0.219	TH	0.343	0.185
HW	0.325	-0.040	-0.072	PGW	0.266	0.241
HAL	0.251	0.065	-0.059	ED	0.250	-0.011
TH	0.248	0.114	0.100	TD	0.219	0.141
HAL	0.237	0.002	-0.052	TIL	0.187	0.017
TIL	0.230	0.051	-0.027	TAL	0.184	0.092
IOD1	0.214	-0.055	0.008	HL	0.167	0.141
SVL	0.213	-0.083	-0.093	EW	0.164	0.111
TAL	0.203	0.008	0.022	HAL	0.161	0.121
FOL	0.199	0.067	-0.072	HAL	0.157	0.127
IOD2	0.195	-0.104	0.079	FOL	0.135	0.105
HL	0.167	-0.002	-0.010	POS	0.131	0.063
SW	0.154	-0.054	-0.074	STCL	0.006	0.337
IND	0.150	0.016	-0.053	HW	0.196	0.219
ED	0.150	0.148	-0.100	SVL	0.129	0.186
ESD	0.136	-0.105	-0.038	SW	0.164	0.183
END	0.005	-0.196	-0.083	IOD2	0.130	0.176
EW	0.288	-0.076	-0.333	ESD	0.077	0.141
STCL	0.108	-0.175	0.257	IOD1	0.098	0.139
TD	0.123	0.057	0.150	END	-0.056	0.118
POS	0.044	-0.013	0.056	IND	0.074	0.098

pas region (Uruguay and Rio Grande do Sul, Brazil; *R. dorbignyi* and *R. fernandezae*) (Fig. 36). In some cases, species are effectively syntopic: *R. bergi, R. fernandezae,* and *R. major* in Argentina; *R. fernandezae* and *R. dorbignyi* in Uruguay and Rio Grande do Sul, and *R. major* and *R. bergi* in Mato Grosso do Sul, Brazil.

Rhinella major, R. fernandezae, R. azarai, and *R. bergi* occur at the Chaco Domain, specifically at the Oriental Chaco, which encompasses the major diversity of the group: four out of twelve species. The area, also referred to as the humid Chaco, has a continental climate with high precipitation (1,300 mm per year), warm summer and moderate winter temperatures. Vegetation in the area is highly diversified and the relief is characterized by wide depressions and valleys, which frequently renders the region to be subjected to flooding (Cabrera, 1994). Apparently, the complexity of the physiognomy of the humid Chaco, along with the availability of temporary and permanent ponds, are sufficient to support four species of the *R. granulosa* group. In no other lowland area of South America, the diversity is so high for the group. This may be explained by the marine transgressions of the interglacial periods in which the "Litoral-Mesopotâmica" area, according to Cei's concept (1980), was completely flooded (Gallardo, 1962; Simpson-Vuilleumier, 1971; Cei, 1993; Mörner *et al.,* 2001). The intermittent sea regressions may have created ecologically distinct micro-areas, allowing speciation. Besides, the also called "Paleoflora Terciária Chaqueña" (Cei, 1993) had been extremely modified (reduced, enlarged, resisted to aridity) during time and was once in contact with Brazil Central Savannas (Cei, 1993); such modifications may have contributed to speciation of the species of the *R. granulosa* group and consequently to the higher diversity that occur in the Chaco Domain.

Rhinella major presents the widest distribution for the group, occurring from Chaco, throughout the Beni Savannas, to the open areas along the Madeira, Tapajós, and Xingú rivers, reaching the mouth of the Amazon river. This wide distribution, encompassing the Chaco, Bolivian Savannas, enclaves of open formations, and riverine habitats in Amazonia, can be either due to a relictual distribution, the result of recent downstream dispersal along the Amazon Basin, or due to collector's effect. Only a molecular oriented phylogeographic study can address these questions.

Contrastingly, three species present very restrict distributions (*R. pygmaea,* restricted to the sandy habitats of Restinga in Rio de Janeiro; *R. azarai,* Mato Grosso do Sul, Provincia Misiones, Argentina, and Paraguay; and *R. nattereri,* known only for three

localities in the Brazil, Guyana, and Venezuela borders). Although the general pattern of distribution of the *R. granulosa* species complex may be partially explained using the Morphoclimatic Domains, other factors, such as topography, type of soil, and climate (temperature and humidity), are probably involved.

Another interesting pattern in the *R. granulosa* group is the fact that the majority of the species are associated to lowlands: *R. pygmaea, R. bergi, R. major, R. mirandaribeiroi, R. azarai, R. fernandezae, R. dorbignyi, R. humboldti,* and *R. centralis* sp. n. These species are usually associated to altitudes lower than 300 m, plane reliefs, and high pluviosity, allowing water accumulation to form the temporary ponds extensively used during their reproduction. Species dependent of similar resources for their reproductive biology, like the hylid *Itapotihyla langsdorffii,* are also associated with flood plains, and its distribution is highly associated with topography (Pavan & Verdade, 1999). Di Tada *et al.* (1999) reported on the preference of *R. fernandezae* for altitudes inferior to 300 m in Cordoba Province, Argentina, and the species was frequently found between 100 and 150 m altitude. The fact that the species were never seen in reproductive activity in lotic sites and are typical explosive breeders of temporary ponds formed after the first heavy rains, restrict their distribution to plane areas, with a mild relief.

During reproduction, toads of the *R. granulosa* group form large congregations of males in temporary ponds after heavy summer rains, generally following the dry season. When not reproducing, they are found under rocks, logs, and inside cylindrical holes they dig in the ground and use as shelter (Vellard, 1948; Langone, 1994; Klappenbach, 1969; Renjifo & Lundberg, 1999; Sanchez & Busch, 2008), foraging for invertebrates that pass near the burrows (Lajmanovich, 1995). At least for one species (*R. fernandezae*), it is known that the frogs can orient themselves and return to their own burrows (Gallardo, 1957). These are some aspects of the biology of the group that may be related to the distribution of the species. The group is known to inhabit open environments in the lowlands of South and Central America. The availability of appropriate sites for reproduction in lowlands, plus the necessity of a soil that is easy to dig in, may explain the occurrence of the species in areas of sedimentary basins.

The lack of a molecular phylogeography for the group is an important barrier to obtain a better picture of its differentiation and pattern of distribution. The phylogenetic topologies available for Bufonidae in which *R. granulosa* group is included, are somewhat congruent and the group seems to be monophyletic (Pramuk, 2002, 2006; Frost *et al.,* 2006; Chaparro *et al.,* 2007; Pramuk *et al.,* 2008). A topology comprising *R. marina* + *R. crucifer* as sister to *R. granulosa* group was supported by DNA analysis and combined data (Pramuk, 2006) and by molecular data (Chaparro *et al.,* 2007). In recent works, *R. marina* is frequently considered sister group to *R. granulosa* (Frost *et al.,* 2006; Pramuk, 2006; Chaparro *et al.,* 2007; Pramuk *et al.,* 2008). The result was unexpected based on our observations on similarities in external morphology. Our primary goal in this work was to clarify the taxonomy of the group, and as such, we did not construct phylogenies. Nevertheless, when comparing the external morphology of *R. granulosa* group and *R. crucifer* and *R. marina,* we found major differences specially regarding type and configuration of cephalic crests and parotoid glands, shape of snout, cutaneous granulation, and tarsal fold. According to Dubois & Ohler (1999), cephalic crests "can be meaningfully used in the diagnoses of species-group." The authors hypothesized "that ridges occupying the same topological position on the head of different toad species are homologous structures, and that their presence/absence is a constant feature within a species." However, phylogenetic studies including only morphological data were not conclusive and pointed out *R. granulosa* as sister group to *Peltophryne lemur* (Pramuk, 2006). Cephalic crests were included in the aforementioned analysis but only regarding presence/absence. Type, shape, and configuration of cephalic crests may also be a useful set of characters to be included in future phylogenetic analysis of Bufonidae species.

We considered this work an important first step to clarify the taxonomy and biogeography of the *R. granulosa* species complex, and strongly advise further studies in the group combining sets of molecular and morphological data, with a more representative sample of species. The resultant topologies could help to elucidate the phylogeny of the group and, therefore, infer about their biogeography in Central and South America, helping to clarify patterns of distribution also for other vertebrates wide distributed East of Andes.

RESUMO

Uma extensa revisão taxonômica das espécies do grupo Rhinella granulosa *foi realizada com base em caracteres morfológicos externos e caracteres morfométricos. Foram analisados 8700 exemplares depositados em 35 coleções nacionais e estrangeiras, representando 865 localidades.*

Doze espécies foram reconhecidas para o grupo, uma delas descrita como nova; são elas: Rhinella granulosa *(Nordeste do Brasil),* R. pygmaea *(Rio de Janeiro, Brasil),* R. bergi *(Paraguai, Noroeste da Argentina, e Mato Grosso, Brasil),* R. major *(Argentina, Bolívia, Paraguai, e Norte e Oeste do Brasil),* R. mirandaribeiroi *(Brasil Central e Bolívia),* R. azarai *(Província de Misiones, Argentina, Paraguai, e Mato Grosso do Sul, Brasil),* R. nattereri *(Venezuela, Guiana e Roraima, Brasil),* R. fernandezae *(Argentina, Uruguai, Paraguai, e Rio Grande do Sul, Brasil),* R. dorbignyi *(Província de Buenos Aires, Argentina, Uruguai, e Rio Grande do Sul, Brasil),* R. merianae *(Venezuela, Suriname, Guiana, e Amazonas e Roraima, Brasil),* R. humboldti *(Colômbia, Venezuela, Suriname, Guiana e Trinidad),* R. centralis *sp. n. (Panamá). Caracteres morfológicos externos, como formato da cabeça e do focinho, tipo de cristas cefálicas, tamanho do tímpano, tamanho e formato das glândulas parotóides e granulação cutânea, são alguns dos atributos utilizados na identificação das espécies. Diagnose comparativa, descrição e sumário de distribuição são fornecidos para cada espécie, assim como uma chave artificial para identificação das espécies do grupo. A distribuição geográfica das espécies de* Rhinella *está amplamente associada às formações abertas da América do Sul e Panamá.*

Palavras-chave: Bufonidae, grupo *Rhinella granulosa,* revisão taxonômica, distribuição geográfica, América Central e do Sul.

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APPENDIX 1

Specimens examined

Numbers in parenthesis refer to the amount of specimens inside a pack.

Rhinella granulosa

Brasil. *Alagoas.* APA de Piaçabuçú: MUFAL 910630-910631, 910647-910648, 920738. Engenheiro Riachão: MZUSP 104436. Estação Ecológica de Xingó: MUFAL 941331, 941333, 941208, 983562, 983742, 993914. Maceió: MUFAL 940979-940980, 930895, 930826-930827, 930836. Mangabeiras (Usina Sinimbú): MZUSP 11911-11939, 104437-104441. Piranhas (Vila Xingó): UMMZ 209801-209817. Reserva Biológica de Murici: MUFAL 993958. Rio Largo: MUFAL 940984-940986. UHE Xingó: MZUSP 70995. Viçosa: MUFAL 952653, 952725. *Bahia.* Andaraí: MZUSP 124285-124290. Bom Jesus da Lapa: UMMZ 108902(6), 108910(3), 108911. Buritirama: MZUSP 22956. Campo Formoso: MZUSP 38799-38805. Carnaíba: MZUSP 124266-124281. Caatinga do Moura: MZUSP 57469-57482. Cocorobó: MZUSP 28130, 38238-38255. Coribe: CHUNB/Fisio 1461-1464. Curuçá: MZUSP 81044-81047. Euclides da Cunha: MZUSP 28107-28109. Feira de Santana: MZUSP 124256-124262. Freitas: CHUNB/Fisio 1646. Ilhéus (Reserva Florestal do Una): CFBH 1769. Iramaia: MZUSP 71235. Irecê: ZUEC 3288, 3291-3298, 3301-07. Itagibá: JJ 7511-7535, 7576-7585; UFC 486-487. Itapetinga: MZUSP 104414-104435; ZUEC 921. Itiúba: MZUSP 38479-38516. Jacobina: MZUSP 54206-54207. Jequié: MZUSP 28114-28121, 124263-124265. Jeremoabo: MZUSP 38061-38126. Joazeiro: UMMZ 108914. Jussari (Serra do Teimoso): MZUSP 125034. Maracás: AMNH 75770; USNM 159141-159142; EI 4734-4739; MCN-FZB 8719, 8721, 8723; JJ 7555-7564; MUSP 98987-99022, 99023-99085, 99086-99149, 104463-104464. Milagres: MZUSP 124282-124284. Mirorós: CHUNB/Fisio 1538. Morro do Chapéu: MZUSP 68946. Mulungu do Morro: MZUSP 54208. Nova Canaã: EI 1519-1521, 2988-2990. Nova Conquista: ZUEC 1504. Paulo Afonso: MZUSP 9525, 76375, 104447-104448. Raso da Catarina: MZUSP 69855. Reserva Biológica de Una: MZUSP 125032, 126275-126306. Rio Grande: UMMZ 108913. Salvador: MZUSP 8190-8191, 9125-9128, 10716, 10718, 10720. São José da Vitória (Fazenda Unacau): MZUSP 125033. Sítio do Mato: MZUSP 80993, 80969. Valença: MNRJ 4613-4698. Vitória da Conquista: MZUSP 104360-104361. *Ceará.* Aiuba: UFC 911-913. Aquiraz: UFC 1347. Arajara: MZUSP 54199. Boa Viagem: UFC 1133, 833. Catunda: UFC 1093-1095. Fortaleza: UFC 1010, 1018, 1034, 1076, 1092, 1096-1097, 1099, 1100-1101, 1130-1131, 1214, 1274, 1313, 1323, 1344, 1372, 1386, 1907-1908. Itapipoca: UFC 1351. Limoeiro do Norte: UFC 1083, 1411. Maranguape: MZUSP 13579-13580. UFC 1024. Mucuripe: MZUSP 104347-104351, 105781. Pacatuba: UFC 975. Pacotí: MZUSP 92027-92030. Quixadá: UFC 934. Reriutaba: UFC 1253. Santana do Cariri: MZUSP 54747-54749. Serra do Mucuripe: MNRJ 2598 (12880-13023). Tauá: UFC 1935, 1937, 1941, 1945, 1947-1949. Ubajara: UFC 966, 1048. *Espírito Santo.* Aracruz: CFBH 3402. Barra de São Francisco (Parque Sombra da Tarde): MBML 1144-1146, 1173-1174. Conceição da Barra: MZ-UFV 3242, 3244-3247, 3249, 3251; MZUSP 125040-125041; MNRJ 20975-21001; CFBH 2455-2457. Fundão (Parque Municipal do Goiapabu Açu): MBML 1256. Fundão (Três Barras): MBML 771-772. Itaúnas: CFBH 1952. Linhares: MBML 231, 612; CFBH 1028-1031. São Mateus: CFBH 1961; MBML 697, 712; MNRJ 22829-22833. *Minas Gerais.* Aimorés: MCN-PUC 1266, 1314, 1497, 1501, 1526. Araçuaí: MCN-PUC 319. Braúnas (UHE Porto Estrela): MCN-PUC 1381, 1941, 2011. Ipaba: MCN-PUC 1228, 1373-74. Itaobim: MZUSP 57515. Jaíba: MZ-UFV 1358, 2033, 2668-2670, 2818, 2821-2825, 2993, 3133-3134, 3462-3464. Januária: UMMZ 108905(2), 108906(2), 108907, 108909(6); USNM 98807-98811. Mantena: JJ 7773-7774. Peçanha: MCN-PUC 1135. Pedra Azul: MZUSP 105788-105792, 108236-108250. Pirapora: CAS 11964, 11966, 11960, 11958, 11971; MZUSP 105782-105785; UMMZ 122426. Porteirinha: MCN-PUC 201-204. Remanso do Anacleto: UMMZ 108909. Resplendor: MCN-PUC 1236, 1288, 1310, 1491. Riacho dos Machados: MCN-PUC 274-277, 280-282. São José do Mantimento: MCN-PUC 2001, 2005. Setubal: MCN-PUC 320-321, 373. *Paraíba.* Boa Vista (Fazenda Bravo): UFPB 11-12, 14, 49, 130, 91, 167-169, 170-171, 173-175, 192, 205-206, 316, 354, 378, 389, 428, 462, 505-506, 517. Cabaceiras: UFPB AL-H 188, 204. Cabedelo: UFPB s/nº (11 specimens). Campina Grande: UFPB 2308-2309. Conde: MZUSP 63021; UFPB 13-15. Coremas: MZUSP 22748-22762. João Pessoa: MZUSP 63099-63100,

115513-115514; UFPB 1-6, 8-12, 16-18. Junco do Seridó: MZUSP 52280, 52321. Patos: ZUEC 8754. Sumé: JJ 6845. *Pernambuco.* Belém de São Francisco (Lago Itaparica): CFBH 450-458. Brejo da Madre de Deus: MCT-PUC 2642-2645. Carnaubeira da Penha: MZUSP 36788. Exu: MZUSP 50096-50099, 50101-50111, 51749-51751, 51777-51781, 51802-51803, 51200-51205, 54200-54201, 58786, 104452-104453; CHUNB/Fisio 1428-1429, 1448. Itacuruba (Lago Itaparica): CFBH 487-490. Ouricuri: MZUSP 108354-108358; CHUNB/Fisio 1430-1444, 1446. Petrolina: MZUSP 58769. Recife: MZUSP 28104-28105, 30525, 50113-50117, 54204-54205, 104446; CFBH 2531, 2536. Salgueiro: MZUSP 54732-54745. Sanharó: MZUSP 104449-104451. Serra dos Cavalos: MZUSP 65334. Serrote: MZUSP 58794-58799. *Piauí.* Canto do Buriti: ZUEC 7058-7062. Lagoa Alegre: MPEG 6778, 6780-6781, 6792-6793, 6795, 6798-6799, 6806, 6811, 6817, 6822, 6825-6828, 3831-6832, 6834-6835. Picos: JJ 6803-6843. Raimundo Nonato: ZUEC 7052-7073, 8820. *Rio Grande do Norte.* Angicos: MZUSP 71232-71233, 71922-71953; CFBH 2458-2459. Ceará Mirim: CAS 49659-49660, 49651-49652. Mossoró: UFPB 19. Natal: MZUSP 28089-28103, 28066-28103. *Sergipe.* Aracajú: MZUSP 28106, 115542-115567. Santo Amaro das Brotas: MZUSP 50100.

Rhinella pygmaea

Brazil. *Rio de Janeiro.* Atafona: MNRJ 3365, 13865-13871. Barra de São João: MZUSP 76403, 98516-98631, 104298-104305, 106068, 125076-125245; EI 3008-3011. Cabo Frio: MZUSP 28110-28113, 28252-28256. Lagoa Feia: MZUSP 1258-1264. Mangaratiba (Ilha da Marambaia): MNRJ 20056, 20084. Rio das Ostras: MZUSP 56124-56125. São João da Barra: MNRJ 2331 (holotype of *R. pygmaea*); MNRJ 2564, 2269, 23761-23766, 2243, 23745-23760; MZUSP 28131; MZUSP 74268-74269 (paratypes of *R. pygmaea*); EI 4939-4944; FML 792 (paratype of *R. pygmaea*).

Rhinella bergi

Argentina. *Chaco.* Puerto Antequera: FML 4347/1-4347/15, 4347-4317, 4257(10). Resistência: MACN-CENAI 7880, 7747-7763. Saenz Peña: FML 5529(8), 5945, 4339, 4279, 4278(8). *Cordoba.* Monte Maíz: MACN-CENAI 5743. Manantiales: FM 1773(3). *Formosa.* Estancia Monte Lindo: FML 5952. Formosa: FML 5956(4). Ibarreta: FML 4001. Las Lomitas: FML 5956(4), 4220. Pirané: FML 8084. Rio Paraguay (a 60km SW de Formosa): AMNH 80668-80670. *Santa Fé.* Arroyo Ceibal: FML 8504-8505. Ceres: MACN-CENAI 10898. Gato Colorado: MACN 26362. Reconquista: FML 4843(5).

Brazil. *Mato Grosso.* Locality unknown: UMMZ 104283(2), 104271. *Mato Grosso do Sul.* Corumbá: CFBH 3240-3248, 3273, 3447-3448, 3450, 3897, 3899, 3901, 4119, 4123, 4127-4128. Passo do Lontra: MZUSP 114328.

Paraguay. *Central.* San Lorenzo: MZUSP 94741. *Concepción.* Concepción: MZUSP 94752; USNM 340593-340606. *Presidente Heyes.* Pozo Colorado, Ruta Transchaco km 222: JJ 6854-6857. Riacho Negro (44 km W de Concepción): USNM 340607. Villa Hayes (86 km NW, Rodovia Transchaco): USNM 340610-340611.

Rhinella major

Argentina. *Chaco.* Arroyo Guaycuru: FML 094. Colonia Benitez: MACN-CENAI 250, 347. Colonias Unidas: FML 2836. Corzuela: MACN 4606. Estancia La Fidelidad: FML 120(2). Las Palmas, Rio del Oro: MACN 14223-14227. Puente Nacional: FML 0097. Roque Saenz Peña: FML 4350, 4361(3); MZUSP 125029. Selva del Rio Oro: MACN-CENAI 975. *Cordoba.* Totoralejos: MACN-CENAI 223, 2648-2651. *Corrientes.* Corrientes: MACN-CENAI 3827-3828; MACN 21212-21220, 33999, 25195-25200. *Formosa.* Bañados del Rio Teuco: FML 1051(56). Clorinda: MACN 33357-33358; FML 5954. Comandante Fontana: FML 2959(5). Estancia Monte Lindo: FML 138(2). Formosa: FML 5955. Ibarreta: FML 4381, 4383. Ingeniero Faure: MZUSP

125042-125043, 125028. Ingeniero Juarez: FML 1076(77), 986(36). Laguna Vaca Perdida: FML 1100(6). Laguna Yema: FML 3887(18). Las Lomitas: MACN 2097, 34111; FML 4219(7), 4222(10). Palma Sola: FML 1060(53). Palo Santo: MACN 35579. Pirané: FML 4238(3). Potrero Norte: FML 928(20). Rio Paraguay, (60 km SW of Formosa): AMNH 80671. *Jujuy.* Yuto: MACN-CENAI 2136; FML 1665(2), 1262(5); TNHC 37061. *Salta.* Embarcación: MACN 18842(13); MACN-CENAI 2513-2518; FML 7962-7981. Finca Los Colorados: FML 5333(13), 5332(5). Hickman: MACN-CENAI 2487-2488; FML 673(19), 1781(4), 2153(12). Joaquim V. Gonzalez: FML 6294(14), 6295(5), 6302(9), 6287(3). Luna Muerta: FML 272(9), 435(28); MZUSP 125038-125039. Orán: MACN-CENAI 2128. Pocitos: MACN 18950-18965. Rio Piedras: FML 861(2). San Ignácio: FML 55. Santa Victorio: MACN 3800. Tabacal: FML 1506(30). *Santa Fe.* Calchaquí: MACN-CENAI 2571. Margarita: MACN-CENAI 7867, 6674-6681. Villa Ana: FML 298(7). *Santiado del Estero.* Caburé y Los Tigres: FML 2832(2). Campo Gallo: MACN 26840-26847; FML 3589(2). El Caburé: MACN 26826-26828, 26855-26861, 26940-26943. Guanaco Sombriana: FML 2231. La Unión: MACN 26837-26838. Matará: MACN 26357-26358. Monte Quemado: FML 3585(8). Monte Quemado (40 km S of): FML 3724, 4363 (7), 3586 (11). Nueva Esperanza: MACN 26876. Pampa de los Guanacos: MACN 26849-26852. Pozo Hondo: MACN 26877-26888. Quimili: MACN 9441-9443, 26848. Sachayoj: MACN 26862-26875. Tintina: MACN 26889-26932. Vilelas: MACN 26361. Weisburd: MACN 26853-26854.

Bolivia. *Chuquisaca.* Chuquisaca: MACN 18984-18989. El Cidral: FML 1832(4). *Cochabamba.* Chapare: USNM 146482-146489. Chipiriri: KU 136042-136046. Villa Tunari: KU 183187-183190. *El Beni.* Casarabe: AMNH 153504-153510. Espiritu: USNM 283280. Estancia San Miguel: MACN 28045-28050. Guayaramerin: AMNH 72102-72105, 78940-78951, 78968, 101745-101762. Ivón: NHM 1967.2052. Magdalena: USNM 162214. Reyes: MACN 4026(2); NHM 1898.6.9.33-34. Riberalta: MACN 3725. Rurrenabaque: AMNH 108306-16; USNM 280453-280454, 280457, 280459-280462, 280464, 280477, 280483; MZUSP 65349-65352. San Javier (23 km W of) (Rio Mamoré): AMNH 78960-78967. San Pedro (Rio Mamoré): AMNH 78952-78959. Santa Rosa (Rio Mamoré): AMNH 72335-72338. Trinidad: USNM 280992. Vaca Diez: USNM 279889-279895. Yacuma (Reserva Beni): USNM 306557-306559, 498232-498234, 283246-283252. Yacuma (45 km N): AMNH 15305. *La Paz.* Alto Beni: MCZ 10089 (holotype of *R. g. mini*); MCZ 10090 (paratype of *R. g. mini*); UMMZ 57912(15). Rio Beni: AMNH 153503. Rio Quiquivé: USNM 280978-280979. San Buena Ventura: USNM 280517-280526. *Santa Cruz.* Abapó: MACN 19109-19112. Buena Vista: USNM 146506. Cabezas (Rio Grande): MACN 14626-14634, 3487(26). Cercado: USNM 146502-146505. Curuyuqui: USNM 336152-336153. El Pailón: MZUSP 21380. Estancia Cachuela Esperanza: AMNH 153501. Estancia San Rafael de Amboro (Buena Vista): NHM 1987.1057-1059. Muyurina: USNM 142103-142104. Nueva Moka: MACN 3462. Parapeti: MZUSP 102333-102335. San José de Chiquitos: MZUSP 21254-21290, 21370-21373, 21375. Tarenda: MACN 18992-18993.

Brazil. *Amapá.* Amapá: CHUNB 00585, 14087-14091. Macapá: MZUSP 99151-99155, 115521-115525. Oiapoque: MZUSP: 50173-50174. Rio Paxacá: MZUSP 99158-99159. Santaná: MZUSP 99156-991157; MPEG 704-707. Serra do Navio: MZUSP 99150. Tartarugalzinho: CHUNB 00584, 01866-01868. Locality unknown: MPEG 709. *Amazonas.* Borba: MZUSP 50123-50129; USNM 201728-201734. Cachoeirinha (Rio Madeira): USNM 201723; MZUSP 50118. Curuçá (Rio Madeira): USNM 201712-201714; MZUSP 50141-50142. Humaitá: CHUNB 803-804; MZUSP 104352-104353. Itacoatiara: EI 2992-2999; MZUSP 16160-16177, 16180-16185; CAS 49747-49749, 49763-49764. Itapiranga: MZUSP 27822. Maués: AMNH 69615-69616. Manicoré: USNM 201715-201722; MZUSP 50130-50139. Nova Olinda: MZUSP 37081-37145, 37167. Novo Aripuanã: MZUSP 50119-50122; USNM 201724-201727. Paraná do Ramos, Rio Amazonas: INPA 1710, 1713. Paraná do Serpa, Rio Amazonas: INPA 1715-1733. Paraná Fins, Lago Pananaima: INPA 2055. Puruzinho (Rio Madeira): USNM 201711; MZUSP 50143. Rio Amazonas: INPA 1708-1709. Raimundo: MPEG 7010-7011, 7055. Silves: MZUSP 27821. Tabatinga: MCT-PUC 1194-1202. *Mato Grosso.* Cáceres: MZUSP 22140-22141, 22154-22156. Cuiabá: MZUSP 128246, 105901; ZUEC 5147-5149; KU 93105-93107. Poconé: MZUSP 57280; UFC 1962-1963. Between Poconé and Porto Cercado: MZUSP 52753. Santo Antonio do Leverger: MZUSP 105902, 124505-124511. Locality unknown: UMMZ 56764-56767, 104284. *Mato Grosso do Sul.* Agachi: MZUSP 10865. Aquidauana: MZUSP 6422, 8315, 7768, 7770-7772, 15797-15798, 67516-67517. Corumbá: CFBH 3272, 3274 3449, 4113-4116, 4122, 4125; MBML 236. Estância Caiman: MZUSP 64855-64902. Miranda: MZUSP 105795-105799;

USNM 302523-302535; NHM 1928.1.8.8. Salobra: MZUSP 21435; MNRJ 2720, 2724, 12429-31; USNM 132907-132908. Taunay: MZUSP 12239-12272, 12275-12288, 27925-27962. *Pará.* Altamira: ZUEC 7200. Alter do Chão: CHUNB 745-750; MZUSP 20409-20410, 29039-29040, 28412-28419, 28421, 35687-35689. Aveiro: MZUSP 27833-27849. Barreiras (Rio Tapajós): MZUSP 35807-35859. Belém: MNRJ 25677; JJ 6791-6792. Breves: MZUSP 28408. Curuá-Una: MZUSP 58388-58395, 58398-58418. Ererê: MZUSP 95625-95628. Faro: MPEG 4547. Fordlândia: MZUSP 35732-35735. Itaituba: USNM 288545-288546. Juruá (Rio Xingú): MZUSP 67093, 63862-63878, 66106-66110. Maicuru: MZUSP 97296-97333; MPEG 475; KU 93099-93100. Monte Alegre: JJ 3000(7); EI 3000-3007; MCT-PUC 2139, 2185; MNRJ 2510, 11395-11397; MZUSP 98108-98114. Óbidos (Oriximiná): MNRJ 25678; MZUSP 27859-27864, 27852-27853. Porto de Moz: MZUSP 27850. Santarém: EI 2991; MCT-PUC 2121-2138, 2140, 2668-2677; UMMZ 122431-122434; MPEG 3317-3319; NHM 1896.6.29.7-9; MZUSP 1005, 27851, 27854-27858, 49672-49674. São Luis (Rio Tapajós): MZUSP 35748-35801. Terra Santa (Boca do Jamari): MZUSP 58133. *Paraná.* Doutor Ulysses: MZUSP 126130-126131. *Rondônia.* Abunã (Rio Madeira): KU 74316-74318. Ariquemes: AMNH 124759-124774; MZUSP 60371-60373, 61130-61133. Cacaulândia: MZUSP 113327. Calama: MZUSP 50140, 50144. Guajará-Mirim: CHUNB 23381-23425, JJ 6786-6788, 6790. Porto Velho: MZUSP 15925, 19813-19913, 50145-50147, 62063-62090; USNM 303850-303861; MCT-PUC 1056. Príncipe da Beira: MZUSP 15900. São Carlos (Foz do Jamari): MZUSP 50148-50155. UHE Samuel: MZUSP 105899-105900. *Roraima.* Boa Vista: MPEG 1086-1098.

Paraguay. *Alto Paraguay.* Parque Nacional "Defensores del Chaco" (Agua Dulce): USNM 340536-340540. Parque Nacional "Defensores del Chaco" (Lagerenza): MNHNP 7160-7161, 7156, 7421. Parque Nacional "Defensores del Chaco" (28 km SE Agua Dulce): MNHP 7203. Parque Nacional "Defensores del Chaco" (Madrejón): MNHNP 7430. *Asunción.* Teniente Fortin Martinez: MACN 31965. *Boqueron.* Colonia Neuland: MNHNP 8081-8082. Doutor Pedro P. Peña: MNHNP 8063. Filadelfia: USNM 340523, 340525-340535. Fortin Madrejon: USNM 205574. Fortín Pozo Hondo (Rio Pilcomayo): USNM 340524. La Gama: MNHNP 7975. Parque Nacional Teniente Enciso: USNM 340544. Teniente Ochoa: USNM 340541. *Concepción.* Concepción: MZUSP 94748-94751. *Cordillera.* San Lorenzo: MZUSP 94744-94745. *Presidente Hayes.* Loma Plata: USNM 340522. Pozo Colorado, Ruta Transchaco km 222: JJ 6846-6853. Riacho Negro (44 km W de Concepción): USNM 340545-340550. Ruta Transchaco (km 322): MNHNP 7436. Ruta Transchaco, Rio Verde (km 323): MNHNP 7429. Locality unknown: Puerto Diana (Rio Paraguay): NHM 1972.6-15.

Rhinella mirandaribeiroi

Bolivia. *Santa Cruz.* Parque Nacional Noel Kampff Mercado: USNM 335072, 336151.

Brazil. *Amazonas.* Humaitá: CHUNB 805-811. Igarapé Belém (Rio Solimões): MZUSP 27830-27832. *Bahia.* Barreiras: MNRJ 1733. Coribe: CHUNB/fisio 1451-1457, 1465. Correntina: CHUNB/Fisio 1392, 1427, 1537. *Goiás.* Aragarças: MPEG 447. Arraias (Córrego Guará): MZUSP 66526. Aruanã: MZUSP 28052-28055. Baliza (Fazenda Bandeirantes): CFBH 603-604, 671-672. Britânia: CNUHB/Fisio 1529-1532. Cana Brava: MZUSP 28056-28059. Goyaz: USNM 130179-130181. Ilha do Bananal: AMNH 70157-70162; MZUSP 12289-12407, 27985-28050, 3951-3956. Jandaia: MZUSP 30468. Jataí. Fazenda Santa Adélia. MZUSP 21010. Fazenda Nova Orlancia: MZUSP 29529. Fazenda Cachoeirinha: MZUSP 30474-30476. Minaçu (UHE Serra da Mesa): MPEG 9067-9068, 9070, 9072-9073, 9077, 9079-9082, 9084-9085, 9087-9094; 89962-90002; CHUNB 567, 574-578, 1870-1899, 1908-1919, 1940-2060, 2063-2064, 2066-2080, 2082-2100, 13088; CHUNB/Fisio 1703, 1725; MCT-PUC 2602, 3022-3112. Niquelândia: MCT-PUC 1187. Peixe: MZUSP 103267-103270. Porto Real: MZUSP 66477. Rio Atalainha: MZUSP 66502. Rio Verde: MZUSP 27970-27982. São Domingos: MZUSP 66604, 125035. Serra da Mesa. Ponto 1: MZUSP 71307-71308. Ponto 2: MZUSP 71721. Ponto 4: MZUSP 72540. *Maranhão.* Barra do Corda: MZUSP 21114-21116, 21118-21119, 21121-21122; Chapadinha: ZUEC 3863-3872, 7746-7751; Imperatriz: MZUSP 99164. Itapicurú-Mirim: ZUEC 823, 870. Peri-Mirim (Fazenda Canaã): MZUSP 104346. Urbano Santos: MZUSP 115532-115541. *Mato Grosso.* Alto Araguaia. Fazenda Taboca: MZUSP 66778. Fazenda Bálsamo: MZUSP 66819. Barra do Graças: MZUSP 70510. Barra do Tapirapé: AMNH 73569-73574; MZUSP 27878-27923, 99172-99178. Cáceres: ZUEC

7080; MZUSP 128247, 105793, 22148; MNRJ 319(2). Capitão Vasconcelos: MZUSP 99170-99171. Chapada dos Guimarães: USNM 507882; CHUNB 21471-21483. Cocalinho: MZUSP 91588-91593. Gaúcha do Norte: MZUSP 83596-83600. Local do Massacre: MZUSP 1039. Mato Verde. MZUSP 27865-27877. Rio Araguaia: AMNH 68066. Pindaíba: MZUSP 91744-91745. Porto Espiridião: MZUSP 54209. Posto Leonardo (Parque Indígena do Xingu): MZUSP 27924, 49149-49192. São Domingos (Rio das Mortes): MZUSP 1610, 1028-1030, 1032-1033, 14727-14728. UHE Manso: CHUNB/Fisio 1466, 1533-34, 1561-62, 1564. Vila Tapirapé: AMNH 68067-68071. Xavantina: MZUSP 21739, 20974-20977. *Mato Grosso do Sul.* Aparecida do Tabuado: JJ 6844. Aquidauana: MNRJ 2359. Três Lagoas: MZUSP 27963-27965. *Minas Gerais.* Arinos: MZUSP 64494-64495. Buritis: MZUSP 64446-64447. Formoso: MZUSP 128268-128272. Francisco Badaró: MNRJ 23741-23743. Itajubá: TNHC 49280. Pirapora: USNM 98244-98246; UMMZ 108903-04, 122427; CAS 11961, 11965. Taiobeiras: MCN-PUC 2016. *Pará.* Aldeia Gorotire: MZUSP 59689. Alto Rio Cururu: MZUSP 99169. Cachimbo: MZUSP 21591-21593, 21733, 22002-22070, 22074-22125, 22621, 64721, 99160-99163, 99165; MCN-FZB 931. Carajás: CHUNB 741, 812-830; CHUNB/Fisio 578-579; ZUEC 6261-6262. Conceição do Araguaia: MZUSP 99166-99168. Ilha de Marajó: NHM 1923.11.9.15 (holotype of *R. g. mirandaribeiroi*), NHM 1923.11.9.16-17 (paratypes of *R. g. mirandaribeiroi*); JJ 6789-6790. Soure: AMNH 46196-46197. Lago Jacaré (Rio Trombetas): MZUSP 29375. Marabá: CFBH 155; MPEG 3201-3202, 3209-3211, 3223, 3235-3236, 3238-3240, 3242, 3244, 3246, 3250, 3271, 3273, 3276, 3281-3284, 3927-3930. Rio Vermelho: MZUSP 70060. *Piauí.* Estação Ecológica Uruçuí-Una: MZUSP 125045-125071. Parque Nacional de Sete Cidades: UFPB 07. Piracuruca: ZUEC 7789-7796. Piripiri: UFC 874-875. São Valença (25 km N): MZUSP 50112. Valença (35 km N): MZUSP 50093-50095. *Rondônia.* Porto Velho: FML 3492(10). *Tocantins.* Araguatins: MZUSP 27966-27969. Babaçulândia: MZUSP 126914-126919. Brejinho de Nazaré: MZUSP 104457. Guaraí: MZUSP 127082-127083. Ipueiras: MZUSP 127428. Palmas: MZUSP 92245-92248; CHUNB 11233-11234, 12311-12341, 12521-12525, 14667, 14720, 16952, 16954-16955, 22078, 23829, 23836. Porto Nacional: MZUSP 69919. São Salvador do Tocantins: MZUSP 114493-114496.

Rhinella azarai

Argentina. *Misiones.* Campo San Juan: MZUSP 115502-115504, 115515. Parque Provincial Fachinal: MZUSP 115516-115517. Posadas: MACN-CENAI 76. Ruta Provincial (between Profundidad and Fachinal): MZUSP 115518-115520. San José de Puidapoy: MZUSP 106046.

Brazil. *Mato Grosso do Sul.* Bela Vista: EI 1438. Maracajú: EI 4740-4741; USNM 107701.

Paraguay. *Central.* Villeta: MNHNP 5040. *Itapúa.* Isla Yacaretá: MNHNP 8161. *San Pedro.* Primavera, Itacurubí del Rosário: NHM 1955.1.5.47 (holotype of *R. g. azarai*). Locality unknown: AMNH 19878-19881; MZUSP 74233 (paratype of *R. g. azarai*).

Rhinella nattereri

Brazil. *Roraima.* Cachoeira Uranduique (Rio Maú): MZUSP 73715 (holotype of *R. g. nattereri*); AMNH 76222; MZUSP 73767-73769, 74358-74359 (paratypes of *R. g. nattereri*); MZUSP 74319-74324. Serra do Sol (Uei-Tepui): MZUSP 74254.

Venezuela. *Bolivar.* Monte Roraima: MCZ 3300. GUIANA: *Cuyuni-Mazaruni.* Monte Roraima: AMNH 39739, 39741-39742, 39745, 39747-39748, 39754; MZUSP 111566-111568.

Rhinella fernandezae

Argentina. *Buenos Aires.* Alberti: MACN 3962. Arroyo Cebey: MACN 3921. Arroyo Vitel: MACN 32927-32930. Azul: MACN-CENAI 3544-3545, 3629, 4347, 3843, 3521. Baradero: MACN 29962-29963,

29346-29349, 29293-29304, 29311-29323, 29329-29331, 29333-29335, 35309. Bella Vista: MACN 10354 (holotype of *R. g. fernandezae*); MZUSP 111575 (paratype of *R. g. fernandezae*); MACN 3951, 10343-10345, 3892, 2381, 24718, 10519-10523, 21854, 2384(7), 18586, 2388(4), 21703, 12802. Boulogne: MACN 18317. Buenos Aires: FML 1108(8); MACN 37a, 3539(2), 9740, 3448, 24174-24175, 18110-18111; AMNH 11962; MZUSP 95674-95676. Cañada de Aguirre: MACN 23470. Carmen del Areco: MACN 23881-23889. Delta del Rio Barca Grande: MACN 29949-29950. El Tigre: MACN 21071, 2167. Estación Carapachay: MACN 18221-18227. Estación Carupá: MACN 3880. Estación Martin Coronado: MACN 27184-27207, 29667-29668, 24656-24660. Ernestina: MACN 20974. Escobar: MACN 3983(2). Fiorito: MACN 20806. Florencio Varella: MACN 2480; FML 2047(7). General Las Heras: MACN 21660-21661. Gorostiaga: MACN 23371. Guernica: MACN 22267-22268. Ingeniero Maschwitz: MACN 3788(7), 32061-32067. Isla Martín Garcia: MACN-CENAI 35(3); MACN 1206. Isla Talavera: MZUSP 115526-115528; MACN-CENAI 1224. José C. Paz: MACN 25422-25426, 18045, 2382, 3878(18), 25993-26001; FML 106(17). La Plata: MZUSP 61096-61099. Lomas de Zamora: MACN 81(3). Magdalena: MCN-FZB 4780. Moreno: FML 162. Morón: MACN 2128. Navarro (Laguna Navarro): MACN 23830-23873. Otamendi: MACN 34842-34856. Pereyra Iraola (Arroyo Pereira): MACN-CENAI 3595-3596. Rojas: MACN 20661. San Isidro: MACN 9005; MACN-CENAI 230(2). San Martin: MACN 24385. San Miguel: MACN 19182-19186, 3812. Sierra de La Ventana: MACN 10059. Temperley: MACN 3934. Wilde: MACN 25537. Zelaya: MACN-CENAI 346. *Chaco.* Puerto Antequera: FML 4347/16. Resistencia: MACN-CENAI 1479, 5730-5731; MZUSP 28246-28251. Roque Saenz Peña: FML 5944(2). *Cordoba.* San Francisco: FML 756. *Corrientes.* Bella Vista (Estación Hidrobiológica): EI 4742-4746; JJ 7366-7423; ZUEC 1144-1147; MACN 22419-22445. Colonia Carlos Pellegrini: MACN 23039-23040. Corrientes: MACN 21205-21211, 3455(8). Curuzú Cuatiá: MACN 22566-22588. Esquina: MACN-CENAI 6637. Felipe Yofré: MACN-CENAI 2373-2376, 2395-2398, 2419-2437, 2438(50), 2439(50). General Alvear: MACN 22895-22896. Goya: MACN 22485-22495. Ita Ibaté: MACN-CENAI 6013, 5923-5925. Itatí: MACN 21278-21281. Ituzaingó: FML 409, 732(6). La Cruz: MACN 22622-22631. Laguna Ibera: FML 765(10). Manantiales: MACN 3313(5), 20715-20718. Mercedes: MACN-CENAI 6039-6042; MACN 22727-22764. Monte Caseros: MACN 22821-22826. Santo Tomé: MACN 2096, 22855-2856. Yofré: MACN-CENAI 3633-3636, 3155-3156. Locality unknown: FML 6688-6700. *Entre Rios.* Concepción del Uruguay: MACN 20066-20070, 18023, 18137-18138. Crespo: MACN 20075-20118, 20175-20226. Diamante: FML sm1-sm2. Gualequaychú: MACN 21176-21178. Isla del Delta del Paraná: FML 2469. La Paz: FML 197(2). Larroque: MACN 25388. Lazo (Estancia La Peregrina): MACN 2395(6), 2397. Leibas: MACN 19320-19323. Los Conquistadores: MACN 32217. Paranacito: MACN 21809-21810. Parque Nacional El Palmar: MZUSP 1332, 61102. Piedras Blancas: MACN 27245-27250. Primeiro de Mayo: MACN-CENAI 4710. Pronunciamento: MACN 27485-27488. Pueblo Gobernador Racedo: MACN-CENAI 229. Puerto Ibicuy: MZUSP 115510-115512, 115530-115531. Rio Paranacito: MACN-CENAI 7863. Segui (Rio Paraná Guazú): MACN 20681-20684. Villa Federal: MACN 29847. Locality unknown: MZUSP 713, 1332. *Formosa.* Clorinda: FML 886(3). Estancia Monte Lindo: FML 5953, 4402-4403. Formosa: FM 927(9). Ingeniero Juarez: FML 5946. Laguna Oca: FML 2042(3). Potrero Norte: FML 6189. Puerto Pilcomayo: FML 3584. Riacho Negro: FML 910. Rio Paraguay (60km SW de Formosa): AMNH 80669. *Santa Fé.* Angélica: MACN 24617-24627. Ceres: MACN-CENAI 7391-7393. Helvécia: MACN 30803-30804, 4301-4306. Isla del Cortado: FML 134. La Califórnia: MACN 29629. Perez: MACN 24405. Reconquista: MZUSP 70805. Between Reconquista and Puerto Reconquista: FML 4849(10), 04843, 4872(6). Reconquista (100km W of): MACN 28620-28621. Recreo: MACN-CENAI 1441. Roldan: MACN 25552-25558. San José del Rincon: FML 4891(2). *Santa Fé.* MACN 4300-4306; FML 1026. Tostado: FML 4833. Vera: MACN-CENAI 4386-4387. Vera y Pintado: MACN-CENAI 8165-8183. Villa Eloisa MACN 24.593. *Santiago del Estero.* Taco Pozo: MACN 33799.

Brazil. *Rio Grande do Sul.* Alvorada: MCN-FZB 3095. Barão do Triunfo: MCT-PUC 370. Bossoroca: MCN-FZB 3112. Cachoeirinha: MCN-FZB 3633-3640, 3642, 3645-3653. Campo Bom: MCN-FZB 4285-4286. Capão da Canoa: MCN-FZB 2154-2160; MCT-PUC 232. Cidreira: MCN-FZB 823, 6992, 12066-12071; MCT-PUC 1133. Estação Ecológica Taim: MCN-FZB 10653. General Câmara: MCT-PUC 3848-51, 3871-72. Gravataí: MCN-FZB 3157-3159, 3270-3283, 3450-3550, 3552-3564, 3520, 3532, 3480, 3482, 3506-3507, 3566-3576, 3619-3628, 3702-3710, 3727-3731, 3892-3956, 3991, 4024-4044, 4046-4052, 4054-4064, 4066-4141, 4149-4151, 10559-10561; ZVCB 2212, 2388, 4101-4103; MZUSP 104261-104272. Guaíba: MCN-FZB 271; MCT-PUC 215-218. Guaíba. Fazenda Guaíba: MCN-FZB 1411, 1416-1417, 1436, 1490,

1539. Guaíba. Ponta da Pintada: MCN-FZB 11795-11796. Imbé: MCT-PUC 1073, 1076-1078, 1207-1211, 1217-1222, 1248. Montenegro: MCN-FZB 10014, 11806-11807, 11809, 11812. Palmares do Sul: MCT-PUC 1463. Porto Alegre: MZUSP 2847, 21692; MACN 18037; MCN-FZB 8607-8608, 21145. Porto Alegre. Agronomia: MCN-FZB 4155-56. Porto Alegre. Alvorada: MCN-FZB 3094-3095. Porto Alegre. Dique do Rio Gravataí: MCN-FZB 2307-2321, 2333-2337. Porto Alegre. Guarujá: MCN-FZB 4861-4863, 8604-8606. Porto Alegre. Ilha das Flores: MCN-FZB 12206-12207. Porto Alegre. Ilha do Lage: MCN-FZB 11799-11802, 11804, 12211. Porto Alegre. Ipanema: MCN-FZB 4487-4450. Porto Alegre. Jardim Sabará: MCN-FZB 701. Porto Alegre. Sarandi: MCN-FZB 3718-3722. Rio Grande: MCN-FZB 11652. Santo Antônio das Missões: MCN-FZB 13369. São Leopoldo: MZUSP 28168-28205. Sapucaia do Sul: MCN-FZB 9052. Taquari: MCT-PUC 1956. Terra de Areia: MCT-PUC 4925. Torres: MCN-FZB 1727-1728, 2499, 2717, 3051-3053, 5227, 7665-7697; MCT-PUC 219-221. Tramandaí: MZUSP 28133-28139, 104312-104317; MCN-FZB 370-371, 4557-4558; MCT-PUC 3757. Uruguaiana: MCT-PUC 1854-55. Viamão: MCN-FZB 1929-30, 1958-59, 13189, 13289-91; MCT-PUC 222-24; ZUEC 10418. Viamão. Passo do Vigário: MCN-FZB 1075-76, 1547, 1832-1833. Locality unknown: MCN-FZB 1855-1858; MCT-PUC 225-226, 231. *Santa Catarina.* Içara (Lagoa dos Esteves): MCN-FZB 10048.

Paraguay. *Alto Paraguay.* Paso Tapiricuay: NHM 1972.84-85. *Central.* Asunción: AMNH 64644-46, 81365. Colonia Nueva Italia: AMNH 50672-50675. Villeta: USNM 340515-340518. *Cordillera.* Santa Elena: USNM 340519-340520. *Presidente Hayes.* Estancia La Golondrina: USNM 340521. *San Pedro.* Puerto Rosário: NHM 1972.19-28.

Uruguay. *Artigas.* Arrocera Conti: ZVCB 3144, 3238, 3025, 1608(2), 2052. Arrocera Riusa: ZVCB 1580. Arroyo Itacumbu: ZVCB 2247, 1675(2), 2334(2), 2334-2335; MZUSP 54210-54211. Barra del Yacaré: ZVCB 16. Belén: ZVCB 779(2). Bella Union: ZVCB 398, 2418. Estancia El Ombú: ZVCB 231. *Canelones.* Arroyo Carrasco: ZVCB 3320, 3326. Arroyo Las Tunas (en Ruta Interbalnearia): ZVCB s/nº (5). Balneario Lagomar: MZUSP 115529; ZVCB 658. Bañados del Carrasco: ZVCB 844(7), 845(10). Canelones: MCT-PUC 3955-3961. Carrasco (Aeropuerto Internacional): MACN-CENAI 3258. Costa Azul: ZVCB 3226, 1136, 1135(2). Las Toscas: ZVCB 484. Parque Roosevelt: ZVCB 818(2). Pinamar: ZVCB 2596-2598. Ruta Interbalnearia, Km 18: ZVCB 2106, Km 47: ZVCB 836, 898(6), Km 63: ZVCB 1025A. Salto: MACN 36324-36326. San José de Carrasco: ZVCB 4210-4211. Sauce: ZVCB 897A. *Colonia.* Carmelo: MACN 8736; ZVCB 3241. Carretera entre Carmelo e V. Palmira: ZVCB 3234, 3240. Juan Lacaze: MZUSP 54213-54214; ZVCB 4168-4183. Nueva Palmira: ZVCB 397(2), 268; MACN 2248. Paso de la Horqueta (Arroyo San Juan): ZVCB 3916. *Lavalleja.* Aguas Blancas: UTA 5899. Cerro del Perdido: ZVCB 902. Penitente: ZVCB 2984. *Maldonado.* Balneario Solis (Arroyo Espinas): ZVCB(nº campo) 163, 497, 6, 138, 110, 192. Isla de Lobos: ZVCB 2803. *Montevideo.* Arroyo Carrasco: ZVCB 394. Montevideo: ZVCB 281. Arroyo Malvin: MACN-CENAI 3351. Pajas Blancas: FML 3677(2); MCN-FZB 5168, 5172; ZVCB 2118, 465, 4136-4143. Playa Carrasco: ZVCB 1099. Playade los Pocitos: ZVCB 3278. Prado (Barrio la Escalada): ZVCB 3598. Santiago Vazquez: MACN-CENAI 3369. *Paisandú.* Arroyo Carpinchurí: ZVCB 2739. Arroyo Negro: ZVCB 4043, 356. Costanera Sur: ZVCB 3791. Santa Rita: ZVCB 395(4), 396. *Rio Negro.* Arroyo Laureles: ZVCB 2487. Boca del Arroyo Negro: ZVCB 4067-4068, 1261. Costa del Rio Negro (Villa Soriano): ZVCB 1341(9). Estancia Francia: ZVCB 4154. Fray Bentos: ZVCB 4127. Isla Vizcaino: ZVCB 3007. San Javier: ZVCB 390. *Salto.* Arroyo el Espinillar: ZVCB 1630(8), 1702, 2087. Constitución: ZVCB 1623(2), 1586(10). Rio Dayman: ZVCB 4118, 1598. Salto: ZVCB 1595(3), 1016 (2), 1562(15); ZVCB 1348A, 1348C, 1522(3). *San José.* Arazati: ZVCB 391, 1273. Arroyo del Tigre: ZVCB (s/nº). Autódromo Nacional: ZVCB 1141-1142. Balneario Kiyú: ZVCB 2668-2669, 3284, 900(2). Barra de Santa Lucia: ZVCB 544(2). Delta del Tigre: ZVCB 4129-4135; ZUEC 10430, 10435-10437. Establecimiento El Relincho: ZVCB 2204-2206, 3457-3458, 2637-2639, 2851. Playa Pascual: ZVCB 1440(8), 2221, 2344, 2254-2258. Sierra de Mahoma: ZVCB 392(3), 822(2), 899(4).

Rhinella dorbignyi

Argentina. *Buenos Aires.* Ariel: MACN 21797. Arroyo Los Huesos: MACN-CENAI 3537-3538, 3574-3575, 3566-3567. Ayacucho: MACN 29517-29521. Azul: MACN 4057. Bonifácio: MACN 4322,

20942. Cacharí (Arroyo del Azul): MACN 29476. Casalins: MACN 328. Chascomus (Estancia "La Eloisa"): MZUSP 115505-115509; MACN 2308(2). Coraceros: MACN 35433. D. Harostegui: MACN 24734-24742. Dolores: MACN 299499-299501. Dorbignyi: MACN 18574, 18584-18585, 3910, 10502-10511, 20758, 18333-18387, 3976, 21726, 3908, 21883-22006. Energía: MACN 7884-7888. Esperanza: 29684. Estancia Cari Lauquen: MACN 3855. General Lavalle: MACN 24380, 30237-30240, 29684, 29638-29642. Juarez: MACN 23518, 23507-23508. La Adela: MACN 3828(3). Laguna del Monte: MACN 21830-21837. Libres del Sur: MACN 25344-25345, 23727-23728, 18177-18195. Mapis: MACN 28363-28364. Mar del Plata: AMNH 33991-33997, 34077-34082; EI 1302. Masurel: MACN 3961. Pila: MACN 23401, 23398-23413. Rosas: MACN 254. Santo Domingo (Estancia El Zoneleiro): MACN 2390, 10389-10393. Santos Unzué: MACN 29941. Tandil: MACN 539(2), 25950. Tapalqué: MACN 30218, 18215-18218. *La Pampa.* General Pico: MACN 1283. *Rio Negro.* Rosas (Bahia de Rosas): MACN 4435.

Brazil. *Rio Grande do Sul.* Arambaré: MCT-PUC 1264. Arroio dos Ratos (Minas do Butiá): MCN-FZB 1042. Canoas (Parque Aeronáutico da FAB): MCN-FZB 1043. Estação Ecológica Taim: MZUSP 52235-52237, 57561-57563; MCN-FZB 13382, 13394, 106405, 10646-10647. Gravataí: ZUEC 1543-1544, 1548. Guaíba: MCN-FZB 3343, 4745. Guaíba. Fazenda Umbu: MCN-FZB 2649, 2726, 2756, 2854. Jaguarão: MZUSP 28140-28167; MCN-FZB 1146. Jaguarão. Jardim Botânico: MCN-FZB 13190, 13206. Montenegro: MCN-FZB 11805, 11808, 11810-11811, 11813, 11839, 11847, 11997-12000, 12072. Osório. Praia de Atlântida: MCN-FZB 9653-9655. Passo do Vigário: MZUSP 104310-104311. Pelotas: MZUSP 28132; MCN-FZB 1681, 9009-9017. Palmares do Sul: MCN-FZB 4639. Porto Alegre: MACN 2398, 18038; MCN-FZB 2011, 2416, 374, 3236, 3309, 3719-3720, 3722, MCT-PUC 227-230, 2561, 3219-3220, 3153, 4912. Porto Alegre. Ilha do Lage: MCN-FZB 11715-11803, 11846. Porto Alegre. Passo do Feijó: MCN-FZB 2087. Porto Alegre. Praia de Belas: MCN-FZB 2408-2410, 2064. Rio Grande. Praia do Cassino: MCN-FZB 10400-10409, 10500-10509, 10642-10653. Santa Vitória do Palmar: MCN-FZB 10301-09, 10597-10626, 10628-41, 10687-90. São Lourenço do Sul: MCN-FZB 9623. Tramandaí: MCN-FZB 403. Triunfo: MCN-FZB 11779-80, 11783. Triunfo. Lagoa do Pontal: MCN-FZB 9652. Triunfo. Fazenda Delapieve: MCN-FZB 11350-51, 11347. Viamão: MCT-PUC 2562-64, 3234-35, 3238; ZUEC 10417. Viamão. Parque Saint Hilaire: MCN-FZB 2404. Locality unknown: MZUSP 1330-1331; MCN-FZB 2494; NHM 1882.10.4.12.

Uruguay. *Artigas.* Arroyo Yacui: ZVCB 4069-4077, 4091-4099. Bella Union: ZVCB 2419. Estância Chico Martinez (Arroyo Catalán Chico): ZVCB 171. Rio Cuareim: ZVCB 1290. *Canelones.* Águas Correntes: ZUEC 10419. Arroyo Pando: ZVCB 369. Atlântida: MACN 36320-36321; ZVCB 643(3). Pinamar: ZVCB 975D-975G. Ruta Interbalnearia, Km 63: ZVCB 1025C. Santa Lucía: MACN-CENAI 178. Sauce: ZVCB 897B-897C. *Cerro Largo.* Arroyo del Cordobés: ZVCB 782(3). Melo: ZVCB 1264, 4062; AMNH 71163-71169. Placido Rosas (20 km NW of): ZVCB 3131. Locality unknown: ZVCB 2384. *Colonia.* Rosario: ZVCB 3132. *Durazno.* Rincón de las Piedras: ZVCB 1381(4). *Flores.* Estación Arroyo Grande: ZVCB 2111. *Florida.* Vinte e Cinco de Agosto: ZVCB 1363. *Lavalleja.* Abra de Zabaleta: ZVCB 4155-4156, 4216. Aguas Blancas: ZVCB 2428; UTA 5899. Cerro Arequita: ZVCB 697. Penitente: ZVCB 2986. Rio Cebollatí: ZVCB 414. *Maldonado.* Isla de Lobos: ZVCB 1296, 1297(2), 4120-4122. Laguna del Diário: MACN-CENAI 2815. Laguna del Sauce: ZVCB 2649-2656. Pan de Azúcar: ZVCB 4119, 2049, 2059, 2061, 2064-2065, 2071. Piriápolis (Arroyo Los Alamos): ZVCB 2434. Punta del Este: ZVCB 2373, 2489, 4117. San Rafael: ZVCB 359(3). *Montevideo.* Punta Espinillo: ZVCB 4104-4110. *Paisandú.* Costanera Sur: ZVCB 1968, 3789-3790. *Rivera.* Arroyo Cuñapirú: ZVCB 797(3). *Rocha.* Cabo Polonio: ZVCB 4209. Chuy (Arroyo Chuy): ZVCB 4197-4202, 4209. La Coronilla: ZVCB 1711, 2774. La Paloma: ZVCB 1179(4). Laguna de Castillos: MZUSP 115501. Parque Nacional San Miguel: ZVCB 1256, 1265, 1294. Parque Santa Teresa: ZVCB 3749. *San José.* Balneário Kiyú: ZVCB 2657-2661. Rio Santa Lucía: ZVCB 738. Villa Rodriguez: ZVCB 2624. *Soriano.* Costa Rio Negro: ZVCB 4214. Estancia Santa Rita: ZVCB 1150(2). *Tacuarembó.* Ansina: ZVCB 2248-2252. Paso Baltasar: ZVCB 3059-3062. Tambores (Pozo Hondo): ZVCB 483, 2342. Tacuarembó (40 km NW): AMNH 71162. *Treinta y Tres.* Arroyo Los Membrillos: ZVCB 612. Arrozal Treinta y Tres: ZVCB 393. La Charqueada: ZVCB 4153. Santa Clara del Olimar: ZVCB 448.

Rhinella merianae

Brazil. *Amazonas.* Coarí: MZUSP 37175, 39665-39969. Codajás: MZUSP 42189-42191. Lago Beruri: MZUSP 27823-27829. Lago Catiá: MZUSP 95640. Manacapuru: MZUSP 42196, 39578, 15948. Manaus: ZUEC 4060-4061; CFBH 1884-1885; MNRJ 1368, 3137, 7513-7517, 13473; MZUSP 747, 749, 71234, 71234, 71879-71880, 96259-96262; MPEG 4968-4969, 4971; INPA 786. Reserva Campina (Rodovia Manaus-Caracaraí km 60): MNRJ 25679-25682. Reservas INPA-WWF: MZUSP 60110, 67773-67776. Cidade Powell: MZUSP 66328. Porto Alegre: MZUSP 60110. Rio Negro: MZUSP 1308-1310. Rio Pitinga: INPA 2040. São Terra Preta (Boca do Manacapuru): MZUSP 39578, 42196. Locality unknown: MZUSP 53673-53615. *Roraima.* Boa Vista: USNM 30294-30295; MZUSP 68755-68756, 65410-65411. Cachoeira do Cujubim (Rio Catrimani): MZUSP 54785-54786. Caracaraí: MPEG 7760. Caracaraná: USNM 302450-302453; MZUSP 67067-67070. Colônia Apiaú: MZUSP 65954, 66069-66083, 66084-66085. Fazenda Fortaleza: MZUSP 66631. Fazenda Salvamento: MZUSP 66029, 66632, 67261, 67262-67263, 67599, 70689. Fazenda São Marcos: MZUSP 104379-104381. Igarapé Cauaruaú: MZUSP 66308-66309, 68247, 68616-68618, 66039-66040. Igarapé Cocal: USNM 302394-302397. Igarapé Murupu: MZUSP 68752. Ilha de Maracá: MZUSP 65575-65578, 65618-65625, 65682, 65708-65711. Maloca Mangueira: MZUSP 65965-65969, 65971-65975. Missão Catrimani: MZUSP 63652-63658. Monte Roraima: AMNH 3750. Mucajaí: USNM 302147-302174. Normandia: MZUSP 70565. Rio Ajarani: MPEG 7646-7647, 7795, 7784, 7848. Rio Mucajaí: MZUSP 29889, 65978, 110999. Serra da Saracura: MZUSP 62456-62457, 65794-65799. Tepequém: USNM 326610; MZUSP 69772-69773, 65988-65990, 65992-65996, 66984-89. Vila Brasil: MZUSP 68634-68635. Vila Surumu: MZUSP 21668-21669, 21781-21784, 65818-65823, 65847, 65848-65853, 105741-150762; MNRJ 24324-24629, 24800-24801. Vila Teresa: MZUSP 73701.

Guiana: *Cuyuni-Mazaruni.* Head Falls of Essequibo River: AMNH 46531 (holotype of *R. g. merianae*); AMNH 101719-101725, 46525-46530 (paratypes of *R. g. merianae*); MZUSP 73573-73574 (paratypes of *R. g. merianae*); MZUSP 111572. Monte Roraima: AMNH 39740, 39743, 39746, 39750, 39760. *Potaro-Siparuni.* Kato, Rio Chiung: MZUSP 110998; USNM 291087-291101. Montanha Pakaraima: NHM 1933.6.19.35. *Upper Demerara-Berbice.* Dubulay (Rio Berbice): AMNH 141065-141080; MZUSP 111574. *Upper Takutu-Upper Essequibo.* Aishalton (Kubanawau Creek): AMNH 139019-132030, 1390132-139033; MZUSP 111573. Alto Rio Rupununi: MZUSP 111569-111571. Isherton: AMNH 70111, 46338-46348. Lethem, Rio Takutu: USNM 497689-497693. Moco-moco: MCZ 50753. Rupununi Savanna: NHM 1933.6.19.33-34. Locality unknown. UMMZ 218763-218764.

Surinam. *Brokopondo.* Browns Berg (Railway km 62): RMNH 29355, 29361-29362, 26364. *Nickerie.* Camp. Hydro: USNM 220061-22064. *Pará.* Krakka: RMNH 26050, 26053-26054. Paranam KU 159623-159624. Zanderij: KU 221526.

Venezuela. *Amazonas.* Puerto Ayacucho, Rio Orinoco: AMNH 23220-23221, 131018. *Bolivar.* Las Majadas (Rio Orinoco): MHNM 504, 531. Santa Elena de Uairen: USNM 258106. *Zulia.* El Laberinto: MACN-CENAI 2629.

Rhinella humboldti

Colombia. *Antioquia.* Medellin: AMNH 39090, 39127-39128. *Arauca.* Arauca: MNHN 5009-5010. Caño Limón: ICN-UNC 27290, 27835. *Atlantico.* Barranquilla: ICN-UNC 1918, 1921; MZUSP 6034-6129. Piojo: USNM 152688-152695. *Bolivar.* Cartagena (Hotel Los Corales): UTA 4980-4982. Santa Rosa: ICN-UNC 2125, 2128. San Cristobal: AMNH 81664-81668, 75649-75654. Sincelejo: USNM 150733-150741. Tolú Viejo: MZUSP 54181, 5420-5435. *Caldas.* Samaná: ICN-UNC 34711, 34715. *Casanare.* Yopal: AMNH 81671-81672. *Cesar.* Becerril: AMNH 84375. Rio Cesar: USNM 117515. *Cordoba.* Caño Bentancí: USNM 144571. *Cundinamarca.* Anapoima: USNM 153928. Fusagasuga: AMNH 71559-71561; USNM 153935. Girardot: MACN-CENAI 3125-3126; AMNH 81658-81663. Melgar: USNM 146635-146636. Tocaima: USNM 146201. *La Guajira.* Pajaro: USNM 151292-151302. Serrania Macuira: USNM 115380. *Magdalena.*

Bonda (Finca El Aranar): MZUSP 111005; USNM 152735-152749. Cienaga: USNM 144153. Fundación: MCZ 8978 (paratype of *Rhinella granulosa humboldti* GALLARDO 1965a). Rio Manzanares (between Santa Marta and Mamatoca): USNM 150892. *Meta.* Acacias: ICN-UNC 39463. Cana Guapaya (Sierra de La Macarena): USNM 147266-147267. Cumaral: ICN-UNC 21307. La Cristalina: USNM 144572. Puerto Lopez: AMNH 75642, 75145-75152; MZUSP 104340-104342. Villavicencio: MZUSP 54452, 105878-105896, 104331-104335; AMNH 75144, 75643, 81669-81670; USNM 158034-158035, 146815, 144573, 146385-146389, 144573. *Norte de Santander.* Astillero: USNM 146816-146817. Barrancabermeja: USNM 146814. Zulia: ICN-UNC 33559, 33562. *Sucre.* Coveñas: FML 2584. *Tolima.* Girardot: AMNH 75139-75143; MZUSP 104336-104339. Gualanday: MCZ 24882 (holotype of *R. g. humboldti*). Honda: ICN-UNC 43169; AMNH 75644-75648, 20358. Mariquita: USNM 15151-15153, 144574-144583; MZUSP 111000. Melgar: USNM 148135. Venadillo: ICN-UNC 43940. *Vaupes.* Amanaven (Boca del Rio Guaviara): USNM 144584.

Guyana: *Cuyuni-Mazaruni.* Bartica: MCZ 50748-50752. *Upper Takutu-Upper Essequibo.* Alto Rio Rupununi: AMNH 101726-101744, 46484-46493, 46446-46450.

Surinam. *Brokopondo.* Brokopondo: RMNH 29309-29330, 29385-29389. Brownsweg: RMNH 26051-26052. *Commewijne.* Nieuw Grond, Rio Coppename: MCZ 98937-98938. *Marowigne.* Christiaakondre: MZUSP 27815-27820. Paloemeu: USNM 158981-158982. *Pará.* Matta: RMNH 29383. Moeroe Kreek: RMNH 260556. Zanderij: USNM 159057-159061; MCZ 89492-89493. *Paramaribo.* Paramaribo: RMNH 26055, 29372-29375. *Sipaliwini.* Foengoe Eiland, Raleighvallen-Voltzberg Reserva Natural: MCZ 92149, 96514. *Surinam.* Rio Surinam: RMNH 29380.

Trinidad. *Arima.* Arima: USNM 306144-306145, 286986-28692; MZUSP 110996; KU 263850-263851; NHM 1897.7.23.116, 1932.9.16.20-22. *Caroni.* Chaguanas: USNM 166290-166295. *Saint George.* Churchill-Roosevelt Higway: AMNH 55774 (holotype of *R. g. beebei*); AMNH 101704-101707, 55771, 55773, 55775 (paratypes of *R. g. beebei*); AMNH 55770, 55772, 55776-55778, 101692-101703; MZUSP 74261-74262 (paratypes of *R. g. beebei*); MZUSP 111561-111565. Piarco: AMNH 79814-79817, 101708-101718; USNM 166296. Saint Augustine: USNM 141533; MCZ 19889, 126240; NHM 1970.546-547, 1971.1548-1549. *Saint Patrick.* Balandra: MCZ 80478. Locality unknown: AMNH 119171-119174; USNM 266101-266102, 5827.

Venezuela. *Amazonas.* Puerto Sanariapo: USNM 80640-80650. San Fernando de Atabapo: MCZ 27825; MZUSP 6325. *Anzoátegui.* Barcelona: MZUSP 8079. *Apure.* Biraquita: MZUSP 31375. *Aragua.* Maracay: AMNH 70525, 70527-70529; TNHC 44063; USNM 196327, 97193-97195, 196327; JJ 6858. Ocumare del Tui: MZUSP 8078. *Bolivar.* El Manteco (25 km SE): AMNH 90201-90202; USNM 216519-216523, 216525. Las Majadas (Rio Orinoco): MNHM 4022. Upata: USNM 216518. *Distrito Federal.* Caracas: TNHC 46530-46539. *Guarico.* Hato Masaguaral: NHM 1976.149-150. *Monagas.* Hato Mata de Bejuco, Rio Tigre: USNM 216526-216527. *Nueva Esparta.* Isla de Margarita: RMNH 10867 (holotype of *R. g. barbouri*); RMNH 10868a-10868d (paratypes of *R. g. barbouri*); MZUSP 8077, 8080. La Asunción: USNM 139066-139068, 216515-216517. Salamanca: USNM 216510-216514. San Juan Bautista: USNM 216509. *Yaracuy.* San Felipe: NHM 1971.1545-1547. *Zulia.* Cerro Azul: USNM 216533-216534. Maracaibo: MZUSP 58848-58850.

Rhinella centralis sp. n.

Panama. *Chiriquí.* TNHC 33425-33426. David: AMNH 69634-69635; TNHC 31289-31295. *Coclé.* UMMZ 167436, 167370-167372. Agua Dulce: KU 107337-43. El Cano: KU 107344. Penonome (Cerro Puerto Posada): AMNH 84888; KU 107345-48, 116844-116845. *Colón.* Isla Barro Colorado: AMNH 22830. *Herrera.* Chitre: USNM 203595-203612 (paratypes of *R. centralis* sp. n.); MZUSP 111002-111003, 110995 (paratypes of *R. centralis* sp. n.). Parita: USNM 127250. *Los Santos.* Lajamina: KU 67756. *Panama.* Albrook: TNHC 24018-24027. Bejuco: AMNH 69628-69631; MZUSP 111559-111560. Canal Zone: MZUSP 104378. Diablo Heights: AMNH 81524. Fort Kobbe: USNM 140493. Isla Nueva Gorgona: AMNH 69632-69633; MZUSP 111560. Panamá: UMMZ 167437. Rio Calobre: USNM 53739. Tocumén: KU 107358-107359. *Veraguas.* Montijo: KU 107353-107357. Locality unknown: TNHC 33427-33431, 33433-33434.

Hybrid specimens

Rhinella bergi/Rhinella major

Brazil. *Mato Grosso do Sul.* Corumbá: CFBH 3898, 4117-4118, 4120-4121, 4124, 4126.

Rhinella major/Rhinella mirandaribeiroi

Brazil. *Mato Grosso.* Cáceres: MZUSP 22142, 22144-22146, 22152.

Rhinella mirandaribeiroi/Rhinella granulosa

Brazil. *Bahia.* Barreiras: UMMZ 108912. Riacho das Neves: CHUNB/Fisio 1563. *Minas Gerais.* Pirapora: CAS 11962-11963 11969-11970 11959 11967. Rio Pandeiros: MZUSP 28060-28065.

Rhinella fernandezae/Rhinella dorbignyi

Argentina. *Buenos Aires.* Juancho: MACN 5133. URUGUAY. *Canelones.* Bañados Salinas: ZVCB 901. Las Tunas: ZVCB 578. Pinamar: ZVCB 975A. Ruta Interbalnearia, Km 63: ZVCB 1025B. Tropas Viejas: MZUSP 104308-104309. *Lavalleja* Cerro del Perdido: ZVCB 2989. *Salto.* Termas del Arapey: ZVCB. BRAZIL. *Rio Grande do Sul.* Osório: EI 1301. Porto Alegre: MACN-CENAI 659-663. São Leopoldo: EI 4936-4938. Sapucaia do Sul: MZUSP 104356-104357. Montenegro. Morro do Pesqueiro: MCN-FZB 11344-46, 11483.

The following specimens belong to the *Rhinella granulosa* group, but they are too young and an accurate identification was not possible. Venezuela. *Bolivar.* Cerro Yuruani: AMNH 129477. San Tomé de Guayana: AMNH 81454. Guiana. *Cuyuni-Mazaruni.* Manarabisi Creek: AMNH 49348. Rodovia Kartabu-Puruni: AMNH 70831. *East Berbice-Corentyne.* King Frederick Willian Falls: NHM 1936.9.3.19-21. *Upper Takutu-Upper Essequibo.* Wismar: AMNH 45761.

The following specimens were mistakenly catalogued as *Rhinella granulosa* but they do not belong to the *R. granulosa* group. Argentina. *Salta.* Rio Zenta: FML 177. Brazil. *Amazonas.* Penedo, Rio Juruá: INPA 2520, 2377. *Bahia.* Jeremoabo: MZUSP 38127. *Mato Grosso do Sul.* Fazenda Barma: MZUSP 69355. Salobra: MZUSP 21426, 21428-21430, 21432-21433. *Pará.* Alter do Chão: MZUSP 29041. *Rio Grande do Sul.* Costa Marques: MCT-PUC 1679. Rio Grande. Estação Ecológica Taim: MZUSP 52238-52239, 52241. *Roraima.* Tepequem: MZUSP 65991. Suriname. *Paramaribo.* Paramaribo: USNM 158947. Uruguay. *Artigas.* Arrocera Conti: ZVCB 3198. *San José.* Autódromo Nacional: ZVCB 1054.

Other specimens examined

Rhinella marina. Brazil. *Amazonas.* Coari: MZUSP 28904-10; *Roraima.* Fazenda Salvamento: MZUSP 71206. *Rhinella crucifer.* Brazil. *Bahia.* Una: MZUSP 126304.