

DESCRIPTION AND PHYLOGENETIC POSITION OF A NEW SPECIES OF *OREOBATES* (ANURA: CRAUGASTORIDAE) FROM NORTHWESTERN ARGENTINA

MARTÍN O. PEREYRA¹, DARÍO E. CARDOZO², JORGE BALDO³, AND DIEGO BALDO^{2,4}

¹ CONICET - División Herpetología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina

² CONICET - Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical, Facultad de Ciencias Exactas Químicas y Naturales, Universidad Nacional de Misiones; Félix de Azara 1552, CPA N3300LQF, Posadas, Misiones, Argentina

³ CONICET - Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, Y4600DTA, San Salvador de Jujuy, Argentina

ABSTRACT: We describe a new species of *Oreobates* from Jujuy, Argentina. The new species is clearly diagnosable from other species of *Oreobates* by a combination of morphological characters and support by molecular evidence (genetic distance and phylogenetic analysis). We also provide taxonomic comments about *O. discoidalis* and *O. barituensis*, emphasizing the need for an exhaustive revision of these species.

Key words: Direct-developing frog; Morphology; Phylogenetic analysis; Taxonomy

THE NEW WORLD direct-developing frogs (Terrarana) constitute a massive radiation of anurans comprising four families (Brachycephalidae, Ceuthomantidae, Craugastoridae, and Eleutherodactylidae) with more than 990 species (Frost, 2014). This monophyletic group was originally defined mostly on the basis of molecular evidence (Hedges et al., 2008; Heinicke et al., 2009), but recently several morphological synapomorphies were proposed (Taboada et al., 2013).

Within Terrarana, *Oreobates* Jiménez de la Espada, 1872 is the genus with the southernmost distribution. Its 22 species are distributed from southern Colombia to northern Argentina and eastwards into western Brazil (Padial et al., 2012; Frost, 2014). This genus was resurrected by Caramaschi and Canedo (2006) and more recently Padial et al. (2008, 2012) addressed its taxonomy and phylogenetic relationships. Currently, the only putative phenotypic synapomorphy of *Oreobates* is the structure of its advertisement call, composed of amplitude-modulated and highly pulsatile notes with little or no frequency modulation (Padial et al., 2012).

Two species of *Oreobates* are recognized in Argentina, *O. discoidalis* (Peracca, 1895) and *O. barituensis* Vaira and Ferrari, 2008, both

distributed in sub-Andean forests in Jujuy, Salta, and Tucumán provinces in the northwest of the country. These species were recovered as closely related in the phylogenetic analysis of Padial et al. (2012) and apparently have extensive areas of sympatry throughout their distributions (Akmentins, 2011; Akmentins et al., 2012).

During recent fieldwork in Jujuy, northwestern Argentina, some specimens of a distinctive species of *Oreobates* were collected. Additional specimens of this new species were discovered after revision of herpetological collections. In this paper we describe it as a new species which is clearly distinguishable from other species by a combination of morphological characters and molecular evidence.

MATERIALS AND METHODS

Molecular Phylogenetic Analyses

We performed a parsimony phylogenetic analysis including DNA sequences of three mitochondrial genes (12S–16S, ≈2400 bp; cytochrome b, 385 bp) and two nuclear genes (recombinase activation 1 [RAG-1] 632 bp; tyrosinase [TYR], 493 bp).

Total genomic DNA was extracted from ethanol-preserved tissues (liver or muscle) of *Oreobates crepitans* and from the new species using the Qiagen DNeasy kit. PCR amplifica-

⁴ CORRESPONDENCE: e-mail, diegobaldo@gmail.com

tions were carried out in 25- μ l reactions using 0.2 μ l Taq (Fermentas). The mitochondrial genes 16S and cytochrome b were amplified for the new species using the pairs of primers 16S-ar/Wilkinson2 (Palumbi, 1996; Wilkinson et al., 1996) and CytbDen3-L/CytbDen1-H (Santos and Cannatella, 2011), respectively. Additionally, we included sequences of the genes 16S and cytochrome b for *O. crepitans*, one of the two species of *Oreobates* not included in the previous phylogenetic analysis of the genus (Padial et al., 2012). The PCR protocol consisted of an initial denaturation step at 94°C (3 min), 35 cycles consisting of 94°C (30 s) for denaturation, 48°C (30 s) for annealing, and 72°C (40 s) for extension followed by a final extension step at 72°C (10 min). PCR-amplified products were cleaned using 10 U of exonuclease plus 1 U of alkaline phosphatase per reaction. The products were sequenced with an automatic sequencer ABI 3730XL (Applied Biosystems, Grand Island, NY, USA) and all samples were sequenced in both directions to check for potential errors. Chromatograms obtained from the automated sequencer were processed using Sequencher v4.5 (Gene Codes, Ann Arbor, MI, USA). Complete sequences were edited with BioEdit (Hall, 1999) and deposited in GenBank under the accession numbers KJ125507–12.

For the phylogenetic analysis we included sequences of all the species and candidate species (see Padial et al., 2012) of *Oreobates* for which there are available sequences in GenBank. Additionally, we included sequences of 34 species representing 13 genera of Craugastoridae (sensu Pyron and Wiens, 2011) selected according to the phylogenetic hypotheses of Hedges et al. (2008), Pyron and Wiens (2011), and Padial et al. (2012). *Adelophryne gutturosa*, a species of Eleutherodactylidae, the sister family of Craugastoridae, was used for rooting the trees. Except for the original sequences of 16S and cytochrome b for the new species and *O. crepitans*, the sequences for all other species used in the phylogenetic analysis were obtained from GenBank. The included nuclear (RAG-1 and TYR) and mitochondrial fragments (12–16S and cytochrome b) are the most-sampled fragments for *Oreobates* and related groups

and were included to test more strictly the monophyly of *Oreobates* and the phylogenetic relationships of the new species. A detailed list of analyzed specimens, collection numbers, and accession numbers of GenBank is available in Appendix I. Phylogenetic analyses were performed under direct optimization in POY 4.1.2.1 (Varón et al., 2010) using equal weights for all transformations (substitution and insertion–deletion events). We considered parsimony as optimality criterion because the cladogram that minimizes transformations to explain the observed variation is the simplest, maximizes evidential congruence, and has the greatest explanatory power (Kluge and Grant, 2006; Wheeler et al., 2006). For the analysis of sequences, we first performed a multiple alignment using the online software MAFFT v6.240 (Kato and Toh, 2008) under the strategy E-INS-i and default parameters for gaps opening and extension. Final alignments for each gene can be accessed in the Dryad Digital Repository (doi:10.5061/dryad.t114v). The ribosomal genes (12S–16S) were preliminarily delimited in sections of putative homology (Wheeler et al., 2006), and equal-length sequences of coding genes (nuclear and cytochrome b fragments) were considered as static alignments to accelerate the searches (Faivovich et al., 2010).

Analyses were performed using the command “Search.” This command implements a driven search building Wagner trees using random addition sequences (RAS), tree bisection and reconnection (TBR), branch swapping followed by ratchet (Nixon, 1999), and tree fusing (Goloboff, 1999). This command stores the shortest trees of each independent run and performs final tree fusing using the pooled trees as a source of topological diversity (Wheeler et al., 2006). The resulting trees were submitted to a final round of swapping using iterative pass optimization (Wheeler, 2003). Implied alignment resulting from POY searches after iterative pass optimization was submitted to TNT (v1.1, Willi Hennig Society Edition; Goloboff et al., 2008) for additional swapping to ensure that all equally optimal solutions for that homology scheme were recovered (Pickett et al., 2006). Parsimony jackknife (Farris et al., 1996)

absolute frequencies were estimated from the original static alignment with TNT, generating 50 RAS + TBR per replicate for a total of 1000 replicates, with removal probability of 36% and considering gaps as a fifth state. Editing of trees was performed with Winclada (Nixon, 2002). Uncorrected p -distances (UPD) of the 16s gene were calculated in PAUP* (Swofford, 2002) for a dataset with all sequences having the same length and no missing data (575 bp including gaps) and containing only samples of some species of *Oreobates* closely related to the new species. These sequences of 16S gene were aligned using the software MAFFT under the strategy G-INS-i with default parameters for gaps opening and extension and are available in the Dryad Digital Repository (doi:10.5061/dryad.t114v).

Morphology

For morphological descriptions, we followed the terminology of Lynch and Duellman (1997), Padial et al. (2008), Duellman and Lehr (2009), and Taboada et al. (2013). Following Fabrezi and Alberch (1996), fingers were numbered II–V. Measurements (± 0.1 mm) were taken with calipers under a stereoscopic microscope. Considered measurements are those that were described by Padial et al. (2008): snout–vent length, SVL; head length, HL; head width, HW; eye length, EL; eye to nostril distance, EN; internarial distance, IND; eye–eye distance, EE; tympanic membrane height (vertical diameter), TYH; tympanic membrane length (horizontal diameter), TYL; arm length (from posterior margin of thenar tubercle to distal point of elbow), FA; tibia length, TL; thigh length, TH (from vent to knee); and foot length, FL. Sex was determined by observation of external secondary sexual characters (nuptial pads and vocal slits) and by direct inspection of gonads.

Reference specimens are deposited in the following herpetological collections: División Herpetología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”—CONICET (MACN), Buenos Aires, Argentina; Instituto de Herpetología, Fundación Miguel Lillo (FML), Tucumán, Argentina; Laboratorio de Genética Evolutiva (LGE), Instituto de Biología Subtropical (CONICET-Universidad Nacional de Misiones), Posadas, Misiones,

Argentina; Museo de Ciencias Naturales (MCN), Universidad Nacional de Salta, Argentina; Museu de Zoología, Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu de História Natural, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil (ZUEC); Museu Nacional do Rio de Janeiro (MNRJ), Universidade Federal de Rio de Janeiro, Rio de Janeiro, Brazil; Museo di Zoologia, Instituto di Zoologia e Anatomia Comparata Università di Torino (MZUT), Torino, Italy. All examined specimens are listed in Appendix II.

RESULTS

Molecular Phylogenetic Analyses

The phylogenetic analysis using direct optimization resulted in a single, most-parsimonious tree of 12,666 steps (Fig. 1). As was defined by Padial et al. (2012), *Oreobates* is recovered as monophyletic with a high support (jackknife = 91%) and as the sister clade of *Lynchius* (77%). The specimens of the new species are recovered as the sister taxon of *O. lundbergi* with low support (<50%). The specimen of *O. crepitans* is recovered as the sister species of *O. remotus*, also with low support (<50%). The other two species that are present in Argentina, *O. barituensis* and *O. discoidalis*, form a clade with *O. ibischi* and are distantly related to the new species. The uncorrected p -distances showed a relatively high genetic differentiation of the new species in regard to other species of *Oreobates* (>12.4%; Table 1, Fig. 1).

Oreobates berdemenos sp. nov. (Figs. 2–4, Table 2)

Holotype.—LGE 2530, an adult female collected on 12 February 2012 in Abra Colorada (23°40'28.7''S, 64°54'18.2''W, datum = WGS84; 1667 m above sea level [asl]), Departamento Ledesma, Jujuy, Argentina, by J. Baldo and Y. Arzamendia (Figs. 2–4A).

Paratopotypes.—Five adult males (FML 24621–2, 24624, 24626, LGE 2531), two adult females (FML 24623, 24625), and two juveniles (LGE 4789–90) collected on 20 February 2012 by D. Baldo and J. Baldo. An adult female (LGE 4779) collected on 15 December 2012 and five adult males (LGE 4787–91)

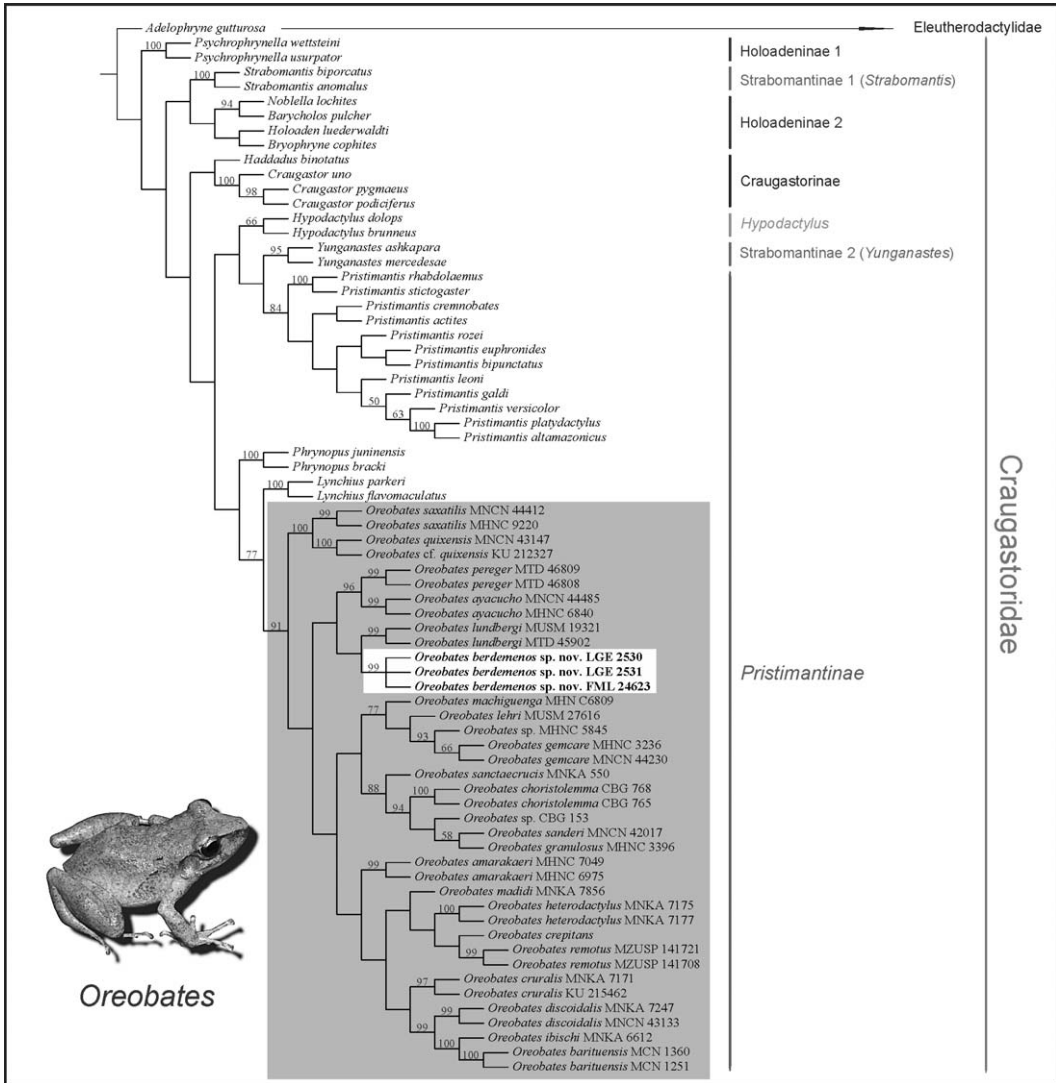


FIG. 1.—The most parsimonious tree of 12,651 equally weighted steps obtained using direct optimization in POY. Parsimony jackknife absolute frequencies support values on each node, calculated from the analysis of the static alignment. *Oreobates berdemenos* sp. nov. is shown in bold. The illustrated specimen is *O. discoidalis*.

TABLE 1.—Percentage of uncorrected *p*-distances of the 16S gene of *Oreobates* species most related to *O. berdemenos* sp. nov. (in bold) in the phylogenetic analysis.

Taxon (n)	1	2	3	4
<i>O. ayacucho</i> (2)	0.00			
<i>O. lundbergi</i> (2)	9.88–10.20	0.00		
<i>O. pereger</i> (2)	5.52–5.66	11.86–12.14	0.00	
<i>O. berdemenos</i> (3)	12.37	13.53–13.83	12.91–13.08	0.00

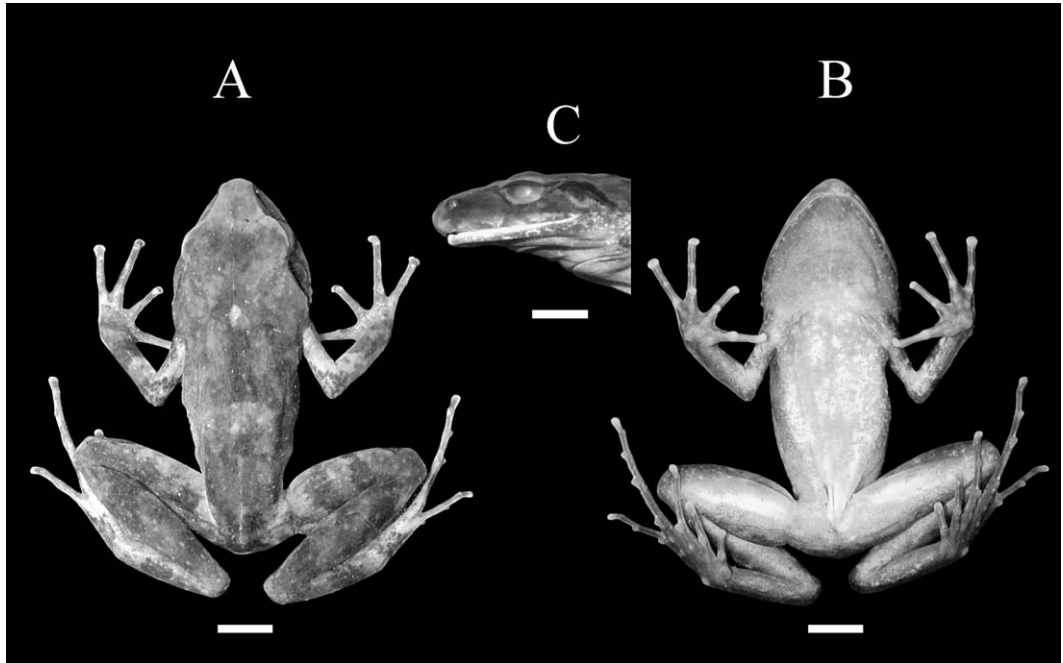


FIG. 2.—Dorsal view (A), ventral view (B), and profile (C), of *Oreobates berdemenos* sp. nov. adult female, SVL 34.7 mm (LGE 2530, holotype). Scale bar = 5 mm.

collected on 17 December 2012, by J.M. Ferro, M. Soliz, A. Taffarel, J. Grosso, and G. Navarro.

Paratypes.—Nine adult males (MACN 45592–600), an adult female (MACN 45603), and a juvenile (MACN 45589) collected on February 1968. Twenty-one adult males (MACN 45644–5, 45652, 45654–5, 45657, 45662, 45665, 45667–9, 45674–6, 45680–1, 45689, 45691–4) and seven adult females (MACN 45607, 45650, 45664, 45682–3, 45686, 45690) collected on October 1968. All the paratypes were collected in Abra de Cañas “Monolito,” 20 km SSE San Francisco along Ruta Provincial 83 (23°40′55″S, 64°54′06″W, 1722 m) at the western boundary of Parque Nacional Calilegua, Departamento Ledesma, Jujuy, Argentina, by A. Barrio.

Referred specimens.—Two adult males (MACN 45576–7) collected in Valle Grande (23°28′32″S, 64°56′32″W, 1609 m) and two adult males (MACN 45585, 45588), three adult females (MACN 45579, 45581, 45586), and four metamorphs (MACN 45578, 45582–4) collected en route to Valle Grande;

Departamento Ledesma, Jujuy, Argentina, on October 1967 by A. Barrio. Three adult males (MACN 45604–6) collected on 28 February 1968 en route from Rio Jordán to Valle Grande, Departamento Ledesma, Jujuy, Argentina, by F. Contino. Eleven adult males (MACN 45653, 45656, 45659–60, 45666, 45672–3, 45679, 45684–5, 45688), five adult females (MACN 45648, 45651, 45661, 45677, 45687), and six metamorphs (MACN 45643, 45647, 45658, 45663, 45670–1) collected on October 1968 at Abra de Cañas “Monolito,” 20 km SSE San Francisco along Ruta Provincial 83 (23°40′55″S, 64°54′06″W, 1722 m) at the western boundary of Parque Nacional Calilegua, Departamento Ledesma, Jujuy, Argentina, by A. Barrio. Two adult males (MACN 45608–9) and an adult female (MACN 45610) collected on October 1968 in Departamento Ledesma (1700 m), Jujuy, Argentina, by A. Barrio. Twenty-four adult males (MACN 45611–4, 45616–8, 45620, 45622, 45624, 45627–31, 45633–40, 45642), five adult females (MACN 45615, 45621, 45623, 45626, 45641), and three metamorphs (MACN 45619, 45625, 45632) collected on

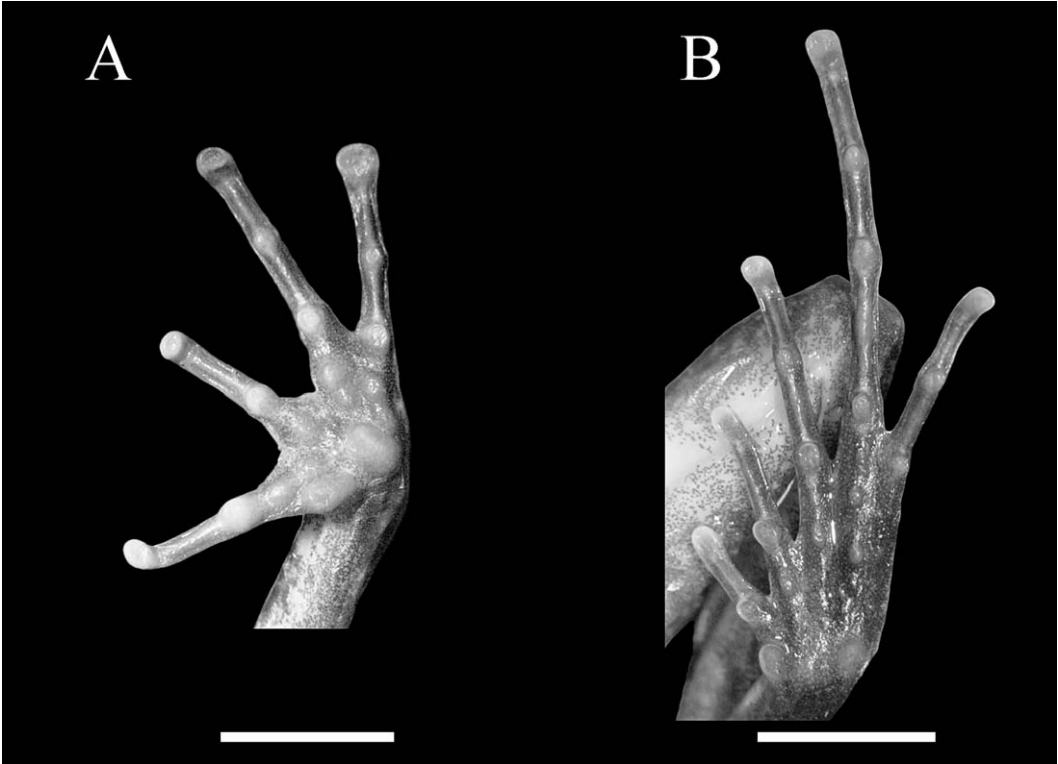


FIG. 3.—*Oreobates berdemenos* sp. nov. Ventral views of hand (A) and foot (B) of the holotype (LGE 2530). Scale bar = 5 mm.

October 1968 in Departamento Ledesma (1500 m), Jujuy, Argentina, by A. Barrio.

Diagnosis.—A species of *Oreobates*, characterized by: (1) small size (SVL ranges from 20.9–30.9 mm in males and from 30.1–40.0 mm in females; Table 2); (2) body slender; (3) head nearly as wide as long; (4) dorsal tegument smooth to finely shagreened; (5) eyelid smooth without tubercles; (6) short

dorsolateral fold; (7) discoidal fold incomplete, although there is an underlying pelvic lymphatic septum; (8) axillary glands present; (9) one or two post-rietal glands; (10) small, rounded, and unpigmented inguinal gland; (11) supratympanic fold well-developed; (12) ulnar tubercles absent; (13) relative length of Finger IV > II = V > III; (14) tips of Fingers IV and V slightly expanded, the remaining

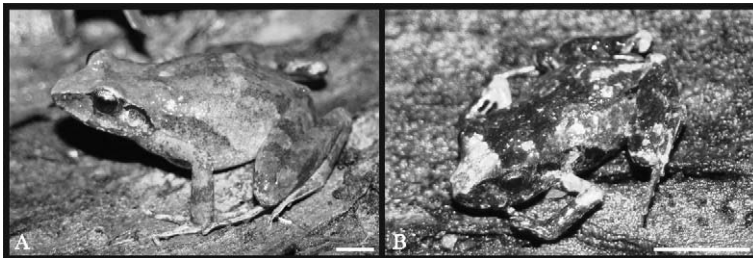


FIG. 4.—*Oreobates berdemenos* sp. nov. in life. (A) Adult female (LGE 2530, holotype). (B) Juvenile (LGE 2532, paratopotype). Scale bar = 5 mm.

unexpanded; (15) circumferential groove in fingers barely visible; (16) unguis flap in fingers present, but poorly defined; (17) lateral fringes or keels on fingers narrow and weak; (18) nuptial pad absent in males; (19) supernumerary tubercles on hands small but defined; (20) relative length of Toes IV > III > V > II > I; (21) basal webbing between toes poorly developed; (22) circumferential groove in toes barely visible; (23) unguis flap in toes present, but poorly evident; (24) lateral fringes on toes narrow and weak; (25) few, small supernumerary tubercles on foot; (26) ulnar tubercle absent; (27) vocal sacs in males indistinguishable externally; (28) Wolffian ducts fused anteriorly (sensu Taboada et al., 2013) in a single, common cloacal opening; (29) posterior dorsolumbar vein present; (30) medial dorsolumbar vein absent; and (31) posterior caval vein originates in the anterior third of kidneys.

The new species can be distinguished from all other nominal species of *Oreobates*, except for *O. pereger*, by the presence of an incomplete discoidal fold (absent in the abdominal region). The presence of a complete discoidal fold was described previously for *O. amarakaeri*, *O. gemcare*, *O. lehri*, *O. machiguenga* (Padial et al., 2012), *O. ayacucho* (Lehr, 2007; Duellman and Lehr, 2009), *O. barituensis* (Vaira and Ferrari, 2008), *O. choristolemma* (Harvey and Sheehy, 2005; Padial et al., 2008), *O. crepitans* (Bokermann, 1965), *O. cruralis* (Lynch, 1989; Padial et al., 2008; Duellman and Lehr, 2009), *O. discoidal* (Peracca, 1895), *O. granulatus* (Padial et al., 2008; Duellman and Lehr, 2009), *O. heterodactylus* (Miranda-Ribeiro, 1937; Padial and de la Riva, 2005; Padial et al., 2008), *O. ibischi* (Reichle et al., 2001; Padial et al., 2008), *O. lundbergi* (Lehr, 2005; Duellman and Lehr, 2009), *O. remotus* (Teixeira et al., 2012), *O. madidi* (Padial et al., 2005a), *O. quixensis* (Padial et al., 2008; Duellman and Lehr, 2009), *O. sanctaerucis* (Harvey and Keck, 1995; Padial et al., 2008), *O. sanderi* (Padial et al., 2005b, 2008), *O. saxatilis* (Duellman, 1990; Padial et al., 2008; Duellman and Lehr, 2009), and *O. zongoensis* (Reichle and Köhler, 1997; Padial et al., 2008). The incomplete discoidal fold of *O.*

TABLE 2.—Measurements (mm) of the adults of the type series of *Oreobates berdemenos* sp. nov. Values are reported as mean \pm 1 SD (range).^a

	Males (n = 40)	Females (n = 12)
SVL	26.69 \pm 2.5 (20.9–30.9)	35.23 \pm 3.6 (30.1–40.0)
EE	4.90 \pm 0.7 (3.4–6.0)	5.63 \pm 1.1 (3.2–6.7)
EL	3.27 \pm 0.6 (2.1–4.2)	4.07 \pm 0.6 (3.0–4.8)
EN	2.95 \pm 0.3 (2.1–3.6)	3.81 \pm 0.4 (3.2–4.3)
TYH	1.63 \pm 0.3 (1.1–2.1)	1.99 \pm 0.3 (1.6–2.4)
TYL	1.44 \pm 0.3 (0.9–1.9)	1.72 \pm 0.2 (1.5–1.9)
HL	9.27 \pm 0.8 (7.0–10.7)	11.47 \pm 0.7 (10.7–12.5)
HW	9.76 \pm 1.3 (6.8–11.4)	12.37 \pm 1.0 (10.9–13.5)
IND	2.46 \pm 0.4 (1.7–2.9)	3.03 \pm 0.3 (2.6–3.3)
FA	6.77 \pm 0.6 (5.0–7.7)	8.59 \pm 0.7 (7.6–9.4)
FL	13.92 \pm 1.5 (9.4–15.9)	18.43 \pm 1.1 (17.0–20.0)
TH	13.56 \pm 1.4 (9.3–15.8)	17.85 \pm 1.4 (16.0–19.3)
TL	14.31 \pm 1.5 (9.6–16.3)	18.82 \pm 1.2 (16.9–20.4)

^a SVL = snout-vent length; EE = eye-eye distance; EL = eye diameter; EN = eye to nostril distance; TYH = tympanic membrane height (vertical diameter); TYL = tympanic membrane length (horizontal diameter); HL = head length; HW = head width; IND = internarial distance; FA = arm length; FL = foot length; TH = thigh length (from vent to knee); and TL = tibia length.

pereger was described by Lynch (1975), and Duellman and Lehr (2009).

The small size of adults in *O. berdemenos* sp. nov. separates it from *O. saxatilis* (SVL = 50.6 mm in a male; 44.5–63.0 mm in females; Duellman, 1990) and possibly from *O. sanctaerucis* (SVL = 31.6 mm in only known male; 43.8 mm in only known female; Harvey and Keck, 1995).

The barely expanded fingertips of digits IV and V differentiate the new species from *O. barituensis* (Vaira and Ferrari, 2008; MOP, personal observation), *O. choristolemma* (Harvey and Sheehy, 2005; Padial et al., 2008), *O. crepitans* (Bokermann, 1965; Heyer and Muñoz, 1999; MOP, personal observation), *O. cruralis* (Reichle et al., 2001; Padial et al., 2008; Duellman and Lehr, 2009), *O. discoidal* (Peracca, 1895; MOP, personal observation), *O. granulatus* (Reichle et al., 2001), *O. heterodactylus* (Reichle et al., 2001; Padial et al., 2008; MOP, personal observation), *O. ibischi* (Reichle et al., 2001; Padial et al., 2008), and *O. remotus* (Teixeira et al., 2012), where the tips of Fingers IV and V are largely expanded.

The lack of nuptial pads on adult males separates *Oreobates berdemenos* sp. nov. from *O. ayacucho* (Padial et al., 2012), *O. barituensis* (Vaira and Ferrari, 2008; MOP, personal observation), *O. choristolemma* (Pa-

dial et al., 2008), *O. granulatus* (Padial et al., 2008; Duellman and Lehr, 2009), *O. heterodactylus* (Padial and de la Riva, 2005; Padial et al., 2008), *O. lundbergi* (Lehr, 2005; Duellman and Lehr, 2009), and *O. sanderi* (Padial et al., 2005b, 2008). There is some controversy concerning the character state in *O. discoidalis* (present according to Lynch, 1989; Reichle and Köhler, 1997; and observed by us; but absent according to Padial et al., 2008; Vaira and Ferrari, 2008) and in *O. ibischi* (absent, Reichle et al., 2001; Padial et al., 2008; present study). We observed that a male of *O. crepitans* (ZUEC 14115) lacks nuptial pads. The character state is unknown in *O. amarakaeri* and *O. machiguenga*.

A distinct tympanum, with horizontal diameter (TYL) less than 50% (range 36–48%) of eye length (EL), separates the new species from *O. amarakaeri* (TYL ranges from 50%–70% of EL; Padial et al., 2012), *O. crepitans* (TYL near 75% of EL; Bokermann, 1965; Padial et al., 2012), *O. discoidalis* (TYL ranges from 50%–75% of EL; Cei, 1980; Lynch, 1989; Padial et al., 2008), *O. heterodactylus* (TYL about 75% of EL; Padial et al., 2008), *O. ibischi* (TYL > 50% of EL; Reichle et al., 2001; Padial et al., 2008), *O. remotus* (TYL = 60% of EL in a paratype; Teixeira et al., 2012), *O. quixensis* (TYL = 60% of EL; Duellman and Lehr, 2009), and *O. saxatilis* (TYL \approx 75% of EL; Padial et al., 2008; Duellman and Lehr, 2009).

The smooth to finely shagreened dorsal skin texture differentiates *Oreobates berdemenos* sp. nov. from *O. choristolemma* (granular; Harvey and Sheehy, 2005; Padial et al., 2008), *O. granulatus* (granular; Boulenger, 1903; Padial et al., 2008; Duellman and Lehr, 2009), *O. quixensis* (granular; Padial et al., 2008; Duellman and Lehr, 2009), *O. lehr* (coarsely shagreened with enlarged keratinized granules; Padial et al., 2007; Duellman and Lehr, 2009); *O. madidi* (dorsum heavily warty; Padial et al., 2008), *O. sanctaerucis* (granular; Harvey and Keck, 1995; Padial et al., 2008), *O. sanderi* (granular; Padial et al., 2005b, 2008), *O. saxatilis* (granular; Duellman, 1990; Padial et al., 2008; Duellman and Lehr, 2009), and *O. zongoensis* (granular; Reichle and Köhler, 1997; Padial et al., 2008).

The presence of supernumerary tubercles on the hands separates the new species from *O. ayacucho* (absent; Lehr, 2007; Duellman and Lehr, 2009) and *O. pereger* (supernumerary tubercles absent or inconspicuous; Lehr and Aguilar, 2006; Padial et al., 2012).

Oreobates berdemenos sp. nov. differs from *O. pereger* by the lack of papillae on finger discs (present in *O. pereger*; Lehr and Aguilar, 2006; Duellman and Lehr, 2009). Furthermore, *O. berdemenos* has a clearly different ventral pattern with throat dark brown (throat yellowish orange in *O. pereger*; Lehr and Aguilar, 2006; Duellman and Lehr, 2009) and chest and belly cream mottled with brown (yellow with dark brown flecks in *O. pereger*; Lehr and Aguilar, 2006; Duellman and Lehr, 2009).

Description of holotype.—Head slightly wider than long; head width 34.9% SVL; snout rounded in dorsal and lateral views; tip of snout overlaps border of lower lip in lateral view; nostrils oval, located near the tip of the snout, slightly protuberant, laterally directed; canthus rostralis straight in dorsal view, nearly straight in profile; loreal region slightly concave, sloping gradually to the lips; lips not flared; upper eyelid smooth; eyes lateral (eye diameter 30.6% of head width); cranial crests absent; supratympanic fold evident; tympanic membrane and annulus distinct; tympanic membrane oval, tympanic ring slightly compressed laterally (vertical diameter larger than horizontal diameter), its horizontal diameter about half of eye length; two conical postrictal glands, posterior larger than anterior; choanae large, widely separated medially, nearly concealed by the palatal shelf of the maxillary arch in ventral view; tongue slightly longer than wide, posterior margin rounded, free posteriorly for about two thirds of length; vomerine dentigerous process large, oval, with four conical teeth, located posteriorly to choanae; vocal slits absent.

Ulnar tubercle absent; thenar tubercle oval; outer metacarpal tubercle oval, about two-thirds larger than inner; medium-sized, rounded and conical palmar supernumerary tubercles; subarticular tubercles of fingers conical, prominent. Fingers bearing narrow, keel-like lateral fringes; relative finger lengths: IV > II = V > III; fingertips rounded, with

the tips of Fingers IV and V barely expanded; unguis flap poorly developed, disc pad defined by a circumferential groove. Tarsus lacking tubercles; inner metatarsal tubercle oval, twice as long as outer metatarsal tubercle (rounded); plantar supernumerary tubercles small, oval shaped; subarticular tubercles conical; toes bearing narrow, keel-like lateral fringes, basal webbing; toes long and slender; toe tips rounded, Toe IV barely expanded distally, unguis flap and circumferential groove poorly developed; terminal knuckle evident; relative toe lengths $IV > III > V > II > I$.

Skin of dorsum and dorsal surfaces of limbs smooth, with scattered small glandular warts; flanks areolated; dorsum with a poorly defined V-shaped scapular fold, and dorsolateral folds composed by small warts; occipital fold absent; ventral skin smooth, with posterior abdominal region slightly granular; ventral surfaces of limbs smooth; discoidal fold incomplete; small, rounded axillary gland; small, rounded and unpigmented inguinal gland. Measurements (mm) of holotype are: SVL 34.7; HL 11.6; HW 12.1; EL 3.7; EN 3.5; IND 2.9; EE 5.6; TYH 2.1; TYL 1.8; FA 9.1; FL 18.4; TH 17.8; TL 18.7.

Variation.—Sexual dimorphism is evident, as males bear vocal slits and are noticeably smaller (20.9–30.9 mm) than females (30.1–40.0 mm). Color pattern is highly variable. Dorsally, it varies from marbled light brown to uniformly dark brown. Ventrally, specimens vary from beige with marbled grey to dark brown. Ten paratypes show a complete vertebral line while in eight there is only a partial line extending medially from the sacral region to the vent. Twenty-six paratypes do not show an evident dorsolateral fold, but this may be an artifact of preservation. Axillary glands are apparently absent in 10 paratypes and barely visible in the other 16. There are notable ontogenetic changes of coloration in the dorsal pattern (see below), but these are not apparently associated with sex or the reproductive condition of the specimens.

Color in life.—In adults, dorsal coloration ranges from brown to reddish-brown, with large irregular, diffuse, dark brown and yellowish blotches in the interocular and scapular regions (holotype and juvenile para-

topotype shown in Fig. 4). A thin vertebral line extends from the tip of the snout to the vent; sacral region with a rectangular light blotch, flanked by two lateral dark spots. Diffuse dark brown transversal bars on upper side of arms and thigh and exposed surfaces of shank and foot; hidden surface of thigh light brown with sparse and irregular creamy mottling. In lateral view, head with poorly defined dark brown labial spots; supratympanic fold black; upper region of tympanic membrane dark ochre; lateral surface of body with a large dark oblique lateral stripe. Ventral surface of head dark brown, mottled with cream, especially along the mandibular arch; belly, chest, and ventral surface of limbs cream mottled with brown; surface of hands and feet dark brown with gray tubercles. The dorsal color of juveniles is similar to that of adult specimens, though they have evident yellowish spots on frontal region of head, arm, elbow, distal region of forearm, heel, and urostilar region. The ventral region of juveniles is whitish and uniformly spotted with black.

Etymology.—The specific name *berdemenos*, meaning “muddled” or “confused,” is a Greek adjective used in reference to the misidentification of the new species in herpetological collections as *Oreobates discoidalis*.

Distribution and habitat.—In addition to the type locality (Fig. 5), the new species was also collected at several nearby localities within Departamento Ledesma, Jujuy, Argentina. Except for Abra de Cañas “Monolito” on Ruta Provincial 83 at the western boundary of Parque Nacional Calilegua and Valle Grande, these localities are vaguely referred to as collecting points along transects between Parque Nacional Calilegua and Valle Grande (Fig. 6; see *Referred specimens* section).

At the type locality, specimens of *Oreobates berdemenos* sp. nov. were collected during the day, being found inactive under rocks on an abrupt slope in the wet eastern foothills of Calilegua hills (part of the geological Province “Sierras Subandinas”). This range represents the first appearance of the Andes after the extensive chaco-paranaense lowlands. This orographic barrier to the humid winds of the Atlantic permits the establishment of jungles and rain forests on its eastern slopes, known

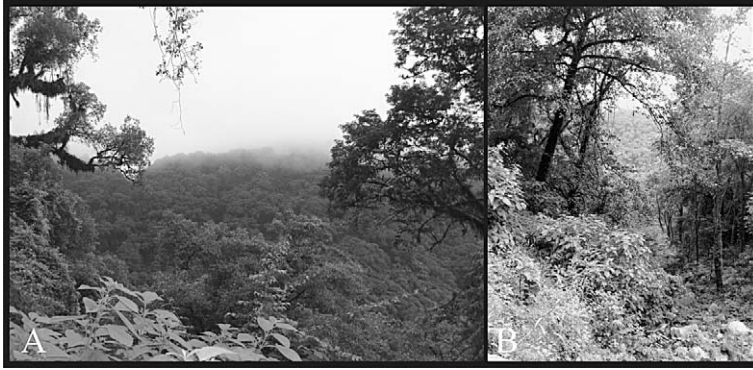


FIG. 5.—General view of habitat (A) and microhabitat (B) of *Oreobates berdemenos* in the type locality Abra Colorada, Jujuy, Argentina.

locally as “Selva tucumano–boliviana” or “Yungas” (Hauman, 1931; Cabrera, 1994). These mountains form the western boundaries of Parque Nacional Calilegua. Within the Neotropical region, the area is included in the Amazon Domain, Yungas Province, and District of Montane Forests (Cabrera, 1994). The altitudinal gradient includes “Cloud Forest” from 1200–2500 m asl. These forests are replaced near the peaks with cloud or montane grasslands, resulting in a landscape of high structural heterogeneity including forests in different successional stages, pastures and lawns, with varying degrees of anthropic pressure (Brown, 1995; Arturi et al., 1998; Grau and Veblen, 2000). At its lower

limits, this cloud forest is replaced by montane rainforest from 550–1200 m asl (Cabrera, 1994).

DISCUSSION

Taxonomy and Phylogenetic Relationships of Oreobates berdemenos sp. nov.

Although this study was designed to describe the phylogenetic position of *Oreobates berdemenos* and not to test phylogenetic hypotheses of Craugastoridae (e.g., Hedges et al., 2008; Heinicke et al., 2009; Pyron and Wiens, 2011), the intergeneric relationships obtained here are similar to the most-inclusive analyses (Pyron and Wiens, 2011; Canedo and

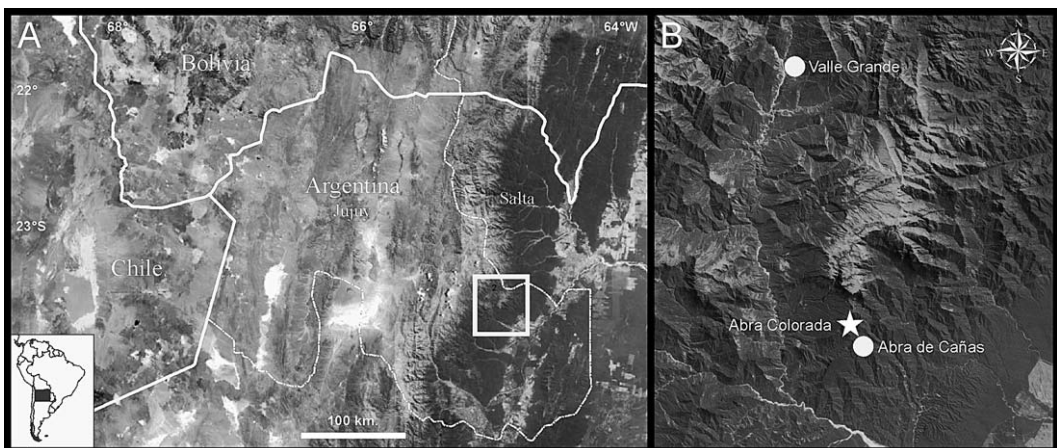


FIG. 6.—Geographic distribution of *Oreobates berdemenos*. (A) Northwest portion of Argentina (inset = South America); the study area is marked. (B) Map showing known localities of *Oreobates berdemenos* sp. nov. (Star = type locality).

Haddad, 2012; Padial et al., 2012). Thus, we found the original Strabomantidae paraphyletic with respect to Craugastoridae, as was recovered in the phylogenetic analysis of Pyron and Wiens (2011). Furthermore, *Yunganastes* was recovered as the sister taxon of *Pristimantis*, supporting the results of Canedo and Haddad (2012) and Padial et al. (2012).

Oreobates was recovered as monophyletic and as the sister group of *Lynchius*, in agreement with the results of Pyron and Wiens (2011) and Canedo and Haddad (2012). Padial et al. (2012:44) noted this relationship in the text but, in their schematic maximum-likelihood tree showing the intergeneric relationships (Fig. 1 of Padial et al., 2012), the sister clade of *Oreobates* is not *Lynchius* but *Phrynomys*.

Recently, *Oreobates* has undergone several changes in its composition, with several new species described since it was resurrected by Caramaschi and Canedo (2006). Although *O. berdemenos* is morphologically similar to other *Oreobates* and shares the typical features of this genus (e.g., cranial crests absent; smooth ventral skin; inguinal glandular pads present; nuptial pads absent, and vocal sac absent or poorly developed in males), it can be confidently assigned to this genus only in the context of a molecular phylogenetic analysis because no morphological synapomorphies exist to support its placement (Padial et al., 2012). The new species was recovered deeply nested in a well-supported *Oreobates* clade and poorly supported as the sister taxon of a geographically distant species, *O. lundbergi*, from which it can be easily differentiated morphologically (see *Diagnosis*) and by a relatively high genetic divergence (Table 1).

Oreobates crepitans, a species not included in previous phylogenetic analyses, is nested in a poorly supported clade (<50%) comprising the species that inhabit dry forests on the Brazilian shield—*O. heterodactylus* and *O. remotus*. This result supports the inclusion of this species in *Oreobates* by Padial et al. (2012). Morphologically these species are characterized for having the fingertips of Fingers IV and V greatly expanded. This condition could represent a putative synapomorphy of this clade.

As expected, the recovered phylogenetic relationships within *Oreobates* are generally similar to those obtained by Padial et al. (2012) because only two species, and relatively few sequences, were included in addition to that analysis. Two exceptions are *O. amarae* and *O. cruralis*, which appear in different positions in both analyses although with weak support. Moreover, although some supraspecific relationships are well supported (e.g., [*O. saxatilis* + *quixensis*], [*O. ibischi* + *O. discoidalis* + *O. barituensis*]), most of the recovered clades are poorly supported in both analyses, suggesting that our knowledge about the phylogenetic relationships of *Oreobates* is still incomplete. A thorough dataset of mitochondrial and nuclear genes is necessary to test the supraspecific relationships in *Oreobates*, and this would be fundamental to understanding the evolution of some phenotypic characters in this group.

The genus *Oreobates* in Argentina

Apart from the species described here, three additional species of *Oreobates* have been reported from Argentina. *Oreobates discoidalis* was described as *Hylodes discoidalis* Peracca, 1895, based on several specimens (syntypes MZUT 427) collected by A. Borelli in Tucumán between 1893 and 1894. More recently, Cei (in Gavetti and Andreone, 1993) designated the specimen MZUT An. 427.1 as the lectotype (Fig. 7A–C). This species has been repeatedly recorded from numerous localities in Tucumán, Salta, and Jujuy provinces (e.g., Cei, 1980; Laurent, 1980; Vaira, 2002).

Oreobates cruralis was reported from Calilegua, Jujuy, Argentina, by Cei (1987; as *Eleutherodactylus cruralis*) based on a personal communication by E.O. Lavilla referring to specimens housed in the Natural History Museum, The University of Kansas (identified by J.D. Lynch and D.C. Cannatella). However, Lynch (1989) subsequently modified his earlier opinion, and Lavilla and Cei (2001) considered all records of *O. cruralis* from Argentina to be referable to *O. discoidalis*.

Oreobates barituensis was described by Vaira and Ferrari (2008) on the basis of material from several localities bordering Parque Nacional Baritú, Salta, Argentina.

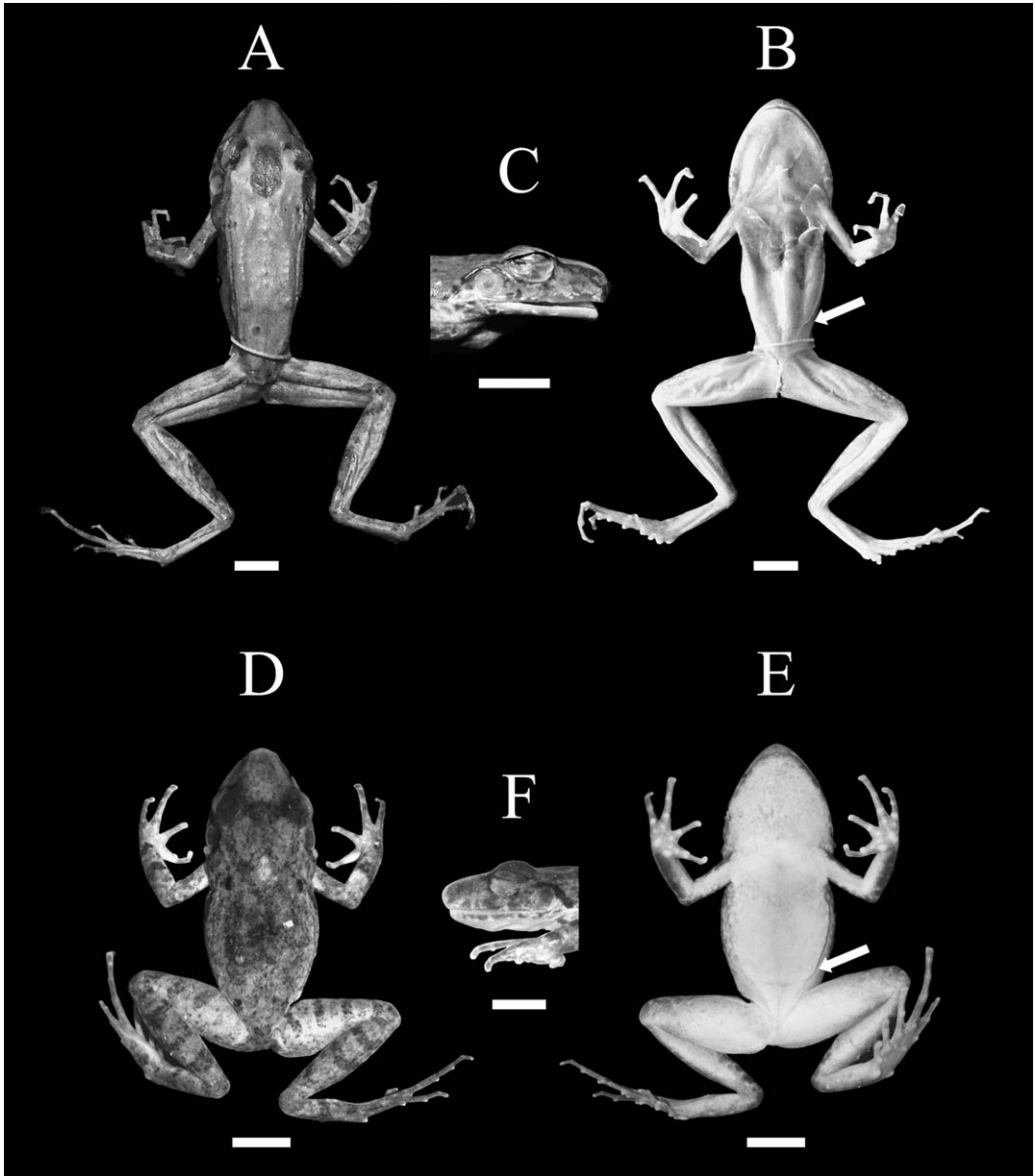


FIG. 7.—Dorsal (A, D), ventral (B, E), and lateral views of the heads (C, F) of the lectotype of *Oreobates discoidalis* (MZUT An. 427.1, A–C) and holotype of *O. barituensis* (FML 21079, D–F). Arrows in Figs. B and E indicate the complete discoidal fold. Scale bar = 5 mm.

The authors differentiated it from *O. discoidalis* by the shape of the head, size of the tympanum, and occurrence of a nuptial pad on the thumb. We examined specimens of *O. discoidalis* from Tucumán but observed no obvious differences with *O. barituensis* (i.e.,

holotype Fig. 7D–F, paratypes, and many specimens from Tucumán; see Appendix II). As no voucher specimens of *O. discoidalis* were cited by Vaira and Ferrari (2008), the identity of the specimens determined as *O. discoidalis* used in that comparison cannot be

verified. Vaira and Ferrari (2008) and Akmentins (2011) indicated that the composition and frequency of the advertisement calls of *O. barituensis* and *O. discoidalis* are different. The voucher specimens identified as *O. discoidalis* (MCN 191 and 361) by Ferrari and Vaira (2008), and reproduced by Vaira and Ferrari (2008), are not from the type locality of *O. discoidalis* but from Abra de Cañas, Parque Nacional Calilegua, Jujuy, Argentina (23°40'35"S, 64°53'49"W), a locality approximately 1 km to the type locality of *O. berdemenos*. Our examination of this material confirmed that it does not correspond to *O. berdemenos* but neither can we confidently ascribe them to *O. discoidalis* sensu stricto.

Akmentins (2011) reported the advertisement, territorial, and aggressive calls of *O. discoidalis* and *O. barituensis*. He recorded several individuals from five different localities in Salta and Jujuy but does not refer these to any voucher specimen, making it impossible to assess their taxonomic identity. In addition, Akmentins et al. (2012) recorded specimens assigned to *O. barituensis* from Ruta Provincial 340, between Las Tipas and San Javier, Tucumán. This location is approximately 15 km from the type locality of *O. discoidalis*, and the specimens recorded (FML 24683–5) are indistinguishable from the lectotype and one of the paralectotypes (MZUT An427.2 [lectotype] of *O. discoidalis*).

The character states that Vaira and Ferrari (2008) assigned to *O. discoidalis* to differentiate it from *O. barituensis* are evident neither in the examined type specimens of *O. discoidalis* nor in specimens from Tucumán. Thus, a thorough revision of *O. discoidalis* and *O. barituensis* along its entire distribution range, considering morphological, bioacoustical, and molecular data, is desirable to assess the taxonomic status of these species.

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APPENDIX I
Species Analyzed in the Phylogenetic Analysis

GenBank accession numbers for the sequences employed in the phylogenetic analysis. Species in bold are those for which we provide original sequences. CytB = cytochrome b; RAG1 = recombinase activation; TYR = tyrosinase.

Species	Voucher	12S	16S	CytB	RAG1	TYR
<i>Adelophryne gutturosa</i>	ROM 39578	EU186679		GQ345201	EU186751	EU186772
<i>Barycholos pulcher</i>	KU 217781	EU186727	EU186709	—	EU186744	EU186765
<i>Bryophryne cophites</i>	KU 173497	EF493537		—	EF493423	EF493508
<i>Craugastor pygmaeus</i>	UTA-A 55241	EF493711		—	EF493451	EF493479
<i>Craugastor podiciferus</i>	MVZFC 13463	EF493360		GQ345197	EF493450	EF493481
<i>Craugastor uno</i>	AMCC 118080	EU186673		—	EU186748	EU186769
<i>Haddadus binotatus</i>	USNM 303077	EF493361		GQ345198	EF493397	—
<i>Holoaden luederwaldti</i>	MZUSP 131872	EU186728	EU186710	—	EU186747	EU186768
<i>Hypodactylus brunneus</i>	KU 178258	EF493357		GQ345203	EF493422	EF493484
<i>Hypodactylus dollops</i>	No voucher	EF493394		—	EF493414	EF493483
<i>Lynchius flavomaculatus</i>	KU 218210	EU186667		—	EU186745	EU186766
<i>Lynchius parkeri</i>	KU 181307	EU186705		—	—	—
<i>Noblella lochites</i>	KU 177356	EU186699		—	EU186756	EU186777
<i>Oreobates amarakaeri</i>	MHNC 6975	—	JF809996	—	—	—
	MHNC 7049	—	JF809998	—	—	—
<i>Oreobates ayacucho</i>	MHNC 6840	—	JF809971	—	—	—
	MNCN 44485	—	JF809972	—	—	—
<i>Oreobates barituensis</i>	MCN 1251	—	JF810001	—	—	—
	MCN 1360	—	JF810000	—	—	—
<i>Oreobates berdemenos</i> sp. nov.	LGE 2530	—	KJ125507	KJ125511	—	—
	LGE 2531	—	KJ125508	—	—	—
	FML 24623	—	KJ125509	—	—	—
<i>Oreobates choristolemma</i>	CBG 768	—	EU368895	—	—	—
	CBG 765	FJ539072	FJ539067	—	—	—
<i>Oreobates crepitans</i>	ZUEC 14119	—	KJ125510	KJ125512	—	—
<i>Oreobates cruralis</i>	KU 215462	EU186666		—	EU186743	EU186764
	MNKA 7171	—	EU192295	EU368881	—	—
<i>Oreobates discoidalis</i>	MNCN 43133	FJ539073	FJ539068	—	—	—
	MNKA 7247	—	EU192254	EU368883	—	—
<i>Oreobates gemcare</i>	MHNC 3223–37	—	JF809952	—	—	—
	MNCN 44230	—	JF809961	—	—	—
<i>Oreobates granulosus</i>	MHNC 3396	FJ539074	EU368897	—	—	—
<i>Oreobates heterodactylus</i>	MNKA 7175	FJ438816	FJ438805	EU368886	—	—
	MNKA 7177	—	EU368898	EU368885	—	—
<i>Oreobates ibischi</i>	MNKA 6612	FJ438817	FJ438806	—	—	—
<i>Oreobates lehri</i>	MUSM 27616	—	JF809957	—	—	—
<i>Oreobates lundbergi</i>	MTD 45902	—	JF809958	—	—	—
	MUSM 19321	—	JF809959	—	—	—
<i>Oreobates machiguenga</i>	MHNC 6809	—	JF809969	—	—	—
<i>Oreobates madidi</i>	MNKA 7856	FJ539075	FJ539070	EU368887	—	—
<i>Oreobates pereger</i>	MTD 46808	—	JF809955	—	—	—
	MTD 46809	—	JF809956	—	—	—
<i>Oreobates quixensis</i>	MNCN 43147	—	EU192297	EU368889	—	—
<i>Oreobates</i> cf. <i>quixensis</i>	KU 212327	EU186726	EU186708	—	EU186742	EU186763
<i>Oreobates remotus</i>	MZUSP 141708	—	JN688273	JN688276	—	—
	MZUSP141721	—	JN688275	JN688278	—	—
<i>Oreobates sanctaecrucis</i>	MNKA5507	—	JF809951	—	—	—
<i>Oreobates sanderi</i>	MNCN42017	—	EU368904	EU368891	—	—
<i>Oreobates saxatilis</i>	MHNC9220	—	JF809985	—	—	—
	MNCN44412	—	JF809965	—	—	—
<i>Oreobates</i> sp.	CBG153	—	EU368903	—	—	—
	MHNC5845	—	JF809995	—	—	—
<i>Phrynopus bracki</i>	USNM 286919	EF493709		GQ345202	EF493421	EF493507
<i>Phrynopus juninensis</i>	MTD 44759	AM039728	AM039660	—	—	—
<i>Pristimantis actites</i>	KU 217830	EF493696		—	EF493432	EF493494
<i>Pristimantis altamazonicus</i>	KU 215460	EF493670		—	EF493441	EU186778

APPENDIX I
Continued.

Species	Voucher	12S	16S	CytB	RAG1	TYR
<i>Pristimantis bipunctatus</i>	KU 291638		EF493702	—	EF493430	EF493492
<i>Pristimantis cremnobates</i>	KU 177252		EF493528	—	EF493424	EF493486
<i>Pristimantis euphronides</i>	BWMC 6918		EF493527	—	EF493427	EF493489
<i>Pristimantis galdi</i>	QCAZ 32368		EU186670	—	EU186746	EU186767
<i>Pristimantis leoni</i>	KU 218227		EF493684	—	EF493433	EF493495
<i>Pristimantis platydactylus</i>	MNCN-DNA 9484	—	EU368902	EU368880	—	—
<i>Pristimantis rhabdolaemus</i>	AMNH-A 165195		AY843586	—	—	AY844035
<i>Pristimantis rozei</i>	No voucher		EF493691	—	EF493429	EF493491
<i>Pristimantis stictogaster</i>	KU 291659		EF493704	—	EF493445	EF493506
<i>Pristimantis versicolor</i>	KU 218096		EF493389	—	EF493431	EF493493
<i>Psychrophrynella usurpator</i>	KU 173495		EF493714	GQ345205	EU186762	EU186780
<i>Psychrophrynella wetsteini</i>	KU 183049		EU186696	—	EU186755	EU186776
<i>Strabomantis anomalus</i>	KU 177627		EF493534	—	EF493447	—
<i>Strabomantis biporcatus</i>	CVULA 7073		EU186691	GQ345204	EU186754	EU186775
<i>Yunganastes ashkapara</i>	ZFMK 70318	FJ438807	FJ438796	—	—	—
<i>Yunganastes mercedesae</i>	ZFMK 72572	FJ539071	FJ539066	—	—	—

APPENDIX II

Specimens Examined

Oreobates barituensis.—ARGENTINA: Salta: Departamento Santa Victoria: Baritú, FML 21079 (holotype), FML 21077–8, 21080 (paratypes); Quebrada “El Lapachar,” in close proximity to Río Sidras, Parque Nacional Baritú, MACN 40528, 45697–703; Tucumán: Departamento Tafí Viejo: Ruta Provincial 340 between Las Tipas and San Javier, FML 24683–5.

Oreobates crepitans.—BRAZIL: Mato Grosso: Cuiabá, São Vicente, MZUSP 85628 (holotype), ZUEC 14114–5, 14119.

Oreobates discoidalis.—ARGENTINA: Jujuy: Departamento Ledesma: Abra de Cañas, Parque Nacional Calilegua, MCN 191, 361. Tucumán: Tucumán, MZUT An427.1 (lectotype), MZUT An427.2 (paralectotype); Departamento Lules: Lules, Finca Nougues, LGE 1330, 6204–5; Ruta Provincial 341 near to Lules, LGE 2537–42. Departamento Tafí Viejo: Río de la Hoyada, FML 7330–1; Departamento Yerba Buena: Horco Molle, FML 1895, 3692, 4405, 4533, MACN 13728–37; San Javier, FML 2628, 5498; Sierra de San Javier, FML 462.

Oreobates heterodactylus.—BRAZIL: Mato Grosso: Gruta da Fazendinha, Cáceres, MNRJ 106 (holotype).