



## A relict new species of *Oreobates* (Anura, Strabomantidae) from the Seasonally Dry Tropical Forests of Minas Gerais, Brazil, and its implication to the biogeography of the genus and that of South American Dry Forests

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### Abstract

A new species of *Oreobates* is described from Cavernas do Peruaçu National Park, Januária, Minas Gerais state, in the Atlantic Dry Forests of Brazil. The new species is distinguished from all other *Oreobates* by having the following combination of characters: large tympanum, discs broadly enlarged and truncate on Fingers III and IV, smooth dorsal skin, nuptial pads absent, snout subacuminate, and a very short pulsatile (2–3 pulses) single-noted advertisement call with dominant frequency of about 3150 Hz, and no harmonic structure. Molecular phylogenetic analyses using partial sequences of the mitochondrial genes cytochrome *b* (cyt *b*) and 16S using multiple outgroups recovered the new species within *Oreobates* and sister to *O. heterodactylus*. The latter species inhabits the Dry Forests of Mato Grosso (Cerrado) and Bolivia (Chiquitano forests), and is strictly associated to these habitats, which suggests a preterit connection between Chiquitano and Atlantic Dry Forests. The discovery of a new *Oreobates* in the Atlantic Dry Forest is of great importance for the conservation of these dry forests, as it is known only from this type of habitat.

**Key words:** Peruaçu valley, Pandeiros River, Terrarana

### Introduction

The distribution patterns of species with physiological restrictiveness to certain kinds of habitats are always of great importance to understanding the biogeographic history of those habitats because of the common history they share (Croizat 1964). Habitat range and connectivity are affected by environmental changes, such as those promoted by climatic fluctuations, resulting generally in species dispersal or isolation, leading ultimately to speciation (Lomolino *et al.* 2006). Therefore phylogenetic relationships among species occurring in different and/or same habitats can inform us about the history of habitats (Crisci *et al.* 2003; Morrone 2009).

Frogs of genus *Oreobates* seem to be habitat-specialists. Most of its 16 species are restricted to Yungas montane forests from the eastern versant of the Cordillera Oriental of the Andes, from northern Argentina to Ecuador. However one species, *O. quixensis*, is an eminently Amazonian lowland dweller that occurs throughout the Upper Amazon Basin, from Colombia to Bolivia. All but one species of *Oreobates* occur in the Andes or close to them in the adjacent Amazonian lowlands. The exception is *O. heterodactylus*, an inhabitant of Cerrado and Chiquitano forests in eastern Bolivia and western Brazil (see Padial & De la Riva 2005; Padial *et al.* 2008a; Duellman & Lehr 2009).

The taxonomy of *Oreobates* has been in constant change since its description, and only recently has a molecular phylogenetic approach been used to infer relationships among its species closely related genera (Hedges *et al.* 2008; Padial *et al.* 2008a; Padial *et al.* 2009; Pyron & Wiens 2011). The genus *Oreobates*, and its type species, *Oreobates quixensis*, were originally described by Jiménez de la Espada (1872) and placed in the family Cystignathidae. A few years later, Boulenger (1882) recognized *Oreobates* as a junior synonym of *Borborocoetes* Cope, 1865. At the end of the 19<sup>th</sup> Century, *Cystignathus* was recognized as a junior synonym of *Leptodactylus*, and *O. quixen-*

*sis* was then placed in Leptodactylidae (Werner 1896). Peters (1955) placed it into the synonymy of *Eusophus* Fitzinger, 1843, where it remained until Lynch and Schwartz (1971) relocated *O. quixensis* to *Ischnocnema* Reinhardt and Lütken, 1862, rendering *Oreobates* a junior synonym of *Ischnocnema*. About 35 years later Caramaschi and Canedo (2006), in their morphological taxonomic reassessment of the genera *Ischnocnema* and *Oreobates*, resurrected *Oreobates* and relocated *I. saxatilis*, *I. sanctaecrucis*, *I. sanderi*, *I. simmonsii* and *I. choristolemma* (by implication) to *Oreobates*. One year later, a molecular phylogenetic study on the once eleutherodactyline frogs, found large, deeply rooted radiations of geographically isolated groups within New World direct-developing frogs (Heinicke *et al.* 2007), which led to a preliminary reorganization of the taxonomy of eleutherodactyline frogs. However, *Oreobates* was not affected by any taxonomic change. On the following year, a morphological and molecular study on *Oreobates* revealed that *Eleutherodactylus cruralis*, *E. discoidalis*, *E. granulosus*, *E. heterodactylus*, *E. ibischi*, *E. lehri*, *E. madidi*, and *E. zongonensis*, clustered together in a clade also containing *O. quixensis*, *I. choristolemma*, *I. sanctaecrucis*, *I. sanderi*, *I. saxatilis*, and *I. simmonsii* (Padial *et al.* 2008a). The genus *Oreobates* was therefore redefined accordingly to include the aforementioned species. That same year a large molecular phylogenetic assessment on eleutherodactyline frogs proposed the name *Terrarana* for a Neotropical group harboring terrestrial breeding frogs with direct development (equivalent to Frost's *et al.* [2006] *Brachycephalidae*) (Hedges *et al.* 2008). Hedges *et al.* (2008) supported Padial *et al.* (2008a) hypothesis and kept *Oreobates* as it was but added *E. pereger*. Finally, that same year a new species, *O. barituensis*, was described from Baritú, Santa Victoria Department, Salta province, Argentina (Vaira & Ferrari 2008), and *Oreobates* achieved the taxonomic content recognized today.

Following Padial *et al.* (2008a) phylogenetic hypothesis for *Oreobates* intrageneric relationships, *O. heterodactylus* originated from Andean ancestor that dispersed throughout the adjacent lowlands, reaching the current Bolivian-Brazilian border (Miranda Ribeiro 1937; Padial & De la Riva 2005), an area now covered by Seasonally Dry Tropical Forest (SDTF) or Chiquitano forests.

These SDTFs ecoregion lies within the Tropical Dry Forest biome (*sensu* Olson *et al.* 2001), within which the Brazilian Atlantic Dry Forest (ADF) ecoregion also occurs, forming a N-S oriented stripe between Brazilian Cerrado and Caatinga. Those dry forests are composed of deciduous and semideciduous arborescent vegetation, that are lower, more open, and poorer in woody species when compared to Rain Forests (Murphy & Lugo 1986; Oliveira-Filho & Ratter 2002). They are found on rich soil, where annual rainfall is less than 1600 mm, and there are at least 5–6 dry months per year (*i.e.* months with rainfall less than 100 mm) (Pennington *et al.* 2000).

SDTFs are among the most endangered tropical environments (Janzen 1988). About 97% of its coverage is in danger and more than a half of these kind of environments are located in South America (Miles *et al.* 2006). In the Neotropics the Rain Forest are the environments that have historically been main targets of biological studies and conservations efforts, leaving less studied environments, such as the dryer ones, with their biotic content virtually unknown and unprotected (Janzen 1988; Redford *et al.* 1990; Sánchez-Azofeifa *et al.* 2005). Within the Brazilian territory only a large patch of SDTFs at Goiás state has been herpetologically surveyed, however it was focused only in lizards (Werneck & Colli 2006).

In Brazil one of the few protected remnant areas covered predominantly with SDTFs is the Peruaçu river valley region (Silva 2001), which harbors a National and a State Park. Although this region is considered a priority for conservation (MMA 2000; Tabarelli & Silva 2003), and is especially important for conservation of the herpetofauna (MMA 2000), the only reptiles and amphibians records from this area are those resulting from surveys for the National Park management plan (Feio 2003).

Feio (2003) in his herpetological survey at Cavernas do Peruaçu National Park recorded a species which he attributed at that time to *Eleutherodactylus*, and which he considered as “certainly new species”. However under the current *Terrarana* taxonomy, and in the light of molecular data we recognize this as a *Oreobates* species. Herein, on the basis of a series of specimens obtained during an extensive herpetofaunal survey at this area, we describe this new species, its advertisement call, and some aspects of its natural history. On the basis of a molecular analysis of mitochondrial genes we also investigate its phylogenetic placement within *Oreobates* and discuss the biogeography of the genus and its implication to SDTFs biogeography.

## Material and methods

**Morphological assessment and distribution.** Morphometric terminology follows a combination of Duellman and Lehr (2009) and Padial *et al.* (2008a) measurements (only adults and sub-adults were measured), and morphological

descriptions follow Padial *et al.* (2008a). Measurements were taken with an electronic caliper after fixation to the nearest 0.1 mm. Observations of morphological characters were performed with a stereomicroscope Zeiss STEMI SV6. Measurements taken were: snout-vent length (SVL); tibia length, from knee to heel (TL); thighs length, measured from mid-cloaca to knee (THL); foot length, measured from proximal end of inner metatarsal tubercle to tip of fourth toe (FL); head length, from tip of snout to posterior end of jaw (HL); head width, the distance between posterior ends of jaw (HW); internarinal distance (IND); eye-eye distance, the distance between anterior corner of eyes (EE); eye-nostril distance, from anterior corner of eye to nostril (EN); eye diameter, horizontal distance between anterior and posterior corners of eyes (ED); tympanum diameter, measured from the edges of tympanic annulus (TD).

Comparisons with other species were based on the original and/or secondary descriptions of those species (Lynch 1975; Padial & De la Riva 2005; Padial *et al.* 2008a; Padial *et al.* 2008b; Duellman & Lehr 2009), holotype pictures from original publications, and comparison of the following voucher specimens housed in Museu de Zoologia da Universidade de São Paulo: *Oreobates discoidalis*, Horco Molle, Tucumán province, Argentina (MZUSP 85542); *Oreobates cruralis*, Sara, Santa Cruz province, Bolivia (MZUSP 119467); *Oreobates heterodactylus*, Fazenda Santa Edwiges, Mato Grosso state, Brazil (MZUSP 71103, 71104).

Records on maps were compiled from the literature (Jiménez de la Espada 1872; Lynch 1975; Duellman 1990; Heyer & Gascon 1995; Alonso & Dallmeier 1998; Doan & Arriaga 2002; Cisneros-Heredia 2003; Pérez *et al.* 2004; Harvey & Sheehy 2005; Padial & De la Riva 2005; Vaira & Ferrari 2008; Ferrari & Vaira 2008; Padial *et al.* 2008a; Padial *et al.* 2008b; Akmentins & Vaira 2009; Duellman & Lehr 2009; UHESA 2011), online databases (GBIF 2011), and vouchers from Museu de Zoologia da Universidade de São Paulo (MZUSP). Redundant records were removed.

**Bioacoustics.** Calls were recorded with sampling rate of 44.1 kHz and 16 bit of resolution, with a Panasonic portable digital audio recorder model RR-US450, using its built-in microphone with recording frequency up to 7 kHz in a mono channel. Audio analysis and generation of audiospectrogram and oscillograms were performed with Sound Ruler v. 0.9.6 software (Gridi-Papp 2007). Air temperatures were taken with quick-reading Miller and Weber Inc. thermometer, model T-6000.

**Field sampling methods.** Specimen collection was made primarily through pitfall traps with drift fences installed throughout the main habits at Cavernas do Peruaçu National Park: 15 on dry forest habitats; 15 on savanna; 17 on the “carrascos” and two on riparian evergreen forest, which remained opened along across January 2008 and 2009 (rainy seasons), and July 2008 and 2009 (dry seasons). Unquantified active search was also performed at areas unsuitable to pitfall installation. Collected individuals were sacrificed with lethal doses of anesthetics, fixed in 10% formalin, preserved in 70% ethanol, and housed at Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

**Phylogenetic analysis.** Partial sequences of the mitochondrial cytochrome *b* (cyt *b*) and 16S genes of the holotype and two paratypes of the new species were obtained. Protocols for DNA extraction, amplification, sequencing, and sequence editing followed Amaro *et al.* (2009). The mitochondrial genic fragments were amplified with primers CB1-L and CB3-H for cyt *b* and 16SAR and 16SBR for 16S (Palumbi 1996). (GenBank accession numbers: JN688273-JN688278).

Sequences were edited in CodonCode Aligner (CodonCode Corporation) and aligned with MEGA 5 (Tamura *et al.* 2011). The matrix of 328 bp of aligned sequences of cyt *b* showed no indels. The alignment of 16S was made based on secondary structure and resulted in a matrix of 529 bp. Both data set were combined in a matrix of 857 bp and 20 terminals, including own sequences and sequences from Padial *et al.* (2008a) that includes species of Strabomantinae genera (*Oreobates*, *Pristimantis*, *Strabomantis*, *Hypodactylus* and *Phrynopus*); *Leptodactylus* species were used as outgroup. We performed a Bayesian phylogenetic analysis in MrBayes 3.0b4 (Ronquist & Huelsenbeck 2003): two independent Bayesian analyses were performed with a random starting tree, four incrementally heated Markov chains, and 10,000,000 generations, with trees sampled every 100 generations to estimate likelihood and sequence evolution parameters. The best-fit model of nucleotide substitution selected using the Akaike information criterion (AIC) in MrModeltest v.2.2 (Nylander 2004) was HKY+I+G for both partitions. Stationarity for each run was detected by plotting the likelihood scores of the trees against generation time, and the topology, posterior probability values, and branch lengths inferences were estimated after discarding 25% of the initial trees of each run as burn-in samples. Nodes with posterior probability  $\geq 0.9$  on a 50% majority rule consensus tree from

both runs were considered significant support for a given clade. The majority 50% consensus tree saved with posterior probabilities on the nodes was visualized using FigTree 1.3.1 (<http://tree.bio.ed.ac.uk/>). Uncorrected genetic distances (p distances) were also calculated using PAUP.

## Results

### Taxon description

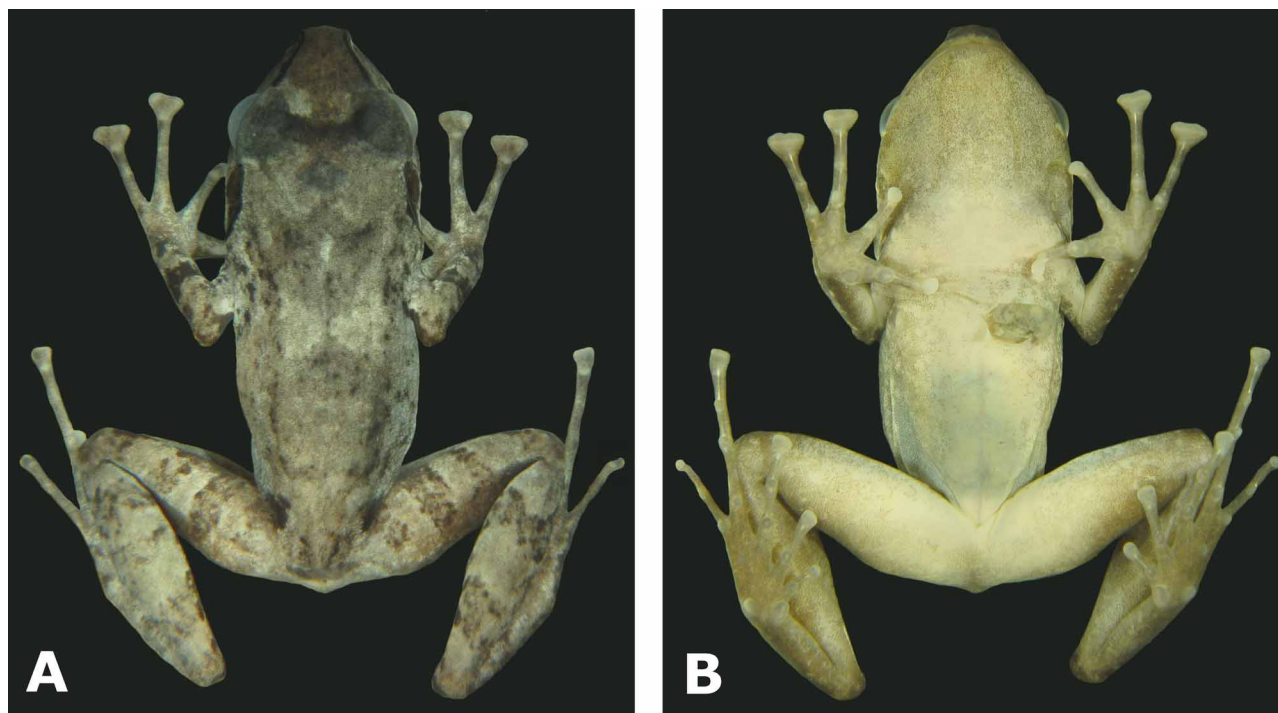
#### *Oreobates remotus* sp. nov.

(Figs. 1–3)

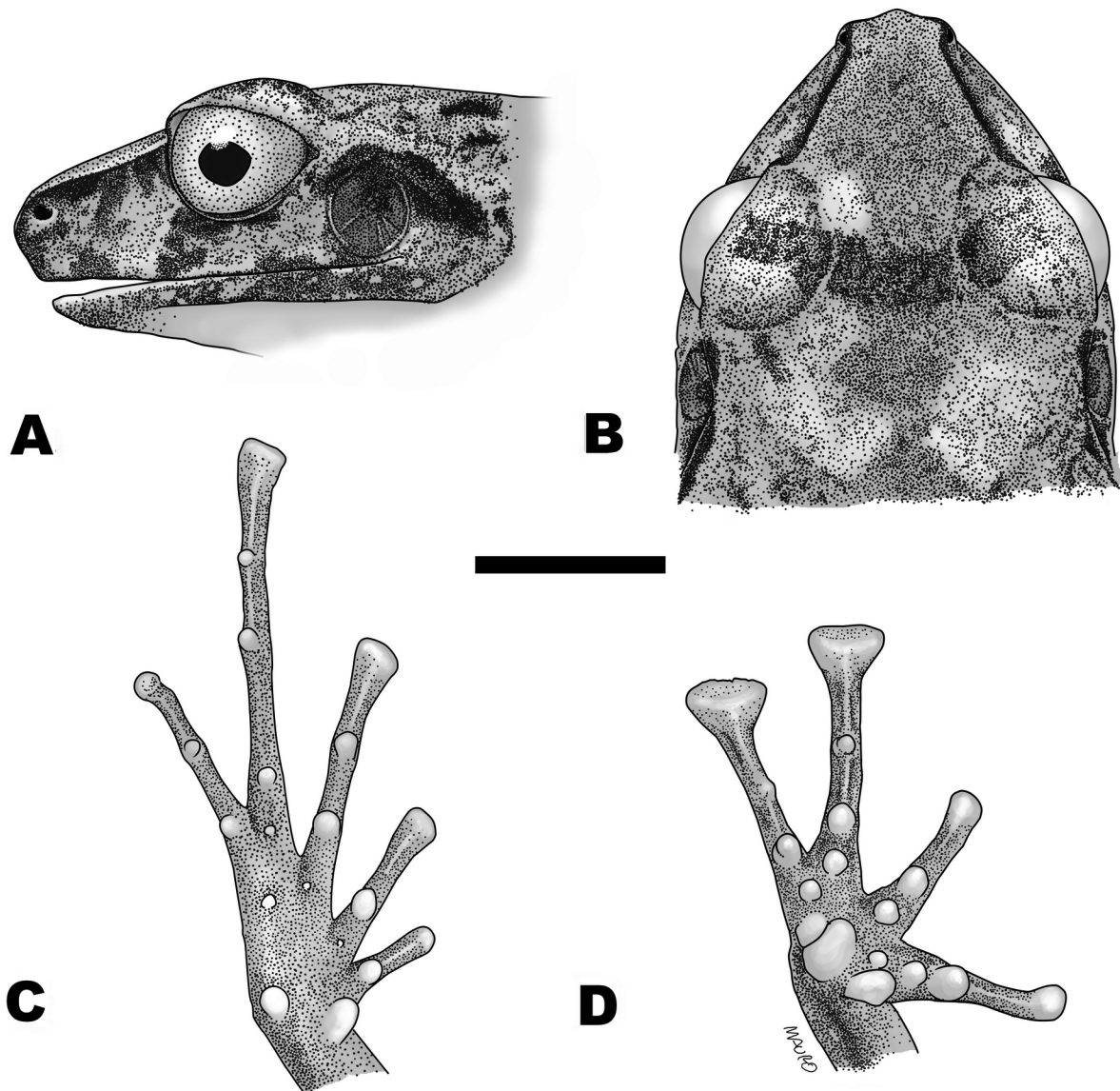
**Holotype.** MZUSP 141708 (Figs. 1, 2), an adult male from “Rochedo” (15°8'43.80"S, 44°14'29.04"W, WGS84, 624 m elevation), a large limestone outcrop crossed by a road, close to Fabião I village, at Cavernas do Peruaçu National Park, Januária municipality, Minas Gerais state, Brazil, collected on January 9<sup>th</sup>, 2009 by M. Teixeira Jr., M. A. de Sena, R. S. Recoder and M. T. Rodrigues; field number MTJ 0430.

**Paratopotypes.** (Fig. 3) MZUSP 141710, an adult female, collected with the holotype; field number MTJ 0426. MZUSP 141711–13, adult males, collected with the holotype; field numbers MTJ 0427–29. MZUSP 141715, a juvenile, collected with the holotype; field numbers MTJ 0431.

**Paratypes.** MZUSP 141709, a juvenile, from the trail between Janelão Cave and Terra Brava farm old headquarters, at Cavernas do Peruaçu National Park, Januária municipality, Minas Gerais, Brazil, collected on January 24<sup>th</sup>, 2008 by M. Teixeira Jr. and R. S. Recoder; field number MTJ 0209. MZUSP 141715–24, juveniles, from an unpaved road that connects Terra Brava farm to Liasa farm, at Cavernas do Peruaçu National Park, Januária municipality, Minas Gerais state, Brazil, collected between January 10<sup>th</sup> and January 23<sup>th</sup> 2009 by M. Teixeira Jr., M. A. de Sena, R. S. Recoder; field numbers MTJ 0432–34, 448, 493, 550–53, 567, 568. MZUSP 23306, an adult, from Pandeiros River, Minas Gerais state, Brazil, collected on 1935 by J. Blaser. MZUFV 5005–10, subadults, from Cavernas do Peruaçu National Park, Januária municipality, Minas Gerais, Brazil, collected between March 12<sup>th</sup> and 19<sup>th</sup> 2003 by R. Feio.



**FIGURE 1.** Holotype of *Oreobates remotus* sp. nov. (MZUSP 141708): Dorsal (A) and ventral (B) views.



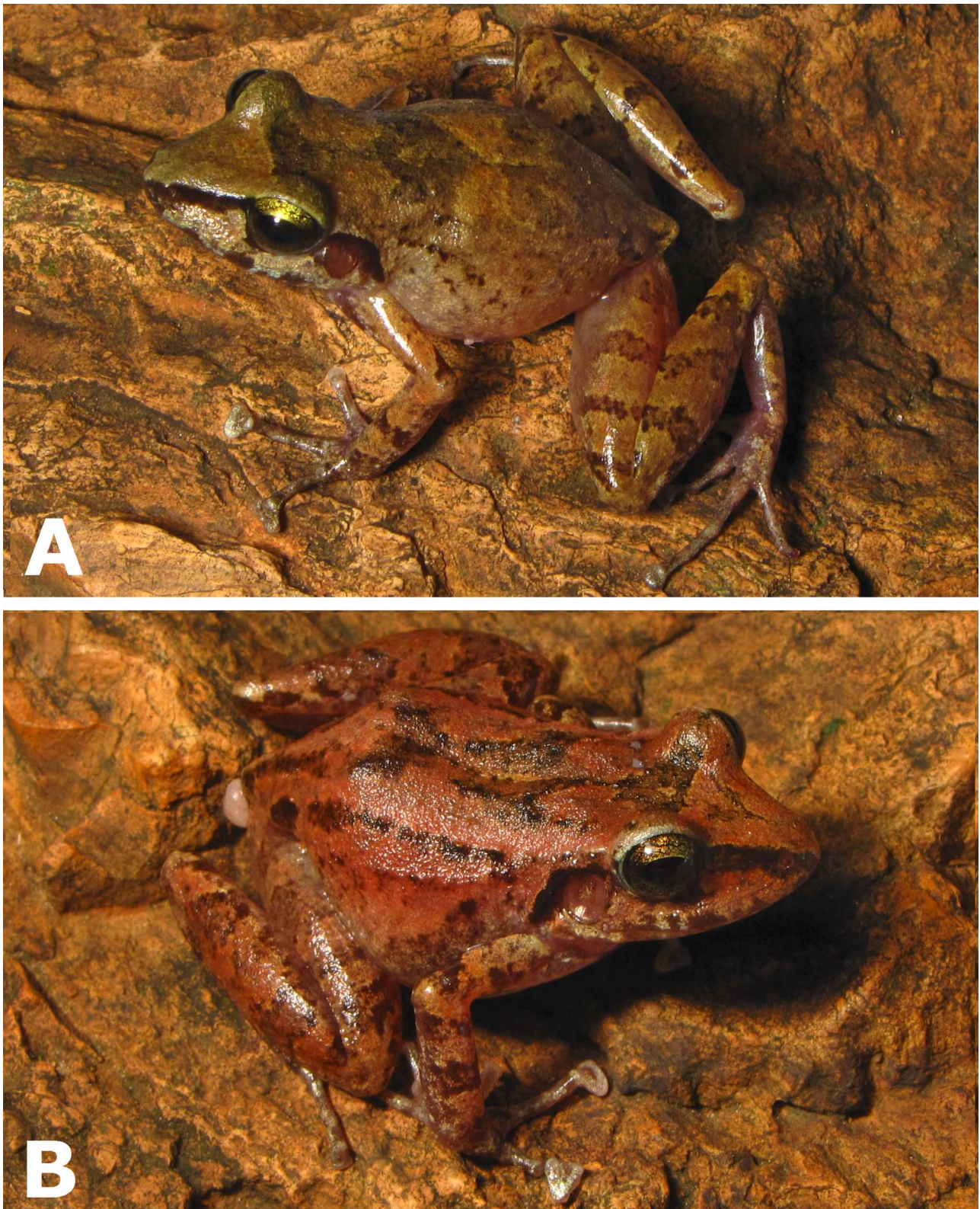
**FIGURE 2.** Holotype (MZUSP 141708) of *Oreobates remotus* **sp. nov.**: Lateral (A), dorsal (B) views of the head; Foot (C) and hand (D). Scale bar = 5 mm.

**Etymology.** The specific epithet is a noun in apposition meaning “remote, distant, far off”, in Latin, in reference to the geographical gap of more than 1.000 km between the area of occurrence of the new species and that of all other *Oreobates*.

**Diagnosis.** A medium-sized *Oreobates* with moderately robust body (SVL of adult males, 29.6–33.1 mm and female, 37.7 mm) characterized as follows: (1) skin on dorsum smooth; venter smooth; posterior surfaces of limbs smooth; discoidal fold slightly visible, thoracic fold absent; postrictal tubercle absent; (2) tympanic membrane and annulus distinct, about 3/5 of eye diameter; supratympanic fold weak; (3) head large, slightly longer than wide; snout subacuminate in dorsal view, slightly protruding in lateral view; canthal ridge straight in dorsal view, slightly concave in profile; (4) cranial crests absent; upper eyelid smooth; (5) dentigerous process of vomers distinct, situated posteromedial to choanae; (6) males with vocal slit and no nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, conical; supernumerary tubercles large, conical, smaller than subarticular tubercles; disks on Fingers III and IV large, broadly expanded, truncated, with circumferential groove and pad; lateral fringes weak; (8) ulnar tubercles absent; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle sub-elliptical, prominent; outer metatarsal tubercle round, prominent; supernumerary tubercles small, weakly distinct; (11) toes long and slender, lateral fringes slightly visible distally, web-



bing absent; fifth and third toes reaching second subarticular tubercle of Toe IV; discs relatively small, slightly expanded, truncated in Toe IV, truncate to rounded in Toes V, III and II, and rounded in Toe I, circumferential grooves and pads present in Toes III, IV and V; (12) axillary gland absent; (13) dorsal coloration olive brown to reddish brown, with W-shaped occipital dark markings poorly evident, dorsolateral dark brown mark may form a longitudinal dark strip; throat and chest grey; belly cream with grey mottling or reticulations on anterior margin.



**FIGURE 3.** Adult paratopotypes of *Oreobates remotus* **sp. nov.** in life: (A) Male (MZUSP 141711) and (B) female (MZUSP 141710).

**Description of the holotype.** An adult male, SVL 32.18 mm, with vocal slits and no nuptial pads; head slightly longer than wide, and slightly wider than body; snout moderate in length, subacuminate in dorsal view, slightly protruding in profile; nostril opening laterally, placed on an elevation on the side of snout; eye large, protruding, placed and directed laterally; canthal ridge straight in dorsal view and slightly concave in profile; loreal region slightly concave; no cranial crests; upper eyelid without tubercles; supratympanic fold present, but not well developed; tympanic membrane and annulus distinct, except on supratympanic region; tympanic membrane vertically elliptical, large, diameter about 3/5 of eye diameter; no postrictal tubercles; choanae small, slightly rounded, not concealed, and placed anterolaterally on roof of mouth, separate by a distance of about four times their diameter; dentigerous process of vomers present, elliptical, forming two small barely separated oblique clumps between, and slightly posterior, to choanae; vocal sac simple, subgular, scarcely developed; vocal slit present, slit-like, laterally to tongue, posteriorly on floor of mouth; tongue lanceolate, not notched posteriorly; Eustachian tube opening posteriorly on eye bulge; dorsal surfaces of head, back and limbs smooth; ventral surfaces of limbs, belly, chest and throat smooth; cloacal region slightly shagreen; no cloacal flap present; no scapular-occipital fold nor middorsal and dorsolateral tubercle or fold; discoidal fold slightly visible, no thoracic fold; arm and forearm slender; ulnar tubercles absent; palmar tubercle elliptical, large, prominent; thenar tubercle ovate, large, prominent; supernumerary tubercles present, large, conical with rounded bases; subarticular tubercles large, larger than supernumerary tubercles, conical and projecting, rounded in the base, distal ones are smaller than proximal ones; disks on Fingers III and IV large, broadly expanded, truncated; small, rounded slightly larger than finger width in Fingers I and II; circumferential groove and pad presents in Fingers III and IV; fingers slender and long, not webbed; fingers weakly fringed laterally; relative finger length  $II < IV < III$ ; legs slender and moderately long; toes slender and long (foot length 49% of SVL), not webbed; heel and tarsal tubercles absent, no tarsal fold; inner metatarsal tubercle slightly developed, longer than wide, sub-elliptical; outer metatarsal tubercle rounded, smaller than inner one; a few supernumerary plantar tubercles present, small, weakly distinct; subarticular tubercles conical, projecting, with rounded bases, subarticular tubercles from outer toes smaller than those from inner toes; discs relatively small, slightly expanded, truncated in Toe IV, truncate to rounded in Toes V, III and II, and rounded in Toe I, disk of Toe I as wide as digit width; circumferential grooves and pads present in Toes III, IV and V; toes slightly laterally fringed distally; relative toes length  $I < II < V < III < IV$ .

**Color in life.** Interorbital bar dark brown, concave anteriorly, with an irregular posterior medial projection expanded across midline of head, and with irregular lateral borders; canthal stripe dark brown, extending longitudinally from tip of snout to anterior margin of eye, ventrally irregularly edged and dorsally sharply edged along canthal ridge. Supratympanic area blackish, extending along supratympanic fold, dark coloration extends ventrally approximately to the level of mid-tympanum length. Two diagonal labial bars dark brown, slightly faded, irregularly edged and discontinuous, one below eye and one crossing loreal region and connecting to canthal stripe, infralabial region with scattered irregular marks. Dorsal background coloration olive brown, with a large dark brown X-shaped mark over scapulae, connecting with the interorbital bar. Dorsal coloration also includes small scattered black dots. Arm light brown with irregular dark brown transversal marks; forearm light brown with transverse dark brown irregular bars and some flecks. Dorsal surfaces of legs light brown with transverse dark brown bars; hidden surfaces of thighs and shanks slightly translucent producing fleshy brown tonalities. Belly cream centrally, ventrolaterally and anteriorly with faint and fine dark brown flecks extending from dorsolateral coloration. Chest lighter than belly, and throat grey with inconspicuous faint vermiculations posteriorly.

**Color in preservative.** Background color light grey, pattern of dark coloration as described above, but turned in to dark grey, and light ventral coloration whitish.

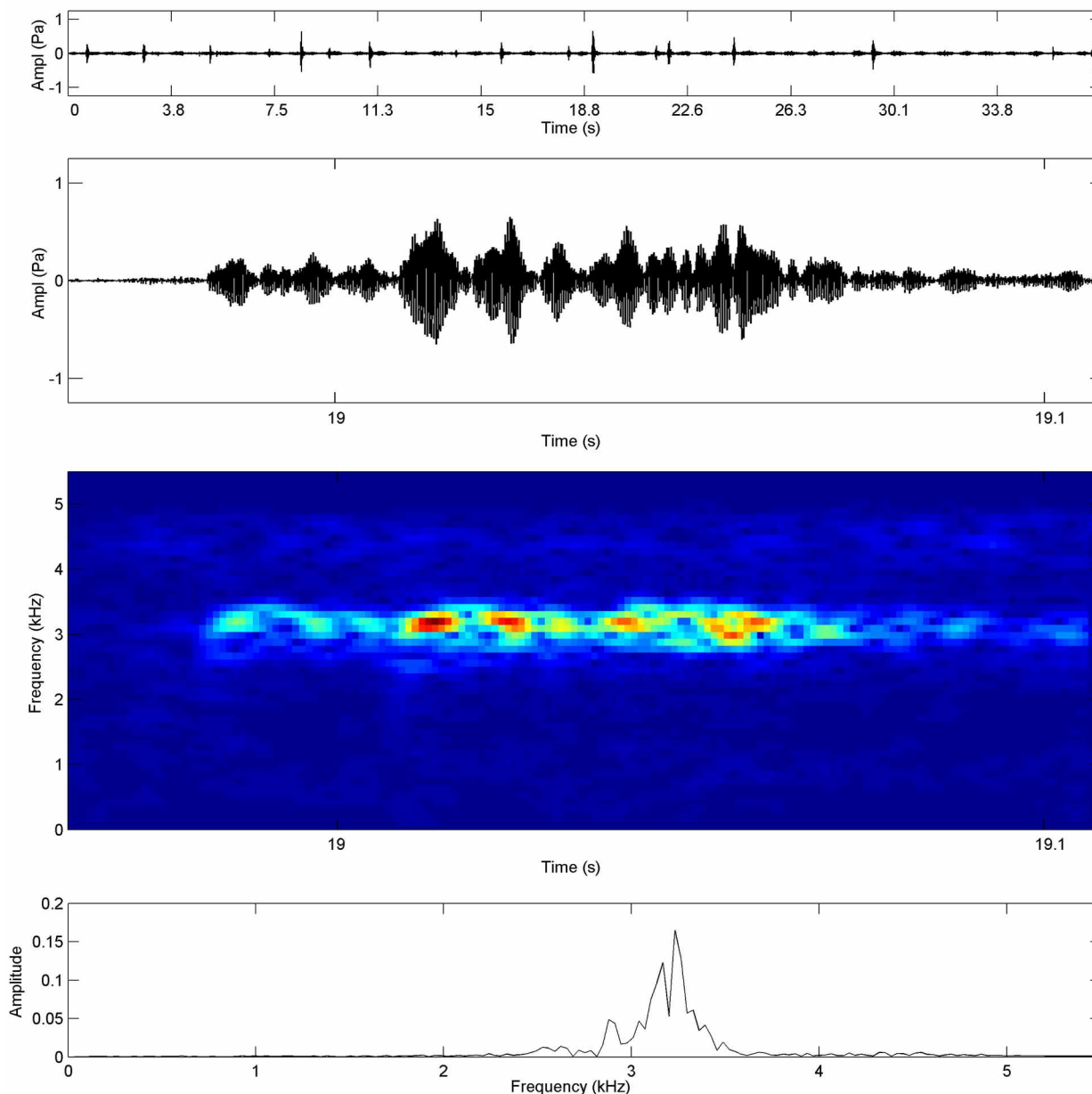
**Measurements of the holotype (mm).** SVL = 32.18; HL = 11.76; HW = 10.93; EN = 4.14; EE = 5.8; ED = 4.5; TD = 2.54; THL = 16.5; TL = 17.03; FL = 15.94; IND = 2.44.

**Variation.** We found little variation on morphological characters among the specimens, varying mainly in body size. Measurements are presented on Table 1. The only adult female has a larger SVL than adult males. The dorsum shows some variation in coloration and patterns, varying from yellowish brown background color with scattered dark marks to reddish brown with dorsolateral dark marks aligned marks, forming an irregular longitudinal stripe (Fig. 3). Some individuals also show a slightly visible middorsal fold.

**Advertisement call.** Calls were recorded on 9<sup>th</sup> January 2009 at 21:16h; air temperature was 21°C. Sixteen calls from four specimens were analyzed. The advertisement call consist on a series of single short pulsed notes averaging 104 ms in length (range = 89–142 ms) having 2–3 pulses each, however the poor quality of the record-



ings do not allow an accurate count of pulses. The calls show no harmonic structure, has no amplitude modulation and pulses are amplitude modulated. The average call repetition rate is 31.6 call/min (18–45 call/min). The average dominant frequency is 3150.7 Hz (2866.5–3395.7 Hz) (Fig. 4).



**FIGURE 4.** Advertisement call of *Oreobates remotus* sp. nov.: (from up to down) Oscillogram of a whole track and; oscillogram of a section comprising one note; Spectrogram of the same note; Amplitude spectrum of the note on the left. The call was recorded about 21:16 h on 9<sup>th</sup> January 2009, air temperature was 21°C.

**Comparison with other species (data for species other than *Oreobates remotus* in parenthesis).** *Oreobates remotus* can be distinguished from *O. barituensis*, *O. choristolemma*, *O. cruralis*, *O. granulosus*, *O. lehri*, *O. madidi*, *O. pereger*, *O. quixensis*, *O. sanctacruis*, *O. sanderi*, *O. saxatilis*, *O. simmonsii*, and *O. zongonensis* by having dorsal skin smooth and broadly enlarged truncate discs on Fingers III and IV (dorsal skin shagreened to granular and discs on Finger III and IV not enlarged). From *O. ibischi* by having dorsal skin smooth, broadly enlarged truncated discs on Fingers III and IV, nuptial pads absent and advertisement call notes having 2–3 pulses each (dorsal skin granular, discs on Finger III and IV only slightly enlarged, nuptial pads present and advertisement call notes having 6–8). From *O. discoidalis* by the absence of toe webbing, larger discs on Fingers III and IV, and advertisement call consisting of a single short pulsed note with 104 ms in length, dominant frequency of about



3150 Hz and 2–3 pulses per note (toes basally webbing, proportionally smaller discs on Fingers III and IV, and call composed of a single longer pulsed note with 582 ms in length, dominant frequency of about 2200 Hz and 8–11 pulses per note). *Oreobates remotus* is more similar to *O. heterodactylus*, from which it can be distinguished by absence of nuptial pads, subacuminated snout in dorsal view, and shorter advertisement call with dominant frequency of about 3150 Hz, no harmonic structure and 2–3 pulses per note (nuptial pads present, slightly truncated snout in dorsal view and call is a single pulsed note with dominant frequency of about 3950 Hz, having 3 to 5 harmonics and 5–9 pulses per note). Additionally *O. remotus* has, proportionally to body size, a larger hand than any other species of *Oreobates*.

**TABLE 1.** Measurements (mm) of *Oreobates remotus* **sp. nov.**: n = number of individuals; mean  $\pm$  standard deviation; range in parentheses.

	Adult males (n=4)	Adult female (n=1)	Subadults (n=6)
SVL	31.6 $\pm$ 1.5 (29.6–33.1)	37.7	25.3 $\pm$ 2 (23.4–28.0)
HL	12 $\pm$ 0.7 (11.4–13.0)	14.0	9.9 $\pm$ 0.8 (9.0–11.0)
HW	11 $\pm$ 0.7 (10.2–12.0)	12.9	9.2 $\pm$ 0.8 (8.3–10.1)
EN	3.9 $\pm$ 0.3 (3.6–4.1.0)	4.6	3.2 $\pm$ 0.2 (2.8–3.5)
EE	5.8 $\pm$ 0.2 (5.6–6.1.0)	7.2	5.4 $\pm$ 0.5 (4.9–6.1)
ED	4.2 $\pm$ 0.2 (3.9–4.5.0)	4.6	3.4 $\pm$ 0.2 (3.0–3.7)
TD	2.5 $\pm$ 0.1 (2.4–2.5)	3.1	2.0 $\pm$ 0.3 (1.6–2.8)
IND	2.5 $\pm$ 0.1 (2.4–2.7)	3.3	2.2 $\pm$ 0.2 (1.9–2.5)
THL	16.2 $\pm$ 0.8 (15.3–17.1)	18.8	13.4 $\pm$ 1 (12.4–15.1)
TL	16.9 $\pm$ 0.6 (16.2–17.7)	19.2	14.1 $\pm$ 1.1 (13–15.6)
FL	15.5 $\pm$ 0.4 (15.1–15.9)	17.6	12.9 $\pm$ 1.4 (10.7–14.4)

**Natural history and distribution.** All individuals of *Oreobates remotus* **sp. nov.** were found only during the rainy seasons. During our first expedition to Peruaçu valley, only one juvenile was found at a semideciduous forest. However that rainy season was atypical as the precipitation was very low (about 500 mm<sup>3</sup>). The second sampled rainy season was a typical one (about 1000 mm<sup>3</sup>) and individuals became very abundant. Many juveniles were found in pitfall traps and along the dry forest floor jumping over the leaf-litter. No individual was found in non-forest environments (e.g. savanna and *carrasco*). All adults were found in wet limestone outcrops covered with mosses on the roadside within the dry forest (Fig. 5). Males were heard calling at night from the wet walls and crevices of the outcrops, especially during rainy days.

The new species is currently known only from the vicinities of the type locality, Peruaçu river valley, and from Pandeiros River, both at northern Minas Gerais state, Brazil (Figs. 6 and 7). Although geographical information for this latter record is imprecise, Pandeiros River is also located at the left margin of São Francisco River, about 70 km SW from Peruaçu region. Both areas lie at the southernmost end of the Atlantic Dry Forest.

**Phylogenetic relationships.** Both individual and combined analyses of mitochondrial genes cytochrome *b* (*cyt b*) and 16S recovered *Oreobates remotus* **sp. nov.** deeply embedded within *Oreobates* and sister to *O. heterodactylus* (Fig. 8), with 10% of interspecific divergence for 16S and 16–17% for *cyt b* between them. The clade comprising *O. cruralis*, *O. discoidalis* and *O. madidi* is recovered as sister to that containing *O. remotus* **sp. nov.** and *O. heterodactylus*, while *O. quixensis* and *O. sanderi* are recovered in a basal position. The remaining relationships within Strabomantinae were poorly supported, similar to results of Padial *et al.* (2008b, 2009).

## Discussion

Although our molecular phylogenetic hypothesis does not include all *Oreobates* species, they recovered *O. heterodactylus* as a sister taxon of *O. remotus* **sp. nov.** with support. The placement of this species in *Oreobates* and its affinities to *O. heterodactylus* are also supported by morphological, ecological and distributional evidence. Both

species are morphologically similar, occur in the same microhabitats, and are biogeographically associated to dry forests. The broadly enlarged and truncated discs in Finger III and IV are the most conspicuous traits shared by both species.



**FIGURE 5.** Habitats: General view of the dry forest during rainy season (A), and during the dry season (B); Limestone outcrops (“Rochedo”) within the dry forest where adult males of *Oreobates remotus* **sp. nov.** were found calling, and where the holotype was collected (C).

Padial *et al.* (2008a) provided a phylogenetic hypothesis for intrageneric relationships in *Oreobates* in which the most parsimonious biogeographical scenario was an origin of *Oreobates* from an ancestor at the upper Amazon basin and Andes foothills. Their hypothesis also implied a subsequent colonization of higher altitudes, in the Andean Cordillera Oriental, and two subsequent radiations, one of robust species and one of smaller species mainly occurring in from Central Bolivia to Argentina across the Andean hills. They also suggested that *O. heterodactylus*, a member of the clade with small species, would have originated from an ancestor that dispersed through the lowlands and reached the Brazilian Precambrian Shield. However their phylogenetic hypothesis used to construct this biogeographical scenario missed *Oreobates* closest related genera, *Lynchi* and *Phrynopus* (Hedges *et al.* 2008, Padial *et al.* 2009, Pyron & Wiens 2011).

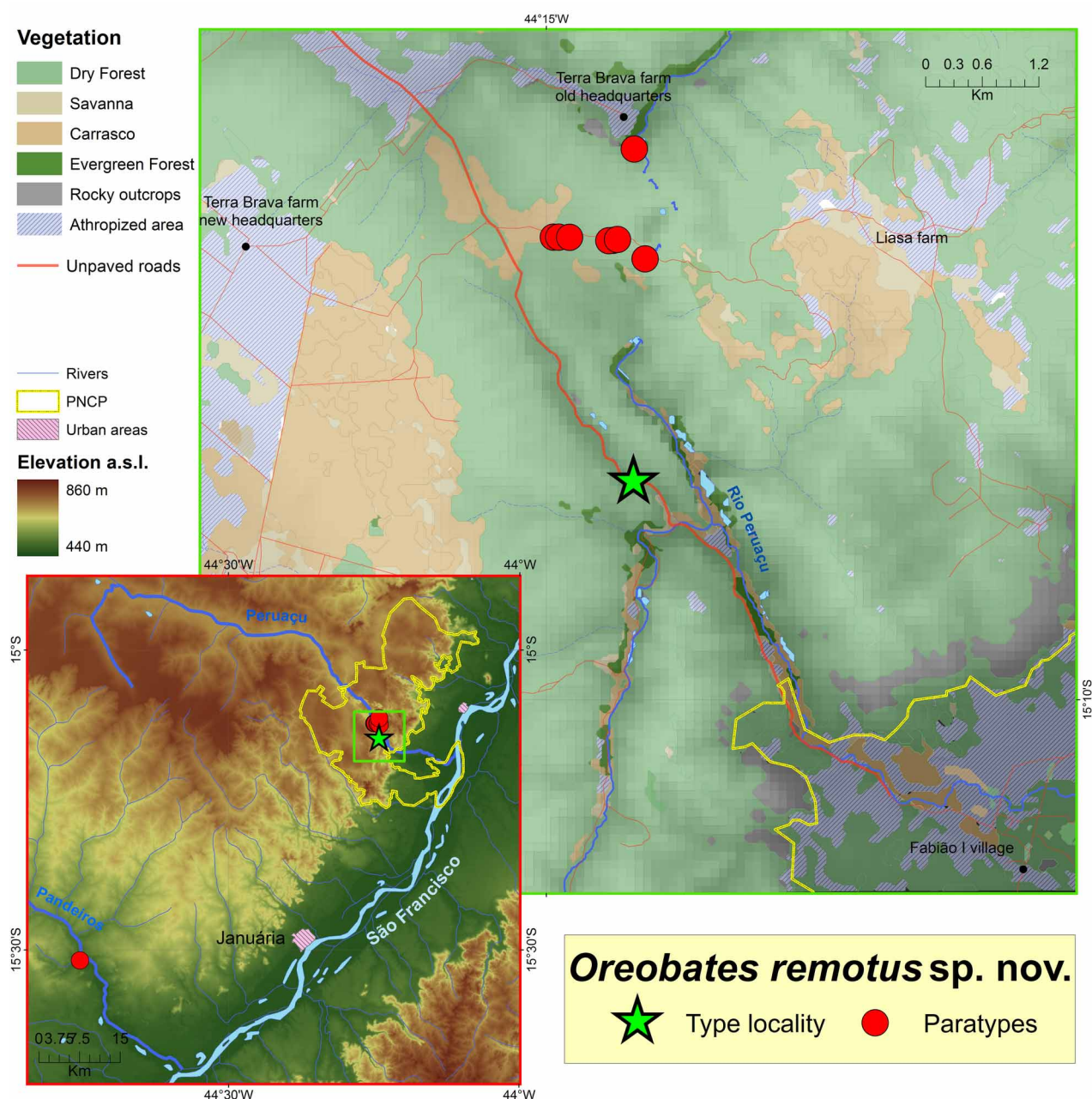
However, given the recently published phylogenetic hypotheses (Hedges *et al.* 2008; Padial *et al.* 2009; Pyron & Wiens 2011) new and more complete view of *Oreobates* biogeography can be drawn. Species within the genus *Phrynopus* occurs at the humid montane forests and supra-tree line grasslands between 2200–4400 m a.s.l. and *Lynchi* in similar habitats between 2200–3100 m a.s.l., both at Andean Cordillera Oriental (Hedges *et al.* 2008).



Therefore the association with Andean habitats seems to be a simplesiomorphic feature for *Oreobates*, *Lynchi* and *Phrynopus*, indicating that their common ancestor was of Andean origin. Therefore, the present association of *Oreobates* to Andean habitats should be considered plesiomorphic, and the occupancy of the lowlands apomorphic. The colonization of the lowland by *O. quixensis* may well be considered an early event. Subsequently, a second, independent colonization of the lowlands, when lowland Chiquitano and Atlantic Dry Forests were colonized, would have taken place from the ancestor of clade of small *Oreobates* (*O. barituensis*, *O. cruralis*, *O. discoidalis*, *O. heterodactylus*, *O. madidi*, and *O. heterodactylus*). Probably the only lowland diversification event within *Oreobates* was the origin of *O. heterodactylus* and *O. remotus* from a common ancestor.



**FIGURE 6.** Map of South America, showing distributional records of *Oreobates*.

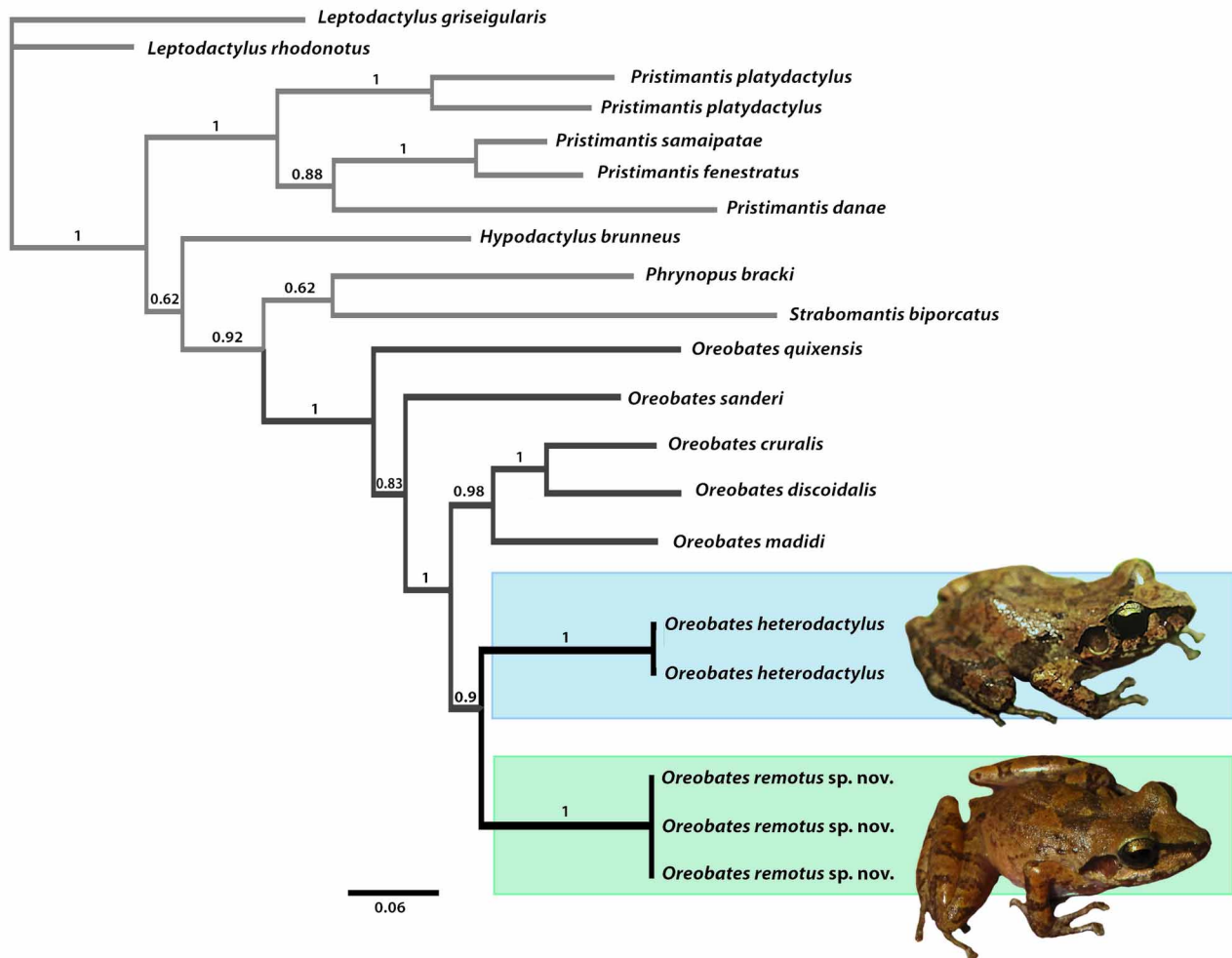


**FIGURE 7.** Map of the current known distribution of *Oreobates remotus* sp. nov.

Currently, Atlantic and Chiquitano Dry Forests are separated from each other by a distance of more than 1,000 km. However, the occurrence of tree species in both areas indicates an ancient connection between those two forests as suggested by the Pleistocene Arc hypothesis (Prado & Gibbs 1993; Pennington *et al.* 2000; Prado 2000). This hypothesis states that during the Last Glacial Maximum, when a cold and dry climate took place over South America, humid habitats, such as those of the Amazon and Atlantic Rain Forests, retracted and fragmented. Plant species adapted to cold/dry climatic conditions spread then over central South America producing a large and continuous cover of dry forests that connected thus the Atlantic Dry Forest and the Chiquitano Forests (Prado & Gibbs 1993; Pennington *et al.* 2000; Prado 2000). Although the current distributional records of plant species associated with dry forests indicates a preterit connection between these forests (Prado & Gibbs 1993; Pennington *et al.* 2000; Prado 2000), recent molecular data on endemic plant species of the SDTFs showed no evidence of vicariance and that their diversification was older than the Pleistocene as originally suggested (Pennington *et al.* 2004). Palynological data of plant species from Chiquitano Dry Forest is absent from Pleistocene pollen records (Mayle 2006), and paleodistribution modeling also indicates an older event of dry forest expansion, as the LGM was too cold and dry



to allow it (Werneck *et al.* 2010). Moreover, the large genetic divergences between *O. heterodactylus* and *O. remotus* also suggest that the splitting was older than the Pleistocene. Faunistic evidence is nonetheless weak to support this Pleistocene Arc hypothesis, and is currently based on shared species between SDTFs of Paran  valley at Goi s state with the Caatingas (Moojen *et al.* 1997; Werneck & Colli 2006), suggesting a larger extension of dry habitats in northeastern Brazil and their connection to eastern Cerrado SDTFs, and not a continuous dry habitat across Central Brazil.



**FIGURE 8.** Bayesian consensus tree topology obtained from the combined molecular data set (cyt b and 16S) showing the placement of *Oreobates remotus* sp. nov. within *Oreobates*, and as sister taxon of *O. heterodactylus*. Numbers above nodes are posterior probabilities.

The new species was recorded only at the southernmost end of the ADF, which was the only area properly sampled along this ecoregion. *Oreobates remotus* may have a wider distribution, which can be only confirmed by additional sampling along the remaining fragments of SDTFs northern from Peru u region. The present status of the original vegetation cover of ADF was never properly addressed, but it seems to be highly fragmented with only few areas protected in conservation unities (Silva 2001; Silva & Casteleti 2005). Although an apparently stable population of *Oreobates remotus* occurs within a national park, undetected populations may be undergoing severe anthropic pressure, as this forests are the main target areas for agriculture along central Brazil (Oliveira-Filho & Ratter 2002). Conservation efforts along the remaining fragments of SDTFs are urgently necessary in order to ensure the detection, investigation and continuity of the evolutionary processes of this biotic domain, which is only beginning to be known.

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