

Systematics of *Oreobates* and the *Eleutherodactylus discoidalis* species group (Amphibia, Anura), based on two mitochondrial DNA genes and external morphology

JOSÉ M. PADIAL¹, JUAN C. CHAPARRO² and IGNACIO DE LA RIVA^{1*}

¹Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales, CSIC. C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

²Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru

Received 25 January 2007; accepted for publication 5 July 2007

We present morphological and molecular (mitochondrial DNA, mtDNA) evidence supporting the validity and monophyly of the genus *Oreobates*. This genus also includes members of the former *Eleutherodactylus discoidalis* species group plus *Eleutherodactylus heterodactylus*. The presence of prominent conical subarticular tubercles and prominent supernumerary tubercles associated with the axis of fingers and toes, the presence of glandular axillary pads, and the absence of vocal sacs are proposed as morphological synapomorphies. Species of this taxon form a well-supported crown clade in a phylogeny including members of the genera *Craugastor* and *Eleutherodactylus s.l.* The sister taxon to *Oreobates* is the *Eleutherodactylus martinicensis* series; *Oreobates* does not appear to be closely related to the *Eleutherodactylus binotatus* series or to members of the *Eleutherodactylus dolops* and *Eleutherodactylus nigrovittatus* species groups. The taxonomic status of all species of *Oreobates* is reassessed. *Hylodes philippi* and *Hylodes verrucosus* are removed from the synonymy of *Oreobates quixensis*. We redescribe *Oreobates cruralis* on the basis of the holotype and new material from Bolivia and Peru, and restrict its distribution to the humid forests of the lowlands and adjacent foothills of the Andes, from southern Peru to central Bolivia. *Oreobates granulosus* is rediscovered, redescribed, and resurrected, on the basis of the examination of the holotype and additional material from Peru. Phylogenetic analyses of partial 16S mtDNA are used to test the independence of lineages (species). The 14 species of *Oreobates* are distributed from southern Ecuador to northern Argentina. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 152, 737–773.

ADDITIONAL KEYWORDS: Amazon – Andes – phylogenetics – South America – taxonomy.

INTRODUCTION

Research on systematics of Neotropical amphibians has experienced a boost in recent decades (Glaw & Köhler, 1998). Nevertheless, many taxonomic problems remain to be solved. New species are being described each year and many phylogenetic hypotheses are under review (Padial & De la Riva, 2006). Moreover, the degree of exploration is still incomplete for lineages, areas (Kress *et al.*, 1998), and DNA sequences (Vences & Köhler, 2006). Among brachycephalids, '*Eleutherodactylus*' are famous for

their incomplete and complex taxonomy, together with the difficulties in their identification. This is probably, at least in part, because of the rarity of many species, which leads to low sampling for species descriptions. In order to facilitate taxonomic work, this large genus has been subdivided into several subgenera, series, and species groups (Lynch & Duellman, 1997). More recently, it has been split into several genera (Crawford & Smith, 2005; Frost *et al.*, 2006). However, the taxonomic status and monophyly of most groups and taxa now included in the family Brachycephalidae have not yet been assessed. Examples of this include the *Eleutherodactylus discoidalis* species group and the genus *Oreobates*.

*Corresponding author. E-mail: iriva@mncn.csic.es

Jiménez de la Espada (1872) described the genus *Oreobates* and the species *Oreobates quixensis* from the Ecuadorian Amazon. Subsequently, Lynch (1971) and Lynch & Schwartz (1971) considered *Oreobates* a synonym of *Ischnocnema*, a genus described by Reinhardt & Lütken (1862) to accommodate *Leiuperus verrucosus* Reinhardt & Lütken, 1862 from Minas Gerais (south-eastern Brazil). Lynch & Schwartz (1971) also placed two *Hylodes* (= *Eleutherodactylus*) species, illustrated by Jiménez de la Espada (1875), as synonyms of *Ischnocnema quixensis*. The types of *Oreobates* and one of the *Hylodes* were considered lost, and *Ischnocnema verrucosa* was only known from the holotype, a badly preserved and broken juvenile specimen. Given this lack of relevant material for study, further taxonomic reassessment has not been possible. Therefore, subsequent authors that discovered new *Ischnocnema* species in the Andes (Lynch, 1974; Duellman, 1990; Harvey & Keck, 1995; Harvey & Sheehy, 2005; Padial, Reichle, & De la Riva, 2005a) followed Lynch & Schwarz's (1971) arrangement. However, Caramaschi & Canedo (2006) rediscovered *I. verrucosa* and placed *Ischnocnema* in the synonymy of *Eleutherodactylus* Duméril & Bibron, 1841. They also resurrected the genus *Oreobates* for *O. quixensis* and the Andean species previously assigned to *Ischnocnema*.

The *E. discoidalis* group was proposed by Lynch (1976), who recognized five species: *Eleutherodactylus cruralis* (Boulenger, 1902), *Eleutherodactylus discoidalis* (Peracca, 1895), *Eleutherodactylus elassodiscus* Lynch, 1973, *Eleutherodactylus granulatus* (Boulenger, 1903), and *Eleutherodactylus nigrovittatus* (Anderson, 1945). He defined this group on the basis of a unique combination of traits and treated it as monophyletic. Additionally, he noted some heterogeneity within the group, as evidenced by the presence of pointed digital tips in *E. elassodiscus* and *E. nigrovittatus*, in contrast to the rounded tips in the three southern species (*E. cruralis*, *E. discoidalis*, and *E. granulatus*). He also pointed out that the southern species resembled the Brazilian species *Eleutherodactylus octavioi* of the *Eleutherodactylus binotatus* species group in having large outer metatarsal tubercles. Later, Lynch (1989) considered *E. granulatus* a junior synonym of *E. cruralis*, and split the former *E. discoidalis* group, leaving it with only the two southern species: *E. discoidalis* and *E. cruralis*. *Ischnocnema* was then considered phylogenetically more primitive, or ancestral to *Eleutherodactylus*, and those species placed in the *E. binotatus* group were proposed as the species most closely related to *Ischnocnema*, and ancestral to the *E. discoidalis* group (Lynch, 1989). He also proposed that a complex of species, the *Eleutherodactylus fitzingeri* group of Lynch (1976) and Lynch & Myers (1983) (later divided

into the genus *Craugastor* and the *Eleutherodactylus conspicillatus* group; Lynch, 1986; Crawford & Smith, 2005) would be advanced in relation to (and/or derived from) the frogs identified as members of the *E. discoidalis* group. Furthermore, Lynch (1989) also rejected Savage's (1987) hypothesis of relationships that considered *Ischnocnema* and the Mexican genus *Tomodactylus* as sister groups.

More recently, molecular phylogenetic analyses placed *I. quixensis* among *Eleutherodactylus* and as sister group of the *E. binotatus* species group (Frost *et al.*, 2006); however, because of the limited taxon sampling, the only supported conclusion was the nonmonophyly of *Eleutherodactylus* (see also Darst & Cannatella, 2004). Hence, the taxonomic status and phylogenetic relationships of *Ischnocnema* could not be assessed, other than saying that *I. quixensis* was close to what we call *Eleutherodactylus* (a position that was already held by Jiménez de la Espada 1872, 1875). With the resurrection of *Oreobates* and its restriction to the Andean and Amazonian species, the hypotheses of relationships are even more uncertain. If *I. verrucosa* is an '*Eleutherodactylus*' and *Oreobates* a valid taxon, which one among the several '*Eleutherodactylus*' species groups is the sister clade of *Oreobates*? Moreover, is *Oreobates* monophyletic? Furthermore, if we assume no relationships of *Oreobates* with south-eastern Brazilian *Eleutherodactylus* (the *E. binotatus* series), a position held by Caramaschi & Canedo (2006), then we have to look for putatively related groups in the Andes or the Amazon. The *E. discoidalis* species group seems to be the best candidate. It shares with *Oreobates* many external morphological features, among them, those proposed by Lynch (1989) as synapomorphies for this group. Moreover, Padial *et al.* (2005a) already pointed out the difficulties of assigning some specimens from the Andes either to what was then considered *Ischnocnema* or to the *E. discoidalis* group. Furthermore, some characteristics of the advertisement call of *Oreobates sanctaerucis* were considered similar, but putatively primitive, to those calls characteristic of the *E. discoidalis* group (Padial *et al.*, 2008). Finally, a species of the Brazilian Shield recently rediscovered, *Eleutherodactylus heterodactylus*, shows morphological characters of both the *E. binotatus* and the *E. discoidalis* groups (Padial & De la Riva, 2005), and its phylogenetic relationships deserve a detailed study (Padial *et al.*, 2008).

None of the previous hypotheses have been tested to date. Hence, the goal of our study is to answer the following questions.

1. Are the *E. discoidalis* group and *Oreobates* monophyletic?
2. What is their phylogenetic relationship?

3. Do former members of the *E. discoidalis* group belong to this group?
4. What is the current species diversity of those taxa?
5. To which group does *E. heterodactylus* belong?

To answer these questions we apply an integrative taxonomic approach, *sensu* Dayrat (2005), Will, Mishler & Wheeler (2005), and Padial & De la Riva (2006). We include molecular phylogenetics (using mitochondrial DNA, mtDNA) and classical taxonomic analyses. We also consider Padial *et al.*'s (2008) analyses on advertisement calls as additional evidence to test our hypothesis. Finally, we provide a taxonomic account, with remarks and redescriptions for several species the taxonomic status of which is unclear or still poorly known.

MATERIAL AND METHODS

EXTERNAL MORPHOLOGY

We followed Lynch (1989) and Lynch & Duellman (1997) for morphological and colour characteristics used in the diagnosis and description. A single person (JMP) took measurements with a digital calliper to the nearest 0.01 mm, but to avoid pseudoprecision (Hayek, Heyer & Gascon, 2001), we rounded all measurements to only one decimal point. Abbreviations are as follows: EE, eye–eye distance; EL, eye length (measured horizontally); EN, eye–nostril distance; FA, arm length (from posterior margin of thenar tubercle to distal point of elbow); FL, foot length (from posterior border of inner metatarsal tubercle to tip of fourth toe); HL, head length (from posterior margin of lower jaw to tip of snout); HW, head width (measured at level of rictus); IND, internarial distance; SVL, snout–vent length; TH, thigh length (from vent to knee); TL, tibia length; TYH, tympanic membrane height; TYL, tympanic membrane length. We do not include values of interorbital distance (IOD) and upper eyelid width (EW). Our experience indicates that these parameters are usually of little utility because the preservation condition of specimens highly influences the measurements, and makes it difficult to obtain precise and comparable values. Colour characteristics were noted in life and in alcohol. We determined the age and sexual condition by dissection or observation of external secondary sexual characters. The condition of the trigeminal nerve (see Lynch, 1986) was determined through dissection of the skin above the tympanic area, and through a horizontal cut of the mandibular joint. Museum abbreviations other than cited by Leviton *et al.* (1985) are: Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia (CBG); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Museo de Historia Natural Noel

Kempff Mercado, Santa Cruz de la Sierra, Bolivia, Amphibian Collection (MNKA, formerly NKA); Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru (MHNSM), Museo de Historia Natural, Universidad Nacional de San Antonio Abad del Cusco, Peru (MHNC). We include a list of specimens examined in the Appendix.

MOLECULAR PROCEDURES AND PHYLOGENETIC ANALYSES

The origin of sequences, collection numbers, and localities for each terminal and corresponding amplified fragment are detailed in Table 1. Following the recent hypotheses of hyloid relationships (Darst & Cannatella, 2004; Frost *et al.*, 2006), we selected *Cryptobranchus* sp., *Rhinella amboroensis* (see Chaparro, Pramuk & Gluesenkamp, 2007), *Leptodactylus griseigularis*, and *Leptodactylus rhodonotus* as the outgroup taxa. Sequences not amplified by us were downloaded from the NCBI database (<http://www.ncbi.nlm.nih.gov>) or were provided by Matt Heinicke and Blair Hedges (*Eleutherodactylus dolops* and *E. elassodiscus*). We used the standard phenol-chloroform extraction protocol (Sambrook, Fritsch & Maniatis, 1989), with minor changes, to isolate genomic DNA. Fragments of approximately 591 bp from the mitochondrial gene 16S and approximately 350 bp of cytochrome *b* (*cytb*) were amplified after previously described PCR conditions (Hillis, Moritz & Mable, 1996), using the universal primers 16Sar-5' and 16Sbr-3', and *cytb*Z15-5' and *cytb*B2-3', respectively (Hillis *et al.*, 1996; Goebel, Donnelly & Atz, 1999). Amplification PCR products were purified and sequenced by SecuGen SA in an ABI-PRISM 3700 instrument. Sequences were edited in Sequencher 4.6 (Gene Codes Corporation). Alignments were performed using the program CLUSTAL X 1.83.1 (Thompson *et al.*, 1997) under default parameters. Ambiguously aligned regions were removed from the analysis (see below). For Bayesian phylogenetic analyses (Rannala & Yang, 1996) we used MrBayes version 3.2.1 (Huelsenbeck & Ronquist, 2001). The majority rule consensus tree was produced from four Metropolis-coupled Monte Carlo Markov chains (MCMC; Yang & Rannala, 1997); each run used one cold chain (the head chain) and three heated chains (scout chains). The analysis was run simultaneously for 10 million generations. Chain swapping and parameters update rates were monitored at the beginning and the end of the analyses to ensure that tree searches were being improved. Trees were sampled every 1000 generations. Burn-in was evaluated by examination of the standard deviation of split frequencies (> 0.01), to determine at what point the values had reached stationarity. Stationarity was reached after the first 1 000 000 generations, and hence the first

Table 1. Localities, voucher information, and GenBank accession numbers for sequences and specimens used in this study

Species	Locality	Museum No.	MNCN DNA collection	16S	Cytb
<i>Craugastor</i>					
<i>C. augusti</i>	México: Sonora, Alamos.	UAZ unnumbered	–	DQ283271 (3)	–
<i>C. fitzingeri</i>	Costa Rica: Limón, Estación Experimental La Lola.	–	–	AY326001	–
<i>C. rhodophis</i>	México: Oaxaca, El Mirador, Municipio Santa María Chilchotla.	JAC 22721	–	DQ283317 (3)	–
<i>Eleutherodactylus</i>					
<i>E. platydactylus</i>	Peru: Cusco, Pantiacolla	JCC (PL025A)	9484	EU368880	EU368902
<i>E. binotatus</i>	Brazil: São Paulo, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, São Luis do Paraitinga.	CFBH 5813	–	DQ283092 (3)	–
<i>E. chloronotus</i>	Ecuador: Napo, 3.5 km east of Santa Bárbara.	KU 202325	–	AY326007 (1)	–
<i>E. danae</i>	Bolivia: La Paz: Santa Cruz de Valle Ameno	IDLR4001	547	EU192260	EU368882
<i>E. dolops</i>	Colombia: Caquetá, municipio Florencia, vereda Santa Elena, 26.5 km (by road) arriba de Florencia ('poste 0'), 940 m a.s.l.	ICNMNH 23809	–	EU368905	–
<i>E. duellmani</i>	Ecuador: Carchi, ~5 km west of La Gruel; 2340 m a.s.l.	KU 202404	–	AY326003 (1)	–
<i>E. elassodiscus</i>	Ecuador: Napo, Cuyujua.	KU 177282	–	EU368906	–
<i>E. fenestratus</i>	Bolivia: Cochabamba, Los Guácharos.	MNK A 6631	4088	EU192275	EU368884
<i>E. thymelensis</i>	Ecuador: Carchi, 12 km west of Tufino, 3520 m a.s.l.	KU 202519	–	AY326009 (1)	–
<i>E. platydactylus</i>	Bolivia: La Paz, Serranía Bellavista.	MNCN-43224	3818	EU368901	EU368888
<i>E. samaipatae</i>	Bolivia: Santa Cruz, Quebrada a 6 km de la Angostura en dirección a Samaipata	MNCN-42987	3899	EU192292	EU368890
<i>E. supernatis</i>	Ecuador: Napo, 3.5 km east of Santa Barbara.	KU 202432	–	AY326005 (1)	–
<i>Oreobates</i>					
<i>O. choristolemma</i>	Bolivia: La Paz, Boquerón.	CBG 765	5715	EU368894	–
<i>O. choristolemma</i>	Bolivia: La Paz, Boquerón.	CBG 768	5745	EU368895	–
<i>O. cruralis</i>	Bolivia: Santa Cruz, Camino a Bella Vista.	MNK A7171	6098	EU192295	EU368881
<i>O. discoidalis</i>	Bolivia: Tarija, Serranía Aguarague.	MNK A 7247	6123	EU192254	EU368883
<i>O. discoidalis</i>	Bolivia: Tarija, Entre Ríos, Chiquiacá.	MNCN-43133	6134	EU368896	–
<i>O. granulatus</i>	Peru: Puno, Santo Domingo, Carabaya.	MHNC 3396	20550	EU368897	–
<i>O. heterodactylus</i>	Bolivia: Santa Cruz, Cerro del Arco, Serranía de Santiago.	MNK A7177	6018	EU368898	EU368885
<i>O. heterodactylus</i>	Bolivia: Santa Cruz, Cerro del Arco, Serranía de Santiago.	MNK A7175	6061	EU192296	EU368886
<i>O. lehri</i>	Peru: Cusco, Cosñipata Valley.	MHNC 3236	20551	EU368899	–
<i>O. madidi</i>	Bolivia: La Paz, Serranía Eslabón.	MNK A7856	5999	EU368900	EU368887

Table 1. *Continued*

Species	Locality	Museum No.	MNCN		
			DNA collection	16S	Cytb
<i>O. quixensis</i>	Bolivia: Pando, San Sebastián.	MNCN-43147	6216	EU192297	EU368889
<i>O. sanctaerucis</i>	Bolivia: Cochabamba, Chaquisacha.	CBG 153	5719	EU368903	–
<i>O. sanderi</i>	Bolivia: La Paz, Santa Cruz de Valle Ameno.	MNCN-42017	3723	EU368904	EU368891
Outgroups					
<i>Leptodactylus griseigularis</i>	Bolivia: La Paz, Serranía Bellavista.	IDLR4118	3815	EU368907	EU368893
<i>Leptodactylus rhodonotus</i>	Bolivia: La Paz, Serranía Bellavista.	–	3836	EU368908	EU368892
<i>Rhinella amboroensis</i>	Bolivia: Santa Cruz, San Juan del Potrero.	MNK-A 5302	–	DQ283386 (3)	
<i>Cryptobatrachus</i> sp.	Colombia: Santander, 7 km by road south-west of San Gil.	JDL 14865		AY326050 (1)	

Numbers in parentheses correspond to sequences used in previous studies: (1) Darst & Cannatella (2004); (2) Faivovich *et al.* (2005); (3) Frost *et al.* (2006).

Abbreviations (other than cited in the text and in Leviton *et al.* 1985): CFBH, Celio F. B. Haddad specimen collection; ICNMNH, Instituto de Ciencias Naturales, Bogotá, Colombia; IDLR, Ignacio de la Riva's field series; JAC, Jonathan A. Campbell's field series; JCC, Juan C. Chaparro's field series; JDL, John D. Lynch's field series; SIUC, Southern Illinois University at Carbondale (USA).

1000 from 10 001 trees were discarded. Following Crawford & Smith (2005), default priors and conditions were used in all cases. Maximum parsimony (MP) analyses were performed in PAUP* 4.0b10 (Swofford, 1998) using heuristic searches under parsimony (with all characters weighted equally), with tree bisection-reconnection (TBR) branch swapping and 1000 random addition sequence replicates, with no limit imposed on the number of trees searched. In order to obtain estimates of clade support, nonparametric bootstrapping was performed with heuristic searches of 1000 replicate datasets, and 100 random addition sequences per dataset, with no limit imposed on the number of trees searched. Gaps were treated as fifth base in both the MP and the Bayesian analyses (Crawford & Smith, 2005).

Phylogenetic analyses are presented in two ways. First, the MP and Bayesian analyses of a 16S plus *cytb*, with a data-partitioned dataset, included 756 equal-weight characters (427 constant, 85 parsimony uninformative, and 224 parsimony informative, with gaps considered as 'fifth-base') of 14 taxa including outgroups. *Leptodactylus griseigularis* and *L. rhodonotus* were used as outgroups for this analysis. We removed 38 and 12 base pairs corresponding to ambiguously aligned regions of the 16S dataset. Second, the MP and Bayesian analyses of the single 16S dataset, with larger taxon sampling, included 479 equal-weight characters (222 constant, 55 parsimony

uninformative, and 192 parsimony informative, with gaps considered as 'fifth-base') of 32 taxa (four outgroups – *Cryptobatrachus* sp., *R. amboroensis*, *L. griseigularis*, and *L. rhodonotus*). Uncorrected pairwise distances for members of *Oreobates* were calculated in PAUP* 4.0b10 from this later dataset after removing ambiguous regions. This larger analysis, and the uncorrected pairwise distances analysis, aimed to test the independence and divergence of species included in *Oreobates* and the *E. discoidalis* group. However, given the limitations of only using mtDNA for phylogenetic inference at the species level (Funk & Omland, 2003), nuclear markers need to be incorporated to complement and/or test our phylogenetic analyses.

RESULTS

Inferred phylogenies and nodal support of Bayesian partitioned analyses of partial 16S and *cytb* support the monophyly of *Oreobates* (bayesian posterior probability, *bpp* = 100), and a group including the *E. conspicillatus* and *Eleutherodactylus martinicensis* series (*sensu* Lynch & Duellman, 1997) (*bpp* = 100; Fig. 1). Maximum parsimony partitioned analysis of partial 16S and *cytb* resulted in two equally most-parsimonious trees, also with statistical support for both clades (bootstrap support, *bss* = 98 and 85 for *Oreobates* and *Eleutherodactylus*, respectively;

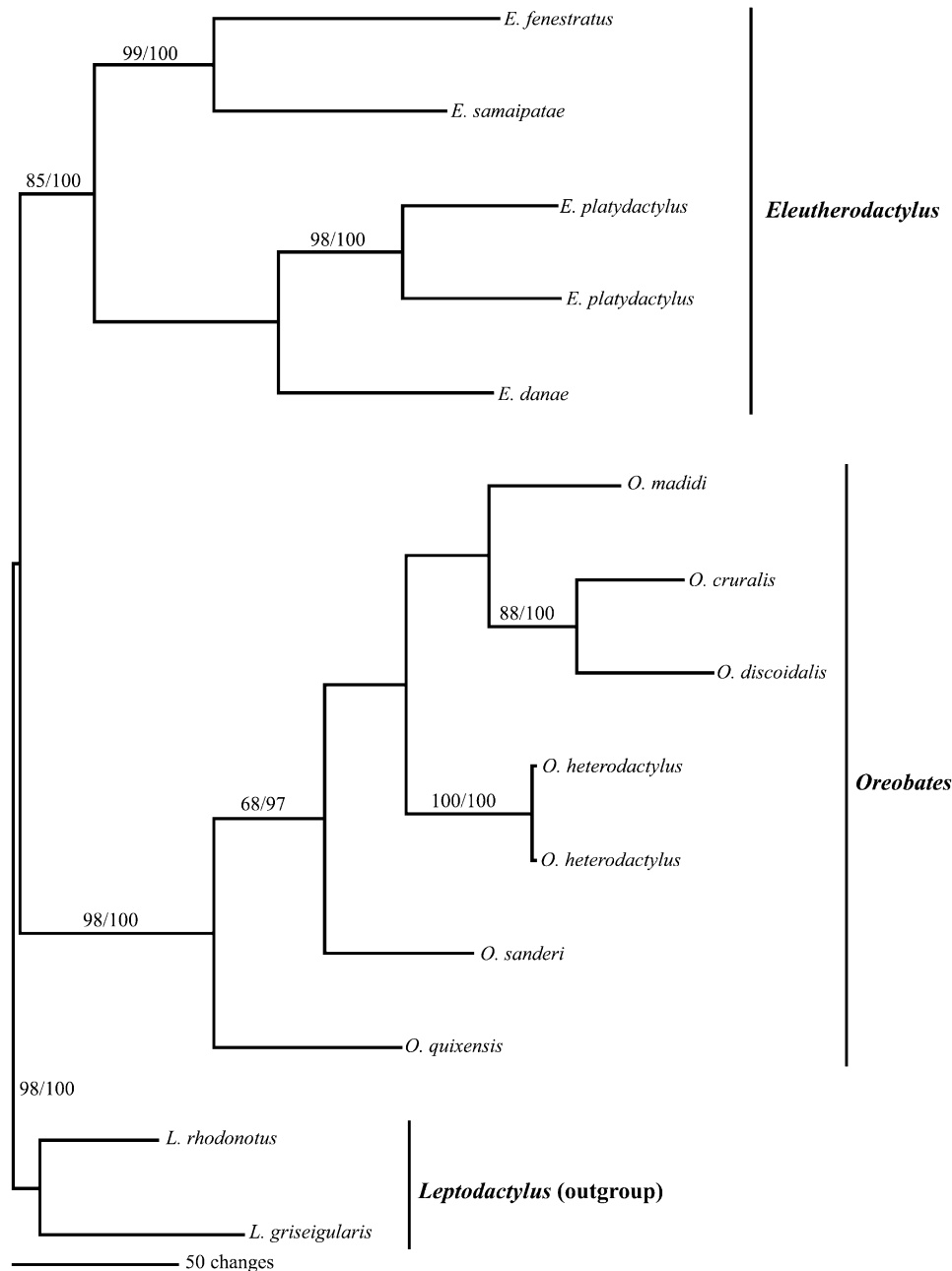


Figure 1. Majority rule consensus tree based on maximum parsimony (MP) and Bayesian phylogenetic analyses of combined data from the partial cytochrome *b* (c. 350 bp) and 16S (c. 590 bp) mitochondrial DNA. The numbers above branches indicate bootstrap support ($\geq 50\%$) for the MP topology, followed by Bayesian posterior probabilities for the Bayesian topology (≥ 95).

Fig. 1). Bayesian analyses of partial 16S alone (with larger taxon sampling) are concordant in their support for the monophyly (bpp = 0.95) of the following main clades: *Oreobates*, *E. conspicillatus* series plus *E. martinicensis* series, *Craugastor*, and *E. dolops* plus *E. nigrovittatus* species groups. Maximum parsimony analysis for the same dataset of partial 16S resulted in three equally most-

parsimonious trees, with statistical support for the monophyly of *Oreobates*, *Craugastor*, and the *E. dolops* group (Fig. 2). Within the clade *Oreobates* there are two evident and well-supported subclades (bpp > 0.98). One clade contains *E. cruralis*, *Eleutherodactylus madidi*, *E. discoidalis*, and *E. heterodactylus*, and the other contains *Oreobates choristolemma*, *O. sanctaerucis*, *Oreobates sanderi* and *Ore-*

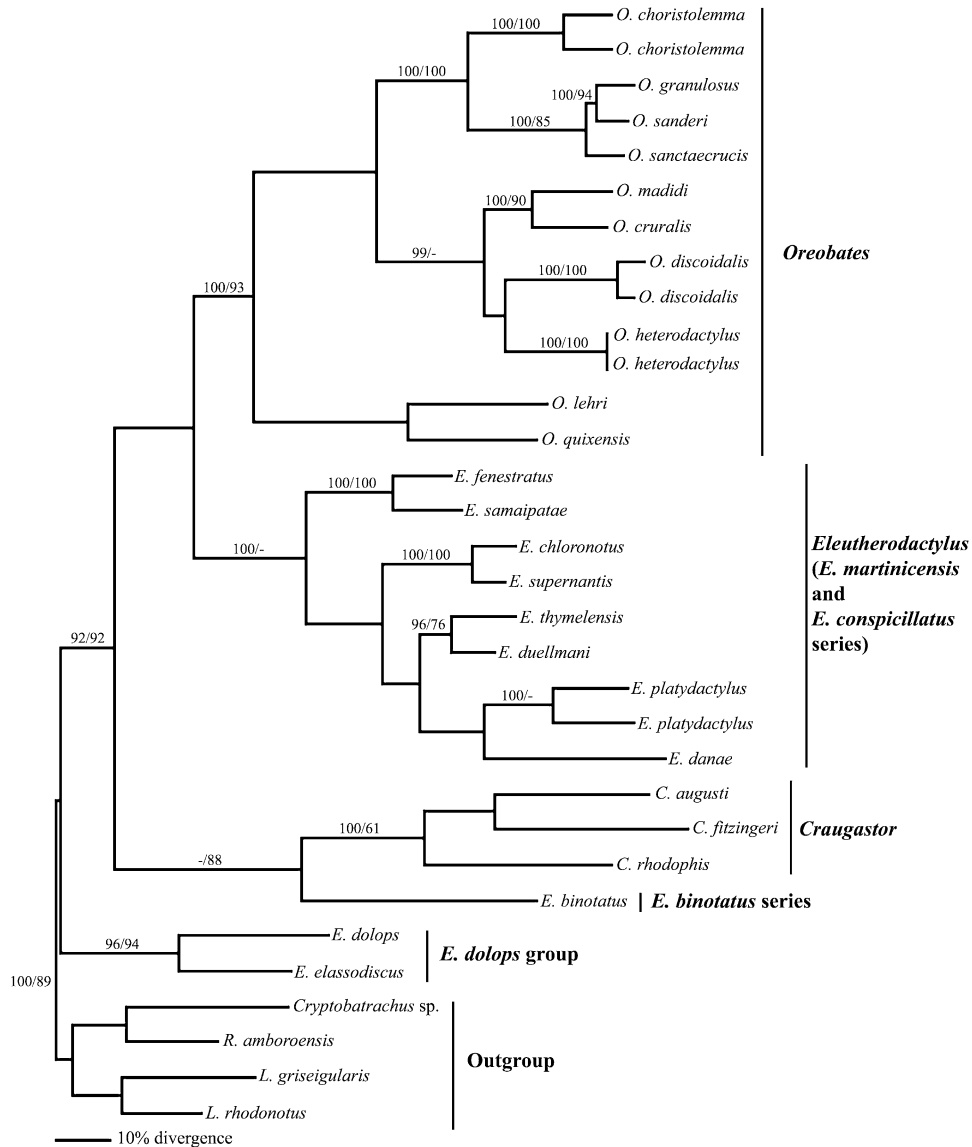


Figure 2. Majority rule consensus tree based on Bayesian phylogenetic analyses of partial 16S (c. 590 bp) mitochondrial DNA of some members of the genera *Oreobates*, *Eleutherodactylus*, and *Craugastor*. The numbers above branches are Bayesian posterior probabilities, followed by bootstrap support for maximum parsimony topology. Values lower than 0.90 Bayesian posterior probability, or lower than 60 for bootstrap, are not depicted.

bates granulosis (Fig. 2). *Oreobates quixensis* and *Oreobates lehri* are the sister group of these two subclades in the Bayesian and MP analyses (Figs 1, 2). The sister group of *Oreobates* is the subgenus *Eleutherodactylus* (including the *E. conspicillatus* and *E. martinicensis* series), and the genus *Eleutherodactylus* turns out to be nonmonophyletic (Fig. 2). The clade that includes species assigned to the Central American genus *Craugastor* (Crawford & Smith, 2005; Frost *et al.*, 2006) has the *E. binotatus* series as sister group, with low bootstrap support (bss = 88%) and no Bayesian support. The *E. dolops* and *E. nigro-*

vittatus species groups are not closely related to *Oreobates*. However, it must be stressed that our taxon and character sampling for all these groups, except our focal groups (*Oreobates* and the *E. discoidalis* group), are incomplete. What is intended herein is to answer the five questions posed in the Introduction.

The clade *Oreobates* includes species assigned to the *E. discoidalis* group by Lynch (1989) and by us (Padiál, González & De la Riva, 2005b; Padiál, Chaparro & De la Riva, 2007; Padiál *et al.*, 2008), and members of the genus *Oreobates* (*sensu* Caramaschi & Canedo, 2006). It also includes *E. heterodactylus*

(Miranda-Ribeiro, 1937), which had already been suggested as belonging to the *E. discoidalis* group (Padial & De la Riva, 2005; Padial *et al.*, 2008). Hence, members of the *E. discoidalis* species group are now included in the genus *Oreobates*. Following the PhyloCode (Cantino & de Queiroz, 2004), the genus *Oreobates* can be node-based defined as the least inclusive crown clade including *Oreobates discoidalis*, *O. lehri*, *O. quixensis*, and *O. sanctaerucis*. Additionally, differences in the 560-bp fragment of the 16S mtDNA also support the specific status of the species assigned to the former *E. discoidalis* group and to *Oreobates* (Table 2), although the value for the pair *O. granulatus*–*O. sanderi* is moderate to low (2.8%).

Regarding external morphology, we propose the presence of enlarged conical plantar supernumerary and subarticular tubercles, together with a smooth texture of the skin covering plantar surfaces, as a synapomorphy for *Oreobates*. Two other putative synapomorphies are the presence of axillary glandular pads and the absence of a vocal sac in males. Harvey & Sheehy (2005) first described the presence of axillary glandular pads for *O. choristolemma*. We additionally found this character in *Oreobates cruralis*, *O. discoidalis*, *O. granulatus*, *Oreobates heterodactylus*, *Oreobates ibischi*, *Oreobates madidi*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, and *O. lehri*. We were not able to look for this character in *Oreobates simmonsii*, *Oreobates saxatilis*, or *Oreobates zongoensis*.

SYSTEMATICS

OREOBATES JIMÉNEZ DE LA ESPADA 1872

Telatrema Miranda-Ribeiro, 1937

Ichnocnema – Lynch & Schwartz (1971)

Oreobates – Caramaschi & Canedo (2006)

Type species: Oreobates quixensis Jiménez de la Espada, 1872: 87. Lectotype: MNCN 1708 (formerly 330).

The genus *Oreobates* includes small to medium-sized frogs (SVL of males, 20–44 mm; of females, 25–63 mm) with the following characters: snout short; sexual dimorphism in size; cranial crests absent; body robust; limbs moderately long; skin of venter smooth; skin on dorsal surfaces from smooth to tuberculate; skin of plantar surfaces smooth (not considering plantar tubercles); axillary and/or inguinal glandular pads present; discoidal fold conspicuous; dorsolateral folds rudimentary or absent; males with faint or absent nuptial pads, vocal slits present, and vocal sac absent; tympanic membrane and annulus conspicuous; finger I longer or equal to finger II; finger tips usually rounded with reduced, or absent, disc struc-

ture, when present only on fingers III and IV, and always with incomplete circumferential grooves and a poorly defined unguis flap; supernumerary and subarticular tubercles present, prominent, subconical to conical, on smooth plantar surface; toe V equal or slightly shorter than toe III, not reaching distal subarticular tubercle of toe IV (condition B *sensu* Lynch & Duellman, 1997); toes lacking discs; webbing absent; no tubercles on heel or tarsus; subarticular tubercles prominent and conical, supernumerary tubercles either absent or few, and round to prominent and conical; dorsal coloration overall brown, with an occipital W-shaped dark mark, an x-shaped mid-dorsal dark mark, and a broad and oblique dark band at the anterior margin of the flanks; dentigerous process of the vomers short, prominent, almost at the level of choanae or between them; mandibular ramus of the trigeminal nerve passing lateral to the m. adductor mandibulae externus (S condition *sensu* Lynch, 1986); reproductive mode by terrestrial eggs with direct development (mode 17 of Duellman & Trueb, 1986); advertisement call consisting of pulsed notes (4–32 pulses), and with low dominant frequency (2000–3800 Hz) (Padial *et al.*, 2008).

The genus *Oreobates* includes 14 species: *O. choristolemma*, *O. cruralis*, *O. discoidalis*, *O. granulatus*, *O. heterodactylus*, *O. ibischi*, *O. lehri*, *O. madidi*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, *O. saxatilis*, *O. simmonsii*, and *O. zongoensis*.

SPECIES ACCOUNTS

OREOBATES CHORISTOLEMMA (HARVEY & SHEEHY, 2005) COMB. NOV.

Ichnocnema choristolemma Harvey & Sheehy, 2005 (Fig. 3A)

Ichnocnema choristolemma Harvey & Sheehy, 2005: 269. Holotype: CBF 5611. Type locality: ‘Serranía de Bellavista, Caranavi Province, La Paz Department, Bolivia, c. 1000 m’ (Fig. 4), coordinates: approx. 15°40’S, 67°30’W.

Diagnosis: A robust *Oreobates* (SVL of adults, 26.7–46.4 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules, and small and large warts; occipital W-shaped fold and/or x-shaped fold on mid-dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present, weak; enlarged warts forming an incomplete dorsolateral fold anteriorly; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length about half to two thirds of eye length; supratympanic fold weak, short; (3) head large, wider than long; snout short, round to subacuminate in dorsal view, round in lateral view;

Table 2. Percentage of divergence based on uncorrected-p distances in partial 16S mitochondrial DNA (c. 560 bp) between several members of *Oreobates*

	<i>choristolemma</i>	<i>cruralis</i>	<i>discoidalis</i>	<i>granulosus</i>	<i>heterodactylus</i>	<i>lehri</i>	<i>madidi</i>	<i>quixensis</i>	<i>sanctaerucis</i>
<i>cruralis</i>	9.2								
<i>discoidalis</i>	10.9	9.8							
<i>granulosus</i>	4.7	9.6	13.0						
<i>heterodactylus</i>	10.2	8.3	9.8	9.5					
<i>lehri</i>	11.0	11.2	10.8	11.2	11.7				
<i>madidi</i>	9.6	6.4	9.6	10.2	9.6	11.1			
<i>quixensis</i>	10.4	11.3	11.2	11.1	11.4	10.9	12.1		
<i>sanctaerucis</i>	3.7	8.5	11.9	3.5	9.3	10.8	9.4	10.9	
<i>sanderi</i>	5.0	9.4	12.4	2.8	10.1	11.7	10.2	11.3	3.2

canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small warts and granules; (5) dentigerous process of the vomers large, triangular, posteromedial to choanae; (6) males with vocal slits and nuptial pads; (7) hands with long and slender fingers, first finger equal or slightly shorter than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large or small, round to conical, smaller than subarticular tubercles; tips of fingers III and IV truncate, slightly enlarged, lacking circumferential grooves and unguis flaps; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles conspicuous, conical; (11) toes long and slender (foot length 50% of SVL), lateral fringes weak or absent, webbing absent; toe V reaching the distal margin of the second subarticular tubercle of toe IV, and toe III reaching the proximal margin; tips of toes moderately enlarged, rounded to truncate, with indented or notched unguis flap; (12) axillary glands present or absent; (13) dorsum brown with darker markings, lips and limbs barred, W-shaped mark in suprascapular region, venter drab brown with cream flecks; posterior surface of thigh and groin unpatterned.

Oreobates choristolemma is most similar to *O. granulosus*, *O. lehri*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, and *O. saxatilis*, from which it can be distinguished by the combination of enlarged finger and toe tips with notched unguis flaps, dorsolateral folds, and iris metallic green. Additionally, it can be distinguished (character of other species in parentheses) from *O. granulosus* by the larger size of females (SVL, 34.4–39.5 mm) (Table 3); from *O. lehri* by shorter feet, FL/SVL = 50% (60–70%); from *O. sanctaerucis* by dorsal coloration without scarlet flecks; from *O. simmonsii* by lacking ulnar tubercles (abundant, round, small, pungent ulnar tubercles), and head wider than long; from *O. zongoensis* by having dorsal skin irregularly covered with enlarged warts and granules (densely and homogeneously granular, round, pungent keratinized granules).

Remarks: This species was only known from the holotype and paratypes collected in the Yungas de la Paz, Bolivia. No additional specimens were known prior to this study. Although we were not able to review the types, the precise original description allowed us to identify some specimens from Bolivia (see Appendix) as *O. choristolemma*. The specimens we studied show three main diagnostic characters: the presence of axillary glandular pads, enlarged discs on fingers III and IV, and a notched unguis flap (Harvey & Sheehy,



2005). However, axillary, inguinal, and sacral glandular pads are present in other species of the genus (see above). Nevertheless, the presence of an indented (notched) unguis flap is exclusive for this species (among members of this genus). The specimen

ZFMK 72569, from Chapare Province, Departamento Cochabamba, Bolivia, represents the southernmost record of this species, and increases its distribution area by about 500 km to the south. This specimen is an adult female (SVL, 41.0 mm), with enlarged and

Figure 3. Photographs of adult specimens of *Oreobates*. A, *Oreobates choristolemma* from Altamachi, Department Cochabamba, Bolivia. B, *Oreobates cruralis* from the road to Bellavista, Department Santa Cruz, Bolivia. C, *Oreobates cruralis* from Chalalán, Department La Paz, Bolivia. D, *Oreobates discoidalis* Serranía Aguaraquí, Department Tarija, Bolivia. E, *Oreobates granulatus* (female) from Santo Domingo, Department Puno, Peru. F, *Oreobates granulatus* (male) from Santo Domingo, Department Puno, Peru. G, *Oreobates heterodactylus* from Serranía de Santiago, Department Santa Cruz, Bolivia. H, *Oreobates ibischi* from Masicurí, Department Santa Cruz, Bolivia. I, *Oreobates lehri* from Cosñipata Valley, Department Cusco, Peru. J, *Oreobates madidi* from Serranía Eslabón, Department La Paz, Bolivia; K, *Oreobates quixensis* from Amacayacu, Department Amazonas, Colombia; L, *Oreobates sanctaerucis* from El Chapé, Department Santa Cruz, Bolivia; M, *Oreobates sanderi* from Santa Cruz de Valle Ameno, Department La Paz, Bolivia. N, *Oreobates saxatilis* from Ponga de Shilcayo, Department San Martín, Peru; O, *Oreobates zongoensis* from Valle de Zongo, Department La Paz, Bolivia.

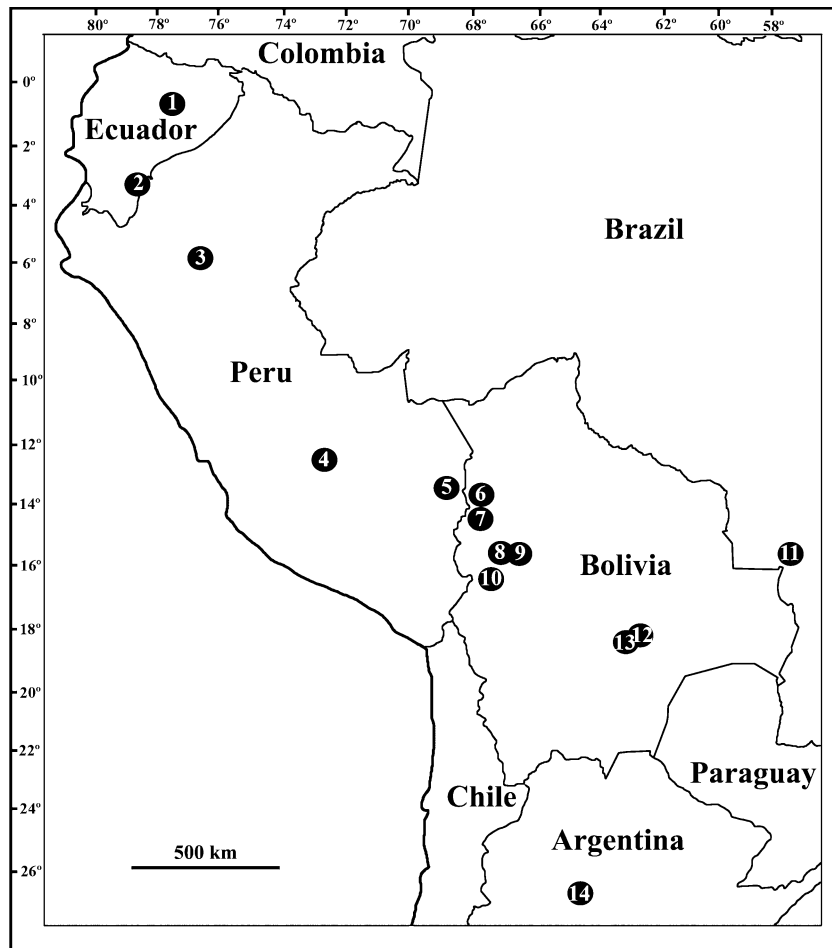


Figure 4. Type localities of members of *Oreobates*: (1) *O. quixensis*, San José de Moti, Prov. Napo, Ecuador; (2) *O. simmonsii*, Río Piuntza, 1830 m a.s.l., Cordillera del Cóndor, Prov. Morona-Santiago, Ecuador; (3) *O. saxatilis*, Ponga de Shilcayo, 470 m a.s.l., Department San Martín, Peru; (4) *O. lehri*, Apurimac River Valley, 2445 m a.s.l., Department Cusco, Peru; (5) *O. granulatus*, Santo Domingo, Carabaya, Department Puno, Peru, 1800 m a.s.l.; (6) *O. madidi*, Arroyo Huacataya, Serranía Eslabón, 1500 m a.s.l., Department La Paz, Bolivia; (7) *O. sanderi*, Arroyo Bilunto, Chunirumi Valley, 1800 m a.s.l., near Santa Cruz de Valle Ameno, Department La Paz, Bolivia; (8) *O. zongoensis*, Valle de Zongo, 1250 m a.s.l., Department La Paz, Bolivia; (9) *O. choristolemma*, Serranía de Bellavista c. 1000 m a.s.l., Department La Paz, Bolivia; (10) *O. cruralis*, Department La Paz, Bolivia, 4000 m a.s.l. (in error); (11) *O. heterodactylus*, gruta Facendinha, State Mato-Grosso, Brazil; (12) *O. ibischi*, km 68.5 on Santa Cruz de la Sierra-Samaipata road c. 750 m a.s.l., Department Santa Cruz, Bolivia; (13) *O. sanctaerucis*, El Chapé, Department Santa Cruz, Bolivia, 2060 m a.s.l.; (14) *O. discoidalis*, Tucumán, Prov. Tucumán, Argentina.

Table 3. Measurements and proportions of the three species of *Oreobates* redescribed herein (mean \pm standard deviation follow ranges in parentheses). See text for abbreviations

	<i>O. cruralis</i>						<i>O. discoidalis</i>						<i>O. granulatus</i>					
	Males (N = 44)		Females (N = 34)		Males (N = 8)		Females (N = 23)		Males (N = 6)		Females (N = 6)							
SVL	20.3–30.2 (24.8 \pm 2.2)	24.9–33.6 (29.3 \pm 2.0)	25.6–30.4 (27.9 \pm 1.4)	29.5–39.7 (34.7 \pm 2.3)	22.6–28.5 (26.6 \pm 2.1)	34.4–39.5 (36.9 \pm 1.7)												
HL	7.6–11.5 (9.4 \pm 0.7)	8.9–11.8 (10.7 \pm 0.7)	9.2–11.3 (10.3 \pm 0.7)	11.3–14.5 (12.5 \pm 0.7)	9.0–11.1 (10.4 \pm 0.8)	13.0–17.5 (14.8 \pm 1.5)												
HW	7.3–10.6 (8.7 \pm 0.7)	9.1–11.6 (10.1 \pm 0.6)	8.4–11.0 (9.6 \pm 0.8)	10.7–13.9 (11.8 \pm 0.8)	9.1–11.4 (10.4 \pm 0.8)	13.3–15.2 (14.4 \pm 0.8)												
EL	2.9–4.6 (3.6 \pm 0.4)	2.9–4.7 (4.0 \pm 0.4)	3.4–4.2 (3.7 \pm 0.3)	3.7–5.5 (4.4 \pm 0.4)	3.2–4.6 (3.8 \pm 0.5)	4.1–5.2 (4.5 \pm 0.5)												
EN	2.0–3.6 (2.8 \pm 0.3)	2.4–3.7 (3.2 \pm 0.3)	2.7–3.6 (3.3 \pm 0.3)	3.1–5.0 (3.9 \pm 0.4)	2.8–3.7 (3.1 \pm 0.3)	3.8–4.7 (4.3 \pm 0.4)												
IND	1.8–3.1 (2.4 \pm 0.3)	2.2–3.3 (2.7 \pm 0.2)	2.2–2.8 (2.5 \pm 0.2)	2.6–3.6 (3.1 \pm 0.2)	2.4–3.1 (2.7 \pm 0.3)	3.2–3.9 (3.6 \pm 0.3)												
EE	2.9–5.1 (4.4 \pm 0.4)	4.4–6.2 (5.0 \pm 0.4)	4.2–5.3 (4.7 \pm 0.3)	5.1–6.5 (5.7 \pm 0.4)	4.1–5.2 (4.8 \pm 0.4)	5.6–6.5 (6.0 \pm 0.4)												
TYH	1.5–2.3 (1.9 \pm 0.2)	0.7–2.6 (2.1 \pm 0.4)	1.5–2.3 (2.0 \pm 0.3)	2.0–2.9 (2.6 \pm 0.2)	1.5–2.1 (1.9 \pm 0.3)	2.4–2.8 (2.6 \pm 0.2)												
TYL	1.4–2.2 (1.7 \pm 0.2)	0.7–2.5 (2.0 \pm 0.3)	1.5–2.3 (2.0 \pm 0.3)	1.8–2.9 (2.3 \pm 0.3)	1.5–2.1 (1.9 \pm 0.2)	2.2–2.6 (2.4 \pm 0.2)												
FA	4.8–6.7 (5.6 \pm 0.5)	5.2–7.3 (6.6 \pm 0.5)	5.5–7.4 (6.3 \pm 0.6)	6.5–9.0 (7.6 \pm 0.7)	5.4–7.4 (6.2 \pm 0.7)	7.8–9.2 (8.4 \pm 0.7)												
TL	11.3–15.5 (13.5 \pm 2.6)	12.3–17.7 (14.5 \pm 1.3)	13.4–15.1 (14.2 \pm 0.5)	15.5–20.3 (17.8 \pm 1.0)	12.3–16.1 (14.4 \pm 1.4)	19.0–21.1 (19.8 \pm 0.8)												
TH	9.0–14.2 (12.5 \pm 1.1)	12.3–17.4 (14.2 \pm 1.2)	12.2–14.8 (13.3 \pm 1.0)	14.7–19.0 (16.8 \pm 1.1)	11.8–15.3 (14.0 \pm 1.2)	16.8–19.4 (18.0 \pm 1.0)												
FL	10.5–15.3 (12.9 \pm 1.1)	1.0–17.7 (14.1 \pm 2.7)	12.5–14.8 (13.4 \pm 0.8)	14.4–20.5 (17.2 \pm 1.4)	12.3–16.4 (14.6 \pm 1.4)	18.9–20.8 (19.9 \pm 0.8)												
TL/SVL	0.7–1.3 (0.9 \pm 0.2)	0.3–0.6 (0.5 \pm 0.0)	0.5–0.5 (0.5 \pm 0.0)	0.5–0.6 (0.5 \pm 0.0)	0.5–0.6 (0.5 \pm 0.0)	0.5–0.6 (0.5 \pm 0.0)												
FL/SVL	0.5–0.6 (0.5 \pm 0.0)	0.5–0.6 (0.5 \pm 0.0)	0.4–0.5 (0.5 \pm 0.0)	0.4–0.6 (0.5 \pm 0.0)	0.5–0.6 (0.6 \pm 0.0)	0.5–0.6 (0.5 \pm 0.0)												
HL/SVL	0.3–0.4 (0.4 \pm 0.0)	0.3–0.4 (0.4 \pm 0.0)	0.4–0.4 (0.4 \pm 0.0)	0.3–0.4 (0.4 \pm 0.0)	0.4–0.4 (0.4 \pm 0.0)	0.4–0.5 (0.4 \pm 0.1)												
HW/SVL	0.3–0.4 (0.4 \pm 0.0)	0.3–0.4 (0.3 \pm 0.0)	0.3–0.4 (0.3 \pm 0.0)	0.3–0.4 (0.3 \pm 0.0)	0.4–0.4 (0.4 \pm 0.0)	0.4–0.4 (0.4 \pm 0.0)												
HW/HL	0.8–1.1 (0.9 \pm 0.1)	0.8–1.1 (0.9 \pm 0.0)	0.9–1.0 (0.9 \pm 0.0)	0.9–1.0 (0.9 \pm 0.0)	0.9–1.1 (1.0 \pm 0.1)	0.8–1.1 (1.0 \pm 0.1)												
EN/EL	0.6–1.0 (0.8 \pm 0.1)	0.6–1.1 (0.8 \pm 0.1)	0.8–1.0 (0.9 \pm 0.1)	0.7–1.1 (0.9 \pm 0.1)	0.7–1.0 (0.8 \pm 0.1)	0.9–1.1 (1.0 \pm 0.1)												
EL/HW	0.4–0.5 (0.4 \pm 0.0)	0.3–0.5 (0.4 \pm 0.0)	0.4–0.4 (0.4 \pm 0.0)	0.3–0.4 (0.4 \pm 0.0)	0.3–0.4 (0.4 \pm 0.0)	0.3–0.3 (0.3 \pm 0.0)												
TYL/TYH	0.7–1.3 (0.9 \pm 0.1)	0.5–1.2 (0.9 \pm 0.1)	0.9–1.0 (1.0 \pm 0.0)	0.7–1.1 (0.9 \pm 0.1)	0.9–1.1 (1.0 \pm 0.1)	0.9–1.0 (0.9 \pm 0.0)												

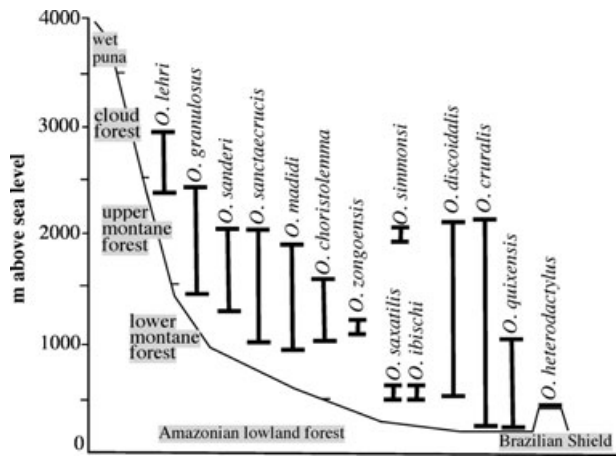


Figure 5. Altitudinal distribution across habitat types of members of the genus *Oreobates*.

indented fingers III and IV, and without axillary glands. Harvey & Sheehy (2005) did not report any condition of nuptial excrescences because the type series is composed of an adult female and a subadult male. The specimen CBG 767, an adult male (SVL, 28.7 mm), has posterolateral vocal slits and a single, white, glandular, nonspinous nuptial pad on the dorsal surface of each thumb. All but one specimen (CBG 765) of the series CBG 765–768, from Yungas de La Paz, show axillary glands. All of these specimens have moderately enlarged discs on fingers III and IV with notched ungual flaps. All the specimens we examined lack toe or finger fringes.

Distribution. This species inhabits the humid forest of the Andean foothills from 1000 to 1500 m a.s.l., from Yungas de Cochabamba to Yungas de La Paz, central Bolivia (Figs 4, 5).

***OREOBATES CRURALIS* (BOULENGER, 1902)**

COMB. NOV.

Hylodes cruralis Boulenger (1902)

Eleutherodactylus cruralis – Stejneger (1904)
(Figs 3B–C, 6A–B)

Hylodes cruralis Boulenger, 1902: 396. Holotype: BM 1947.2.15.70 (formerly 1901.8.2.44). Type locality: ‘La Paz, Bolivia, 4000 m’ (Fig. 4).

Lynch (1989) redescribed this species after examining the holotype. He also studied numerous specimens from Bolivia and Peru deposited in several collections. He confronted two problems. One, the type locality of *H. cruralis* was La Paz, Bolivia, 4000 m a.s.l. (type collected by P. O. Simmons). Lynch considered this locality to be in error, which was subsequently supported by De la Riva (1990), De la

Riva (1993), and De la Riva *et al.* (2000). The second problem was the great variability in the size of adults. Most of these specimens were in very poor preservation condition, and therefore many subtle morphological characters were difficult or impossible to observe or identify with confidence. Moreover, the specimens studied by Lynch came from very different altitudes and habitats. For example, the largest sample available to him was the series AMNH 6060–73, and the locality of procedence ‘Juliaca’ was also in error, as it lies in the dry altiplano of southern Peru.

De la Riva *et al.* (2000) previously stated that what was considered *E. cruralis* could be in reality a composite of more than one species. Some species described recently were similar in external appearance to *E. cruralis* (*O. ibischi* and *O. madidi*), and differences in advertisement calls were pivotal for assessing their distinctness (Reichle, Lötters, & De la Riva, 2001; Padial *et al.*, 2005b; Padial *et al.*, 2008). We studied 181 specimens of *E. cruralis* from Bolivia and Peru, collected by us as well as those deposited in various collections, including the holotype and almost all specimens studied by Lynch (1989). After recognizing *O. granulatus* (see below), *O. ibischi*, *O. madidi*, *O. sanderi*, and *O. lehri*, *O. cruralis* can be defined with confidence. The redescription of *E. cruralis* by Lynch (1989) is not only based on the holotype, but on a series of specimens. Furthermore, in our point of view, the series examined by him contain three different species (*O. cruralis*, *O. granulatus*, and *O. sanderi*). Hence, in order to avoid confusion we provide a thorough diagnosis of *O. cruralis* and a redescription based exclusively on the holotype. The study of the intraspecific variation is based on additional specimens listed in the Appendix.

Diagnosis: A small *Oreobates* (SVL of adults, 20.3–33.6 mm) characterized as follows: (1) skin on dorsum coarsely shagreened without keratinized granules, texture composed of small, round, low, flat warts, regular in size, only some of them slightly enlarged; warts on flanks slightly larger than those of dorsum; a pair of incomplete dorsolateral folds composed by enlarged warts; venter smooth; posterior surfaces of limbs smooth; discoidal fold present; postrictal glands present; (2) tympanic membrane and annulus distinct, about half the eye length; supratympanic fold weak and short; (3) head large, slightly longer than wide; snout round in dorsal and lateral views; canthus rostralis sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small granules; (5) dentigerous process of vomers large, situated posteromedial to choanae; (6) males with vocal slits and no nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent,



Figure 6. Type specimens of some members of *Oreobates*. A–B, holotype of *O. cruralis* (BM 1947.2.15.70); C–D, holotype of *O. simmonsii* (KU 147068); E–F, paralectotype of *O. discoidalis* (BM 1947.2.15.63); G–H, holotype of *O. granulatus* (BM 1947.2.15.72); I–J, lectotype of *O. quixensis* (MNCN 1708).

conical; supernumerary tubercles large, prominent, round to conical, smaller than subarticular tubercles; tips of fingers III and IV truncate, slightly enlarged, lacking circumferential grooves and unguis flaps; lateral fringes and keels on fingers from moderate to absent; (8) ulnar tubercles absent; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle ovate to round, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles conical, prominent; (11) toes long and slender (foot length 50% of SVL), lateral fringes weak or absent, webbing absent; fifth and third toes reaching mid-point of second subarticular tubercle of toe IV; tips of toes moderately enlarged, rounded, unguis flap not indented; (12) axillary gland present; (13) dorsal coloration pale brown to dark brown or greyish-brown, with W-shaped occipital and mid-dorsal X-shaped dark marks, or a pair of cream dorsolateral stripes and a short longitudinal sacral stripe; throat and chest light grey to dark brown; belly cream with brown mottling or reticulations on anterior margin.

Oreobates cruralis can be distinguished from other *Oreobates* (characters of other species in parentheses) as follows: from *O. choristolemma* by lacking keratinized granules on dorsum, smaller size (SVL of the single known adult female, 46.4 mm) (Table 3), and lacking indented unguis flap on finger discs; from *O. discoidalis* by having warty dorsal skin (finely shagreened with few enlarged warts in some specimens); moderately enlarged and truncate tips on fingers III and IV (enlarged and ovate); dentigerous process of vomers posteromedial to choanae (between choanae); canthus rostralis sinuous in dorsal view and round in lateral profile (straight and sharp); differences in advertisement call and habitat (Padial *et al.*, 2008). From *O. granulatus* by having slightly enlarged and truncate tips on fingers III and IV (rounded, not enlarged); dorsal skin coarsely shagreened, composed of round low warts, without keratinized granules on dorsum (dorsal skin with low, round, nonpungent keratinized granules and warts); smaller SVL of adult females, 24.9–33.6 mm (SVL, 34.4–39.5 mm), and head longer than wide (equal) (Table 3); by having numerous, conical, and prominent supernumerary tubercles on feet (supernumerary tubercles low, few, round). From *O. heterodactylus* by having coarsely shagreened dorsal skin with enlarged warts (smooth); slightly enlarged and truncate tips of fingers III and IV (very enlarged and ovate); numerous, conical, and prominent supernumerary tubercles on feet (supernumerary tubercles low, few, round); advertisement call, and habitat (Padial *et al.*, 2008). From *O. ibischi* by having tympanum length half or less than half of eye length (more than half of eye length); coarsely shagreened dorsal skin with enlarged warts (smooth to finely shagreened with some enlarged warts); slightly

enlarged and truncate tips on fingers III and IV (enlarged and ovate, finger tips two times wider than the digit); numerous, conical, and prominent supernumerary tubercles on feet (supernumerary tubercles low, scarce, round); head longer than wide (wider than long); differences in advertisement call and habitat (Padial *et al.*, 2008). From *O. lehri* by having slightly enlarged and truncate tips on fingers III and IV (finger tips not expanded); first finger longer than second (finger I equal to finger II); smaller size of adult males and females (SVL, 31.0–39.9 mm) (Table 3); shorter feet, FL/SVL = 50% (60%); numerous conical and prominent supernumerary tubercles on feet (supernumerary tubercles low, few, round). From *O. madidi* by having dorsal skin with small, round, uniform warts, with sparse enlarged warts (homogeneously warty, larger warts), slightly enlarged and truncate tips on fingers III and IV (rounded finger tips), and advertisement call (Padial *et al.*, 2005b, 2008). From *O. quixensis* by smaller size, mean SVL of males and females, 24.8 and 29.3 mm, respectively (mean SVL of adult males, 39.0 mm, $N = 9$; mean SVL of adult females, 50.4 mm, $N = 14$) (Table 3); coarsely shagreened dorsal skin with enlarged warts (dorsal skin coarsely tuberculate, with enlarged and prominent warts and granules, some of them keratinized); slightly enlarged and truncate tips on fingers III and IV (rounded finger tips). From *O. sanctaerucis* by smaller size, mean SVL of males and females, 24.8 and 29.3 mm, respectively (mean SVL of adult males, 35.2 mm, $N = 3$; mean SVL of adult females, 46.0 mm, $N = 3$) (Table 3); coarsely shagreened dorsal skin with enlarged warts (dorsal skin coarsely tuberculate, with enlarged and prominent warts and granules, some of them keratinized); slightly enlarged and truncate disc on fingers III and IV (rounded finger tips). From *O. sanderi* it differs by smaller size (mean SVL of adult males, 29.2 mm, $N = 6$; mean SVL of adult females, 36.5 mm, $N = 4$) (Table 3); head longer than wide (wider than long); coarsely shagreened dorsal skin with enlarged warts (dorsal skin covered by sparse keratinized granules and some warts); slightly enlarged and truncate tips on fingers III and IV (rounded finger tips). From *O. saxatilis* by smaller size, mean SVL of females, 29.3 mm (49.0 and 43.7 mm, holotype and paratype, respectively) (Table 3); coarsely shagreened dorsal skin with enlarged warts (dorsal skin coarsely tuberculate, with enlarged and prominent warts and granules, some of them keratinized); slightly enlarged and truncate disc on fingers III and IV (rounded finger tips). From *O. simmonsii* by having coarsely shagreened dorsal skin with enlarged warts (densely granular with round, pungent, keratinized granules); slightly enlarged and truncate tips on fingers III and IV (rounded finger tips); ulnar tubercles absent (abundant, round, small). From *E. zongoensis*

by having coarsely shagreened dorsal skin with enlarged warts (densely granular with round, pungent, keratinized granules); slightly enlarged and truncate tips on fingers III and IV (rounded finger tips); head longer than wide (wider than long).

Description of the holotype: An adult female (small ovarian eggs) with head slightly longer than wide; snout round in dorsal view, and round to subacuminate in lateral profile; nostrils slightly protuberant, orientated dorsolaterally; canthus rostralis straight in dorsal view, round in frontal profile; loreal region slightly concave, sloping gradually to the lips; lips not flared; upper eyelid without tubercles, but covered by small warts; no cranial crests. Supratympanic fold distinct, thin, short; tympanic membrane and its annulus, distinct; tympanic membrane slightly ovate vertically, its length about two-fifths of eye length; two postrectal glands. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae large, round, lateral, separated by distance equal to four times the diameter of a choana; the specimen has one discernible vomerine odontophore, situated posteromedial to and far from the choanae. Skin texture of dorsal surfaces and posterior parts of hind limbs composed of small, low, round warts; ventral surfaces smooth; a W-shaped occipital fold; no dorsolateral folds; discoidal fold evident.

Ulnar tubercles absent; palmar tubercle bifid, flat, prominent; thenar tubercle ovate, prominent, two-thirds of the size of the palmar tubercle; supernumerary tubercles large, round, prominent, smaller than subarticular tubercles; subarticular tubercles large, prominent, subconical; tips of fingers I and II round, not enlarged, and those of fingers III and IV moderately enlarged, truncate; basal lateral fringes on fingers I–III; relative length of fingers: $II < I \leq IV < III$.

Toes long and slender (foot length 50% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle round, prominent, slightly larger than outer metatarsal tubercle; outer metatarsal tubercle round, conical; six supernumerary tubercles, small, round to elongate; subarticular tubercles prominent, subconical to conical; toes with basal lateral fringes; toes I and II with tips rounded, not expanded, toes III–V with slightly enlarged and truncate tips; unguis not indented; relative length of toes, $I < II < V < III < IV$; toes III and V reaching penultimate subarticular tubercle of toe IV.

Dorsal surfaces reddish brown, with darker marks including a W-shaped occipital dark brown mark, an interocular bar, two subocular dark brown stripes, and a supratympanic stripe. Arms and hindlimbs light brown with transverse brown stripes; concealed sur-

faces of hindlimbs brown; flanks beige with dark brown spots that merge in an oblique wide band posterior to the arm insertion; ventrally cream with fine grey mottling on throat, chest, and anterior margin of belly.

Measurements of the holotype: SVL, 27.4 mm; HL, 8.9 mm; HW, 9.2 mm; EL, 4.1 mm; EN, 3.2 mm; IND, 2.4 mm; EE, 4.4 mm; TYH, 1.7 mm; TYL, 1.4 mm; FA, 5.6 mm; TL, 14.6 mm; TH, 14.1 mm; FL, 14.0 mm.

Variation: The most variable characters of *O. cruralis* are the size of adults and the coloration. These two characters can lead to confusion with other species. Although we have removed several taxa (with different adult sizes) from what was thought to be '*O. cruralis*' (see remarks section below and on *O. granulatus*), the variation in size of this species is still considerably high compared with other members of this genus. However, this is the species for which the largest data set has been analysed, and hence such observed variability may be influenced by sample size. Adult males of *O. cruralis* range from 20.3 to 30.2 mm, and females from 24.9 to 33.6 mm. The sizes of males and females overlap broadly. Another very relevant character is skin texture, but this character is easily diagnosable under a stereomicroscope. The dorsal skin texture of this species varies from scarcely warty (almost smooth) to densely and homogeneously warty with few or abundant enlarged warts. We consider the skin texture to be warty, although it has also been considered as rugose (Boulenger, 1902), shagreened, or smooth to finely areolate (Padial *et al.*, 2005a, b). The relevant distinction is that the dorsal skin of this species lacks granules (i.e. hard, keratinized structures, usually rounded or conical) or tubercles (enlarged, prominent, conical warts). All dorsal warts are always flat, low, and constitute soft structures. As in *O. granulatus* and *O. sanderi*, there are two colour morphs. The most common morph consists of a pale to dark brown or reddish brown dorsum, with pale and dark irregular flecks, a W-shaped mark on occipital region, and a x-shaped mark on the mid-dorsum, one or two broad dark oblique bands on flanks, and dark interocular, labial, and transversal bars on the extremities. This pattern occurs in 60 of 91 (66%) specimens for which the colour pattern was noted. Another 26 specimens (29%) show the following colour pattern: a pale to dark brown or reddish brown dorsum outlined by a pair of pale dorsolateral bands, a sacral stripe, and two wide dark brown stripes on flanks, one anterior to the groin and one posterior to the arm insertion, with the transverse bars on the extremities less evident. The intensity and tonalities of both patterns varies. A third, rare colour pattern, shared only with *E. madidi*, is the presence of a thin, white (in alcohol,

yellow in life) mid-dorsal stripe from snout to vent. This pattern was observed in five specimens (one female and four males). In all three morphs, the ventral pattern is similar: overall cream with fine mottling on throat and chest, mottling varying in density, intensity, and colour, from grey to dark brown. Other variable characters are as follows. Although breeding males of *O. cruralis* do not have nuptial pads, a nonswollen white region can be observed on the dorsal surface of the thumbs of some individuals. Axillary glands can be present or absent, or present on only one side; finger fringes can be present (weak) or absent; a faint thin mid-dorsal fold is shown in some specimens; the number of supernumerary tubercles on a single toe varies from two to four, and from weak to prominent; the degree of enlargement of finger tips of fingers III and IV varies, although this variation seems to be related to fixation. The most divergent specimens studied by us are those from La Hoyada (MNK A 5577 and ZFMK 72644), which are overall dark greyish-brown, and have conspicuous finger and toe fringes. Specimens from the lowlands of Peru (KU207749, 215461–2) seem to have slightly indented unguis flaps on the fingers. Specimens from higher altitudes are more affected by parasitic subdermal mites (see Wohltmann, Köhler & Martin, 2006), which may lead one to think they have unusual skin structures.

Remarks: The specimens AMNH 91579, 153046, 153085, 153086, and KU 173230–32 were identified in collections as *O. cruralis*, but they are neither *O. cruralis* nor any other known species of *Oreobates*. The specimens AMNH 91579, KU 173230–32, and MZUM 64120 and 135341, identified by Lynch (1989) as *O. cruralis*, do not correspond with any known species of *Oreobates*. The specimen KU 182814 illustrated as *O. cruralis* (see Harvey & Keck 1995: fig 3) is an adult female of *O. discoidalis*. The comparison between *O. discoidalis* and *O. cruralis* provided by Ceï (1987) includes some observations that do not correspond with characters of *O. cruralis*. The broad range of adult size and intraspecific genetic distances, the broad altitudinal gradient occupied by this species (including several life zones), and the broad latitudinal distribution, together with some differences in advertisement calls (Padial *et al.*, 2008), suggest that the name *O. cruralis* is perhaps still being applied to more than one species. The best candidates to be recognized as new species are those populations from humid montane forests and cloud forests in the departments of Cochabamba and Santa Cruz, Bolivia, but our data are still inconclusive.

Distribution: This species inhabits the lowland rainforests, humid forests, and cloud forests of the Andean foothills from 200 to 2000 m a.s.l., from

Department Cusco in southern Peru to Department Santa Cruz in central Bolivia (Figs 4, 5). This species also reaches the semideciduous forests of the inter-Andean valleys of central Bolivia. Ceï (1987) tentatively cited *O. cruralis* for Argentina without locality, but Lavilla & Ceï (2001) discarded this possibility. Köhler (2000), Reichle *et al.* (2001), and Padial *et al.* (2008) described its advertisement call. Some data on its biology and ecology can be found in Köhler (2000), Doan & Arizábal (2002), and Duellman (2005).

OREOBATES DISCOIDALIS (PERACCA, 1895)

COMB. NOV.

Hylodes discoidalis Peracca, 1895

Eleutherodactylus discoidalis – Stejneger (1904) (Figs 3D, 6E–F)

Hylodes discoidalis Peracca, 1895: 24. Lectotype: MZUT An 427.1. Type locality: ‘Tucumán (Argentina)’ (Fig. 4), coordinates approx. 26°50’S, 65°13’W.

Lynch (1989) redescribed this species based on type material, but neither Peracca (1895) nor Lynch designated one of the syntypes as a lectotype. Lynch’s (1989) redescription is based on the syntypes BM 1947.2.15.63–65 and several syntypes deposited in the MZUT, Torino, Italy. The lectotype was designated by Gavetti & Andreone (1993) from the MZUT series. Although they mention that the lectotype was in a good state of preservation, the plate provided evidence that the specimen was not very well preserved. Moreover, the description of the lectotype is rather incomplete (for example it does not include data on skin texture, tubercles on plantar surfaces, or the degree of development of finger and toe tips). The BM series that we studied is better preserved and, in order to avoid future misidentification, we herein describe the best-preserved specimen of this series (BM 1947.2.15.63) (Fig. 6E, F), which is in general very similar to the lectotype.

Diagnosis: a medium-sized *Oreobates* (SVL of adults, 25.6–39.7 mm) characterized as follows: (1) skin of dorsum finely shagreened or smooth, with low warts; posterior surfaces of limbs smooth; discoidal fold present; no dorsolateral folds; large postrictal glands; (2) tympanic membrane and annulus distinct, its length longer than half of the eye length; supratympanic fold prominent; (3) head longer than wide; snout long, subacuminate in dorsal view, round in lateral profile; canthus rostralis straight in dorsal view, sharp in profile; (4) cranial crests absent; eyelid tubercles absent; (5) dentigerous process of vomers medial to choanae; (6) males with vocal slits; nuptial pads absent; (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; terminal tips of fingers III and IV truncate or ovate, enlarged, circumferential grooves weak or absent, unguis flap not indented; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles inconspicuous; (11) toes long and slender (foot length 40–60% of SVL, see Table 3), lateral fringes absent, webbing present, rudimentary; (12) axillary, sacral, and inguinal glands present; (13) dorsal coloration pale brown, greyish brown, reddish brown, or dark brown with cream flecks, sometimes with W-shaped occipital and/or mid-dorsal X-shaped dark marks; belly cream with brown mottling or reticulations on anterior margin.

Oreobates discoidalis can be distinguished from *O. choristolemma*, *O. cruralis*, *O. granulatus*, *O. lehri*, *O. madidi*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, *O. saxatilis*, *O. simmonsii*, and *O. zongoensis* by having dorsal skin smooth to finely shagreened, and enlarged and ovate finger tips on fingers III and IV. These two characters are shared with *O. heterodactylus* and *O. ibischi*. Nevertheless, *O. heterodactylus* exhibits a pattern of dorsal coloration consisting of arrow-shaped and X-shaped dark dorsal marks, and it occurs on the Brazilian Shield; *O. ibischi* has moderately enlarged and truncate finger tips, low warts on dorsal skin, and head wider than long. These three species can be further distinguished by differences in advertisement calls (see Padial & De la Riva, 2005; Padial *et al.*, 2008).

Description of BM 1947.2.15.63: An adult female (SVL, 39.9 mm), with head slightly longer than wide; snout subacuminate in dorsal view and round in lateral profile; nostrils slightly protuberant, orientated dorsolaterally; canthus rostralis straight in dorsal view, sharp in frontal profile; loreal region flat; lips not flared; upper eyelid without tubercles or warts; no cranial crests. Supratympanic fold prominent; tympanic membrane and annulus distinct; tympanic membrane large, round, longer than half of the eye length; two postrictal glands on each side of the head. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae large, round, lateral, separated by distance equal to seven times the diameter of a choana; dentigerous process of vomers ovate, medial to choanae, slightly separated from each other, but far from choanae. Skin texture of dorsal surfaces smooth to finely shagreened; ventral surfaces smooth; no occipital or dorsolateral folds; discoidal fold conspicuous.

Ulnar tubercles absent; palmar tubercle round, flat, prominent; thenar tubercle ovate, prominent, two-thirds of the size of palmar tubercle; supernumerary tubercles large, conical, prominent, smaller than subarticular tubercles; subarticular tubercles large, prominent, conical; tips of fingers I and II round, not enlarged, and those of fingers III and IV very large and truncate; lateral fringes absent; relative length of fingers: $II < I \leq IV < III$.

Toes moderately long (foot $\leq 50\%$ of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle ovate, prominent, slightly larger than outer metatarsal tubercle; outer metatarsal tubercle large, round, conical; three inconspicuous supernumerary tubercles, small, round; subarticular tubercles prominent, conical; toes with faint basal membrane between toes II and III; toes I, II and V with rounded, not expanded, tips; toes III and IV with slightly enlarged and truncate tips; unguis flap not indented; relative length of toes $I < II < V < III < IV$; toes III and V reaching penultimate subarticular tubercle of toe IV.

Colour in preservative: Dorsal surfaces reddish brown, with many irregular dark and light (cream, grey, and brown) marks. Tympanic fold almost black; subocular bars dark brown; flanks as dorsum, but with a dark brown, irregular, oblique wide band posterior to the arm insertion; ventrally cream, with intense reddish brown mottling on throat, chest, anterior margin of belly, and proximate surfaces of flanks.

Measurements of BM 1947.2.15.63: SVL, 39.1 mm; HL, 13.3 mm; HW, 13.0 mm; EL, 5.0 mm; EN, 4.7 mm; IND, 3.1 mm; EE, 6.4 mm; TYH, 2.9 mm; TYL, 2.9 mm; FA, 8.7 mm; TL, 18.3 mm; TH, 17.5 mm; FL, 17.9 mm.

Remarks: In the label of the jar containing *O. discoidalis* specimens catalogued as BM 98.7.7.1920 there is a hand-written note with the word 'Types'. Nevertheless, these specimens are not types. They were collected by Dr Borelli at San Lorenzo, Province Jujuy, Argentina, and were probably sent to the BM by Peracca with the types [Peracca (1895, 1897) studied Borelli's collections]. San Lorenzo is also the locality of the two syntypes catalogued as NMW 16510 (Häupl, Tiedeman & Grillitsch, 1994). The locality 'Tucumán' of the lectotype designated by Gavetti & Andreone (1993) is quite ambiguous, as it may refer to Province Tucumán or to San Miguel de Tucumán (popularly known as Tucumán). We suspect that these specimens may originate from near the town of San Miguel de Tucumán, probably from the Sierra de San Javier, as do the paralectotypes BM 1947.2.15.63–65. The specimen KU 182814 (see

Harvey & Keck 1995: fig. 3) that was reported as *O. cruralis* is in fact an adult female of *O. discoidalis*. Cei (1980) provided a basic but accurate description of this species and an inaccurate illustration of the plantar surfaces. He also provides an illustration of the pectoral girdle. Padial *et al.* (2008) first described the advertisement call. Alcaide de Pucci, De Mopty & Terán (1992), and De Mopty, Terán & Alcaide de Pucci (1992) provided information about the lingual structures in relation to feeding habits. Lavilla & Cei (2001) consider this species as a poorly known taxon.

Distribution: In Argentina, *O. discoidalis* occurs in subtropical forest from Province Jujuy to Province Tucumán (Cei, 1980). De la Riva *et al.* (2000) and Köhler (2000) cite this species for Tucumani-Bolivian montane forests and cloud forests from southern Bolivia (Department Tarija) to cloud forests of Parque Nacional Amboro (Department Santa Cruz) in central Bolivia (Figs 4, 5).

***OREOBATES GRANULOSUS* (BOULENGER, 1903)
COMB. NOV.**

Hylodes granulosis Boulenger, 1903

Eleutherodactylus granulosis – Stejneger (1904)
(Figs 3E–F, 6G–H)

Hylodes granulosis Boulenger, 1903: 553. Holotype: BM 1947.2.15.72 (formerly 1902.11.28.15). Type locality: 'Santo Domingo, Carabaya, S.E. Peru, 6000 feet' (Fig. 4), coordinates: 13°49'59.6"S, 69°38'31.8"W.

Lynch (1989) synonymized *E. granulosis* with *E. cruralis*. He was probably influenced by his broad concept that *E. cruralis* included specimens from very different sizes, altitudes, and habitats. Indeed, the series he studied included several species: *O. cruralis*, *O. granulosis*, and *O. sanderi*. After studying the holotype of both *O. cruralis* and *O. granulosis*, and additional specimens from around the type locality of *O. granulosis*, we concluded that *O. granulosis* is a valid species (see diagnosis and redescription of the holotype below). Moreover, recently collected specimens of *O. granulosis* by JC at the type locality (Santo Domingo, Cordillera de Carabaya, Provincia Sandia, Department Puno, Peru) confirm this position. This represents a remarkable discovery, because no specimen of this species had been found since Mr Ockenden's expedition at the end of the 19th century.

Diagnosis: A medium-sized *Oreobates* (SVL of adults, 22.6–36.9 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules and small, sparse, low, flat warts, only some of them slightly enlarged; warts on flanks slightly larger than

those of dorsum; occipital W-shaped fold and/or x-shaped fold on mid-dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present; no dorsolateral folds; large postrietary glands; (2) tympanic membrane and annulus distinct, both with length about half of the eye length; supratympanic fold weak and short; (3) head large, as wide as long; snout short, round in dorsal and lateral views; canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small warts; (5) dentigerous process of vomers large, oblique, almost in contact, situated posteromedial to choanae; (6) males with vocal slits and nuptial pads; (7) hands with long and slender fingers, first finger equal or slightly shorter than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large or small, round to conical, smaller than subarticular tubercles; tips of fingers III and IV round, slightly enlarged, lacking circumferential grooves and unguis flap; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles inconspicuous, small, or absent; (11) toes long and slender (foot length 50–60% of SVL), lateral fringes weak or absent, webbing absent; toe V reaching the distal margin of the second subarticular tubercle of toe IV, and toe III reaching the proximal margin; tips of toes moderately enlarged, rounded, with unguis flap not indented; (12) axillary, sacral, and inguinal glands present; (13) dorsal coloration pale brown to dark brown with cream flecks, sometimes with W-shaped occipital and/or mid-dorsal X-shaped dark marks, or a pair of cream dorsolateral stripes and a short longitudinal sacral stripe; throat and chest cream with fine brown mottling; belly cream with brown mottling or reticulations on anterior margin.

Oreobates granulosis can be distinguished from other *Oreobates* (characters of other species in parentheses) as follows: from *O. choristolemma* by smaller size of females [SVL of the only known adult females, 46.4 mm (holotype) and 41.0 mm (ZFMK 72569)] (Table 3), and lacking indented unguis flap on discs. From *O. discoidalis* by having warty and granular dorsal skin (finely shagreened with few enlarged warts in some specimens); tips of fingers III and IV rounded (enlarged and ovate); dentigerous process of vomers posteromedial to choanae (between choanae); canthus rostralis convex or sinuous in dorsal view, and round in lateral profile (straight and sharp). From *O. cruralis* by having slightly rounded, not enlarged, finger tips (enlarged and truncate tips on fingers III and IV); dorsal skin with low, round, nonpungent keratinized granules and warts (dorsal skin coarsely shagreened,

composed of round low warts, without keratinized granules on dorsum); larger size, mean SVL of adult females, 36.9 mm (mean SVL of adult females, 29.3 mm) and head as long as wide (head longer than wide) (Table 3); inconspicuous supernumerary tubercles, low, few, round (numerous, conical, and prominent supernumerary tubercles on feet). From *O. heterodactylus* by having dorsal skin with low, round, nonpungent keratinized granules and warts (smooth); rounded, slightly developed tips of fingers III and IV (enlarged and ovate). From *O. ibischi* by having tympanum length half or less than half of the eye length (more than half of the eye length); granular and warty dorsal skin (smooth to finely shagreened with some enlarged warts); rounded, slightly developed tips of fingers III and IV (enlarged and ovate discs two times wider than the digit); head as long as wide (wider than long). From *O. lehri* by having dorsal skin with low, round, nonpungent keratinized granules and warts (homogeneously warty); by smaller size, mean SVL of adult males, 26.6 mm (mean SVL of adult males, 32.1 mm) (Table 3); shorter feet, FL/SVL = 50–60% (60–70%). From *O. madidi* by having dorsal skin with low, round, nonpungent keratinized granules and warts (homogeneously warty); head as wide as long (longer than wide); shorter feet, FL/SVL = 50–60% (50%). From *O. quixensis* by smaller size, mean SVL of males and females, 26.6 and 36.9 mm, respectively [mean SVL of adult males, 39.0 mm, $N = 9$; mean SVL of adult females, 50.4, $N = 14$] (Table 3); dorsal skin with low, round, nonpungent keratinized granules and warts (dorsal skin coarsely tuberculate, with enlarged and prominent warts and granules, some of them keratinized); inconspicuous supernumerary tubercles on feet, low, scarce, round (numerous, conical and prominent supernumerary tubercles on feet). From *O. sanctaerucis* by the smaller size of adult females, 36.9 mm (mean SVL of adult females, 46.0, $N = 3$) (Table 3); dorsal coloration without scarlet flecks; supernumerary tubercles inconspicuous, scarce (numerous supernumerary tubercles, prominent); longer feet, FL/SVL = 50–60% (50%). From *O. sanderi* by having supernumerary tubercles inconspicuous, scarce (numerous supernumerary tubercles, prominent); longer feet, FL/SVL = 50–60% (FL/SVL = 50%); head as long as wide (wider than long). From *O. saxatilis* by its smaller size, mean SVL of females 36.9 (adult females, 49.0 and 43.7 mm, holotype and paratype, respectively) (Table 3); dorsal skin with low, round, nonpungent keratinized granules and warts (dorsal skin coarsely tuberculate, with enlarged and prominent warts and granules, some of them keratinized); head as long as wide (wider than long). From *O. simmonsii* by having dorsal skin with low, round, nonpungent keratinized granules and warts (densely granular, round, pungent, keratinized granules); ulnar

tubercles absent (abundant, round, small, pungent); head as long as wide (longer than wide). From *O. zongoensis* by having dorsal skin with low, round, nonpungent keratinized granules and warts (densely granular, round, pungent keratinized granules); slightly enlarged and truncate discs on fingers III and IV (rounded finger tips); head as long as wide (wider than long).

Description of the holotype: An adult male with vocal slits and single faint white, glandular, nonspinous nuptial pad on each thumb; head as long as wide; snout round in dorsal view and lateral profile; nostrils small, orientated dorsolaterally; canthus rostralis slightly convex in dorsal view, round in frontal profile; loreal region slightly concave, sloping gradually to the lips; lips not flared; upper eyelid without tubercles but covered by small granules; no cranial crests. Supratympanic fold indistinct; tympanic membrane and annulus distinct; tympanic membrane nearly round, its length about half of the eye length; two or three postrictal glands. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae large, round, anterolateral, separated by distance equal to five times the diameter of a choana; dentigerous process of the vomers larger than choanae, oblique, large, prominent, almost in contact, situated posteromedial to choanae, bearing vomerine teeth; vocal slits short, placed posterolaterally. Skin of dorsal surfaces and posterior parts of hind limbs granular, with round, low, keratinized granules and sparse, low, irregular warts; ventral surfaces smooth; W-shaped occipital fold; no dorsolateral folds; a thin mid-dorsal fold; discoidal fold evident, almost reaching the groin.

Ulnar tubercles absent; palmar tubercle round, large, flat; thenar tubercle ovate, large, prominent, its size around two-thirds of the size of the palmar tubercle; supernumerary tubercles low, round, small; subarticular tubercles round, larger than supernumerary tubercles; finger tips round, slightly enlarged, but almost the same width as corresponding digits; fingers lacking lateral fringes and keels; relative length of fingers: $I < IV < II < III$.

Toes long and slender (foot length 54% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle oval to round, prominent, slightly larger than outer metatarsal tubercle; metatarsal tubercle round, conical; supernumerary tubercles small, elongate, inconspicuous; subarticular tubercles prominent, conical, elongate; toes apparently without lateral fringes and keels; toe tips rounded, slightly enlarged; ungual flap not indented; relative length of toes: $I < II < V < III < IV$.

Colour: In preservative, the dorsal coloration is pale brown to dark brown with cream flecks, a W-shaped occipital dark mark, a pair of faint cream dorsolateral stripes from posterior margin of eyes to occipital region, and a white spot on the middle of the occipital region; head brown with cream flecks, two dark subocular bars; throat and chest cream with fine brown mottling; belly cream with brown mottling or reticulations on anterior margin; flanks cream with fine brown mottling, coalescing in an oblique, broad band posterior to arm insertion; extremities pale brown with diffuse reddish brown transverse bars.

Measurements of the holotype: SVL, 27.6 mm; HL, 10.67 mm; HW, 10.5 mm; EL, 4.6 mm; EN, 3.2 mm; IND, 3.1 mm; EE, 5.2 mm; TYH, 2.1 mm; TYL, 2.1 mm; FA, 6.5 mm; TL, 14.5 mm; TH, 14.4 mm; FL, 14.9 mm.

Variation: There is scarce variation in the qualitative characters other than colour pattern. Juveniles are almost identical to adults. There is marked sexual dimorphism in size (females are larger than males), and males have longer feet and larger EL in relation to HW and EN (see Table 3). There are two basic colour morphs. One is the colour pattern of the holotype, consisting of a pale to dark brown dorsum, with pale and dark irregular flecks, and a W-shaped dark brown or cream mark on the occipital region, and a x-shaped dark or pale mark on mid-dorsum, a pale sacral stripe, and dark transverse bars on extremities (Fig. 6G). The alternative colour pattern (present on five of 26 specimens) consists of a dark brown dorsum delimited by a pair of pale dorsolateral bands, a sacral stripe and two wide dark brown stripes on flanks, one anterior to groin and one posterior to arm insertion, and transverse bars on extremities that are less evident than in the first colour pattern. Both colour patterns are shared by *O. cruralis*, *O. lehri*, and *O. sanderi*. The intensity of brown mottling on the throat and chest also varies. Glandular pads are present on axillary, groin, and sacral regions, but are sometimes completely absent or absent from only one side. The adult breeding males USNM 299011–12 present glandular pads on axillary, groin, sacral regions, and thumb. It is likely that the development of these glandular pads occurs only during the breeding season. In life, the dorsal texture and folds are also similar to preserved specimens. For example, the specimen MHNC 5328 shows incomplete dorsolateral folds composed of warts, an occipital W-shaped fold a x-mid-dorsal fold, and three enlarged round warts on the dorsal surface of the snout.

Description of colour patterns in life are based on the specimens MHNC 5328 and MHNC 5335 (Fig. 3E, F). The adult female MHNC 5328 showed the follow-

ing coloration. Head greenish brown, two subocular and one labial irregular dark brown bars, canthus and loreal region with the same coloration; tympanic fold dark brown; lower lip barred with broad dark brown bars separated by light yellow stripes; postrectal glands orange; tympanic membrane purplish brown, annulus greenish brown; an interocular dark brown bar. Dorsum reddish brown with greenish brown tonalities; some scattered red and orange warts on sacral and occipital regions; dark brown W-shaped occipital mark interiorly outlined by orange tones; mid-dorsum with an irregular X-shaped dark brown mark; sacral region with a transverse dark brown mark that continues towards the groin, forming two oblique bands in the posterior margin of the flanks; flanks light orange to pinkish cream, with some dark brown flecks; a broad irregular, oblique band on the anterior and posterior margins of each flank; groin orange. Arms greenish brown with irregular, transverse bands; arm insertion orange; limbs greenish brown with well-defined transverse dark brown bands and orange granules; plantar surfaces dark brown with grey tubercles. Throat purple, with irregular yellow spots; chest purple; belly yellowish; ventral and posterior surfaces of limbs orange. Iris coloration composed of metallic green, yellow, and orange tones, and black reticulations. Pupil horizontal, black, with a vertical black stripe ventrally. The adult male MHNC 5335 showed the following coloration. Head brown with two subocular and one labial irregular dark brown bars, canthus and loreal region with the same coloration; tympanic fold black; lower lip barred with broad dark brown bars separated by light yellow stripes; postrectal glands orange; tympanic membrane purplish brown, annulus brown; an interocular dark brown bar outlined anteriorly with two cream spots. Dorsum dark reddish brown with some scattered orange warts on sacral and occipital regions; dark brown W-shaped occipital mark interiorly outlined by orange; a pair of bold black spots in the dorsolateral region; sacral region with a thin transverse black stripe that continues toward the groin, forming two oblique bands on the posterior margin of the flanks; flanks brown with some light flecks; groin orange. Arms and limbs brown with diffuse transverse bars and orange warts. Throat brown, with white spots; belly yellow with white spots on dark brown groin anterolaterally; ventral and posterior surfaces of limbs fleshy orange. Iris bronze with black reticulations. Pupil horizontal, black, with a vertical black stripe ventrally.

Remarks: The original description by Boulenger (1903) is short but accurate. Although he overlooked the difference in relation to the degree of development of supernumerary tubercles between *O. granulosus*

and *O. cruralis*, he did note the pivotal difference in skin texture. He mentioned 'skin slightly rugose' (Boulenger, 1902: 580) for *O. cruralis*, and 'granulate with small warts' for *O. granulatus* (Boulenger, 1903: 553). This species, which was known from the holotype only, is now known from 25 additional specimens (see Appendix). BM 1905.5.31.21 corresponds to seven specimens (two small juveniles, two young females, a subadult female, and two adult males) collected at Limbani, Carabaya, Department Puno, Peru, by Ockenden. Boulenger identified them as *O. granulatus*, but he did not include them as types. BM 1905.5.31.14.20 includes four specimens (two juveniles, a subadult male, and a subadult female) from Agualani, Carabaya, Department Puno, Peru. BM 1907.5.7.17–18 correspond to an adult female and a subadult female, respectively. Both specimens were collected by Ockenden very close to the type locality. A series of specimens (USNM 299006–299012) collected by John Cadle at Ollachea 1800 m a.s.l., Department Puno, Peru, are also *O. granulatus*. From the series of specimens AMNH 6060–6073 identified as *O. cruralis* we were able to study the specimens 6060–6064. These include four specimens of *O. granulatus* and one of *O. sanderi* from Department Puno, collected by H. Keays. The specimens MHNC 5328 and MHNC 5335 (Fig. 3E, F) were recently collected by JCC at Santo Domingo, Distrito de Limbani, Provincia de Sandia, Departamento de Puno, Peru (13°49'59.6"S, 69°38'31.8"W), at 1400–1500 m a.s.l. The specimen MHNC 5328 (field number 3396) is an adult female collected on 11 November 2006 along the Santo Domingo stream, 1400 m a.s.l., on a rock 1.5 m above ground. The specimen MHNC 5335 (field number 3403) is an adult male collected on 11 November 2006 on the main path to Santo Domingo, 1500 m a. s. l.; it was found calling close to a small waterfall.

Distribution: This species inhabits humid montane forests and cloud forests of the eastern versant of Cordillera Carabaya, Puno, Peru (Figs 4, 5). It is known from four localities between 1400 and 2000 m a.s.l. The most distant localities are Limbani and Ollachea, separated by approximately 200 km.

OREOBATES HETERODACTYLUS (MIRANDA-RIBEIRO, 1937) COMB. NOV.

Teletrema heterodactylum Miranda-Ribeiro, 1937

Eleutherodactylus heterodactylus – Myers (1962) (Fig. 3G)

Teletrema heterodactylum Miranda-Ribeiro, 1937: 67. Lectotype: MN 106A, by Miranda-Ribeiro, 1955.

Type locality: 'gruta dita Facendinha', Matto-Grosso, Cáceres, Brazil (Fig. 4), coordinates: 16°00'S, 57°36'W.

Diagnosis: A small *Oreobates* (SVL of adults, 24.6–30.8 mm) characterized as follows: (1) skin on dorsum finely shagreened to smooth; venter smooth; posterior surfaces of limbs smooth; discoidal fold present; post-tritral glands present; (2) tympanic membrane and annulus distinct, its length about two-thirds of the eye length; supratympanic fold well developed; (3) head longer than wide; snout slightly pointed in dorsal view, round in lateral profile; canthus rostralis sharp, slightly concave; (4) cranial crests absent; upper eyelid tubercles absent; (5) dentigerous process of the vomers medial to choanae; (6) males with vocal slits and a single faint nuptial pad; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles enlarged and subconical; supernumerary tubercles small, rounded; terminal discs of fingers I and II rounded, not enlarged, those of fingers III and IV markedly enlarged, ovate; lateral fringes and keels on fingers absent; (8) between two and four small ulnar tubercles; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle small, high, ovoid; outer more rounded, subequal; supernumerary tubercles round to conical; (11) lateral fringes absent, webbing absent; fifth toe shorter than third; tips of toes moderately enlarged, rounded, ungual flap not indented; (12) axillary gland present; (13) dorsal coloration light reddish brown with dark brown to black spots and marks, outlined by cream; in preservative, dorsal regions brownish grey; snout dark grey with darker marks; throat cream with dense and fine brown mottling; venter immaculate.

Oreobates heterodactylus can be distinguished from *O. choristolemma*, *O. cruralis*, *O. granulatus*, *O. lehri*, *O. madidi*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, *O. saxatilis*, *O. simmonsii*, and *O. zongoensis* by having dorsal skin smooth to finely shagreened, and enlarged and ovate finger tips on fingers III and IV. These two characters are shared with *O. discoidalis*. Nevertheless, *O. heterodactylus* exhibits a pattern of dorsal coloration consisting of arrow-shaped and X-shaped dark dorsal marks, and it occurs on the Brazilian Shield. *Oreobates ibischi* has moderately enlarged and truncate finger tips, low warts on dorsal skin, and head wider than long. These three species can be further distinguished by differences in advertisement calls (see Padial & De la Riva, 2005; Padial *et al.*, 2008).

Remarks: Padial & De la Riva (2005) and Padial *et al.* (2008), based on the similarity of external morphology and advertisement calls, already noted that this species could belong to the *E. discoidalis* group.

Distribution: It is only known from three localities in the semideciduous forest of the Precambrian Brazilian Shield of western Brazil and eastern Bolivia (Heyer & Muñoz, 1999; Padial & De la Riva, 2005) (see Figs 4, 5).

***OREOBATES IBISCHI* (REICHLÉ ET AL., 2001) COMB. NOV.**

Eleutherodactylus ibischi Reichle et al., 2001 (Fig. 3H)

Eleutherodactylus ibischi Reichle, Lötters & De la Riva, 2001. Holotype: CBF 3341, by original designation. Type locality: 'km 68.5 on Santa Cruz de la Sierra-Samaipata road, close to the village of Bermejo, Provincia Florida, Departamento Santa Cruz, Bolivia', coordinates: 18°11'S, 63°34'W, approximately 750 m a.s.l. (Fig. 4).

Diagnosis: A small *Oreobates* (SVL of adults, 31.3–38.7 mm) characterized as follows: (1) skin on dorsum finely shagreened with some low, inconspicuous warts; venter smooth; posterior surfaces of limbs smooth; discoidal fold present; postrictal glands present; (2) tympanic membrane and annulus distinct, its length slightly more than two-thirds of the eye length; supratympanic fold weak; (3) head wider than long; snout round in dorsal view and lateral profile; canthus rostralis slightly convex, round; (4) cranial crests absent; upper eyelid tubercles absent; (5) dentigerous process of vomers medial and almost at the level of choanae; (6) males with vocal slits and a single faint nuptial pad; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles enlarged and subconical; supernumerary tubercles small, rounded; terminal discs of fingers I and II rounded, not enlarged, but with those of fingers III and IV markedly enlarged and ovate; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle small, high, ovoid; outer more rounded, subequal; supernumerary tubercles round, small; (11) lateral fringes absent, webbing absent; fifth toe shorter than third; tips of toes scarcely enlarged, rounded, unguis flap not indented; (12) axillary gland present; (13) dorsal coloration cream to pale brown with dark brown to black spots and undefined marks, outlined by cream; in preservative, dorsal regions pinkish grey with undefined dark brown marks; venter immaculate.

Oreobates ibischi can be distinguished from *O. cholestolemma*, *O. cruralis*, *O. granulosus*, *O. lehri*, *O. madidi*, *O. quixensis*, *O. sanctaerucis*, *O. sanderi*, *O. saxatilis*, *O. simmonsii*, and *O. zongoensis* by having dorsal skin finely shagreened and enlarged,

and ovate finger tips on fingers III and IV. *O. ibischi* can be easily distinguished from the most similar species (*O. discoidalis*, *O. heterodactylus*, and *O. cruralis*) by having a head wider than long. Moreover, *O. discoidalis* and *O. heterodactylus* have sharp, distinct canthus rostralis in frontal profile, whereas the canthus rostralis is round and indistinct in *O. ibischi*.

Remarks: The original description and diagnosis are accurate (Reichle et al., 2001). Nevertheless, the authors mention that the dorsal skin is finely tuberculate, but following Lynch & Duellman's (1997) terminology the dorsal skin of this species is finely shagreened with some low, inconspicuous warts. Moreover, Reichle et al. (2001) mention the absence of nuptial pads in males of *O. ibischi*, but re-examination of the adult holotype revealed single, white, glandular nuptial pads on the dorsal surface of each thumb. They distinguished this species from *O. discoidalis* on the basis of enlarged tips of fingers III and IV, but this character is present in both species (*O. discoidalis* has more developed finger tips). In contrast, the presence of nuptial pads was mentioned for *O. discoidalis*, but we were not able to detect this structure in any adult male of *O. discoidalis*. Moreover, a diagnostic character provided by Reichle et al. (2001) that allows for the separation of *O. cruralis* from *O. ibischi* ($TYL > 1/2EL$) is not applicable for distinguishing *O. ibischi* from *O. discoidalis*, because both share a large tympanic membrane.

Distribution: Only known from the semideciduous forests of the type locality and a nearby locality in Central Bolivia (see Appendix and Figs 4, 5). It is expected to occur in the semideciduous forests from Department Santa Cruz to Northern Argentina.

***OREOBATES LEHRI* (PADIAL ET AL., 2007) COMB. NOV.**

Eleutherodactylus lehri Padial et al., 2007 (Fig. 3I)

Eleutherodactylus lehri Padial, Chaparro & De la Riva, 2007: 115. Holotype: USNM 537848. Type locality: 'Apurimac River Valley, Camisea Natural Gas Pipeline, Wayrapata Camp, 2445 m asl (12°50'10"S, 73°29'43"W), Department Cusco, Peru' (Fig. 4).

Diagnosis: A robust *Oreobates* (SVL of adults, 28.5–39.9 mm) characterized as follows: (1) skin on dorsum coarsely shagreen with enlarged keratinized granules, granules regular in size, small, round, with only some of them slightly enlarged; granules on flanks slightly larger than those of dorsum; venter smooth; posterior surfaces of limbs smooth; discoidal fold present; no dorsolateral folds; postrictal glands weak

or absent; (2) tympanic membrane and annulus distinct, their length about half of the eye length; supratympanic fold weak, short; (3) head large, slightly longer than wide or subequal; snout round in dorsal and lateral views; canthus rostralis sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small granules; (5) dentigerous process of vomers large, situated posteromedial to choanae; (6) males with vocal slits; (7) hands with long and slender fingers, first finger about the same length as second; subarticular tubercles round to conical, well developed; supernumerary tubercles low, not prominent, round to conical, smaller than subarticular tubercles; terminal discs of fingers truncate to round, not enlarged, lacking circumferential grooves and unguis flap; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle ovate to round, prominent; outer smaller, round, prominent; supernumerary tubercles absent; (11) toes long and slender (foot length 60–70% of SVL), lacking lateral fringes or keels (or very weak at the base of toe III), webbing absent; fifth and third toes reaching midpoint of second subarticular tubercle of toe IV; tips of toes moderately enlarged, rounded, with unguis flap not indented; (12) axillary glands present; (13) dorsal coloration pale brown to dark brown or grayish brown, with darker marks and bold spots; a pair of cream dorsolateral stripes and a short longitudinal sacral stripe present in some specimens; snout dark brown with darker bars; throat and chest light grey to dark brown; belly cream with brown mottling or reticulations on anterior margin.

Oreobates lehri can be distinguished from all other species of the genus by the combination of long feet, fingers I, II, and IV of the same length, the absence or weakly developed supernumerary tubercles on the feet, round and not enlarged finger tips, and granular dorsal skin. In most species of *Oreobates* the foot length = 50% of the SVL, whereas in *O. lehri* the foot length \geq 60% of the SVL. For additional differences refer to Padial *et al.* (2007).

Distribution: *Oreobates lehri* is known from the type locality (Fig. 4) and from two localities in the Cosñipata Valley, Cusco, Peru. Both localities are situated in cloud forests (Fig. 5) and are separated by a distance of approximately 200 km. Nothing is known about its natural history.

OREOBATES MADIDI (PADIAL *ET AL.*, 2005)

COMB. NOV.

Eleutherodactylus madidi Padial *et al.*, 2005 (Fig. 3J)

Eleutherodactylus madidi Padial, González & De la Riva, 2005: 319. Holotype: MNK-A 7856. Type

locality: 'Arroyo Huacataya, Serranía Esclabón, Área Natural de Manejo Integrado Madidi, Provincia Franz Tamayo, Departamento La Paz, Bolivia (14°20'12"S, 68°05'57"W), c. 1500 m a.s.l.' (Fig. 4).

Diagnosis: A small *Oreobates* (SVL of adults, 27.9–33.0 mm) characterized as follows: (1) skin on dorsum heavily warty, warts regular in size, low, small, rounded, some of them enlarged on the posterior part of the head and scapular region; warts on flanks larger and more elongate than those of dorsum; venter smooth; posterior surfaces of limbs uniformly warty; discoidal fold present, barely visible; no dorsolateral folds; postrectal glands well developed; (2) tympanic membrane and annulus distinct, about half of the eye length; supratympanic fold weak, short; (3) head large, longer than wide; snout round to subacuminate in dorsal and lateral views; canthus rostralis rounded; (4) cranial crests absent; upper eyelid tubercles absent; (5) dentigerous process of vomers large, situated posteromedial to choanae; (6) males with vocal slits and a single faint nuptial pad on thumb; (7) first finger longer than second; subarticular tubercles enlarged and subconical to conical in profile; supernumerary tubercles small; terminal discs of fingers rounded, not enlarged; tips of fingers III and IV round; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle ovoid, outer more rounded, subequal; (11) toes lacking lateral fringes or keels; webbing absent; fifth toe shorter than third; discs of toes moderately enlarged, rounded; supernumerary tubercles conical, prominent; (12) axillary gland present; (13) dorsal coloration dark brown to black, with diffuse dark marks; in preservative, dorsal regions brownish grey or purplish grey; snout dark grey with darker marks; throat cream with dense and fine brownish grey mottling; venter cream with scarce to dense brownish grey fine mottling.

Oreobates madidi is most similar to *O. cruralis*. It differs from *O. cruralis* by having a homogeneously warty dorsal surface, large warts (skin with small, round, uniform warts, smaller warts with sparse enlarged warts), rounded finger tips (slightly enlarged and truncate tips on fingers III and IV), and a different advertisement call (Padial *et al.*, 2005b, 2008). It can be distinguished from other small *Oreobates* (*O. discoidalis*, *O. heterodactylus*, and *O. ibischi*) by having rounder finger discs (truncate and enlarged on fingers III and IV); it can be distinguished from larger species of *Oreobates* by lacking keratinized granules on dorsum.

Remarks: Its advertisement call allows for an unequivocal identification of live male frogs (Padial *et al.*, 2005b; Padial *et al.*, 2008).

Distribution: *Oreobates madidi* inhabits the humid montane forests of the Andean slopes of northern Bolivia, at elevations of 900–1500 m a.s.l. (Figs 4, 5). The species is only known from La Cascada and Serranía Eslabón, two localities in the Department La Paz, separated by a distance of 150 km.

OREOBATES QUIXENSIS JIMÉNEZ DE LA
ESPADA, 1872

Hylodes verrucosus Jiménez de la Espada, 1872

Hylodes philippi Jiménez de la Espada, 1875

Borborocoetes quixensis – Boulenger (1882)

Leptodactylus tuberculatus Andersson, 1945

Eupsophus quixensis – Peters (1955)

Eleutherodactylus philippi – Gorham (1966)

Eleutherodactylus verrucosus – Gorham (1966)

Ischnocnema quixensis – Lynch & Schwartz (1971)

Oreobates quixensis – Caramaschi & Canedo (2006)
(Figs 3K, 6I–J)

Oreobates quixensis Jiménez de la Espada, 1872: 87. Types: not given in the original descriptions. Type locality: San José de Moti, Province Napo, Ecuador (Fig. 4).

Diagnosis: A large *Oreobates* (SVL of adults, 35–63 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules and small, sparse, prominent, and enlarged warts; occipital W-shaped fold and/or x-shaped fold on mid-dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present; no dorsolateral folds; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length about half of the eye length; supratympanic fold weak and short; (3) head large, wider than long; snout short, round in dorsal and lateral views; canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by prominent warts and granules; (5) dentigerous process of vomers large, oblique, almost in contact, situated posteromedial to choanae; (6) males with vocal slits, no nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large, prominent, round to conical, smaller than subarticular tubercles; tips of fingers III and IV round, not enlarged, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) either one or two ulnar tubercles, round, low; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatar-

sal tubercle smaller, round, prominent; supernumerary tubercles large, prominent, conical, smaller than subarticular tubercles; (11) toes long and slender (foot length 50–60% of SVL), lateral fringes weak or absent, webbing absent; tips of toes round; (12) axillary glands present; (13) dorsal coloration pale brown to dark brown with purple tonalities and cream flecks, sometimes with W-shaped occipital and/or mid-dorsal X-shaped dark marks, and a short longitudinal sacral stripe; ventral surfaces cream with fine to dense brown mottling or reticulations.

Oreobates quixensis is the largest species of the genus. It differs from all small species of *Oreobates* by the combination of dorsum with enlarged warts and keratinized granules, head wider than long, and rounded finger discs. Among the medium-sized and large *Oreobates*, it is most similar to *O. saxatilis*, but *O. quixensis* has larger subconical tubercles on dorsum and a more heavily mottled venter.

Remarks: The original description by Jiménez de la Espada (1872) is very succinct, but the redescription by Jiménez de la Espada (1875) is very accurate. Several authors have subsequently diagnosed this species (e.g. Lynch & Schwartz, 1971; Duellman, 1978; Rodríguez & Duellman, 1994).

Lynch & Schwartz (1971) placed *O. quixensis* in the genus *Ischnocnema*, and considered *Hylodes philippi* Jiménez de la Espada, 1875 and *Hylodes verrucosus* Jiménez de la Espada, 1875 as junior synonyms of *O. quixensis*. These two *Hylodes* were not described and were only illustrated (Jiménez de la Espada, 1875). Based on the illustrations, Lynch & Schwartz (1971) considered that the variability of *O. quixensis* included what Jiménez de la Espada described as *H. verrucosus* and *H. philippi*. Moreover, as Duellman was not able to examine the types of *O. quixensis* and *O. verrucosus* in the MNCN, Lynch & Schwartz (1971: 107) considered all of the types lost. This status prevailed until this paper (see Frost, 2006). The type locality of *O. quixensis* was considered 'la provincia de Quijos' by Lynch & Schwartz (1971), following the original description. The type locality of *H. verrucosus* was considered unknown. For *H. philippi* they provided the correct former holotype number (MNCN 202) and the corresponding locality of origin: San José de Motí, Provincia Napo, Ecuador. Although Jiménez de la Espada never mentioned catalogue numbers in his publications, the types are preserved in the amphibian collection of the Museo Nacional de Ciencias Naturales de Madrid [see González (2006) for a detailed catalogue of the Espada's collection at the MNCN]. Our examination of the types revealed significant differences between the two *Hylodes* taxa and *O. quixensis*. For example, both *H. verrucosus* and *H. philippi* lack supernumerary plantar

tubercles, a character illustrated in detail by Jiménez de la Espada (1875) for *O. quixensis*. Moreover, none of the latter species belongs to the genus *Oreobates*, and both belong to the *E. dolops* species group (*sensu* Lynch, 1989). The taxonomic status of these two species will be discussed elsewhere.

Jiménez de la Espada (1875) mentioned 11 specimens of *O. quixensis* on which he based a more accurate description. In the MNCN there are 14 specimens collected and identified by Jiménez de la Espada. One comes from San José de Moti, Municipio San José de Mote (or Nuevo), Provincia Napo; the other 13 specimens come from Municipio Archidona de Quijos, Provincia Napo, Ecuador. The specimen MNCN 1708 (formerly 330), an adult female from San José de Moti, corresponds to the specimen measured by Jiménez de la Espada (1875: 104). On the reverse of the original catalogue card corresponding to this specimen there is the inscription 'Cotipo' (= cotype); at the back, there is the inscription 'genotipo' (= type of the genus). Moreover, the card states that this specimen was illustrated in Jiménez de la Espada (1875). The original catalogue number 1154 corresponds to 13 specimens (MNCN 1709–21) from Archidona de Quijos, Napo, Ecuador. Nevertheless, Jiménez de la Espada (1875) only mentioned 11 specimens for this locality. González (2006) mentioned that two of these specimens could correspond to *H. verrucosus* or *H. philippi*; however, we find them all assignable to *O. quixensis*.

We consider the specimen MNCN 1708 (formerly 330), an adult female from San José de Moti (from Municipio San José de Mote (or Nuevo), Provincia Napo, Ecuador, collected in June 1885 by Marcos Jiménez de la Espada, the lectotype of *O. quixensis* (Fig. 6I–J), and the specimens MNCN 1709–21 (formerly 1154) from Archidona, Ecuador, collected by Marcos Jiménez de la Espada on 4 May 1865, the paralectotypes of *O. quixensis*. The lectotype corresponds with the specimen measured and illustrated by Jiménez de la Espada (1875).

Distribution: Upper Amazon Basin in Colombia, Ecuador, Peru, Bolivia (Department of Pando), and western Brazil, up to 1000 m a.s.l. (Frost, 2006). The advertisement call was described by Duellman (1978) and Heyer & Gascon (1995), both of which also provide natural history information.

OREOBATES SANCTAECRUCIS (HARVEY &
KECK, 1995)

Ischnocnema sanctaegrucis Harvey & Keck, 1995

Oreobates sanctaegrucis – Caramaschi & Canedo (2006) (Fig. 3L)

Ischnocnema sanctaegrucis Harvey & Keck, 1995: 57. Holotype: MNKA 1198, by original designation. Type locality: 'El Chapé, Provincia Florida, Departamento de Santa Cruz, Bolivia, 2060 m' (Fig. 4), coordinates: 18°03'34'S, 63°54'36'W.

Diagnosis: A medium-sized *Oreobates* (SVL of adults, 35.1–48.1 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules and small, sparse, low, flat warts, some of them slightly enlarged; warts on flanks slightly larger than those of dorsum; occipital W-shaped fold and/or x-shaped fold on mid-dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present; no dorsolateral folds; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length about half of the eye length; supratympanic fold weak, short; (3) head large, wider than long; snout short, round in dorsal and lateral views; canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small granules; (5) dentigerous process of vomers large, oblique, almost in contact, situated posteromedial to choanae; (6) males with vocal slits, no nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large or small, round to conical, smaller than subarticular tubercles; tips of fingers III and IV round, not enlarged, lacking circumferential grooves and unguis flap; lateral fringes and keels on fingers absent or weak; (8) single ulnar tubercle, weak; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles round, low; (11) toes long and slender (foot length 50% of SVL), lateral fringes weak or absent, webbing absent; tips of toes round, with unguis flap not indented; (12) axillary glands present; (13) dorsal coloration pale brown to dark brown with cream flecks, sometimes with W-shaped occipital and/or mid-dorsal X-shaped dark marks; a short longitudinal sacral stripe; throat and chest cream with brown mottling; belly cream with brown mottling; in life, conspicuous red to scarlet spots in axiles, dorsum, and shanks.

Oreobates sanctaegrucis can be distinguished from the rest of the species of *Oreobates* by the combination of dorsum with warts and keratinized granules, round finger and toe tips, and red to scarlet spots in axiles, dorsum, and shanks.

Remarks: Its advertisement call allows for an unequivocal identification of active male frogs (Reichle, 1999; Köhler, 2000).

Distribution: *Oreobates sanctaerucis* inhabits the humid montane forests and cloud forests of the Andean slopes of central Bolivia, in Departments Cochabamba and Santa Cruz, at elevations of 1000–2100 m a.s.l. (Figs 4, 5).

OREOBATES SANDERI (PADIAL *ET AL.*, 2005)

Ischnocnema sanderi Padial *et al.*, 2005

Oreobates sanderi – Caramaschi & Canedo (2006) (Fig. 3N)

Ischnocnema sanderi Padial, Reichle, & De la Riva, 2005: 187. Holotype: CBF 5385. Type locality: 'Arroyo Bilunto (14°38'24"S, 68°31'45"W), Chunirumi Valley, Bilunto Mountains, Área Natural de Manejo Integrado Madidi, near Santa Cruz de Valle Ameno, Province Franz Tamayo, Departament La Paz, Bolivia, 1800 m' (Fig. 4).

Diagnosis: A medium-sized *Oreobates* (SVL of adults, 28–38 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules and small, sparse, low, flat warts, only some of them slightly enlarged; warts on flanks slightly larger than those of dorsum; occipital W-shaped fold and/or x-shaped fold on mid-dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present; dorsolateral folds weak; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length of about half of the eye length; supratympanic fold weak, short; (3) head large, as wide as long; snout short, round in dorsal and lateral views; canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small warts; (5) dentigerous process of vomers large, oblique, almost in contact, situated posteromedial to choanae; (6) males with vocal slits and nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large or small, round to conical, smaller than subarticular tubercles; tips of fingers III and IV round, not enlarged, lacking circumferential grooves and unguis flap; lateral fringes and keels weak; (8) ulnar tubercles absent; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles conspicuous, conical; (11) toes long and slender (foot length 50% of SVL), lateral fringes weak or absent, webbing absent; tips of toes round, with unguis flap not indented; (12) axillary glands present; (13) dorsal coloration pale brown to dark brown with cream flecks, sometimes with W-shaped occipital and/or mid-dorsal X-shaped dark marks, or a pair of cream dorsolateral stripes and

a short longitudinal sacral stripe; throat and chest cream with fine brown mottling; belly cream with brown mottling or reticulations on anterior margin.

Among the medium-sized and large species of *Oreobates*, *O. sanderi* is most similar to *O. granulosus*, from which it can be distinguished by having conspicuous supernumerary tubercles (weak or absent), shorter feet, FL/SVL = 50% (50–60%), and incipient dorsolateral folds (absent). It can be distinguished from small species of *Oreobates* by the combination of keratinized granules on dorsum, and fingertips round and not enlarged.

Remarks: The original description and diagnosis are accurate (Padial *et al.*, 2005a). For distinguishing this species from other members of *Oreobates* see the operational key below. Its advertisement call is unknown.

Distribution: *Oreobates sanderi* inhabits the humid montane forests and cloud forests of the Andean slopes of northern Bolivia, in Department La Paz, at elevations of 1300–2000 m a.s.l. (Figs 4, 5). Two specimens from Department Puno, Peru, one from Abra de Maruncuna, 10 km south-west of San Juan del Oro, 1650 m a.s.l. (KU 206101), and one from Juliaca (AMNH 6063; locality in error given that Juliaca lies in the dry Altiplano – this specimen was probably sent to Juliaca from somewhere else in the humid montane forests of Department Puno, Peru), are tentatively assigned to this species.

OREOBATES SAXATILIS (DUELLMAN, 1990)

Ischnocnema saxatilis Duellman, 1990

Oreobates saxatilis – Caramaschi & Canedo (2006) (Fig. 3N)

Ischnocnema saxatilis Duellman, 1990: 1. Holotype: KU 212556. Type locality: 'Ponga de Shilcayo, about 4 km NNW of Tarapoto, 470 m (6°31'S, 76°53'W), Provincia de San Martín, Departamento de San Martín, Peru' (Fig. 4).

Diagnosis: A large *Oreobates* (SVL of adults, 44.5–50.0 mm) characterized as follows: (1) skin of dorsum granular, with round keratinized granules and small, sparse, low, flat warts, only some of them slightly enlarged; warts on flanks slightly larger than those of dorsum; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present; no dorsolateral folds; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length of about two thirds of the eye length; supratympanic fold weak, short; (3) head large, wider than long; snout short, round in dorsal and lateral views;

canthus rostralis slightly convex or sinuous in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small warts and granules; (5) dentigerous process of vomers large, transverse, situated posteromedial to choanae; (6) vocal slits and nuptial pads condition unknown; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, round to conical; supernumerary tubercles large, conical, smaller than subarticular tubercles; tips of fingers III and IV round, not enlarged, lacking circumferential grooves and unguis flap; lateral fringes and keels on fingers absent; (8) single round, low, ulnar tubercle; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles conspicuous, conical; (11) toes long and slender (foot length 50% of SVL), lateral fringes absent, webbing absent; tips of toes rounded, not enlarged, with unguis flap not indented; (12) condition of axillary, sacral, and inguinal glands unknown; (13) dorsal coloration greyish brown with darker brown markings; throat and chest cream with dense brown mottling; belly immaculate.

Among the large *Oreobates*, *O. saxatilis* is most similar to *O. quixensis*, but differs by being smaller and having more scattered warts, and by having an immaculate belly. From all small *Oreobates* it differs by its larger size and by having keratinized granules on dorsum and non-enlarged fingertips.

Remarks: The original description and diagnosis are accurate (Duellman, 1990). However, Duellman (1990) mentioned the presence of narrow lateral fringes on fingers and toes, a character that we did not find in the specimens examined. Its advertisement call is unknown; nothing is known about the natural history of this species.

Distribution: Known only from the type locality (Fig. 4).

OREOBATES SIMMONSI (LYNCH, 1974)

Ischnocnema simmonsii Lynch, 1974

Oreobates simmonsii – Caramaschi & Canedo (2006) (Fig. 6C–D)

Ischnocnema simmonsii Lynch, 1974: 85. Holotype: KU 147068, by original designation. Type locality: 'Río Piuntza, Cordillera del Cóndor, Morona-Santiago Prov. Ecuador 1830 m' (Fig. 4).

Diagnosis: An small *Oreobates* (SVL of a subadult female, 26.0 mm) characterized as follows: (1) skin of dorsum homogeneously granular, with small, round,

elevated, keratinized granules; venter granular; posterior surfaces of limbs granular, groin granular; discoidal fold absent; no dorsolateral folds; large postrictal glands; (2) tympanic membrane and annulus distinct, both with length of about two thirds of the eye length; supratympanic fold absent; (3) head longer than wide; snout short, round in dorsal and lateral views; canthus rostralis slightly concave in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by small granules; (5) dentigerous process of vomers large, transversal, situated posteromedial to choanae; (6) vocal slits and nuptial pads condition of males unknown; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, conical; supernumerary tubercles large, round, prominent, smaller than subarticular tubercles; tips of fingers pointed, lacking circumferential grooves and unguis flaps; lateral fringes and keels on fingers absent; (8) ulnar tubercles abundant, round; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles conspicuous, conical; (11) toes long and slender (foot length 55% of SVL), lateral fringes present, webbing absent; tips of toes rounded; (12) condition of axillary, sacral and inguinal glands unknown; (13) dorsal coloration reddish brown with dark brown marks on dorsum; belly reddish brown with irregular white spots.

Oreobates simmonsii can be distinguished from all species of *Oreobates* by the combination of homogeneously granular dorsal surfaces and extremities, venter granular, and long feet with conspicuous supernumerary tubercles.

Remarks: The original description and diagnosis are accurate. It is based on two specimens (Lynch, 1974). Its advertisement call is unknown. Nothing is known about the natural history of this species. It is only known from the types. The assignment to *Oreobates* is tentative.

Distribution: Only known from the type locality (Fig. 4).

OREOBATES ZONGOENSIS (REICHLÉ & KÖHLER, 1997) **COMB. NOV.**

Eleutherodactylus zongoensis Reichle & Köhler, 1997 (Fig. 3Q)

Eleutherodactylus zongoensis Reichle & Köhler, 1997: 33. Holotype: CBF 2503. Type locality: 'Valle del Zongo (16°03'31 S, 68°00'72 W), 1250 m above sea level, Departamento La Paz, Bolivia' (Fig. 4).

Diagnosis: A medium sized *Oreobates* (SVL of a single adult male, 30.6 mm) characterized as follows: (1) skin of dorsum homogeneously granular, with small, conical, elevated, keratinized granules; skin on arms smooth; venter smooth, slightly granular close to groin; posterior surfaces of limbs granular, groin granular; discoidal fold present; no dorsolateral folds; large postictal glands; (2) tympanic membrane and annulus distinct, both with length of about half of the eye length; supratympanic fold absent; (3) head wider than long; snout short, round in dorsal and lateral views; canthus rostralis slightly concave in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered by granules; (5) dentigerous process of vomers large, oblique, situated posteromedial to choanae; (6) males without vocal slits and nuptial pads; (7) hands with long and slender fingers, first finger longer than second; subarticular tubercles large, prominent, round; supernumerary tubercles small and round, smaller than subarticular tubercles; tips of fingers rounded, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles round, small; (11) toes long and slender (foot length 50% of SVL), lateral fringes absent, webbing absent; tips of toes rounded; (12) condition of axillary, sacral, and inguinal glands unknown; (13) dorsal coloration in alcohol homogeneously dark brown, almost black; ventral surfaces dark brown, lighter than dorsum.

Oreobates zongoensis is most similar to *O. simonsi*, from which it can be distinguished by a head wider than long, smooth skin on arms, and rounded and small supernumerary tubercles. It can be distinguished from other *Oreobates* species by the combination of homogeneously granular dorsum, head wider than long, supernumerary tubercles round and small, and dorsal and ventral surfaces homogeneously dark brown.

Remarks: The original description and diagnosis are accurate, even though they are based on a single specimen (Reichle & Köhler, 1997). For distinguishing this species from other members of *Oreobates* see the operational key below. Its advertisement call is unknown; nothing is known about the natural history of this species. It is only known from the holotype. The assignment to *Oreobates* is tentative.

Distribution: Known only from the type locality (Fig. 4).

DISCUSSION

HYPOTHESES OF RELATIONSHIPS

Phylogenetic analyses of mtDNA support the hypothesis of monophyly for the genus *Oreobates*. The monophyly is also supported by the presence of three putative morphological synapomorphies. The genus *Oreobates* now comprises all members of the former *E. discoidalis* group (*sensu* Padial *et al.*, 2007) and *Oreobates* (*sensu* Caramaschi & Canedo, 2006). The structure of the advertisement calls in *Oreobates* also suggests close relationships (Padial *et al.*, 2008). The sister group of *Oreobates* is a well-supported clade including the *E. conspicillatus* and *E. martinicensis* series of the subgenus *Eleutherodactylus* (Figs 1, 2). However, as *E. binotatus*, *E. dolops*, and *E. elassodiscus* (representing the *E. binotatus*, *E. dolops*, and *E. nigrovittatus* species groups of the subgenus *Eleutherodactylus*) do not cluster with the *E. martinicensis* series (which includes the type species of *Eleutherodactylus*), we consider *Eleutherodactylus* to be nonmonophyletic. This conclusion is also supported by Darst & Cannatella (2004) and Frost *et al.*'s (2006) molecular phylogenies. The genus *Eleutherodactylus* should probably be restricted to the *E. martinicensis* and *E. conspicillatus* series. Our data also support the hypothesis of monophyly of *Craugastor* (Crawford & Smith, 2005), but *E. binotatus* clusters with no statistical support with this taxon. Hence, either the *E. binotatus* series is the sister taxon of *Craugastor* or *Craugastor* includes members of this series. However, our limited dataset and scarce taxon sampling for these groups do not allow for definitive conclusions.

The most important synapomorphy suggested by us for *Oreobates* was already proposed by Lynch (1989) for two species (*O. cruralis* and *O. discoidalis*): presence of conical subarticular and supernumerary plantar tubercles. Jiménez de la Espada (1875) also described this character for *O. quixensis*. This character is also present in all other species assigned to *Oreobates* by Caramaschi & Canedo (2006). Lynch (1989) compared the skull morphology of several putatively related species, but he only selected this synapomorphy to split the former *E. discoidalis* species group (which by that time included species without conical subarticular tubercles, and without supernumerary tubercles). The two other remaining groups (*E. dolops* and *E. nigrovittatus* species groups) were considered very closely related to each other, but not to the *E. discoidalis* group. This hypothesis is corroborated by our mtDNA analyses (Fig. 2). Although the presence of conical subarticular and supernumerary plantar tubercles may be considered of doubtful phylogenetic utility because of its potential adaptive function, and hence being more likely to result from convergent evolution (Hennig, 1966), the degree of development does not

seem to be directly related to habitat use. For example, it could be hypothesized that those species with more terrestrial habits or those that live on hard substrates may show the most enlarged tubercles. Nevertheless, species such as *O. cruralis*, *O. discoidalis*, *O. heterodactylus*, and *O. ibischi* usually perch on bushes or are found on leaves, yet they present different degrees of development in plantar tubercles. In two terrestrial species, *O. granulatus* and *O. lehri*, the supernumerary tubercles of the feet are reduced in number and size. On the other hand, the degree of development of external finger discs seems to be associated to the arboreal life of these frogs. For example, terrestrial and rock-dwelling species such as *O. saxatilis*, *O. quixensis*, or *O. granulatus* have less developed finger discs.

As stated above, Lynch (1971) and Lynch & Schwartz (1971) considered *Oreobates* a junior synonym of *Ischnocnema*. More recently, Caramaschi & Canedo (2006) resurrected *Oreobates* and placed *Ischnocnema* in the synonymy of *Eleutherodactylus*. Both Lynch (1971) and Caramaschi & Canedo (2006) used some osteological differences to support their positions, but these characters were neither proposed nor tested as synapomorphies. The most significant difference mentioned by Caramaschi & Canedo (2006) to synonymize *Ischnocnema* was the presence of 'T-shaped terminal phalanges'. Jiménez de la Espada (1872, 1875) also described the osteology of *O. quixensis* and stated that the moderate bifurcation of the terminal phalanges was an intermediate character between *Hylorhina sylvatica* and *Hylodes* (= *Eleutherodactylus*). Nevertheless, members of what we consider *Oreobates* have very well bifurcated T-shaped terminal phalanges (e.g. *O. discoidalis* and *O. heterodactylus*).

The presence of conical supernumerary and subarticular tubercles probably influenced the synonymization of *Oreobates* with *Ischnocnema*, and led to the hypothesis of the relationship proposed by Lynch (1989), in which *Ischnocnema* was the ancestor of members of the *E. discoidalis* group. Indeed, *E. verrucosus* (formerly *I. verrucosa*) or *E. octavioi* (of the *E. binotatus* series), from south-eastern Brazil, also show prominent conical subarticular tubercles. Nevertheless, the development of plantar tubercles in *E. verrucosus* and *E. octavioi* seems to be associated with skin texture. These species have general granular skin texture that extends to the plantar surfaces, which contain some scattered enlarged granules similar to supernumerary tubercles. In the genus *Oreobates* the supernumerary tubercles are strictly associated with the axis of the phalanges, whereas in *E. verrucosus* the plantar tubercles are randomly distributed on the plantar surface. Furthermore, although in *Oreobates* each finger or toe bears

between one and three supernumerary tubercles, in *E. verrucosus* there are only between one and three supernumerary tubercles for the whole plantar surface. Unfortunately, we were not able to test the relationships of *Oreobates* with *E. verrucosus* from south-eastern Brazil in our phylogeny. Nevertheless, no synapomorphy is shared by these species and *Oreobates* to suggest a close relationship. Indeed, the degree of development of the terminal phalanges seems to be associated with the degree of development of disc structures. The development of these structures is also variable within *Oreobates*, which suggests its limited utility for inferring phylogenetic relationships. Hence, until these hypotheses of relationships can be empirically tested, we agree with the biogeographical argument of Caramaschi & Canedo (2006) that considers the relationship of *Oreobates* (Andean and Amazonian species) with *E. verrucosus* (south-eastern Brazil) as doubtful.

Another hypothesis of relationship proposed by Lynch (1989) suggests that members of the *E. binotatus* series are intermediate between *Ischnocnema* and members of the *E. discoidalis* group, and that the latter would be annectant to the *E. fitzingeri* group (now *Craugastor*). However, although our molecular phylogeny is insufficient to address this problem, it does not show any close phylogenetic relationship of *E. binotatus* or *Craugastor* with the *Oreobates* clade. Examination of Lynch's (1971, 1989) illustrations of the skulls of *O. quixensis* and *O. discoidalis* reveals a morphology of the vomers similar to that of members of the *E. binotatus* series and *Euhyas*. This is the only character that suggests close relationships, but, as Lynch (2001) stated, this character seems to be non-homologous for both *Euhyas* and *E. binotatus*. We extend this assumption to *Oreobates*. Thus, there is no putative synapomorphy to support this hypothesis.

HYPOTHESES OF ORIGIN

Combining our information about distribution, habitat use, and phylogenetic relationships, we can hypothesize about the origin of the taxa under study (Graham *et al.*, 2004). The highest diversity and endemism of *Oreobates* is reached in the Eastern Cordillera of the Central Andes (*sensu* Gregory-Wodzicki, 2000). This diversity seems to be related to vicariant events as a result of Andean orogeny (Lynch & Duellman, 1997; Gregory-Wodzicki, 2000; Doan, 2003), and/or habitat fragmentation promoted by climatic changes (Weir, 2006; Hughes & Eastwood, 2006). Only three species are found in the lowlands (*O. quixensis*, *O. cruralis*, and *O. heterodactylus*). *Oreobates quixensis* occurs in the Upper Amazon Basin and invades the Andean foothills, where it reaches altitudes of 1000 m a.s.l. (Frost, 2006). *Oreobates cruralis*

also inhabits the humid forests of the Andean foothills up to 2000 m a.s.l. Some members of the group, such as *O. ibischi* and *O. discoidalis*, occupy the semideciduous forests of the inter-Andean dry valleys, from Central Bolivia to northern Argentina, and *O. cruralis* reach the northern limit of this habitat (close to the Amazonian forests).

Padial *et al.* (2008) found that differences in calls of some *Oreobates* were related to distribution in a certain habitat, and suggested that these differences could reflect consequences of isolation together with adaptation to a particular environment. Moreover, they found a geographical pattern in call variation along the latitudinal axis of the Andes, and proposed two possible scenarios for explaining these patterns. In the first, the colonization of the Andes by ancestors of the *E. discoidalis* group could have taken place in southern or central Bolivia, with subsequent expansion to the north (Peru) and to the south (northern Argentina). This hypothesis requires the *E. discoidalis* group to be related to the *E. binotatus* group (as hypothesized by Lynch, 1989). As the *E. binotatus* series is not closely related to *Oreobates* (Fig. 2), we reject this hypothesis.

In the second hypothesis, members of the *E. discoidalis* group would have emerged from a common ancestor of *O. quixensis* or a northern member of the *E. binotatus* series (Lynch, 1989). Our data discard the possibility of the *E. binotatus* series being related to *Oreobates*, but rather we suggest that *O. quixensis* could be the sister species to the rest of *Oreobates* (Figs 1, 2). In this case, the origin of *Oreobates* would be the Upper Amazon Basin or the Andean foothills. Indeed, members of *Oreobates* are direct-developing frogs that require moist conditions for reproduction, and the greatest species diversity in the genus occurs in humid forests of the Andean slopes from 1000 to 2000 m a.s.l. (Fig. 5). Those species inhabiting drier forests always seem to be restricted to humid microhabitats, such as for example the vegetation close to streams or caves. Moreover, there are two well-supported clades within *Oreobates* (Fig. 2), one including former members of *Oreobates* (robust frogs with marked granular skin and very short, weakly pulsed calls) and another including former members of the *E. discoidalis* group (small and slender frogs, with warty or shagreened dorsal skin, and longer calls with higher numbers of pulses). These facts suggest two events of diversification, one involving more robust *Oreobates* species (i.e. *O. choristolemma*, *O. granulatus*, *O. sanctaerucis*, *O. sanderi*, and *O. saxatilis*) in the Andean hills close to the Upper Amazon Basin, with a subsequent colonization to the south, and another diversification of smaller *Oreobates* species (*O. discoidalis*, *O. cruralis*, *O. ibischi*, and *O. madidi*) in the Andes from Bolivia to Argentina.

The most isolated species, from other members of *Oreobates*, is *O. heterodactylus*, which occurs in two isolated mountain ranges of the Precambrian Brazilian Shield (Heyer & Muñoz, 1999; Padial & De la Riva, 2005). This species inhabits relictual humid forests in small canyons and hills of isolated rocky outcrops. The distribution of this species is interesting because this area lacks any other brachycephalid species. This area lies in between the range of Andean and eastern Brazilian taxa. The occurrence of *E. heterodactylus* in this area probably made the correct assignment of this species to any species group difficult. For example, Lynch & Myers (1983) placed this species in the former *E. fitzingeri* group, whereas Lynch & Duellman (1997) included it in the *E. binotatus* group from the Atlantic Forests, something that Heyer & Muñoz (1999) considered as not making zoogeographical sense. Padial & De la Riva (2005) pointed out that *O. heterodactylus* resembles species of the *E. binotatus* (Lynch & Duellman, 1997) and *E. discoidalis* (*sensu* Lynch, 1989) species groups. Subsequently, Padial *et al.* (2008) suggested putative relationships with members of the *E. discoidalis* group based on similarities in advertisement calls. However, according to our analyses *O. heterodactylus* clearly belongs to *Oreobates*. Moreover, our phylogeny supports a close relationship of *O. heterodactylus* with the clade including putatively advanced *Oreobates* in the Andes of Bolivia and Argentina. Indeed, *O. discoidalis*, *O. ibischi*, and *O. heterodactylus* are very similar in morphology, and share a similar habitat (semideciduous forests). Therefore, the distribution pattern of these species indicates a broader distribution of *Oreobates* in the lowlands during more humid periods, and evidences a biogeographical connection between the Andes and the Precambrian Brazilian Shield (see also Pennington, Prado & Pendry, 2000).

CONCLUSIONS

Phylogenetic analyses of mtDNA, together with morphological synapomorphies and bioacoustical similarities, support the monophyly of *Oreobates* and the nonmonophyly of *Eleutherodactylus*. *Oreobates* contains 14 species, including former members of the *E. discoidalis* species group, *E. heterodactylus* and species assigned to *Oreobates* by Caramaschi & Canedo (2006). This genus is the sister group of the *E. martinicensis* and *E. conspicillatus* series of the subgenus *Eleutherodactylus*, and it is not closely related to members of the *E. dolops* or *E. nigrovittatus* groups, nor is it closely related to members of the *E. binotatus* series or *E. verrucosus* (formerly *I. verrucosa*). Members of *Oreobates* occur from Amazonian Colombia to northern Argentina, with an isolated vicariant species in the Precambrian Brazilian Shield

OPERATIONAL KEY TO THE SPECIES OF THE GENUS *OREOBATES*

1. Dorsal skin smooth to finely shagreened, enlarged discs on fingers III and IV, dentigerous process of vomers between choanae.....2
Dorsal skin with warts, granules, and/or tubercles.....4
2. Discs on fingers III and IV large, ovate; few or no warts on dorsum.....3
Discs moderately enlarged, truncate, low warts on dorsal skin.....*O. ibischi*
3. Dorsal coloration with arrow-shaped and X-shaped dorsal marks, Brazilian Shield distribution.....
.....*O. heterodactylus*
Dorsal coloration plain, or with irregular marks and spots, Andean distribution.....*O. discoidalis*
4. Dorsal skin coarsely shagreened or warty, keratinized granules absent.....5
Dorsal skin coarsely warty or tuberculate, keratinized granules present.....7
5. Dorsal warts homogeneous in size, finger tips rounded, adult SVL, 20.3–33.6 mm.....6
Dorsal warts of different sizes sometimes coalesce in dorsolateral ridges, fingers III and IV moderately enlarged.....*O. cruralis*
6. Foot length > 50% of SVL, supernumerary tubercles inconspicuous or absent.....*O. lehri*
Foot length < 50% of SVL, supernumerary tubercles conspicuous, numerous.....*O. madidi*
7. Dorsal skin granular.....8
Dorsal skin tuberculate, composed of enlarged warts, subconical tubercles, and granules.....10
8. Dorsal skin with pungent keratinized granules both on dorsum and extremities.....9
Dorsal skin with small, round, keratinized granules, low warts, extremities less granular.....11
9. Pungent granules on forearm present.....*O. simmonsii*
Pungent granules on forearm absent.....*O. zongoensis*
10. Abundant large subconical tubercles on dorsum, heavily mottled venter.....*O. quixensis*
Few large subconical tubercles on dorsum, faintly mottled venter.....*O. saxatilis*
11. Finger tips not enlarged.....12
Finger tips enlarged and with indented unguis flap.....*O. choristolemma*
12. Supernumerary tubercles conspicuous, prominent, abundant, conical; FL = 50% of SVL.....13
Supernumerary tubercles inconspicuous, low, between one and three; FL ≥ 50% of SVL.....*O. granulosis*
13. Dorsal coloration brownish grey, red or scarlet spots absent, head as wide as long.....*O. sanderi*
Red to scarlet spots in axiles, dorsum, and shanks, head wider than long.....*O. sanctaerucis*

(*O. heterodactylus*). The highest diversity of *Oreobates* occurs in humid montane forests of the Andean Cordillera Oriental (1000–2000 m a.s.l.).

ACKNOWLEDGEMENTS

Most of Padial's field work in Bolivia was financed by a grant of the Mutis programme of the MAE-AECI (Spain); his trip to visit the museums in the USA was funded by an Ernst Mayr Travel Grant in Animal Systematics (Museum of Comparative Zoology, Harvard University), and his trip to visit the British Museum was funded by the 'European Commission's Research Infrastructure Action' via the 'SYNTHESYS Project'. JCC's fieldwork was funded by APECO and by a Koepcke grant. We are grateful to the following people for the loan of specimens, support, and/or space provided at their institutions: R. Bain, D. Frost, T. Grant, and D. Kizirian (AMNH); B. Clarke and M. Wilkinson (BM); J. Aparicio (CBF); R. Aguayo and A. Muñoz (CBG); W. E. Duellman, J. Simmons, and L. Trueb (KU); J. Hanken and J. Rosado (MCZ); O. Aguilar (MHNC); Cesar Aguilar (MHNSM); B. Álvarez, J. E. González-Fernández, and I. Rey (MNCN); L. González, A. Justiniano, R. Montaña,

M. Suárez, and R. Vespa (MNK); P. E. Vanzolini, and H. Zaher (MZUSP); D. Cannatella, and T. LaDuc (TNHC); R. A. Nussbaum, and G. Schneider (UMMZ); K. de Queiroz, W. R. Heyer, R. McDiarmid, and R. V. Wilson (USNM); J. A. Campbell (UTA); W. Böhme, S. Lötters, and J. Köhler (ZFMK); and J. B. Rasmussen and M. Andersen (ZMUC). We thank R. Aguayo, E. Ávila, P. Comas, R. de Sá, D. Embert, J. M. Gil-Sánchez, M. González-Osto, J. Heredia, P. Macuapa, M. Moleón, J. Pérez-Marín, D. Ramos, C. Rojas, S. Ten, and C. Ureña, for their valuable help and companionship in the field. We are indebted to S. Castroviejo-Fischer, P. Flores, A. Machordom, and M. García-París for their perennial disposition to help us in the lab and with the phylogenetic analyses. G. Parra-Olea, B. Hedges, and M. Heinicke provided pivotal sequences for this study. W. E. Duellman, A. Muñoz, and S. Reichle provided the pictures of *O. choristolemma*, *O. saxatilis*, and *O. zongoensis*, respectively. We thank F. Palacios for his decisive support, and J. Köhler and S. Reichle for their constructive discussion over many years. We appreciate A. Crawford, W. R. Heyer, J. Köhler, and S. Castroviejo-Fischer for their valuable comments on the manuscript. This work was partially funded by

projects REN/GLO 2001–1046 and CGL2005-03156 of the Spanish Ministry of Education and Science (I. De la Riva, Principal Investigator).

NOTE ADDED IN PROOF

While this paper was in press, two important publications appeared (Heinicke, Duellman & Hedges, 2007; Hedges, Duellman & Heinicke, 2008) in which former families Brachycephalidae and Eleutherodactylae are revised. The genus *Oreobates* is placed in the new family Strabomantidae, and presumably would include also the former species *Phrynopus pereger*.

REFERENCES

- Alcaide de Pucci MFS, De Mopty S, Terán HR. 1992.** Análisis histoquímico de las mucinas de la lengua de tres especies de la fam. Leptodactylidae (Anura). *Acta Zoologica Lilloana* **42**: 35–40.
- Boulenger GA. 1902.** Description of new batrachians and reptiles from the Andes of Peru and Bolivia. *Annals and Magazine of Natural History* **7**: 394–402.
- Boulenger GA. 1903.** Descriptions of new Batrachians in the British Museum. *Annals and Magazine of Natural History* **7**: 552–557.
- Cantino PD, de Queiroz K. 2004.** *Phylocode: a phylogenetic code of biological nomenclature*, version 2b. Available at <http://www.ohiou.edu/phylocode/>
- Caramaschi U, Canedo C. 2006.** Reassessment of the taxonomic status of the genera *Ischnocnema* Reinhardt and Lütken, 1862 and *Oreobates* Jiménez de la Espada 1872, with notes on the synonymy of *Leiuperus verrucosus* Reinhardt and Lütken, 1862 (Anura: Leptodactylidae). *Zootaxa* **1116**: 43–54.
- Cei JM. 1980.** Amphibians of Argentina. *Monitore Zoológico Italiano. Monografie* **2**: 1–609.
- Cei JM. 1987.** Additional notes to ‘Amphibians of Argentina’: an update, 1980–86. *Museo Regionale Di Scienze Naturali Torino, Monografie* **21**: 209–272.
- Chaparro JC, Pramuk JB, Gluesenkamp AG. 2007.** A new species of arboreal *Rhinella* (Anura: Bufonidae) from cloud forest of southeastern Peru. *Herpetologica* **63**: 203–212.
- Crawford AJ, Smith EE. 2005.** Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleutherodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* **35**: 536–555.
- Darst CR, Cannatella DC. 2004.** Novel relationships among hylid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **31**: 462–475.
- Dayrat B. 2005.** Toward integrative taxonomy. *Biological Journal of the Linnean Society* **85**: 407–415.
- De la Riva I. 1990.** Lista preliminar comentada de los anfibios de Bolivia con datos sobre su distribución. *Bolletino Del Museo Regionale Di Scienze Naturali, Torino* **8**: 261–319.
- De la Riva I. 1993.** Sinopsis del género *Eleutherodactylus* (Amphibia, Anura, Leptodactylidae) en Bolivia y adición de tres especies nuevas para el país. *Revista Española de Herpetología* **7**: 97–105.
- De la Riva I, Köhler J, Lötters S, Reichle S. 2000.** Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetología* **14**: 19–164.
- De Mopty S, Terán HR, Alcaide de Pucci MFS. 1992.** Histomorfológia lingual en relación con los hábitos alimenticios en tres especies de anuros (Fam. Leptodactylidae). *Acta Zoologica Lilloana* **42**: 143–148.
- Doan TM. 2003.** A south-to-north biogeographic hypothesis for Andean speciation: evidence from the lizard genus *Protoporus* (Reptilia: Gymnophthalmidae). *Journal of Biogeography* **30**: 361–374.
- Doan TM, Arizábal W. 2002.** Microgeographic variation in species composition of the herpetofauna communities of Tambopata region, Peru. *Biotropica* **34**: 101–117.
- Duellman WE. 1978.** The biology of an Equatorial herpetofauna in Amazonian Ecuador. *University of Kansas Museum of Natural, History Miscellaneous Publications* **55**: 1–352.
- Duellman WE. 1990.** A new species of leptodactylid frog, genus *Ischnocnema*, from Peru. *Occasional Papers of the Museum of Natural History of the University of Kansas* **138**: 1–7.
- Duellman WE. 2005.** *Cusco Amazónico: the Lives of Amphibians and Reptiles in an Amazonian Rainforest*. Ithaca: Cornell University Press.
- Duellman WE, Trueb L. 1986.** *The Biology of Amphibians*. New York: McGraw-Hill Co.
- Faivovich J, Hadad CFB, Garcia PCA, Frost DR, Campbell JA, Wheeler WC. 2005.** Systematic review of the frog family Hylidae, with special reference to the Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* **294**: 1–240.
- Frost DR. 2006.** *Amphibian species of the world 4.0, an online reference*. New York: American Museum of Natural History. 17 September 2006. Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>
- Frost D, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, De Sá R, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC. 2006.** The Amphibia tree of life. *Bulletin of the American Museum of Natural History* **297**: 1–370.
- Funk DJ, Omland KE. 2003.** The frequency, causes and consequences of species level paraphyly and polyphyly: insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution and Systematics* **34**: 397–423.
- Gavetti E, Andreone F. 1993.** Revised catalogue of the herpetological collection in Turin University. I. Amphibia. *Museo Regionale Di Scienze Naturali Di Torino, Cataloghi* **10**: 1–185.
- Glaw F, Köhler J. 1998.** Amphibian species diversity exceeds that of mammals. *Herpetological Review* **29**: 11–12.
- Goebel AM, Donnelly JM, Atz ME. 1999.** PCR Primers and

- amplification methods for 12S Ribosomal DNA, the Control Region, Cytochrome Oxidase I, and Cytochrome b in bufonids and other frogs, and an overview of PCR primers which have amplified DNA in amphibians successfully. *Molecular Phylogenetics and Evolution* **11**: 163–199.
- González JE. 2006.** Anfíbios colectados por la Comisión Científica del Pacífico (entre 1862 y 1865) conservados en el Museo Nacional de Ciencias Naturales de Madrid. *Graellsia* **62**: 111–158.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C. 2004.** Integrating phylogenetics and environmental niche models to explore speciation mechanisms in Dendrobatid frogs. *Evolution* **58**: 1781–1793.
- Gregory-Wodzicki KM. 2000.** Uplift history of the Central and Northern Andes: a review. *GSA Bulletin* **112**: 1091–1105.
- Harvey MB, Keck MB. 1995.** A new species of *Ischnocnema* (Anura: Leptodactylidae) from high elevations in the Andes of central Bolivia. *Herpetologica* **51**: 56–66.
- Harvey MB, Sheehy CM. 2005.** A new species of *Ischnocnema* (Anura: Leptodactylidae) from La Paz, Bolivia. *Herpetologica* **61**: 268–275.
- Häupl M, Tiedeman F, Grillitsch H. 1994.** Katalog der Typen der Herpetologischen Sammlung nach dem Stand vom 1. Jänner 1994. Teil I: Amphibia. *Kataloge der wissenschaftlichen Sammlungen des Naturhistorischen Museum in Wien, Vertebrata* **9**: 1–46.
- Hayek LA, Heyer WR, Gascon C. 2001.** Frog morphometrics: a cautionary tale. *Alytes* **18**: 153–177.
- Hedges SB, Duellman WE, Heinicke MP. 2008.** New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, in press.
- Heinicke MP, Duellman WE, Hedges SB. 2007.** Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the USA* **104**: 10092–10097.
- Hennig W. 1966.** *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.
- Heyer WR, Gascon C. 1995.** Collection notes and call characteristics for *Ischnocnema quixensis* and *Phyzelaphryne miriamae* (Amphibia: Anura; Leptodactylidae). *Journal of Herpetology* **29**: 304–307.
- Heyer WR, Muñoz AM. 1999.** Validation of *Eleutherodactylus crepitans* Bokermann, 1965, notes on the types and type locality of *Telatrema*[sic] *heterodactylum* Miranda-Ribeiro, 1937, and description of a new species of *Eleutherodactylus* from Mato Grosso, Brazil (Amphibia: Anura: Leptodactylidae). *Proceedings of the Biological Society of Washington* **112**: 1–18.
- Hillis DM, Moritz C, Mable BK, eds. 1996.** *Molecular systematics*, 2nd edn. Sunderland, MA: Sinauer.
- Huelsenbeck JP, Ronquist F. 2001.** MrBAYES: Bayesian inferences of phylogenetic trees. *Bioinformatics* **8**: 754–755.
- Hughes C, Eastwood R. 2006.** Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences USA* **103**: 10334–10339.
- Jiménez de la Espada M. 1872.** Nuevos Batracios Americanos. *Anales de la Sociedad Española de Historia Natural* **1**: 85–88.
- Jiménez de la Espada M. 1875.** *Vertebrados Del Viaje Al Pacífico. Batracios*. Madrid: Imprenta Miguel Ginesta.
- Köhler J. 2000.** Amphibian diversity in Bolivia: a study with special reference to montane forest regions. *Bonner Zoologische Monographien* **48**: 1–243.
- Kress WJ, Heyer WR, Acevedo P, Coddington J, Cole D, Erwin TL, Meggers BJ, Pogue M, Thorington RW, Vari RP, Weitzman MJ, Weitzman SH. 1998.** Amazonian biodiversity: assessing conservation priorities with taxonomic data. *Biodiversity and Conservation* **7**: 1577–1587.
- Lavilla EO, Cei JM. 2001.** Amphibians of Argentina. A second update, 1987–2000. *Museo Regionale Di Scienze Naturali Torino, Monografie* **28**: 1–177.
- Leviton AER, Gibbs H, Heal E, Dawson CE. 1985.** Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **3**: 802–832.
- Lynch JD. 1971.** Evolutionary relationships, osteology, and zoogeography of Leptodactylid frogs. *University of Kansas, Museum of Natural History Miscellaneous Publications* **53**: 1–238.
- Lynch JD. 1974.** A new species of leptodactylid frog (*Ischnocnema*) from the Cordillera del Cóndor in Ecuador. *Journal of Herpetology* **8**: 85–87.
- Lynch JD. 1976.** The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Occasional Papers of the Museum of Natural History, University of Kansas* **61**: 1–24.
- Lynch JD. 1986.** The definition of the Middle American clade of *Eleutherodactylus* based on jaw musculature (Amphibia: Leptodactylidae). *Herpetologica* **42**: 248–258.
- Lynch JD. 1989.** Intrageneric relationships of mainland *Eleutherodactylus* (Leptodactylidae). I. A review of the frogs assigned to the *Eleutherodactylus discoidalis* species group. *Milwaukee Public Museum, Contributions in Biology and Geology* **79**: 1–25.
- Lynch JD. 2001.** Four osteological synapomorphies within *Eleutherodactylus*: (Amphibia: Leptodactylidae) and their bearing on subgeneric classifications. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* **25**: 127–136.
- Lynch JD, Duellman WE. 1997.** Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: systematics, ecology, and biogeography. *University of Kansas Natural History Museum Special Publications* **23**: 1–236.
- Lynch JD, Myers CW. 1983.** Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocóan South America (Leptodactylidae). *Bulletin of the American Museum of Natural History* **175**: 481–572.
- Lynch JD, Schwartz A. 1971.** Taxonomic disposition of some 19th Century leptodactylid frog names. *Journal of Herpetology* **5**: 103–114.
- Padial JM, Chaparro JC, De la Riva I. 2007.** A new species of the *Eleutherodactylus discoidalis* group (Anura: Brachycephalidae) from cloud forests of Peru. *Herpetologica* **63**: 114–122.

- Padial JM, De la Riva I. 2005.** Rediscovery, redescription and advertisement call of *Eleutherodactylus heterodactylus* (Miranda Ribeiro, 1937) (Anura: Leptodactylidae), and notes on other *Eleutherodactylus*. *Journal of Herpetology* **39**: 372–379.
- Padial JM, De la Riva I. 2006.** Taxonomic inflation and the stability of species lists: the perils of ostrich's behavior. *Systematic Biology* **55**: 859–867.
- Padial JM, González L, De la Riva I. 2005b.** A new species of the *Eleutherodactylus discoidalis* group (Anura: Leptodactylidae) from Andean humid montane forest of Bolivia. *Herpetologica* **61**: 318–325.
- Padial JM, Köhler J, Muñoz A, De la Riva I. 2008.** Assessing the taxonomic status of tropical frogs through bioacoustics: geographical variation in the advertisement call in the *Eleutherodactylus discoidalis* species group (Anura: Brachycephalidae). *Zoological Journal of the Linnean Society* **152**: 353–365.
- Padial JM, Reichle S, De la Riva I. 2005a.** A new species of *Ischnocnema* (Anura: Leptodactylidae) from the Andes of Bolivia. *Journal of Herpetology* **39**: 186–191.
- Pennington RT, Prado DE, Pendry CA. 2000.** Neotropical seasonally dry forest and Quaternary vegetation changes. *Journal of Biogeography* **27**: 261–273.
- Peracca MG. 1895.** Viaggio del Dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. Rettili e Anfibi. *Bollettino di Musei di Zoologia ed Anatomia comparata de lla R. Università di Torino* **10**: 1–32.
- Peracca MG. 1897.** Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. Rettili e Anfibi. *Bollettino di Musei di Zoologia ed Anatomia comparata de lla R. Università di Torino* **12**: 1–19.
- Rannala B, Yang Z. 1996.** Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *Journal of Molecular Evolution* **43**: 304–311.
- Reichle S. 1999.** Zur Kenntnis dreier Leptodactylidae aus Bolivien, *Ischnocnema sanctaecrucis* Harvey & Keck, 1995, *Eleutherodactylus fenestratus* (Steindachner, 1864) und *Eleutherodactylus samaipatae* Köhler & Jungfer, 1995. *Herpetofauna* **123**: 5–9.
- Reichle S, Köhler J. 1997.** A new species of *Eleutherodactylus* (Anura: Leptodactylidae) from the Andean slopes of Bolivia. *Amphibia-Reptilia* **18**: 333–337.
- Reichle S, Lötters S, De la Riva I. 2001.** A new species of the *discoidalis* group of *Eleutherodactylus* (Anura, Leptodactylidae) from inner-Andean dry valleys of Bolivia. *Journal of Herpetology* **35**: 21–26.
- Reinhardt J, Lütken Ch. 1862.** Bidrag til kundsrab on Brasiliens paddes og krybdyr. *Vodenskabelgige Meddelelser Fra Dansk Naturhistorisk Forening I Kjøbenhavn, Series 2*: 143–242.
- Rodríguez LO, Duellman WE. 1994.** Guide to the frogs of the Iquitos Region, Amazonian Peru. *University of Kansas Museum of Natural History Special Publications* **22**: 1–80.
- Sambrook E, Fritsch F, Maniatis T. 1989.** *Molecular cloning*. New York: Cold Spring Harbor Press.
- Savage JM. 1987.** Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibian: Leptodactylidae). *Fieldiana Zoologica* **33**: 1–57.
- Swofford DL. 1998.** *PAUP**. *Phylogenetic analysis using parsimony* and other methods, version 4b10*. Sunderland, MA: Sinauer Associates.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997.** The CLUSTALX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**: 4876–4882.
- Vences M, Köhler J. 2006.** The current status of genetic exploration in amphibians: taxonomic and geographical disparities. In: Vences M, Köhler J, Ziegler T, Böhme W, eds. *Herpetologica Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. Bonn: SHE, 193–195.
- Weir JT. 2006.** Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* **60**: 842–855.
- Will KW, Mishler BD, Wheeler QD. 2005.** The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology* **54**: 844–851.
- Wohltmann A, Köhler J, Martin P. 2006.** Endoparasitic mite infections of anuran amphibians from Bolivian montane rain forests, with descriptions of two new *Hannemania* species (Acari: Parasitengona: Trombiculidae: Leeuwenhoekinae). *Organisms Diversity and Evolution* **6**: 141–150.
- Yang Z, Rannala B. 1997.** Bayesian phylogenetic inference using DNA sequences: a Markov Chain Monte Carlo method. *Molecular Biology and Evolution* **14**: 717–724.

APPENDIX

SPECIMENS EXAMINED

- ELEUTHERODACTYLUS BABAX* (two specimens). Colombia: Departamento Nariño: 7 km south de Chucunes, Reserva Natural La Planada, KU 200201–2 (paratypes).
- ELEUTHERODACTYLUS DOLOPS* (two specimens). Ecuador: Provincia Napo: Loreto, USNM 199990 (paratype); Salto de Agua, 2.5 km north north-east of Río Reventador, 1660 m a.s.l., KU 143505 (holotype); Provincia Pastaza: Río Villano, USNM 199991–2 (paratypes).
- ELEUTHERODACTYLUS ELASSODISCUS* (two specimens). Ecuador: Provincia Napo: Cuyuja, 2360 m a.s.l., USNM 167668 (holotype), 167669 (paratype).
- ELEUTHERODACTYLUS OCTAVIOI* (three specimens). Brazil: Rio do Janeiro: Tijuca, Guanabara & BM 1964.2008 (paratype), USNM 152767 (paratype), MCZ 64361 (paratype).
- ELEUTHERODACTYLUS VERRUCOSUS* (one specimen). Brazil: Minas Gerais: 'Byen (= city) Juiz de Fora i Minas Geraes' ZMUC 51 (R 1180) (holotype).
- OREOBATES CHORISTOLEMMA* (five specimens). Bolivia: Departamento Cochabamba: 'Old' Chapare road, 1300–1500 m a.s.l., ZFMK 72569; Departa-

mento La Paz: Provincia Sud Yungas, Boquerón, CBG 765–68.

OREOBATES CRURALIS (181 specimens). Bolivia: Departamento Beni: Areruta, CBG 1545–7; Asunción, Biosphere Reserve Pilón Lajas, MNKA 4074; Buena Vista, MZUM 66609–10; Huachi, MZUM 58987, 135343; Laguna Azul, Biosphere Reserve Pilón Lajas, MNKA 3975–76, 3979, 3985–87, 4003; Rurrenabaque, CBG 3667, MNCN 42558–9; San Luis Chico, MNKA 4027, 4030; Serranía del Pilón, Biosphere Reserve Pilón Lajas, MNKA 4182–83, 4209–13; Departamento Cochabamba: Bulo Bulo, TIPNIS, CBG 350, 380, 382–3, 393; Chaquisacha, 1300–1500 m a.s.l., Parque Nacional Carrasco, CBG 198, 199, 1140; de Paracti a El Palmar, ZFMK 66964, ZFMK 66971–2; El Palmar, 1300 m. Parque Nacional Carrasco, CBG 276, 956, ZFMK 72570; entre Paractito y El Palmar, ZFMK 66964, ZFMK 66971–2, ZFMK 72541–3; Los Guácharos (Chapare, 500 m a.s.l.), CBG 308, MNKA 6617–19, MNCN 43018–9, ZFMK 72532; on Villa Tunari road, USNM 146577; Puerto Villaroel, CBG 1337; Río Grande, 1000 m a.s.l., Parque Nacional Carrasco, CBG 275; San José de la Angostura, TIPNIS, CBG952–54; Santa Anita, TIPNIS, CBG 739; Santo Domingo 800 m, TIPNIS, CBG 596–7; Serranía de Mosenes 1580 m, MNCN 43155; Valle de Sajta, MNKA 3633, 1489; Villa Tunari, MNKA 1492; Departamento La Paz: Arroyo Pico Plancha, San José y Apolo, ANMI-Parque Nacional Madidi, MNKA 7180; Aserradero San Francisco, Ixiamas, CBG 1133; Boquerón, Biosphere Reserve Pilón Lajas, CBG 789–93; Camino a Bella Vista, Sud Yungas, MNKA 3792; Camino maderero El Chaval, Arroyo Mikai, Biosphere Reserve Pilón Lajas, MNKA 3759–61; Chalalán, ANMI-Parque Nacional Madidi, MNCN 42560, 43021–2, 43058, 43222, 43223; Flor de Mayo, La Asunta, CBG 2936; Flor de Mayo, río Boopi, CBG 1791; Hornuni, Parque Nacional AMNI-Cotapata, CBG 4208; Irupana, CBG 529; La Paz (locality in error), BM 1947.2.15.70 (holotype); CBG 2484; Puerto Linares, 360 m a.s.l., USNM 281100–30; road from Caranavi to Palos Blancos, ZFMK 80599; Serranía Tequeje, CBG 5104–7; Serranía del Pilón, Biosphere Reserve Pilón Lajas MNKA 4182–6, 4201, 4208–13, 4218; Torno Azul, Biosphere Reserve Pilón Lajas, CBG 1004; Tumupassa, MZUM 58985–6, 58988; Tunquini, Parque Nacional AMNI-Cotapata, CBG 4224; 5 km west of San Buenaventura USNM 280617; Departamento Pando: Florida, Reserva Manuripi, MNKA 5086, 5122; Lago Bay, Reserva Manuripi, MNKA 6120–21; Departamento Santa Cruz: Buena Vista, USNM 118686; camino a BellaVista desde la carretera a Samaipata, MNCN 42557, 42977, MNKA 7171, ZFMK 71997; La Hoyada, Parque Nacional Amboró, MNKA 5577, ZFMK 72644;

Mataracú, Parque Nacional Amboró, MNKA 3950, 3952, 3954, 3968; Santa Cruz de la Sierra, BM 1904.10.29.102–107; south of Cuevas ZFMK 72644; Víbora, CBG 3638. Peru: Departamento Madre de Dios: Colpa de Guacamayos, Zona Reservada Tambopata-Candamo, USNM 332436–37; Puerto Maldonado, 30 km south south-west of Tambopata, USNM 284267, 343240, 342989–92; 15 km east of Puerto Maldonado, 200 m a.s.l., KU 207749, 215461–62, 215479–80; Departamento Cusco: Río los Amigos, MHNC 3170, 3172, 3177.

OREOBATES DISCOIDALIS (113 specimens). Argentina: Province Tucumán: El Indio, km 28 Tafi del Valle-Amaicha del Valle road, 960 m a.s.l., KU 182815; Horco Molle, '13 km west of Tucumán', Sierra de San Javier, c. 1200 m a.s.l., BM 1947.2.15.63–65 (syn-types), KU 154521–29; MCZ 35583; 24 km west of Tucumán, KU 206434–38; without locality, MCZ 117097; Province Jujuy: Abra de las Cañas, Serranía de Calilegua, 1550 m a.s.l., KU 182813–14; Arroyo Agua Negra, near border Salta-Jujuy, 10 km up to Manolito and Valle Grande, from Yuto to Ledesma, TNHC 36776, 36778–93; San Lorenzo, BM 98.7.7.19.20. Bolivia: Departamento Chuquisaca: Río Pilipili, CBG 1396–7; Departamento Santa Cruz: Río Parabano, MNKA 5582; Departamento Tarija: Bajada de la Escalera, Reserva Nacional Tariquía, CBG 4978–9; Cambarí. Reserva Nacional de Tariquía, CBG 4889–90; Chiquiacá MNKA 7262–3, MNCN 43133–35; Entre Ríos, MNKA 7257–59, MNCN 43132; La Planchada, CBG 3773, 3780–4; Potrerillas, Reserva Nacional Tariquía, CBG 4891; Serranía Aguarague, a 17 km de Villa Montes en dirección a Entre Ríos, MNKA 7246–56, MNCN 43123, 43125–31, 43136–9; Serranía Aguarague, a 40 km de Yacuiba, CBG 1411–17; subida a Palo Marcado, Reserva Nacional Tariquía, CBG 4970; 12.3 km north-west of Entre Ríos on the road to Tarija 1900 m a.s.l., MNKA 3877–97, UTA 45645, 45648–50, 45652, 45658–62.

OREOBATES GRANULOSUS (26 specimens). Peru: Department Puno: Agualani, Carabaya, 2740 m a.s.l., BM 1905.5.31.14.20 (four specimens); Limbani, Carabaya, 2740 m a.s.l., BM 1905.5.31.21 (formerly 1904.10.26.94–99); Ollachea, 11 km (north north-east), 1800 m a.s.l., USNM 299006–12; Santo Domingo, Carabaya, 1400–1500 m a.s.l., MHNC 5328, 5335; Santo Domingo, Carabaya, 6000 ft (1800 m a.s.l. approx.), BM 1947.2.15.72 (holotype); Santo Domingo, Carabaya, 6500 ft (2000 m a.s.l. approx.), BM 1907.5.7.17–18; Juliaca (locality in error), AMNH 6060–2, 6064.

OREOBATES HETERODACTYLUS (seven specimens). Bolivia: Departamento Santa Cruz: Bella Boca, MNKA 6482; Cerro del Arco, Serranía de Santiago, MNKA 6356–7, 7175–6, MNCN 43055–6.

OREOBATES IBISCHI (four specimens). Bolivia: Departamento Santa Cruz: km 68.5 on Santa Cruz de la Sierra-Samaipata road, 750 m a.s.l. elevation, CBF 3341 (holotype); km 60 on Santa Cruz de la Sierra-Samaipata road, MNKA 6612, MNCN 42959; Samaipata, ZFMK 60402 (paratype).

OREOBATES LEHRI (31 specimens). Peru: Departamento Cusco: Apurimac River Valley, Camisea Natural Gas Pipeline, Wayrapata Camp, 2445 m a.s.l. (12°50'10"S, 73°29'43"W), USNM 537848 (holotype), USNM 537846–57 (paratopotypes); Buenos Aires, 2400 m a.s.l., KU 173231; Esperanza, Kosñipata Valley, 2600–2800 m a.s.l. (13°10'56"S, 71°36'22"W), MHNC 3223–31 (paratype), 3234–37 (paratype), MNCN 43740–1 (paratype); Paucartambo, AMNH 153087; Pillahuata, between Puente Kosñipata and road, 2430 m a.s.l. (13°09'52"S, 71°35'46"W), AMNH 11831 (paratype).

O. OREOBATES MADIDI (six specimens). Bolivia: Departamento La Paz: Arroyo Huacataya, Serranía Eslabón, Área Natural de Manejo Integrado Madidi, MNKA 7856 (holotype), 7197 (paratype), MNCN 42014–15 (paratypes); La Cascada, Biosphere Reserve Pilon Lajas, MNKA 4137–38 (paratypes).

OREOBATES QUIXENSIS (59 specimens). Bolivia: Departamento Pando: Luz de América, Reserva Nacional de Vida Silvestre Manuripi-Heath, MNKA 6525; Mukden, 4591; Reserva Nacional de Vida Silvestre Manuripi-Heath, MNKA 3640–1, 6099; Reserva Nacional de Vida Silvestre Tahuamanu, NKA 4586–90; Río Negro, MNKA 6525–27, 6900; San Antonio, Reserva Nacional de Vida Silvestre Manuripi-Heath, MNKA 6526–27. Colombia: Departamento Amazonas: Puerto Nariño MCZ 93777–80; Río Amaca-Yacu, MCZ 95734. Ecuador: Provincia Morona-Santiago: Sucua, MCZ 91361; Provincia Napo: AMO-II drill site, MCZ 111776–7; Archidona, MNCN 1709–21 (paralectotypes); Coca, MCZ 105868, 106017–19, 124825; Hacienda Primavera, MCZ 97881; La Cruz Blanca, South side of Río Napo,

MCZ 109213–14, 119093; Limón Cocha, MCZ 56307; near Tarapoa, MCZ 101262; Santa Cecilia, MCZ 57793–97, 57799; San José de Moti, MNCN 1708 (lectotype); Provincia Oriente: Canelos MCZ19734–6. Peru: Departamento Amazonas: MCZ 125896–7.

OREOBATES SANCTAECRUCIS (13 specimens). Bolivia: Departamento Cochabamba: Chaquisacha, 1300–1500 m a.s.l., Parque Nacional Carrasco, CBG 152–3; Diampampa, Parque Nacional Carrasco, CBG 634; Karahuasi, ZFMK 72647; Río Grande, 1000 m a.s.l., Parque Nacional Carrasco, CBG 291–292; Departamento Santa Cruz: El Bibosi, Parque Nacional Amboró, MNKA 6697; El Chapé, Parque Nacional Amboró, 2060 m a.s.l. elevation, MNKA 1198 (holotype), 7158, MNCN 42010–13.

OREOBATES SANDERI (19 specimens). Bolivia: Department La Paz: Arroyo Bilunto, Chundurumi Valley, Bilunto Mountains, Área Natural de Manejo Integrado Madidi, near Santa Cruz de Valle Ameno, CBF 5385 (holotype), MNCN 42016–7 (paratypes), CBF 5383–4 (paratypes); Bajo Hornuni, CBF 4119–22, 4218–19, 4223 (paratypes); Colonia Eduardo Avaroa, c. 30 km north of Caranavi on the road from Caranavi to Yucumo, ZFMK 80600–1 (paratypes), MNKA 6563 (paratypes); road from Apolo to Sarayo, MNKA 6695–6 (paratypes). Peru: Departamento Puno: Abra de Maruncuna, 10 km south-west of San Juan del Oro, 1650 m a.s.l., KU 206101; Juliaca (locality in error), AMNH 6063.

OREOBATES SAXATILIS (two specimens). Peru: Departamento San Martín: Ponga de Shilcayo, about 4 km north north-west of Tarapoto, 470 m a.s.l., KU 212556 (holotype), MHNSM 8431 (paratype).

OREOBATES SIMMONSI (one specimen). Ecuador: Provincia Morona-Santiago: Río Piuntza 1830 m a.s.l., KU 147068 (holotype).

OREOBATES ZONGOENSIS (one specimen). Bolivia: Departamento La Paz: Valle de Zongo, 1250 m a.s.l., CBF 2503 (holotype).