A Revision of Species Diversity in the Neotropical Genus Oreobates (Anura: Strabomantidae), with the Description of Three New Species from the Amazonian Slopes of the Andes

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Source: American Museum Novitates, 2012(3752) : 1-55

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/3752.2

AMERICAN MUSEUM NOVITATES

Number 3752, 55 pp. July 20, 2012

A revision of species diversity in the Neotropical genus *Oreobates* (Anura: Strabomantidae), with the description of three new species from the Amazonian slopes of the Andes

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ABSTRACT

We revisit species diversity within *Oreobates* (Anura: Strabomantidae) by combining molecular phylogenetic analyses of the 16S rRNA amphibian barcode fragment with the study of the external morphology of living and preserved specimens. Molecular and morphological evidence support the existence of 23 species within *Oreobates,* and three additional candidate species (*Oreobates* sp. [Ca JF809995], *Oreobates* sp. [Ca EU368903], *Oreobates cruralis* [Ca

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ISSN 0003-0082

EU192295]). We describe and name three new species from the Andean humid montane forests of Departamento Cusco, southern Peru: *O. amarakaeri* New Species from Río Nusinuscato and Río Mabe, at elevations ranging from 670 to 1000 m in the Andean foothills; *O. machiguenga,* new species, from Río Kimbiri (1350 m), a small tributary of the Apurimac River, in the western versant of Cordillera Vilcabamba; and *O. gemcare,* new species, from the Kosñipata Valley at elevations ranging from 2400 to 2800 m. The three new species are readily distinguished from all other *Oreobates* by at least one qualitative morphological character. Three species are transferred to *Oreobates* from three genera of Strabomantidae: *Hypodactylus lundbergi*, *Pristimantis crepitans*, and *Phrynopus ayacucho* (for which the advertisement call, coloration in life, and male characteristics are described for first time). *Oreobates simmonsi* is transferred to the genus *Lynchius*. *Hylodes verrucosus* is considered a junior synonym of *Hylodes philippi*. In addition, *H. philippi* is removed from the synonymy of *O. quixensis* and considered a nomem dubium within *Hypodactylus*. The inclusion of *Phrynopus ayacucho* in *Oreobates* extends the ecological range of the genus to the cold Andean puna. *Oreobates* is thus distributed from the Amazonian lowlands in southern Colombia to northern Argentina, reaching the Brazilian Atlantic dry forests in eastern Brazil, across an altitudinal range from ca. 100 to 3850 m.

INTRODUCTION

The genus *Oreobates* (Jiménez de la Espada, 1872) has, in a figurative sense, experienced a rapid radiation in species numbers since Caramaschi and Canedo (2006) resurrected it for six Andean species historically associated with *Ischnocnema* (see Lynch and Schwartz, 1971). Shortly after the recognition of the genus, Padial et al. (2008a) assessed the phylogenetic relationships of *Oreobates* and putatively related groups and proposed a monophyletic *Oreobates* composed of 14 species, most of them former members of the *Eleutherodactylus discoidalis* group (Lynch, 1989). The monophyly of the group was further supported by a larger phylogenetic analysis that included more characters but fewer species of *Oreobates* (Hedges et al., 2008a). That same year, two more species were placed in *Oreobates*: *O. barituensis*, a new species from the Yungas of northern Argentina (Vaira and Ferrari, 2008), and *Oreobates pereger*, an inhabitant of montane forests in southern Peru, which was transferred from *Phrynopus* to *Oreobates* by Hedges et al. (2008a). More recently, a new species was surprisingly found as far east as the Atlantic dry forests in eastern Brazil (Teixeira et al., 2012). Subsequently, three other phylogenetic analyses provided support for the monophyly of *Oreobates*, although taxon sampling was still incomplete (Padial et al., 2009a; Teixeira et al., 2012; Pyron and Wiens, 2011).

From south to north, the current geographical and ecoregional distribution of the 17 species of *Oreobates* extends as follows (see Padial et al., 2008a; Vaira and Ferrari, 2008; Frost, 2011; Teixeira et al., 2012): *Oreobates barituensis* inhabits humid Yungas in northern Argentina, and probably occurs in adjacent Bolivia as well. *Oreobates discoidalis* has a large distribution in the Andean hills, from Central Bolivia to northern Argentina, and inhabits Yungas montane forests as well as semideciduous forests of the inter-Andean dry valleys; it is sympatric with *O. barituensis* and mostly parapatric with *O. ibischi*. *Oreobates ibischi* inhabits semideciduous forests of the inter-Andean dry valleys in Central Bolivia, where it may come in contact with *O. discoidalis* and southern populations of the eminently Amazonian *O. cruralis*. Also in dry forests occur the vicariants *O. heterodactylus* and *O. remotus*, inhabitants of wet microhabitats in the otherwise xeric formations of the rocky outcrops of the Precambrian Shield of Bolivia and Brazil, with *O. remotus* representing the easternmost distribution of the genus. Two species, *O. cruralis* and *O. quixensis,* have broad distributions in the Amazonian lowlands, and both of them have sister species inhabiting the Andean hills. The former taxon, as we will show here, is most likely a composite of two species, and its current distribution includes humid and semideciduous Andean montane forests in Central Bolivia, humid forests of the Andean foothills from Central Bolivia to Manu National Park in southern Peru, as well as the adjacent Amazonian lowlands along the Andean hills. *Oreobates quixensis* occurs in the Upper Amazon Basin from Colombia, through Ecuador and Peru, reaching northern Bolivia (Pando) and western Brazil, and climbing the Andean hills up to 1000 m in Peru. The remaining species are strictly high Andean species occurring in humid montane forest and cloud forest from Bolivia to Ecuador. *Oreobates sanctaecrucis* is found in cloud forests of central Bolivia from 1000–2100 m. Toward the north of Bolivia occurs *O. madidi*, the parapatric sister species to *O. cruralis*, which is found in humid montane forests of the lower Andean hills. Roughly at the same latitude, but higher elevation, four other Andean species occur in humid montane forests and cloud forests: *O. granulosus* in southern Peru and *O. choristolemma, O. sanderi*, and *O. zongoensis* in northern Bolivia. From there, a large gap exists until reaching the cloud forest populations of Manu National Park doubtfully assigned to *O. lehri* (see Padial et al., 2007), or its type locality farther north in the western versant of Cordillera Vilcabamba. The distributional gap of *Oreobates* in southern Peru is probably due to incomplete sampling of huge areas in the Peruvian Departaments of Puno and Cusco. Another species known from Cordillera Vilcabamba, and from the eastern versant of the Andes in the Apurimac River Basin, is *O. pereger*, a species occurring in elfin forests at high elevations, around 2500–2600 m (Lehr and Aguilar, 2006). Again a large distribution gap is apparent north of Vilcabamba, until reaching the known range of *O. saxatilis*—the putative sister species of *O. quixensis*—which is parapatric to the latter and occurs in the Andean foothills of northern Peru at elevations between 350–600 m. The northernmost Andean species is *O. simmonsi*, known only from the holotype from a locality in humid montane forest in the Ecuadorian versant of the Cordillera del Cóndor.

The purpose of this paper is to review species diversity within the genus by compiling recently collected data from countries where *Oreobates* occurs. We analyze the species diversity within *Oreobates* based on morphological and genetic (DNA sequences of a short fragment of the mitochondrial 16S rRNA gene) characters. We show that there are six putative new species in *Oreobates*, three of which are formally described and named herein and three are proposed as candidate species (sensu Padial et al., 2010). We also provide new distributional records expanding the known distributions of most species, and produce gene sequences for nine taxa that had not yet been placed in a molecular phylogeny (*Hypodactylus lundbergi*, *O. barituensis*, nominal *O. lehri*, *O. pereger, O. simmonsi*, *Phrynopus ayacucho*, and the three new species), and which suggest generic changes for several species. As a result the content of *Oreobates* is largely modified.

MATERIAL AND METHODS

Species concept and candidate species

We consider a species as the single lineage segment of ancestor-descendant populations or metapopulations delimited by one splitting event. Under this theoretical perspective, species exist and evolve regardless of our ability to discover them, and are discoverable to the degree that footprints of their evolutionary history allow us to infer their existence (Ghiselin, 1975; Wiley, 1978; Hull, 1976; Frost and Kluge, 1994). A species is supported by morphological evidence when it exhibits at least one fixed character state relative to its sister species. The underlying assumption is that fixed differences in morphology is strong evidence of reduced or absent gene flow between populations or metapopulations (Frost and Hillis, 1990; for a review see Padial and De la Riva, 2010). Monophyly of neutral gene genealogies is also considered evidence of species divergence on the assumption that character fixation in gene genealogies across populations is indicative of lineage independence (reviewed by Padial et al., 2010).

When a population shows genetic or morphological divergence from the other populations within the same nominal species, but evidence of lineage divergence is inconclusive, we flag those populational level lineages as UCS (unconfirmed candidate species; Vieites et al., 2009; Padial et al., 2010). If evidence is conclusive about the existence of a new species but the available material is considered insufficient to provide an accurate species description, we consider the lineage at the population level as a CCS (confirmed candidate species; Vieites et al., 2009; Padial et al., 2010). Both CCS and UCS are flagged following the proposal of Padial et al. (2010). Candidate species are referred through the combination of the binomial species name of the most similar or closely related nominal species (or just the genus name), followed (in square brackets) by the abbreviation "Ca" (for candidate) with an attached numerical code referring to the particular candidate species, followed by the GenBank accession number for the sequence of reference deposited in GenBank, and terminating with the author name and year of publication of the article in which the respective lineage was first discovered.

Morphology

We follow Padial et al. (2008a) and Duellman and Lehr (2009) for morphological and color characteristics used in the diagnosis and description. Measurements were taken with a digital caliper to the nearest 0.01 mm and rounded to the nearest 0.1 mm to avoid pseudoprecision. Abbreviations for measurements are as follows: snout-vent length, SVL; head length (from posterior margin of lower jaw to tip of snout), HL; head width (measured at level of rictus), HW; eye length (measured horizontally), EL; eye to nostril distance, EN; internarial distance, IND; eye-eye distance, EE; tympanic membrane height, TYH; tympanic membrane length, TYL; arm length (from posterior margin of thenar tubercle to distal point of elbow), FA; tibia length, TL; thigh length, TH (from vent to knee); foot length (from proximal border of inner metatarsal tubercle to tip of fourth toe), FL. 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 have precise and comparable values. Color characteristics were

TABLE 1. Localities, voucher information, and GenBank accession numbers for sequences and specimens of *Oreobates* used in this study. Accession numbers in **boldface** correspond to sequences produced for this study. DNA collection refers to DNA and tissue collection from National Museum of Natural History in Madrid.

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
39964	*Oreobates amarakaeri*	MHNC6975	Peru	Cusco	Distrito Camanti: Provincia Quispicanchi: Río Nusiniscato 685 m	13.4703	70.8516	**JF809996**
39972	*O. amarakaeri*	MHNC7017	Peru	Cusco	Distrito de Camanti: Provincia Quispicanchi: Cabecera Mabe, 1000 m	13.0188	70.9155	**JF809997**
39975	*O. amarakaeri*	MHNC7049	Peru	Cusco	Distrito de Camanti: Provincia Quispicanchi: Cabecera Mabe, 1000 m	13.0188	70.9155	**JF809998**
23337	*O. ayacucho*	MNCN44484	Peru	Ayacucho	Provincia La Mar: entre Punqui y Anco, 3 km antes de Anco, 3850 masl	13.1038	73.6983	**JF809970**
23338	*O. ayacucho*	MHNC6840	Peru	Ayacucho	Provincia La Mar: entre Punqui y Anco, 3 km antes de Anco, 3850 m	13.1038	73.6983	**JF809971**
23339	*O. ayacucho*	MNCN44485	Peru	Ayacucho	Provincia La Mar: entre Punqui y Anco, 3 km antes de Anco, 3850 m	13.1038	73.6983	**JF809972**
39985	*O. barituensis*	MCN1359	Argentina	Jujuy	Departamento Ledesma: Caimancito, 556 m	23.6313	64.6014	**JF809999**
39986	*O. barituensis*	MCN1360	Argentina	Jujuy	Departamento Valle Grande: Ruta provincial N° 83 entre las localidades de Valle Grande y Valle Colorado, 1660 m	23.4864	64.9454	**JF810000**
39987	*O. barituensis*	MCN1251	Argentina	Salta	Departamento Santa Victoria: El Arazay, 1680 m	22.3203	64.7164	**JF810001**
5715	*O. choristolemma*	CBG765	Bolivia	La Paz	Provincia Sud Yungas: Boqueron, Pilon Lajas, 1000 m	15.3769	67.3769	**EU368894**
5745	*O. choristolemma*	CBG768	Bolivia	La Paz	Provincia Sud Yungas: Boqueron, Pilon Lajas, 1000 m	17.4117	65.2519	**EU368895**
4003	*O. cruralis*	MNCN42977	Bolivia	Cochabamba	Provincia Chapare: Los Guácharos, Parque Nacional Carrasco, 500 m	17.0643	65.4763	**FJ438795**
4078	*O. cruralis*	MNKA5351	Bolivia	Cochabamba	Provincia Chapare: Los Guácharos, Parque Nacional Carrasco, 500 m	17.0643	65.4763	**JF809941**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
4082	*O. cruralis*	MNCN43019	Bolivia	Cochabamba	Provincia Chapare: Los Guácharos, Parque Nacional Carrasco, 500 m	17.0643	65.4763	**JF809942**
4083	*O. cruralis*	MNKA5352	Bolivia	Cochabamba	Provincia Chapare: Los Guácharos, Parque Nacional Carrasco, 500 m	17.0643	65.4763	**JF809943**
4089	*O. cruralis*	MNCN43022	Bolivia	Cochabamba	Provincia Chapare: Los Guácharos, Parque Nacional Carrasco, 500 m	17.0643	65.4763	**JF809944**
4106	*O. cruralis*	MNKA5353	Bolivia	Cochabamba	Provincia Chapare: Road Los Guácharos El Palmar. A 8 Km de los Guácharos, ca. 400 m	17.05	65.4666	**JF809945**
5759	*O. cruralis*	CBG792	Bolivia	La Paz	Provincia Sud Yungas: Boqueron, Pilon Lajas, 1000 m	17.4117	65.2519	**JF809946**
5769	*O. cruralis*	CBG790	Bolivia	La Paz	Provincia Sud Yungas: Boqueron, Pilon Lajas, 1000 m	17.4117	65.2519	**JF809947**
5770	*O. cruralis*	CBG793	Bolivia	La Paz	Provincia Sud Yungas: Boqueron, Pilon Lajas, 1000 m	17.4117	65.2519	**JF809948**
5864	*O. cruralis*	MNCN42559	Bolivia	Beni	Provincia Ballivian: Rurrenabaque, 230 m	14.4686	67.5672	**JF809949**
6098	*O. cruralis [Ca EU192295]*	MNKA7171	Bolivia	Santa Cruz	Provincia Florida: Camino a Bella Vista, 1250 m	18.189	63.7147	**EU192295**
9507	*O. cruralis*	MHNC4959	Peru	Madre de Dios	Provincia Tambopata: Río los Amigos, 229 m	12.5769	70.071	**JF809953**
9509	*O. cruralis*	MHNC4966	Peru	Madre de Dios	Provincia Tambopata: Río los Amigos, 229 m	12.5769	70.071	**JF809954**
34719	*O. cruralis*	MNCN44756	Bolivia	La Paz	Provincia Iturralde: Heath River Wildlife Centre, en la orilla boliviana del Río Heath, 184 m	12.6801	68.7118	**JF809994**
-	*O. cruralis*	KU215462	Peru	Madre de Dios	Provincia Tambopata: Cusco Amazonico, 15 km E of Puerto Maldonado, 214 m	12.5669	69.0711	**EU186666**
5982	*O. discoidalis*	MNKA5598	Bolivia	Tarija	Provincia Oconnor: near Entre Ríos, Chiquiacá, 1763 m	21.4805	64.2029	**JF809950**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
6123	*O. discoidalis*	MNKA7247	Bolivia	Tarija	Provincia Gran Chaco: Serranía Aguarague, 17 km from Villa Montes to Entre Ríos, 478 m	21.2303	63.5612	**EU192254**
6134	*O. discoidalis*	MNCN43133	Bolivia	Tarija	Provincia Oconnor: near Entre Ríos, Chiquiacá, 1763 m	21.4805	64.2029	**EU368896**
9499	*O. gemcare*	one from the series MHNC3223–31,3234–37	Peru	Cusco	Provincia Paucartambo: Esperanza, Valle de Kosñipata, 2700 m	13.1824	71.6036	**JF809952**
20688	*O. gemcare*	MHNC6687	Peru	Cusco	Provincia Paucartambo: Esperanza, Valle de Kosñipata, 2700 m	13.1824	71.6036	**JF809960**
20689	*O. gemcare*	MNCN44230	Peru	Cusco	Provincia Paucartambo: Esperanza, Valle de Kosñipata, 2700 m	13.1824	71.6036	**JF809961**
39920	*O. sp. [(Ca JF809995]*	MHNC5845	Peru	Cusco	Distrito de Camanti: Provincia Quispicanchis: Culebrayoc, 1606 m	13.49031	70.89707	**JF809995**
20550	*O. granulosus*	MHNC3396	Peru	Puno	Provincia Carabaya: Santo Domingo de Carabaya, 1800 m	13.8332	69.6422	**EU368897**
6018	*O. heterodactylus*	MNKA7177	Bolivia	Santa Cruz	Provincia Chiquitos: Cerro del Arco, Santiago de Chiquitos, 800 m	18.3527	59.543	**EU368898**
6061	*O. heterodactylus*	MNKA7175	Bolivia	Santa Cruz	Provincia Chiquitos: Cerro del Arco, Santiago de Chiquitos, 800 m	18.3474	59.8936	**EU192296**
3894	*O. ibischi*	MNCN42959, MNKA6612	Bolivia	Santa Cruz	Provincia Florida: Quebrada, 6 km from la Angostura in directióon to Samaipata, 800 m	18.1833	63.5666	**FJ438794**
17004	*O. lehri*	MUSM27616	Peru	Cusco	Provincia Grau: cloud forest next to road leading to Vilcabamba, ca. km 40; ca. 2850 m	13.0475	72.9248	**JF809957**
17008	*O. lundbergi*	MTD45902	Peru	Pasco	Provincia Huanchon: from Auquimarca to Uchuerta, 2760 m	10.7341	75.7029	**JF809958**
17009	*O. lundbergi*	MUSM19321	Peru	Pasco	Provincia Huanchon: Carretera Puagmaray Oxapampa km 77, 2550 m	10.6599	75.7692	**JF809959**
23233	*O. machiguenga*	MHNC6809	Peru	Cusco	Provincia La Convención: Río Kimbiri, 1300 m	12.5783	73.6725	**JF809969**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
5999	*O. madidi*	MNKA7856	Bolivia	La Paz	Provincia Franz Tamayo: Arroyo Huacataya, Senda entre San José y Apolo, 1300 m	14.3367	68.0993	**EU368900**
17002	*O. pereger*	MTD46808	Peru	Ayacucho	Provincia Lamar: Yanamonte, 2600 m	12.7903	74	**JF809955**
17003	*O. pereger*	MTD46809	Peru	Ayacucho	Provincia Lamar: Yanamonte, 2600 m	12.7903	74	**JF809956**
6216	*O. quixensis*	MNCN43417	Bolivia	Pando	Provincia Tahuamanu: San Sebastián, Estación Biológica Tahuamanu, 280 m	11.4075	69.0186	**EU192297**
26608	*O. quixensis*	MHNC8918	Peru	Loreto	Provincia Mariscal Ramón Castillo: Umarital, Río Ampiyacu, 92 m	3.26659	72.2673	**JF809973**
26690	*O. quixensis*	MNCN45106	Peru	Loreto	Provincia Mariscal Ramón Castillo: Confluencia de los Ríos Supai y Sábalo, 86 m	3.06479	72.1684	**JF809974**
26734	*O. quixensis*	MHNC8997	Peru	Loreto	Provincia Mariscal Ramón Castillo: Pucaurquillo, Río Ampiyacu, 99 m	3.3307	71.9168	**JF809975**
26822	*O. quixensis*	MHNC8832	Peru	Loreto	Provincia Maynas: Camino a Zungarococha y Arboreto de la Universidad de Iquitos, Camino a Puerto Alendras, 103 m	3.8308	73.3733	**JF809976**
26960	*O. quixensis*	MHNC8809	Peru	Loreto	Provincia Maynas: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m	3.8307	73.3732	**JF809977**
27354	*O. quixensis*	MNCN45103	Peru	Loreto	Provincia Maynas: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m	3.8307	73.3732	**JF809990**
27458	*O. quixensis*	MNCN45104	Peru	Loreto	Provincia Maynas: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m	3.8307	73.3732	**JF809991**
27522	*O. quixensis*	MHNC8805	Peru	Loreto	Provincia Maynas: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m	3.8307	73.3732	**JF809992**
27523	*O. quixensis*	MNCN45105	Peru	Loreto	Provincia Maynas: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m	3.8307	73.3732	**JF809993**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
-	*O. quixensis*	KU178249	Ecuador	Sucumbios	Limoncocha, 248 m	0.4	76.6	**EF493662**
-	*O. quixensis*	KU218150	Ecuador	Napo	Jatun Sacha, 400 m	1.0666	77.6	**DQ679380**
-	*O. quixensis*	QZ25520	Ecuador	Pastaza	Kapawi Lodge, 250 m	2.5387	76.8583	**JF810002**
-	*O. quixensis*	QZ31186	Ecuador	Pastaza	Parroquia Teniente Hugo Ortíz, 951 m	1.3541	77.8616	**JF810003**
	O. remotus	MZUSP 141708	Brazil	Minas Gerais	Januária: Parque Nacional Cavernas do Peruaçu, 624 m	15.1455	44.2414	**JN688273**
	O. remotus	MZUSP 141720	Brazil	Minas Gerais	Januária: Parque Nacional Cavernas do Peruaçu, 624 m	15.1455	44.2414	**JN688274**
	O. remotus	MZUSP 141721	Btazil	Minas Gerais	Januária: Parque Nacional Cavernas do Peruaçu, 624 m	15.1455	44.2414	**JN688275**
6097	*O. sanctaecrucis*	MNKA5507	Bolivia	Santa Cruz	Provincia Florida: La Yunga de Mairana, 2060 m	18.0594	63.91	**JF809951**
3723	*O. sanderi*	MNCN42017	Bolivia	La Paz	Provincia Franz Tamayo: Arroyo Bilunto, Chunirumi Valley, Bilunto Mountains, Area Natural de Manejo Integrado Madidi, near Santa Cruz de Valle Ameno, 1800 m	14.6366	68.5325	**EU368904**
23151	*O. saxatilis*	MHNC6775	Peru	Cusco	Provincia La Convención: Río Kimbiri, 1000 m	12.5895	73.703	**JF809962**
23152	*O. saxatilis*	MHNC6776	Peru	Cusco	Provincia La Convención: Río Kimbiri, 1000 m	12.5895	73.703	**JF809963**
23156	*O. saxatilis*	MHNC6777	Peru	Cusco	Provincia La Convención: Río Kimbiri, 1000 m	12.5895	73.703	**JF809964**
23176	*O. saxatilis*	MNCN44412	Peru	Cusco	Provincia La Convención: Río Kimbiri, Comunidad Machiguenga Pomoreni, 1100 m	12.5907	73.6935	**JF809965**
23188	*O. saxatilis*	MNCN44426	Peru	Cusco	Provincia La Convención: Río Kimbiri, Comunidad Machiguenga Pomoreni, 1100 m	12.5907	73.6935	**JF809966**
23189	*O. saxatilis*	MNCN44427	Peru	Cusco	Provincia La Convención: Río Kimbiri, Comunidad Machiguenga Pomoreni, 1100 m	12.5907	73.6935	**JF809967**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
23190	*O. saxatilis*	MNCN44428	Peru	Cusco	Provincia La Convención: Río Kimbiri, Comunidad Machiguenga Pomoreni, 1100 m	12.5907	73.6935	**JF809968**
27182	*O. saxatilis*	MHNC9200	Peru	San Martín	Provincia Lamas: San Roque de Cumbasa, 609 m	6.3848	76.4376	**JF809978**
27185	*O. saxatilis*	MHNC9202	Peru	San Martín	Provincia Lamas: 2 km al Este de Roque, 1138 m	6.3592	76.7535	**JF809979**
27226	*O. saxatilis*	MHNC9219	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809980**
27227	*O. saxatilis*	MNCN45205	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809981**
27228	*O. saxatilis*	MNCN45206	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809982**
27229	*O. saxatilis*	MNCN45207	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809983**
27230	*O. saxatilis*	MNCN45208	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809984**
27231	*O. saxatilis*	MHNC9220	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809985**
27232	*O. saxatilis*	MHNC9221	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809986**
27233	*O. saxatilis*	Tissue only	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809987**
27234	*O. saxatilis*	Tissue only	Peru	San Martín	Provincia Lamas: 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 m	6.3592	76.7535	**JF809988**

DNA collection	Species	Voucher	Country	Region	Locality	Latitude S	Longitude W	GenBank
27257	*O. saxatilis*	Tissue only	Peru	San Martín	Provincia Lamas: Carretera Tarapoto Yurimaguas, Km 26, 668 m	6.4119	76.3175	**JF809989**
-	*O. saxatilis*	MJH7058	Peru	Huanuco	Provincia Puerto Inca: Estacion Biologica Panguana (lower Río Llullapichis, ca. 140 km SSW Pucallpa), 233 m	9.6167	74.9333	**DQ283061**
-	*O. saxatilis*	KU212327	Peru	San Martín	Provincia Lamas: Ponga de Shilcayo, ca. 4 km NNW, Tarapoto, 470 m	6.5167	76.8833	**EU186708**
5719	*O. sp.* *[Ca EU368903]*	CBG153	Bolivia	Cochabamba	Provincia Carrasco: Chaquisacha, Parque Nacional Carrasco, 1500 m	17.6833	65.4166	**EU368903**
-	*Lynchius simmonsi*	QZ41639	Ecuador	Zamora Chinchipe	Miazi Alto, Cordillera del Condor 1300 m	4.25656	78.62246	**JF810004**
-	*Lynchius simmonsi*	QZ41640	Ecuador	Zamora Chinchipe	Miazi Alto, Cordillera del Condor 1300 m	4.25656	78.62246	**JF810005**

noted in life and in alcohol. We determined sexual condition and maturity by dissection or observation of external secondary sexual characters. Museum acronyms are those cited by Frost (2011), except that MHNC refers to Museo de Historia Natural de Cusco (MHNCP by Frost, 2011), and MCN-UNSA refers to Museo de Ciencias Naturales de la Universidad Nacional de Salta. In appendix 1, we include a list of specimens examined.

Molecular phylogenetics analyses

Our phylogenetic analyses rely on the short fragment of the 16S rRNA gene that is commonly used as the barcode for amphibians to identify species, assess the monophyly of species, and/or to discover divergent lineages (Vences et al., 2005; Padial et al., 2009b; Vie-

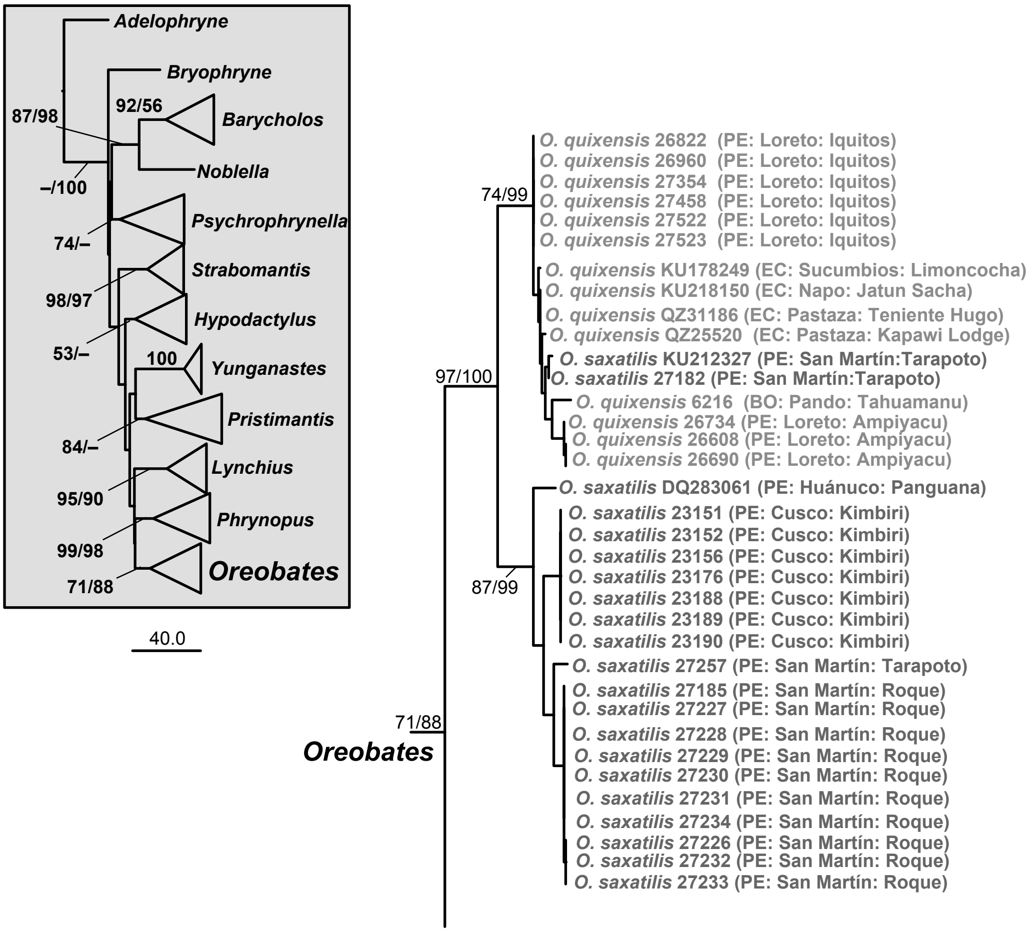


FIG. 1. Main tree (left and right pages): one of 16 equally optimal maximum parsimony trees with branch length depicting phylogenetic relationships of species of *Oreobates* (3936 steps; differences with the strict consensus only affect unresolved intraspecific relationships). Schematic tree (far left): maximum likelihood best tree topology for 145 terminals of Strabomantid frogs inferred from the 16S rRNA barcode fragment of amphibians (see methods). Numbers above nodes for both trees are maximum parsimony bootstrap values followed by maximum likelihood bootstrap values.

ites et al., 2009; Crawford et al., 2010). Tissue fragments were obtained from specimens avoiding any damage to structures and organs used for morphological analyses. Tissue samples and extractions are preserved at the public DNA and tissue collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain). In order to determine generic placement of putative members of *Oreobates*, we include GenBank sequences for all genera of Strabomantidae for which that fragment was available (appendix 2). We used 83 sequences from GenBank and produced sequences for 65 terminals. For information on vouchers, DNA collection numbers, GenBank accession numbers, and locality data of the samples of *Oreobates* used for this study see table 1. The geographic origin of samples is depicted in maps 1–4.

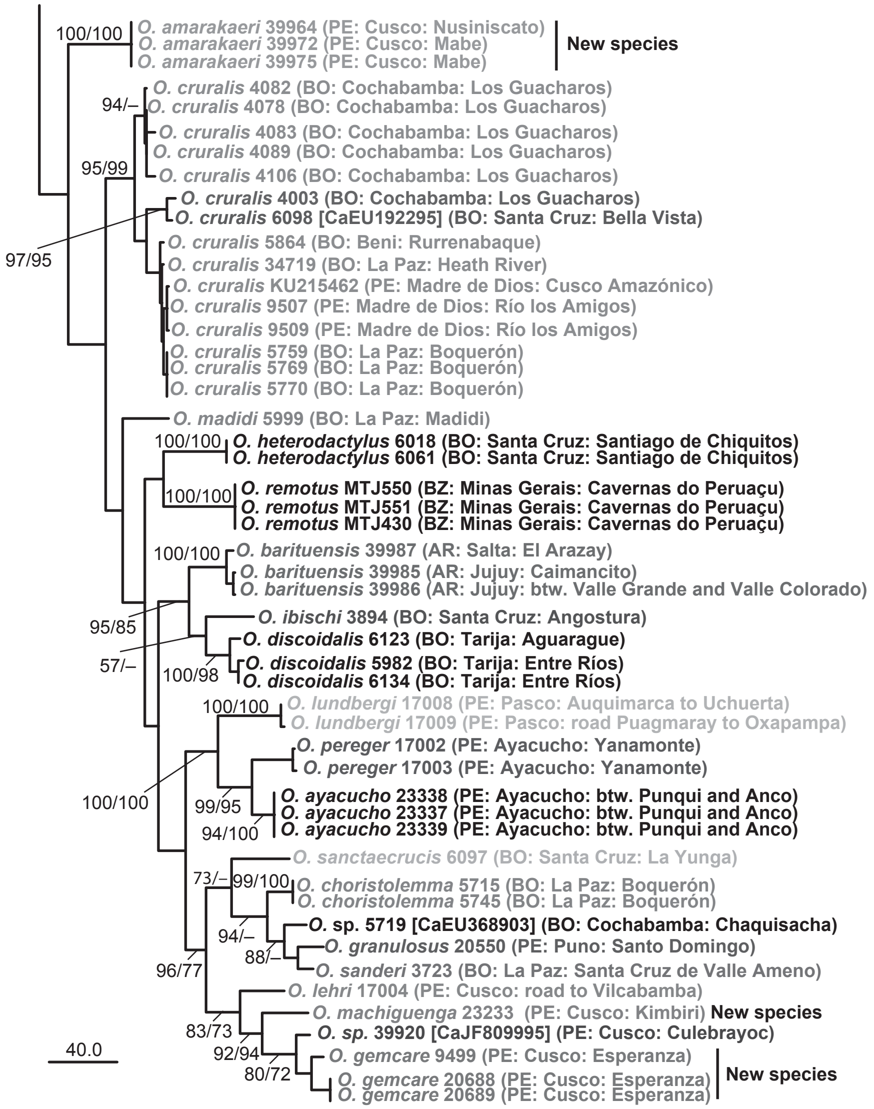


TABLE 2. Characters values for the advertisement call of *Oreobates ayacucho*.

Call parameters			Note parameters									
			Note duration (ms)					Pulses per note				
Call Length (ms) (n = 11)	Dominant Frequency (n = 11)	Fundamental Frequency (Hz) (n = 11)	Note I (n = 11)	Note II (n = 11)	Note III (n = 11)	Note IV (n = 7)	Note V (n = 3)	Note I (n = 11)	Note II (n = 11)	Note III (n = 11)	Note IV (n = 7)	Note V (n = 3)
691–890 (756)	1178–2283 (1560)	1116–2370 (1902)	218–302 (248)	85–116 (98)	87–116 (98)	89–94 (92)	91–94 (92)	9–10 (10)	4–4 (4)	4–4 (4)	4–4 (4)	4–4 (4)

TABLE. 3. Intraspecific and interspecific uncorrected p-distances based on a 586 base pair fragment of the 16S rRNA for members of *Oreobates*. Sample size in parentheses follows species names.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1 *O. amarakaeri* (3)	0.0																						
2 *O. ayacucho* (3)	13.0	0.0																					
3 *O. barituensis* (3)	16.1–16.3	12.9–13.5	0.0–1.4																				
4 *O. choristolemma* (2)	13.1–13.2	11.3	13.1–13.2	0.0																			
5 *O. cruralis* (15)	10.4–12.2	10.2–12.5	11.6–	11.7–12.4	0.0–4.7																		
6 *O discoidalis* (3)	14.7–15.1	13.0–13.1	7.1–8.2	11.8–12.0	11.4–12.5	0.2–1.2																	
7 *O. gemcare* (4)	15.3–15.7	10.6	15.0–15.6	12.1–13.2	12.1–14.3	13.8–14.7	0.0–3.2																

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
8 *O. granulosus* (1)	13.5	12.5	15.1–15.5	6.5	11.6–13.3	15.3–15.7	12.9–13.3	—															
9 *O. heterodactylus* (2)	15.0	13.4	12.1–12.3	13.0	10.4–11.8	11.4–12.3	14.7–15.1	12.2	0.0														
10 *O. ibischi* (1)	16.8	14.9	7.2–7.5	13.2	13.1–14.6	7.4–8.1	15.9–16.5	15.9	14.9	—													
11 *O. lehri* (1)	15.8	11.5	14.4–14.6	12.9	12.5–14.1	14.2–14.6	10.1–10.9	13.9	15.0	17.0	—												
12 *O. lundbergi* (2)	14.7	14.7	14.2–14.6	12.5–12.6	12.0–13.4	13.4–13.8	12.0–12.3	14.3	13.9	15.7–15.8	15.0	0.0											
13 *O. machiguenga* (1)	16.0	10.8	15.4–15.6	12.0	13.7–15.2	14.0–14.4	9.5–9.7	13.9	16.9	16.9	11.6	13.6–13.9	—										
14 *O. madidi* (1)	12.7	11.3	10.3–10.8	11.5	8.4–9.5	10.9–11.1	12.6–13.1	12.7	12.1	13.0	13.3	13.6–13.7	14.1	—									
15 *O. pereger* (2)	15.2–15.3	5.7–6.0	15.0–15.3	13.5–13.6	13.0–15.2	15.2–15.9	11.7–12.6	13.8–14.3	14.7–15.0	17.3–17.6	12.6–12.9	12.5–12.8	11.9–12.4	12.9–13.0	0.2								
16 *O. quixensis* (14)	12.0–13.8	11.2–12.4	13.0–14.4	11.8–12.9	10.8–14.8	12.2–14.0	13.2–15.0	12.5–14.0	11.9–14.0	14.9–16.8	14.1–15.3	11.4–12.9	11.2–13.2	12.7–14.1	12.2–13.8	0.0–3.5							
17 *O. remotus* (3)	14.7	13.5	13.2–13.5	11.3	10.9–12.2	12.5–12.7	12.8–13.4	14.2	12.3	14.1	15.0	12.4–12.5	12.8	11.6	14.9–15.2	12.6–14.5	0.0						
18 *O. sanctaecrucis* (1)	15.2	13.4	14.9–15.1	11.2	12.5–14.0	14.3–14.5	14.2–14.6	11.6	14.7	15.6	14.0	16.1–16.2	15.0	14.2	14.2–14.7	13.9–14.6	14.4	—					
19 *O. sanderi* (1)	12.9	12.0	14.3–14.5	6.4	11.0–11.8	13.3–14.1	12.4–12.6	4.0	12.4	15.5	13.2	14.1	13.1	11.4	13.8–14.3	12.4–13.7	13.4	11.4	—				
20 *O. saxatilis* (21)	12.9–14.5	11.4–14.0	13.7–16.6	12.3–14.8	12.3–14.3	13.1–16.4	13.4–15.1	13.0–15.8	13.4–15.2	16.1–18.9	14.9–16.3	11.6–14.6	11.6–14.4	13.5–15.1	12.8–15.4	0.6–7.9	13.2–15.0	13.9–17.1	13.4–15.5	0.0–7.3			
21 *O.* sp 5719 (1)	12.2	11.4	13.9–14.0	5.7	9.8–12.3	13.9–14.1	12.4	5.5	12.7	14.6	12.6	13.7	12.6	12.0	12.9–13.2	11.8–13.1	13.8	9.5	4.6	12.3–14.9	—		
22 *O.* sp 39920 (1)	14.3	9.8	14.0–14.3	11.3	11.8–13.0	13.7–13.8	4.6	13.0	14.6	14.6	10.3	11.6–11.8	8.7	12.3	11.8–12.0	12.1–13.6	11.9	13.9	12.2	12.6–13.8	10.7	—	
23 *O. cruralis* Ca (2)	11.7–12.2	10.7–12.0	10.9–12.1	11.2–11.9	3.3–5.2	11.1–12.4	12.4–13.1	11.9–12.7	10.0–11.9	14.0–14.6	13.3–13.4	12.6–13.6	13.4–13.9	8.4–8.6	13.2–14.2	11.7–14.4	11.3–11.5	12.6–12.9	11.9–12.1	12.4–14.1	10.7–11.3	11.9–12.4	1.5

Genomic DNA was extracted from ethanol-preserved tissues using standard phenol-chloroform extraction protocols. A fragment of the 16S rRNA gene was amplified and sequenced using the universal primers 16Sar-5′ and 16Sbr-3′ (Hillis et al., 1996). The polymerase chain reaction (PCR) amplification protocols were as follows: 95° C/15 sec; 35 cycles of 95° C/30 sec, 50° C/ 30 sec, 72° C/1 min; and 72° C/10 min. PCR products were visualized in agarose gels, and unincorporated primers and dNTPs were removed from PCR products using ExoSap purification (ExoSap-it, GE Healthcare). Cycle sequencing reactions were completed using the corresponding PCR primers and BigDye Terminator 3.1 chemistry (Applied Biosciences), with a standard cycle sequencing profile (96° C/3 min; 35 cycles of 96° C/10 sec, 50° C/15 sec, 60° C/3 min; and 72° C/7 min). Reaction products were purified using ethanol precipitation and sent to Macrogen Inc. for sequencing. Data from two complementary strands were compared to generate a consensus sequence for each DNA fragment using Sequencher 4.6 (Gene Codes Corporation, 2006).

A static alignment was obtained using the web version of the software Mafft version 6.5 under the Q-INS-I strategy (Katoh et al., 2005). Maximum parsimony (MP) analyses were performed in TNT considering gaps as fifth character, and using New Technology searches at level 100, including sectorial searches, ratchet, drift and tree fusing. Bootstrap support was evaluated through 500 replicates using New Technology searches (Goloboff et al., 2008). Maximum likelihood (ML) analyses were performed in Garli2.0 (Zwickl, 2006; https://www.nescent.org/wg_garli/Main_Page) under default parameters and a GTR+I+G model of evolution. Fifty replicates where performed to assess consistency of results during the best-tree search. Bootstrap support was evaluated through 500 replicates. All trees were rooted with *Adelophryne adiastola*, a member of the distantly related family Eleutherodactylidae (Hedges et al., 2008a). Uncorrected p-distances (UPD) were calculated in PAUP for a dataset with all sequences having the same length and no missing data (586 bp including gaps) and containing only samples of *Oreobates*.

Pyron and Wiens (2011) synonymized Strabomantidae (Hedges et al., 2008a) with Craugastoridae (Hedges et al., 2008a) because they found *Craugastor* and *Haddadus* deeply embedded within Strabomantidae, rendering Strabomantidae paraphyletic. However, we prefer to follow Hedges et al. (2008a) and recognize Strabomantidae for the time being because ongoing studies suggest that the classification of Terrarana will soon undergo additional changes.

Bioacoustics

Advertisement calls of *Oreobates ayacucho* were recorded with a Marantz PMD-670 digital sound recorder, and a Sennheiser Me-80 directional microphone (temperature not recorded). They are deposited at Fonoteca Zoológica, Museo Nacional de Ciencias Naturales, CSIC, Madrid (http://www.fonozoo.com/). All calls were edited with Audacity 1.2.6 for MacOS X (Mazzoni and Dannenberg, 1999). Praat 4.5.02 for MacOS X (Boersma and Weenink, 2006) software was used to generate audiospectrograms and oscillograms. Frequency information was obtained through fast Fourier transformations (FFT) (width of 1024 points). We analyzed the following quantitative characters (Padial et al., 2008b; table 2): Call length (ms), call rate (calls per minute), dominant frequency (Hz), lower limit of dominant frequency (Hz), upper limit of dominant frequency (Hz), fundamental frequency (Hz), number of harmonics, number of notes per call, note duration (ms), and number of pulses per note. In addition, we considered the following three qualitative characters: presence/absence of frequency modulation in notes; presence/absence of amplitude modulation in notes; presence/absence of amplitude modulation in pulses.

RESULTS

Species monophyly and genetic divergences

After alignment, our data set is composed of 148 terminals and 609 character columns. Both MP and ML topologies were basically identical. The MP strict-consensus tree of 16 equally optimal trees (3936 steps) and the best maximum-likelihood tree (ln likelihood = -14466.183) recovered the monophyly of all genera except *Oreobates*, *Phrynopus*, and *Hypodactylus* (*Psychrophrynella* is paraphyletic in MP analyses, with *Psychrophrynella usurpator* basal to all Strabomantids except for *Noblella* and *Barycholos* without support) (fig. 1). In all analyses, *Oreobates simmonsi* is the sister species of *Lynchius* with high support; *Phrynopus ayacucho* is within *Oreobates*, sister to *Oreobates pereger*, with high support; and *Hypodactylus lundbergi* is also recovered within *Oreobates* with unclear relationships.

In order to render a monophyletic *Oreobates*, *Hypodactylus*, and *Phrynopus*, we transfer *Hypodactylus lundbergi* and *Phrynopus ayacucho* to the genus *Oreobates* and *Oreobates simmonsi* to *Lynchius* (fig. 1). This rearrangement renders all genera included in the tree monophyletic, and the clade of *Oreobates* is well supported in all analyses.

Within *Oreobates*, all but two species (*Oreobates quixensis* and *O. saxatilis*) are recovered as monophyletic with support or are sister to monophyletic groups (species for which there was only one terminal). In addition, UPD are high for all species pair comparisons (table 3), ranging from 4.0% for the pair of sister species *O. granulosus*–*O. sanderi* to 17.6% between *O. pereger* and *O. ibischi*. The only exception is the pair *O. quixensis*–*O. saxatilis*, which is paraphyletic in ML and MP analysis, and show a UPD of 0.6%–7.9%. In the MP strict consensus (not shown), two reciprocally monophyletic groups divide this pair of species, with one clade including only specimens of *O. saxatilis* and the other including all samples of *O. quixensis* plus two of *O. saxatilis* from the type locality (one a paratype of *O. saxatilis*). In the ML analysis, *O. quixensis* is not recovered as monophyletic, whereas most samples of *O. saxatilis* (including some but not all from the type locality) form a clade equal to the clade recovered by MP.

In addition to the currently recognized nominal species, six divergent lineages are identified by combining the results of phylogenetic analyses and genetic distances. The terminal *Oreobates lehri* from Vilcabamba (*Oreobates lehri* 17004), which is considered conspecific with nominal *O. lehri* (see below under comments to *O. gemcare* and *O. lehri*), is sister of a clade containing terminals from Kosñipata and Marcapata valleys, and from which it is separated by large divergences (UPD = 10.1%–11.3%) (see also morphology below). The specimens from Kosñipata we consider distinct species (*O. gemcare*), and the specimen from Culebrayoc (*Oreobates* sp. 39920 in fig. 1; see locality in map 2), sister of *O. gemcare* with a UPD of 4.6%, we regard as an unconfirmed candidate species and is referred to as *Oreobates* sp. [Ca JF809995].

Also from Vilcabamba is another divergent lineage identified under the name *O. machiguenga* in figure 1, which is named herein as a new species. *Oreobates machiguenga* is sister of the pair *O. lehri*–*O. gemcare*, with a UPD of the latter two taxa 11.6% and 9.5–9.7%, respectively.

Another divergent lineage (*Oreobates* sp. 5719 in fig. 1), from a montane forest in Parque Nacional Carrasco in central Bolivia (map 3), is sister to the pair *O. granulosus*–*O. sanderi* with which it has a UPD of 5.5% and 4.6%, respectively, and is considered herein a confirmed candidate species and is referred to as *Oreobates* sp. [Ca EU368903] Nevertheless, we refrain from naming this species herein because adequate comparisons with related species could not be performed.

The fourth unnamed lineage is represented by three specimens from two geographically close localities in southern Peru (fig. 1; labeled as *Oreobates amarakaeri*). This lineage is described herein as a new species. In the ML analysis *O. amarakaeri* is sister to the clade composed by *O. choristolemma*, *O. granulosus*, *O. sanctaecrucis*, *O. sanderi*, and *Oreobates* sp. [Ca EU368903], with the smallest UPD to related taxa 12.9% (to *O. sanderi*).

The fifth lineage is embedded in what is currently recognized as *Oreobates cruralis*. *Oreobates cruralis* 4003 in figure 1 from Amazonian forests at Los Guácharos is sympatric with several other specimens of "*O. cruralis,*" with which it has a UPD of 4.7; they are not closely related (fig. 1). Instead, *O. cruralis* 4003 clusters with a specimen from inter-Andean dry valleys (*O. cruralis* 6098). Thus, we suggest that the pair *O. cruralis* 4003 and *O. cruralis* 6098 represent an undescribed species, which is considered here an unconfirmed candidate species, and is here referred to as *Oreobates cruralis* [Ca EU192295]. We refrain from describing this species herein because *O. cruralis* is a widespread polymorphic species (Padial et al., 2008a) and an accurate diagnosis of the new taxon would require a detailed analysis after the acquisition of additional specimens from its distribution area.

Morphology

Detailed comparisons of museum specimens are described below, and qualitative morphological characters support the three new species described herein (see diagnoses). Moreover, the examination of the holotypes of *Hylodes philippi* and *H. verrucosus* (Jiménez de la Espada, 1875) revealed that they are not members of *Oreobates* and are, therefore, not synonyms of *O. quixensis*. Morphological characters also support the placement of *Pristimantis crepitans* in *Oreobates*, for which molecular data is missing. After the inclusion of several species into *Oreobates* (*O. ayacucho*, *O. crepitans*, *O. lundbergi*, and *O. pereger*), the current diagnosis of the genus is no longer accurate; therefore, we provide a new diagnosis for the genus below (see Discussion).

SYSTEMATICS

Oreobates amarakaeri, new species

Figures 2, 3A–B

Holotype: MHNC 6975 (fig. 2A–B and fig. 3A–B), an adult male from Río Nusinuscato (13°08′13.1″S, 70°51′05.8″W; 685 m), Distrito Camanti, Provincia Quispicanchi, Departamento

Cusco, Peru (map 1), collected by J.C. Chaparro, R. Velázquez, F. Najas, J. Chata, and E. Yabar on 16 April 2008.

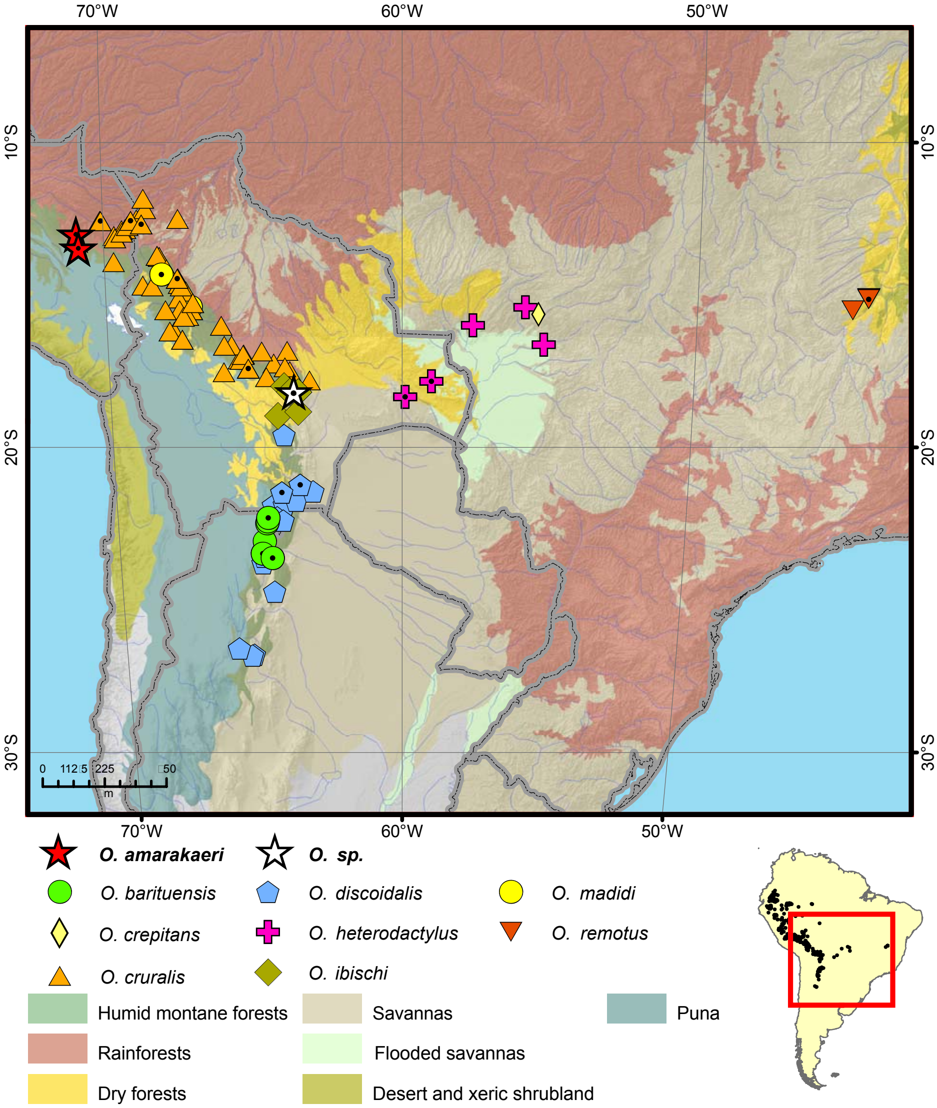
Paratypes: MHNC 7017 (fig. 2E–F) and 7049 (fig. 3C–D), adult males from headwaters of Río Mabe (13°06′31.5″ S, 70°54′ 56.0″W; 1000 m), Distrito Camanti, Provincia Quispicanchi, Departamento Cusco, Peru (map 1), collected by J.C. Chaparro, R. Velázquez, F. Najas, J.C. Irway, and E. Yabar on 20–21 April 2008.

Diagnosis: A small species of *Oreobates* (max. SVL of adult male 30.8) characterized as follows: (1) skin of dorsum warty, warts rounded at the base, generally with rounded tips, some slightly pointed, disparate in size, flanks much less warty than dorsum; incomplete occipital W-shaped fold composed of elongated to triangular warts; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present, weak; postrictal gland present or absent, conical when present; (2) tympanic membrane and annulus distinct, large, about 50%–70% of length of eye; supratympanic fold absent; (3) head as long as wide; snout short, round in dorsal view and in lateral view; canthus rostralis straight in dorsal view, round in profile; (4) cranial crests absent; upper eyelid covered with few and conspicuous round warts; (5) dentigerous process of the vomers large, prominent, triangular in shape, situated posteromedial to choanae (posterior margin at level of choanae), their width about 1.5 times diameter of choanae, bearing 2 and 7 vomerine teeth; (6) males with vocal slits and no vocal sacs; (7) hands with long and slender fingers, first longer than second; subarticular tubercles very large and prominent, round to conical; supernumerary tubercles large, round to conical, smaller than subarticular tubercles; fingertips round, slightly enlarged, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) ulnar region bearing inconspicuous low, round warts (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, very prominent; outer metatarsal tubercle equal in size, conical, inclined, prominent; subarticular tubercles, conical, prominent, supernumerary tubercles smaller than subarticular tubercles, conspicuous, small, round to conical; (11) toes long and slender (foot length 50%–60% SVL), lateral fringes and webbing absent; toe V reaching the proximal margin of the second subarticular tubercle of toe IV; toe III reaching the midpoint or distal margin of the second subarticular tubercle; tips of toes slightly enlarged, rounded, ungual flap and circumferential groove absent; (12) axillary glands absent; (13) in life, dorsum light brown to pinkish brown with black and pale blotches, lips and extremities barred, dark W-shaped mark in suprascapular region, venter dark or light gray with orange blotches, and/or cream and white dots, throat dark or light gray with white, cream, or orange blotches; hidden and ventral surfaces of hind limbs, groin, and axillae orange, iris golden intensively marbled with fine black.

Oreobates amarakaeri differs from all other *Oreobates* by the unique combination of a warty dorsal skin lacking keratinized granules, absence of supratympanic folds, finger I longer than finger II, finger discs not enlarged, rounded, subarticular and supernumerary tubercles prominent and conical, and orange blotches on axillae, belly, throat, chest and hidden surfaces of limbs. *Oreobates amarakaeri* is most similar to *O. cruralis* and *O. madidi*. From *O. cruralis* it can be distinguished (characters of other species in parentheses) by having a warty dorsal skin (shagreen with scattered nonconical warts), and by lacking expanded fingertips (expanded on finger III and finger IV), by having orange blotches on hidden surfaces of limbs, belly and throat (absent). From *O. madidi*, *O. amarakaeri* differs by having conical warts on dorsum, and warts differing in size (warts flat, homogeneously and densely distributed on dorsum), and by having orange blotches on hidden surfaces of limbs, belly, and throat (orange blotches absent). *Oreobates amarakaeri* can be distinguished from *O. barituensis*, *O. choristolemma, O. discoidalis*, *O. heterodactylus*, *O. ibischi*, *O. lundbergi*, and *O. remotus* by having fingertips not expanded (expanded in finger III and finger IV). From *O. granulosus* and *O. sanderi*, it can be distinguished by having finger I longer than finger II (shorter), by a dorsal skin lacking conical keratinized granules (dorsal skin warty and coarsely granular), and by having orange blotches on axillae, belly, throat and chest, and hidden surfaces of limbs (absent). From *O. lehri* and *O. gemcare* it differs by having a warty dorsal skin lacking conical keratinized granules (shagreen with enlarged granules), feet with prominent supernumerary tubercules (absent), foot length 50% of SVL (60%–70% of SVL), and orange blotches on axillae, belly, throat and chest, and hidden surfaces of limbs (absent). From *O. machiguenga* it differs by having a warty dorsum (coarsely granular dorsum, lacking enlarged warts) and belly with orange and/or gray blotches (immaculate). *Oreobates amarakaeri* differs from *O. quixensis*, *O. sanctaecrucis,* and *O. saxatilis* by having a head as wide as long (wider than long), and a dorsal skin with low warts and no conical keratinized granules (coarsely warty and granular skin). From *O. ayacucho* it differs by lacking dorsolateral and supratympanic folds (present), by having conical supernumerary and subarticular tubercles (supernumerary absent, and subarticular round), and by having orange blotches on axillae, belly, throat and chest, and hidden surfaces of limbs (absent). From *O. zongoensis* it differs by having a dorsal skin lacking conical keratinized granules (dorsal skin coarsely granular), by well-developed conical supernumerary tubercles (round and small), and by having orange blotches on axillae, belly, throat and chest, and hidden surfaces of limbs (absent). From *O. pereger*, it differs by lacking a supratympanic fold (well developed), by having well-developed supernumerary tubercles (absent or inconspicuous), and by lacking a disc papilla on finger disc (present).

Description of the holotype: Head as long as wide; snout round in dorsal view and profile; nostrils slightly protuberant, oriented laterally; canthus rostralis straight in dorsal view, round in frontal profile; loreal region slightly concave, sloping gradually to the lips; lips not flared; upper eyelid covered with small round warts; cranial crests absent. Supratympanic fold indistinct; tympanic membrane and annulus distinct; tympanic membrane nearly round, its length about half of eye length; postrictal gland single, small, conical. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth viewed from below; choanae large, round, medial, separated by distance equal to 5–6 times diameter of choana; dentigerous process of the vomers large, prominent, triangular in shape, situated posteromedially to choanae (posterior margin at level of choanae), their width about 1.5 times diameter of choanae, each bearing 2 or 3 vomerine teeth. Skin of dorsum and dorsal surfaces of limbs warty, warts round at the base, generally with rounded tips, some slightly pointed, disparate in size, flanks much less warty than dorsum; incomplete occipital W-shaped fold composed of elongated to triangular warts; venter smooth; posterior surfaces of limbs smooth, groin areolate; discoidal fold present, weak; postrictal gland present, conical. Ulnar region with small round warts; palmar tubercle elongate, large, prominent;

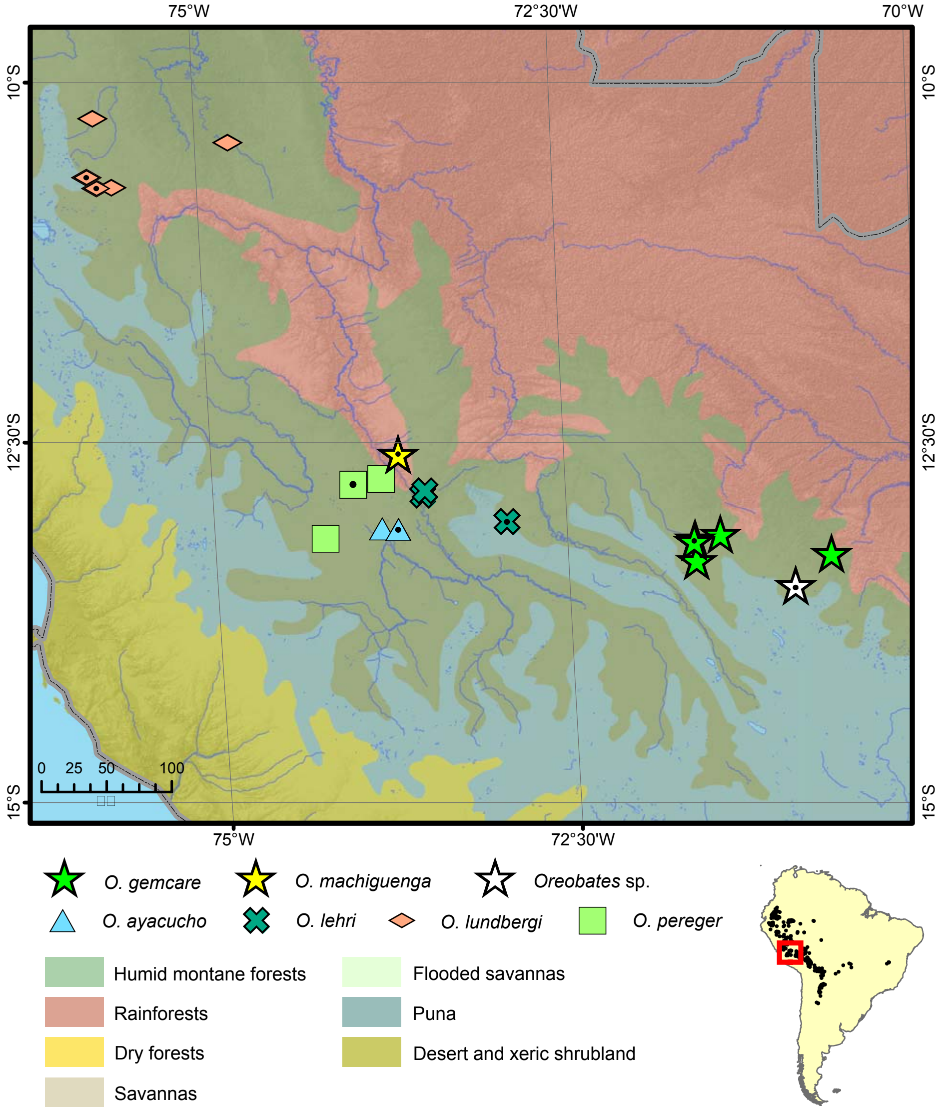
thenar tubercle elongate, prominent, about half size of palmar tubercle; subarticular tubercles very prominent, conical, larger than supernumerary tubercles, supernumerary round to conical, prominent; fingertips round, slightly enlarged; lateral fringes and keels on fingers absent; relative length of fingers: II ≈ IV< I < III. Toes long and slender (foot length 50% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle oval, prominent, slightly larger than outer metatarsal tubercle; metatarsal tubercle round, conical; toes lacking lateral fringes and webbing; toe tips rounded, slightly enlarged, ungual flap absent; relative length of toes IV > III > V ≈ II >



MAP 1. Geographic distribution of nine species of *Oreobates* and one candidate species from Argentina, Bolivia, Brazil, and Peru, based on specimens listed in appendix 1 and in Duellman and Lehr (2009) and Teixeira et al. (2012). Symbols corresponding to localities from which tissue samples were sequenced for this study have a small black dot in the middle. The candidate species are represented by a white star.

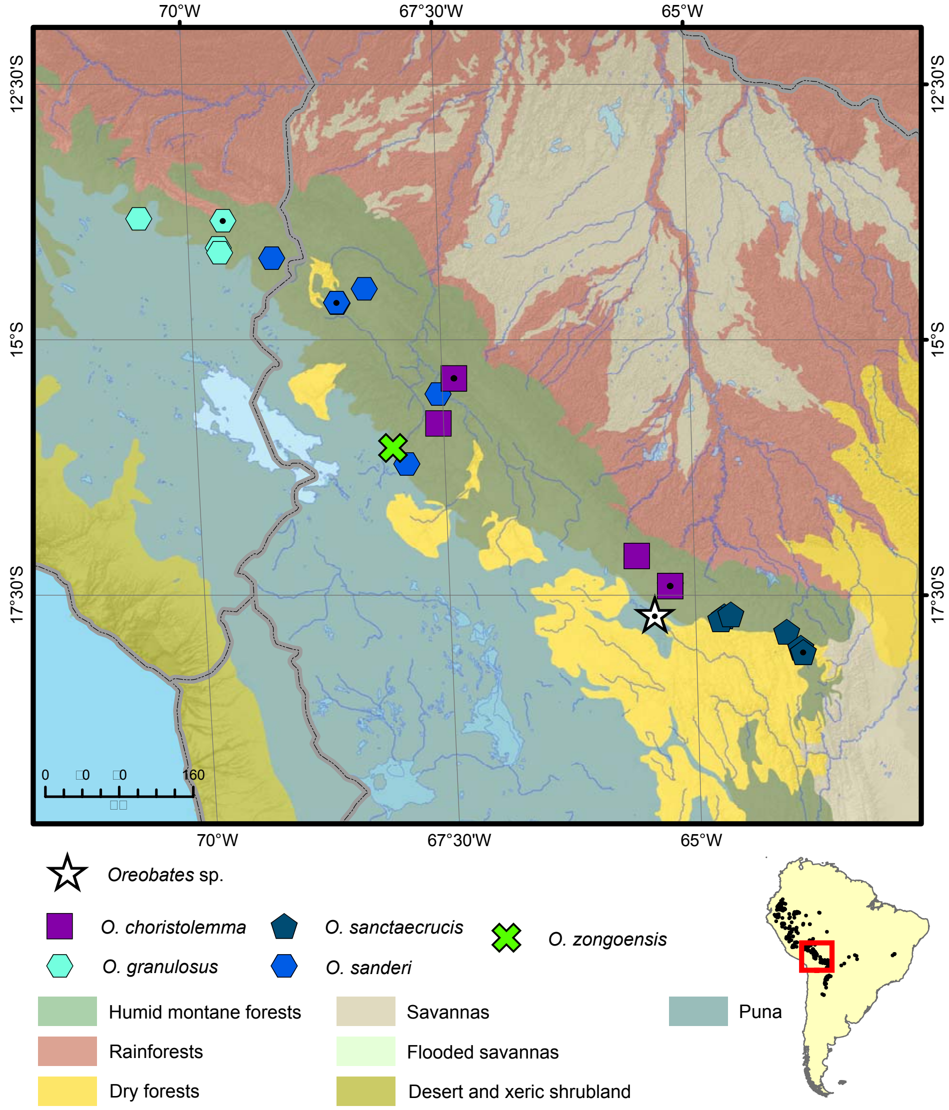
I; toe V reaching the proximal margin of the second subarticular tubercle of toe IV, and toe III reaching midpoint of the second subarticular tubercle of toe IV.

In preservative, dorsal surfaces pale brown, with abundant dark brown, black and pale irregular blotches; dorsal marks include a dark brown to black W-shaped occipital mark, outlined with white blotches anteriorly, a middorsal black mark shaped like close-to-open parentheses, i.e.,)(, and two symmetric, bold, large black dots behind the W-shaped occipital mark; canthus rostralis dark brown, almost black; two subocular dark brown stripes; tym-



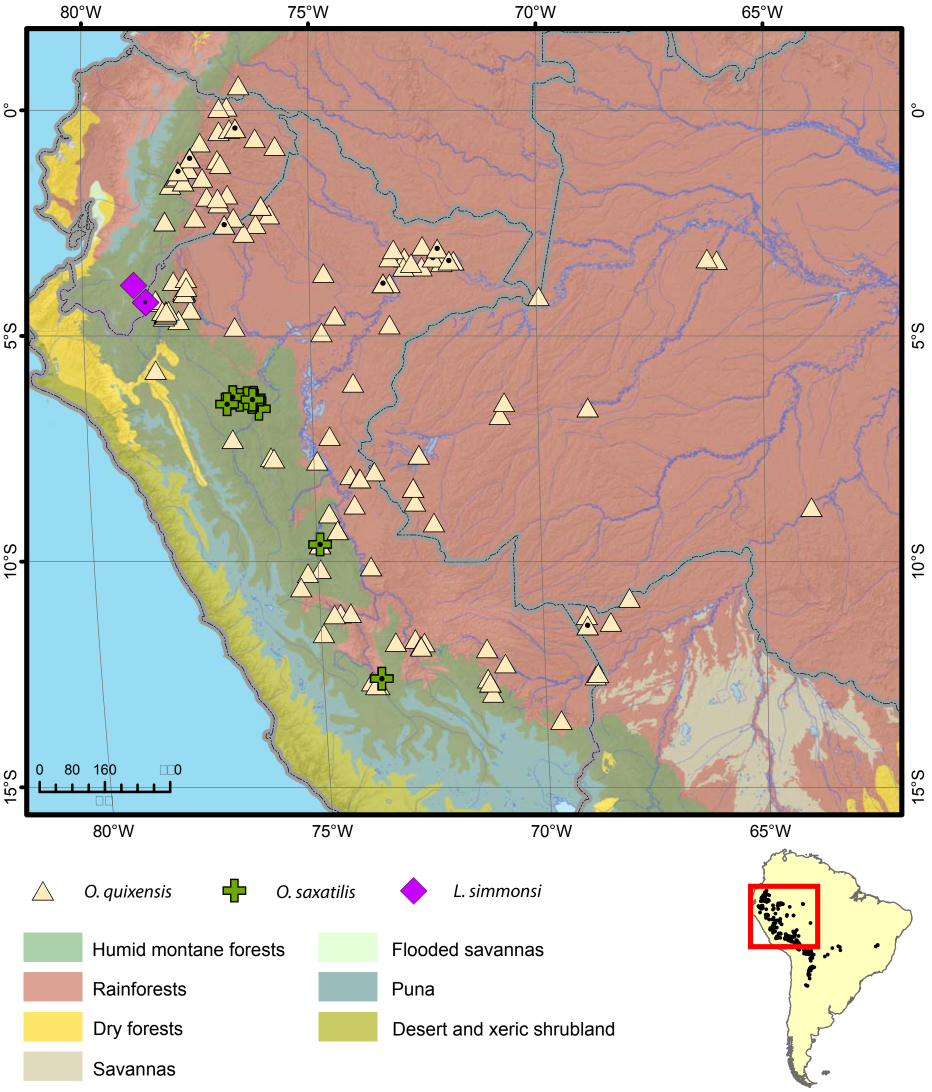
MAP 2. Geographic distribution of six Peruvian species of *Oreobates* and one candidate species based on specimens listed in appendix 1 and in Duellman and Lehr (2009) and Teixeira et al. (2012). Symbols corresponding to localities from which tissue samples were sequenced for this study have a small black dot in the middle. The candidate species are represented by a white star.

panic membrane pale brown. Extremities brown, limbs with dark brown to black transverse bars; flanks dark brown with white marbling. Throat, belly, and posterior and anterior surfaces of hind limbs gray with large white blotches. In life, the same pattern exists, but the dorsum is pinkish brown with black blotches, transversal bars on limbs, and subocular bars are a mix of black with gold and brown, the belly and throat is dark gray with white to cream blotches, and hidden surfaces of arms and limbs are pale salmon to orange. The iris is golden intensively marbled with fine black, and the pupil has a ventral black notch.



MAP 3. Geographic distribution of five species of *Oreobates* and one candidate species from Bolivia and Peru based on specimens listed in appendix 1 and in Duellman and Lehr (2009) and Teixeira et al. (2012). Symbols corresponding to localities from which tissue samples were sequenced for this study have a small black dot in the middle. The candidate species are represented by a white star.

VARIATION: All three males vary little in skin texture characteristics or body structures. Appreciable differences can be observed in coloration. Whereas MHNC 6975 and 7017 have a dark gray belly with white and orange spots or blotches, most ventral surfaces of MHNC 7049 are orange, with few gray blotches. Dorsal and iris coloration are similar among the three specimens. Although testis and vocal slits were evident in the three males specimens, they greatly differ in size (20.7–30.8 SVL), which might indicate that males reach maturity early in development.



MAP 4. Geographic distribution of *Oreobates quixensis*, *Oreobates saxatilis*, and *Lynchius simmonsi* based on specimens listed in appendix 1 and in Duellman and Lehr (2009) and Teixeira et al. (2012). Symbols corresponding to localities from which tissue samples were sequenced for this study have a small black dot in the middle.

Measurements of the holotype (those of paratypes MHNC 7017 and MHNC 7049 in parenthesis): SVL, 24.9 (20.7, 30.8); HL, 9.0 (8.3, 11.5); HW, 9.2 (7.7, 12.2); EL, 3.8 (3.7, 5.2); END, 3.3 (3.0, 4.4); IND, 2.5 (1.7, 2.7); EE, 4.7 (3.8, 5.8); TYH, 2.4 (2.0, 3.3); TYL, 2.4 (2.0, 3.2); FA, 7.6 (6.4, 7.6); TL, 14.3 (11.8, 16.6); THL, 13.3 (11.2, 15.5); FL, 13.6 (10.7, 15.7).

Distribution and ecology: *Oreobates amarakaeri* is known from two localities that are 8 km apart, one at Río Mabe and one at Río Nusinuscato, both tributaries of the Río

FIG. 2. **A–B**. Adult male holotype of *Oreobates amarakaeri* from Río Nusinuscato, 685 m, Cusco, Peru (MHNC 6975, SVL 24.9). **C–D.** Adult male paratype of *Oreobates amarakaeri* from Río Mabe, 1000 m, Cusco, Peru (MHNC 7049, SVL 30.8). **E–F.** Male paratype of *Oreobates amarakaeri* from Río Mabe, 1000 m, Cusco, Peru (MHNC 7017, SVL 20.7).

Araza, in the headwaters of the Río Madre de Dios basin (map 1). The area belongs to the Andean foothills and is covered by Amazonian forest with *Guadua* spp. formations as well as primary forest with predominant presence of trees of the genera *Erythrina*, *Ormosia*, *Inga*,

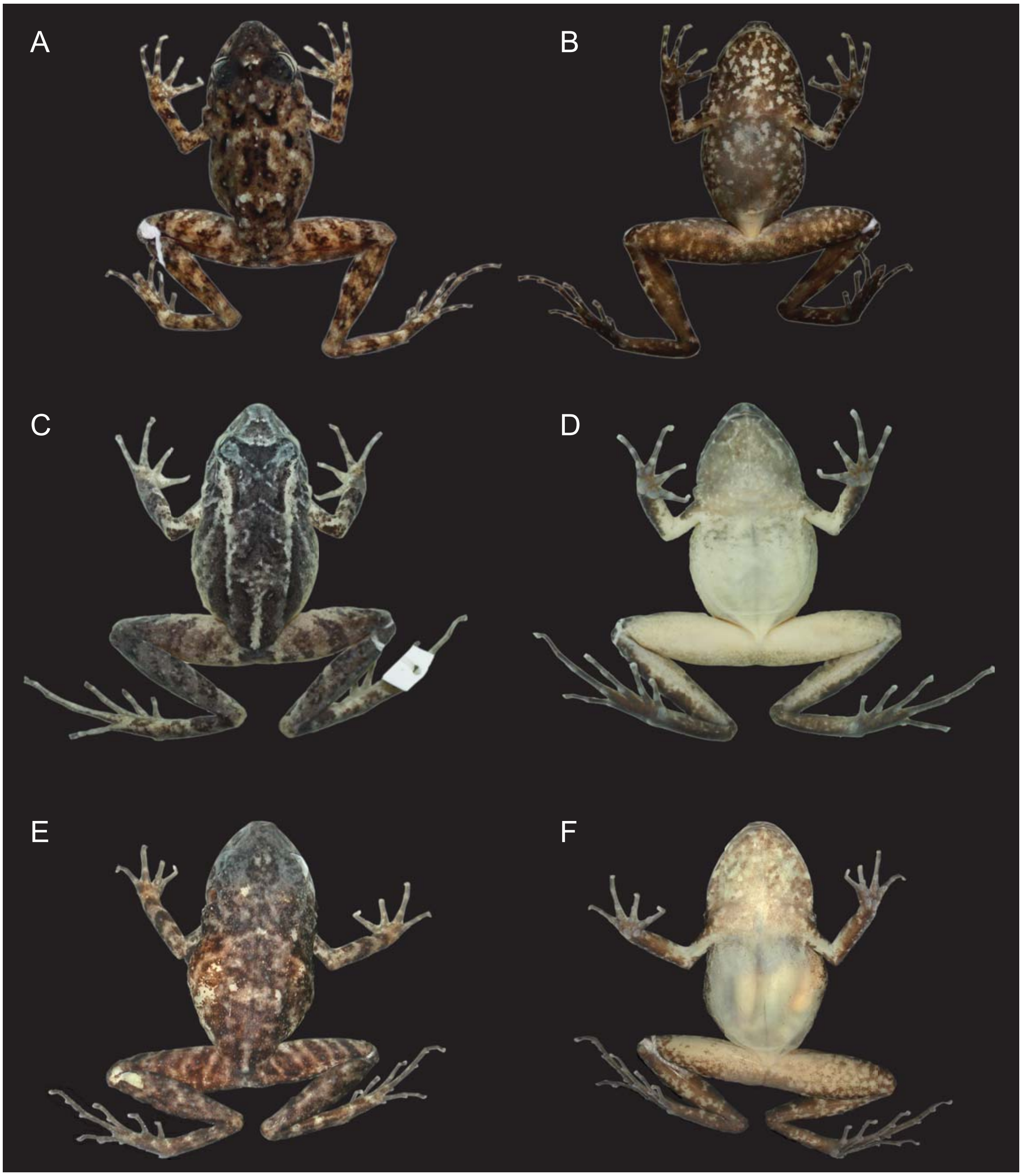


FIG. 3. **A–B.** Adult male holotype of *Oreobates amarakaeri* (MHNC 6975, SVL 24.9). **C–D.** Adult male holotype of *O. gemcare* (MNCN 44230, SVL 33.6). **E–F.** Adult female holotype of *Oreobates machiguenga* (MHNC 6809, SVL 32.7).

FIG. 4. Riverine forest and forested Andean slopes at the type locality of *Oreobates amarakaeri*, Río Nusinuscato, 685 m, Cusco, Peru.

Hevea, and *Virola* (fig. 4). The frogs were active on the ground at night during the end of the rainy season.

ETYMOLOGY: The species epithet is used as a substantive in apposition, and it refers to the Amazonian indigenous group Amarakaeri. Like *Oreobates amarakaeri*, Amarakaeris are intimately associated with the Amazonian forests; the future of both is largely interdependent.

Oreobates ayacucho (Lehr, 2007), new combination

Figure 5A–B

Phrynopus ayacucho: Lehr, 2007: 167.

Molecular analyses of the 16S rRNA gene fragment (fig. 1), and additional analyses with larger character sampling (not shown), show that this species belongs to *Oreobates*, formerly known only from one adult female specimen and a juvenile from Rapi, Provincia de la Mar, Departamento de Ayacucho, Peru (Lehr, 2007) (map 2). Fieldwork in Ayacucho in 2008 added two adult males (MNCN 44484, SVL = 25.0; MHNC 6840, SVL = 19.0) and a juvenile (MNCN 44485, SVL = 13.0) of this species from a locality on the road from Punqui to Anco, 3 km before Anco (Departamento Ayacucho, Peru), at an elevation of 3850 m, 4.7 km from the type locality (map 2; see table 1 for coordinates). The specimens were readily identified as *Phrynopus ayacucho* following Lehr (2007). Males of this species have nuptial pads and vocal slits, but vocal sac was not evident. In life, the dorsum and venter are dark brown. The dorsal skin has low, round warts and two rows of incomplete dorsolateral folds. The folds and some warts are almost black. The iris is almost black, with some golden reticulation.

Several males were heard calling during the day in cold grassland puna (or wet puna). Frogs where hidden under thick layers of moss near the ground or within piles of stones. We analyzed 11 calls from one male (MNCN 44484, SVL 25.0 mm). The call is composed of a

FIG. 5. **A–B.** Adult male of *Oreobates ayacucho* from between Punki and Anco, 3850 m, Ayacucho, Peru (MNCN 44484, SVL 25.0); **C–D.** Adult female of *Oreobates lehri* from ca. 40 km from Vilcabamba, 2850 m, Cusco, Peru (MUSM 27616, SVL 28.0). **E–F.** Adult female of *Oreobates lundbergi* from between Auquimarca and Uchuerta, 2760 m, Pasco, Peru (MTD 45902, SVL 48.0). **G–H.** Adult female of *Oreobates pereger* from Yanamonte, 2600 m, Ayacucho, Peru (MUSM 19982, SVL 31.2).

group of 3–5 pulsed, amplitude-modulated notes with harmonic structure (fig. 6, table 2). Average call length was 756 ms, ranging from 691 to 756 ms. Call rate varied with motivation. When highly motivated, males called at a rate of 2.5–2.9 calls per minute. Most energy was distributed in a band from 1583 to 2703 Hz, with an average fundamental frequency of 1902 Hz (range = 1116–2370), and an average dominant frequency of 1560 Hz (range = 1178–2283), but with additional energy distributed in up to seven harmonics. The first note was always the longer ($\overline{X}$ = 248 ms, range = 218–303 ms), having 9–10 pulses ($\overline{X}$ = 10), and with the amplitude of pulses increasing toward the end of the notes, with a slow decay in the last pulses. Subsequent notes were always shorter, ranging from 85–116 ms, having only four pulses, and decreasing in amplitude toward the end of the note.

Oreobates crepitans (Bokermann, 1965), new combination

Figure 7

Eleutherodactylus crepitans Bokermann, 1965: 262.
Pristimantis crepitans: Heinicke et al., 2007: Supplementary information table 2
Pristimantis (Pristimantis) crepitans: Hedges et al., 2008a: 165.

Oreobates crepitans (Bokermann, 1965) was described from a tableland of the Brazilian shield near São Vicente, a locality located in the Cerrado forest of Mato Grosso, Brazil, not far from the northeastern Bolivian border (map 1). The original description of the species is very accurate and the species is readily distinguishable, but it was placed in the synonymy of *Eleutherodactylus fenestratus* by Lynch (1980), from where it was resurrected by Heyer and Muñoz (1999), a position later supported by Padial and De la Riva (2005). Subsequently, it was transferred to *Pristimantis* (Hedges et al., 2008a). Recent examination of the paratype of *Eleutherodactylus crepitans* (fig. 7) and the holotype of *Telatrema heterodactylum* at MNRJ (a Cerrado species placed in *Oreobates* by Padial et al., 2008a) has led us to conclude that the species indeed belongs to *Oreobates*. *Oreobates crepitans* has enlarged conical and subconical tubercles on plantar surfaces, and lacks circumferential grooves on finger discs. Nonetheless, it has a characteristic that differentiates it from all other *Oreobates* described to date: it has a subgular vocal sac only slightly developed. The only other direct-

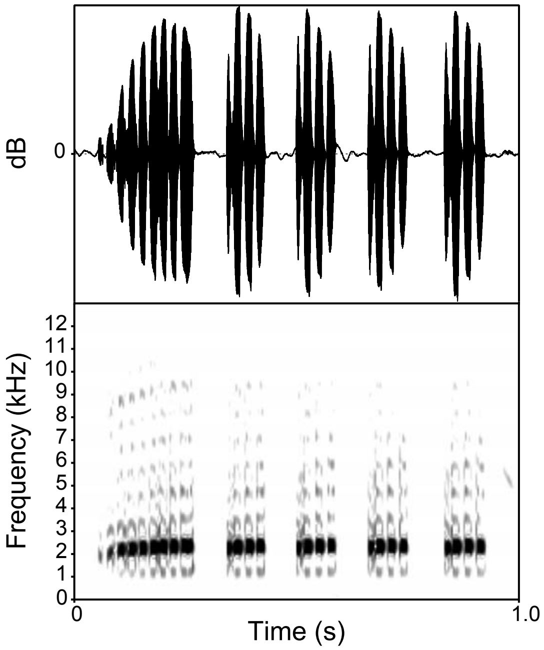


FIG. 6. Oscillogram and sound spectrogram of the advertisement call of *Oreobates ayacucho*, recorded on 28 February 2008 at 12:15 h in the Andean puna between Punki and Anco, 3850 m, Ayacucho, Peru (temperature not recorded). The specimen voucher is the one depicted in figure 6A–B.

developing frogs from the lowlands (i.e., not from the Andes or from the Mata Atlantica) that are similar to *O. crepitans* are members of *Ischnocnema* and *Pristimantis* from the *P. conspicillatus* group. Members of the *P. conspicillatus* group east of the Andes have disc structures with circumferential grooves, and supernumerary tubercles are absent or are not large and conical (Padial and De la Riva, 2009). Some species of *Ischnocnema* resemble members of *Oreobates* and some also have expanded discs, but when these are present they have circumferential grooves (Hedges et al., 2008a). Moreover, no species of *Ischnocnema* is known to reach the Cerrado in western Brazil. In addition, *O. crepitans* has some characteristics that distinguish it from *O. heterodactylus*, which also inhabits the Cerrado in the same region. Although the type of *O. heterodactylus* is poorly preserved, strongly enlarged finger discs (FIII, FIV) are still evident, where *O. crepitans* has moderately enlarged discs. The type localities of both species are far apart (ca. 300 km; Miranda-Ribeiro, 1937; Heyer and Muñoz, 1999). Moreover, Bolivian populations assigned by Padial and De la Riva (2005) to *O. heterodactylus* might indeed represent a third species. Bolivian populations inhabit a distant outcrop of the Brazilian shield, ca. 500 km southwest (map 1); they have smooth skin (warty in nominal *O. crepitans*) and less-developed finger discs than the type of *O. heterodactylus*. However, a rigorous reassessment of the identity of the Bolivian populations would require gathering additional specimens from the type localities of *O. crepitans* and *O. heterodactylus* to assess intraspecific variation.

Oreobates gemcare**,** new species

Figures 3C–D, 8, and 9A

Holotype: MHNC 6687 (field number IDlR 4826), an adult male from Esperanza (13.1824°S, 71.6036°W; 2700 m above the sea level), Kosñipata Valley, Departamento Cusco,

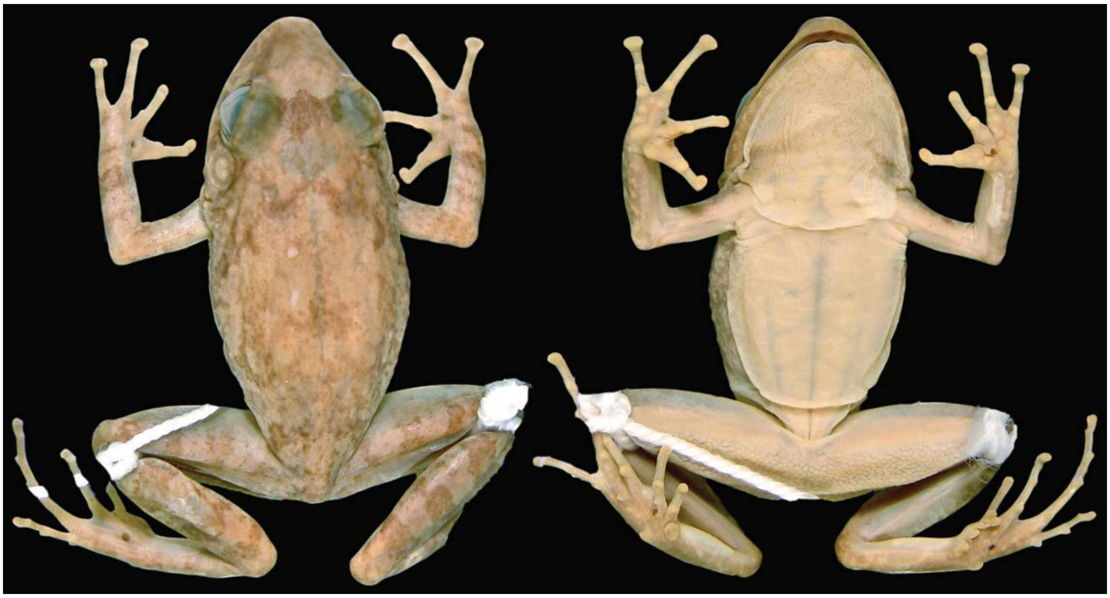


FIG. 7. Male paratopotype of *Eleutherodactylus crepitans* Bokermann, 1965 from São Vicente, Cuiba, Mato Grosso, Brazil (MNRJ 3985, SVL 27.7 mm).

Peru (map 2), one of a series collected on 11th February 2007 by I. De la Riva, J.M. Padial, S. Castroviejo-Fisher and J.C. Chaparro (fig. 3C–D, fig. 8A).

Paratypes: AMNH 11831, an adult male from Pillahuata (13°09′52″S, 71°35′46″W; 2430 m) between Puente Kosñipata and road, Departamento Cusco, Peru (map 2), collected by L.O. Rodríguez on 15 January 1998. MNCN 44230 (field number IDlR 4827) an adult male from Esperanza (13.1824°S, 71.6036°W; 2700 m), Kosñipata Valley, Departamento Cusco, Peru (map 2), collected on 11th February 2007 by I. De la Riva, J.M. Padial, S. Castroviejo-Fisher and J.C. Chaparro. New museum numbers for MHNC are provided here (old museum numbers used for the original description of *O. lehri* in parenthesis): MHNC 4557 (MHNC 3223), 4564–4567, (MHNC 3224–3227) MHNC 4583–4586 (MHNC 3228–3231), MHNC 4587 (MHNC 3232), MHNC 4589 (MHNC 3233), MHNC 4601–4602 (MHNC 3234–3235) MHNC 4682–4683 (MHNC 3236–3237) MHNC 4389 (MHNC 3238), MHNC 4218 (MHNC 3239) and MNCN 43740–1, Esperanza (13° 10′ 56″ S, 71° 36′ 227″ W; 2600–2800 m), Kosñipata Valley, Departamento Cusco, Peru (map 2), collected by Juan C. Chaparro and A. Mendoza between 26th January to 23rd February 2003 (MHNC 4557, 4564, 4602, 4683 and MNCN 43741, adult males;

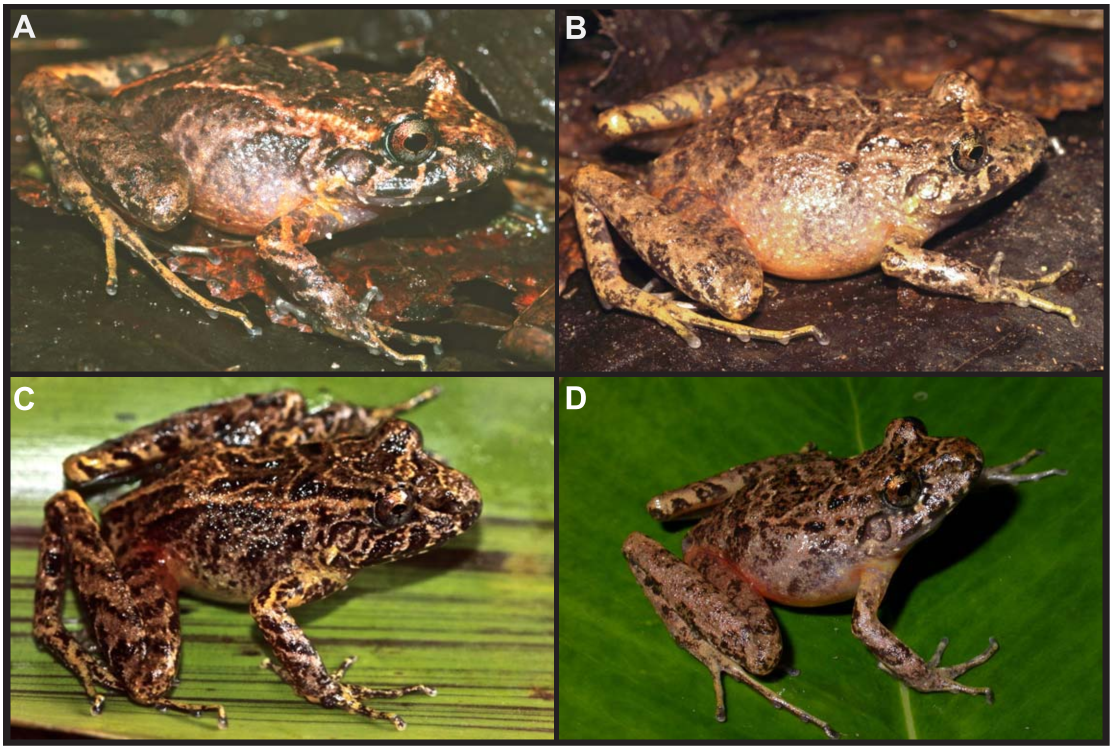


FIG. 8. **A.** Adult male holotype of *Oreobates gemcare* from Esperanza, Kosñipata Valley, 2700 m, Cusco, Peru (MHNC 6687, SVL 33.5). **B.** Adult male paratype of *O. gemcare* from Esperanza, Kosñipata Valley, 2700 m, Cusco, Peru (MNCN 44230, SVL 33.6). **C.** Adult male of *O. gemcare* from Esperanza, Kosñipata Valley, 2790 m, Cusco, Peru (MHNC 10792, SVL 28.2). **D.** Adult male paratype of *O. gemcare* from Esperanza, Kosñipata Valley, 2700 m, Cusco, Peru (MHNC 4564, SVL 32.1).

MHNC 4683 and MNCN 43740, adult females; MHNC 4565, 4601, subadult females; MHNC 4566–4567, 4583–4586, juveniles).

Diagnosis: A robust *Oreobates* (SVL of adult females 35.5–39.9; adult males 31.8–34.3) characterized as follows: (1) skin on dorsum shagreen with enlarged granules and low warts, granules regular in size, small, round, flat, some slightly enlarged; granules scarce on flanks, but slightly larger than those of dorsum; venter smooth; posterior surfaces of limbs smooth; discoidal fold present; dorsolateral folds irregular, formed by connected granular warts, or absent; postrictal glands present, large, prominent; (2) tympanic membrane and annulus distinct, their length about half eye length; supratympanic fold present, conspicuous; (3) head large, as long as wide or longer; snout round in dorsal and lateral views; canthus rostralis straight 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, nuptial pads absent; (7) hands with long and slender fingers, first finger about same length as second; subarticular tubercles round to conical, well developed; supernumerary tubercles prominent, round to conical, smaller than subarticular tubercles; terminal discs of fingers truncate to round, not enlarged, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent, round, low; (9) tubercles absent on heel and tarsus; (10) inner metatarsal tubercle ovate to round, prominent, outer smaller, round, prominent; supernumerary tubercles absent; (11) toes long, slender (foot length 60%–70% SVL), lacking lateral fringes or keels (or very weak at the base of toe III), webbing absent; toe III and V reaching midpoint of second subarticular tubercle of toe IV; tips of toes moderately enlarged, rounded, with ungual flap not indented; (12) axillary glands present; (13) dorsal

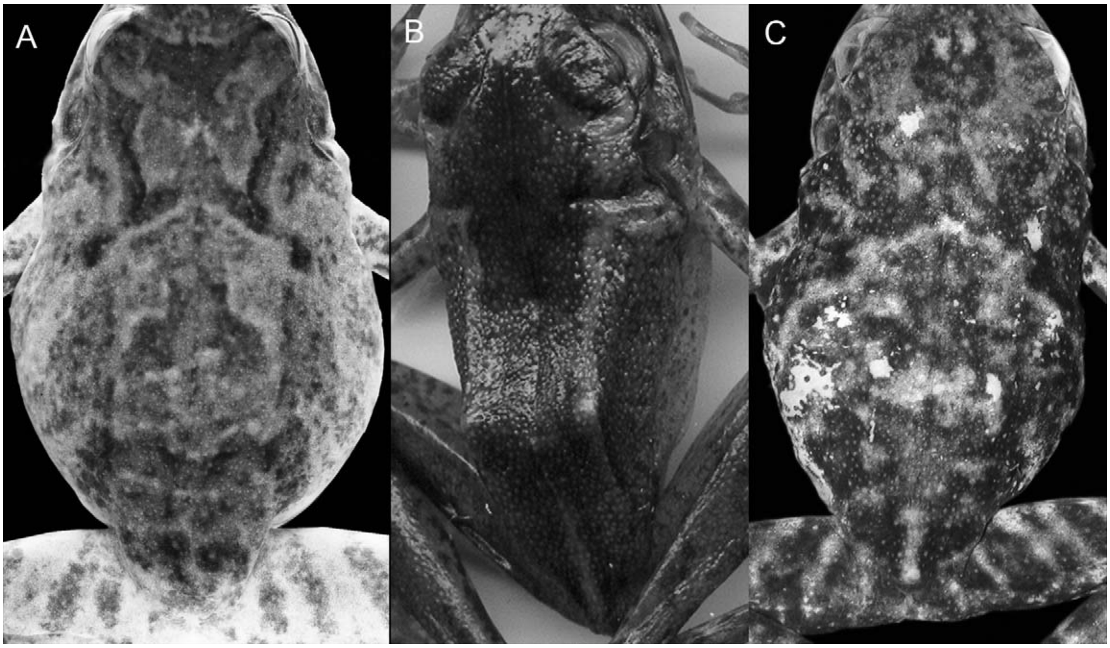


FIG. 9. Details of the dorsal skin of **A.** *Oreobates gemcare*, **B.** *O. lehri*, and **C.** *O. machiguenga*.

FIG. 10. Cloud forests around the type locality of *Oreobates gemcare* in the Kosñipata Valley, 2700 m, Cusco, Peru.

coloration in life pale to dark brown or grayish brown with darker color marks and bold spots, pair of cream dorsolateral stripes, and short longitudinal sacral stripe 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; hidden surfaces of arms and shanks orange or with orange or yellow blotches.

Oreobates gemcare is distinguished from all other species of the genus (except *O. lehri*) by the combination of long feet (≥ 60% SVL), presence of supratympanic fold, absence of supernumerary tubercles on feet, round not enlarged fingertips, shagreen dorsal skin with enlarged granules, and by having orange hidden surfaces of extremities. *Oreobates gemcare* and *O. lehri* are morphologically similar and the only conspicuous difference between them is skin texture (compare fig. 9A and 9B). In *O. lehri,* the dorsal skin is homogeneously granular, with small, low granules covering every spot on the dorsal skin. In *O. gemcare* granules do not cover all areas of flanks and dorsum, and granules are irregular in size. In addition, large warts appear in the dorsum, which are covered with granules, some of them forming incomplete dorsolateral folds. In life, they differ in coloration; *O. gemcare* is mostly brown, whereas in *O. lehri* green patterns prevail (fig. 5C). Also, *O. gemcare* is more robust and larger than *O. lehri* (adult females 35.5–39.9 in *O. gemcare* vs. 31.0–32.9 in *O. lehri*). *Oreobates gemcare* also is similar to *O. machiguenga* (character of *O. machiguenga* in parentheses), from which it can be distinguished by longer feet, FL/SVL = 60–70% (50%), by lacking basal membrane between toes III and IV (present), by having a well developed supratympanic fold (absent), by having a dorsal skin shagreen with most granules being poorly elevated and poorly defined (skin coarsely shagreen, granules very conspicuous and elevated), and by lacking prominent conical supernumerary tubercles on hands (well developed). In addition, *O. gemcare* can be distinguished from *O. barituensis*, *O cruralis*, *O. discoidalis, O. heterodactylus*, *O. ibischi*, *O. lundbergi*, and *O. remotus* by having fingertips not enlarged (enlarged on finger III and IV), and from *O. ayacucho* and *O. pereger*, by lacking well-defined dorsolateral folds (present), and by having a smooth belly (areolate in *O. ayacucho*), and lacking papillae on finger discs (present in *O. pereger*).

FIG. 11. Adult female holotype of *Oreobates machiguenga* from Río Kimbiri, 1400 m, Cusco, Peru (MHNC 6809, SVL 32.7).

Description of the holotype: Head longer than wide; snout round in dorsal view and in profile; nostrils slightly protuberant, oriented laterally; canthus rostralis sinuous in dorsal view, round to slightly sharp in frontal profile; loreal region slightly concave, sloping gradually to lips; lips not flared; upper eyelid without tubercles but covered by small granules; cranial crests absent. Supratympanic fold distinct, conspicuous; tympanic membrane and its annulus distinct; tympanic membrane nearly round, its length about half length of eye; postrictal gland large, sharp and elongated. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae large, round, medial, separated by distance equal to 6–7 times diameter of choana; dentigerous processes of vomers large, prominent, triangular in shape, situated posteromedial to choanae (posterior margin at level of choanae), their width about 1.5 times diameter of choanae, bearing 3–2 vomerine teeth; vocal slits short, placed posterolaterally. Skin of dorsal surfaces and posterior parts of hind limbs shagreen with enlarged granules and low warts also covered with granules; dorsolateral folds low and inconspicuous, incipient, formed by granular warts; ventral surfaces smooth; W-shaped occipital fold weak; discoidal fold conspicuous, posterior surfaces of thighs areolate.

Ulnar tubercles present; palmar tubercle large, cordiform, flat, larger than elongate, prominent thenar tubercle; supernumerary tubercles prominent, round to conical; subarticular tubercles round to subconical, larger than supernumerary tubercles; fingertips round, not enlarged, of same width as corresponding digits; fingers lacking lateral fringes and keels; relative length of fingers: III > I > IV ≈ II.

FIG. 12. Montane forests of Río Kimbiri at ca. 1400 m, near the type locality of *Oreobates machiguenga*, on the western slopes of Cordillera Vilcabamba, Cusco, Peru.

Toes long and slender (foot length 60% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle large, oval prominent, larger than outer metatarsal tubercle; metatarsal tubercle prominent, inclined, conical; supernumerary tubercles absent; subarticular tubercles prominent, round to conical, inclined; toes without lateral fringes and keels, except thin, short keel at base of internal side of toe III; toe tips rounded, slightly enlarged; ungual flap not indented; relative length of toes IV > III > V≈ II > I; toe III and V reaching penultimate subarticular tubercle of toe IV.

In preservative, dorsal surfaces brown with one dorsolateral pale brown stripe on each side of dorsum, from posterior margin of eyelid almost to groin; dorsum brownish gray with black blotches, and W-shaped occipital black mark, an interocular dark color triangle, and two symmetrical middorsal black marks (occipital W-shaped, and middorsal inverted Y-shaped); dorsolateral folds cream; granules on dorsum gray; short cream stripe on sacrum; flanks yellowish gray with dark gray to black blotches; canthus dark brown, almost black; three black labial bars, two of them subocular; tympanic membrane dark brown; tympanic fold black. Limbs pale brown with diffuse transverse bars; hands and feet slightly paler brown; plantar surfaces gray. Throat brownish-gray with cream mottling; chest, belly, and groin cream with fine brown mottling; posterior and anterior surfaces of hind limbs cream with dense brown mottling.

FIG. 13. Adult female holotype of *Hylodes philippi* from San José de Moti (= San José de Mote o Nuevo), Napo, Ecuador (MNCN 1599, formerly MNCN 1155, SVL 49.5). This is the specimen figured on plate 3bis, figure 1 of Jiménez de la Espada (1875).

Measurements of the holotype: SVL, 33.5; HL, 11.2; HW, 12.5; EL, 3.2; END, 3.7; IND, 3.3; EE, 5.7; TYH, 2.7; TYL, 2.4; FA, 8.8; TL, 20.6; TH, 18.85; FL, 19.6.

Variation: Females are larger than males, and proportions are almost identical (see table 4). Males have posterolateral vocal slits but no nuptial pads. Skin texture is homogeneous, although there are more enlarged granules in some specimens than in others. A faint middorsal fold is present in some individuals, as in the holotype. The degree of development of W-shaped occipital fold and)(-shaped middorsal ridges is variable. Dorsal color patterns vary from dark brown with some irregular bold marks to pale reddish brown with irregular brown marks, some of which are outlined with cream. Common dorsal marks are an occipital W-shaped mark, an arrow-shaped middorsal mark, and a transversal irregular ellipse in the presacral region. A vertical pale color sacral stripe is present in all but some specimens. Some specimens have a dorsolateral cream stripe on each side of dorsum, from posterior margin of eye to the level of middorsum or to groin. Bold spots and lines usually outline the W-shaped occipital fold, the supratympanic fold, the)(-shaped middorsal fold, and the upper marging of flanks. Labial bars also vary; darker individuals have less conspicuous bars. The tympanic membrane and annulus are brown in all specimens. The throat pattern varies from pale gray to dark brown. Some specimens have a fine light cream line in the middle of the throat. The chest usually is mottled which diminishes on the belly. The belly varies from white to cream and usually has fine brown mottling on the sides and anterior margin. Transversal irregular bars or irregular ellipses are present on the dorsal surfaces of the

Table 4. Morphometrics of two adult females and seven adult males of *Oreobates gemcare*. Mean ± standard deviation in parentheses follows range (in mm). For abbreviations see Material and Methods.

	Female (MHNC3236)	Female (MHNC3233)	Males (n = 7)
SVL	39.9	35.5	31.8–34.3 (33.1 ± 1.0)
HL	16.0	14.0	12.1–13.6 (12.8 ± 0.8)
HW	15.2	13.8	11.8–13.1 (12.6 ± 0.5)
EL	4.8	4.5	3.2–5.1 (4.5 ± 0.7)
EN	4.8	4.1	3.4–4.1 (3.8 ± 0.3)
IND	4.4	3.9	3.1–3.9 (3.5 ± 0.3)
EE	6.3	6.2	5.1–5.9 (5.4 ± 0.3)
TYH	2.3	2.6	2.1–2.8 (2.5 ± 0.3)
TYL	2.7	2.1	2.0–2.7 (2.4 ± 0.3)
ARM	8.7	8.4	7.3–7.6 (7.5 ± 0.2)
TL	25.4	23.4	19.6–20.8 (20.4 ± 0.5)
TH	21.3	21.7	18.0–19.1 (18.5 ± 0.4)
FL	24.3	23.4	19.7–20.8 (20.1 ± 0.4)
TL/SVL	0.6	0.7	0.6–0.6 (0.6 ± 0.0)
FL/SVL	0.6	0.7	0.6–0.6 (0.6 ± 0.0)
HL/SVL	0.4	0.4	0.4–0.4 (0.4 ± 0.0)
HW/SVL	0.4	0.4	0.4–0.4 (0.4 ± 0.0)
HW/HL	1.0	1.0	1.0–1.1 (1.0 ± 0.1)
EN/EL	1.0	0.9	0.8–1.1 (0.9 ± 0.1)
EL/HW	0.3	0.3	0.2–0.4 (0.4 ± 0.1)
TYL/TYH	1.2	0.8	0.9–1.0 (1.0 ± 0.1)

hind limbs, irregular brown marks are present on the arms. Plantar surfaces vary from dark gray to dark brown with gray or cream plantar tubercles.

In life (based on MHNC 3224, and MNCN 44230) the dorsum is pale brown to dark brown or reddish brown, with irregular dark brown or black spots and marks surrounded by beige, and some small red or orange spots. Some of the dorsolateral warts are black, and the flanks are mostly pale brown to gray with black blotches. The lips have three bold black bars, two subocular separated by cream spots. The tympanic membrane is pale brown. The belly is white, and the throat has brown mottling. The inner surfaces of limbs are red to orange. The axillae and shoulders have yellow and/or orange blotches, and the hind limbs and arms are brown with dark brown irregular bars. The iris is golden dorsally and ventrally, with a bronze transverse stripe. The pupil has a black ventral notch.

Distribution and Ecology: *Oreobates gemcare* is known from cloud forests in the Kosñipata Valley, Departamento Cusco, Peru (map 2) at elevations of 2400–2800 m (fig. 10).

The frogs were active at night on the ground during the rainy season, and males called from the leaf litter. The call consisted of a single pulsed note.

Etymology: The species epithet is used as a substantive in apposition and refers to the company name GEMCare (Golden Empire Managed Care), a medical group that supported J.C.C.'s taxonomic research in southern Peru.

Comments: Except for the specimens MHNC 6687 and MNCN 44230, all specimens of the type series of *O. gemcare* were originally part of the type series of *O. lehri* (Padial et al., 2007). The name *O. lehri* was initially ascribed to two distant populations (200 km airline distance), one in Cordillera Vilcabamba, which is now considered typical *O. lehri*, and one in the Andean hills of the Kosñipata Valley, to which we now assign the name *O. gemcare*. Although Padial et al. (2007) were aware of differences between specimens from both populations, they refrained from recognizing them as different species until living individuals of both populations were available for more accurate comparisons and genetic analysis. Because the diagnosis of *O. lehri* (Padial et al., 2007, 2008a) was based on specimens of what are now recognized as *O. lehri* and *O. gemcare*, we provide a new diagnosis and distributional account for *O. lehri.*

Oreobates lehri (Padial, Chaparro and De la Riva, 2007)

Figures 5C–D, 13B

Eleutherodactylus lehri Padial et al., 2007: 115.
Oreobates lehri: Padial et al., 2008a: 759.

Diagnosis: A slender *Oreobates* (SVL of adult females 31.0–32.9) characterized as follows: (1) skin on dorsum, flanks, and dorsal surfaces of hind limbs coarsely shagreen, granules regular in size, small, round or conical, few of them slightly enlarged; venter smooth; posterior surfaces of limbs areolate; discoidal fold present; dorsolateral folds irregular, formed by granules, or absent; postrictal glands present, large, prominent; (2) tympanic membrane and annulus distinct, their length about half length of eye; supratympanic fold present, conspicuous; (3) head large, as long as wide; snout round in dorsal and lateral views; canthus rostralis straight in dorsal view, round in section; (4) cranial crests absent; upper eyelid bearing by small granules; (5) dentigerous process of vomers large, situated posteromedial to choanae; (6) males with vocal slits but no nuptial pads; (7) hands with long, slender fingers, finger I shorter than finger II; subarticular tubercles round to conical, well developed; supernumerary tubercles round to conical, smaller than subarticular tubercles; terminal discs of fingers round, not enlarged, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers absent; (8) ulnar tubercles absent, round, low; (9) no tubercles on heel and tarsus; (10) inner metatarsal tubercle ovate to round, prominent; outer metatarsal tubercle smaller, round, prominent; supernumerary tubercles absent; (11) toes long and slender (foot length 60–70% SVL), lacking lateral fringes or keels (or very weak at 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 ungual flap not indented; (12) axillary glands present; (13) dorsal coloration in life olive green with dark brown to black marks, outlined with pale green, in occipital region and middorsum; belly yellowish white, throat gray with brown mottling or reticulations on anterior margin, hidden surfaces of hind limbs and groin orange.

Comments: This species is now restricted to Cordillera Vilcabamba, where it is known from two localities in Departamento Cusco (map 2), the type locality (Apurimac River Valley, Camisea Natural Gas Pipeline, Wayrapata Camp, 2445 m, 12° 50′ 10″ S, 73° 29′ 43″ W) and from 40 km from Vilcabamba, ca. 2850 m, (13°02′51.1″ S, 072°55′29.4″ W) (MUSM 27616). The localities are separated by an airline distance of ca. 60 km. Originally this species was discovered from a series of specimens collected at the first locality and deposited at USNM in Washington. One of the authors (EL), collected a specimen at the second locality, which has been sequenced (fig. 1), and which permitted the description of the coloration in life (fig. 5C–D).

Oreobates lundbergi (Lehr, 2005), new combination

Figure 5E–F

Eleutherodactylus lundbergi Lehr, 2005: 200.
"Eleutherodactylus" lundbergi: Heinicke et al., 2007: Supplementary information 4 (removed from *Eleutherodactylus* without providing a new generic name).
Isodactylus lundbergi: Hedges et al., 2008a: 108.
Hypodactylus lundbergi: Hedges et al., 2008b: 67 (replacement name for *Isodactylus*).

Oreobates lundbergi is only known from the type locality in the humid montane forests on the Amazonian slopes of the Cordillera Oriental in central Peru in the Departamento Pasco, 1800–2760 m elevation (map 2). In the original description this species was placed in the *Eleutherodactylus nigrovittatus* species group. Species in this group were placed in *Isodactylus* by Hedges et al. (2008a), a generic name that was later replaced with *Hypodactylus* (Hedges et al., 2008b). Phylogenetic analyses of a short fragment of the 16rRNA gene and additional analyses with larger character sampling (not shown) place this species in *Oreobates* (fig. 1). The specimens sequenced represent the holotype and one paratype of this species.

Oreobates machiguenga, new species

Figures 3E–F, 9C, and 11

Holotype: MHNC 6809 (field number IDLR 4922) (fig. 3E–F, fig. 11), an adult female from Maguireni (12°34′42″ S, 73°40′21″ W, 1400 m), Río Kimbiri, Apurimac River Basin, Provincia La Convención, Departamento Cusco, Peru (map 2), collected by I. De la Riva, J.M. Padial, S. Castroviejo-Fisher, J.C. Chaparro, and C. Vilà, on 18th February 2008.

Diagnosis: A moderately robust species of *Oreobates* (SVL of adult female 32.7) characterized as follows: (1) skin of dorsum granular, granules conspicuous, well defined, round to conical, homogeneous in size on middorsum, smaller posteriorly, decreasing in density and increasing in size toward flanks, warts and tubercles absent; occipital W-shaped fold and/or)(-shaped fold on middorsum absent; venter smooth; posterior surfaces of limbs smooth, groin smooth; discoidal fold present, weak; postrictal glands small, conical; (2) tympanic membrane and annulus distinct, both with length about half of eye length; supratympanic fold absent; (3) head slightly longer than wide; snout short, round in dorsal view, round in lateral view; canthus rostralis convex in dorsal view, round in profile; (4) cranial crests absent; upper eyelid bearing small granules; (5) dentigerous process of vomers large, triangular, posteromedial to choanae, with a single row of teeth; (6)

gravid females with large, orange eggs; (7) hands with long and slender fingers, first longer than second; subarticular tubercles large and prominent, round to conical; supernumerary tubercles large, round to conical, smaller than subarticular tubercles; fingertips round, slightly enlarged, lacking circumferential grooves and ungual flap; lateral fringes and keels on fingers present between fingers II and III, basal; (8) ulnar region bearing low, round granules, one on wrist enlarged and flat; (9) no tubercles on heel or tarsus; (10) inner metatarsal tubercle ovate, very prominent; outer metatarsal tubercle equal in size, conical, inclined, prominent; subarticular tubercles, conical, prominent, supernumerary tubercles smaller than subarticular tubercles, conspicuous, small, round; (11) toes long and slender (foot length 50% SVL), lateral fringes basal between toe II and toe III, basal webbing between toe III and toe IV; toe V reaching the proximal margin of second subarticular tubercle of toe IV, and toe III reaching distal margin; tips of toes slightly enlarged, rounded, ungual flap absent; (12) axillary glands absent; (13) in life, dorsum dark brown with black and pale brown blotches, lips and extremities barred, dark brown W-shaped mark in suprascapular region, venter white, throat white with orange blotches; hidden and ventral surfaces of hind limbs, groin, and axillae orange.

Oreobates machiguenga differs from all other *Oreobates* by the unique combination of granular dorsal skin lacking warts and folds, the lack of occipital and middorsal tubercles, finger I longer than finger II, finger discs not enlarged, rounded, subarticular and supernumerary tubercles prominent and conical, head longer than wide, basal membrane between toe III and IV, FL/SVL = 50%, and orange blotches in axillae and on throat, chest, and hidden surfaces of limbs. *Oreobates machiguenga* is most similar to *O. gemcare* and *O. lehri* (characters of other species in parentheses), from which it can be distinguished by shorter feet, FL/SVL = 50% (60–70%), by having a basal membrane between toe III and IV (absent), a dorsal skin covered by conspicuous and elevated keratinized granules, and conical supernumerary tubercles on feet (absent) and by lacking a supratympanic fold. It can be distinguished from *O. choristolemma, O. granulosus*, *O. pereger*, *O. quixensis*, *O. sanctaecrucis*, *O. sanderi*, and *O. saxatilis* by lacking enlarged warts and/or folds (present), having finger I longer than finger II (shorter), basal webbing between toe III and IV present (absent), orange blotches on axillae, throat and chest, and hidden surfaces of limbs (absent). It differs from *O. amarakaeri* by having a granular dorsum with no enlarged warts (enlarged warts present) and by having an immaculate belly (orange and/or gray blotches). It can be distinguished from *O. barituensis*, *O. cruralis*, *O. discoidalis, O. heterodactylus*, *O. ibischi*, *O. lundbergi*, and *O. remotus* by having granular dorsal skin (shagreen), fingertips rounded and not enlarged (enlarged on finger III and IV), and basal webbing present between toes III and IV (absent). It can be distinguished from *O. madidi* by having granular dorsal skin (small warts), basal webbing between toes III and IV (absent), and orange blotches on axillae, throat and chest, and hidden surfaces of limbs. It can be distinguished from *O. zongoensis* by having conical and conspicuous supernumerary tubercles on hands (small and round), basal webbing between toes III and IV (absent), and orange blotches on axillae, throat and chest, and hidden surfaces of limbs. It differs from *O. ayacucho* and *O. pereger* by lacking conspicuous dorsolateral and tympanic folds (present).

Description of the holotype: Head slightly longer than wide (head width/head length = 0.95); snout round in dorsal view and lateral profile; nostrils slightly protuberant, oriented laterally; canthus rostralis 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 having small granules; cranial crests absent. Supratympanic fold indistinct; tympanic membrane and its annulus distinct; tympanic membrane nearly round, its length about half of eye length; postrictal gland single, small, conical. Choanae not concealed by palatal shelf of the maxillary arch when roof of mouth is viewed from below; choanae large, round, separated by distance equal to 5–6 times diameter of choana; dentigerous process of the vomers large, prominent, triangular in shape, situated posteromedial to choanae (posterior margin at level of choanae), width about 1.5 times diameter of choanae, bearing 7 and 9 teeth. Skin of dorsal surfaces coarsely shagreen, very granular behind tympanic region and middorsum, decreasing posteriorly, hind limbs with less granules and more disparate in size than on dorsum, forelimbs with few granules; ventral surfaces smooth; occipital folds and dorsolateral folds absent; discoidal fold weak. Ulnar region with small round warts and one white low tubercle; palmar tubercle divided in two ovate prominent subunits, inner larger than outer; thenar tubercle prominent, ovate; subarticular tubercles prominent, conical, larger than supernumerary tubercles, supernumerary tubercles round to conical, prominent; fingertips round, slightly enlarged; lateral fringes and keels between fingers II and III, basal; relative length of fingers: II = IV < I < III. Toes long and slender (foot length 50% of SVL); heel and tarsus lacking tubercles or folds; inner metatarsal tubercle oval, prominent, slightly larger than outer metatarsal tubercle; metatarsal tubercle round, conical; toes with lateral fringes basal between toes II and III, basal webbing between toes III and IV; toe tips rounded, slightly enlarged, ungual flap absent; relative length of toes IV > III > V = II > I; toe V reaching proximal margin of second subarticular tubercle of toe IV, toe III reaching distal margin.

In preservative, dorsal surfaces of head and body brown, with dark brown, black and pale brown irregular blotches, granules of dorsum grayish brown; a dark brown to black W-shaped occipital mark; canthus rostralis dark brown, almost black; lips barred with two subocular dark brown stripes; tympanic membrane dark brown, annulus dark brown anteriorly. Extremities brown, limbs with well-defined dark brown transverse bars, diffuse on shanks and arms; short cream stripe on sacrum; flanks dark brown with pale brown granules. Throat white with fine brown mottling; belly white; groin cream; posterior and anterior surfaces of hind limbs brown with cream mottling. In life, coloration has same pattern and tones; belly white; throat, axillae, chest, and hidden surfaces of limbs orange or having orange blotches; iris bronze reticulated with black, and with a narrow range ring around the pupil, which has a black ventral notch.

Measurements of the holotype: SVL, 32.7; HL, 13.4; HW, 13.2; EL, 4.9; EN, 4.1; IND, 3.1; EE, 5.9; TYH, 2.5; TYL, 2.3; FA, 8.9; TL, 17.0; TH, 16.1; FL, 17.2.

Distribution and ecology: *Oreobates machiguenga* is known only from the type locality on the slopes of Cordillera Vilcabamba, in the Río Kimbiri Valley, which is part of the Río Apurimac Basin, Provincia La Convención, Departamento Cusco, Peru (map 2). The area supports humid montane forest (fig. 16). The frog was on the forest floor at night during the rainy season. Several large, orange ovarian eggs could be observed through the ventral skin.

ETYMOLOGY: The specific name is a substantive in apposition, and refers to the Amazonian indigenous group Machiguenga. We name this species after the inhabitants of the Reserva Comunal Machiguenga, situated in the oriental versant of Cordillera Vilcabamba, who authorized our work and helped us during our expedition. Like *Oreobates machiguenga*, Machiguengas are intimately associated with the Amazonian forests, and the future of both depends on the same governances and decisions.

Oreobates pereger (Lynch, 1975)

Figure 5G–H

Phrynopus pereger Lynch, 1975: 32.
Eleutherodactylus pereger: Lehr and Aguilar, 2006: 60.
"Eleutherodactylus" pereger: Heinicke et al., 2007: Supplementary information 3. (Removed from *Eleutherodactylus* without placement in another genus.)
Oreobates pereger: Hedges et al., 2008a: 111.

Oreobates pereger is known from elevations of 1650–2900 m on the eastern slopes of the Cordillera Oriental and Cordillera Vilcabamba in central Peru (Lynch, 1975; Lehr and Aguilar, 2006) (map 2). In the original description, this species was placed in *Phrynopus* (Lynch, 1975), from where it was removed by Lehr and Aguilar (2006). Phylogenetic analyses of a short fragment of the 16rRNA gene and additional analyses with larger character sampling (not shown) support the placement of this species in *Oreobates*, where it was placed by Hedges et al. (2008a). The specimens sequenced are those described by Lehr and Aguilar (2006).

HYLODES PHILIPPI AND *H. VERRUCOSUS*

Lynch and Schwartz (1971) placed *Hylodes philippi* Jiménez de la Espada, 1875 and *Hylodes verrucosus* Jiménez de la Espada, 1875 in the synonymy of *O. quixensis*. Recently, Padial et al. (2008a) reviewed Jiménez de la Espada's type specimens that were considered lost by Lynch and Schwartz (1971), who tentatively placed them in the *Eleutherodactylus dolops* Group, nowadays in the genus *Hypodactylus* (Hedges et al., 2008a) without further discussion. The taxonomic status of both taxa remained uncertain.

The holotypes of *Hylodes philippi* (MNCN 1600, sex unknown) and *H. verrucosus* (MNCN 1599, sex unknown) come from the locality San José de Moti, Orellana, Ecuador. This locality lies in the northeastern slopes of Volcán Reventador, but its exact location has not yet been established (see González-Fernández, 2006; Páez-Vacas et al., 2010). The holotype of *H. philippi* (fig. 13) is well preserved, and the following characters are recognizable: (1) skin on dorsum, head, and thighs granular, granules conical and keratinized; ventral skin smooth, discoidal fold present; (2) tympanic membrane and annulus distinct, about 1/3 eye length, supratympanic fold present; (3) head large, longer than wide; snout short, sinuous in dorsal view, round in lateral profile; (4) cranial crests absent; (5) dentigerous process of the vomers large, triangular, situated posteromedial to choanae; (6) hands with long and slender fingers, relative length of fingers III > IV = I > II; subarticular tubercles round, prominent; supernumerary tubercles absent; tips of fingers only slightly enlarged, round, with weak circumferential grooves; (7) toes long and slender, toe tips enlarged, round, with barely appreciable disc structure; no tubercles on heel or tarsus; supernumerary tubercles absent; relative length of fingers IV > V > III > II > I.

The holotype of *Hylodes verrucosus* is similar to the holotype of *H. philippi*; in the original illustrations in Jiménez de la Espada (1875) both are almost identical. Unfortunately, most character states can no longer be determined in the holotype of *H. verrucosus* because it has been dehydrated. Therefore, we consider them to be synonyms. They were first illustrated on the same page but not described (name availability by indication); we choose to apply the name *H. philippi* given that the holotype is better preserved.

With the information at hand, it is impossible for us to apply the name *Hylodes philippi* to any known species of *Hypodactylus*. If the type locality of *H. philippi* lies on the hills of Volcán Reventador, the only two *Hypodactylus* species with which its distribution may coincide are *Hypodactylus dolops* and *H. nigrovittatus*. The former closely resembles *H. philippi* in general appearance, and the latter is completely different. However, we refrain from synonymizing *H. philippi* with *H. dolops* because data at hand are inconclusive. Fresh material from the type locality of *H. philippi* needs to be gathered and compared with *H. dolops* to solve the issue. Therefore, we prefer to keep *H. philippi* as a nomem dubium within *Hypodactylus*, and *H. verrucosus* as a junior synonym of *H. philippi*.

DISCUSSION

Generic assignments and the redefinition of *Oreobates*

With the new additions to the genus, especially *Oreobates ayacucho* and *O. pereger*, which are morphologically different from the other species of *Oreobates*, a redefinition of the genus is granted, and we provide it below. However, it is important to note that we have not yet found any morphological synapomorphy for the genus, and neither did Hedges et al. (2008a). With the inclusion of *Oreobates ayacucho*, *Oreobates* shares the distinctive paramo-adapted morphology characteristic of other paramo- or puna-dwelling species of strabomantids like *Bryophryne*, *Lynchius*, *Phrynopus*, *Psychrophrynella*, or even some *Pristimantis*. Indeed, recurrent evolution of paramo-adapted morphologies has historically hampered the identification of monophyletic groups within what is today known as Strabomantidae (see Hedges et al., 2008a). Thus, for example, most species sharing that morphology were usually included in the genus *Phrynopus* (e.g. Lynch, 1975), as happened to *O. ayacucho* (Lehr, 2007). In this sense, and following the results of our study, the use of the short 16S rRNA fragment for amphibians as the standard DNA barcode (Vences et al., 2005; Fouquet et al., 2007; Padial et al., 2009b; Vieites et al., 2009; Crawford et al., 2010) seems to be promising in assigning new species to genera of Terrarana in the absence of consistent morphological diagnostic characters.

Interestingly, the only potential synapomorphy for *Oreobates* is the structure of its advertisement call (amplitude-modulated and highly pulsatile notes with little or no frequency modulation). Even the general structure of the advertisement call of *Oreobates ayacucho* is identical to the call structure of all other species of *Oreobates* (Padial et al., 2008b; Vaira and Ferrari, 2008), including the rather short call of the recently described *O. remotus* (Teixeira et al., 2012). However, *O. ayacucho* is the only species routinely emitting groups of well-separated notes. Terminology plays a role in interpreting call structure. The long single-noted, multi-pulsed calls of species like *O. madidi* and *O. cruralis* are easily interpreted as such. Also, the notes in the call of *O. ayacucho* are herein considered pulsatile notes. Nonetheless, in some species the pulses could be also considered separate notes because the amplitute drops to zero between "pulses." Thus, the calls of *O. barituensis*, *O. discoidalis*, *O. ibischi*, and *O. remotus*, are composed of short "pulsatile-pulses," which can be also interpreted as single pulsatile notes. Nevertheless, the general structure is common across all the calls of *Oreobates* described to date. It is also worth noting that Goicoechea et al. (2010) discovered phylogenetic information in advertisement calls characters of some Terrarana groups including *Oreobates*. Theoretically, anatomical structures might restrict call evolution and impede sexual selection the complete extirpation of shared derived features. This finding also suggests that anatomical structures not studied to date may provide synapomorphies for the clade. Indeed, one important characteristic of *Oreobates* is the strong reduction (to near absence) of the vocal sac, a state that also seems to be shared with *Lynchius*, its sister group. Unfortunately, only the calls of nine species of *Oreobates* have been described to date, and the calls of species in *Lynchius* are unknown, which hinders the proposition of any well-grounded synapomorphy or hypothesis on call evolution in this group of frogs, subjects that surely deserve future research.

The genus *Oreobates* now includes species with the following characters: snout short; sexual dimorphism in size (SVL of males 20–44 mm, of females 25–63 mm); cranial crests absent; body robust; skin of venter usually smooth (areolate in *O. ayacucho*); skin on dorsal surfaces smooth to tuberculate; skin of plantar surfaces smooth (exclusive of plantar tubercles); axillary and/or inguinal glandular pads present (not confirmed for all species); discoidal fold conspicuous; dorsolateral folds rudimentary or absent; males with faint or absent nuptial pads, vocal slits present, vocal sac reduced; tympanic membrane and annulus present, conspicuous; finger I longer than or equal to finger II; fingertips rounded and not expanded in fingers I and II, rounded or ovate and expanded in fingers III and IV, and always with absent or incomplete circumferential grooves and absent or poorly defined ungual flap (circumferential groves interrupted by a finger disc papilla in *O. pereger*); supernumerary and subarticular tubercles present, prominent, round, 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 and Duellman, 1997); toes lacking disc structures; webbing absent (basal in *O. lehri*); no tubercles on heel or tarsus; subarticular tubercles prominent, conical, supernumerary tubercles from absent or low and round to prominent and conical; dorsal coloration overall brown with variable dorsal marks, but usually including an occipital W-shaped dark mark, an X-shaped middorsal dark mark and a broad and oblique dark band at the anterior margin of the flanks; dentigerous process of the vomers short, prominent, at the level of choanae or placed posteromedially to them; mandibular ramus of the trigeminal nerve passing lateral to the m. adductor mandibulae externus (S condition sensu Lynch, 1986); reproduction by terrestrial eggs with direct-development (mode 17 of Duellman and Trueb, 1986) inferred from circumstantial evidence (egg size and numbers in female oviducts); advertisement call always consisting of highly pulsed, amplitude-modulated notes with little or no frequency modulation, with 4–12 pulses, and with low dominant frequencies (2000–3800 Hz).

Oreobates includes 23 nominal species (all authors of species are in parentheses because species names are being properly cited as scientific contributions): *O. amarakaeri,* new species, *O. ayacucho* (Lehr, 2007), *O. barituensis* (Vaira and Ferrari, 2008), *O. choristolemma* (Harvey and Sheehy, 2005), *O. crepitans* (Bokermann, 1965), *O. cruralis* (Boulenger, 1902), *O. discoidalis* (Peracca, 1895), *O. gemcare,* new species, *O, granulosus* (Boulenger, 1903), *O. heterodactylus* (Miranda-Ribeiro, 1937), *O. ibischi* (Reichle et al., 2001), *O. lehri* (Padial et al., 2007), *O. lundbergi* (Lehr, 2005), *O. madidi* (Padial et al., 2005a), *O. machiguenga,* new species, *O. pereger* (Lynch, 1975), *O. quixensis* (Jiménez de la Espada, 1872), *O. remotus* (Teixeira et al., 2012), *O. sanctaecrucis* (Harvey and Keck, 1995), *O. sanderi* (Padial et al., 2005b), *O. saxatilis* (Duellman, 1990), and *O. zongoensis* (Reichle and Köhler, 1997).

All currently recognized species of *Oreobates* (except *O. crepitans* and *O. zongoensis*) were included in our molecular phylogenetic analyses. Moreover, all but the pair *O. quixensis* and *O. saxatilis* received support by morphological and molecular evidence, which following Padial et al. (2009b), suggest that they are potentially stable species. Nonetheless, this species pair is reciprocally diagnosable morphologically, which suggest that the paraphyly of mtDNA gene genealogies may be the result of hybridization or incomplete lineage sorting (Funk and Omland, 2003). However, some other taxonomic problems exist. As mentioned above, *O. cruralis* might be a composite of two species. Vaira and Ferrari (2008) described *O. barituensis* from northern Argentina and suggested that Bolivian populations of *O. discoidalis* might represent a different species than nominal *O. discoidalis* (the type locality is in northern Argentina). However, topotypic specimens of *O. discoidalis* have not yet been sequenced, and, therefore, the status of both *O. barituensis* and *O. discoidalis* from Bolivia with respect to nominal *O. discoidalis* remains uncertain. Vaira and Ferrari (2008) observed that advertisement calls of populations of *O. cruralis* from central Bolivia were similar to the calls of *O. barituensis* and considered that these lineages might be conspecific. However, our results here confirm that they are two different distinct lineages, because the Bolivian populations mentioned by Vaira and Ferrari (2008) correspond to the candidate species *Oreobates cruralis* [CaEU192295], which is not sister to *O. barituensis*. As mentioned above, Bolivian populations under the name *O. heterodactylus* will need further attention; they might represent an undescribed species.

With the removal of *Oreobates simmonsi* (Lynch, 1974) from the genus, the Andean distribution of *Oreobates* ranges from northern Peru (*O. saxatilis* reaches the border with Ecuador in the Andean hills) to northern Argentina (*O. discoidalis*). The northernmost distribution is that of *O. quixensis* in the Amazonian lowlands of Colombia. Only four species have broad distributions—*O. quixensis* and *O. cruralis* in the Amazonian lowlands and *O. discoidalis* and *O. saxatilis* in the Andean hills, whereas all the others are local endemisms of the Andean forests above 1500 m or of tablelands of the Brazilian shield. All but one species (*O. ayacucho*) are forest dwellers, and most of them inhabit humid montane forests. The exceptions are the species in dry forests on the Brazilian shield (*O. crepitans*, *O. heterodactylus*, and *O. remotus*) and the species inhabiting the inter-Andean dry valleys of central and southern Bolivia (*O. ibischi* and some populations of *O. cruralis* and *O. discoidalis*). With the addition of *O. ayacucho* to the genus, the ecological distribution of *Oreobates* is extended to the cold grassland puna of the Andes. Thus, the genus constitutes a small but interesting radiation of members of such disparate habitats as the Amazonian lowlands, the Cerrado, the Chiquitano Forest, the Brazilian dry forests, the inter-Andean dry valleys, the cold Yungas of Argentina, and the humid montane forests, elfin forests, and puna of the Andes. The phylogenetic relationships of members of *Oreobates* are not fully resolved (fig. 1), a subject that deserves further study and that should shed light on the origin and diversification of the group in those habitats.

Candidate species and incomplete taxonomies

In addition to the 22 nominal species, we propose three candidate species within *Oreobates*. The term "candidate species" has a long history in bacteriology, where species are not formally recognized until they meet some minimal criteria established in the bacteriological code (Murray and Schleifer, 1994). However, as those criteria are relatively restrictive, candidate species were routinely informally named and considered in microbiology studies. The concept was only recently used in vertebrate taxonomy to cope with the high number of new species being discovered but not described, especially after the advent of molecular methods (Morando et al., 2003; Köhler et al., 2005, Fouquet et al., 2007; Vences and Wake, 2007; Vieites et al., 2009; Köhler et al., 2010). Interestingly, recent analyses (Joppa et al., 2011) have shown that despite the increase in number of new species (including amphibians) and of taxonomists, the rate at which new species are being described by taxonomists is decreasing. Joppa et al. (2011) provided an explanation: there is a shortage of new species to be described by taxonomists for several groups of organisms (including amphibians). Surprisingly, the term *candidate species* was first introduced into vertebrate taxonomy by taxonomists working on amphibians for exactly the opposite reason: herpetologists are not able to cope with the huge number of new species being discovered. However, an alternative explanation seems to us more likely and quotidian. Describing species and writing lengthy taxonomic revisions is not the only task of taxonomists. Inferring evolutionary history through phylogenetics constitutes an important activity of most taxonomists, especially now that analytical tools are broadly available, and that publishing evolutionary studies is more profitable under the current system of evaluating professional scientific curricula (Agnarson and Kunstner, 2007; Werner, 2007; Ebach et al., 2011; Valdecasas, 2011).

Vieites et al. (2009) proposed subdivision of candidate species depending on the amount of evidence supporting the discovery of a putatively diverging lineage. Thus, groups of individuals within nominal species having large genetic distances, but without further information, are considered unconfirmed candidate species (UCS) deserving further study. When additional data indicate that these genealogical units are not differentiated at the species level, they are considered deep conspecific lineages (DCL). The third category, confirmed candidate species (CCS), applies to those deep genealogical lineages that can be considered good species following standards of divergence for the group under study but that have not yet been formally described and named. For example, confirmed candidate species can be sister lineages in syntopy showing no evidence of interbreeding, or allopatric lineages with distinct morphological or bioacoustical character divergences. Padial et al. (2010) proposed a naming system for candidate species with the goal of inventorying and tracking those divergent lineages that might eventually be named as Linnaean species. The naming system has been applied herein to three UCS of *Oreobates*: *Oreobates* sp. [Ca JF809995], *Oreobates* sp. [Ca EU368903], *Oreobates cruralis* [Ca EU192295]. The binomial species name of the most similar or closely related nominal species, if any, is followed (in brackets) by the abbreviation "Ca" (for candidate) and a numerical code that in this case refers to the GenBank accession number that serves as the "type" sequence. However, the candidate code species could be any equivalent information, such as MorphoBank accession numbers for morphological candidate species or a voucher specimen number from a public collection. Herein we use GenBank numbers because the candidate species were discovered using genetic evidence.

The term candidate species should not be confounded with cryptic or sibling species. Candidate species can be readily evident by morphological or any other kind of evidence, and the concept of candidate does not mandate or even suggest the amount or kind of evidence necessary to designate a diverging lineage as candidate or to describe it as a new species within a particular group of organisms. Candidate species can be good species as much as any other formally named species; they are just assigned the status of candidate until someone finds the time to put together the necessary evidence to describe the candidate species as formal Linnaean species under the rules of the International Code of Zoological Nomenclature. In this study, we refrained from formally naming three species because we lacked enough data to provide an accurate morphological diagnosis for the new taxa. However, because these discovered species are now highlighted as candidate taxa, other herpetologists will be aware of their existence and, it is hoped, this will encourage the collection of more specimens and the description of the new taxa if additional evidence supports our findings. Moreover, the term *candidate* and the candidate species proposed herein by us do not conflict with the International Code of Zoological Nomenclature. They are not diagnosed and no Linnaean binomia are assigned to them.

Future prospects in the taxonomy of *Oreobates*

The way taxonomists are working in herpetology is changing quickly. The previous centuries saw most taxonomic papers, and especially single species descriptions, ascribed to single authors, with very few of them published by three or more (Frost, 2011). Also, the pace for revisiting the taxonomy of groups was slow, with revisions for the same group appearing distantly in time. Collaborative efforts are now changing that pattern, and the present paper might well be a good example of the new trend. Also, the incorporation of genetics into taxonomy is encouraging, if not forcing, fast collaborative projects. Tissue samples for many species and different populations across large areas are difficult to get by a single person, but thorough taxonomic revisions are becoming more and more dependent on a good sample of sequenced specimens. The number of new discoveries through the addition of missing taxa to new phylogenies is also promoting a faster pace of revisionary work for some groups of organisms. In the case of *Oreobates*, shortly after the resurrection of the genus by Caramaschi and Canedo (2006), Padial et al. (2008a) reviewed species diversity and supported its monophyly by placing together 14 species—all species of *Oreobates* plus all members of the *Eleutherodactylus discoidalis* group sensu Lynch (1989). Subsequently, one new species was described from northern Argentina (Vaira and Ferrari, 2008), an additional species—*Phrynopus pereger* (Lynch, 1975) (see also Lehr and Aguilar, 2006)—was added to the genus (Hedges et al., 2008a), and more recently a new species from the Atlantic Dry Forests has been described (Teixeira et al., 2012). At this point, it is interesting to look back in time and see that five years ago only six species where placed in *Oreobates* (Caramaschi and Canedo, 2006) and that we now recognize 23. But what is more important is that only three years after Padial's et al. (2008a) paper, a reanalysis of *Oreobates* was more than granted. Under this panorama, it is difficult to imagine how many more *Oreobates* will be discovered in the future, but surely it will be many.

ACKNOWLEDGMENTS

We are grateful to the following persons for the loan of specimens, support and/or space provided at their institutions: D. Frost and D. Kizirian, (AMNH), B. Clarke and M. Wilkinson (BM), J. Aparicio (CBF), R. Aguayo and A. Muñoz (CBG), W.E. Duellman, and L. Trueb (KU), J. Hanken and J. Rosado (MCZ), O. Aguilar and R. Orellana (MHNC), C. Aguilar (MUSM), B. Álvarez, J.E. González-Fernández and I. Rey (MNCN), L. González, A. Justiniano, R. Montaño, M. Suárez and R. Vespa (MNK), J. Pombal (MNRJ), 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 (ZFMK), and J.B. Rasmussen and M. Andersen (ZMUC). R. Márquez, M. Pérez, and L. González kindly processed and archived sound recordings at Fonozoo (MNCN). This work was partially funded by projects CGL2005-03156 and CGL2008-04164 of the Spanish Ministry of Science and Innovation (I. De la Riva, Principal Investigator). J.C.C.'s research was partially funded by J. Bustamante, from the GEMCare organization located in Bakersfield, California, and DOMUS Consultoria Ambiental. Research by J.M.G. is supported by the Centro para la Investigación de la Biodiversidad y el Cambio Climático, Universidad Tecnológica Indoamérica. The work of S.C.F. was financed by a Fulbright/Ministry of Education post-doctoral research contract. Padial's research is founded by a Gerstner Postdoctoral Fellowship at the American Museum of Natural History. Research and collecting permits in Peru, were provided by Ministerio del Ambiente (ex Ministerio de Agricultura), authorizations N° 035-2008-INRENA-IFFS-DCB, N° 014-2003-INRENA-IFFS-DCB, N° 447-2009-AG-DGFFS-DGEFFS. This article has benefited from criticisms made by Darrel Frost, Joern Koehler, and Willian E. Duellman.

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APPENDIX 1

Specimens Examined

Hypodactylus dolops (1 specimen): ECUADOR: Provincia Napo: Salto de Agua, 2.5 km NNE Río Reventador, Ecuador, 1660 m, KU 143505 (holotype). ***Hypodactylus elassodiscus*** (2 specimens): ECUADOR: Provincia Napo: Cuyuja, 2830 m, USNM 197668 (holotype), 167669 (paratype). ***Hypodactylus nigrovittatus*** (1 specimen): ECUADOR: Provincia Pastaza: near Mera, cerros de Abitagua, 1200 m above the sea level, NHRM 4998. ***Lynchius simmonsi*** (5 specimens): ECUADOR: Provincia Morona de Santiago: Río Piuntza, 1830 m, KU 147068 (holotype); Provincia de Zamora Chinchipe: Cordillera del Cóndor, Cóndor Mirador (03°18′25″ S, 78°23′36″ W, 1850 m), QCAZ 30829–30; Miazi Alto, 1300 m (04.25656°S, 78.62246°W), QCAZ 41639–40. ***Oreobates amarakaeri*** (3 specimens): PERU: Departamento Cusco: Río Nusinuscato, 685 m (13° 08′ 13.1″ S, 70° 51′ 05.8″ W), MHNC 6975 (holotype); Río Mabe, 1000 m, (13° 06′ 31.5″ S, 70° 54′ 56.0″ W), MHNC 7017 (paratype), MHNC 7049 (paratype). ***Oreobates ayacucho*** (3 specimens): PERU: Departamento Ayacucho: road between Punqui and Anco, 3 km before Anco, 3850 m (13.1038°S, 73.6983°W), MNCN 44484–5, MHNC 6840. ***Oreobates crepitans*** (3 specimens): BRAZIL: Mato Grosso: São Vicente, Cuiabá, MZUSP 85628 (holotype), MZUSP 73671 (allotype), MNRJ 33985 (paratype). ***Oreobates choristolemma*** (5 specimens): BOLIVIA: Departamento Cochabamba: "Old" Chapare road, 1300–1500 m, ZFMK 72569; Departamento La Paz: Provincia Sud Yungas, Boquerón, CBG 765–68. ***Oreobates cruralis*** (184 specimens): BOLIVIA: Departamento Beni: Areruta, CBG 1545–7; Asunción, Biosphere Reserve Pilón Lajas, MNK A 4074; Buena Vista, MZUM 66609–10; Huachi, MZUM 58987, 135343; Laguna Azul, Biosphere Reserve Pilón Lajas, MNK A 3975–76, 3979, 3985–87, 4003; Rurrenabaque, CBG 3667, MNCN 42558–9; San Luis Chico, MNK A 4027, 4030; Serranía del Pilón, Biosphere Reserve Pilón Lajas, MNK A 4182–83, 4209–13; Departamento Cochabamba: Bulo Bulo, TIPNIS, CBG 350, 380, 382–3, 393; Chaquisacha, 1300–1500 m, 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), CBG 308, MNK A 6617–19, MNCN 43018–9, ZFMK 72532; on Villa Tunari road, USNM 146577; Puerto Villaroel, CBG 1337; Río Grande, 1000 m, 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 Mosetenes 1580 m, MNCN 43155; Valle de Sajta, MNK A 3633, 1489; Villa Tunari, MNK A 1492; Departamento La Paz: Arroyo Pico Plancha, San José y Apolo, ANMI-Parque Nacional Madidi, MNK A 7180; Aserradero San Francisco, Ixiamas, CBG 1133; Boquerón, Biosphere Reserve Pilón Lajas, CBG 789–93; Camino a Bella Vista, Sud Yungas, MNK A 3792; Camino maderero El Chaval, Arroyo Mikai, Biosphere Reserve Pilón Lajas, MNK A 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, USNM 281100–30; road from Caranavi to Palos Blancos, ZFMK 80599; Serranía Tequeje, CBG 5104–7; Serranía del Pilón, Biosphere Reserve Pilón Lajas MNK A 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 W of San Buenaventura USNM 280617; Departamento Pando: Florida, Reserva Manuripi, MNK A 5086, 5122; Lago Bay, Reserva Manuripi, MNK A 6120–21; Departamento Santa Cruz: Buena Vista, USNM 118686; camino a BellaVista desde la carretera a Samaipata, MNCN 42557, 42977, MNK A 7171, ZFMK 71997; La Hoyada, Parque Nacional Amboró, MNK A 5577, ZFMK 72644; Mataracú, Parque Nacional Amboró, MNK A 3950, 3952, 3954, 3968; Santa Cruz de la Sierra, BM 1904.10.29.102–107; S of Cuevas, ZFMK 72644; Sara, MZUSP 119467; Víbora, CBG 3638. PERU: Departamento Madre de Dios: Colpa de Guacamayos, Zona Reservada Tambopata-Candamo, USNM 332436–37; Puerto Maldonado, 30 km SSW of Tambopata, USNM 284267, 343240, 342989–92; 15 km E of Puerto Maldonado, 200 m, KU 207749, 215461–62, 215479–80; Departamento Cusco: Río los Amigos, MHNC 3170, 3172, 3177, 4959, 4966. ***Oreobates discoidalis*** (114 specimens): ARGENTINA: Province Tucumán: El Indio, km 28 Tafí del Valle-Amaicha del Valle road, 960 m, KU 182815; Horco Molle, “13 km W of Tucumán,” Sierra de San Javier, ca. 1200 m, BM 1947.2.15.63–65 (syntypes), KU 154521–29; MCZ 35583, MZUSP 85542; 24 km W of Tucumán, KU 206434–38; without locality, MCZ 117097; Province Jujuy: Abra de las Cañas, Serranía de Calilegua, 1550 m, KU 182813–14; Arroyo Agua Negra, near border Salta-Jujuy, 10 km up to Monolito 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, MNK A 5582; Departamento Tarija: Bajada de la Escalera, Reserva Nacional Tariquía, CBG 4978–9; Cambarí, Reserva Nacional de Tariquía, CBG 4889–90; Chiquiacá MNK A 7262–3, MNCN 43133–35; Entre Ríos, MNK A 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, MNK A 7246–56, MNCN 43123, 43125–31, 43136–9; Serrania Aguarague, a 40 km de Yacuiba, CBG 1411–17; subida a Palo Marcado, Reserva Nacional Tariquía, CBG 4970; 12.3 km NW of Entre Ríos on the road to Tarija, 1900 M, MNK A 3877–97, UTA 45645, 45648–50, 45652, 45658–62. ***Oreobates gemcare*** (33 specimens): PERU: Departamento Cusco: Buenos Aires, 2400 m, KU 173231; Esperanza, Kosñipata Valley, 2700 m (13.1824°S, 71.6036°W), MHNC 4557, 4564–4567, 4583–4586 (paratype), MHNC 4601–4602 (paratype), MHNC 6687 (holotype), MNCN 43740–41 (paratype), MNCN 44230 (paratypes); Paucartambo, AMNH 153087; Pillahuata, between Puente Kosñipata and road, 2430 m asl, (13° 09′ 52″ S, 71° 35′ 46″ W), AMNH 11831 (paratype). ***Oreobates granulosus*** (26 specimens): PERU: Department Puno: Agualani, Carabaya, 9000 ft, BM 1905.5.31.14.20 (four specimens); Limbani, Carabaya, 9000 ft, BM 1905.5.31.21 (formerly 1904.10.26.94–99); Ollachea, 11 km (airline NNE of), 1800 m, USNM 299006–12; Santo Domingo, Carabaya, 1400–1500 m, MHNC 5328, 5335; Santo Domingo, Carabaya, 6000 ft (1800 m aprox.), BM 1947.2.15.72 (holotype); Santo Domingo, Carabaya, 6500 ft (2000 m aprox.), BM 1907.5.7.17–18; Juliaca (locality in error), AMNH 6060–2, 6064. ***Oreobates heterodactylus*** (10 specimens): BOLIVIA: Departamento Santa Cruz: Bella Boca, MNK A 6482; Cerro del Arco, Serranía de Santiago, MNK A 6356–7, 7175–6, MNCN 43055–6. BRAZIL: Mato Grosso: Gruta da Fazendinha, Cáceres, MNRJ 106 (holotype); Fazenda Santa Edwiges, MZUSP 71103–4. ***Oreobates ibischi*** (4 specimens): BOLIVIA: Departamento Santa Cruz: km 68.5 on Santa Cruz de la Sierra-Samaipata road, 750 m elevation, CBF 3341 (holotype); km 60 on Santa Cruz de la Sierra-Samaipata road, MNK A 6612, MNCN 42959; Samaipata, ZFMK 60402 (paratype). ***Oreobates lehri*** (32 specimens): PERU: Departamento Cusco: Apurimac River Valley, Camisea Natural Gas Pipeline, Wayrapata Camp, 2445 m asl, (12° 50′ 10″ S, 73° 29′ 43″ W), USNM 537848 (holotype), USNM 537846–57 (paratopotypes);

ca. 40 km from Vilcabamba, 2850 m (13°02′51.1″S, 072°55′29.4″W), MUSM 27616. ***Oreobates lundbergi*** (2 specimens): PERU: Departamento Pasco: from Auquimarca to Uchuerta, 2760 m, MTD 45902 (paratype); road Puagmaray Oxapampa km 77, 2550 m, MUSM 19321 (paratype). ***Oreobates machiguenga*** (1 specimen): PERU: Departamento Cusco: Maguireni (12°34′42″S/73°40′21″W), Río Kimbiri, Apurimac River Basin, MHNC 6809 (holotype). ***Oreobates madidi*** (6 specimens): BOLIVIA: Departamento La Paz: Arroyo Huacataya, Serranía Eslabón, Área Natural de Manejo Integrado Madidi, MNK A 7856 (holotype), 7197 (paratype), MNCN 42014–15 (paratypes); La Cascada, Biosphere Reserve Pilón Lajas, MNK A 4137–38 (paratypes). ***Oreobates pereger*** (40 specimens): PERU: Departamento Ayacucho: Provincia La Mar, Yanamonte (12°47′25,0″S, 74°00′02,4″W), 2600 m, MUSM 19982–19984, MTD 46807–09, FMNH 39747–65, 39768–70, 39773–78, 39780, 39782, 39837; Mitupucuru on Tambo-Valle del Apurimac path, KU 151908-09 (paratypes), KU 196595. ***Oreobates quixensis*** (69 specimens): BOLIVIA: Departamento Pando: Luz de América, Reserva Nacional de Vida Silvestre Manuripi-Heath, MNK A 6525; Mucden, 4591; Reserva Nacional de Vida Silvestre Manuripi-Heath, MNK A 3640–1, 6099; Reserva Nacional de Vida Silvestre Tahuamanu, NKA 4586–90; Río Negro, MNK A 6525–27, 6900; San Antonio, Reserva Nacional de Vida Silvestre Manuripi-Heath, MNK A 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 MCZ 19734–6; Provincia de Zamora: sourroundigs of Villano, 430 m, QCAZ 38670, 38693, 39215, 39217, 39244. PERU: Departamento Amazonas: MCZ 125896–7; Departamento Loreto: Arboretum de la UNAM, camino hacia Puerto Almendras, 103 m, MHNC 8805, 8809; Camino a Zungarococha y Arboreto de la Universidad de Iquitos, Camino a Puerto Almendras, 103 m, MHNC 8832; Pucaurquillo, Río Ampiyacu, 99 m, MHNC 8997; Río Ampiyacu, 92 m, MHNC 8918. ***Oreobates remotus*** (24 specimens): BRAZIL: Minas Gerais: Januária, Parque Nacional Cavernas do Peruaçu, 624 m, MZUSP 141708 (holotype), MZUSP 141709–724, MZUFV 5005–10 (paratypes); Rio Pandeiros, MZUSP 23306. ***Oreobates sanctaecrucis*** (13 specimens): BOLIVIA: Departamento Cochabamba: Chaquisacha, 1300–1500 m, Parque Nacional Carrasco, CBG 152–3; Diampampa, Parque Nacional Carrasco, CBG 634; Karahuasi, ZFMK 72647; Río Grande, 1000 m, Parque Nacional Carrasco, CBG 291–292; Departamento Santa Cruz: El Bibosi, Parque Nacional Amboró, MNK A 6697; El Chapé, Parque Nacional Amboró, 2060 m elevation, MNK A 1198 (holotype), 7158, MNCN 42010–13. ***Oreobates sanderi*** (19 specimens): BOLIVIA: Department La Paz: Arroyo Bilunto, Chunirumi Valley, Bilunto Mountains, Area 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, ca. 30 km north of Caranavi on the road from Caranavi to Yucumo, ZFMK 80600–1 (paratypes), MNK A 6563 (paratypes); road from Apolo to Sarayo, MNK A 6695–6 (paratypes). PERU: Departamento Puno: Abra de Maruncuna, 10 km SW of San Juán del Oro, 1650 m, KU 206101; Juliaca (locality in error), AMNH 6063. ***Oreobates saxatilis*** (14 specimens): PERU: Departamento Cusco: Río Kimbiri, 1000 m, MHNC 6775–77; Río Kimbiri, Comunidad Machiguenga Pomoreni, 1100 m, MNCN 44412, 44426–28; Departamento San Martín: Pongo de Shilcayo, about 4 km NNW of Tarapoto, 470 m, KU 212556 (holotype), MUSM 8431 (paratype); San Roque de Cumbasa, 609 m, MHNC 9200; 2 km al Este de Roque, 1138 m, MHNC 9202; 6 km S of Roque, on Río Sisa, Catarata de Pueblo Nuevo, 1086 mals, MHNC 9219–21. ***Oreobates zongoensis*** (1 specimen): BOLIVIA: Departamento La Paz: Valle de Zongo, 1250 m, CBF 2503 (holotype).

APPENDIX 2

Accession Numbers for 16S rRNA GenBank Sequences of Strabomantid Species Used as Outgroups

Adelophryne gutturosa	EU186679
Barycholos pulcher	EU186709
Barycholos ternetzi	DQ283094
Bryophryne cophites	EF493537
Hypodactylus brunneus	EF493357
Hypodactylus dolops	EF493394
Hypodactylus elassodiscus	EF493358
Hypodactylus peraccai	EF493710
Lynchius nebulanastes	EU186704
Lynchius parkeri	EU186705
Lynchius flavomaculatus	EU186667
Noblella lochites	EU186699
Phrynopus auriculatus	EF493708
Phrynopus barthlenae	AM039653
Phrynopus bracki	EF493709
Phrynopus bufoides	AM039645
Phrynopus heimorum	AM039635
Phrynopus horstpauli	AM039651
Phrynopus juninensis	AM039657
Phrynopus kauneorum	AM039655
Phrynopus pesantesi	AM039656
Phrynopus tautzorum	AM039652
Phrynopus tribulosus	EU186725
Pristimantis actites	EF493696
Pristimantis altamazonicus	EF493670
Pristimantis bipunctatus	EF493702
Pristimantis colomai	EF493354
Pristimantis condor	EF493701
Pristimantis conspicillatus	EF493529
Pristimantis cremnobates	EF493528
Pristimantis curtipes	EF493513
Pristimantis duellmani	AY326003
Pristimantis euphronides	EF493527
Pristimantis galdi	EU186670
Pristimantis leoni	EF493684
Pristimantis nyctophylax	EF493526
Pristimantis ockendeni	EF493519
Pristimantis reichlei	EF493707
Pristimantis rozei	EF493691
Pristimantis sagittulus	EF493705
Pristimantis stictogaster	EF493704
Pristimantis thymelensis	EF493516
Pristimantis unistrigatus	EF493387
Pristimantis urichi	EF493699
Pristimantis versicolor	EF493389
Pristimantis walkeri	EF493518
Psychrophrynella guillei	AY843720
Psychrophrynella iatamasi	AM039644
Psychrophrynella saltator	AM039642
Psychrophrynella usurpator	EF493714
Psychrophrynella wettsteini	EU186696
Strabomantis anomalus	EF493534
Strabomantis biporcatus	EU186691
Strabomantis bufoniformis	DQ283165
Strabomantis necerus	EF493535
Strabomantis sulcatus	EF493536
Yunganastes ahskapara	EU192233
Yunganastes bisignatus	EU192235
Yunganastes fraudator	FJ539065
Yunganastes mercedesae	FJ539066
Yunganastes pluvicanorus	EU192247

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