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Molecular phylogenetics, species diversity, and biogeography of the Andean lizards of the genus *Proctoporus* (Squamata: Gymnophthalmidae)

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ABSTRACT

The family Gymnophthalmidae comprises ca. 220 described species of Neotropical lizards distributed from southern Mexico to Argentina. It includes 36 genera, among them *Proctoporus*, which contains six currently recognized species occurring across the yungas forests and wet montane grasslands of the Amazonian versant of the Andes from central Peru to central Bolivia. Here, we investigate the phylogenetic relationships and species limits of *Proctoporus* and closely related taxa by analyzing 2121 base pairs of mitochondrial (12S, 16S, and ND4) and nuclear (c-mos) genes. Our taxon sampling of 92 terminals includes all currently recognized species of *Proctoporus* and 15 additional species representing the most closely related groups to the genus. Maximum parsimony, maximum likelihood and Bayesian phylogenetic analyses recovered a congruent, fully resolved, and strongly supported hypothesis of relationships that challenges previous phylogenetic hypotheses and classifications, and biogeographic scenarios. Our main results are: (i) discovery of a strongly supported clade that includes all species of *Proctoporus* and within which are nested the monotypic *Opipeuter xestus* (a genus that we consider a junior synonym of *Proctoporus*), and two species of *Euspondylus*, that are therefore transferred to *Proctoporus*; (ii) the paraphyly of *Proctoporus bolivianus* with respect to *P. subsolanus*, which is proposed as a junior synonym of *P. bolivianus*; (iii) the detection of seven divergent and reciprocally monophyletic lineages (five of them previously assigned to *P. bolivianus*) that are considered confirmed candidate species, which implies that more candidate species are awaiting formal description and naming than currently recognized species in the genus; (iv) rejection of the hypothesis that *Proctoporus* diversified following a south to north pattern parallel to the elevation of the Andes; (v) species diversity in *Proctoporus* is the result of in situ diversification through vicariance in the grasslands of the high Andes, with at least five dispersals contributing to montane forest species.

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1. Introduction

The family Gymnophthalmidae is an assemblage of 36 genera of highly diversified (roughly 220 species) Neotropical lizards that occur from southern Mexico to Argentina (Uetz, 2012). Within gymnophthalmids, the genus *Proctoporus* has received considerable attention during the last decade (Doan, 2003; Doan and Castoe, 2003, 2005; Doan et al., 2005). As currently defined, the genus *Proctoporus* comprises six species: *Proctoporus pachyurus* Tschudi, *Proctoporus bolivianus* Werner, *Proctoporus guentheri* Boettger, *Proctoporus sucullucu* Doan and Castoe, *Proctoporus unsaacae* Doan and Castoe, and *Proctoporus subsolanus* Doan, Castoe and Arizábal. They are medium-sized (snout-vent length 27–78 mm), semi-fossorial lizards that occur in yungas forests and wet montane grasslands, between 1000 and 4000 m, along the Amazonian versant of the Andes from central Peru to central Bolivia (Doan and Castoe, 2005; Doan et al., 2005; Uzzell, 1970).

After the synonymization of the genera *Riama* Gray, *Oreosaurus* Peters, and *Emphrassotis* OShaughnessy with *Proctoporus*, the genus *Proctoporus* included species distributed along the Andes from Venezuela to Bolivia, as well as Trinidad and Tobago (Doan and Castoe, 2003; Doan and Schargel, 2003; Kizirian, 1996; Uzzell, 1958, 1970). During the last decade, phylogenetic analyses conducted by Castoe et al. (2004) found *Proctoporus* to be polyphyletic. Following Castoe et al. (2004) and Doan and Castoe (2005) provided a monophyletic taxonomy by restricting *Proctoporus* to the

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P. pachyurus group (Uzzell, 1970), placing species from Ecuador, Colombia, Venezuela, and Trinidad and Tobago into the resurrected genus *Riama*, and naming a new genus (*Petracola*) to include members of the *Proctoporus ventrimaculatus* group.

Despite the important contribution of the above-mentioned studies, they present some limitations that need to be addressed in order to attain an accurate picture of the diversity and phylogenetic relationships of *Proctoporus*. Doan and Castoe (2003) found that *P. bolivianus* was composed of three different lineages, and named two of them as new species. Subsequently, Doan et al. (2005) described *P. subsolanus* from southern Peru and recognized and undescribed species from the same region (herein referred as *Proctoporus* sp. 3). The type specimens of two species (*P. bolivianus* and *P. guentheri*) are lost, and the accurate assignment of populations to their corresponding species based on molecular data would have required sampling their type localities. Moreover, several populations tentatively assigned to *P. bolivianus* by Uzzell (1970) have not yet been properly studied. These issues seem to be especially important given that *P. subsolanus* overlaps in range with what is now considered *P. bolivianus*. Indeed, as already noted by Uzzell (1970), and as can be observed in Doan and Castoe (2003), *P. bolivianus* presents a large morphological variation across its distributional range, which overlaps with that of other species in the genus. Additionally, several names are available for populations that might represent distinct species, such as *Oreosaurus* (*Proctoporus*) *lacertus* Stejneger from Middle Urubamba valley (Cusco, Peru), *Proctoporus longicaudatus* Andersson from Pelechuco (La Paz, Bolivia), and *Proctoporus obesus* Barbour and Noble from Ñusta Hispana (Cusco, Peru). All these forms were tentatively synonymized with *P. bolivianus* by Uzzell (1970) based on overlapping morphological characters in relatively small sample sizes.

The relationships of *Proctoporus* with its closer relatives within Gymnophthalmidae also need to be explored. A sister relationship of *Proctoporus* with *Euspondylus* and *Opipeuter* has been suggested by several authors (Chávez et al., 2011; Doan, 2003; Köhler and Lehr, 2004; Presch, 1980), but no phylogenetic analysis to date has addressed the relationships of all these genera, which renders their position within Gymnophthalmidae uncertain.

Recent extensive fieldwork in Peru and Bolivia allowed us to obtain 59 samples from 32 different localities of four recognized species of *Proctoporus*, including topotype material of *Proctoporus bolivianus* and synonymous taxa, as well as specimens of *Opipeuter xestus* and two species of *Euspondylus*. By combining our molecular data with sequences used by Castoe et al. (2004), Doan et al. (2005), and Pellegrino et al. (2001), we test the monophyly of *Proctoporus*, assess the phylogenetic position of *Opipeuter* and *Euspondylus* within Gymnophthalmidae, and evaluate species diversity within *Proctoporus*. Additionally, we use our phylogenetic hypothesis and distributional data to discuss the biogeography and diversification mode of *Proctoporus*.

2. Material and methods

2.1. Taxon sampling

Our study includes 215 sequences from 59 tissue samples produced for this study and 115 sequences from Castoe et al. (2004), Doan et al. (2005), and Pellegrino et al. (2001). The final data set contains 92 terminals listed in Table 1, including: six recognized species of *Proctoporus* [including samples from southern Peruvian populations previously studied and assigned to *P. bolivianus* by Doan and Castoe (2003), Doan et al. (2005), and Uzzell (1970)], *Opipeuter xestus, Euspondylus chasqui* Chávez, Siu-Ting, Duran and Venegas, and an undescribed species of *Euspondylus*.

Following previous phylogenetic studies of Gymnophthalmidae (Castoe et al., 2004; Pellegrino et al., 2001) we used *Alopoglossus atriventris* Duellman, *Placosoma cordylinum* Tschudi, *Placosoma glabellum* (Peters), *Neusticurus bicarinatus* (Linnaeus), *Neusticurus rudis* Boulenger, *Riama orcesi* (Kizirian), *Riama cashcaensis* (Kizirian and Coloma), *Riama colomaromani* (Kizirian), *Pholidobolus macbrydei* Montanucci, *Pholidobolus montium* (Peters), *Petracola ventrimaculatus* (Boulenger), *Cercosaura schreibersii* Wiegmann, *Cercosaura eigenmanni* (Griffin), *Potamites ecpleopus* (Cope) and *Potamites strangulatus* (Cope) as outgroups. *Alopoglossus atriventris* was used to root all trees.

2.2. DNA extraction, amplification, and sequencing

We collected tissue samples in the field and preserved them in 96° ethanol. Samples were deposited at the tissue and DNA collection of the Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain); corresponding voucher specimens are listed on Table 1. Total DNA was extracted from tissue samples using the Qiagen DNeasy extraction kit and protocol (Qiagen Inc., Hilden, Germany). Fragments of the mitochondrial NADH dehydrogenase subunit 4 (ND4), mitochondrial small subunit rRNA gene (12S), mitochondrial large subunit rRNA gene (16S), and the nuclear oocyte maturation factor gene (c-mos) genes were amplified by polymerase chain reaction (PCR) using the primers and protocols specified in Table 2.

Purified PCR products were sent to Macrogen Inc. (Seoul, Republic of Korea) for sequencing in both directions with the amplification primers. Raw sequence chromatographs for sequences generated in this study were edited using Sequencher 4.9 (Gene Codes Corp., 2009).

2.3. Molecular phylogenetics

DNA sequences of each marker were independently aligned in Mafft online version 6 (Katoh et al., 2005). Sequences of coding genes were aligned using the G-INS-i strategy, which assumes that the entire region can be aligned globally, while 12S and 16S sequences were aligned under the Q-INS-i strategy, which considers secondary structure of RNA (Katoh and Toh, 2008). We used three methods of phylogenetic inference: maximum parsimony (MP), maximum likelihood (ML), and Bayesian (BI), for the four independent gene partitions separately and for a combined dataset (see below).

Parsimony analyses were performed using TNTv.1.1 (Goloboff et al., 2008). Tree searches were performed with gaps coded as a fifth state, so that gaps contribute to the cost of the tree. Numerous search methods available in TNT were utilized to search tree space but the following approach was found to consistently recover trees with minimum lengths for our datasets. The implemented search was driven under new technology search (level 100). Default settings for sectorial searches (RSS and CSS) and tree fusing were used, with 20 replicates per repetition and the requirement that the global optimum be found 100 times. TBR branch swapping was performed on the resulting trees and a strict consensus was calculated. Bootstrap support (BSS) was calculated in TNT through 1000 pseudoreplicates consisting of 10 random-addition replicates using TBR branch swapping.

For parametric methods (ML and BI) we used the program Modeltest 3.7 (Posada and Crandall, 1998) combined with PAUP* 4.0b10 (Swofford, 2002) to select the model of sequence evolution for each marker under the Akaike Information Criterion (Akaike, 1974). For the protein coding genes (ND4 and c-mos) models were determined also for each codon position. We partitioned the dataset by gene and codon position.

Table 1
List of sequences used for this study with GenBank accession numbers by locus. Museum acronyms are: CBF (Colección Boliviana de Fauna), KU (University of Kansas Biodiversity Institute – Herpetology Collection), UTA (University of Texas at Arlington), AMNH (American Museum of Natural History – Herpetology Collection), MHNC (Museo de Historia Natural de la Universidad Nacional de San Antonio Abad, Cusco, Peru) and MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain). Sequences generated for this study are in boldface.

Species	Locality (ID No. in Fig. 2)	Coordinates	Museum number	MNCN DNA collection	ND4	c-mos	12S	16S
Alopoglossus atriventris	–	–	–		AF420908	AF420821	AF420695	AF420746
Cercosaura eigenmanni	–	–			AF420895	AF420828	AF420690	AF420728
Cercosaura schreibersii	–	–	–		AF420911	AF420817	AF420686	AF420749
Neusticurus bicarinatus	–	–	–		–	AF420816	AF420671	AF420708
Neusticurus rudis	–	–	–		AF420905	–	AF420689	AF420709
Petracola ventrimaculatus	–	–	KU219838		AY507894	AY507910	AY507863	AY507883
Pholidobolus macbrydei	–	–	KU218406		AY507886	AY507896	AY507848	AY507867
Pholidobolus montium	–	–	–		AF420884	AF420820	AF420701	AF420756
Placosoma cordylinum	–	–	–		AF420879	AF420823	AF420673	AF420734
Placosoma glabellum	–	–	–		AF420907	AF420833	AF420674	AF420742
Potamites ecpleopus	–	–	–		AF420890	AF420829	AF420656	AF420748
Potamites strangulatus	–	–	KU21677		AY507885	–	AY507847	AY507866
Riama cashcaensis	–	–	KU217205		AY507887	–	AY507852	AY507870
Riama colomaromani	–	–	KU217209		AY507888	AY507899	AY507853	AY507871
Riama orcesi	–	–	KU221772		AY507889	–	AY507855	AY507874
Proctoporus bolivianus	Peru:Puno:Sandia (9)	–	UTA R-52944		AY968814	–	AY968826	AY968833
Proctoporus bolivianus	Peru:Puno:Sandia (9)	–	UTA R-52946		AY968811	–	AY968822	AY968831
Proctoporus bolivianus	Peru:Puno:Between Cuyo Cuyo and Sandia (29)	14°26′05.5″S/69°31′38.3″W	MNCN43660	5203	JX436061	–	JX435931	**JX435989**
Proctoporus bolivianus	Peru:Puno:Between Cuyo Cuyo and Sandia (29)	14°26′05.5″S/69°31′38.3″W	MHCN5333	5204	JX436064	JX436033	JX435932	**JX435990**
Proctoporus bolivianus	Peru:Puno:Between Cuyo Cuyo and Sandia (29)	14°26′05.5″S/69°31′38.3″W	MHNC5334	5205	JX436062	–	JX435933	**JX435991**
Proctoporus bolivianus	Peru:Puno:Between Cuyo Cuyo and Quebrada Sayaco (29)	14°26′32.5″S/69°31′43.7″W	MHNC5348	5438	–	JX436034	JX435935	**JX435992**
Proctoporus bolivianus	Peru:Puno:Between Cuyo Cuyo and Quebrada Sayaco (29)	14°26′32.5″S/69°31′43.7″W	MNCN43662	5439	JX436063	JX436035	JX435934	**JX435993**
Proctoporus bolivianus	Peru:Puno:Patambuco (30)	14°23′24.6″S/69°35′44.0″W	MHNC5357	5452	JX436065	JX436036	JX435936	**JX435998**
Proctoporus bolivianus	Peru:Puno:Patambuco (30)	14°23′24.6″S/69°35′44.0″W	MNCN43663	5453	JX436066	JX436037	JX435937	**JX436000**
Proctoporus bolivianus	Peru:Puno:Patambuco (30)	14°23′24.6″S/69°35′44.0″W	MNCN43664	5454	–	JX436038	JX435938	**JX435999**
Proctoporus bolivianus	Bolivia:La Paz:Sorata Valley (31)	15°51′30.2″S/68°37′37.6″W	MNCN43678	5573	JX436067	JX436039	JX435939	–
Proctoporus bolivianus	Bolivia:La Paz:Sorata Valley (31)	15°51′30.2″S/68°37′37.6″W	–	8989	JX436071	JX436040	JX435940	**JX435994**
Proctoporus bolivianus	Bolivia:La Paz:Sorata Valley (31)	15°51′30.2″S/68°37′37.6″W	–	8990	JX436070	JX436041	JX435941	**JX435995**
Proctoporus bolivianus	Bolivia:La Paz:Sorata Valley (31)	15°51′30.2″S/68°37′37.6″W	–	8991	JX436068	JX436042	JX435942	**JX435996**
Proctoporus bolivianus	Bolivia:La Paz:Sorata Valley (31)	15°51′30.2″S/68°37′37.6″W	MNCN43679	8992	JX436069	JX436043	JX435943	**JX435997**
Proctoporus bolivianus Ca1	Peru:Puno:Laracani (16)	–	UTA R-52945		AY968813	–	AY968825	AY968832
Proctoporus bolivianus Ca1	Peru:Puno:Between Trapiche and Sina (32)	14°30′20.0″S/69°16′57.0″W	MHNC5322	5180	–	JX436045	**JX435945**	**JX435988**
Proctoporus bolivianus Ca1	Peru:Puno:Between Cuyo and Quebrada Sayaco (29)	14°26′32.5″S/69°31′43.7″W	MHNC5346	5436	JX436099	–	JX435944	–
Proctoporus bolivianus Ca2	Bolivia:Santa Cruz:Amboró (1)	–	AMNH R-150695		AY225175	–	AY507851	AY968828
Proctoporus bolivianus Ca3	Peru:Puno:Between Huancasarani and Limbani (22)	14°10′29.4″S/69°41′36.1″W	MNCN43666	5462	JX436072	JX436008	JX435922	**JX435957**
Proctoporus bolivianus Ca3	Peru:Puno:Between Huancasarani and Limbani (22)	14°10′29.4″S/69°41′36.1″W	MHNC5359	5463	JX436074	JX436009	JX435923	**JX435958**
Proctoporus bolivianus Ca3	Peru:Puno:Between Huancasarani and Limbani (22)	14°10′29.4″S/69°41′36.1″W	MHNC6360	5464	JX436075	JX436010	JX435924	**JX435959**
Proctoporus bolivianus Ca3	Peru:Puno:Between Huancasarani and Limbani (22)	14°10′29.4″S/69°41′36.1″W	MHNC5361	5465	JX436076	–	JX435925	**JX435960**
Proctoporus bolivianus Ca3	Peru:Puno:Between Ollachea and Corani (23)	13°53′18.8″S/70°30′37.0″W	MNCN43668	5562	JX436089	JX436014	JX435911	**JX435962**
Proctoporus bolivianus Ca3	Peru:Puno:Between Ollachea and Corani (23)	13°53′18.8″S/70°30′37.0″W	MHNC5417	5563	JX436088	JX436015	JX435916	**JX435963**
Proctoporus bolivianus Ca3	Peru:Puno:Between Ollachea and Corani (23)	13°53′18.8″S/70°30′37.0″W	MHNC5421	5569	JX436087	–	JX435917	**JX435964**
Proctoporus bolivianus Ca3	Peru:Puno:Between Ollachea and Corani (23)	13°53′18.8″S/70°30′37.0″W	MNCN43669	5570	JX436090	JX436031	JX435918	**JX435965**
Proctoporus bolivianus Ca3	Peru:Puno:Between Usicayos and Quetapalo (24)	14°07′21.1″S/70°57′06.7″W	MNCN44222	20651	JX436077	–	JX435919	**JX435985**
Proctoporus bolivianus Ca3	Peru:Puno:Between Usicayos and Quetapalo (24)	14°07′21.1″S/70°57′06.7″W	MNCN44223	20652	–	JX436020	JX435926	**JX435986**
Proctoporus bolivianus Ca3	Peru:Puno:Between Usicayos and Quetapalo (24)	14°07′21.1″S/70°57′06.7″W	MNCN44224	20653	JX436078	JX436021	JX435920	**JX435987**
Proctoporus bolivianus Ca3	Peru:Puno:Between Huancasarani and Limbani (22)	14°10′29.4″S/69°41′36.1″W	MHNC5651	21323	JX436073	–	JX435921	**JX435961**
Proctoporus bolivianus Ca3	Peru:Cusco:Kosñipata Valley (25)	13°36′10.4″S/70°57′15.3″W	MHNC4600	21343	JX436080	JX436025	JX435928	**JX435974**
Proctoporus bolivianus Ca3	Peru:Cusco:Kosñipata Valley (25)	13°36′10.4″S/70°57′15.3″W	MHNC4661	21345	JX436081	JX436027	JX435929	**JX435975**
Proctoporus bolivianus Ca3	Peru:Cusco:Kosñipata Valley (25)	13°36′10.4″S/70°57′15.3″W	MHNC4629	21346	JX436082	–	JX435930	**JX435976**
Proctoporus bolivianus Ca3	Peru:Cusco:Kosñipata Valley (25)	13°36′10.4″S/70°57′15.3″W	MHNC6005	21318	JX436079	JX436049	JX435927	**JX435966**
Proctoporus bolivianus Ca4	Peru:Puno:Tambillo (21)	13°52′40.9″S/70°12′57.2″W	MHNC5428	5580	JX436083	JX436016	JX435912	**JX435979**
Proctoporus bolivianus Ca4	Peru:Puno:Tambillo (21)	13°52′40.9″S/70°12′57.2″W	MNCN43675	5581	JX436084	JX436017	JX435913	**JX435980**
Proctoporus bolivianus Ca4	Peru:Puno:Tambillo (21)	13°52′40.9″S/70°12′57.2″W	MNCN43676	5582	JX436085	JX436018	JX435914	**JX435981**

(*continued on next page*)

Table 1 (*continued*)

Species	Locality (ID No. in Fig. 2)	Coordinates	Museum number	MNCN DNA collection	ND4	c-mos	12S	16S
Proctoporus bolivianus Ca4	Peru:Puno:Tambillo (21)	13°52′40.9″S/70°12′57.2″W	MHNC5429	5583	JX436086	JX436019	JX435915	**JX435982**
Proctoporus bolivianus Ca5	Peru:Cusco:Between Marcapata and Tambopampa (19)	13°35′00.4″S/71°02′05.1″W	MNCN43670	5475	–	JX436032	JX435906	**JX435967**
Proctoporus bolivianus Ca5	Peru:Cusco:Between Marcapata and Tambopampa (19)	13°35′00.4″S/71°02′05.1″W	MHNC5367	5477	JX436091	JX436011	JX435907	**JX435978**
Proctoporus bolivianus Ca5	Peru:Cusco:Between Marcapata and Tambopampa (19)	13°35′00.4″S/71°02′05.1″W	MHCN43671	5478	–	JX436012	JX435910	**JX435968**
Proctoporus bolivianus Ca5	Peru:Cusco:Between Marcapata and Tambopampa (19)	13°35′00.4″S/71°02′05.1″W	MHCN5370	5484	JX436092	–	JX435909	**JX435970**
Proctoporus bolivianus Ca5	Peru:Cusco:Between Marcapata and Tambopampa (19)	13°35′00.4″S/71°02′05.1″W	MHCN5371	5485	JX436093	JX436013	JX435908	**JX435969**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MNCN44216	20608	JX436096	JX436022	JX435900	**JX435972**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MNCN44217	20609	JX436094	–	JX435905	**JX435971**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MNCN44218	20610	–	JX436023	JX435903	**JX435973**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MHNC4750	20614	JX436098	JX436046	JX435901	**JX435984**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MHNC4751	20615	JX436097	JX436048	JX435904	**JX435977**
Proctoporus bolivianus Ca5	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MNCN4221	20613	JX436095	JX436047	JX435902	**JX435983**
Proctoporus bolivianus Ca6	Peru:Cusco:Canchayoc (2)	–	UTA R-51484		AY22518	–	AY968820	AY968827
Proctoporus bolivianus Ca6	Peru:Cusco:Carrizales (3)	–	UTA R-51487		AY225180	AY507897	AY507850	AY507869
Proctoporus bolivianus Ca6	Peru:Cusco:Piscacucho (4)	–	UTA R-51506		AY225175	AY507898	AY507851	AY507869
Proctoporus chasqui	Peru:Ayacucho:Between Abra Tapuna and San Francisco (26)	13°01′59.7″S/73°40′46″W	MNCN6771	23140	JX436051	**JX436003**	JX435887	**JX435946**
Proctoporus chasqui	Peru:Ayacucho:Between Abra Tapuna and San Francisco (26)	13°01′59.7″S/73°40′46″W	MNCN44407	23141	JX436052	JX436004	JX435888	**JX435947**
Proctoporus chasqui	Peru:Ayacucho:Between Abra Tapuna and San Francisco (26)	13°01′59.7″S/73°40′46″W	MNCN44408	23142	JX436053	JX436005	JX435889	**JX435948**
Proctoporus guentheri	Peru:Cusco:Chocalloc (5)	–	UTA R-51515		AY225185	AY507900	AY507849	AY507872
Proctoporus guentheri	Peru:Cusco:Machu Picchu (6)	–	UTA R-51517		AY225169	AY507901	AY507854	AY507873
Proctoporus pachyurus	Peru:Cusco:Marcapata Valley (20)	13°36′10.4″S/70°57′15.3″W	MHNC11439	21335	JX436056	JX436050	JX435893	**JX435950**
Proctoporus pachyurus	Peru:Cusco:Kosñipata Valley (25)	13°10′56.5″S/71°36′13″W	MHCNC4599	21342	JX436055	JX436024	JX435891	**JX435952**
Proctoporus pachyurus	Peru:Cusco:Kosñipata Valley (25)	13°10′56.5″S/71°36′13″W	MHNC4689	21344	JX436057	JX436026	JX435892	**JX435951**
Proctoporus pachyurus	Peru:Junín:Muruhuay (7)	–	UTA R-52949		AY968816	–	AY968824	AY968834
Proctoporus pachyurus	Peru:Junín:Palca (8)	–	MHNC TMD1203		AY968815	–	AY968823	AY968829
Proctoporus sp.	Peru:Cusco:Kimbiri River (27)	12°34′S/73°39′W	MHNC6834	23305	JX436054	JX436006	JX435890	**JX435949**
Proctoporus sucullucu	Peru:Ayacucho:Between Punqui and Anco (28)	13°06′13.7″S/73°41′53.7″W	MNCN44474	23325	–	JX436028	JX435894	**JX435953**
Proctoporus sucullucu	Peru:Ayacucho:Between Punqui and Anco (28)	13°06′13.7″S/73°41′53.7″W	MNCN44475	23326	JX436058	JX436029	JX435895	**JX435954**
Proctoporus sucullucu	Peru:Ayacucho:Between Punqui and Anco (28)	13°06′13.7″S/73°41′53.7″W	MNCN44476	23327	JX436060	JX436030	JX435897	**JX435955**
Proctoporus sucullucu	Peru:Ayacucho:Between Punqui and Anco (28)	13°06′13.7″S/73°41′53.7″W	MNCN44478	23328	JX436059	JX436044	JX435896	**JX435956**
Proctoporus sucullucu	Peru:Apurımac:Abancay (10)	–	UTA R-52950		AY968817	–	–	AY968830
Proctoporus sucullucu	Peru: Cusco:Kusilluchayoc (11)	–	UTA R-51478		AY225171	AY507903	AY507857	AY507878
Proctoporus sucullucu	Peru:Cusco:Piscacucho (12)	–	UTA R-51496		AY225177	AY507904	AY507858	AY507879
Proctoporus unsaacae	Peru:Cusco:Pisac (13)	–	UTA R-51475		AY225174	–	AY968819	AY507869
Proctoporus unsaacae	Peru:Cusco:Pisac (13)	–	UTA R-51479		AY225172	–	AY968818	–
Proctoporus unsaacae	Peru:Cusco:Quellouno (14)	–	UTA R-51488		AY225186	AY507908	AY507859	AY507882
Proctoporus unsaacae	Peru:Cusco:Saqsayhuaman (15)	–	UTA R-51477		AY225170	AY507909	AY507860	AY507881
Proctoporus xestus	Bolivia:Cochabamba:Cochabamba (17)	–	–	6160	JX436101	–	JX435898	**JX436002**
Proctoporus xestus	Bolivia:La Paz:Between Lambate and Totoral (18)	–	–	2425	JX436100	JX436007	JX435899	**JX436001**

Table 2
Genes and primers used in this study.

Gene	Primers (forward/reverse)	Source	Conditions
ND4	ND4/LEU	Arévalo et al. (1994)	94 °C/3 min; 35 × (94 °C/45s, 50 °C/45 s, 72 °C/1 min); 72 °C/6 min
12S	12SA4 L/12SB-H	Hillis et al. (1996)	95 °C/15 s; 35 × (95 °C/30 s, 50 °C/30 s, 72 °C/1 min); 72 °C/10 min
16S	16Sar-5′/16Sbr-3′	Hillis et al. (1996)	95 °C/15 s; 35 × (95 °C/30 s, 50 °C/30 s, 72 °C/1 min); 72 °C/10 min
c-mos	G73/G74	Pellegrino et al. (2001) and Saint et al. (1998)	94 °C/2 min; 35 × (94 °C/1 min, 56 °C/45 s, 72 °C/1 min); 72 °C/7 min

Maximum likelihood analyses were performed in Garli 2.0 (Zwickl, 2006; available at http://www.nescent.org/informatics/download.php?software_id=4) under default parameters. We did a total of 100 independent searches to reduce the probability of inferring a suboptimal likelihood solution. Node support was assessed by 1000 bootstrap pseudoreplicates.

For Bayesian phylogenetic analyses (Rannala and Yang, 1996), we used MrBayes 3.2.1 (Ronquist and Huelsenbeck, 2003). Eight Monte Carlo Markov chains (MCMCs) with default heating parameters were run for 20 million generations and with sampling intervals of 1000 generations. We determined the "burn-in" by examining the log likelihood (lnL) plots using the program Tracer version 1.3 (Rambaut and Drummond, 2003). To assess whether the MCMC reached stationarity we checked that the standard deviation of split frequencies was <0.01. After verifying stationarity, a 50% majority rule consensus tree and Bayesian posterior clade probabilities (BPPs) were inferred from the remaining (post-"burn-in") trees.

We interpreted BSS $\geqslant$ 70 and BPP $\geqslant$ 0.95 as indicating strong support (Hillis and Bull, 1993; Alfaro et al., 2003; Erixon et al., 2003). Intraspecific and interspecific sequence variation of concatenated mtDNA was assessed with uncorrected proportional distances (p-distances) calculated in PAUP* 4.0b10 (Swofford, 2002).

Divergent lineages considered putative new species are referred to as candidate species following the scheme developed by Padial et al. (2010): the binomial species name of the closely related species is followed in squire brackets by the abbreviation "Ca" and a numerical code (GenBank number, sequence, collection specimen, etc.) referring to the voucher of the particular candidate species, and terminating with the author name and year of publication of the article in which the lineage was first discovered.

2.4. Dispersal-vicariance analyses

Potential biogeographical events (vicariance, dispersal, and extinction) that shaped species diversity within *Proctoporus* were inferred by optimizing ancestral areas on our phylogenetic hypothesis considering the distributional data. We used two methods: Maximum parsimony reconstructions (MPRs) and dispersal-vicariance (DIVA) analysis (Ronquist, 1997). MPRs were performed in Mesquite v2.6 (Maddison and Maddison, 2009) with states unordered. DIVA optimizes the ancestral distribution areas onto a fully resolved phylogeny by minimizing the number of duplications and extinctions required to explain the distribution of the terminals. As opposed to cladistic biogeography, it does not assume a hierarchical organization of the areas under study (Ronquist, 1997). However, it becomes more ambiguous towards the root, inferring wide ancestral distributions, a problem that can be addressed by constraining the maximum number of ancestral areas (Ronquist, 1997). Because we obtained congruent species relationships among methods we did not need to address phylogenetic uncertainty with respect to optimization methods. We used DIVA as implemented in RASP v2.0b. Biogeographic reconstructions were simultaneously inferred (after trimming all outgroups but *Potamites* and removing branch lengths) with the maximum upper bound to tree length of the optimal reconstruction (Bound = 32767). Because the maximum number of areas occupied by any species in our tree is two, we constrained the maximum number of ancestral areas inferred for a node to that value.

We recognize three main ecoregions in the distribution area of *Proctoporus* and its sister group (*Potamites*, see below): lowland forests, yungas (montane forests) and wet montane grasslands. also recognized these areas, but provided a more fine-grained classification of all three areas. The yungas, or montane forest of the eastern versant of the Andes, comprise an area from ca. 500 to 2700–3000 m along the Andean hills, and constitute the transition zone between the warm Amazonian lowland forests (from ca. 50 to 500 m) and the cold grasslands (paramo and puna) that irregularly appear above 2700–3500 m depending of local conditions and latitude (see Olson et al. (2001) for a more detailed description of the ecoregions in the area). The ecoregional and altitudinal distribution for each ingroup species is detailed in Table 4. Both species of *Potamites* in the sister group inhabit both the Andean hills and the adjacent Amazonian lowland forests (Chávez and Vásquez, 2012; Doan and Castoe, 2005). To construct GIS-referenced distribution maps of all species we used ArcMap v.9.3.

3. Results

3.1. Phylogenetic analysis

The combined dataset included 92 terminals and 2115 aligned characters, of which 1141 were constant, 248 were parsimony uninformative, and 726 were parsimony informative (Data deposited in the Dryad Repository: doi:10.5061/dryad.364j2). Character diagnostics for the individual genes and the models of sequence evolution for each partition are included in Table 3.

Inferred trees for each locus under the three optimality criteria were either topologically similar (16S, 12S, ND4), or unresolved for many nodes (c-mos). No well-supported conflicting topologies were recovered. For the combined data set, all optimization methods produced almost identical results and no strongly supported conflicting topologies were recovered (Fig. 1). The MP search recovered 152 most parsimonious trees (L = 4591, consistency index = 0.492, retention index = 0.607). Relationships among equally short trees are stable among species (sensu this work) only varying on the branching pattern of specimens within species. For the Bayesian analyses, stationarity was always reached after 700,000 generations (in all partitions), and the majority consensus trees were obtained from the 13,000 trees remaining after burn-in. The maximum likelihood analysis recovered one tree with ln likelihood = −22619.61. The ML topology is shown in Fig. 1 with support values for MP, ML, and BI analyses.

All analyses recovered with strong support the monophyly of a clade formed by all *Proctoporus* species, with the genera *Opipeuter* and two species of *Euspondylus* deeply nested within it (Clade A: Fig. 1). Within *Proctoporus*, the first two splits (clades B and C) are recovered with strong support. Clade B contains topotypic samples of *P. bolivianus*, along with topotypic *P. subsolanus* from Sandia and a divergent lineage from Laracani (Puno, Peru) referred to as *Proctoporus* sp. 3 by Doan et al. (2005), and which is also considered a candidate species herein (see below).

Clade C contains five subclades including all other nominal species of *Proctoporus* (*P. pachyurus*, *P. sucullucu*, *P. unsaacae*, *P. guen-*

Table 3
Characteristics of each gene and model of nucleotide substitution for the partitions used in the parametric phylogenetic analyses.

Gene	Number of Characters	Constant	Parsimony uninformative	Parsimony informative	Partition	Selected model
12S	404	224	43	137	12S	GTR + I + G
16S	449	286	42	121	16S	GTR + I + G
ND4	860	354	97	409	Codon	GTR + I + G for 1st, HKY + I + G for 2nd and GTR + G for 3rd
c-mos	402	277	66	59	Codon	GTR + I + G for 1st, HKI for 2nd and HKI + G for 3rd

Table 4
Distribution by habitat and elevation (meters above sea level) for species of *Proctoporus* sampled in this study.

Species	Habitat	Elevation
1. *P. bolivianus*	Yungas, Wet Montane Gransslads	2100–3743
2. *P. bolivianus* Ca1	Wet Montane Gransslads	3105–3500
3. *P. bolivianus* Ca2	Yungas	1800
4. *P. bolivianus* Ca3	Wet Montane Grasslands	2700–3600
5. *P. bolivianus* Ca4	Wet Montane Grasslads	3800
6. *P. bolivianus* Ca5	Wet Montane Grasslands	2700–3850
7. *P. bolivianus* Ca6	Wet Montane Grasslands	3100–3500
8. *P. chasqui*	Yungas, Wet Montane Gransslads	1850–2780
9. *P. guentheri*	Yungas	1000–2000
10. *P. pachyurus*	Wet Montane Grasslands	2770–3800
11. *P. sucullucu*	Wet Montane Grasslands	3000–3300
12. *P. unsaacae*	Wet Montane Grasslands	3152–3600
13. *P. xestus*	Yungas, Wet Montane Gransslads	1000–2900
14. *Proctoporus* sp.	Yungas	1131

theri, and purported *P. bolivianus*), along with *Opipeuter xestus*, *Euspondylus chasqui*, and *Euspondylus* sp. Clade D includes *P. sucullucu* as sister taxon to *P. pachyurus* and *Euspondylus*. Clade E contains *Opipeuter xestus*, which is basal to Clade F. The latter contains a specimen from Santa Cruz (Bolivia), identified as *P. bolivianus* by Doan et al. (2005), and which we consider an undescribed species (see below), plus clades G and H. Clade G includes *P. guentheri* and *P. unsaacae*. Clade H includes four divergent lineages from different populations of Cusco and Puno in southern Peru, traditionally identified as *P. bolivianus* (Doan and Castoe, 2003; Doan et al., 2005; Uzzell, 1970), and that we consider undescribed species (see below).

3.2. Genetic divergences

Comparison of the *p*-distances of the mitochondrial dataset showed marked genetic differentiation among all recognized species of *Proctoporus* (Table 5). Comparatively, the lowest divergences are shown between the species pair *Euspondylus chasqui*-*Euspondylus* sp. (2.7–2.8%). In some cases intraspecific divergence values for some species pairs are similar or even overlap with inter-lineage divergence values for other species pairs. Thus, genetic divergences among populations of *P. pachyurus* (0.6–6.4%), and *P. unsaacae* (0.5–7.1%) have larger values than divergence between *E. chasqui*-*Euspondylus* sp. or between the candidate species *Proctoporus bolivianus* ca3, *Proctoporus bolivianus* ca4, and *Proctoporus bolivianus* ca5 (Table 5).

3.3. Biogeography

Amongst 14 species of *Proctoporus* included in our analysis, eight are exclusive of high altitude montane grasslands, three species occurs in grasslands and adjacent yungas forests, and the remaining three dwell exclusively in yungas forests. MPRs and DIVA resulted in an optimal solution requiring a minimum of five dispersals between different areas (Fig. 3). The main differences between MPRs and DIVA are that the latter infers up to four ancestors with wide distributions (yungas + montane grasslands) and that one of the alternative solutions of DIVA implies a dispersal from yungas to montane grasslands (MCRA of *P. chasqui*-*P.* sp.). Both species of *Potamites* are polymorphic for yungas and lowland forests, and the distribution of the common ancestor with *Proctoporus* is unresolved, with a broad distribution involving either Amazonian lowlands plus grasslands, Amazonian lowland plus yungas, or even all the three areas. Therefore, a unique origin of *Proctoporus* in grasslands seems to be supported by data at hand, but the distribution of the common ancestor with other gymnophtalmids remains unknown.

4. Discussion

4.1. Phylogeny and taxonomic implications

According to our results, *Potamites* is the sister group of *Proctoporus* with maximum support values for all methods (Fig. 1). This result is not congruent with previous hypotheses of relationships within the family Gymnophthalmidae that recovered the genus *Petracola* as sister to *Proctoporus* (Castoe et al., 2004; Doan and Castoe, 2005). In our analyses *Petracola* is recovered as sister taxon of the genus *Cercosaura*, although with moderate support (Fig. 1). Our phylogenetic hypothesis received maximum support in all methods for all basal splits; however, our outgroup sampling is limited relative to the species diversity of gymnophthalmids and we interpret our results with caution. Nonetheless, our results provide novel and strongly supported relationships among gymnophthalmids, which should be tested in future studies.

The monophyly of *Proctoporus* including the monotypic genus *Opipeuter* and two species of *Euspondylus* is fully supported. The genus *Opipeuter* was described by Uzzell (1969) on the basis of one specimen collected in Incachaca (Cochabamba, Bolivia). Since its original description this genus has been considered as closely related to *Proctoporus* and *Euspondylus* (Köhler and Lehr, 2004; Presch, 1980; Uzzell, 1969). *Proctoporus* and *Opipeuter* have been distinguished by the presence of prefrontal scales in *Opipeuter* and absence in *Proctoporus*, but this character has been demonstrated to be highly variable within members of the family Gymnophthalmidae (Köhler and Lehr, 2004). Indeed, prefrontal scales are present in both *O. xestus* and the two species of *Euspondylus* that are nested within *Proctoporus* in our analyses, proving the highly homoplastic condition of this character state. *Proctoporus* species and *O. xestus* also share the condition of a transparent disc in the lower eyelid, a character that nonetheless appears in *Potamites* and other Gymnophtalmids (Doan and Castoe, 2005), being thus either homoplastic or symplesiomorphic. Given the results of this study, and the fact that the genus *Proctoporus* was described before *Opipeuter* we consider *Opipeuter* to be a junior synonym of *Proctoporus* and, consequently, we propose *Proctoporus xestus* (Uzzell, 1969) as a new combination, which extends the distribution of the genus *Proctoporus* to northern Argentina (Laurent et al., 1979).

The genus *Euspondylus* was described by Tschudi (1845). This ill-defined genus (Kok and Rivas, 2011; Tschudi, 1845) was also

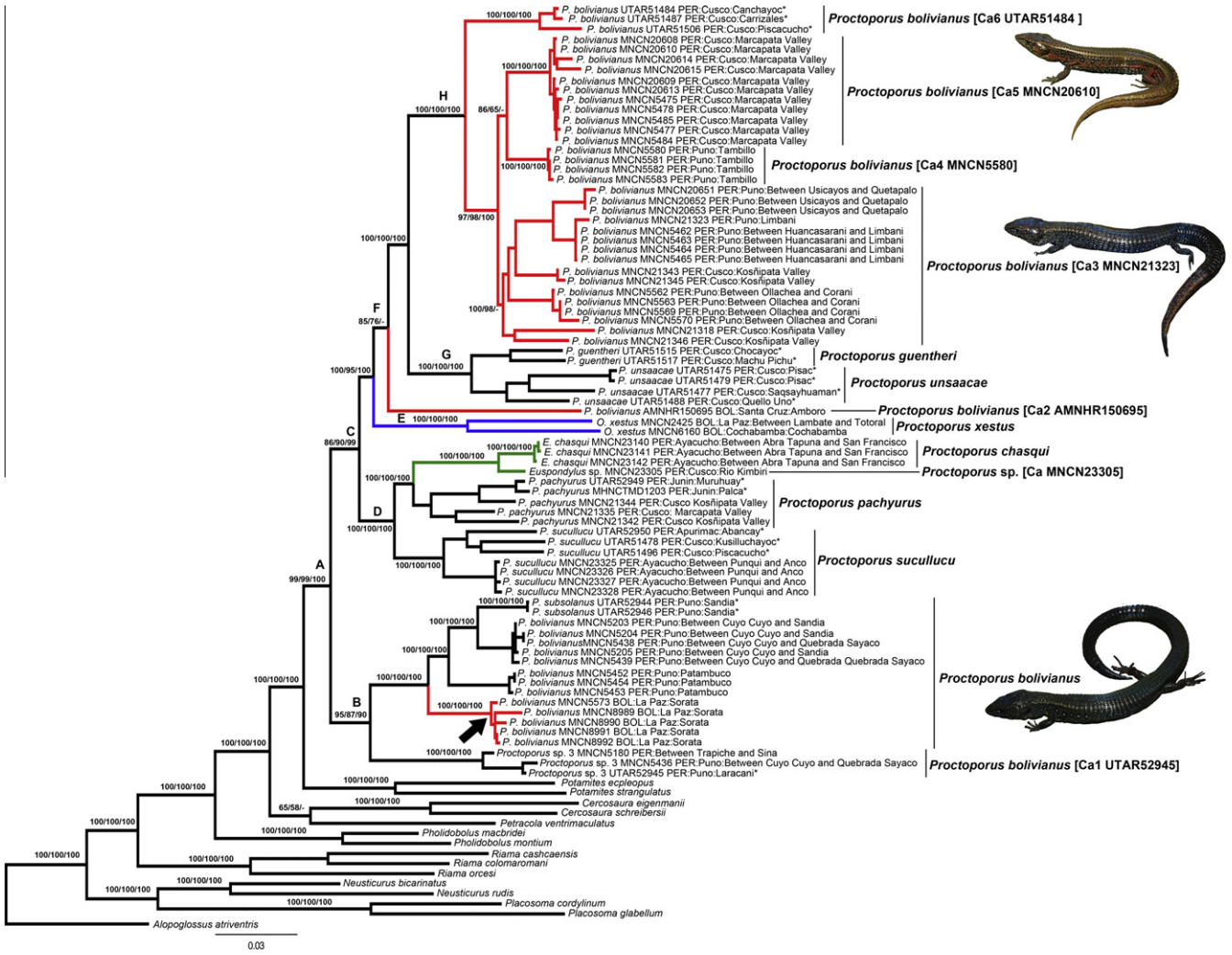

Fig. 1. Maximum likelihood tree of *Proctoporus* and allies based on 2121 bp of combined mitochondrial (ND4, 12S and 16S) and nuclear (c-mos) gene sequences. Values above nodes represent maximum likelihood and maximum parsimony bootstrap values, and Bayesian posterior clade probabilities. Scientific names on terminals reflect the taxonomy in use previous to this work and are followed by tissue or voucher collection code and locality (BOL = Bolivia, PER = Peru). Asterisks denote sequences gathered from GenBank. Black vertical lines delimit the taxonomy proposed in this work. Red branches correspond to populations assigned to *P. bolivianus* by Doan and Castoe (2003), Doan et al. (2005), and Uzzell (1970). The arrow indicates samples from the type locality of *P. bolivianus*. Blue branches correspond to samples of *Opipeuter xestus* and green to species of *Euspondylus*.

purported to be distinguished from *Proctoporus* by the presence of prefrontal scales (Kizirian, 1996; Köhler and Lehr, 2004; Peters and Donoso-Barros, 1970). As mentioned above, this distinction does not hold. Currently, 13 species are assigned to *Euspondylus*, which are distributed along the Tepuis of the Guianan shield and the Andes, between Venezuela and southeastern Peru (Chávez et al., 2011; Köhler, 2003; Köhler and Lehr, 2004; Mijares-Urrutia et al., 2001). Five members of *Euspondylus* (*E. acuirostris* Peters, *E. auyanensis* Myers, Rivas and Jadin, *E. guentheri* ÓShaughnessy, *E. maculatus* Tschudi and *E. monsfumus* Urrutia) are found in Colombia, Ecuador, Venezuela, as well as in northern Peru. These species seem to differ greatly from remaining Peruvian *Euspondylus*. They are "long-snouted" forms that have been suggested to be related to the genus *Anadia* (Mijares-Urrutia et al., 2001; Montero et al., 2002; Oftedal, 1974; Uzzell, 1973).

The eight Peruvian species of *Euspondylus* [*E. caideni* Köhler, *E. chasqui* Chávez, Siu-Ting, Durán and Venegas, *E. josyi* Köhler, *E. nellycarrillae* Köhler and Lehr, *E. oreades* Chávez, Siu-Ting, Durán and Venegas, *E. rahmi* (De Grijs), *E. simonsii* Boulenger and *E. spinalis* (Boulenger)] are found along central and southern Peru, overlapping with the distribution of *Proctoporus*. Furthermore, species of *Proctoporus* and Peruvian *Euspondylus* share several derived features including the presence of an undivided palpebral eye disc (Chávez et al., 2011; Köhler and Lehr, 2004).

Although our results support a clade with *Euspondylus* and *Opipeuter* nested within the diversity of *Proctoporus* and our study constitutes the first phylogenetic test of the relationships and monophyly of *Euspondylus* and *Opipeuter*, we prefer to be cautious and consider that there is not enough evidence to place all species (or even the eight Peruvian species) of *Euspondylus* within *Proctoporus*. Accordingly, we assign *Euspondylus chasqui* from Ayacucho to *Proctoporus* and propose the new combination *Proctoporus chasqui* (Chávez, Siu-Ting, Durán and Venegas, 2011). The second species of *Euspondylus* included in this study, referred herein to as *Euspondylus* sp. is sister to *E. chasqui*. It was collected at Río Kimbiri, Cusco, Peru and its genetic distance from *P. chasqui* is moderate (2.7–2.8%, Table 5). Despite the lower divergence between these lineages in comparison with other species of *Proctoporus* (Table 5), we found that *Euspondylus* sp. and *P. chasqui* differ both in morphology and distribution (the former inhabiting lower yungas forest at ca. 1000 m.a.s.l, and the later inhabiting transitional areas between yungas forest and montane grasslands at ca. 2780 m). Therefore,

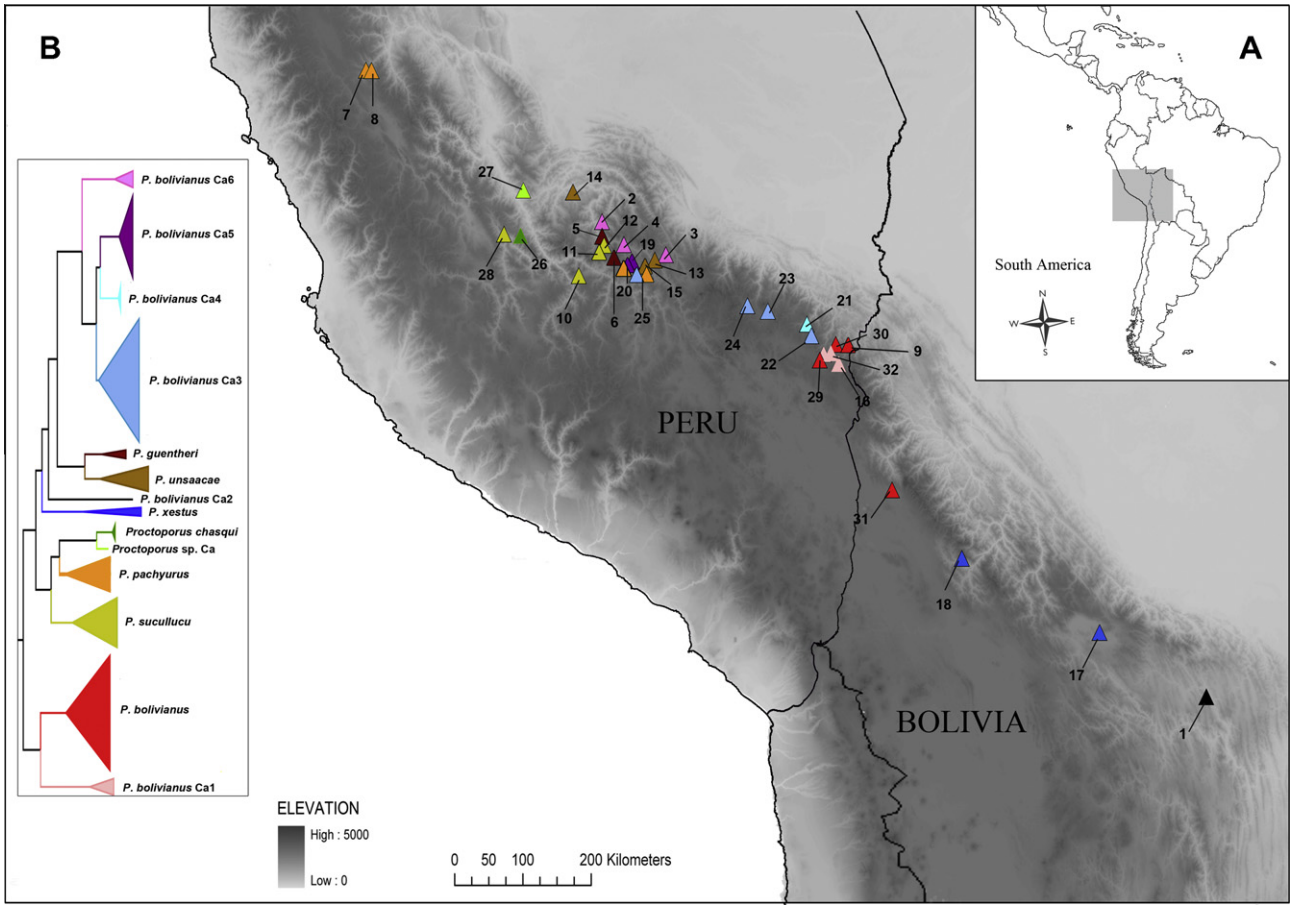

Fig. 2. (A) Location of the study area in South America and (B) Simplified phylogeny of *Proctoporus* and map of the Andes of southern Peru and northern Bolivia showing samples used for this study. Locality numbers correspond to those in Table 1.

we consider *Euspondylus* sp. as a confirmed candidate species and refer to it as *Proctoporus* sp. [Ca MNCN23305]. The proper generic allocation of the remaining species that are currently grouped under *Euspondylus* must wait until a phylogenetic analysis based on a denser taxon sampling and thorough analyses of the pholidosis and morphometrics of these genera of lizards become available.

Within *Proctoporus*, we found *P. bolivianus* as currently defined to be polyphyletic. Populations identified as *P. bolivianus* are found in three different places in our tree (clades B and H and *Proctoporus bolivianus* Ca2: Fig. 1). Clade B contains specimens from near the type locality of *P. bolivianus* in northern Bolivia, populations from Puno identified as *P. subsolanus* by Doan et al. (2005), and a candidate species from Puno, near Bolivia. We consider samples from near the type locality as nominal *P. bolivianus* as well as the samples from Sandia (southern Peru) that are nested with topotypic samples. Accordingly, *P. subsolanus* is embedded within nominal *P. bolivianus*. Our preliminary survey of available specimens of *P. subsolanus* and nominal *P. bolivianus* failed to identify any morphological or color pattern characters that could unequivocally distinguish these two species. In fact, Doan et al. (2005) described *P. subsolanus* on the basis of the presence of a frontonasal scale larger than frontal, a character that is also present in nominal *P. bolivianus* (unpublished data). Although populations of these two taxa are separated by moderate genetic divergence (5.5–5.4%; Table 5), these values overlap with the genetic differentiation observed between the different populations of nominal *P. bolivianus* (0.1–5.7%; Table 5). Therefore, we consider *P. subsolanus* as a junior synonym of *P. bolivianus*.

Proctoporus sp. 3 of Doan et al. (2005) from Laracani (Puno, Peru) has no morphological differences that distinguish it from *P. bolivianus*. Nevertheless, *P. bolivianus* and *Proctoporus* sp. 3 share a small area of sympatry in Puno. These two lineages are separated by large genetic distances (9.9–12.1%; Table 5). Therefore, we considered *Proctoporus* sp. 3 as a confirmed candidate species and we refer to it as *Proctoporus bolivianus* [Ca1 UTAR52945 Doan et al., 2005].

A sample of *Proctoporus* from Amboró (Santa Cruz: Bolivia) was assigned to *P. bolivianus* by Doan et al. (2005). This specimen is not closely related to nominal *P. bolivianus*, from which it is also separated by substantial *p*-distances (11.1–13.6; Table 5). Although the specimen (voucher number AMNH 150695) is a juvenile, it shows marked morphological differences with nominal *P. bolivianus*. Given morphological, genetic and distributional evidence, we consider that *P. bolivianus* from Amboró represents a confirmed candidate species and we refer to it as *Proctoporus bolivianus* [Ca2 AMNHR150695 Doan et al., 2005].

Another major clade of *Proctoporus* identified by us (clade H) includes samples exclusively from southern Peru. We have arranged its diversity in four main well-supported clades that are considered confirmed candidate species on the basis of morphological (unpublished) and genetic evidence. Each of these lineages differs from all others by a genetic divergence of at least 3.9% (Table 5), whereas the genetic divergence within lineages is 0.1–3.6%. Uncorrected *p*-distances between these four lineages are smaller than divergence between the remaining species of *Proctoporus*. Furthermore, intraspecific divergences in some species as *P. pachyurus* or *P. guentheri* are larger than divergence between these four lineages (Table 5). But, in spite of the lower levels of genetic differentiation observed within this clade in comparison with levels of divergence observed between the remaining species of the genus, we found

Table 5
Uncorrected *p*-distances calculated from the mitochondrial data set for eight nominal species and seven candidate species of *Proctoporus*.

Proctoporus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *xestus*	0.0–9.0														
2. *subsolanus*	12.6–13.1	0.1													
3. *bolivianus*	12.2–12.4	5.5–5.4	0.1–5.7												
4. *bolivianus* Ca1	13.1–15.8	10.3–12.9	9.9–12.1	0.6–2.1											
5. *pachyurus*	10.6–11.7	9.6–10.5	9.8–11.1	9.9–13	0.6–6.4										
6. *chasqui*	11.3–11.8	9.2–9.3	8.75–10.0	10.8–10.9	6.6–7.6	0.12–0.4									
7. sp. 1	11.1–11.3	9.5–9.6	8.8–10.40	10.5	6.6–7.4	2.7–2.8	–								
8. *suculucu*	10.6–13.5	9.3–10.3	9.8–11	10.5–5.8	7.6–8.9	8.1–9.2	7.7–8.13	0.1–4.9							
9. *bolivianus* Ca2	13.0–13.2	11.0	11.0	12.6–15.3	9.7–10.4	10.8–10.9	11.06	10.8–12	–						
10. *guentheri*	11.7–12.6	10.4–10.7	9.6–10.2	11.2–14.2	9.5–10.5	10.32–10.83	9.9–10.4	9.6–10.3	10.3–10.5	0.0–4.1					
11. *unsaacae*	11.9–14.6	11.0–13.1	10.6–12.9	11.1–13.6	9.5–12	10.4–11.47	9.7–10.5	9.2–14.3	10.5–13	7.4–9.2	0.5–7.1				
12. *bolivianus* Ca6	11.2–13.3	11.2–11.7	10.2–11.2	11.6–15.9	9.4–12	10.79–12.0	10.4–11.3	9.5–11.8	10.8–11.5	9.4–9.9	9.3–13.7	0.5–2.4			
13. *bolivianus* Ca5	11.0–11.3	10.0–10.7	9.4–9.8	10.7–14	8.7–9.6	9.1–9.8	8.9–9.22	8.4–10.4	10.9–11.1	8.8–9.5	8.6–11.9	6.8–7.1	0.1–0.8		
14. *bolivianus* Ca4	11.3–12.4	10.6–10.9	10.4–10.7	11.5–14.9	9.6–10.4	10.25–10.78	9.8–10.09	8.9–10.9	10.6–10.7	9.3–9.5	9.2–12	6.3–6.7	3.9–4.1	0.2–0.4	
15. *bolivianus* Ca3	11.1–12.1	9.9–10.4	9.8–10.1	11.2–15	9.6–10	9.5–10.8	9.1–10.4	8.5–10.4	10.8–11.5	8.7–9.2	8.0–12.2	6.5–7.9	3.9–5.1	4.1–5.2	0.1–3.6

that each of this four reciprocally monophyletic groups have unique morphologies (unpublished data). We refer to the four candidate species as *Proctoporus bolivianus* [Ca3 MNCN21323], *Proctoporus bolivianus* [Ca4 MNCN5580], *Proctoporus bolivianus* [Ca5 MNCN20610], and *Proctoporus bolivianus* [Ca6 UTAR51484 Doan et al., 2005].

As stated above some of these populations might be assigned to *Oreosaurus* (*Proctoporus*) *lacertus* Stejneger (from Tinccochaca, Cusco, Peru), *P. longicaudatus* Andersson (from Pelechuco, La Paz, Bolivia), or *P. obesus* Barbour and Noble (from Ñusta Hispana, Cusco, Peru), which were synonymized with *P. bolivianus* by Uzzell (1970). Thus, a detailed taxonomic revision is needed in order to uncover species diversity.

4.2. Genetic divergence and species delimitation

Although levels of genetic divergence can help to identify divergent lineages that may truly represent species-level lineages (e.g. Avise and Aquadro, 1982; Castresana, 2001; Fouquet et al., 2007; Johns and Avise, 1998; Lumbsch, 2002; Nimis, 1998; Vences et al., 2005; Vieites et al., 2009), our study shows that intraspecific and interspecific variation can largely vary even between closely related species. Similar cases have been found, for example, for Amazonian and Andean frogs (Padial et al., 2009; Funk et al., 2011), a situation that is well supported by our current understanding on how different speciation scenarios affect rates of genetic divergence for neutral characters and characters under selection (Padial and De la Riva, 2010; Padial et al., 2010).

Uncorrected *p*-distances (Table 5) between *Proctoporus* species ranged from 2.7% (*Proctoporus chasqui-Proctoporus* sp.) to 15.9% (*Proctoporus bolivianus* Ca1-*P. xestus*). Besides the pair *Proctoporus chasqui-Proctoporus* sp., the lowest interspecific divergence values are found among *Proctoporus bolivianus* Ca5, *Proctoporus bolivianus* Ca4, and *Proctoporus bolivianus* Ca3. The divergence between these lineages is lower than intraspecific divergence for other species of *Proctoporus*. For example, intraspecific divergence for *P. pachyurus* range from 0.6% to 6.4%, and from 0.5% to 7.1% in *P. unsaacae*, whereas divergence between *Proctoporus bolivianus* Ca5 and *Proctoporus bolivianus* Ca4 range from 3.9% to 4.1% (Table 5).

However, given the limited knowledge on the morphological variation within most species of *Proctoporus*, the limited geographical sampling used in both morphological and molecular analyses, and the fact that *Proctoporus bolivianus* Ca5 and *Proctoporus bolivianus* Ca3 are morphologically well-distinguished (unpublished), we suspect that the high genetic divergences observed among some populations within several nominal species of *Proctoporus* could reflect the existence of even more unnamed species.

4.3. Biogeographic patterns

Most species of *Proctoporus* are found in the cold grasslands habitats of the Andes locally known as "páramos" or "wet puna", with few known species occurring in the adjacent montane forest, or in both types of habitats. Our study reveals that *Proctoporus* are not only diverse in the high montane grasslands but that they diversified there as a result of vicariance within the area. Additionally, our study revealed that species diversity within *Proctoporus* is still vastly understimated, a pattern probably mirrored by other Andean lizards and other kinds of organisms. These findings reinforces the mostly overlooked conclusion that diversification in montane grasslands has largely contributed to the overall Andean species diversity, a pattern that has mainly been reported for plants (e.g. Hughes and Eastwood, 2006; Särkinen et al., 2012). As inferred from our work, the high montane grasslands also seem to have played an important role as a source for montane forest lineages (a transitional zone between the Andean high montane

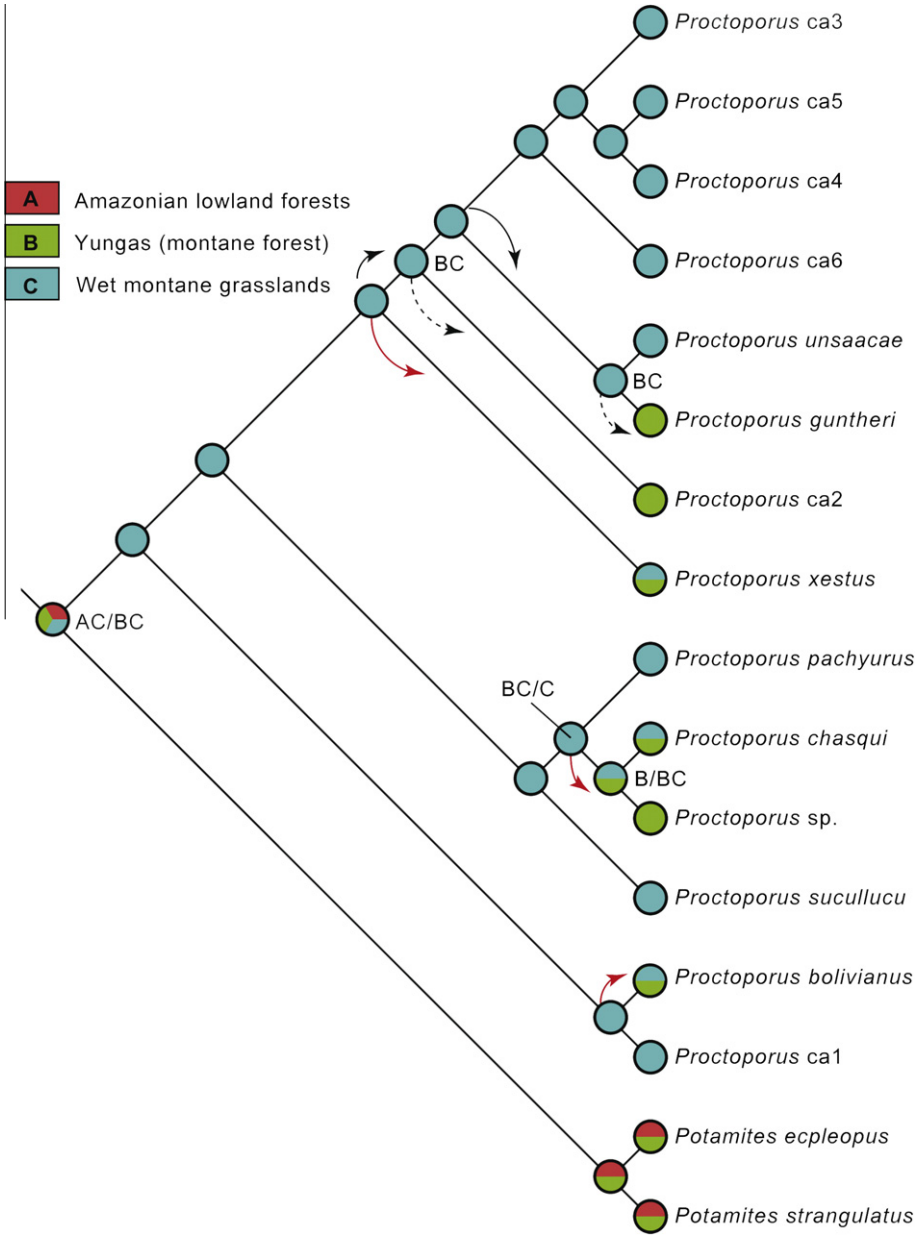

Fig. 3. Phylogenetic relationships, as revealed in this study, of the 14 species of *Proctoporus* recognized in this work and its sister group (*Potamites*) showing the reconstruction of ancestral distributions according to maximum parsimony (MPR) and dispersal-vicariance analyses (DIVA). Colored circles indicate the distribution of species, with internal nodes showing ancestral states and tips current known distribution. More than one color at a given node indicates wide distribution (i.e. species present in more than one area). Letters close to nodes indicate alternative DIVA reconstructions when differing from MPRs. Arrows mark the minimum number of dispersals between areas inferred by DIVA (black), MPRs (dashed) or common to both methods (red). For a definition of areas and the altitudinal distribution of *Proctoporus* species see Table 4 and Material and Methods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

grasslands and the Amazonian lowlands). The montane forest vegetation belt has been found to be extremely important for the building of neotropical diversity (Roberts et al., 2006, 2007; Smith et al., 2007; Wiens et al., 2007). For *Proctoporus*, speciation within montane forests does not seem yet to be especially relevant, although future discovery of species might well change this still incomplete pattern. A scenario that largely remains to be explored in animals is that montane forests also contribute to species diversity in the higher, colder, and structurally different neighbor habitat of the grasslands, as it could be the case in frogs of the species rich clade Terrarana (Hedges et al., 2008) or some marsupial frog species of the genus *Gastrotheca* (Wiens et al., 2007). Indeed, these two habitats, in conjunction with the Amazonian lowlands, seem to form a feedback-driven system where species diversify after colonizing their respective adjacent habitat (e.g. Guayasamin et al., 2008; Lim, 2008; Santos et al., 2009). This scenario, no doubt, remains to be tested with larger taxon sampling and across different groups or organisms, but some hints are provided by our results. The closest relative to *Proctoporus* is the genus *Potamites*, whose species are in general distributed at lower altitudes across the Amazonian slopes of the Andes (Doan and Castoe, 2005). Other more distantly related groups such as *Cercosaura* are also distributed across the Amazon forest, while *Petracola* inhabits the high Andean grasslands of northern Peru (Doan and Castoe, 2005; Duellman, 1979; Kizirian et al., 2008). Thus, shifts in altitudinal distribution of lineages across habitats of the Andes, most likely promoted by the Andean uplift or recurrent climatic changes, seem to be promoting the formation of new species on each vegetation belt, as a

result of local adaptation and subsequent vicariance. In other words, a bi-directional (or multidirectional) system resulting from recurrent exchanges and diversification events among faunas of the high Andes, montane forests, and lowland forests, might explain the high species diversity of the Andean hills and adjacent lowlands.

Our molecular phylogeny of *Proctoporus* further provides the opportunity to revisit the south-to-north hypothesis (SNSH) of diversification in the Andes (Doan, 2003). Doan (2003) predicted that because the Andean orogeny proceeded from south to north (Garzione et al., 2008; Gregory-Wodzicki, 2000; Hartley, 2003), we should expect a pattern of cladogenesis of Andean species following the rise of the Andes, with basal lineages occurring in the southern areas and derived ones toward lower latitudes. The analyses of Doan (2003) were based on a morphological phylogeny of *Proctoporus* including *Riama* and *Petracola*, a group that was found to be paraphyletic with respect to genera such as *Potamites*, *Cercosaura*, and *Pholidobolus* (Castoe et al., 2004; Doan and Castoe, 2005; this work). For *Proctoporus* sensu stricto (as defined here) we found well-supported optimal topologies incongruent with a SNSH at the geographic scale of our study (northern Bolivia and southern Peru). None of the species with southernmost ranges occupies a basal position in the tree (Fig. 2). The phylogeny supports instead an ancient split between a clade containing species from northern Bolivia and southern Peru, from a clade that contains species encompassing the entire range of the genus, from central Peru to northern Argentina. Torres-Carvajal (2007) evaluated the SNSH for the genus *Stenocercus* (Tropiduridae), and despite one of the clades within *Stenocercus* followed the prediction of SNSH, overall the cladogenetic pattern was incongruent with a SNSH. However, the intense Andean orogeny coupled with climatic changes might have modified an original south to north pattern, especially in the Central Andes, where elevation increased in ca. 3000 m during the last 10 Ma (Garzione et al., 2008). As suggested by Torres-Carvajal (2007), the northern portion of the Andes might constitute a better scenario to test the SNSH, where putatively young species would have diversified during a more recent uplift. However, as revealed by this study, our still more than fragmentary knowledge of species diversity of Andean lizards make our phylogeny-based inferences on biogeographic patterns ineluctably fragile.

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