



Phylogeny of Neotropical *Cercosaura* (Squamata: Gymnophthalmidae) lizards[☆]



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ARTICLE INFO

Article history:

Received 12 February 2015

Revised 24 July 2015

Accepted 28 July 2015

Available online 7 August 2015

Keywords:

Andes

Cercosaurini

Gymnophthalmidae

Lizards

Phylogenetics

South America

ABSTRACT

Among Neotropical lizards, the geographically widespread gymnophthalmid *Cercosaura* as currently defined includes lowland and highland taxa from Panama to Argentina, with some species occurring in the northern Andes. In this study we analyze three mitochondrial (12S, 16S, ND4) and one nuclear (*c-mos*) gene using Bayesian methods to clarify the phylogenetic relationships among most species of *Cercosaura* based on a well-supported phylogenetic hypothesis that also includes a large sample of other taxa within Cercosaurini. The phylogenetic tree obtained in this paper shows that *Cercosaura* as currently defined is not monophyletic. Two species from the northern Andes (*C. dicra* and *C. vertebralis*) are nested within *Pholidobolus*, which has been formerly recognized as a major radiation along the Andes of Ecuador and Colombia. Therefore, *Cercosaura* has probably not diversified in the northern Andes, although the phylogenetic position of *C. hypnoides* from the Andes of Colombia remains unknown. Tree topology and genetic distances support both recognition of *C. ocellata bassleri* as a distinct species, *C. bassleri*, and recognition of *C. argula* and *C. oshaughnessyi* as two different species. In the interest of promoting clarity and precision regarding the names of clades of gymnophthalmid lizards, we propose a phylogenetic definition of *Cercosaura*.

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1. Introduction

The gymnophthalmid lizard *Cercosaura* as currently defined (Doan, 2003) is nested within the clade Cercosaurini (Pellegrino et al., 2001) and contains 13 species that occur in Panama and most South American countries, ranging from temperate regions in the south, through the Amazon basin, the Andes from northern Peru to Colombia, the Chocó region, Guianan Shield and north-central Brazil between 0 and 2500 m (Avila-Pires, 1995; Doan, 2003; Ruibal, 1952; Uzzell, 1973). To date the only published phylogenetic tree of *Cercosaura* was reconstructed using morphological evidence (Doan, 2003) and only two other species of Cercosaurini. Thus, a new phylogenetic analysis of *Cercosaura* using molecular data and more outgroups seems appropriate, as many questions on systematics and biogeography remain unanswered. For example, the morphological tree (Doan, 2003) has *C. dicra* and *C. vertebralis* (both from the northern Andes), along with *C. manicata* (central and northern Andes), in a clade sister to all other species of *Cercosaura*, which suggests a northern Andean radiation

within *Cercosaura* as has been observed in other lizard taxa (e.g., *Stenocercus*, *Pholidobolus*; Torres-Carvajal, 2007; Torres-Carvajal and Mafla-Endara, 2013). Alternatively, *Cercosaura* as currently defined might not be monophyletic, and some or all species from the northern Andes currently allocated within *Cercosaura* might belong to a different clade. This would not be surprising as recent molecular phylogenetic studies of Cercosaurini lizards have shown that traditional, morphology-based hypotheses, have led to wrong classification schemes. For example, “*Pholidobolus*” *annectens* was found to be nested within *Macropholidus* (Torres-Carvajal and Mafla-Endara, 2013), and “*Opieuteus xestus*” is a member of *Protoporus* (Goicoechea et al., 2012). In an attempt to clarify the phylogeny of species currently allocated in *Cercosaura*, in this paper we use mitochondrial and nuclear DNA sequence data to analyze phylogenetic relationships of most species of *Cercosaura* and a large taxon sampling within Cercosaurini.

2. Materials and methods

2.1. Character and taxon sampling

We obtained nucleotide (nt) sequences from three mitochondrial genes, ribosomal small (12S, 367 nt) and large (16S, 529 nt)

[☆] This paper was edited by the Associate Editor J.A. Schulte.

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subunit genes, subunit IV of NADH dehydrogenase (*ND4*, 621 nt), as well as one nuclear gene, oocyte maturation factor *mos* (*c-mos*, 387 nt). For all these genes we generated novel DNA sequences from 49 specimens representing *Cercosaura argula*, *C. dicra*, *C. manicata*, *C. ocellata*, *C. oshaughnessyi*, *C. vertebralis*, and *C. sp. nov.* from Ecuador and Peru (Fig. 1), as well as two other undescribed species of cercosaurines from Peru (*Macropholidus sp. nov.*, *Pholidobolus sp. nov.*). We were unable to obtain tissue samples of *C. hypnoides* from Colombia. We also generated *c-mos* sequences for *Macropholidus annectens*, *M. huanacabambae*, *Pholidobolus affinis*, *P. hillisi*, *P. macbrydei*, *P. montium*, and 12S, 16S and *c-mos* sequences for *Alopoglossus viridiceps*. In addition, we obtained sequences of five species of *Cercosaura* from GenBank (*C. eigenmanni*, *C. ocellata*, *C. oshaughnessyi*, *C. quadrilineata*, *C. schreibersii*) and other taxa ranked as genera within Cercosaurini, as well as outgroup taxa based on previous phylogenetic hypotheses (Castoe et al., 2004; Pellegrino et al., 2001). All specimens used in our analyses along with their GenBank numbers are listed in Table 1.

2.2. Laboratory protocols

Genomic DNA was isolated from frozen muscle or liver tissues using a guanidinium isothiocyanate extraction protocol. Polymerase Chain Reaction (PCR) amplification of gene fragments was performed in a final volume of 25 µl reactions using 1× PCR Buffer (-Mg), 3 mM MgCl₂, 0.2 mM dNTP mix, 0.2 µM of each primer, 0.1 U/µl of Platinum® Taq DNA Polymerase (Invitrogen, Carlsbad, CA) and 1 µl of extracted DNA. Negative controls were run on all amplifications to check for contamination. Primers and PCR amplification protocols are presented in Table 2. PCR products were analyzed on 1% agarose gels by horizontal electrophoresis (the target fragment size was estimated from molecular weight markers), using SYBR® Safe (Invitrogen, Carlsbad, CA) staining, and analyzed with a Molecular Imager® Gel Doc™ XR+ Imaging System (Bio Rad, Hercules, CA). Amplified products were treated with ExoSAP-IT (Affymetrix, Cleveland, OH) to remove remaining dNTPs and primers, and extraneous single-stranded DNA produced in the PCR. Double stranded sequencing of the PCR products were performed in both directions by MacroGen Inc. New sequences were deposited in GenBank (Table 1).

2.3. Alignment, model selection, and phylogenetic analyses

Data were assembled and aligned in Geneious v5.5 (Drummond et al., 2010) under default settings for MAFFT (Katoh and Toh, 2010). *ND4* and *c-mos* sequences were translated into amino acids for confirmation of alignment. The best-fit nucleotide substitution models and partitioning scheme were chosen simultaneously using PartitionFinder v1.1.1 (Lanfear et al., 2012) under the Bayesian Information Criterion (BIC). The “greedy” algorithm was used with branch lengths of alternative partitions “linked” to search for the best-fit scheme, which consisted of six partitions: (i) 12S + 16S [GTR + I + G]; (ii) *ND4*, 1st codon position (GTR + I + G); (iii) *ND4*, 2nd codon position [HKY + I + G]; (iv) *ND4*, 3rd codon position (GTR + G); (v) *c-mos*, 3rd codon position [K80 + G]; and (vi) *c-mos*, 1st and 2nd codon positions (HKY + G).

Bayesian inference was used to obtain a phylogenetic tree of the combined dataset using the program MrBayes v3.2.1 (Ronquist et al., 2012). All parameters were unlinked between partitions (except topology and branch lengths), and rate variation (prset ratepr = variable) was invoked. Four independent runs, each with four MCMC chains, were run for 10⁷ generations, sampling every 1000 generations. Results were analyzed in Tracer v1.6 (Rambaut and Drummond, 2007) to assess convergence and effective sample sizes (ESS) for all parameters. Additionally, we verified that the

average standard deviation of split frequencies between chains and the potential scale reduction factor (PSRF) of all the estimated parameters approached values of ≤0.01 and 1, respectively. Of the 10,000 trees resulting per run, 1000 were arbitrarily discarded as “burn-in”. The resultant 36,000 trees were used to calculate posterior probabilities (PP) for each bipartition in a 50% majority-rule consensus tree. The phylogenetic tree was visualized and edited using FigTree v1.4.2 (Rambaut, 2014).

2.4. Sequence divergence

Interspecific sequence divergence among species of Cercosaurini and intraspecific divergence within species of *Cercosaura* with more than one sample were assessed with uncorrected distances for all genes using MEGA v6 (Tamura et al., 2013).

3. Results

3.1. Phylogeny of *Cercosaura* and Cercosaurini

The 50% majority-rule consensus tree resulting from our phylogenetic analysis does not support the monophyly of *Cercosaura* as currently recognized (Fig. 2). Two species, *C. dicra* and *C. vertebralis* are nested within *Pholidobolus* (from now on referred to as *Pholidobolus dicrus* and *P. vertebralis*, respectively). The remaining species of *Cercosaura* form a strongly supported clade (PP = 1.00), and the relationships among them are fully resolved and strongly supported. Within *C. ocellata*, *C. ocellata ocellata* is separated from *C. ocellata bassleri* by branches that are similar in length to other branches separating sister species within *Cercosaura* (e.g., *C. manicata* and *C. sp.*; Fig. 2). There is a basal split between the clades (*C. manicata*, *C. sp.*) and (*C. quadrilineata*, ((*C. eigenmanni*, *C. ocellata*), (*C. schreibersii*, (*C. oshaughnessyi*, *C. argula*))))).

Although the phylogenetic relationships of *Pholidobolus dicrus* and *P. vertebralis* (sister taxa with PP = 0.99) to other species of *Pholidobolus* are not clearly resolved, they were inferred in a strongly supported clade (PP = 1) with all other species of *Pholidobolus* except *P. hillisi* and *P. sp. nov.* The last two species are sister taxa (PP = 1) and form a clade weakly supported (PP = 0.65) as sister to the remaining species of *Pholidobolus*.

Within Cercosaurini (PP = 1.00; Fig. 2), *Cercosaura* is nested within the strongly supported (PP = 1.00) clade (*Petracola*, (*Potamites*, (*Proctoporus*, *Cercosaura*))). Within this clade, all relationships among taxa traditionally ranked as genera are strongly supported (PP = 0.99–1.00). The clade (*Petracola*, (*Potamites*, (*Proctoporus*, *Cercosaura*))) is sister (PP = 1.00) to the strongly supported (PP = 1.00) clade (*Macropholidus*, *Pholidobolus*). They form a larger clade sister (PP = 0.50) to (*Neusticurus*, *Placosoma*). This larger clade is sister (PP = 1.00) to *Riama*.

3.2. Sequence divergence

Uncorrected genetic distances for all genes and specimens of Cercosaurini included in this study are presented in the supplementary material. For this analysis we treat subspecies of *C. ocellata* as different species (see Section 4.3).

Interspecific sequence divergence within *Cercosaura* ranged from 0.035 (*C. argula* and *C. schreibersii*) to 0.168 (*C. eigenmanni* and *C. quadrilineata*) for 12S, 0.043 (*C. oshaughnessyi* and *C. schreibersii*) to 0.105 (*C. quadrilineata* and *C. sp.*) for 16S, 0.084 (*C. oshaughnessyi* and *C. sp.*) to 0.293 (*C. argula* and *C. sp.*) for *ND4*, and 0.004 (*C. manicata* and *C. sp.*) to 0.052 (*C. argula* and *C. manicata*; *C. argula* and *C. quadrilineata*; *C. ocellata* and *C. quadrilineata*) for *c-mos*.

Table 1

Vouchers, locality data, and GenBank accession numbers of taxa and gene regions included in this study. Asterisks indicate new sequences obtained for this study. CORBIDI (División de Herpetología, Centro de Ornitología y Biodiversidad, Lima, Peru), KU (University of Kansas Biodiversity Institute–Herpetology Collection), LSUMZ (Louisiana State University Museum of Natural Science), MHNC (Museo de Historia Natural de la Universidad Nacional de San Antonio Abad, Cusco, Peru), MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador), UTA (University of Texas at Arlington).

Taxon	Voucher and locality	Genbank accession number			
		12S	16S	ND4	c-mos
Cercosaurini					
<i>Cercosaura</i>					
<i>C. argula</i>	QCAZ 4888 ; Ecuador: Orellana: Parque Nacional Yasuní, km 49–50 on road Pompeya-Iro	KP874738*	KP874790*	KP874900*	KP874842*
<i>C. argula</i>	QCAZ 5217 ; Ecuador: Orellana: Parque Nacional Yasuní, SPF road	KP874739*	KP874791*	KP874901*	KP874843*
<i>C. bassleri</i>	CORBIDI 6374 ; Peru: San Martín: Picota: Chambirillo (puesto de control 16, Parque Nacional Cordillera Azul)	KP874740*	KP874792*	KP874902*	KP874844*
<i>C. bassleri</i>	CORBIDI 6382 ; Peru: San Martín: Picota: Chambirillo (puesto de control 16, Parque Nacional Cordillera Azul)	KP874741*	KP874793*	KP874903*	KP874845*
<i>C. bassleri</i>	CORBIDI 6384 ; Peru: San Martín: Picota: Chambirillo (puesto de control 16, Parque Nacional Cordillera Azul)	KP874742*	KP874794*	KP874904*	KP874846*
<i>C. bassleri</i>	CORBIDI 10711 ; Peru: Cusco: La Convención: KP 55, Bajo Puyantimari	KP874743*	KP874795*	KP874905*	KP874847*
<i>C. bassleri</i>	CORBIDI 11218 ; Peru: Madre de Dios: Tambopata: Baltimore	KP874744*	KP874796*	KP874906*	KP874848*
<i>C. eigenmanni</i>	MRT 976979 ; Brazil: Mato Grosso: Jurueña	AF420690 ^a	AF420728 ^a	AF420895 ^a	AF420828 ^a
<i>C. manicata</i>	CORBIDI 8837 ; Peru: San Martín: Picota: Chambirillo (puesto de control 16, Parque Nacional Cordillera Azul)	KP874745*	KP874797*	KP874907*	KP874849*
<i>C. manicata</i>	QCAZ 5793 ; Ecuador: Pastaza: Campo Oglán (Agip Oil)	KP874746*	KP874798*	KP874908*	KP874850*
<i>C. manicata</i>	QCAZ 5821 ; Ecuador: Pastaza: Campo Oglán (Agip Oil)	KP874747*	KP874799*	KP874909*	KP874851*
<i>C. ocellata</i>	MRT 977406 ; Brazil: Mato Grosso: Aripuanã	AF420677 ^a	AF420731 ^a	AF420883 ^a	AF420834 ^a
<i>C. oshaughnessyi</i>	LSUMZ H12591 ; Ecuador: Sucumbíos: Reserva de Producción Faunística Cuyabeno	AF420698 ^a	AF420751 ^a	AF420896 ^a	AF420838 ^a
<i>C. oshaughnessyi</i>	LSUMZ H13584 ; Brazil: Acre: Porto Walter	AF420696 ^a	AF420750 ^a	AF420893 ^a	AF420852 ^a
<i>C. oshaughnessyi</i>	QCAZ 4623 ; Ecuador: Morona Santiago: km 83–85 on road Payapas-Santiago, nearby military camp	KP874748*	KP874800*	KP874910*	KP874852*
<i>C. oshaughnessyi</i>	QCAZ 4809 ; Ecuador: Pastaza: Canelos, Hostería Huella Verde	KP874749*	KP874801*	KP874911*	KP874853*
<i>C. oshaughnessyi</i>	QCAZ 4842 ; Ecuador: Pastaza: Comunidad Jatun Yaku	KP874750*	KP874802*	KP874912*	KP874854*
<i>C. oshaughnessyi</i>	QCAZ 4891 ; Ecuador: Orellana: Parque Nacional Yasuní, km 108 on road Pompeya-Iro	KP874751*	KP874803*	KP874913*	KP874855*
<i>C. oshaughnessyi</i>	QCAZ 4903 ; Ecuador: Pastaza: Comunidad Puka Yaku	KP874752*	KP874804*	KP874914*	KP874856*
<i>C. oshaughnessyi</i>	QCAZ 4925 ; Ecuador: Pastaza: Comunidad Campus	KP874753*	KP874805*	KP874915*	KP874857*
<i>C. oshaughnessyi</i>	QCAZ 5178 ; Ecuador: Orellana: Dayuma	KP874754*	KP874806*	KP874916*	–
<i>C. oshaughnessyi</i>	QCAZ 5195 ; Ecuador: Orellana: Parque Nacional Yasuní	KP874755*	KP874807*	KP874917*	KP874858*
<i>C. oshaughnessyi</i>	QCAZ 5246 ; Ecuador: Orellana: Estación Científica Yasuní, PUCE	KP874756*	KP874808*	KP874918*	KP874859*
<i>C. oshaughnessyi</i>	QCAZ 5828 ; Ecuador: Pastaza: Campo Oglán (Agip Oil)	KP874757*	KP874809*	KP874919*	KP874860*
<i>C. oshaughnessyi</i>	QCAZ 6750 ; Ecuador: Napo: Guagua Sumaco, on trail to rio Pinguyo waterfall	KP874758*	KP874810*	KP874920*	KP874861*
<i>C. oshaughnessyi</i>	QCAZ 6751 ; Ecuador: Napo: Guagua Sumaco, on trail to rio Pinguyo waterfall	KP874759*	KP874811*	KP874921*	KP874862*
<i>C. oshaughnessyi</i>	QCAZ 7048 ; Ecuador: Sucumbíos: Zábalo	KP874760*	KP874812*	KP874922*	KP874863*
<i>C. oshaughnessyi</i>	QCAZ 7337 ; Ecuador: Napo: Tena	KP874761*	KP874813*	KP874923*	KP874864*
<i>C. oshaughnessyi</i>	QCAZ 7603 ; Ecuador: Napo: Río Hollín	KP874762*	KP874814*	KP874924*	KP874865*
<i>C. oshaughnessyi</i>	QCAZ 7855 ; Ecuador: Pastaza: Bobonaza	KP874763*	KP874815*	KP874925*	KP874866*
<i>C. oshaughnessyi</i>	QCAZ 8156 ; Ecuador: Pastaza: Villano B, Campo Villano, Bloque 10-Agip Oil	KP874765*	KP874817*	KP874927*	KP874868*
<i>C. oshaughnessyi</i>	QCAZ 8162 ; Ecuador: Pastaza: Campo Villano (Agip Oil), K4 oil camp	KP874766*	KP874818*	KP874928*	–
<i>C. oshaughnessyi</i>	QCAZ 8384 ; Ecuador: Pastaza: K10 camp, Campo Villano, Bloque 10-Agip Oil	KP874767*	KP874819*	KP874929*	KP874869*
<i>C. oshaughnessyi</i>	QCAZ 9482 ; Ecuador: Orellana: southern bank of Río Napo, Sector La Primavera	KP874768*	KP874820*	KP874930*	KP874870*
<i>C. oshaughnessyi</i>	QCAZ 9537 ; Ecuador: Orellana: southern bank of Río Napo, Edén	KP874769*	KP874821*	KP874931*	KP874871*
<i>C. oshaughnessyi</i>	QCAZ 10526 ; Ecuador: Morona Santiago: Comunidad Shuar “El Tiink”	KP874770*	KP874822*	KP874932*	KP874872*
<i>C. oshaughnessyi</i>	QCAZ 10720 ; Ecuador: Sucumbíos: La Selva	KP874771*	KP874823*	KP874933*	KP874873*
<i>C. oshaughnessyi</i>	QCAZ 11407 ; Ecuador: Orellana: Comunidad Sinchichikta	KP874772*	KP874824*	KP874934*	KP874874*
<i>C. quadrilineata</i>	LG 936 ; Brazil: Goiás: Caldas Novas	AF420672 ^a	AF420717 ^a	–	AF420830 ^a
<i>C. schreibersii</i>	LG 1168 ; Brazil: São Paulo: São Paulo	AF420658 ^a	AF420729 ^a	AF420882 ^a	AF420882 ^a
<i>C. schreibersii</i>					
<i>C. schreibersii</i>	LG 927 ; Brazil: São Paulo: São Paulo	AF420686 ^a	AF420749 ^a	AF420911 ^a	AF420911 ^a
<i>C. sp.</i>	CORBIDI 650 ; Peru: San Martín: Mariscal Cáceres: Laguna Negra	KP874773*	KP874825*	KP874935*	KP874875*
<i>Macropholidus</i>					
<i>M. annectens</i>	QCAZ 11120 ; Ecuador: Loja: 15 km E Loja	KC894341 ^b	KC894355 ^b	KC894369 ^b	KP874876*
<i>M. annectens</i>	QCAZ 11121 ; Ecuador: Loja: 15 km E Loja	KC894342 ^b	KC894356 ^b	KC894370 ^b	KP874877*
<i>M. huancabambae</i>	CORBIDI 10492 ; Peru: Piura: Huancabamba: Las Pozas	KC894343 ^b	KC894357 ^b	KC894371 ^b	KP874878*
<i>M. huancabambae</i>	CORBIDI 10493 ; Peru: Piura: Huancabamba: Las Pozas	KC894344 ^b	KC894358 ^b	KC894372 ^b	KP874879*
<i>M. huancabambae</i>	CORBIDI 10496 ; Peru: Piura: Huancabamba: Las Pozas	KC894345 ^b	KC894359 ^b	KC894373 ^b	KP874880*
<i>M. ruthveni</i>	CORBIDI 4281 ; Peru: Lambayeque: El Totoral	KC894354 ^b	KC894368 ^b	KC894382 ^b	–
<i>M. sp.</i>	CORBIDI 12932 ; Peru: Piura: Ayabaca: Bosque de Cuyas	KP874774*	KP874826*	KP874936*	KP874881*
<i>Neusticurus</i>					
<i>N. bicarinatus</i>	MRT 968462 ; Brazil: Mato Grosso: Apiacás	AF420671 ^a	AF420708 ^a	–	AF420816 ^a
<i>N. rudis</i>	MRT 926008 ; Brazil: Amapá: Serra do Navio	AF420689 ^a	AF420709 ^a	AF420905 ^a	–
<i>Petracola</i>					
<i>P. ventrimaculata</i>	CORBIDI 9235 ; Peru: Cajamarca	KJ948193 ^c	KJ948144 ^c	KJ948145 ^c	KJ948220 ^c
<i>P. waka</i>	KU 212687 ; Peru: Cajamarca: Celendin: E slope Abra Gelic, 20 km E Celendin	AY507864 ^d	AY507876 ^d	–	AY507903 ^d

(continued on next page)

Table 1 (continued)

Taxon	Voucher and locality	Genbank accession number			
		12S	16S	ND4	c-mos
<i>Pholidobolus</i>					
<i>P. affinis</i>	QCAZ 9641 ; Ecuador: Cotopaxi: San Miguel de Salcedo	KC894348 ^b	KC894362 ^b	KC894376 ^b	KP874883*
<i>P. affinis</i>	QCAZ 9900 ; Ecuador: Chimborazo: Colta	KC894349 ^b	KC894363 ^b	KC894377 ^b	KP874884*
<i>P. dicrus</i>	QCAZ 5304 ; Ecuador: Azuay: Guarumales	KP874776*	KP874828*	KP874938*	KP874885*
<i>P. dicrus</i>	QCAZ 6936 ; Ecuador: Tungurahua: Río Blanco	–	KP874829*	KP874939*	KP874886*
<i>P. hillisi</i>	QCAZ 4998 ; Ecuador: Loja: Vía Loja-Zamora, near Estación San Francisco	KP090167 ^c	KP090170 ^c	KP090173 ^c	–
<i>P. hillisi</i>	QCAZ 4999 ; Ecuador: Loja: Vía Loja-Zamora, near Estación San Francisco	KP090169 ^c	KP090172 ^c	KP090175 ^c	KP874887*
<i>P. hillisi</i>	QCAZ 5000 ; Ecuador: Loja: Vía Loja-Zamora, near Estación San Francisco	KP090168 ^c	KP090171 ^c	KP090174 ^c	KP874888*
<i>P. macbrydei</i>	KU 218406	AY507848 ^d	AY507867 ^d	AY507886 ^d	AY507896 ^d
<i>P. macbrydei</i>	QCAZ 9914 ; Ecuador: Azuay: Guablid	KC894352 ^b	KC894366 ^b	KC894380 ^b	–
<i>P. macbrydei</i>	QCAZ 9932 ; Ecuador: Azuay: 20 km W Cuenca	KC894353 ^b	KC894367 ^b	KC894381 ^b	KP874889*
<i>P. montium</i>	KU 196355 ; Ecuador: Cotopaxi	AF420701 ^a	AF420756 ^a	AF420884 ^a	AF420820 ^a
<i>P. montium</i>	QCAZ 4051 ; Ecuador: Pichincha: Quito	KC894346 ^b	KC894360 ^b	KC894374 ^b	KP874890*
<i>P. montium</i>	QCAZ 9044 ; Ecuador: Pichincha: Tababela	KC894347 ^b	KC894361 ^b	KC894375 ^b	–
<i>P. prefrontalis</i>	QCAZ 9908 ; Ecuador: Chimborazo: Alausí	KC894350 ^b	KC894364 ^b	KC894378 ^b	–
<i>P. prefrontalis</i>	QCAZ 9951 ; Ecuador: Chimborazo: Tixán	KC894351 ^b	KC894365 ^b	KC894379 ^b	–
<i>P. vertebralis</i>	QCAZ 5057 ; Ecuador: Carchi: Chilma Bajo	KP874778*	KP874830*	KP874940*	KP874891*
<i>P. vertebralis</i>	QCAZ 8687 ; Ecuador: Carchi: Finca de Aníbal Pozo, Chilma Bajo	KP874779*	KP874831*	KP874941*	–
<i>P. vertebralis</i>	QCAZ 8688 ; Ecuador: Carchi: Finca de Aníbal Pozo, Chilma Bajo	KP874780*	KP874832*	KP874942*	KP874892*
<i>P. vertebralis</i>	QCAZ 8689 ; Ecuador: Carchi: Finca de Aníbal Pozo, Chilma Bajo	KP874781*	KP874833*	KP874943*	–
<i>P. vertebralis</i>	QCAZ 8717 ; Ecuador: Carchi: Chilma Bajo, on trail to Cascada Tres Marías	KP874782*	KP874834*	KP874944*	KP874893*
<i>P. vertebralis</i>	QCAZ 8724 ; Ecuador: Carchi: Chilma Bajo, on trail to Cascada Tres Marías	KP874783*	KP874835*	KP874945*	–
<i>P. vertebralis</i>	QCAZ 10667 ; Ecuador: Pichincha: Santa Lucía de Nanegal	KP874784*	KP874836*	KP874946*	KP874894*
<i>P. vertebralis</i>	QCAZ 10750 ; Ecuador: Pichincha: Santa Lucía de Nanegal	KP874785*	KP874837*	KP874947*	KP874895*
<i>P. sp.</i>	CORBIDI 1679 ; Peru: Cajamarca: Chota: Región Cajamarca, La Granja	KP874786*	KP874838*	–	KP874896*
<i>P. sp.</i>	CORBIDI 12735 ; Peru: Cajamarca: Jaen: Bosque de Huamantanga	KP874787*	KP874839*	KP874948*	KP874897*
<i>P. sp.</i>	CORBIDI 12737 ; Peru: Cajamarca: Jaen: Bosque de Huamantanga	KP874788*	KP874840*	KP874949*	KP874898*
<i>Placosoma</i>					
<i>P. cordylinum</i>	LG 1006 ; Brazil: Rio de Janeiro: Teresópolis	AF420673 ^a	AF420734 ^a	AF420879 ^a	AF420823 ^a
<i>P. glabellum</i>	LG 940 ; Brazil: São Paulo	AF420674 ^a	AF420742 ^a	AF420907 ^a	AF420833 ^a
<i>Potamites</i>					
<i>P. ecleopus</i>	MRT 0472 ; Brazil: Mato Grosso	AF420656 ^a	AF420748 ^a	AF420890 ^a	AF420829 ^a
<i>P. strangulatus</i>	KU 21677 ; voucher number probably in error	AY507847 ^d	AY507866 ^d	AY507885 ^d	–
<i>Proctoporus</i>					
<i>P. bolivianus</i> Ca1	MHNC 5322 ; Peru: Puno: between Trapiche and Sina	JX435945 ^f	JX435988 ^f	–	JX436045 ^f
<i>P. bolivianus</i> Ca1	UTA R-52945 ; Peru: Puno: Laracani	AY968825 ^g	AY968832 ^g	AY968813 ^g	–
<i>P. bolivianus</i> Ca3	MHNC 6005 ; Peru: Cusco: Kosn-ipata Valley	JX435927 ^f	JX435966 ^f	JX436079 ^f	JX436049 ^g
<i>P. bolivianus</i> Ca5	MNCN 4221 ; Peru: Cusco: Marcapata Valley	JX435902 ^f	JX435983 ^f	JX436095 ^f	JX436047 ^f
<i>P. bolivianus</i>	MNCN 43679 ; Bolivia: La Paz: Sorata Valley	JX435943 ^f	JX435997 ^f	JX436069 ^f	JX436043 ^f
<i>P. carabaya</i>	MHNC 5428 ; Peru: Puno: Tambillo	JX435912 ^f	JX435979 ^f	JX436083 ^f	JX436016 ^f
<i>P. chasqui</i>	MHNC 6771 ; Peru: Ayacucho: Between Abra Tapuna and San Francisco	JX435887 ^f	JX435946 ^f	JX436051 ^f	JX436003 ^f
<i>P. guentheri</i>	UTA R-51515 ; Peru: Cusco: Chocalloc	AY507849 ^d	AY507872 ^d	AY225185 ^h	AY507900 ^d
<i>P. guentheri</i>	UTA R-51517 ; Peru: Cusco: Machu Picchu	AY507854 ^d	AY507873 ^d	AY225169 ^h	AY507901 ^d
<i>P. pachyurus</i>	MHNC 11439 ; Peru: Cusco: Marcapata Valley	JX435893 ^f	JX435950 ^f	JX436056 ^f	JX436050 ^f
<i>P. succullucu</i>	UTA R-51478 ; Peru: Cusco: Kusilluchayoc	AY507857 ^d	AY507878 ^d	AY225171 ^h	AY507905 ^d
<i>P. succullucu</i>	UTA R-51496 ; Peru: Cusco: Piscacucho	AY507858 ^d	AY507879 ^d	AY225177 ^h	AY507906 ^d
<i>P. unsaaca</i>	UTA R-51477 ; Peru: Cusco: Saqsayhuaman	AY507860 ^d	AY507882 ^d	AY225170 ^h	AY507909 ^d
<i>P. unsaaca</i>	UTA R-51488 ; Peru: Cusco: Quellouno	AY507859 ^d	AY507881 ^d	AY225186 ^h	AY507908 ^d
<i>P. xestus</i>	MNCN 2425 ; Bolivia: La Paz: Between Lambate and Totoral	JX435899 ^f	JX436001 ^f	JX436100 ^f	JX436007 ^f
<i>P. sp.</i>	MHNC 6834 ; Peru: Cusco: Kimbiri River	JX435890 ^f	JX435949 ^f	JX436054 ^f	JX436006 ^f
<i>Riama</i>					
<i>R. cashcaensis</i>	QCAZ 10754 ; Ecuador: Bolivar: Road Guanujo-Salinas, near Río Moya	KJ948181 ^c	KJ948126 ^c	KJ948163 ^c	KJ948219 ^c
<i>R. colomaromani</i>	KU 217209 ; Ecuador: Carchi: 26.9–27.3 km from Maldonado on road to Tulcan	AY507853 ^d	AY507871 ^d	AY507888 ^d	AY507899 ^d
<i>R. orcesi</i>	KU 221772 ; Ecuador: Napo: 31 km N Jondachi	AY507855 ^d	AY507874 ^d	AY507889 ^d	–
<i>R. simotera</i>	KU 217207 ; Ecuador: Carchi: 15.3 km from Tulcan on road to Tufino	AY507856 ^d	AY507875 ^d	AY507890 ^d	AY507902 ^d
<i>R. unicolor</i>	QCAZ 9682 ; Ecuador: Imbabura: Reserva Ecológica Cotacachi-Cayapas, trail near Cuicocha Lake	KJ948188 ^c	KJ948138 ^c	KJ948157 ^c	KJ948205 ^c
Outgroups					
<i>Alopoglossus viridiceps</i>	QCAZ 10670 ; Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KP874789*	KP874841*	KJ705316 ⁱ	KP874899*
<i>Bachia flavescens</i>	LSUMZ H12977 ; Brazil: Pará: Agropecuária Treviso, Santarém	AF420705 ^a	AF420753 ^a	AF420869 ^a	AF420859 ^a
<i>Ecleopus gaudichaudii</i>	LG 1356 ; Brazil: São Paulo: Boissucanga	AF420660 ^a	AF420738 ^a	AF420901 ^a	AF420855 ^a
<i>Gymnophthalmus leucomystax</i>	MRT 946613 ; Brazil: Roraima: Fazenda Salvamento	AF420675 ^a	AF420715 ^a	AF420906 ^a	AF420824 ^a
<i>Rhachisaurus brachylepis</i>	MRT 887336 ; Brazil: Minas Gerais: Serra do Cipó	AF420665 ^a	AF420737 ^a	AF420877 ^a	AF420853 ^a

^a Pellegrino et al. (2001).^b Torres-Carvajal and Mafía-Endara (2013).^c Aguirre-Peñafiel et al. (2014).^d Castoe et al. (2004).^e Torres-Carvajal et al. (2014).^f Goicoechea et al. (2012).^g Doan et al. (2005).^h Doan and Castoe (2003).ⁱ Torres-Carvajal and Lobos (2014).

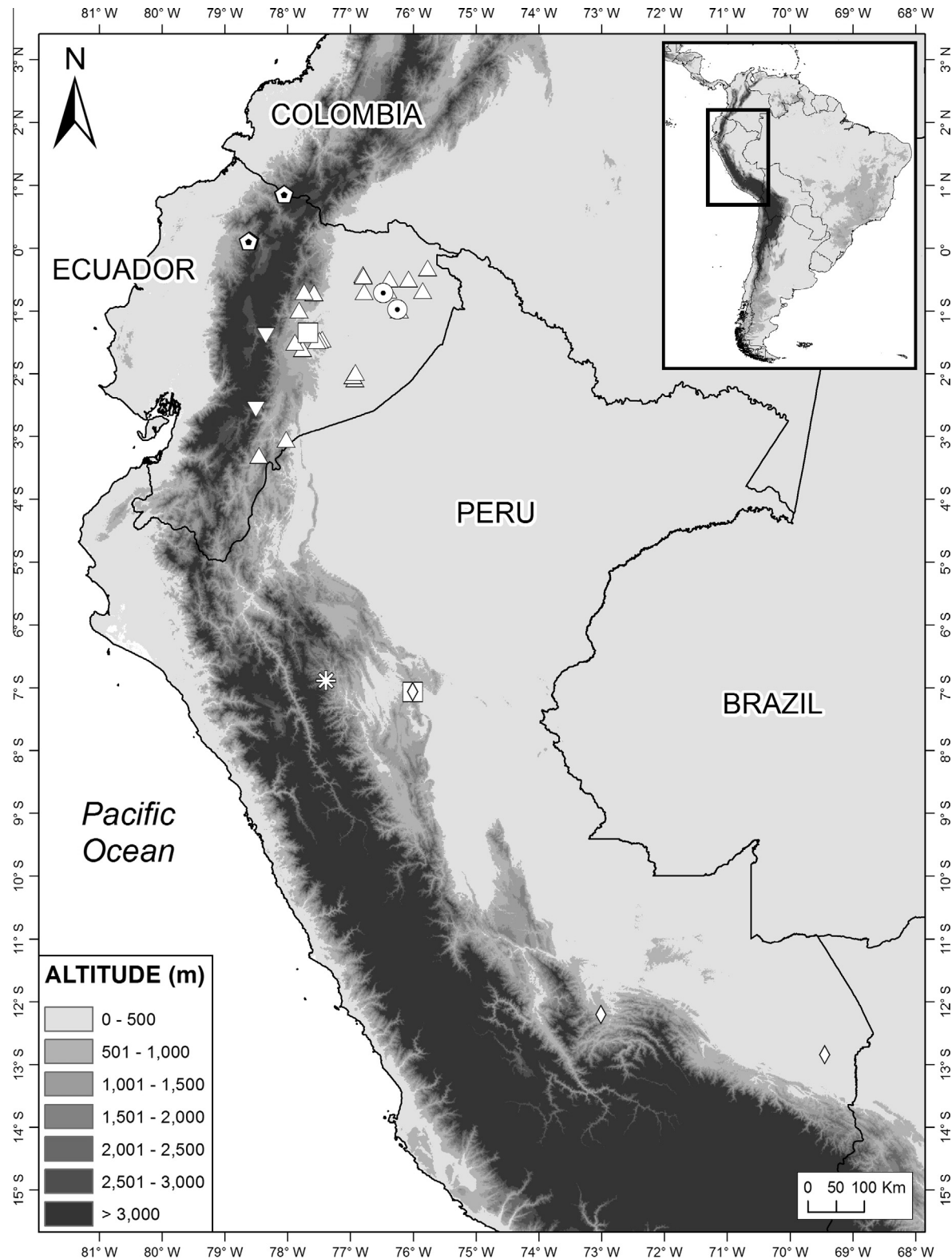


Fig. 1. Map of western South America showing sampling localities of DNA sequences generated in this study for taxa traditionally recognized as *Cercosaura*. Circles: *C. argula*; diamonds: *C. bassleri*; squares: *C. manicata*; triangles: *C. oshaughnessyi*; asterisk: *C. sp.*; inverted triangles: *Pholidobolus dicrus*; pentagons: *P. vertebralis*. Taxonomic details are presented in the Section 4. Locality details, as well as voucher and GenBank accession numbers are listed in Table 1.

Among species of *Cercosaura* for which we had more than one sample (i.e., all except *C. eigenmanni*, *C. ocellata*, *C. quadrilineata* and *C. sp.*), intraspecific genetic distances ranged between 0.004 (S.E. 0.003) in *C. argula* and 0.038 (S.E. 0.012) in *C. schreibersii* for

12S, 0.006 (S.E. 0.004) in *C. argula* and 0.029 (S.E. 0.009) in *C. schreibersii* for 16S, 0.014 in *C. argula* (S.E. 0.008) and 0.189 in *C. schreibersii* (S.E. 0.044) for ND4, and 0.000 in all species for *c-mos*.

Table 2
Gene regions, primers and PCR protocols used in this study.

Gene region	Primers sequence (5'–3')	PCR protocol
12S	12S1L (Kocher et al., 1989) CAAACCTGGGATTAGATACCCACTAT	1 cycle: 3 min 94 °C 33 cycles: 30 s 92 °C, 30 s 57 °C, 1:50 min 72 °C 1 cycle: 10 min 72 °C
	12s2H (Kocher et al., 1989) AGGGTGACGGCGGTGTGT	
16S	16sF.0 (Pellegrino et al., 2001) CTGTTTACCAAAAACATMRCCTYTACG	1 cycle: 3 min 96 °C 40 cycles: 30 s 95 °C, 1 min 51 °C, 1 min 72 °C 1 cycle: 10 min 72 °C
	16sR.0 (Whiting et al., 2003) TAGATAGAAACCGACTGATT	
	16SL (Harris et al., 1998) CGCCTGTTTACCAAAAACAT	
	16Sh (Harris et al., 1998) CCGGTCTGAACCTCAGATCACGT	
	ND412931L (Blair et al., 2009) CTACCAAAAGCTCATGTAGAAGC	1 cycle: 3 min 96 °C 40 cycles: 30 s 95 °C, 1 min 52 °C, 1 min 72 °C 1 cycle: 10 min 72 °C
c-mos	ND413824H (Arévalo et al., 1994) CATTACTTTTACTTGGATTTCACCA	1 cycle: 3 min 96 °C 35 cycles: 25 s 95 °C, 1 min 52 °C, 2 min 72 °C 1 cycle: 10 min 72 °C
	G73 (Saint et al., 1998) GCGGTAAAGCAGGTGAAGAAA	
	G74 (Saint et al., 1998) TGAGCATCAAAGTCTCCAATC	

4. Discussion

4.1. *Cercosaura* in the northern Andes

The 2000 km-long northern Andes (12°N–5°S) have a NNE–SSW orientation, and extend from easternmost Venezuela to northernmost Peru. They are part of the Tropical Andes hotspot, which is regarded as one of the world's greatest biodiversity hotspots, harboring high levels of vertebrate and plant endemism (Myers et al., 2000). Physiographically, the northern Andes include two cordilleras in Ecuador, three in Colombia and two in Venezuela (Schubert and Clapperton, 1990). In spite of its recognition as an important hotspot, our knowledge on the evolution of organisms in the northern Andes from a phylogenetic perspective is limited. Among lizards, molecular phylogenies are available for the iguanids *Stenocercus*, *Anolis heterodermus*, and the gymnophthalmid *Pholidobolus*, all of which have successfully diversified along the northern Andes (Torres-Carvajal, 2007; Torres-Carvajal and Mafla-Endara, 2013; Torres-Carvajal et al., 2014; Vargas-Ramírez and Moreno-Arias, 2014). In this paper we show that *Cercosaura* has not diversified in the Andes of Ecuador; two northern Andean species traditionally placed in this genus (i.e., *C. dicra* and *C. vertebralis*) belong in the clade *Pholidobolus*, which has radiated along the Andes of northern Peru, Ecuador, and Colombia (Figs. 1 and 2; Torres-Carvajal and Mafla-Endara, 2013). The phylogenetic position of *C. hypnoides* from the Colombian highlands remains unknown. This species is known from a single locality at 1640 m on the eastern slopes of the Eastern Cordillera. If *C. hypnoides* is a member of *Cercosaura*, then it probably represents a lineage derived from an Amazonian ancestor, as other species of *Cercosaura* are known to occur in Amazonian Colombia.

In addition, the taxonomic identity of populations of “*Cercosaura*” *vertebralis* from Colombia, Venezuela and Panama should be assessed in more detail. Records of “*C.*” *vertebralis* from Peru (Doan and Cusi, 2014; Uzzell, 1973) are based on misidentified specimens, some of which correspond to an undescribed species of *Pholidobolus* (unpublished results, *P. sp.* in our phylogenetic tree; Fig. 2).

4.2. Phylogeny of *Cercosaurini*

The phylogeny of *Cercosaurini* inferred in this study (Fig. 2) is different from the morphology-based phylogeny presented by Doan (2003), except for the sister taxon relationship between *Pholidobolus dicrus* and *P. vertebralis*, both placed within *Cercosaura*. In addition to *C. ocellata*, the taxonomic sampling in Doan (2003) was restricted to the former genera *Prionodactylus* and *Pantodactylus*, which she synonymized with *Cercosaura*, as well as “outgroup” taxa *Euspondylus spinalis* and *Protoporus xestus*. Therefore, in that study incomplete taxonomic sampling prevented the possibility of inferring both *Pholidobolus dicrus* and *P. vertebralis* as members of *Pholidobolus*.

On the other hand, even though our inferred phylogeny is fully congruent with previous molecular phylogenies (Castoe et al., 2004; Pellegrino et al., 2001), our study is the first to include *Cercosaura manicata*, *Pholidobolus dicrus* and *P. vertebralis* in a DNA-sequence-based phylogenetic analysis. Generic misplacement of other species of *Cercosaurini* has been demonstrated with phylogenetic analyses of DNA sequence data elsewhere (Castoe et al., 2004; Goicoechea et al., 2012; Torres-Carvajal and Mafla-Endara, 2013), and some taxa traditionally ranked as genera have not been sampled yet (i.e., *Anadia*, *Echinosaura*, *Teuchocercus*). This reveals that our knowledge of the phylogenetic relationships among taxa within the clade *Cercosaurini* is still incomplete, and future phylogenetic analyses are likely to lead to further taxonomic changes.

4.3. Taxonomy

Based on the phylogenetic hypothesis presented in this paper (Fig. 2), the genus *Cercosaura* as currently defined (Doan, 2003) is paraphyletic. Therefore, we propose to place *C. dicra* and *C. vertebralis* within the genus *Pholidobolus* as defined by Torres-Carvajal and Mafla-Endara (2013).

Within *Cercosaura*, our phylogenetic tree shows a clear distinction between subspecies *C. ocellata ocellata* and *C. ocellata bassleri*, which have an average genetic distance of 0.065 for 12S, 0.072 for 16S, 0.204 for ND4, and 0.013 for *c-mos*. These values fall within interspecific distance ranges observed among other species of *Cercosaura* (see supplementary material). Furthermore, *C. ocellata bassleri* and *C. ocellata ocellata* occur in allopatry and can be distinguished from each other morphologically (Avila-Pires, 1995). We therefore recognize *C. ocellata bassleri* as a distinct species, *C. bassleri* Ruibal, 1952. Within *C. bassleri*, two distinct clades suggest the existence of two species, which is further supported by their disjunct distribution. One clade (CORBIDI 6374, 6382, 6384; Fig. 2) contains specimens from a single locality in San Martín, northern Peru (~7°S; Fig. 1), whereas the second clade (CORBIDI 10711, 11218; Fig. 2) is represented by specimens from Madre de Dios and Cusco in southern Peru (~12–13°S; Fig. 1). However, we recognize that only a more exhaustive morphological and molecular study of populations currently assigned to *C. bassleri* will clarify their taxonomic status. Similarly, the large genetic distance values between subspecies of *C. schreibersii* (see supplementary material) suggest that their taxonomic status should be rigorously evaluated.

Another taxonomic issue that deserves attention is the distinction between *C. argula* Peters, 1863 and *C. oshaughnessyi* Boulenger, 1885. Based on morphological traits, these species were synonymized by Uzzell (1973), recognized back as two distinct species by Avila-Pires (1995), and later synonymized again by Doan (2003). Based on our experience, these two species can be readily distinguished from each other following Avila-Pires' (1995) identification key. Even though our sampling of *C. argula* is poor (*n* = 2) as opposed to *C. oshaughnessyi* (*n* = 26), our phylogenetic hypothesis (Fig. 2) further supports recognition of *C. argula* and *C. oshaughnessyi* as two distinct species because they are reciprocally monophyletic.

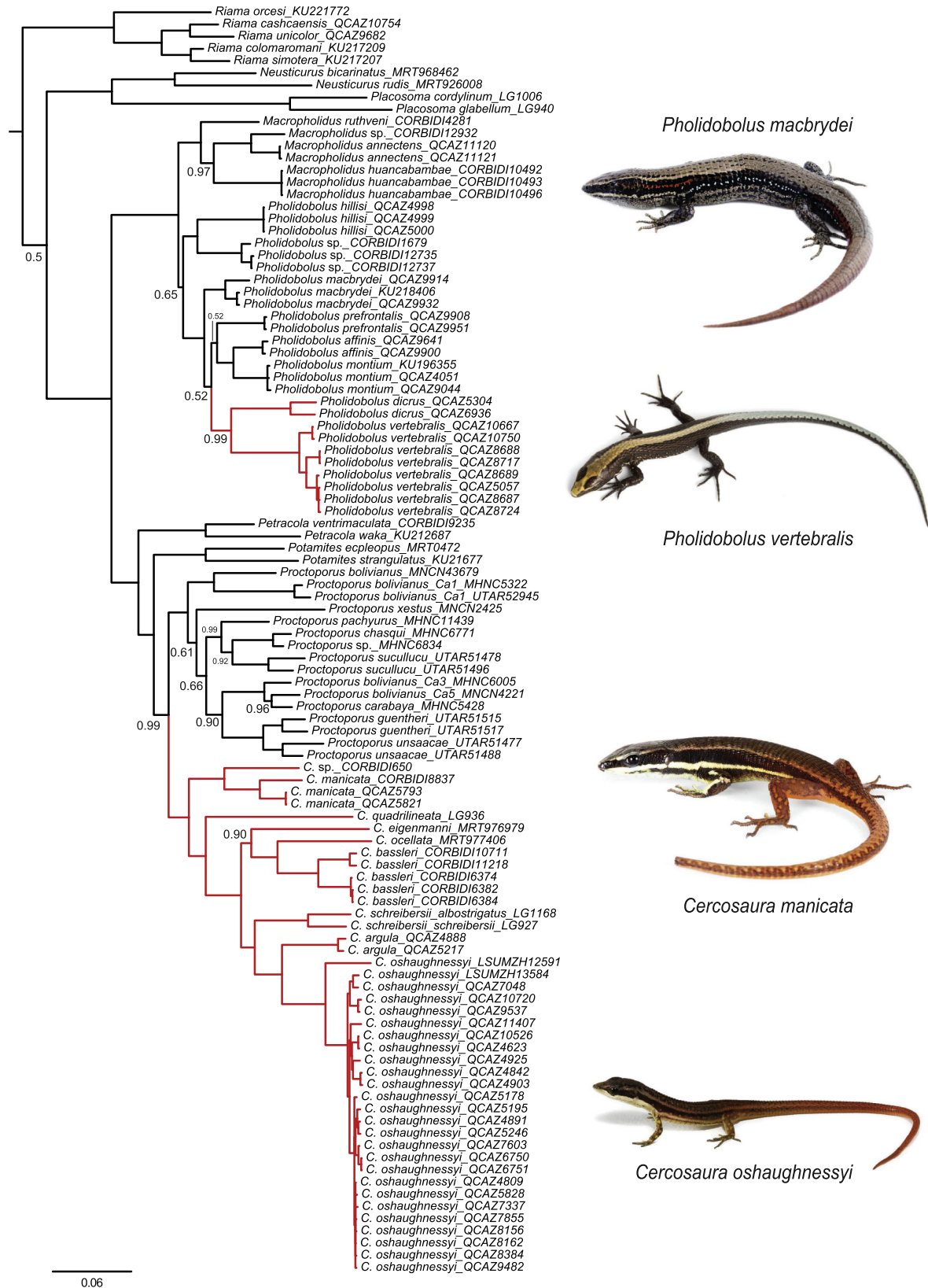


Fig. 2. Phylogeny of Cercosaurini. Majority rule (50%) consensus tree of 36,000 trees obtained from a Bayesian analysis of 110 specimens, four mitochondrial genes (12S, 16S, ND4) and one nuclear gene (*c-mos*). Outgroup taxa (Table 1) are not shown. Numbers next to branches correspond to posterior probability values. All bipartitions have PP values of 1 unless otherwise noted; PP values on intraspecific branches are not shown for clarity. Voucher numbers of sequences are indicated for each terminal. Taxonomic changes proposed in this paper (see Section 4) are adopted; red branches indicate all lineages formerly placed within *Cercosaura* (= *C.*). Photographs were taken from ReptiliaWebEcuador (<http://zoologia.puce.edu.ec/Vertebrados/Reptiles/ReptilesEcuador>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Genetic distance values between these species are low, on average on the lower limit of the interspecific ranges reported above ($12S = 0.045$, $16S = 0.061$, $ND4 = 0.130$, $c-mos = 0.043$). However, this might be an artifact of our geographic sampling, as all our samples of *C. argula* and *C. oshaughnessyi*, except for one, are from eastern Ecuador (Table 1). The only sample of *C. oshaughnessyi* from Brazil (LSUMZ H13584) is also the most basal in the clade (Fig. 2), with a relatively long branch that suggests strong genetic differences between populations from Brazil and Ecuador.

In the interest of promoting clarity and precision regarding the names of clades of gymnophthalmid lizards, we propose the following phylogenetic definition (de Queiroz and Gauthier, 1994) for *Cercosaura* according to the rules of the draft International Code for Phylogenetic Nomenclature (ICPN, Cantino and de Queiroz, 2007).

Cercosaura Wagler, 1830 (converted clade name). Definition: The crown clade originating with the most recent common ancestor of *Cercosaura ocellata* Wagler, 1830, *C. manicata* O'Shaughnessy, 1881, *C. (Prionodactylus) eigenmanni* (Griffin, 1917), and *C. argula* Peters, 1862. Reference phylogeny: Fig. 2 of this paper. Hypothesized composition: *Cercosaura* is currently hypothesized to include *Cercosaura argula* Peters, 1862, *C. bassleri* Ruibal, 1952, *C. (Prionodactylus) eigenmanni* (Griffin, 1917), *C. hypnoides* Doan and Lamar, 2012, *C. manicata* O'Shaughnessy, 1881, *C. (Prionodactylus) nigroventris* (Gorzula and Senaris, 1999), *Cercosaura ocellata* Wagler, 1830, *C. (Prionodactylus) oshaughnessyi* (Boulenger, 1885), *C. (Pantodactylus) parkeri* (Ruibal, 1952), *C. (Euspondylus) phelpsorum* (Lancini, 1968), *C. quadrilineata* Boettger, 1876, *C. schreibersii* Wiegmann, 1834, and *C. (Pantodactylus) steyeri* (Tedesco, 1998). Comments: Inclusion of *C. hypnoides*, *C. nigroventris*, *C. parkeri*, *C. phelpsorum*, and *C. steyeri* within *Cercosaura* needs to be confirmed with a robust phylogeny that includes those taxa, as well as a large taxon sampling within Cercosaurini. Morphological diagnostic apomorphies of *Cercosaura*, as defined here, should be reassessed with further phylogenetic data.

Acknowledgments

We thank G. Castillo and L. Jaramillo for laboratory work. This project was funded by Secretaría de Educación Superior, Ciencia, Tecnología e Innovación del Ecuador (SENESCYT) and Pontificia Universidad Católica del Ecuador. Specimens from Ecuador were collected under collection permits 001-10 IC-FAU-DNB/MA, 001-11 IC-FAU-DNB/MA, 002-2012-CA-FAU-MAE-DPO-PNY, 005-12-IC-FAU-DNB/MA, 006-2012-FAU-MAE-DPO-PNY, 008-09 IC-FAU-DNB/MA, and 015-2012-FAU-MAE-DPO issued by Ministerio del Ambiente and were deposited at Museo de Zoología (QCAZ), Pontificia Universidad Católica del Ecuador. Specimens from Peru were collected under collection permits 110-2007-INRENA-IFFS-DCB, N°08 C/C – 2008-INRENA-IANP, 118-2007-INRENA-IFFS-DCB, 0581-2011-AG-DGFFS-DGEFFS and were deposited at Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2015.07.025>.

References

- Aguirre-Peñafiel, V., Torres-Carvajal, O., Nunes, P.M.S., et al., 2014. A new species of *Riama* Gray, 1858 (Squamata: Gymnophthalmidae) from the Tropical Andes. *Zootaxa* 3866, 246–260.
- Arévalo, E.S., Davis, S.K., Sites Jr., J.W., 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of

- the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Syst. Biol.* 43, 387–418.
- Avila-Pires, T.C.S., 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Nationaal Natuurhistorisch Mus. Zool. Verhandelingen* 299, 1–706.
- Blair, C., Mendez de la Cruz, F.R., Ngo, A., Lindell, J., Lathrop, A., Murphy, R.W., 2009. Molecular phylogenetics and taxonomy of leaf-toed geckos (Phyllodactylidae: Phyllodactylus) inhabiting the peninsula of Baja California. *Zootaxa* 2027, 28–42.
- Cantino, P.D., de Queiroz, K., 2007. International Code of Phylogenetic Nomenclature. Version 4. <<http://www.ohio.edu/phylocode/>>.
- Castoe, T.A., Doan, T.M., Parkinson, C.L., 2004. Data partitions and complex models in Bayesian analysis: the phylogeny of gymnophthalmid lizards. *Syst. Biol.* 53, 448–469.
- de Queiroz, K., Gauthier, J., 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9, 27–31.
- Doan, T.M., Castoe, T.A., 2003. Using morphological and molecular evidence to infer species boundaries within *Proctoporus bolivianus* Werner (Squamata: Gymnophthalmidae). *Herpetologica* 59, 432–449.
- Doan, T.M., 2003. A new phylogenetic classification for the gymnophthalmid genera *Cercosaura*, *Pantodactylus* and *Prionodactylus* (Reptilia: Squamata). *Zool. J. Linn. Soc.* 137, 101–115.
- Doan, T.M., Castoe, T.A., Arizabal, W., 2005. Phylogenetic relationships of the genus *Proctoporus* sensu stricto (Squamata: Gymnophthalmidae), with a new species from Puno, southeastern Peru. *Herpetologica* 61, 325–336.
- Doan, T.M., Cusi, J.C., 2014. Geographic distribution of *Cercosaura vertebralis* O'Shaughnessy, 1879 (Reptilia: Squamata: Gymnophthalmidae) and the status of *Cercosaura ampuedai* (Lancini, 1968). *Check List* 10, 1195–1200.
- Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Heled, J., Kearse, M., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T., Wilson, A., 2010. Geneious v5.5. Biomatters. <<http://www.geneious.com>>.
- Goicoechea, N., Padial, J.M., Chaparro, J.C., Castroviejo-Fisher, S., De la Riva, I., 2012. Molecular phylogenetics, species diversity, and biogeography of the Andean lizards of the genus *Proctoporus* (Squamata: Gymnophthalmidae). *Mol. Phylogenet. Evol.* 65, 953–964.
- Harris, D.J., Arnold, E.N., Thomas, R.H., 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proc. Roy. Soc. Lond. B Biol. Sci.* 265, 1939–1948.
- Katoh, K., Toh, H., 2010. Parallelization of the MAFFT multiple sequence alignment program. *Bioinformatics* 26, 1899–1900.
- Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc. Natl. Acad. Sci. USA* 86, 6196–6200.
- Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. Partition-finder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* 29, 1695–1701.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Pellegrino, K.C.M., Rodrigues, M.T., Yonenaga-Yassuda, Y., Sites, J.W., 2001. A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. *Biol. J. Linn. Soc.* 74, 315–338.
- Rambaut, A., Drummond, A.J., 2007. Tracer v1.4. <<http://beast.bio.ed.ac.uk/Tracer>>.
- Rambaut, A., 2014. FigTree Version 1.4.2. <<http://tree.bio.ed.ac.uk/software/figtree/>>.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542.
- Ruibal, R., 1952. Revisionary studies of some South American Teiidae. *Bull. Mus. Comp. Zool.* 106, 475–529.
- Saint, K.M., Austin, C.C., Donnellan, S.C., Hutchinson, M.N., 1998. C-mos, a nuclear marker useful for Squamate phylogenetic analysis. *Mol. Phylogenet. Evol.* 10, 259–263.
- Schubert, C., Clapperton, C.M., 1990. Quaternary glaciations in the northern Andes (Venezuela, Colombia and Ecuador). *Quatern. Sci. Rev.* 9, 123–135.
- Tamura, K., Stecher, G., Peterson, D., Filipiński, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. *Mol. Biol. Evol.* 30, 2725–2729.
- Torres-Carvajal, O., 2007. Phylogeny and biogeography of a large radiation of Andean lizards (Iguania, *Stenocercus*). *Zool. Scr.* 36, 311–326.
- Torres-Carvajal, O., Mafía-Endara, P., 2013. Evolutionary history of Andean *Pholidobolus* and *Macropholidus* (Squamata: Gymnophthalmidae) lizards. *Mol. Phylogenet. Evol.* 68, 212–217.
- Torres-Carvajal, O., Venegas, P.J., Lobos, S.E., Mafía-Endara, P., Nunes, P.M.S., 2014. A new species of *Pholidobolus* (Squamata: Gymnophthalmidae) from the Andes of southern Ecuador. *Amphib. Reptile Conserv.* 8, 76–88.
- Torres-Carvajal, O., Lobos, S.E., 2014. A new species of *Alopoglossus* lizard (Squamata, Gymnophthalmidae) from the tropical Andes, with a molecular phylogeny of the genus. *ZooKeys* 410, 105–120.
- Uzzell, T.M., 1973. A revision of lizards of the genus *Prionodactylus*, with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). *Postilla*, 1–67.
- Vargas-Ramírez, M., Moreno-Arias, R., 2014. Unknown evolutionary lineages and population differentiation in *Anolis heterodermus* (Squamata: Dactyloidae) from the Eastern and Central Cordilleras of Colombia revealed by DNA sequence data. *S. Am. J. Herpetol.* 9, 131–141.
- Whiting, A.S., Bauer, A.M., Sites Jr., J.W., 2003. Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). *Mol. Phylogenet. Evol.* 29, 582–598.