



## Phylogeny and biogeography of the most diverse clade of South American gymnophthalmid lizards (Squamata, Gymnophthalmidae, Cercosaurinae) ☆



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### ABSTRACT

Nearly 50% of the diversity of the speciose Neotropical lizard clade Gymnophthalmidae is nested within the subclade Cercosaurinae. The taxonomy of Cercosaurinae lizards has been historically confusing because many diagnostic characters of those clades traditionally ranked as genera do not represent true diagnostic apomorphies. Even though molecular phylogenies of several 'genera' have been presented in the last few years, some of them remain poorly sampled (e.g., *Anadia*, *Echinosaura*, *Potamites*, *Riama*). In this paper we present a more comprehensive phylogeny of Cercosaurinae lizards with emphasis on Andean taxa from Ecuador and Peru, as well as a time-calibrated phylogeny with reconstruction of ancestral areas. Our analysis includes 52% of all recognized species of Cercosaurinae (67 species) and 1914 characters including three mitochondrial and one nuclear gene. We find that *Anadia*, *Echinosaura*, *Euspondylus*, *Potamites*, *Proctoporus*, and *Riama* are not monophyletic: the Tepuian *Anadia mcdiarmidi* is not sister to Andean species of *Anadia*; *Echinosaura sulcarostrum* is not included in the same clade formed by other species of *Echinosaura* and their more recent common ancestor; *Teuchocercus* is nested within *Echinosaura*; species of *Euspondylus* included in this study are nested within *Proctoporus*; *Riama laudahnae* is included in *Proctoporus*; and *Potamites* is paraphyletic and split in two separate clades, one of which we name *Gelanesaurus*, also a new genus-group name. Within *Potamites*, *P. ecleopus* is paraphyletic, and *P. strangulatus strangulatus* and *P. strangulatus trachodus* are recognized as two distinct species. We also identify three unnamed clades (i.e., not nested within any of the recognized 'genera') from Andean populations in Ecuador and Peru. The estimated age of the clade Cercosaurinae (~60 Ma) corresponds to the early stages of the northern Andes. Even though the distribution of the most recent common ancestor of Cercosaurinae remains equivocal, our analysis shows that these lizards colonized and radiated along the northern Andes before reaching the central Andes in Peru. Finally, we present phylogenetic definitions for some of the recovered clades to promote a clear and precise classification of Cercosaurinae lizards.

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### 1. Introduction

With 253 species (Uetz and Hošek, 2016), the lizard clade Gymnophthalmidae is one of the most diverse lizard taxa in the Neotropics. As expected from its high diversity, many questions on the systematics and biogeography of this clade remain unanswered. This problem is aggravated by the rarity of some taxa in collections, convergent morphological characters confusing

classifications (Pellegrino et al., 2001; Presch, 1980), and large unsampled geographical areas. More than a decade ago, Pellegrino et al. (2001) published the first molecular phylogeny of Gymnophthalmidae based on DNA sequence data along with the corresponding taxonomic classification. These authors recognized four major clades—Alopoglossinae, Rachisaurinae, Gymnophthalminae, and Cercosaurinae—which they ranked as subfamilies. Subsequently, Castoe et al. (2004) published a phylogeny of Gymnophthalmidae based on a broader taxonomic sampling and more sophisticated phylogenetic analyses. Their tree was generally similar to the tree presented by Pellegrino et al. (2001); among the few differences Ecleopodini, one of two

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subclades recovered by Pellegrino et al. (2001) within Cercosaurinae, was instead distantly related to that clade in the phylogeny by Castoe et al. (2004), who recognized it as a fifth “subfamily” (Eclepodinae) of Gymnophthalmidae. Similarly, in a large-scale phylogeny of Squamata, Pyron et al. (2013) recognized a sixth “subfamily” (Bachiinae), which was formerly referred to as Bachiini, one of the two “tribes” recognized by Castoe et al. (2004) within Cercosaurinae. More recently, Kok (2015) showed that *Riolama*, traditionally recognized as part of Cercosaurinae, was not included in that clade or any of the previously proposed clades; consequently, he erected the “subfamily” Riolaminae. Except for Alopoglossinae, Riolaminae is sister to all other gymnophthalmids (Kok, 2015).

One of the least-known clades within Gymnophthalmidae is Cercosaurinae (sensu Pyron et al., 2013), which contains ~50% of the species of gymnophthalmid lizards. A comprehensive phylogeny of Cercosaurinae (~128 species) has not been published yet. Based on the phylogenetic hypothesis proposed by Castoe et al. (2004), Doan and Castoe (2005) proposed three new taxon names (ranked as genera)—*Potamites*, *Petracola* and *Riama*—within Cercosaurinae. More recently, several authors have published molecular phylogenies of taxa traditionally ranked as genera within Cercosaurinae, such as *Proctoporus* (Goicoechea et al., 2012), *Pholidobolus* and *Macropholidus* (Torres-Carvajal and Mafla-Endara, 2013), and *Cercosaura* (Torres-Carvajal et al., 2015). As a result, several species have been shown to be nested in different clades than those implied under traditional, usually non-phylogenetic, morphology-based hypotheses. For example, *Opipeuter xestus* was found to be nested within *Proctoporus*, which rendered *Opipeuter* as a junior synonym of *Proctoporus* (Goicoechea et al., 2012). Both “*Cercosaura*” *dicra* and “*C.*” *vertebralis* were found to be nested within *Pholidobolus*, a clade distantly related to *Cercosaura* (Torres-Carvajal et al., 2015). More strikingly, Kok (2015) showed that *Riolama* is not nested within Cercosaurinae as previously suggested (Castoe et al., 2004). In spite of these efforts, major questions on the systematics of Cercosaurinae remain unanswered due to incomplete taxonomic sampling. The phylogenetic position of *Euspondylus* has been poorly explored (Goicoechea et al., 2012), whereas the phylogenetic affinities of *Anadia*, *Echinosaura*, and *Teuchocercus* have not been yet assessed with DNA sequence data, except for the non-Andean species *A. mcdiarmidi* and *E. sulcarostrum* (Kok, 2015). *Anadia*, *Echinosaura*, *Euspondylus*, and *Teuchocercus* occur mostly along the Central and Northern Andes from Peru to Venezuela. In this paper we use mitochondrial and nuclear DNA sequence data of nearly 50% of all species of Cercosaurinae, with emphasis on Andean taxa, to (1) infer phylogenetic relationships among species and subclades within Cercosaurinae; (2) address monophyly of taxa traditionally ranked as genera; and (3) propose an updated phylogeny-based classification scheme for Cercosaurinae lizards. In addition, we conduct a Bayesian chronobiogeographic analysis and discuss the biogeography of Cercosaurinae lizards.

## 2. Materials and methods

### 2.1. Character and taxon sampling

We obtained nucleotide (nt) sequences from three mitochondrial genes, ribosomal small (12S, 368 nt) and large (16S, 538 nt) 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 these genes we generated novel DNA sequences from 71 specimens representing 25 species currently allocated to *Anadia*, *Cercosaura*, *Echinosaura*, *Euspondylus*, *Potamites*, *Proctoporus*, *Riama* and *Teuchocercus*, as well as 10 specimens that we could not assign to any of the recognized genus-ranked taxa within

Cercosaurinae based on morphology (Fig. 1, Table 1). In addition, we obtained sequences from GenBank representing 42 additional species of Cercosaurinae, as well as seven outgroup taxa based on previous phylogenetic hypotheses (Table 1; Castoe et al., 2004; Kok, 2015; Pellegrino et al., 2001). Thus, our analysis includes 67 species of Cercosaurinae, 52% of all recognized species in this clade.

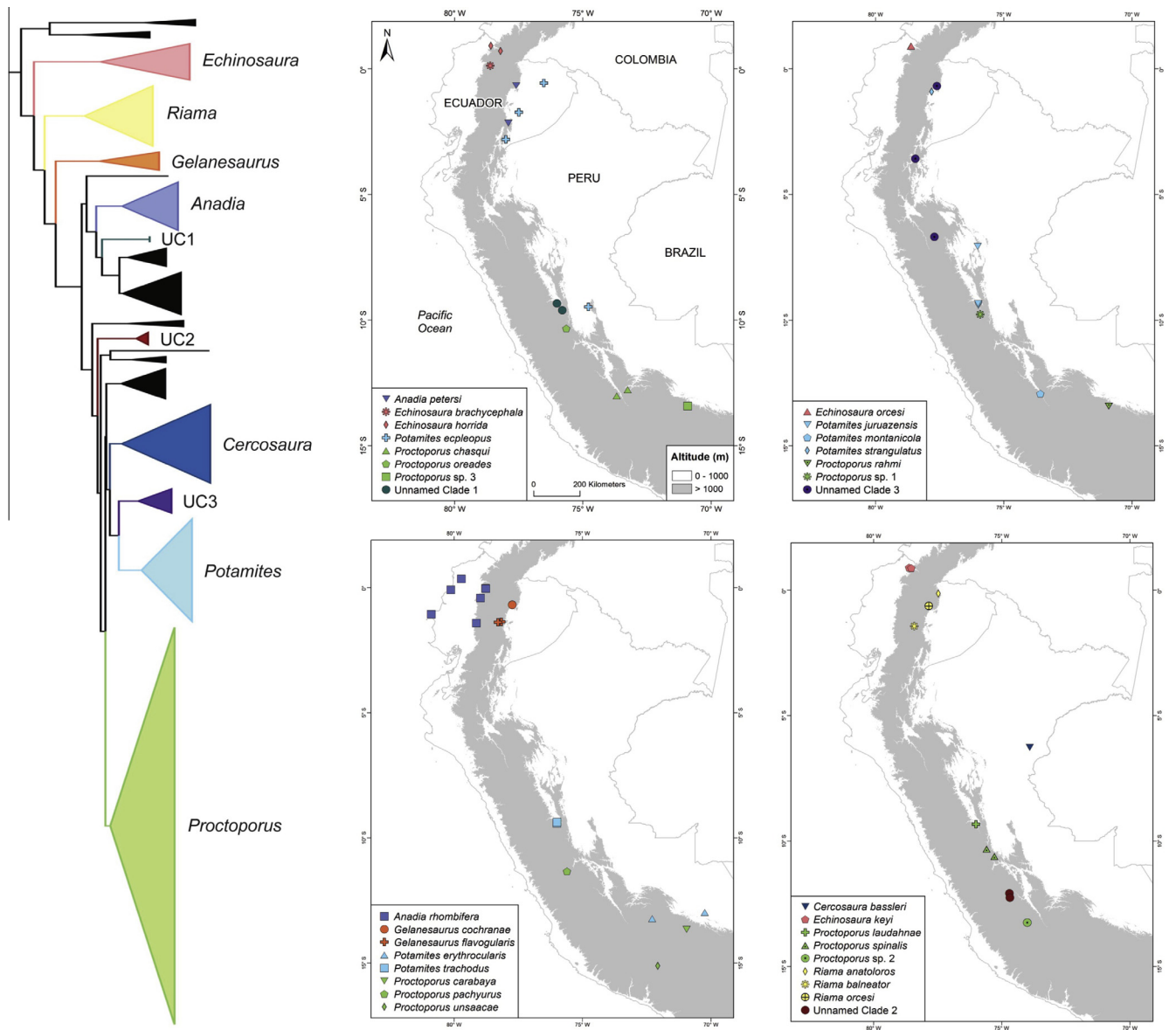
### 2.2. Laboratory protocols

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  $\mu$ l reactions using 1 $\times$  PCR Buffer (–Mg), 3 mM MgCl<sub>2</sub>, 0.2 mM dNTP mix, 0.2  $\mu$ M of each primer, 0.1 U/ $\mu$ l of Platinum<sup>®</sup> Taq DNA Polymerase (Invitrogen, Carlsbad, CA) and 1  $\mu$ l of extracted DNA. Negative controls were run on all amplifications to check for contamination. Primers and PCR amplification protocols were presented elsewhere (Table 2 in Torres-Carvajal et al., 2015). PCR products were analyzed on 1% agarose gels by horizontal electrophoresis (the target fragment size was estimated from molecular weight markers), using SYBR<sup>®</sup> Safe (Invitrogen, Carlsbad, CA) staining, and analyzed with a Molecular Imager<sup>®</sup> Gel Doc<sup>™</sup> 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 v7.1.5 (Kearse et al., 2012) under default settings for MAFFT (Katoh and Standley, 2013). Ribosomal (12S and 16S) gene regions with multiple gaps were realigned to minimize indels and optimize nucleotide identities among different individuals. *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 [GTR + 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).

Both maximum likelihood (ML) and Bayesian inference methods were used to obtain the optimal tree topology of the combined, partitioned dataset using the programs RAxML v8.2.4 (Stamatakis, 2006) and MrBayes v3.2.1 (Ronquist et al., 2012), respectively. The ML analysis was performed under the GTRCAT approximation using eight partitions (12S, 16S, and 1st, 2nd and 3rd codon positions of both *ND4* and *c-mos*); nodal support was assessed with the fast bootstrapping (BB) algorithm (Stamatakis et al., 2008) letting RAxML halt bootstrapping automatically (total number of replicates = 156). For the Bayesian analysis we used the partitions selected by PartitionFinder. Four independent runs, each with four MCMC chains, were run for 10<sup>7</sup> 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



**Fig. 1.** Simplified phylogeny of Cercosaurinae and maps of western South America showing sampling localities of DNA sequences of Cercosaurinae lizards generated in this study. Taxonomic details are presented in Sections 3 and 4. Locality details, as well as voucher and GenBank accession numbers are listed in Table 1.

parameters approached values of  $\leq 0.01$  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. Phylogenetic trees were rooted with *Alopoglossus* (Castoe et al., 2004; Pellegrino et al., 2001; Pyron et al., 2013), visualized and edited using FigTree v1.4.2 (Rambaut, 2014).

#### 2.4. Biogeographical analysis

We used the program BEAST 1.8.3 (Drummond et al., 2012) to infer simultaneously the phylogeny, divergence times, and ancestral distributions of Cercosaurinae lizards. To reconstruct ancestral distributions we used the Bayesian stochastic search variable selection (BSSVS; Lemey et al., 2009) of the discrete phylogeographic model. Based on the classification presented by Duellman (1999), with slight modifications by Castroviejo-Fisher et al. (2014; see their Fig. 1), we identified six biogeographical areas where species of Cercosaurinae lizards and their immediate

relatives occur: Chocó, Amazon, Guiana Shield, Northern Andes, Central Andes, and Atlantic Forest. All species included in this study are restricted to one of these areas, except for *Echinosauro horrida*, *E. keyi*, *E. orcesi*, *Cercosaura manicata*, and *Potamites ecleopus*, which occupy two areas. Based on node ages estimated by Zheng and Wiens (2016) for well-supported clades in their phylogeny, we applied the following calibrations: (1) a normally distributed prior with a mean of  $59.23 \pm 1$  SD Ma representing the node age of Cercosaurinae; (2) a normally distributed prior with a mean of  $44.36 \pm 1$  SD Ma representing the split between *Placosoma* and *Neusticurus*; (3) a normally distributed prior with a mean of  $36.55 \pm 1$  SD Ma representing the node age of the clade including *Pholidobolus*, *Proctopus*, *Cercosaura* and *Potamites*, but not *Riama* or *Gelanesaurus*; and (4) a normally distributed prior with a mean of  $16.40 \pm 1$  SD Ma representing the node age of the least inclusive clade containing *Riama unicolor*, *R. simotera* and *R. colomaromani*.

For this analysis we pruned our dataset to select only one sample per species, except for species occupying two areas, in which case each area was represented by one sample specimen. Based

**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. AMNH (American Museum of Natural History – Herpetology Collection), CORBIDI (División de Herpetología, Centro de Ornitología y Biodiversidad, Lima, Peru), IRSNB (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium), KU (University of Kansas Biodiversity Institute–Herpetology Collection, Kansas, United States), LSUMZ (Louisiana State University Museum of Natural Science, Louisiana, United States), 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), ROM (Royal Ontario Museum, Toronto, Canada), UTA (University of Texas at Arlington, Texas, United States).

Taxon	Voucher and locality	GenBank accession number			
		12S	16S	ND4	c-mos
<b>Cercosaurinae</b>					
<b>Anadia</b>					
"A". <i>mcclarmidi</i>	IRSNB 2674; Venezuela: Bolívar: Abakapá-tepui	–	JQ742263 <sup>a</sup>	KP283392 <sup>b</sup>	KP283385 <sup>b</sup>
<i>A. petersi</i>	QCAZ 5068; Ecuador: Napo: Wildsumaco Wildlife Sanctuary, Wildsumaco Biological Station, approx. 1 km S Pacto Sumaco	KU902127*	KU902208*	KU902283*	KU902048*
<i>A. petersi</i>	QCAZ 10087; Ecuador: Morona-Santiago: Nuevo Israel	KU902130*	KU902211*	KU902286*	KU902050*
<i>A. rhombifera</i>	QCAZ 5782; Ecuador: Manabí: Martínez estate, Tres Bosques trail	KU902128*	KU902209*	KU902284*	–
<i>A. rhombifera</i>	QCAZ 6873; Ecuador: Esmeraldas: Bilsa Biological Station	KU902129*	KU902210*	KU902285*	KU902049*
<i>A. rhombifera</i>	QCAZ 10537; Ecuador: Pichincha: Mindo, halfway between highway and Mindo	KU902131*	KU902212*	KU902287*	–
<i>A. rhombifera</i>	QCAZ 10556; Ecuador: Pichincha: Mindo, Yellow House trails & lodge	KU902132*	KU902213*	KU902288*	KU902051*
<i>A. rhombifera</i>	QCAZ 11061; Ecuador: Bolívar: 3 km on road Mulidiaguán-Río Verde	KU902133*	KU902214*	KU902289*	KU902052*
<i>A. rhombifera</i>	QCAZ 11510; Ecuador: Manabí: Pacoche Lodge	KU902134*	KU902215*	KU902290*	–
<i>A. rhombifera</i>	QCAZ 11862; Ecuador: Cotopaxi: San Francisco de Las Pampas	KU902135*	KU902216*	KU902291*	KU902053*
<b>Cercosaura</b>					
<i>C. argula</i>	QCAZ 4888; Ecuador: Orellana: Yasuni National Park, km 49–50 on road Pompeya-Iro	KP874738 <sup>c</sup>	KP874790 <sup>c</sup>	KP874900 <sup>c</sup>	KP874842 <sup>c</sup>
<i>C. bassleri</i>	CORBIDI 11218; Peru: Cusco: La Convención: Pagoreni Oeste	KP874744 <sup>c</sup>	KP874796 <sup>c</sup>	KP874906 <sup>c</sup>	KP874848 <sup>c</sup>
<i>C. bassleri</i>	CORBIDI 15187; Peru: Loreto: Requena: Tapiche River	KU902136*	KU902217*	KU902292*	KU902054*
<i>C. doanae</i>	CORBIDI 650; Peru: San Martín: Mariscal Cáceres: Laguna Negra	KP874773 <sup>c</sup>	KP874825 <sup>c</sup>	KP874935 <sup>c</sup>	KP874875 <sup>c</sup>
<i>C. eigenmanni</i>	MRT 976979; Brazil: Mato Grosso: Jurueña	AF420690 <sup>d</sup>	AF420728 <sup>d</sup>	AF420895 <sup>d</sup>	AF420828 <sup>d</sup>
<i>C. manicata</i>	CORBIDI 8837; Peru: San Martín: Picota: Chambirillo (Checkpoint 16, Cordillera Azul National Park)	KP874745 <sup>c</sup>	KP874797 <sup>c</sup>	KP874907 <sup>c</sup>	KP874849 <sup>c</sup>
<i>C. manicata</i>	QCAZ 5793; Ecuador: Pastaza: Oglán (Agip Oil)	KP874746 <sup>c</sup>	KP874798 <sup>c</sup>	KP874908 <sup>c</sup>	KP874850 <sup>c</sup>
<i>C. ocellata</i>	MRT 977406; Brazil: Mato Grosso: Aripuanã	AF420677 <sup>d</sup>	AF420731 <sup>d</sup>	AF420883 <sup>d</sup>	AF420834 <sup>d</sup>
<i>C. oshaughnessyi</i>	LSUMZ H12591; Ecuador: Sucumbíos: Cuyabeno Wildlife Production Reserve	AF420698 <sup>d</sup>	AF420751 <sup>d</sup>	AF420896 <sup>d</sup>	AF420838 <sup>d</sup>
<i>C. oshaughnessyi</i>	LSUMZ H13584; Brazil: Acre: Porto Walter	AF420696 <sup>d</sup>	AF420750 <sup>d</sup>	AF420893 <sup>d</sup>	AF420852 <sup>d</sup>
<i>C. oshaughnessyi</i>	QCAZ 4623; Ecuador: Morona-Santiago: km 83–85 on road Payapas-Santiago, nearby military camp	KP874748 <sup>c</sup>	KP874800 <sup>c</sup>	KP874910 <sup>c</sup>	KP874852 <sup>c</sup>
<i>C. quadrilineata</i>	LG 936; Brazil: Goiás: Caldas Novas	AF420672 <sup>d</sup>	AF420717 <sup>d</sup>	–	AF420830 <sup>d</sup>
<i>C. schreibersii</i>	LG 1168; Brazil: São Paulo: São Paulo	AF420658 <sup>d</sup>	AF420729 <sup>d</sup>	AF420882 <sup>d</sup>	AF420856 <sup>d</sup>
<i>C. schreibersii</i>	LG 927; Brazil: São Paulo: São Paulo	AF420686 <sup>d</sup>	AF420749 <sup>d</sup>	AF420911 <sup>d</sup>	AF420817 <sup>d</sup>
<b>Echinosaura</b>					
<i>E. brachycephala</i>	QCAZ 10824; Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KU902137*	KU902218*	KU902293*	KU902055*
<i>E. horrida</i>	QCAZ 6666; Ecuador: Esmeraldas: Alto Tambo, El Placer-La Carolina	KU902138*	KU902219*	KU902294*	KU902056*
<i>E. horrida</i>	QCAZ 8788; Ecuador: Esmeraldas: Alto Tambo, El Placer	KU902139*	KU902220*	KU902295*	KU902057*
<i>E. keyi</i>	QCAZ 8074; Ecuador: Esmeraldas: 5 km on road Alto Tambo-El Placer, Otokiki Reserve	KU902140*	KU902221*	KU902296*	KU902058*
<i>E. keyi</i>	QCAZ 12485; Ecuador: Esmeraldas: Chuchubí, on path above Chuchubí Resort	KU902141*	KU902222*	KU902297*	KU902059*
<i>E. orcesi</i>	QCAZ 6299; Ecuador: Esmeraldas: Alto Tambo, El Placer	KU902142*	KU902223*	KU902298*	KU902060*
<i>E. orcesi</i>	QCAZ 10022; Ecuador: Esmeraldas: Alto Tambo, Otokiki Reserve	KU902143*	KU902224*	KU902299*	KU902061*
"E". <i>sulcarostrum</i>	ROM 22892; Guyana: Baramita, approximately 1 km S airstrip	AF206584 <sup>e</sup>	AF206584 <sup>e</sup>	–	–
<b>Gelanesaurus</b>					
<i>G. cochranae</i>	QCAZ 5587; Ecuador: Napo: Río Hollín	KU902144*	KU902225*	KU902300*	KU902062*
<i>G. cochranae</i>	QCAZ 6120; Ecuador: Napo: Río Hollín, Jondachi-Loreto road	KU902145*	KU902226*	KU902301*	KU902063*
<i>G. flavogularis</i>	QCAZ 4611; Ecuador: Tungurahua: Río Zuñac Reserve	KU902146*	KU902227*	KU902302*	KU902064*
<i>G. flavogularis</i>	QCAZ 6943; Ecuador: Tungurahua: Machay River, Baños-Puyo road	KU902147*	KU902228*	KU902303*	KU902065*
<b>Macropholidus</b>					
<i>M. annectens</i>	QCAZ 11121; Ecuador: Loja: 15 km E Loja	KC894342 <sup>f</sup>	KC894356 <sup>f</sup>	KC894370 <sup>f</sup>	KP874877 <sup>c</sup>
<i>M. huancabambae</i>	CORBIDI 10493; Peru: Piura: Huancabamba: Las Pozas	KC894344 <sup>f</sup>	KC894358 <sup>f</sup>	KC894372 <sup>f</sup>	KP874879 <sup>c</sup>
<i>M. ruthveni</i>	CORBIDI 4281; Peru: Lambayeque: El Totoral	KC894354 <sup>f</sup>	KC894368 <sup>f</sup>	KC894382 <sup>f</sup>	–
<i>M. sp.</i>	CORBIDI 12932; Peru: Piura: Ayabaca: Bosque de Cuyas	KP874774 <sup>c</sup>	KP874826 <sup>c</sup>	KP874936 <sup>c</sup>	KP874881 <sup>c</sup>
<b>Neusticurus</b>					
<i>N. bicarinatus</i>	MRT 968462; Brazil: Mato Grosso: Apiacás	AF420671 <sup>d</sup>	AF420708 <sup>d</sup>	–	AF420816 <sup>d</sup>
<i>N. rudis</i>	MRT 926008; Brazil: Amapá: Serra do Navio	AF420689 <sup>d</sup>	AF420709 <sup>d</sup>	AF420905 <sup>d</sup>	–
<b>Petracola</b>					
<i>P. ventrimaculata</i>	CORBIDI 9235; Peru: Cajamarca	KJ948193 <sup>g</sup>	KJ948144 <sup>g</sup>	KJ948145 <sup>g</sup>	KJ948220 <sup>g</sup>
<i>P. waka</i>	KU 212687; Peru: Cajamarca: Celendin: E slope Abra Gelic, 20 km E Celendin	AY507864 <sup>h</sup>	AY507876 <sup>h</sup>	–	AY507903 <sup>h</sup>
<b>Pholidobolus</b>					
<i>P. affinis</i>	QCAZ 9641; Ecuador: Cotopaxi: San Miguel de Salcedo, Cutuchi River	KC894348 <sup>f</sup>	KC894362 <sup>f</sup>	KC894376 <sup>f</sup>	KP874883 <sup>c</sup>
<i>P. dicrus</i>	QCAZ 5304; Ecuador: Morona-Santiago: Guarumales	KP874776 <sup>c</sup>	KP874828 <sup>c</sup>	KP874938 <sup>c</sup>	KP874885 <sup>c</sup>
<i>P. hillisi</i>	QCAZ 5000; Ecuador: Zamora-Chinchipe: near San Francisco Research Station on Loja-Zamora road	KP090168 <sup>i</sup>	KP090171 <sup>i</sup>	KP090174 <sup>i</sup>	KP874888 <sup>c</sup>
<i>P. macbrydei</i>	QCAZ 9932; Ecuador: Azuay: 20 km on road Cuenca-El Cajas	KC894353 <sup>f</sup>	KC894367 <sup>f</sup>	KC894381 <sup>f</sup>	KP874889 <sup>c</sup>
<i>P. montium</i>	QCAZ 4051; Ecuador: Pichincha: Quito	KC894346 <sup>f</sup>	KC894360 <sup>f</sup>	KC894374 <sup>f</sup>	KP874890 <sup>c</sup>
<i>P. prefrontalis</i>	QCAZ 9908; Ecuador: Chimborazo: Alausí	KC894350 <sup>f</sup>	KC894364 <sup>f</sup>	KC894378 <sup>f</sup>	–



Table 1 (continued)

Taxon	Voucher and locality	GenBank accession number			
		T2S	I6S	ND4	c-mos
<i>P. vertebralis</i>	<b>QCAZ 8688</b> ; Ecuador: Carchi: Chilma Bajo	KP874780 <sup>c</sup>	KP874832 <sup>c</sup>	KP874942 <sup>c</sup>	KP874892 <sup>c</sup>
<i>P. sp.</i>	<b>CORBIDI 12737</b> ; Peru: Cajamarca: Jaen: Huamantanga Forest	KP874788 <sup>c</sup>	KP874840 <sup>c</sup>	KP874949 <sup>c</sup>	KP874898 <sup>c</sup>
<b>Placosoma</b>					
<i>P. cordylinum</i>	<b>LG 1006</b> ; Brazil: Rio de Janeiro: Teresópolis	AF420673 <sup>d</sup>	AF420734 <sup>d</sup>	AF420879 <sup>d</sup>	AF420823 <sup>d</sup>
<i>P. glabellum</i>	<b>LG 940</b> ; Brazil: São Paulo: Iguape	AF420674 <sup>d</sup>	AF420742 <sup>d</sup>	AF420907 <sup>d</sup>	AF420833 <sup>d</sup>
<b>Potamites</b>					
<i>P. ecleopopus</i>	<b>CORBIDI 14382</b> ; Peru: Huánuco: Puerto Inca: Hospital camp from Cordillera del Sira, Lullapichis District	KU902148*	KU902229*	KU902304*	KU902066*
<i>P. ecleopopus</i>	<b>QCAZ 4699</b> ; Ecuador: Pastaza: Sarayacu, on path to Palandayacu River	KU902149*	KU902230*	KU902305*	KU902067*
<i>P. ecleopopus</i>	<b>QCAZ 5208</b> ; Ecuador: Orellana: Yasuni National Park (km 22)	KU902150*	KU902231*	KU902306*	KU902068*
<i>P. ecleopopus</i>	<b>QCAZ 10071</b> ; Ecuador: Morona-Santiago: Napimias	KU902151*	KU902232*	KU902307*	KU902069*
<i>P. ecleopopus</i>	<b>MRT 0472</b> ; Brazil: Mato Grosso: Apicás	AF420656 <sup>d</sup>	AF420748 <sup>d</sup>	AF420890 <sup>d</sup>	AF420829 <sup>d</sup>
<i>P. erythrocularis</i>	<b>CORBIDI 15153</b> ; Peru: Madre de Dios: Tambopata: Manu-Tambopata Corridor	KU902152*	KU902233*	KU902308*	KU902070*
<i>P. erythrocularis</i>	<b>MHNC 10946</b> ; Peru: Cusco: Urubamba	KU902153*	KU902234*	KU902309*	KU902071*
<i>P. juruazensis</i>	<b>CORBIDI 9951</b> ; Peru: San Martín: Picota: Chambirillo (Checkpoint 16, Cordillera Azul National Park)	KU902154*	KU902235*	KU902310*	KU902072*
<i>P. juruazensis</i>	<b>CORBIDI 15479</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	–	KU902236*	KU902311*	KU902073*
<i>P. juruazensis</i>	<b>CORBIDI 15504</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902155*	KU902237*	KU902312*	KU902074*
<i>P. juruazensis</i>	<b>CORBIDI 15550</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902156*	KU902238*	KU902313*	KU902075*
<i>P. juruazensis</i>	<b>CORBIDI 15579</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902157*	KU902239*	KU902314*	KU902076*
<i>P. montanicola</i>	<b>CORBIDI 10791</b> ; Peru: Ayacucho: La Mar: Pampa Aurora	KU902158*	KU902240*	KU902315*	KU902077*
<i>P. strangulatus</i>	<b>KU 212677<sup>h</sup></b> ; Peru: San Martín: Ahuashiyacu falls	AY507847 <sup>h</sup>	AY507866 <sup>h</sup>	AY507885 <sup>h</sup>	–
<i>P. strangulatus</i>	<b>QCAZ 6133</b> ; Ecuador: Napo: Archidona	KU902159*	KU902241*	KU902316*	KU902078*
<i>P. trachodus</i>	<b>CORBIDI 15489</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902160*	KU902242*	KU902317*	KU902079*
<i>P. trachodus</i>	<b>CORBIDI 15514</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902161*	KU902243*	KU902318*	KU902080*
<i>P. trachodus</i>	<b>CORBIDI 15515</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902162*	KU902244*	KU902319*	KU902081*
<b>Proctoporus</b>					
<i>P. bolivianus</i>	<b>MHNC 5357</b> ; Peru: Puno: Patambuco	JX435936 <sup>j</sup>	JX435998 <sup>j</sup>	JX436065 <sup>j</sup>	JX436036 <sup>j</sup>
<i>P. bolivianus</i>	<b>MNCN 43662</b> ; Peru: Puno: between Cuyo and Quebrada Sayaco	JX435934 <sup>j</sup>	JX435993 <sup>j</sup>	JX436063 <sup>j</sup>	JX436035 <sup>j</sup>
<i>P. bolivianus</i>	<b>MNCN 43679</b> ; Bolivia: La Paz: Sorata Valley	JX435943 <sup>j</sup>	JX435997 <sup>j</sup>	JX436069 <sup>j</sup>	JX436043 <sup>j</sup>
<i>P. bolivianus</i>	<b>MNCN 8989</b> ; Bolivia: La Paz: Sorata Valley	JX435940 <sup>j</sup>	JX435994 <sup>j</sup>	JX436071 <sup>j</sup>	JX436040 <sup>j</sup>
<i>P. bolivianus</i> Ca1	<b>MHNC 5322</b> ; Peru: Puno: between Trapiche and Sina	JX435945 <sup>j</sup>	JX435988 <sup>j</sup>	–	JX436045 <sup>j</sup>
<i>P. bolivianus</i> Ca1	<b>UTA R-52945</b> ; Peru: Puno: Laracani	AY968825 <sup>k</sup>	AY968832 <sup>k</sup>	AY968813 <sup>k</sup>	–
<i>P. bolivianus</i> Ca2	<b>AMNH R-150695</b> ; Bolivia: Santa Cruz: Amboró	AY968821 <sup>k</sup>	AY968828 <sup>k</sup>	AY968812 <sup>k</sup>	–
<i>P. bolivianus</i> Ca3	<b>MHNC 6005</b> ; Peru: Cusco: Kosñipata Valley	JX435927 <sup>j</sup>	JX435966 <sup>j</sup>	JX436079 <sup>j</sup>	JX436049 <sup>j</sup>
<i>P. bolivianus</i> Ca5	<b>MHNC 5367</b> ; Peru: Cusco: between Marcapata and Tambopampa	JX435907 <sup>j</sup>	JX435978 <sup>j</sup>	JX436091 <sup>j</sup>	JX436011 <sup>j</sup>
<i>P. bolivianus</i> Ca5	<b>MHNC 5371</b> ; Peru: Cusco: between Marcapata and Tambopampa	JX435908 <sup>j</sup>	JX435969 <sup>j</sup>	JX436093 <sup>j</sup>	JX436013 <sup>j</sup>
<i>P. bolivianus</i> Ca6	<b>UTA R-51487</b> ; Peru: Cusco: Carrizales	AY507850 <sup>h</sup>	–	AY225180 <sup>j</sup>	AY507897 <sup>h</sup>
<i>P. bolivianus</i> Ca6	<b>UTA R-51506</b> ; Peru: Cusco: Piscacucho	AY507851 <sup>h</sup>	AY507869 <sup>h</sup>	AY225175 <sup>j</sup>	AY507898 <sup>h</sup>
<i>P. carabaya</i>	<b>CORBIDI 14709</b> ; Peru: Cusco: Quispicanchis: Capiere	KU902163*	–	KU902320*	KU902082*
<i>P. carabaya</i>	<b>CORBIDI 14710</b> ; Peru: Cusco: Quispicanchis: Capiere	KU902164*	KU902245*	KU902321*	KU902083*
<i>P. carabaya</i>	<b>CORBIDI 14711</b> ; Peru: Cusco: Quispicanchis: Capiere	KU902165*	–	KU902322*	KU902084*
<i>P. carabaya</i>	<b>MHNC 5428</b> ; Peru: Puno: Carabaya: Tambillo	JX435912 <sup>j</sup>	JX435979 <sup>j</sup>	JX436083 <sup>j</sup>	JX436016 <sup>j</sup>
<i>P. carabaya</i>	<b>MHNC 5429</b> ; Peru: Puno: Tambillo	JX435915 <sup>j</sup>	JX435982 <sup>j</sup>	JX436086 <sup>j</sup>	JX436019 <sup>j</sup>
<i>P. carabaya</i>	<b>MNCN 43675</b> ; Peru: Puno: Tambillo	JX435913 <sup>j</sup>	JX435980 <sup>j</sup>	JX436084 <sup>j</sup>	JX436017 <sup>j</sup>
<i>P. carabaya</i>	<b>MNCN 43676</b> ; Peru: Puno: Tambillo	JX435914 <sup>j</sup>	JX435981 <sup>j</sup>	JX436085 <sup>j</sup>	JX436018 <sup>j</sup>
<i>P. chasqui</i>	<b>CORBIDI 8416</b> ; Peru: La Mar: Ayacucho, Chiquintirca	KU902166*	KU902246*	KU902323*	KU902085*
<i>P. chasqui</i>	<b>CORBIDI 8431</b> ; Peru: La Mar: Ayacucho, Chiquintirca	KU902167*	KU902247*	KU902324*	KU902086*
<i>P. chasqui</i>	<b>CORBIDI 8478</b> ; Peru: Cusco: La Convención: KP 55, Poyentimari Native Community	KU902168*	KU902248*	KU902325*	KU902087*
<i>P. chasqui</i>	<b>MNCN 6771</b> ; Peru: Ayacucho: between Abra Tapuna and San Francisco	JX435887 <sup>j</sup>	JX435946 <sup>j</sup>	JX436051 <sup>j</sup>	JX436003 <sup>j</sup>
<i>P. chasqui</i>	<b>MNCN 44407</b> ; Peru: Ayacucho: between Abra Tapuna and San Francisco	JX435888 <sup>j</sup>	JX435947 <sup>j</sup>	JX436052 <sup>j</sup>	JX436004 <sup>j</sup>
<i>P. chasqui</i>	<b>MNCN 44408</b> ; Peru: Ayacucho: between Abra Tapuna and San Francisco	JX435889 <sup>j</sup>	JX435948 <sup>j</sup>	JX436053 <sup>j</sup>	JX436005 <sup>j</sup>
<i>P. guentheri</i>	<b>UTA R-51515</b> ; Peru: Cusco: Chocalloc	AY507849 <sup>h</sup>	AY507872 <sup>h</sup>	AY225185 <sup>j</sup>	AY507900 <sup>h</sup>
<i>P. guentheri</i>	<b>UTA R-51517</b> ; Peru: Cusco: Machu Picchu	AY507854 <sup>h</sup>	AY507873 <sup>h</sup>	AY225169 <sup>j</sup>	AY507901 <sup>h</sup>
<i>P. iridescens</i>	<b>MHNC 5651</b> ; Peru: Puno: between Huancasarani and Limbani	JX435921 <sup>j</sup>	JX435961 <sup>j</sup>	JX436073 <sup>j</sup>	–
<i>P. iridescens</i>	<b>MNCN 43666</b> ; Peru: Puno: between Huancasarani and Limbani	JX435922 <sup>j</sup>	JX435957 <sup>j</sup>	JX436072 <sup>j</sup>	JX436008 <sup>j</sup>
<i>P. iridescens</i>	<b>MNCN 43668</b> ; Peru: Puno: between Ollachea and Corani	JX435911 <sup>j</sup>	JX435962 <sup>j</sup>	JX436089 <sup>j</sup>	JX436014 <sup>j</sup>
<i>P. iridescens</i>	<b>MNCN 44224</b> ; Peru: Puno: between Usicayos and Quetapalo	JX435920 <sup>j</sup>	JX435987 <sup>j</sup>	JX436078 <sup>j</sup>	JX436021 <sup>j</sup>
<i>P. kiziriani</i>	<b>MNCN 4751</b> ; Peru: Cusco: Marcapata Valley	JX435904 <sup>j</sup>	JX435977 <sup>j</sup>	JX436097 <sup>j</sup>	JX436048 <sup>j</sup>
<i>P. kiziriani</i>	<b>MNCN 44218</b> ; Peru: Cusco: Marcapata Valley	JX435903 <sup>j</sup>	JX435973 <sup>j</sup>	–	JX436023 <sup>j</sup>
<i>P. kiziriani</i>	<b>MNCN 44221</b> ; Peru: Cusco: Marcapata Valley	JX435902 <sup>j</sup>	JX435983 <sup>j</sup>	JX436095 <sup>j</sup>	JX436047 <sup>j</sup>
<i>P. lacertus</i>	<b>UTA R-51484</b> ; Peru: Cusco: Canchayoc	AY968820 <sup>k</sup>	AY968827 <sup>k</sup>	AY225182 <sup>j</sup>	–
<i>P. laudahnae</i>	<b>CORBIDI 15558</b> ; Peru: Huánuco: Leoncio Prado: La Garganta camp-Tingo María National Park	KU902171*	KU902250*	KU902328*	KU902090*
<i>P. laudahnae</i>	<b>CORBIDI 15743</b> ; Peru: Huánuco: Leoncio Prado: La Garganta camp-Tingo María National Park	KU902172*	KU902251*	KU902329*	KU902091*
<i>P. oreades</i>	<b>CORBIDI 7217</b> ; Peru: Pasco: Oxapampa: Santa Barbara	KU902173*	KU902252*	KU902330*	KU902092*
<i>P. oreades</i>	<b>CORBIDI 7218</b> ; Peru: Pasco: Oxapampa: Santa Barbara	KU902174*	KU902253*	KU902331*	KU902093*
<i>P. oreades</i>	<b>CORBIDI 7225</b> ; Peru: Pasco: Oxapampa: Santa Barbara	KU902175*	KU902254*	KU902332*	KU902094*
<i>P. pachyurus</i>	<b>CORBIDI 11807</b> ; Peru: Junín: Tarma: Palca District (Anexo Huandunga)	KU902176*	–	KU902333*	KU902095*
<i>P. pachyurus</i>	<b>CORBIDI 11810</b> ; Peru: Junín: Tarma: Palca District (Anexo Huandunga)	KU902177*	–	KU902334*	KU902096*
<i>P. pachyurus</i>	<b>CORBIDI 11811</b> ; Peru: Junín: Tarma: Palca District (Anexo Huandunga)	KU902178*	KU902255*	KU902335*	KU902097*

(continued on next page)

Table 1 (continued)

Taxon	Voucher and locality	GenBank accession number			
		12S	16S	ND4	c-mos
<i>P. pachyurus</i>	<b>MHNC 4689</b> ; Peru: Cusco: Kosñipata Valley	JX435892 <sup>j</sup>	JX435951 <sup>j</sup>	JX436057 <sup>j</sup>	JX436026 <sup>i</sup>
<i>P. rahmi</i>	<b>CORBIDI 14705</b> ; Peru: Cusco: Quispicanchi: Capire	KU902179*	KU902256*	KU902336*	KU902098*
<i>P. rahmi</i>	<b>CORBIDI 14706</b> ; Peru: Cusco: Quispicanchi: Capire	KU902180*	KU902257*	KU902337*	KU902099*
<i>P. rahmi</i>	<b>CORBIDI 14707</b> ; Peru: Cusco: Quispicanchi: Capire	KU902181*	KU902258*	KU902338*	KU902100*
<i>P. spinalis</i>	<b>CORBIDI 7234</b> ; Peru: Pasco: Oxapampa: Osaplaya	KU902182*	KU902259*	KU902339*	KU902101*
<i>P. spinalis</i>	<b>CORBIDI 7241</b> ; Peru: Pasco: Oxapampa: Osaplaya	KU902183*	KU902260*	KU902340*	KU902102*
<i>P. spinalis</i>	<b>CORBIDI 7246</b> ; Peru: Pasco: Oxapampa: Osaplaya	KU902184*	KU902261*	KU902341*	KU902103*
<i>P. spinalis</i>	<b>CORBIDI 11573</b> ; Peru: Pasco: Oxapampa: Sholl'et Forest	KU902185*	–	KU902342*	KU902104*
<i>P. spinalis</i>	<b>CORBIDI 11575</b> ; Peru: Pasco: Oxapampa: Sholl'et Forest	KU902186*	–	KU902343*	KU902105*
<i>P. sucullucu</i>	<b>MNCN 44475</b> ; Peru: Ayacucho: between Punqui and Anco	JX435895 <sup>j</sup>	JX435954 <sup>j</sup>	JX436058 <sup>j</sup>	JX436029 <sup>i</sup>
<i>P. sucullucu</i>	<b>MNCN 44476</b> ; Peru: Ayacucho: between Punqui and Anco	JX435897 <sup>j</sup>	JX435955 <sup>j</sup>	JX436060 <sup>j</sup>	JX436030 <sup>i</sup>
<i>P. sucullucu</i>	<b>MNCN 44478</b> ; Peru: Ayacucho: between Punqui and Anco	JX435896 <sup>j</sup>	JX435956 <sup>j</sup>	JX436059 <sup>j</sup>	JX436044 <sup>j</sup>
<i>P. sucullucu</i>	<b>UTA R-51478</b> ; Peru: Cusco: Kusilluchayoc	AY507857 <sup>h</sup>	AY507878 <sup>h</sup>	AY225171 <sup>l</sup>	AY507905 <sup>h</sup>
<i>P. sucullucu</i>	<b>UTA R-51496</b> ; Peru: Cusco: Piscacucho	AY507858 <sup>h</sup>	AY507879 <sup>h</sup>	AY225177 <sup>l</sup>	AY507906 <sup>h</sup>
<i>P. unsaacae</i>	<b>CORBIDI 10562</b> ; Peru: Cusco: Colquemarca-Charamuray	KU902187*	KU902262*	–	KU902106*
<i>P. unsaacae</i>	<b>UTA R-51475</b> ; Peru: Cusco: Pisac	AY968819 <sup>k</sup>	–	AY225174 <sup>l</sup>	–
<i>P. unsaacae</i>	<b>UTA R-51477</b> ; Peru: Cusco: Saqsayhuaman	AY507860 <sup>h</sup>	AY507882 <sup>h</sup>	AY225170 <sup>l</sup>	AY507909 <sup>h</sup>
<i>P. unsaacae</i>	<b>UTA R-51479</b> ; Peru: Cusco: Pisac	AY968818 <sup>k</sup>	–	AY225172 <sup>l</sup>	–
<i>P. unsaacae</i>	<b>UTA R-51488</b> ; Peru: Cusco: Quellouno	AY507859 <sup>h</sup>	AY507881 <sup>h</sup>	AY225186 <sup>l</sup>	AY507908 <sup>h</sup>
<i>P. xestus</i>	<b>MNCN 2425</b> ; Bolivia: La Paz: between Lambate and Totoral	JX435899 <sup>j</sup>	JX436001 <sup>j</sup>	JX436100 <sup>j</sup>	JX436007 <sup>i</sup>
<i>P. xestus</i>	<b>MNCN 6160</b> ; Bolivia: Cochabamba: Cochabamba	JX435898 <sup>j</sup>	JX436002 <sup>j</sup>	JX436101 <sup>j</sup>	–
<i>P. sp.</i>	<b>MHNC 6834</b> ; Peru: Cusco: Kimbiri River	JX435890 <sup>j</sup>	JX435949 <sup>j</sup>	JX436054 <sup>j</sup>	JX436006 <sup>i</sup>
<i>P. sp.</i>	<b>MHNC 11439</b> ; Peru: Cusco: Marcapata Valley	JX435893 <sup>j</sup>	JX435950 <sup>j</sup>	JX436056 <sup>j</sup>	JX436050 <sup>i</sup>
<i>P. sp. 1</i>	<b>CORBIDI 14624</b> ; Peru: Huánuco: Huánuco: Huanacaure community	KU902188*	KU902263*	KU902344*	KU902107*
<i>P. sp. 1</i>	<b>CORBIDI 14625</b> ; Peru: Huánuco: Huánuco: Huanacaure community	KU902189*	KU902264*	KU902345*	KU902108*
<i>P. sp. 1</i>	<b>CORBIDI 14626</b> ; Peru: Huánuco: Huánuco: Huanacaure community	KU902190*	KU902265*	KU902346*	KU902109*
<i>P. sp. 2</i>	<b>CORBIDI 9636</b> ; Peru: Ayacucho: Yuccay river	KU902191*	KU902266*	KU902347*	KU902110*
<i>P. sp. 2</i>	<b>CORBIDI 10753</b> ; Peru: Ayacucho: Yuccay	KU902192*	KU902267*	KU902348*	KU902111*
<i>P. sp. 2</i>	<b>CORBIDI 10754</b> ; Peru: Ayacucho: Yuccay	KU902193*	KU902268*	KU902349*	KU902112*
<i>P. sp. 2</i>	<b>CORBIDI 10755</b> ; Peru: Ayacucho: Yuccay	KU902194*	KU902269*	KU902350*	KU902113*
<i>P. sp. 3</i>	<b>CORBIDI 14692</b> ; Peru: Cusco: Quispicanchis: Capire	KU902169*	–	KU902326*	KU902088*
<i>P. sp. 3</i>	<b>CORBIDI 14693</b> ; Peru: Cusco: Quispicanchis: Capire	KU902170*	KU902249*	KU902327*	KU902089*
<b>Riama</b>					
<i>R. anatorloros</i>	<b>QCAZ 9203</b> ; Ecuador: Napo: Santa Rosa, Tigre protected forest, La Cascada protected forest and Sumaco Biosphere Reserve	KU902195*	KU902270*	KU902351*	KU902114*
<i>R. balneator</i>	<b>QCAZ 11099</b> ; Ecuador: Tungurahua: San Antonio de Puntzan (mountains), Don Nelson Palacios estate	KU902196*	KU902271*	KU902352*	KU902115*
<i>R. cashcaensis</i>	<b>QCAZ 10754</b> ; Ecuador: Bolívar: La Moya, on road Guanujo-Salinas	KJ948181 <sup>g</sup>	KJ948126 <sup>g</sup>	KJ948163 <sup>g</sup>	KJ948219 <sup>g</sup>
<i>R. colomaromani</i>	<b>KU 217209</b> ; Ecuador: Carchi: 26.9–27.3 km on road Maldonado-Tulcán	AY507853 <sup>h</sup>	AY507871 <sup>h</sup>	AY507888 <sup>h</sup>	AY507899 <sup>h</sup>
<i>R. labionis</i>	<b>QCAZ 10411</b> ; Ecuador: Cotopaxi: Naranjito, Bosque Integral Otonga reserve	KJ948171 <sup>g</sup>	KJ948120 <sup>g</sup>	KJ948147 <sup>g</sup>	KJ948218 <sup>g</sup>
<i>R. meleagris</i>	<b>QCAZ 9840</b> ; Ecuador: Tungurahua: Mucubí	KJ948182 <sup>g</sup>	KJ948129 <sup>g</sup>	KJ948164 <sup>g</sup>	KJ948214 <sup>g</sup>
<i>R. orcesi</i>	<b>QCAZ 10569</b> ; Ecuador: Napo: Antisana Ecological Reserve, Virgen de Guacamayos	KU902197*	KU902272*	KU902353*	KU902116*
<i>R. simotera</i>	<b>KU 217207</b> ; Ecuador: Carchi: 15.3 km on road Tulcán-Tufino	AY507856 <sup>h</sup>	AY507875 <sup>h</sup>	AY507890 <sup>h</sup>	AY507902 <sup>h</sup>
<i>R. stigmatoral</i>	<b>QCAZ 11412</b> ; Ecuador: Azuay: San Vicente, road to the antennas	KJ948189 <sup>g</sup>	KJ948124 <sup>g</sup>	KJ948158 <sup>g</sup>	KJ948209 <sup>g</sup>
<i>R. unicolor</i>	<b>QCAZ 9682</b> ; Ecuador: Imbabura: Cotacachi-Cayapas Ecological reserve, trail near Cuicocha Lake	KJ948188 <sup>g</sup>	KJ948138 <sup>g</sup>	KJ948157 <sup>g</sup>	KJ948205 <sup>g</sup>
<i>R. yumborum</i>	<b>QCAZ 10827</b> ; Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KJ948195 <sup>g</sup>	KJ948142 <sup>g</sup>	KJ948170 <sup>g</sup>	KJ948216 <sup>g</sup>
<b>Unnamed clade 1</b>					
Cercosaurinae sp. 1	<b>CORBIDI 14965</b> ; Peru: Huánuco: Huánuco: Santa Clara	KU902198*	KU902273*	KU902354*	KU902117*
Cercosaurinae sp. 1	<b>CORBIDI 15573</b> ; Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902199*	KU902274*	KU902355*	KU902118*
<b>Unnamed clade 2</b>					
Cercosaurinae sp. 2	<b>CORBIDI 8815</b> ; Peru: Huancavelica: Mantaro Valley	KU902200*	KU902275*	KU902356*	KU902119*
Cercosaurinae sp. 2	<b>CORBIDI 13634</b> ; Peru: Huancavelica: Tayacaja: Colcabamba-Quinta District	KU902201*	KU902276*	KU902357*	KU902120*
Cercosaurinae sp. 2	<b>CORBIDI 13636</b> ; Peru: Huancavelica: Tayacaja: Colcabamba-Quinta District	KU902202*	KU902277*	KU902358*	KU902121*
<b>Unnamed clade 3</b>					
Cercosaurinae sp. 3	<b>CORBIDI 15117</b> ; Peru: San Martín: Mariscal Cáceres: Laurel	KU902203*	KU902278*	KU902359*	KU902122*
Cercosaurinae sp. 3	<b>CORBIDI 15118</b> ; Peru: San Martín: Mariscal Cáceres: Laurel	KU902204*	KU902279*	KU902360*	KU902123*
Cercosaurinae sp. 3	<b>CORBIDI 15119</b> ; Peru: San Martín: Mariscal Cáceres: Laurel	KU902205*	KU902280*	KU902361*	KU902124*
Cercosaurinae sp. 3	<b>QCAZ 12798</b> ; Ecuador: Napo: Wildsumaco Wildlife Sanctuary, Wildsumaco Lodge, surroundings of the lodge	KU902206*	KU902281*	KU902362*	KU902125*
Cercosaurinae sp. 3	<b>QCAZ 12891</b> ; Ecuador: Zamora-Chinchi: El Pangui, Wawayme River Basin, Concession ECSA-viewpoint	KU902207*	KU902282*	KU902363*	KU902126*
<b>Outgroups</b>					
<i>Alopoglossus viridiceps</i>	<b>QCAZ 10670</b> ; Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KP874789 <sup>c</sup>	KP874841 <sup>c</sup>	KJ705316 <sup>m</sup>	KP874899 <sup>c</sup>
<i>Bachia flavescens</i>	<b>LSUMZ H12977</b> ; Brazil: Pará: Santarém: Agropecuária Treviso	AF420705 <sup>d</sup>	AF420753 <sup>d</sup>	AF420869 <sup>d</sup>	AF420859 <sup>d</sup>
<i>Eclipseus gaudichaudii</i>	<b>LG 1356</b> ; Brazil: São Paulo: Boissucanga	AF420660 <sup>d</sup>	AF420738 <sup>d</sup>	AF420901 <sup>d</sup>	AF420855 <sup>d</sup>

Table 1 (continued)

Taxon	Voucher and locality	GenBank accession number			
		12S	16S	ND4	c-mos
<i>Gymnophthalmus leucomystax</i>	<b>MRT 946613</b> ; Brazil: Roraima: Fazenda Salvamento	AF420675 <sup>d</sup>	AF420715 <sup>d</sup>	AF420906 <sup>d</sup>	AF420824 <sup>d</sup>
<i>Rhachisaurus brachylepis</i>	<b>MRT 887336</b> ; Brazil: Minas Gerais: Serra do Cipó	AF420665 <sup>d</sup>	AF420737 <sup>d</sup>	AF420877 <sup>d</sup>	AF420853 <sup>d</sup>
<i>Riolama inopinata</i>	<b>IRSNB 2680</b> ; Venezuela: Bolívar: Murisipán-tepui	–	KP283384 <sup>b</sup>	KP283395 <sup>b</sup>	KP283388 <sup>b</sup>
<i>R. leucosticta</i>	<b>VUB 3767</b> ; Venezuela: Bolívar: Yuruani-tepui	–	JQ742254 <sup>a</sup>	KP283396 <sup>b</sup>	KP283389 <sup>b</sup>

<sup>a</sup> Kok et al. (2012).<sup>b</sup> Kok (2015).<sup>c</sup> Torres-Carvajal et al. (2015).<sup>d</sup> Pellegrino et al. (2001).<sup>e</sup> Fu (2000).<sup>f</sup> Torres-Carvajal and Mafra-Endara (2013).<sup>g</sup> Aguirre-Peñañiel et al. (2014).<sup>h</sup> Castoe et al. (2004).<sup>i</sup> Torres-Carvajal et al. (2014).<sup>j</sup> Goicoechea et al. (2012).<sup>k</sup> Doan et al. (2005).<sup>l</sup> Doan and Castoe (2003).<sup>m</sup> Torres-Carvajal and Lobos (2014).

<sup>n</sup> This specimen was originally listed as KU 21677 by Castoe et al. (2004); however, this number does not correspond to any specimen of *Potamites* deposited at KU. Most likely, the specimen sequenced by Castoe et al. (2004) was KU 212677, a *P. strangulatus* from the Ahuashiyacu falls in Peru.

on preliminary analyses, we simplified the model partition scheme for nucleotide data described in Section 2.3 in order to reach convergence and obtain acceptable ESS values (i.e., ESS > 200) for all parameters as follows: (1) all mitochondrial genes (GTR + G); (2) *c-mos* (HKY + G). The analyses were conducted under a model with uncorrelated substitution rates among branches and the rate for each branch drawn independently from an underlying lognormal distribution (Drummond et al., 2006); a Yule prior was used for the tree. Ancestral areas were inferred under a symmetric substitution model and a strict clock. We performed three runs of 10<sup>7</sup> generations sampling parameters and trees every 1000 generations. Results were analyzed in Tracer v1.6 (Rambaut and Drummond, 2007) to assess convergence and effective sample sizes for all parameters. After a 10% burn-in, we selected the maximum clade credibility tree (i.e., the tree in the posterior sample that has the maximum sum of posterior probabilities on its *n* – 2 internal nodes) from a sample of 27,000 trees, and calculated posterior probabilities on that tree using TreeAnnotator 1.8.3 (Rambaut and Drummond, 2016). Additional details on the analysis performed in BEAST are included in the corresponding xml file presented as Supplementary material. Both BEAST and RAxML analyses were carried out in the CIPRES Science Gateway (Miller et al., 2010).

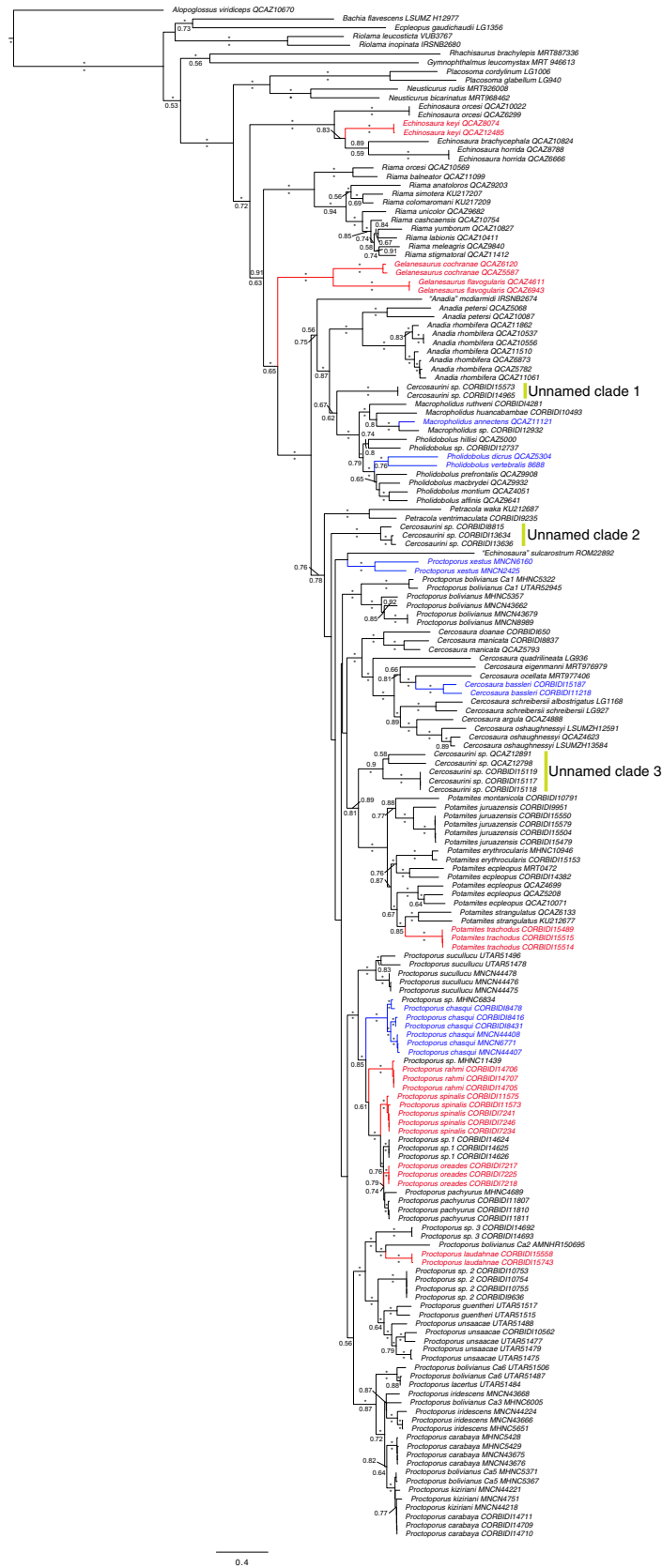
### 3. Results

ML and Bayesian analyses yielded similar tree topologies, with discrepancies occurring at nodes with low support. The differences between both trees are restricted to the position of four taxa: *Petracola waka*, *Echinosaura sulcarostrum*, *Proctoporus xestus* and an unnamed clade. Here we choose the ML tree as our preferred hypothesis of phylogenetic relationships among Cercosaurinae lizards (Fig. 2). The Bayesian tree is presented as Supplementary material.

#### 3.1. Paraphyletic taxa and new clades

While our tree supports strongly (PP = 1; BB = 1) the monophyly of Cercosaurinae, it shows that six taxa traditionally ranked as genera of Cercosaurinae—*Anadia*, *Echinosaura*, *Euspondylus*, *Potamites*, *Proctoporus*, and *Riama*—are not monophyletic (Fig. 2). The two Andean species of *Anadia* included in this study, *Anadia petersi*

and *A. rhombifera* are not sister to the Tepuian *A. mcdiarmidi*. Relationships among included species of *Echinosaura* (i.e., *E. brachycephala*, *E. horrida*, *E. orcesi*, *E. sulcarostrum*) show that *E. sulcarostrum* is not included within *Echinosaura*; instead, this species is sister with low support to *Proctoporus xestus*. Moreover, remaining species of *Echinosaura* form a strongly supported clade (PP = 1; BB = 1) that includes *Teuchocercus keyi*; for this reason, we propose *Echinosaura keyi* as a new combination for this taxon. Species of *Riama* form a clade (PP = 1; BB = 1), except for *R. laudahnae*, which is nested within a distantly related clade with other species currently allocated in *Proctoporus* (see below). Within *Riama*, there is a basal split between two strongly supported clades, (*R. balneator*, *R. orcesi*) and (*R. anatoloros*, ((*R. simotera*, *R. colomaromani*), (*R. unicolor*, (*R. cashcaensis*, ((*R. meleagris*, *R. stigmatoral*), (*R. yumborum*, *R. labionis*)))))). Species of *Potamites* form a strongly supported clade (PP = 1; BB = 1) except for *P. cochranae* and *P. flavogularis*, which are distantly related to the remaining species of *Potamites*, and form a previously unidentified clade (PP = 1; BB = 1) herein named *Gelanesaurus* (see Section 4.4). Within *Potamites*, *P. ecleopus* is paraphyletic, with samples from Ecuador forming a clade sister to *P. strangulatus*. Within the latter, we recognize *P. strangulatus trachodus* and *P. strangulatus strangulatus* as two distinct species (*P. trachodus* and *P. strangulatus*, respectively) because they are separated by branches that are similar in length to other branches separating sister species within *Potamites* (e.g., *P. montanica* and *P. juruazensis*). Moreover, allopatry and morphology also support recognition of *P. trachodus* and *P. strangulatus* as two distinct species (Uzzell, 1966). The clade ((*P. strangulatus*, *P. trachodus*), *Potamites ecleopus* [Ecuador]) is sister to (*P. ecleopus* [Peru and Brazil], *P. erythrocularis*); together they form a clade sister to (*P. montanica*, *P. juruazensis*). Species of *Euspondylus* included in our study (i.e., *E. oreades*, *E. rahmi*, and *E. spinalis*) are nested within a strongly supported clade that also includes *Proctoporus succullucu*, *P. chasqui*, *P. pachyurus*, and one undescribed species of *Proctoporus* (*P. sp. 1*). This clade is sister, although with low support, to another clade containing ((*P. sp. 2*, (*P. guentheri*, *P. unsaaca*)), ((*"Riama"* *laudahnae*, *P. bolivianus* [part]), *P. sp. 3*)) as sister to a clade including *P. lacertus* and paraphyletic taxa *P. bolivianus*, *P. iridescens*, *P. kizirianus*, and *P. carabaya*. Other species of *Proctoporus* are split into two separate clades. One clade includes *P. bolivianus* (part), while the other contains *P. xestus* as sister to *Echinosaura sulcarostrum*.



**Fig. 2.** Phylogeny of Cercosaurinae. Maximum-likelihood tree obtained from an analysis of 175 specimens, three mitochondrial genes (12S, 16S, ND4) and one nuclear gene (*c-mos*). Numbers above branches correspond to Bayesian posterior probability (PP) values; asterisks represent  $PP \geq 0.95$ . Numbers below branches are ML bootstrap support (BB) values; asterisks represent  $BB \geq 0.90$ . PP and BB values  $< 0.50$  are not shown. Monophyly of Cercosaurinae has maximum support ( $PP = 1$ ,  $BB = 1$ ). Voucher numbers of specimens are indicated for each terminal. Taxonomic changes proposed in this paper are adopted; new combinations are shown in red. Recent combinations based on molecular phylogenies (Goicoechea et al., 2012; Torres-Carvajal and Mafra-Endara, 2013; Torres-Carvajal et al., 2015) are shown in blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Both Bayesian and ML analyses also yielded three unnamed clades (UC) composed of specimens that we could not assign to any of the currently recognized clades traditionally ranked as genera. UC1 is sister to the (*Macropholidus*, *Pholidobolus*) clade, although with low support (Fig. 2). UC2 is sister to a large clade containing UC3, *Echinosaura sulcarostrum*, *Cercosaura* (Torres-Carvajal et al., 2015), “*Euspondylus*”, “*Proctoporus*”, and *Potamites*. UC3 is sister to *Potamites*.

### 3.2. Phylogeny of Cercosaurinae

Our tree (Fig. 2) is generally congruent with previous molecular phylogenies (Castoe et al., 2004; Kok, 2015; Torres-Carvajal et al., 2015). The clade (*Neusticurus*, *Placosoma*) is placed basally as sister to all other Cercosaurinae taxa. Following branching order in Fig. 2, the same is true for *Echinosaura*, *Riama*, and *Gelanesaurus*, respectively. The remaining taxa are nested in two large clades. The first clade has *Anadia mcdiarmidi* as sister to clade (*Anadia rhombifera*, *A. petersi*), (UC1, (*Macropholidus*, *Pholidobolus*)). In the second clade *Petracola*, UC2, and subclade (*Proctoporus xestus*, *Echinosaura sulcarostrum*) are each placed, in branching order, as sister to all remaining species, which are in turn nested within the following clades: *Cercosaura*, *Potamites*, UC3 and two “*Proctoporus*” clades (see Section 3.1). Deep relationships within the largest *Proctoporus* clades are not clearly resolved (Fig. 2, see also Supplementary material).

### 3.3. Ancestral areas and divergence times

Results of the chronobiogeographical analysis are summarized in Fig. 3 and Table 2. Cercosaurinae lizards originated 59.25 Ma (high posterior density interval [HPD] = 57.35–61.09), most likely in the Northern Andes (43.07% probability), although the other areas, except the Central Andes, have probabilities between ~11% and 20% of representing the ancestral area for this clade. If we exclude the basal lineages *Placosoma* and *Neusticurus*, currently distributed in the Atlantic forest, Guiana Shield and Amazon basin, the Northern Andes represent the ancestral area of remaining Cercosaurinae taxa with a probability of 90.28% (Fig. 3). Cercosaurinae lizards colonized the Central Andes multiple times in subsequent splits. The clade containing *Petracola*, *Cercosaura*, *Potamites*, *Proctoporus*, and Unnamed Clades 2 & 3, mostly represented by Central Andean taxa, originated 32.42 Ma (HPD = 29.58–35.25) in the Central Andes with a probability of 54.73% (Northern Andes = 45.26%). Moreover, the least inclusive clade containing *Potamites*, *Proctoporus*, and Unnamed Clades 2 & 3 originated 26.48 Ma (HPD = 23.41–29.51) in the Central Andes with a probability of 93.77%. Node ages of other taxa are presented in Table 2.

## 4. Discussion

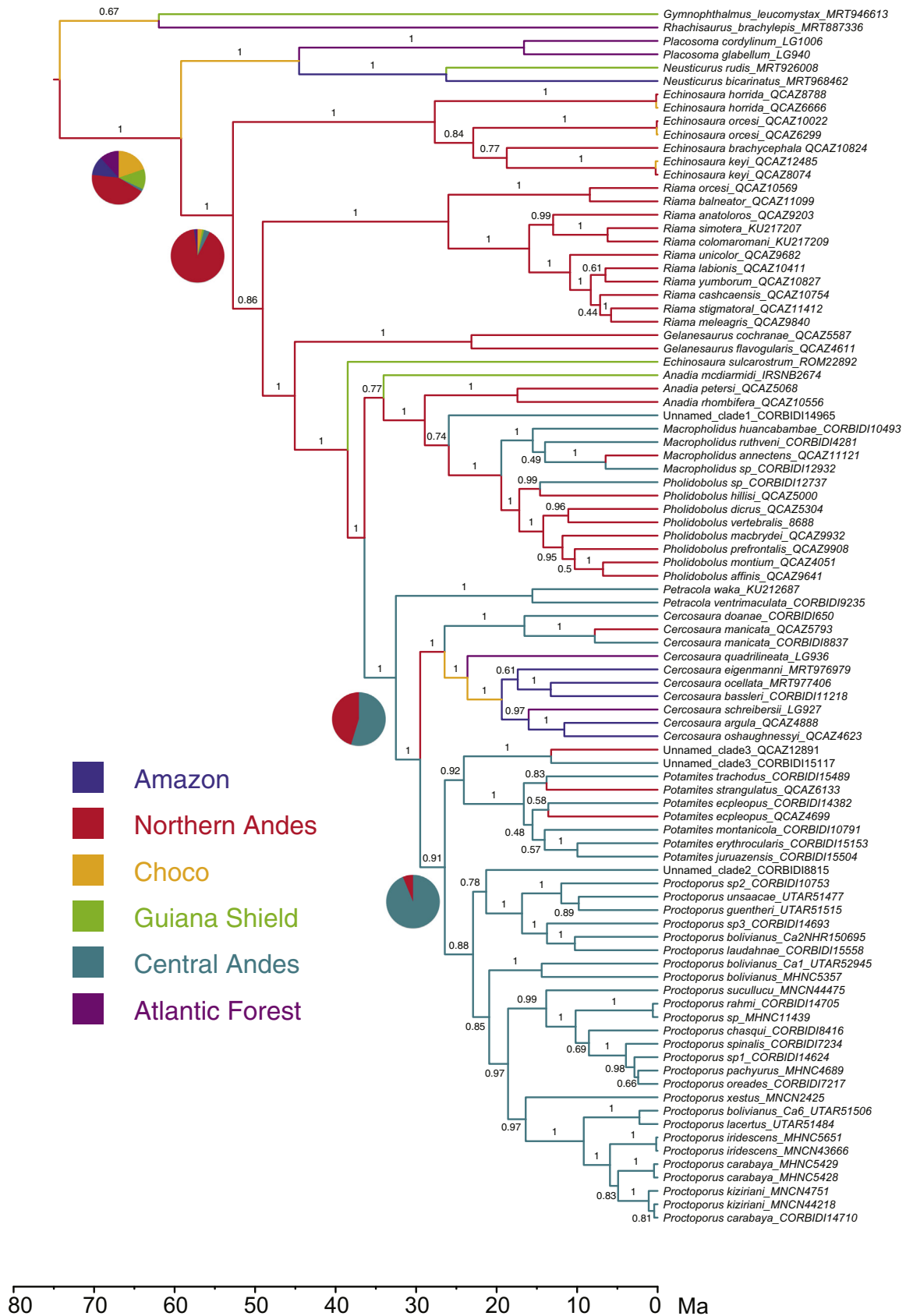
### 4.1. Radiation of Cercosaurinae lizards along the Andes

The complex geography, orogeny and biodiversity of the Andes mountains of South America have attracted the attention of many biologists interested in explaining the evolution and distribution of Andean organisms (e.g., Castroviejo-Fisher et al., 2014; Chaves et al., 2011; Goicoechea et al., 2012; Graham et al., 2004; Hillis, 1985; Patton and Smith, 1992; Torres-Carvajal, 2007; Vuilleumier, 1969). This 8000-km-long mountain chain is divided in three main segments of distinct orientation separated by two major bends (Jaillard et al., 2000). One of these segments corresponds to the 2000 km-long northern Andes (NA), which have a NNE–SSW orientation, and extend from easternmost Venezuela

to northernmost Peru (12°N–5°S). Similar in length to the NA, the central Andes (CA) have a NW–SE orientation and extend from northern Peru to Bolivia and northern Chile (5°S–18°S). It has long been known that most species of Cercosaurinae lizards occur either in the NA or CA (Fig. 3), but the question of how these lizards radiated along these Andean segments has been poorly explored. Based on a phylogenetic analysis of *Proctoporus/Riama* lizards, Doan (2003) proposed the south-to-north speciation hypothesis (SNSH), which predicts a pattern of cladogenesis of Andean species following the rise of the Andes (i.e., from south to north), with basal lineages occurring in southern areas and derived ones in northern areas. Interestingly, the SNSH was later rejected for *Proctoporus* lizards based on a phylogenetic analysis with increased character and taxon sampling (Goicoechea et al., 2012), as it has been rejected for other organisms such as glassfrogs (Castroviejo-Fisher et al., 2014). However, the SNSH seems to hold true at least for some taxa in the NA (e.g., *Pholidobolus*; Torres-Carvajal and Mafla-Endara, 2013). Our results are not in agreement with the SNSH, at least at a large phylogenetic scale. First, the distribution of the most recent common ancestor of Cercosaurinae remains equivocal, possibly because in addition to the Andean taxa, the most basal lineages (*Placosoma* and *Neusticurus*) also occur in the Atlantic forest, Amazon and Guiana Shield (Fig. 3). Nonetheless, according to our chronobiogeographical analysis, ancestors of the ‘Major Andean Clade’ (MAC; i.e., Cercosaurinae excluding *Placosoma* and *Neusticurus*) first colonized the NA most likely in the Paleocene ~60 Ma, when the NA were starting to rise (Gregory-Wodzicki, 2000). The most basal lineages in the MAC—*Echinosaura*, *Riama*, *Gelanesaurus*—are 23–27 Ma old and have mostly radiated along the NA, suggesting that the uplift of the NA had a major impact on their evolution. Only subsequent splits in the MAC led to lineages colonizing the CA for the first time, as well as others spreading back into the Guiana Shield (e.g., “*Echinosaura*” *sulcarostrum*), Amazon (e.g., *Cercosaura argula*), and Atlantic forest (e.g., *Cercosaura quadrilineata*). Among the Central Andean taxa, some are members of clades that also include NA species (e.g., *Macropholidus*, *Pholidobolus*, *Potamites*), whereas others have radiated exclusively along the CA, with *Proctoporus* + Unnamed Clade 2 (if monophyletic, see Section 4.3.2) being the most successful radiation (~22 Ma old) in terms of diversity.

### 4.2. Phylogeny of Cercosaurinae

As with other diverse taxa (e.g., *Anolis*), an accurate estimation of the phylogeny of Gymnophthalmidae is hampered by limited taxon and character sampling (Graybeal, 1998; Heath et al., 2008; Zwickl and Hillis, 2002). Consequently, proposing a taxonomic classification that reflects phylogeny is challenging. The clade Cercosaurinae is of special interest because it includes about 50% of the diversity of gymnophthalmid lizards. Although recent molecular phylogenies of Cercosaurinae include a limited number of taxa, they demonstrate frequently that some traditional classifications based on morphological characters are misleading (Castoe et al., 2004; Goicoechea et al., 2012; Kok, 2015; Pellegrino et al., 2001; Torres-Carvajal and Mafla-Endara, 2013; Torres-Carvajal et al., 2015), highlighting the importance of using DNA sequences to infer the phylogeny of gymnophthalmid lizards as a framework to achieve more appropriate classifications. In this study we focused on increasing taxon sampling and analyzed more than twice the species of Cercosaurinae presented in previous studies. One of the most dramatic results of this study is the paraphyly of *Potamites*, which led us to propose a new clade name, *Gelanesaurus*, that includes two species distantly related to *Potamites*: *G. cochraniae* and *G. flavogularis*. Previous studies included only one specimen each of *Potamites ecleopus*, *P. juruazensis* and *P.*



**Fig. 3.** Phylogenetic tree of Cercosaurinae, with divergence time estimates in millions of years. This maximum clade credibility tree (Log Clade Credibility =  $-9.07828$ ) was chosen from 27,000 trees resulting from a Bayesian chronobiogeographic analysis of 91 taxa, 1844 nucleotide positions and one discrete character (geographical distribution, see Section 2.4). Numbers next to branches correspond to posterior probability (PP) values. Branches are colored according to the most probable posterior location of their child nodes. A pie chart describing the probability of each inferred area is presented near nodes discussed in the text (see Sections 3.3 and 4.1). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

Node ages of representative Cercosaurinae lizard lineages in millions of years. For each node the estimated age along with the 95% high posterior density interval (95% HPD, the shortest interval that contains 95% of the sampled values) are presented. Node ages correspond to the calibrated tree presented in Fig. 3.

Clade/taxon	Node age	
	Age	95% HPD
Cercosaurinae	59.25	57.35–61.09
( <i>Neusticurus</i> , <i>Placosoma</i> )	44.52	42.62–46.43
<i>Neusticurus</i>	26.38	17.97–34.93
<i>Placosoma</i>	16.80	11.48–22.22
Cercosaurinae except ( <i>Neusticurus</i> , <i>Placosoma</i> )	52.79	48.23–57.15
<i>Echinosaura</i> <sup>a</sup>	27.68	21.41–34.11
<i>Riama</i>	26.28	21.21–31.63
<i>Gelanesaurus</i>	23.19	15.20–30.64
<i>Macropholidus</i>	15.60	12.36–18.90
<i>Pholidobolus</i>	17.25	14.48–20.00
( <i>Petracola</i> , <i>Cercosaura</i> , <i>Potamites</i> , <i>Proctoporus</i> , unnamed clades 2 & 3)	32.42	29.58–35.25
<i>Petracola</i>	15.66	9.76–21.93
<i>Cercosaura</i>	26.35	23.11–29.48
( <i>Potamites</i> , <i>Proctoporus</i> , unnamed clades 2 & 3)	26.48	23.41–29.51
<i>Potamites</i>	16.76	14.00–19.55
( <i>Proctoporus</i> , unnamed clade 2)	22.86	19.79–26.09

<sup>a</sup> *Echinosaura sulcarostrum* excluded.

*strangulatus*, whereas in this study we used 22 specimens of all recognized species of *Potamites* (9) except *P. apodemus* and *P. ocellatus*.

In addition to novel relationships among Cercosaurinae lizards, we discovered unexpected levels of clade diversity. We found three clades that were not included in any clade traditionally ranked as a genus (Fig. 2); moreover, we were unable to assign specimens in those three clades to any of the recognized ‘genera’ based on morphology. Therefore, a formal description of these unnamed clades is underway.

#### 4.3. Problematic taxa within Cercosaurinae

##### 4.3.1. *Riama*

As currently defined (Doan and Castoe, 2005), *Riama* is composed of 31 species that occur throughout the Andes of central Peru, Ecuador, Colombia, Venezuela, the Cordillera de la Costa of Venezuela and Trinidad and Tobago (Aguirre-Peñañafiel et al., 2014). Here we show that this definition does not reflect phylogeny, because “*Riama*” *laudahnae* is nested within “*Proctoporus*” as sister to *P. bolivianus* (Fig. 2). This is not surprising given that “*Riama*” *laudahnae*, which occurs in central Peru, was always recognized as having a remarkable disjunct distribution relative to all other species of *Riama*, which occur further north from Ecuador to Venezuela and Trinidad and Tobago. Therefore, we transfer “*Riama*” *laudahnae* to *Proctoporus* and note that *Riama* is restricted to the northern Andes and Trinidad and Tobago.

##### 4.3.2. *Proctoporus* and *Euspondylus*

Regarding *Proctoporus*, our tree (Fig. 2) is similar to the phylogeny of *Proctoporus* presented by Goicoechea et al. (2012), except that the monophyly of *Proctoporus* is not supported. Both hypotheses support a clade containing *Petracola*, *Cercosaura*, *Potamites* and *Proctoporus*, but they differ in the relationships among these taxa. According to Goicoechea’s hypothesis, *Petracola* and *Cercosaura* form a weakly supported clade sister to the strongly supported clade (*Potamites*, *Proctoporus*). In our ML tree (Fig. 2), *Petracola* is weakly supported as sister to all other taxa, which form a large clade where an unnamed clade (UC2) and (*Echinosaura sulcarostrum*, *Proctoporus xestus*) are, in that branching order, sister to the remaining taxa with low support. These remaining taxa are nested in five major clades—two separate clades of *Proctoporus*,

*Cercosaura*, *Potamites*, and an unnamed clade 3 (UC3)—but the relationships among them are poorly resolved. Therefore, we prefer not to propose any taxonomic changes in *Proctoporus*, but note that one of the two *Proctoporus* clades contains the type species *P. pachyurus* Tschudi 1845 (Fig. 2). If future studies show that *Proctoporus* is not monophyletic, this clade should retain the name *Proctoporus*.

Goicoechea et al. (2012) demonstrated that “*Euspondylus*” *chasqui* was nested within *Proctoporus*, and transferred it to *Proctoporus*. They noted that *P. chasqui* is part of the Peruvian (i.e., central and southern Peru) group of species of “*Euspondylus*”, which share with *Proctoporus* several derived characters, such as the presence of an undivided palpebral disc (Köhler and Lehr, 2004). As suggested by Goicoechea et al. (2012), in this study we show that other three species of “*Euspondylus*” in the Peruvian group—*Euspondylus oreades*, *E. rahmi*, and *E. spinalis*—are also nested within the same *Proctoporus* clade as *P. chasqui*. Accordingly, here we propose the following new combinations for these taxa: *Proctoporus oreades*, *P. rahmi*, and *P. spinalis*. The remaining ‘Peruvian species’ of *Euspondylus*—*E. caideni*, *E. josyi*, *E. nellycarrillae* and *E. simonsii*—are most likely members of the same ‘*Proctoporus* clade’. The ‘northern species group’ (i.e., Venezuela, Colombia, Ecuador and northern Peru) of *Euspondylus*, which includes *E. acuirostris*, *E. auyanensis*, *E. guentheri*, *E. maculatus*, and *E. monsfumus*, remains unsampled in molecular phylogenies; however, given its disjunct distribution relative to the ‘Peruvian group’, as well as morphological differences, it is unlikely that this group is nested within *Proctoporus*. Moreover, if the ‘northern group’ is shown to form a distinct clade within Cercosaurinae (i.e., not nested within other clades traditionally ranked as genera), that clade should be named *Euspondylus*, as *E. maculatus* Tschudi 1845 is the type species.

Interestingly, inclusion of three species of the Peruvian group of “*Euspondylus*” in our phylogenetic analyses shows that *P. pachyurus*, as delimited by Goicoechea et al. (2012) based on samples from Cusco and Junin, is not monophyletic. Consequently, we restrict the name *P. pachyurus* to populations from Junin, as they lie closer to the type locality of this species (Valley of Chanchamayo river); samples from Cusco included in Goicoechea et al. (2012) were collected approximately 570 km SE in a straight line, and most likely correspond to a different species of *Proctoporus*. Furthermore, our results suggest that the only Cusco sample of “*P. pachyurus*” from Goicoechea et al. (2012) included in our analyses as *P. sp.* (MHNC 11439) corresponds to a misidentified specimen of *Proctoporus rahmi* (Fig. 2).

#### 4.4. Phylogenetic nomenclature of Cercosaurinae

In the interest of promoting clarity and precision regarding the names of well-supported clades of Cercosaurinae lizards, we propose the following phylogenetic definitions (de Queiroz and Gauthier, 1994). We do not take into consideration those clades with poor taxonomic and/or geographic sampling (e.g., *Riama*, *Anadia*) to avoid taxonomic confusion.

*Cercosaurinae* Gray 1838 (*nomen cladi conversum*)

Definition: The crown clade originating with the most recent common ancestor of *Placosoma cordylinum* Fitzinger, 1847, *Neusticurus* (*Lacerta*) *bicarinatus* (Linnaeus, 1758), *Echinosaura horrida* Boulenger, 1890, *Riama unicolor* Gray, 1858, *Anadia* (*Cercosaurus*) *rhom bifera* (Günther, 1859), *Macropholidus ruthveni* Noble, 1921, *Pholidobolus* (*Ecleopus* [*Pholidobolus*]) *montium* (Peters, 1863), *Petracola* (*Proctoporus*) *ventrimaculata* (Boulenger, 1900), *Proctoporus pachyurus* Tschudi, 1845, *Cercosaura ocellata* Wagler, 1830, and *Potamites* (*Neusticurus*) *ecleopus* (Cope, 1876). Reference phylogeny: Fig. 2 of this paper. Hypothesized composition: *Anadia*, *Cercosaura*, *Echinosaura*, *Euspondylus*, *Gelanesaurus*, *Macropholidus*,



*Neusticurus*, *Petracola*, *Pholidobolus*, *Placosoma*, *Potamites*, *Proctoporus*, *Riama*, and the three unnamed clades in Fig. 2 of this paper. Comments: The validity of the name *Euspondylus* should be further tested in a phylogenetic context. In agreement with previous work (Goicoechea et al., 2012), we show that three species traditionally placed in the 'Peruvian group' of *Euspondylus* are nested within *Proctoporus*; nonetheless, we did not include in our analyses any of the 'northern species' of *Euspondylus*, which might form a separate clade, for which the name *Euspondylus* is available. Morphological diagnostic apomorphies of Cercosaurinae, as defined here, should be reassessed with further phylogenetic data.

*Placosoma* Tschudi 1847 (*nomen cladi conversum*)

Definition: The most inclusive clade containing *Placosoma cordylinum* Fitzinger, 1847, but not *Neusticurus (Lacerta) bicarinatus* (Linnaeus, 1758). Reference phylogenies: Fig. 4 in Pellegrino et al. (2001), Fig. 6 in Castoe et al. (2004), Fig. 2 of this paper. Hypothesized composition: *Placosoma cipoense* Cunha, 1966, *Placosoma cordylinum* Fitzinger, 1847, and *Placosoma (Cercosaura [Urosaura]) glabellum* (Peters, 1870). Comments: Morphological diagnostic apomorphies of *Placosoma*, as defined here, should be reassessed with further phylogenetic data.

*Echinosaura* Boulenger, 1890 (*nomen cladi conversum*)

Definition: The most inclusive clade consisting of *Echinosaura horrida* Boulenger, 1890, but not *Riama unicolor* Gray, 1858, *Riama kizirianii* Sánchez-Pacheco et al., 2012, or *Riama (Proctoporus [Oreosaurus]) shrevei* (Parker, 1935). Reference phylogeny: Fig. 2 of this paper. Hypothesized composition: *Echinosaura brachycephala* Köhler et al., 2004, *Echinosaura horrida* Boulenger, 1890, *Echinosaura (Teuchocercus) keyi* (Fritts and Smith, 1969), *Echinosaura orcesi* Fritts et al., 2002, *Echinosaura palmeri* Boulenger, 1911, and *Echinosaura panamensis* Barbour, 1924. Comments: We exclude "*E.*" *sulcarostrum* from *Echinosaura* because this species is not part of this clade (Fig. 2). Although we did not include *E. palmeri* and *E. panamensis* in our analyses, we are confident that they are part of *Echinosaura* because of strong morphological similarity with *E. horrida*. This similarity led Uzzell (1965) to designate both species as subspecies of *E. horrida*, although Fritts et al. (2002) later resurrected both taxa as valid species based on tail morphology and other scutellational characters.

*Gelanesaurus* (*nomen cladi novum*)

Definition: The most inclusive clade containing *Gelanesaurus (Neusticurus) cochranae* (Burt and Burt, 1931), but not *Placosoma cordylinum* Fitzinger, 1847, *Neusticurus (Lacerta) bicarinatus* (Linnaeus, 1758), *Echinosaura horrida* Boulenger, 1890, *Riama unicolor* Gray, 1858, *Anadia (Cercosaurus) rhombifera* (Günther, 1859), *Macropholidus ruthveni* Noble, 1921, *Pholidobolus (Eupleopus [Pholidobolus]) montium* (Peters, 1863), *Petracola (Proctoporus) ventrimaculata* (Boulenger, 1900), *Proctoporus pachyurus* Tschudi, 1845, *Cercosaura ocellata* Wagler, 1830, and *Potamites (Neusticurus) eupleopus* (Cope, 1876). Reference phylogeny: Fig. 2 of this paper. Etymology: The name *Gelanesaurus* derives from the Greek words *gelanes* (=laughing, cheerful) and *sauros* (=lizard), and refers to the joker-looking head color pattern of the included species, more marked in *G. flavogularis*. Composition: *G. cochranae* (Burt and Burt, 1931) and *G. flavogularis* (Altamirano-Benavides et al., 2013). Comments: Based on morphological similarity, and without a reference phylogeny, *G. cochranae* has been recognized, in chronological order, as a subspecies of *Potamites (Neusticurus) eupleopus* (Burt and Burt, 1931), a species of *Neusticurus* (Uzzell, 1966), and a species *Potamites* (Doan and Castoe, 2005). Similarly, the more recently described *G. flavogularis* was only assigned to *Potamites* based on its morphological resemblance to *G. cochranae*. Here we show that both species form a distinct clade, *Gelanesaurus*, which is not even sister to *Potamites* or *Neusticurus*, revealing the poor accuracy of morphology-based taxonomic classifications of Cercosaurinae lizards (Doan and Castoe, 2005; Presch, 1980;

Uzzell, 1966). Within Cercosaurinae, *Gelanesaurus* differs from all clades traditionally ranked as genera except *Echinosaura*, *Neusticurus*, and *Potamites* in having heterogeneous dorsal scalation. A black ring around the nostril (more conspicuous in *G. flavogularis* than *G. cochranae*) might be a diagnostic apomorphy of *Gelanesaurus*. Because it is not included in any of the clades of Cercosaurinae traditionally ranked as genera, we also present *Gelanesaurus* as a genus-group name, with *G. cochranae* (Burt and Burt, 1931) as type species, and define it as follows: A gymnophthalmid lizard with the tongue covered in imbricate, scale-like papillae; moveable eyelids; external ear opening, with a slightly recessed tympanum; heterogeneous dorsal scalation; subimbricate ventral scales; slightly compressed tail without conical scales; hemipenes with calcareous spinules on flounces and no basal spines.

*Petracola* Doan and Castoe 2005 (*nomen cladi conversum*)

Definition: The most inclusive clade containing *Petracola (Proctoporus) ventrimaculata* (Boulenger, 1900), but not *Proctoporus pachyurus* Tschudi, 1845, *Proctoporus (Riama) laudahnae* (Köhler and Lehr, 2004), *Proctoporus (Opipeuter) xestus* (Uzzell, 1969), *Cercosaura ocellata* Wagler, 1830, and *Potamites (Neusticurus) eupleopus* (Cope, 1876). Reference phylogeny: Fig. 2 of this paper. Hypothesized composition: *Petracola (Proctoporus) labioocularis* (Köhler and Lehr, 2004), *Petracola (Proctoporus) ventrimaculata* (Boulenger, 1900), *Petracola waka* (Kizirian et al., 2008). Comments: Morphological diagnostic apomorphies of *Petracola*, as defined here, should be reassessed with further phylogenetic data.

*Potamites* Doan and Castoe 2005 (*nomen cladi conversum*)

Definition: The crown clade containing *Potamites (Neusticurus) eupleopus* (Cope, 1876), *Potamites erythrocularis* Chávez and Catenazzi, 2014, *Potamites (Neusticurus) juruazensis* (Avila-Pires and Vitt, 1998), *Potamites montanicola* Chávez and Vásquez, 2012, and *Potamites (Euspondylus) strangulatus* (Cope, 1868). Reference phylogeny: Fig. 2 of this paper. Hypothesized composition: *Potamites (Neusticurus) apodemus* (Uzzell, 1966), *Potamites (Neusticurus) eupleopus* (Cope, 1876), *Potamites erythrocularis* Chávez and Catenazzi, 2014, *Potamites (Neusticurus) juruazensis* (Avila-Pires and Vitt, 1998), *Potamites montanicola* Chávez and Vásquez, 2012, *Potamites (Neusticurus) ocellatus* (Sinitin, 1930), *Potamites (Euspondylus) strangulatus* (Cope, 1868), and *Potamites (Neusticurus) trachodus* (Uzzell, 1966). Comments: All recognized species of *Potamites*, as defined here, occur in the Amazon basin and adjacent Andean slopes, except for *P. apodemus*, which is known from Costa Rica and Panama. Although we did not have access to DNA sequences of *P. apodemus*, and could therefore not infer its phylogenetic position, we recognize that an alternative scenario to this apparent disjunct distribution within *Potamites* is that *P. apodemus* is not truly a member of *Potamites*. This would not be surprising given the lack of clear morphological diagnostic apomorphies of *Potamites*, as well as this and recent molecular studies proving morphology-based taxonomies of several Cercosaurinae taxa wrong (Goicoechea et al., 2012; Torres-Carvajal and Mafla-Endara, 2013; Torres-Carvajal et al., 2015).

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## 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.2016.03.006>.

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