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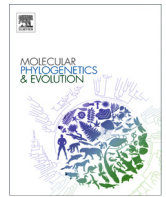
Short Communication

Evolutionary history of Andean *Pholidobolus* and *Macropholidus* (Squamata: Gymnophthalmidae) lizards

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ABSTRACT

Andean *Pholidobolus* and *Macropholidus* lizards contain seven and two species, respectively, as currently recognized. We analyze three mitochondrial loci (12S, 16S, ND4) using Bayesian methods to clarify the phylogenetic relationships between these genera based on a well-supported phylogenetic hypothesis. The phylogenetic tree obtained in this paper includes two main clades and shows that both *Pholidobolus* and *Macropholidus* are not monophyletic. A chronophylogenetic analysis indicates that the southernmost clade, occurring in the Huancabamba Depression, diversified earlier than the northern-Andes clade. Bayesian hypothesis tests reject previous phylogenetic hypotheses. We propose phylogenetic definitions for the main clades inferred herein.

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1. Introduction

The Andes form a nearly continuous 8000-km-long mountain belt that extends along the western border of South America. Its complex geography, orogeny and biodiversity have attracted the attention of many biologists interested in explaining the evolution and distribution of Andean organisms (e.g., Doan, 2003; Duellman, 1979; Graham et al., 2004; Hillis, 1985; Patton and Smith, 1992; Torres-Carvajal, 2007; Vuilleumier, 1969). This exceptionally long mountain chain is composed of three main segments of distinct orientation separated by two major bends (Jaillard et al., 2000). The northern Andes (12°N–5°S) are 2000 km long, have a NNE–SSW orientation, and extend from easternmost Venezuela to northernmost Peru. The central Andes (5°S–18°S) also are about 2000 km long, have a NW–SE orientation, and extend from northern Peru to Bolivia and northern Chile; they are separated from the northern Andes by the Huancabamba Depression (Aleman and Ramos, 2000; Jaillard et al., 2000). The southern Andes (18°S–56°S) are 4000 km long and have a N–S orientation; they are separated from the central Andes by the Arica bend (Jaillard et al., 2000). This portion of the Andes was formed much earlier than the central and northern Andes, possibly prior to the Tertiary (Simpson, 1979). The central Andes were next, followed by the northern Andes, which did not reach their current high elevations before the mid-Pliocene (Aleman and Ramos, 2000; Simpson, 1979). A single date for the uplift of any of the three Andean segments is unrealistic because the Andes are not a single entity; uplift did not happen instantaneously, and its timing probably varied latitudinally and longitudinally (Gregory-Wodzicki, 2000).

The gymnophthalmid lizard *Pholidobolus* as currently defined (Montanucci, 1973) contains six species—*P. annectens*, *P. affinis*, *P. huancabambae*, *P. macbrydei*, *P. montium*, *P. prefrontalis*. They occur between 1800 and 4000 m in the southern portion of the northern Andes between the Huancabamba Depression in northern Peru and extreme southern Colombia. In spite of the low number of species in this genus, several systematic problems persist. First, allocation of a species from southern Peru within *Pholidobolus* (*P. anomalus*) remains controversial (Montanucci, 1973; Reeder, 1996). Second, the limits between this genus and *Macropholidus*, which occurs in the Andes of northern Peru, are not clear (Cadle and Chuna, 1995; Montanucci, 1973; Parker, 1930). Third, a robust phylogeny of *Pholidobolus* has not been published; the phylogenetic relationships among species in this genus have been addressed with morphological and allozyme data under Wagner and UPGMA methods (Hillis, 1985; Montanucci, 1973). In this paper we address the second and third problems mentioned above by using mitochondrial DNA sequence data to analyze phylogenetic relationships of all species of *Pholidobolus* (except *P. anomalus*) and the type species of *Macropholidus* using Bayesian methods.

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2. Materials and methods

2.1. Character and taxon sampling

We obtained nucleotide (nt) sequences from mitochondrial ribosomal small (*12S*, 344 nt) and large (*16S*, 548 nt) subunit genes, as well as mitochondrial subunit IV of NADH dehydrogenase (*ND4*, 680 nt). For all these genes we generated novel DNA sequences from 13 specimens representing six species of *Pholidobolus*, and one specimen of *Macropholidus ruthveni* (Table 1). We were unable to obtain tissue samples of *P. anomalus* and *M. ataktolepis*. In addition, we obtained sequences from GenBank representing six genera of the tribe Cercosaurini and one of the tribe Bachini (Table 1; Castoe et al., 2004; Pellegrino et al., 2001).

2.2. Laboratory protocols

Genomic DNA was isolated from frozen muscle or liver tissues with salt-precipitation protocols. Mitochondrial ribosomal genes *12S* and *16S* were amplified via polymerase chain reaction (PCR) using the primers 12Sa, 12Sb, 16SL, 16SH, 16SF.0, and 16SR.0, whereas the *ND4* gene was amplified with the primers ND4F and ND4R (Pellegrino et al., 2001). The amplification protocol consisted of 1 cycle of initial denaturation for 3 min at 96 °C, 40–45 cycles of denaturation for 30 s at 95 °C, annealing for 1 min at 52 °C, and extension for 1 min at 72 °C, as well as a final extension for 10 min at 72 °C. Positive PCR products were visualized in agarose electrophoretic gels and treated with ExoSAP-it to remove unincorporated primers and dNTPs. Cycle sequencing reactions were carried out by Macrogen Inc.

2.3. Alignment, model selection, and chronophylogenetic analyses

Data were assembled and aligned in Geneious v5.5 (Drummond et al., 2010) under default settings for MAFFT (Katoh and Toh, 2010). *ND4* sequences were translated into amino acids for confirmation of alignment. Evolutionary models for each gene were selected using jModeltest (Posada, 2008) under the Akaike information criterion (AIC), which avoids some limitations of the likelihood-ratio test (LRT), in particular the inability to compare non-nested models.

All genes were combined into a single matrix with three partitions (*12S*, *16S*, *ND4*). Co-estimation of rates, divergence times, and phylogeny was conducted under the Bayesian framework implemented in Beast 1.7 (Drummond et al., 2012). The analyses were conducted under a model with uncorrelated substitution rates among branches and the rate for each branch independently drawn from an underlying lognormal distribution (Drummond et al., 2006). The mean of branch rates parameter (ucld.mean) was fixed to 1.0 reflecting the absence of calibration dates and resulting in time being measured in units that have been arbitrarily chosen so that 1 time unit corresponds to the mean time required for the accumulation of 1 substitution per site (Drummond and Rambaut, 2007; Drummond et al., 2006). We performed four independent 10^7 generation runs with random starting trees, sampling every 1000 generations. Results were analyzed in Tracer to assess convergence and effective sample sizes (ESS) for all parameters, after which 1000 samples were arbitrarily discarded as "burn-in". The resultant 36,000 trees were used to calculate posterior probabilities (PP) for each bipartition in a maximum clade credibility tree in TreeAnnotator 1.7.2 (Rambaut and Drummond, 2010).

2.4. Sequence divergence

Interspecific sequence divergence for each gene was assessed with uncorrected distances, which were obtained in PAUP* (Swofford, 2003).

2.5. Hypothesis tests

The monophyly of *Pholidobolus* as defined by Montanucci (1973) and the alternative phylogenetic hypothesis presented by Hillis (1985) were tested under a Bayesian approach to tree topology tests by determining the posterior probability of each alternative topology (Torres-Carvajal and de Queiroz, 2009). For these tests we loaded into PAUP* the post-burn-in trees resulting from a Bayesian phylogenetic analysis conducted in MrBayes 3.2.0 (Ronquist and Huelsenbeck, 2003) (NRUNS = 4, NGEN = 10,000,000, SAMPLEFREQ = 1000, BURNIN = 1000) using the same dataset and models described above. We then filtered using each alternative topology to determine the frequency (i.e., posterior probability) of that topology within the sample. If the alternative topology

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.

Taxon	Voucher	Locality	Genbank accession number		
			12S	16S	ND4
Bachia flavescens	LSUMZ H12977	Brazil: Pará	AF420705	AF420753	AF420869
Cercosaura quadrilineata	LG 936	Brazil: Goiás	AF420672	AF420717	AF420880
Macropholidus ruthveni	CORBIDI 4281	Peru: Lambayeque: El Totoral	*KC894354	*KC894368	*KC894382
Neusticurus rudis	MRT 926008	Brazil: Amapá	AF420689	AF420709	AF420905
"*Pholidobolus*" *annectens*	QCAZ 11120	Ecuador: Loja: 15 km E Loja	*KC894341	*KC894355	*KC894369
"*P*". *annectens*	QCAZ 11121	Ecuador: Loja: 15 km E Loja	*KC894342	*KC894356	*KC894370
"*P*". *huancabambae*	CORBIDI 10492	Peru: Huancabamba: Las Pozas	*KC894343	*KC894357	*KC894371
"*P*". *huancabambae*	CORBIDI 10493	Peru: Huancabamba: Las Pozas	*KC894344	*KC894358	*KC894372
"*P*". *huancabambae*	CORBIDI 10496	Peru: Huancabamba: Las Pozas	*KC894345	*KC894359	*KC894373
Pholidobolus affinis	QCAZ 9641	Ecuador: Cotopaxi: San Miguel de Salcedo	*KC894348	*KC894362	*KC894376
P. affinis	QCAZ 9900	Ecuador: Chimborazo: Colta	*KC894349	*KC894363	*KC894377
P. macbrydei	QCAZ 9914	Ecuador: Azuay: Guablid	*KC894352	*KC894366	*KC894380
P. macbrydei	QCAZ 9932	Ecuador: Azuay: 20 km W Cuenca	*KC894353	*KC894367	*KC894381
P. montium	QCAZ 4051	Ecuador: Pichincha: Quito	*KC894346	*KC894360	*KC894374
P. montium	QCAZ 9044	Ecuador: Pichincha: Tababela	*KC894347	*KC894361	*KC894375
P. prefrontalis	QCAZ 9908	Ecuador: Chimborazo: Alausí	*KC894350	*KC894364	*KC894378
P. prefrontalis	QCAZ 9951	Ecuador: Chimborazo: Tixán	*KC894351	*KC894365	*KC894379
Placosoma glabellum	LG 940	Brazil: São Paulo	AF420674	AF420742	AF420907
Potamites ecpleopus	MRT 0472	Brazil: Mato Grosso	AF420656	AF420748	AF420890
Proctoporus bolivianus	UTA R-51487	Peru: Cusco: Carizales	AY507850	AY507868	AY225180
Riama cashcaensis	KU 217205	Ecuador: Chimborazo: 30.5 km SW Cajabamba	AY507852	AY507870	AY507887

was not within the 95% credible set of trees, we considered it rejected by the observed data.

3. Results

3.1. Chronophylogenetic analyses

The maximum clade credibility tree resulting from the chronophylogenetic analysis does not support the monophyly of *Pholidobolus* as currently recognized (Fig. 1). All species of *Pholidobolus* were included in a strongly supported clade (PP = 1.00) with a basal split into two strongly supported subclades (PP = 1.00). One of the subclades contained *Macropholidus ruthveni* as sister to a clade containing both *P. annectens* and *P. huancabambae* (PP = 0.91). The other subclade contained *P. macbrydei* as sister to a clade with the three remaining species of *Pholidobolus*; the latter clade included *P. prefrontalis* as sister to a clade (PP = 0.94) containing *P. affinis* and *P. montium* as sister taxa. According to the chronophylogenetic tree inferred in this paper (Fig. 1), diversification of the clade (*M. ruthveni* (*P. annectens, P. huancabambae*)) occurred earlier than that of the clade containing all remaining species of *Pholidobolus*.

3.2. Sequence divergence

Sequence divergence between ingroup species (i.e., clade containing all species of *Pholidobolus* and *Macropholidus* included in this study) and the outgroups ranged from 0.083 (*P. prefrontalis* and *Cercosaura*) to 0.223 (*P. huancabambae* and *Placosoma*) for 12S, 0.063 (*M. ruthveni* and *Proctoporus*) to 0.164 (*P. annectens* and *Placosoma*) for 16S, and 0.176 (*P. prefrontalis* and *Proctoporus*) to 0.284 (*P. huancabambae* and *Neusticurus*) for ND4. Interspecific

sequence divergence within the ingroup clade ranged from 0.024 (*P. affinis* and *P. montium*; *P. macbrydei* and *P. prefrontalis*) to 0.074 (*P. huancabambae* and *M. ruthveni*, *P. huancabambae* and *P. macbrydei*) for 12S, 0.020 (*P. montium* and *P. macbrydei*) to 0.062 (*P. annectens* and *P. affinis*) for 16S, and 0.106 (*P. affinis* and *P. montium*) to 0.237 (*P. affinis* and *P. huancabambae*) for ND4. Interspecific sequence divergence ranged from 0.053 (*P. annectens* and *P. huancabambae*) to 0.074 (*M. ruthveni* and *P. huancabambae*) for 12S, 0.031 (*M. ruthveni* and *P. huancabambae*) to 0.041 (*M. ruthveni* and *P. annectens*) for 16S, and 0.153 (*M. ruthveni* and *P. annectens*) to 0.188 (*P. annectens* and *P. huancabambae*) for ND4 within ingroup subclade (*M. ruthveni*, (*P. annectens, P. huancabambae*)). Sequence divergence values ranged from 0.024 (*P. affinis* and *P. montium*; *P. prefrontalis* and *P. macbrydei*) to 0.049 (*P. affinis* and *P. macbrydei*) for 12S, 0.020 (*P. montium* and *P. macbrydei*) to 0.032 (*P. montium* and *P. prefrontalis*) for 16S, and 0.106 (*P. affinis* and *P. montium*) to 0.136 (*P. affinis* and *P. prefrontalis*) for ND4 within ingroup subclade (*P. macbrydei*, (*P. prefrontalis*, (*P. affinis*, *P. montium*))).

3.3. Test of alternative hypotheses

Ingroup topology of the phylogenetic tree resulting from the analyses in MrBayes was identical to the topology of the chronophylogenetic tree obtained in BEAST; branch support values were nearly identical. Both the monophyly of *Pholidobolus* as defined by Montanucci (1973; i.e., all ingroup species included here except *Macropholidus ruthveni*), and the alternative phylogenetic hypothesis presented by Hillis (1985) were rejected. Neither of these topologies were present in the 95% credible set of trees.
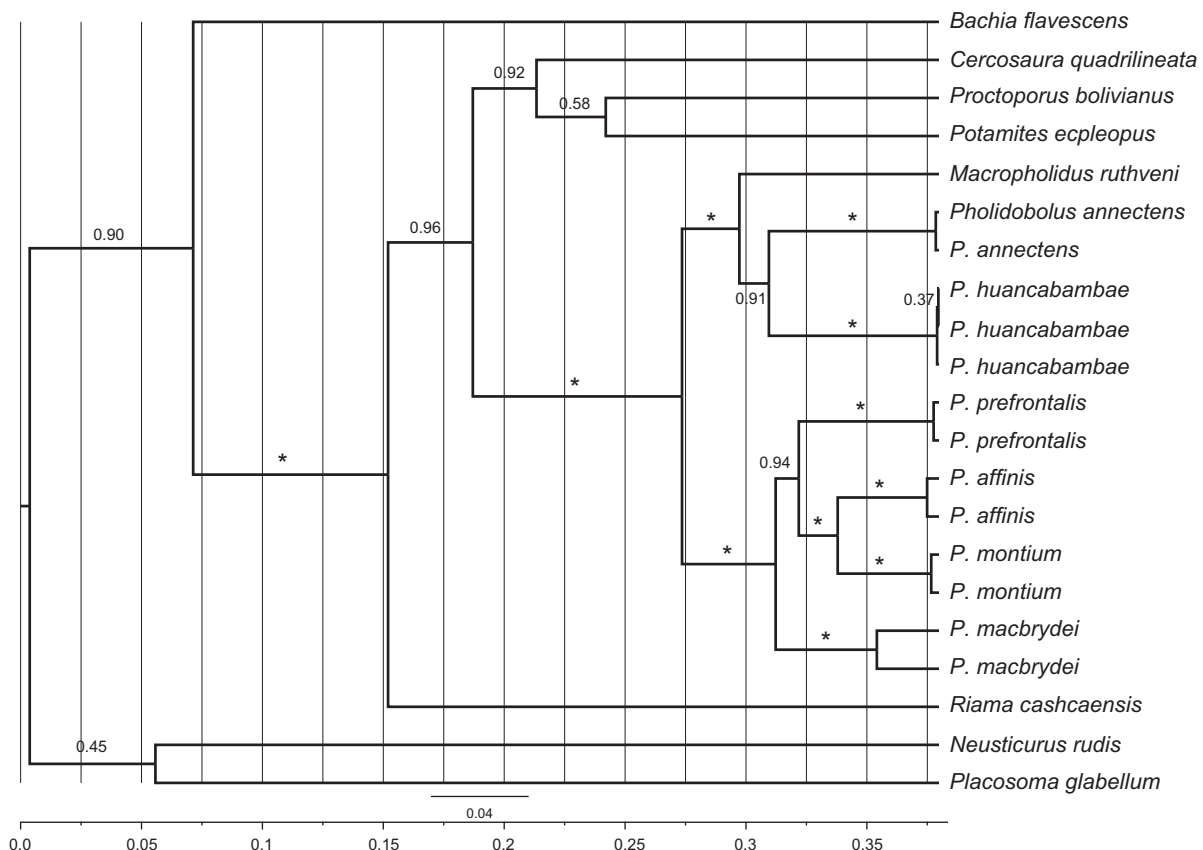

Fig. 1. Maximum clade credibility tree inferred from the analysis of a dataset containing three mitochondrial loci under uncorrelated, log normally distributed rates; branch lengths are in substitutions per site. Posterior probability values are shown above branches; asterisks correspond to values of 1.

4. Discussion

4.1. Biogeography

The chronophylogenetic tree presented in this paper shows a basal split in the phylogeny of *Pholidobolus* (including *Macropholidus*). One of the clades, (*M. ruthveni*, (*P. annectens*, *P. huancabambae*)), is restricted in distribution to the Huancabamba Depression, a region in the Andes that has been recognized as a major biogeographic barrier for Andean organisms (e.g., Cadle, 1991; Duellman, 1979; Vuilleumier, 1969). In this region, which runs approximately between 4°S and 7°S, the relatively low altitude of the Andes causes fragmentation of montane habitats and creation of a mixture of environments (Cadle, 1991). The complex orogeny in the Huancabamba Depression possibly influenced the radiation of *Pholidobolus/Macropholidus* and other Andean lizards (e.g., *Stenocercus*) in this region. All remaining species of *Pholidobolus* included in this study are nested in a second clade, which is primarily distributed along the southern part of the northern Andes (i.e., Ecuador and southern Colombia). Only one species in this clade, *P. macbrydei*, occurs also in the Huancabamba Depression (Fig. 2). A northern-Andes radiation has been documented for other Andean lizards, such as *Riama* (Doan, 2003) and *Stenocercus* (Torres-Carvajal, 2007), suggesting that there are possibly at least some common geological or climatic events that have influenced the diversification of extant lizard clades in the Northern Andes. Furthermore, it is likely that species of *Riama*, *Stenocercus* and *Pholidobolus* inhabiting the northern Andes have diverged recently because of the relatively recent geological uplift of this part of the Andes (i.e., Aleman and Ramos, 2000; Simpson, 1979) to elevations at which these species live, and because of morphological similarity among some of these species. The phylogenetic tree in this paper shows a south-to-north sequence of speciation events (Fig. 2), which is congruent with the south-to-north uplift of the Andes (Simpson, 1979; Aleman and Ramos, 2000). This is in agreement with the south-to-north speciation hypothesis (SNSH) proposed by Doan (2003) for Andean *Proctoporus/Riama* lizards,

although a fine-scale south-to-north speciation sequence is not necessarily a prediction of the SNSH (Torres-Carvajal, 2007).

4.2. Systematics and character evolution

The systematics of *Pholidobolus* Peters, 1863 and *Macropholidus* Noble, 1921 has been controversial because some of the diagnostic morphological characters used by previous authors are not apomorphic. Noble (1921) erected the genus *Macropholidus* for a species of gymnophthalmid lizard (i.e., *M. ruthveni*) diagnosed by (1) two medial longitudinal rows of enlarged dorsal scales, and (2) the lack of reduced scales on the flanks. Choice of inappropriate diagnostic characters has led to confusion in the generic allocation of some species of *Pholidobolus/Macropholidus*. Parker (1930) described *M. annectens*, which shares characters with both *Macropholidus* and *Pholidobolus*. Giving special importance to the distinctive enlarged rows of dorsal scales present in *M. ruthveni* (lacking in *M. annectens*), Montanucci (1973) assigned *M. annectens* to *Pholidobolus* and left *Macropholidus* as a monotypic genus. Following Montanucci's generic arrangement, Cadle and Chuna (1995) described *M. ataktolepis*, and Reeder (1996) described *P. huancabambae*, both species from northern Peru (Fig. 2). Reeder (1996) also proposed a clade containing *P. annectens* and *P. huancabambae* based on two synapomorphies: possession of a single transparent palpebral disc and absence of a lateral fold. In agreement with the phylogenetic hypothesis presented here (Figs. 1 and 2), these characters are shared by species currently assigned to *Macropholidus* (*M. ataktolepis* and *M. ruthveni*), but not by the remaining species of *Pholidobolus* except *P. anomalus*. Thus, we agree with Reeder's synapomorphies and predict that *M. ataktolepis*, not included in our analysis, is part of the "Huancabamba" clade inferred by our analysis. This prediction is consistent with the geographic distribution of this species (i.e., northwestern Peru). If *P. anomalus* is indeed closely related to other *Pholidobolus* species, then it probably belongs to the same clade because it shares the two synapomorphies mentioned above (Reeder, 1996). Nonetheless, the disjunct distribution of this species (Cuzco, Peru, nearly
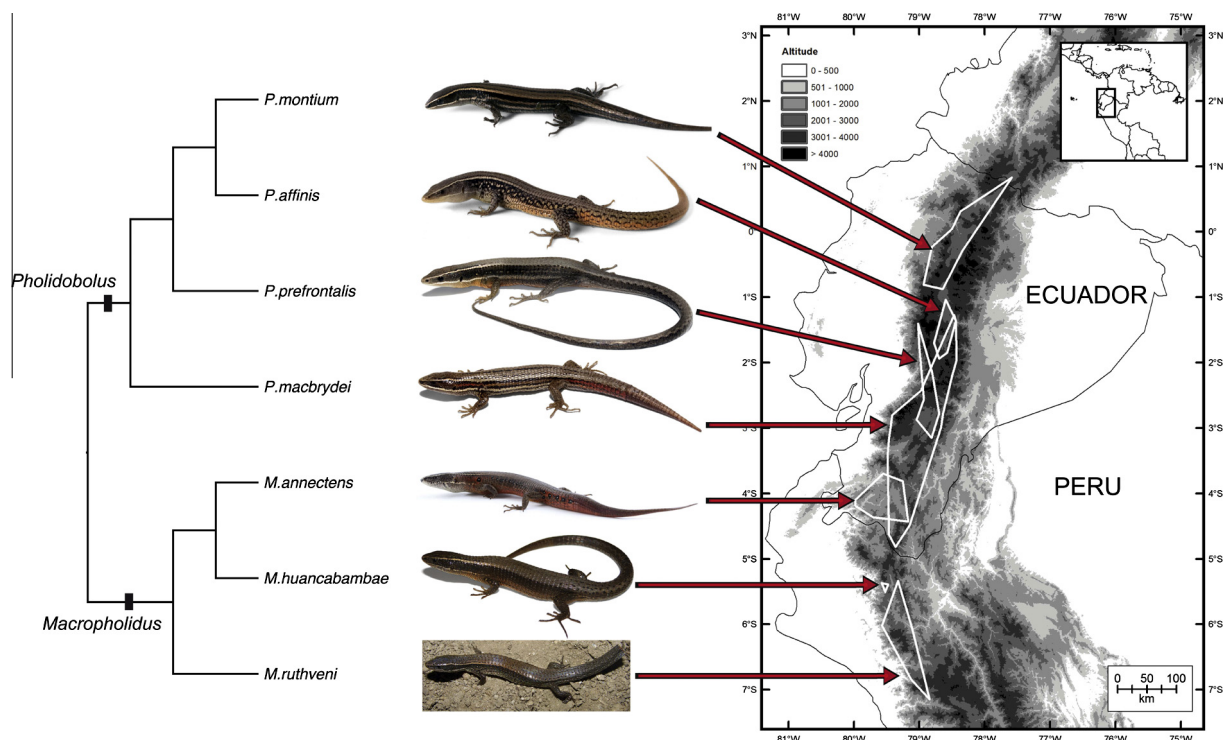

Fig. 2. Summarized phylogeny and distribution of species of *Pholidobolus* and *Macropholidus* included in this study.

1000 km southeast) when compared to other *Pholidobolus* species raises questions on its generic assignment, as it would be a unique distribution pattern among Andean reptiles. We prefer to conclude that the generic allocation of *P. anomalus* remains to be established.

4.3. Taxonomy

Based on the phylogenetic hypothesis presented in this paper (Figs. 1 and 2), the genus *Pholidobolus* as currently defined (Montanucci, 1973) is paraphyletic. Therefore, we propose to place *P. annectens* and *P. huancabambae* within the genus *Macropholidus*. More importantly, in the interest of promoting clarity and precision regarding the names of clades of gymnophthalmid lizards, we propose phylogenetic definitions (de Queiroz and Gauthier, 1994) for two clade names according to the rules of the draft International Code for Phylogenetic Nomenclature (ICPN, Cantino and de Queiroz, 2007).

Macropholidus Noble, 1921 (converted clade name). Definition: The largest crown clade containing *Macropholidus ruthveni* Noble, 1921, but not *Pholidobolus montium* Peters, 1863. Reference phylogeny: Fig. 1 of this paper. Hypothesized composition: *Macropholidus* is currently hypothesized to include *Macropholidus ruthveni* Noble, 1921, *M. annectens* Parker, 1930, *M. ataktolepis* Cadle and Chuna, 1995, and *M.* (*Pholidobolus*) *huancabambae* Reeder, 1996. Comments: Diagnostic morphological apomorphies of *Macropholidus*, as conceptualized here, are currently unclear. Possession of a single transparent palpebral disc in the lower eyelid, and absence of a lateral fold between fore and hind limbs were originally proposed by Reeder (1996) as diagnostic apomorphies for a clade within *Pholidobolus* containing *P. annectens* and *P. huancabambae*. These characters are shared by other members of *Macropholidus* but not *Pholidobolus* as conceptualized here, and their polarity remains to be established.

Pholidobolus Peters, 1863 (converted clade name). Definition: The largest crown clade containing *Pholidobolus montium* Peters, 1863, but not *Macropholidus ruthveni* Noble, 1921. Reference phylogeny: Fig. 1 of this paper. Hypothesized composition: *Pholidobolus* is currently hypothesized to include *Pholidobolus affinis* Peters, 1863, *P. montium* Peters, 1863, *P. macbrydei* Montanucci, 1973, and *P. prefrontalis* Montanucci, 1973. Comments: Morphological diagnostic apomorphies of *Pholidobolus*, as conceptualized here, are currently unclear. In contrast to *Macropholidus* (see Comments on that taxon), members of *Pholidobolus* lack a transparent palpebral disc in the lower eyelid and have a lateral fold between fore and hind limbs; however, the polartiy of these characters remains to be established.

Acknowledgments

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.2013.03.013.

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