Unravelling interspecific relationships among highland lizards: first phylogenetic hypothesis using total evidence of the *Liolaemus montanus* group (Iguania: Liolaemidae)

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The South American lizard genus *Liolaemus* comprises > 260 species, of which > 60 are recognized as members of the *Liolaemus montanus* group, distributed throughout the Andes in central Peru, Bolivia, Chile and central Argentina. Despite its great morphological diversity and complex taxonomic history, a robust phylogenetic estimate is still lacking for this group. Here, we study the morphological and molecular diversity of the *L. montanus* group and present the most complete quantitative phylogenetic hypothesis for the group to date. Our phylogeny includes 103 terminal taxa, of which 91 are members of the *L. montanus* group (58 are assigned to available species and 33 are of uncertain taxonomic status). Our matrix includes 306 morphological and ecological characters and 3057 molecular characters. Morphological characters include 48 continuous and 258 discrete characters, of which 70% (216) are new to the literature. The molecular characters represent five mitochondrial markers. We performed three analyses: a morphology-only matrix, a molecular-only matrix and a matrix including both morphological and molecular characters (total evidence hypothesis). Our total evidence hypothesis recovered the *L. montanus* group as monophyletic and included ≥ 12 major clades, revealing an unexpectedly complex phylogeny.

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INTRODUCTION

The genus *Liolaemus* Wiegmann, 1834 currently includes 267 species of lizards (updated from Gutiérrez *et al.*, 2018) that are distributed from Tierra del Fuego in southern Argentina and Chile to central Peru. The most widely accepted phylogenetic hypothesis for *Liolaemus* is that of Schulte *et al.* (2000), which provided molecular support to Laurent's (1983) division of the genus into two subgenera: *Liolaemus s.s.* (or the 'Chilean group') and *Eulaemus* 1858 (or the 'Argentinean group'). It was Etheridge (1995) who first proposed the division of the genus into groups based on morphological synapomorphies. Various arrangements of species groups have been proposed within *Eulaemus*, as summarized in Table 1. Etheridge (1995) proposed the *Liolaemus montanus* group for species with the following combination of characters: presence of pigmented epimysium of the m. pterygomandibularis, medial head of m. flexor tibialis internus covered by hypetrophied m. tibials anticus (Abdala *et al.*, 2006), a sharp, bladelike process on the posterior distal tibia, associated with a greatly hypertrophied m. tibialis anterior and the absence of a patch of enlarged scales located in the posterior region of the thigh.

Since the first formal phylogenetic hypothesis for *Liolaemus* (Ortiz, 1981), several phylogenies for the genus have been proposed (Young-Downey, 1998; Etheridge, 1995; Schulte *et al.*, 2000; Espinoza *et al.*, 2004). Likewise, phylogenies have been proposed for different groups and subgroups of the genus; for example, *Liolaemus s.s.* (Morando, 2004; Medina *et al.*, 2014), *Eulaemus* (Fontanella *et al.*, 2012; Olave *et al.*, 2014), the *Liolaemus boulengeri* group (Avila *et al.*, 2006; Abdala, 2007), the *Liolaemus lineomaculatus* group (Breitman *et al.*, 2011, 2013), the *Liolaemus elongatus–kriegi* group (Lobo, 2001, 2005), the *Liolaemus alticolor–bibronii* group (Morando *et al.*, 2007; Quinteros, 2013; Portelli & Quinteros, 2018), the *Liolaemus anomalus* group (Abdala & Juarez Heredia, 2013) and the *Liolaemus archeforus–kingii* group (Breitman *et al.*, 2015). The most inclusive phylogenies of Squamata (Pyron *et al.*, 2013; Zheng & Wiens, 2016) or *Liolaemus* broadly (Schulte *et al.*, 2000; Valladares *et al.*, 2002; Espinoza *et al.*, 2004; Schulte, 2013; Olave *et al.*, 2014) have included some species of the *L. montanus* Koslowsky, 1898, group, but never > 25% of the members of this group. Aguilar *et al.* (2017) performed an integrative taxonomical study including a phylogeny of the species (21 terminal taxa) of the *L. montanus*

group from Peru, and Aguilar-Puntriano *et al.* (2018) included 57 terminals corresponding to 43 available names and 14 candidate species of the *L. montanus* group, including populations from Bolivia, Chile and Argentina. Several informal phylogenetic hypotheses have been proposed (Cei, 1986, 1993; Pincheira-Donoso & Núñez, 2005; Díaz Gómez, 2007; Pincheira-Donoso *et al.*, 2008; Lobo *et al.*, 2010a), but these proposals were not based on quantitative phylogenetic methods and were based on few morphological characters. As illustrated in Table 2, the *L. montanus* group has had a complex taxonomic history, with several genera erected and eliminated, and numerous unresolved synonymies and debates on the identities of poorly understood species, all in the absence of a robust phylogenetic hypothesis.

The species of the *L. montanus* group are found from central Peru to central-west Argentina, also occupying areas of northern Chile and the Andean region of Bolivia (Fig. 1). These taxa largely inhabit high elevations (2500–5000 m a.s.l.) in Andean, pre-Puna and Puna regions, with some additional taxa in lower-elevation arid regions of the Pacific slope of Chile and Peru (Fig. 1; Abdala & Quinteros, 2014). The *L. montanus* group includes species that are more widely distributed, such as *Liolaemus orientalis* Müller, 1924 (Puna of Argentina and Bolivia), *Liolaemus schmidti* Marx, 1960 (Puna of south-western Bolivia and Chile) and *Liolaemus signifer* (Duméril & Bibron, 1837) (Puna of Bolivia and Peru). In contrast, there are numerous species with a marked endemism, such as *Liolaemus halonastes* Lobo *et al.*, 2010a (southern region of Salar de Arizaro, Argentina), *Liolaemus porosus* Abdala *et al.*, 2013 (around Volcán Socompa, Argentina and Chile) and *Liolaemus fittkaui* Laurent, 1986 (humid Puna of Cochabamba, Bolivia). Also, there are endemics along the Sierras Pampeanas of Argentina: *Liolaemus famatinae* Cei, 1980 (Sierra de Famatina), *Liolaemus huacahuasicus* Laurent, 1985 (Sierra de Aconquija) and *Liolaemus orko* Abdala & Quinteros, 2008 (Sierra de Fiambalá). Most of the members of the *L. montanus* group are distributed in Chile (27 species; Demangel, 2016), followed by 25 in Argentina (Abdala & Quinteros, 2014), 13 in Bolivia (Etheridge & Frost, 2010; Aguilar-Kirigin *et al.*, 2016) and 15 in Peru (Aguilar *et al.*, 2019) (Table 3). In recent years, there have been many studies on the distribution of species

Table 1. Summary of the proposed groupings within the subgenus *Eulaemus*

Author	Subgenus or Supergroup	Section or main group	Clade or series or group
Laurent (1983, 1985)	*Eulaemus*		*L. fitzingerii* group
			L. signifer group
Cei (1986, 1993	Supergroup Argentina		*L. andinus* group
			L. montanus group
			L. ruibali group
			L. signifer group
Etheridge (1995)	*signifer* group	*L. montanus* group	*L. boulengeri* group, 38 taxa
Schulte *et al.* (2000)	*Eulaemus*	*L. montanus* section	*L. boulengeri* series
		L. lineomaculatus section*	*L. montanus* series
Pincheira-Donoso & Núñez (2005)‡	*Eulaemus*	*L. fitzingerii* complex	*L. darwinii* group
		L. signifer complex	*L. fitzingerii* group
			L. fabiani group
			L. jamesi group
			L. ruibali group
			L. signifer group
Pincheira-Donoso *et al.* (2008)	*Eulaemus*		*L. montanus* clade
			L. anomalus clade
			L. boulengeri clade
Lobo *et al.* (2010a)	*Eulaemus*	*L. montanus* section	*L. montanus* series
		L. lineomaculatus section*	*L. boulengeri* series
		unnamed clade†	
Olave *et al.* (2012, 2014)§	*Eulaemus*	*L. montanus* section	*L. melanops* series
		lineomaculatus section	*L. anomalus* series
			L. montanus group
			L. darwinii group
			L. wiegmannii group
Fontanella *et al.* (2012)§	*Eulaemus*	*L. montanus* section	*L. melanops* series
		L. lineomaculatus section	*L. boulengeri* complex
			L. rothi complex
			L. donosobarrosi complex
			L. fitzingerii complex
			L. nigriceps series
			L. montanus group
			L. darwinii group
			L. anomalus group
			L. wiegmannii group
Schulte *et al.* (2013)	*Eulaemus*	*L. montanus* section	*L. montanus* series
		L. lineomaculatus section	*L. wiegmannii* series
			L. melanops group
			L. darwinii complex

Modified from Quinteros & Abdala (2011).
*The *L. lineomaculatus* section resembles the *L. lineomaculatus* group of Etheridge (1995), but the latter is located in the subgenus *Liolaemus s.s.*
†Includes the *L. magellanicus* and the *L. kingii–archeforus* groups.
‡Classification based on character combination, not on a formal cladistic analysis.
‡Recovers the *L. boulengeri* group (*sensu* Abdala, 2007; Schulte *et al.*, 2000) as paraphyletic. See main text for details.

in the *L. montanus* group (Aparicio & Ocampo, 2010; Paz *et al.*, 2013; Ruiz de Gamboa Astroza & González, 2013; Troncoso-Palacios & Ferri-Yáñez, 2013; Díaz-Vega, 2014; Aguilar-Kirigin *et al.*, 2016; Aguilar-Kirigin & Abdala, 2016; Jiménez-Robles, 2016), allowing us to gain a better understanding of the latitudinal and elevational distributions and the environments that they inhabit. Some species of the *L. montanus* group were included in biogeographical studies (Díaz Gómez, 2007; Quinteros & Díaz Gómez, 2011; Andrade-Díaz *et al.*, 2017), aiding further knowledge.

Table 2. Historical nomenclatural acts proposed for members of the *Liolaemus montanus* group

Current taxonomic state	Proposal	Authors (year)	Nomenclatural act
	Ctenoblepharis audituvelatus	Núñez & Yáñez (1983)	Original description
Liolaemus audituvelatus	*Phrynosaura audituvelata*	Laurent (1984)	Assigned to *Phrynosaura*
	Liolaemus audituvelatus	Etheridge (1995)	Assigned to *Liolaemus*
	Velosaura aymararum	Núñez & Yañez (1984)	Assigned to a new genus
Liolaemus aymararum	*Liolaemus aymararum*	Laurent (1984)	Assigned to a new genus
	Liolaemus jamesi	Pincheira-Donoso & Núñez (2005)	Synonym
	Liolaemus aymararum	Langstroth (2011)	Revalidation
Liolaemus erguetae	*Liolaemus islugensis erguetae*	Laurent (1995)	Original description
	Liolaemus erguetae	Pincheira-Donoso & Núñez (2002)	Assigned to species status
	Ctenoblepharys erroneus	Núñez & Yáñez (1984)	Original description
Liolaemus erroneus	*Phrynosaura erroneus*	Pincheira-Donoso (2005)	Assigned to a new genus
	Liolaemus erroneus	Pincheira-Donoso *et al.* (2008)	Assigned to a new genus
	Abas fabiani	Núñez & Yáñez (1984)	Assigned to a new genus
Liolaemus fabiani	*Ceiolaemus fabiani*	Veloso & Navarro (1988)	Assigned to a new genus
	Liolaemus fabiani	Laurent (1992)	Assigned to a new genus
Liolaemus filiorum	*Liolaemus puritamensis*	Troncoso-Palacio (2014)	Synonym
	Liolaemus filiorum	Pincheira-Donoso (2014)	Revalidation
Liolaemus insolitus	*Abas insolitus*	Núñez & Yáñez (1984)	Assigned to a new genus
	Liolaemus insolitus	Etheridge (1995)	Assigned to a new genus
	Ctenoblepharis jamesi	Boulenger (1891)	Original description
Liolaemus jamesi	*Liolaemus jamesi*	Cei (1979)	Assigned to a new genus
	Velosaura jamesi	Núñez & Yáñez (1984)	Assigned to a new genus
	Liolaemus jamesi	Etheridge (1995)	Assigned to a new genus
Liolaemus manueli	*Phrynosaura manueli*	Núñez *et al.*, 2003	Original description
	Liolaemus manueli	Schulte *et al.* (2004)	Assigned to a new genus
Liolaemus molinai	*Liolaemus andinus*	Pincheira-Donoso & Núñez (2005)	Synonym
	Liolaemus molinai	Lobo *et al.* (2010)	Revalidation
	Helocephalus nigriceps	Philippi (1860)	Original description
Liolaemus nigriceps	*Liolaemus signifer* var. *nigriceps*	Koslowsky (1898)	Assigned to a new genus
	Ctenoblepharis nigriceps	Donoso-Barros (1966)	Assigned to a new genus
	Liolaemus nigriceps	Laurent (1984)	Assigned to a new genus
Liolaemus orientalis	*Liolaemus annectens orientalis*	Müller (1924)	Original description
	Liolaemus orientalis	Laurent (1992)	Assigned to species status
Liolaemus chlorostictus	*Liolaemus orientalis chlorostictus*	Laurent (1991)	Original description
	Liolaemus chlorostictus	Schulte *et al.*, 2000	Assigned to species status
Liolaemus pachecoi	*Liolaemus jamesi pachecoi*	Laurent (1995)	Original description
	Liolaemus pachecoi	Langstroth (2011)	Assigned to species status
Liolaemus pantherinus	*Liolaemus islugensis*	Pincheira-Donoso & Núñez (2005)	Synonym
Liolaemus poecilochromus	*Liolaemus andinus*	Pincheira-Donoso & Núñez (2005)	Synonym
	Liolaemus poecilochromus	Lobo *et al.* (2010b)	Revalidation
	Phrynosaura reichei	Werner (1907)	Original description
	Ctenoblepharys reichei	Donoso-Barros (1972)	Assigned to a new genus
Liolaemus reichei	*Liolaemus reichei*	Etheridge (1995)	Assigned to a new genus
	Liolaemus stolzmanni	Langstroth (2011)	Synonym
	Liolaemus reichei	Valladares *et al.* (2018)	Revalidation
	Ctenoblepharis schmidti	Marx (1960)	Original description
Liolaemus schmidti	*Liolaemus andinus*	Pincheira-Donoso & Núñez (2005)	Synonym
	Liolaemus schmidti	Lobo *et al.* (2010b)	Revalidation
	Proctotretus Signifer	Duméril & Bibron (1837)	Original description
	Ptychodeira signifera	Fitzinger (1843)	Assigned to a new genus
	Leiolaemus signifer	Gray (1845)	Assigned to a new genus
	Eulaemus signifer	Girard (1858)	Assigned to a new genus

Table 2. Continued

Current taxonomic state	Proposal	Authors (year)	Nomenclatural act
	Proctotretus multiformis	Cope (1875)	Assigned to a new genus
Liolaemus signifer	*Liolaemus multiformis*	Halloy & Laurent (1988)	Synonym
	Liolaemus lenzi	Burt & Burt (1931)	Synonym
	Liolaemus variabilis var. *Crequii*	Peters & Donoso-Barros (1970)	Synonym
	Liolaemus variabilis var. *Neveui*	Peters & Donoso-Barros (1970)	Synonym
	Liolaemus variabilis var. *Courtyi*	Peters & Donoso-Barros (1970)	Synonym
	Liolaemus bolivianus	Donoso-Barros (1966)	Synonym
	Ctenoblepharis Stolzmanni	Steindachner (1891)	Original description
Liolaemus stolzmanni	*Phrynosaura stolzmanni*	Laurent (1984)	Assigned to a new genus
	Liolaemus stolzmanni	Etheridge (1995)	Assigned to a new genus
	Liolaemus reichei	Langstroth (2011)	Synonym
Liolaemus torresi	*Phrynosaura torresi*	Núñez *et al.* (2003)	Original description
	Liolaemus torresi	Pincheira-Donoso *et al.* (2008)	Assigned to a new genus
Liolaemus tropidonotus	*Liolaemus multiformus*	Burt & Burt (1931)	Synonym
	Liolaemus signifer	Laurent (1984)	Synonym

We included only those species members of the *L. montanus* group that show nomenclatural acts. We have not included a complete list of synonyms (see Etheridge & Frost, 2010).

The aim of this work is to elucidate the evolutionary relationships and species richness of the *L. montanus* group further by obtaining more robust and comprehensive phylogenetic hypotheses based on the available total evidence, including morphological, ecological, biogeographical and molecular evidence. Additionally, we use these hypotheses to clarify some outstanding taxonomic issues in the *L. montanus* group.

MATERIAL AND METHODS

SPECIMEN COLLECTION AND PREPARATION

More than 600 specimens of *Liolaemus* were collected during 24 collecting trips in Argentina, Bolivia, Chile and Peru, all with the required national or provincial authorizations required for scientific collections of fauna in each country. We were able to collect specimens of the majority of the described species of the *L. montanus* group, plus > 100 specimens of uncertain taxonomic status but clearly belonging to the group. We prioritized collections from the type localities of described species to prevent regional variability. Specimens were captured with a noose, with a fork or by hand, avoiding the use of harmful methods (handgun, stones, etc.) in order to maintain integrity of the samples. During fieldwork, we also obtained data on the coloration in life by description and digital photography. Specimens were killed with 1% sodium pentothal, then injected with 10% formaldehyde and preserved in 70% alcohol. All procedures were conducted in accordance with international standards on animal welfare and were compliant with national regulations and the 'Comité Nacional de Ética en la Ciencia y la Tecnología' of Argentina (Expte. 5344/99 Res. 1047). Most samples were deposited in the herpetological collections of Fundación Miguel Lillo (FML), Colección Boliviana de Fauna (CBF), Museo de Historia Natural de la Universidad Nacional de San Agustín, Arequipa (MUSA) and Museo de Ciencias Naturales, Salta (MCN).

We included 56 described species (87.5%) of the *L. montanus* group and an additional 37 terminal taxa belonging to the group, but which were not assignable to any available names. We did not include *Liolaemus chiribaya*, Aguilar *et al.*, 2019, *Liolaemus duellmani* Cei, 1978, *Liolaemus erroneus* Núñez & Yáñez, 1983, *Liolaemus nazca*, Aguilar *et al.*, 2019, *Liolaemus omorfi* Demangel *et al.*, 2015, *Liolaemus pantherinus* Pellegrin, 1909 and *Liolaemus victormoralesi*, Aguilar *et al.*, 2019, because we did not have access to specimens of these species, some of which are known reliably only from type material, which is lost in the case of *L. erroneus*. As outgroup taxa, we include members of each of the genera included in Liolaemidae and different groups of *Liolaemus*: *Ctenoblepharys adspersa* (Tschudi, 1845), *Phymaturus palluma* (Molina, 1782), *Liolaemus abaucan* Etheridge, 1993, *Liolaemus inacayali* Abdala, 2013, *Liolaemus kingii* (Bell, 1843), *Liolaemus kolengh* Abdala & Lobo, 2006, *Liolaemus pseudoanomalus* (Cei, 1981), *Liolaemus robertmertensi* Hellmich, 1964 and *Liolaemus tiranti* Avila *et al.*, 2017. Specimens studied are listed in the Supporting Information (Appendix S1).

Figure 1. Map showing distribution of the *Liolaemus montanus* group.

DATA MATRIX

Morphological characters

We included a combination of characters based on lepidosis, morphometrics and coloration. Lepidosis was studied under a stereoscope (×10–×40). Morphometric characters were measured with a ± 0.01 mm precision digital calliper. Coloration was based on photographs of live animals and was analysed in conjunction with direct observation of preserved specimens. Terminology of colour patterns is shown in Figure 2. Terminology

Table 3. Political distribution of the valid species of the *Liolaemus montanus* group

Argentina (25)	Bolivia (13)	Chile (31)	Peru (15)
L. cazianiae	***L. chlorostictus***	*L. andinus*	*L. annectens*
L. chlorostictus	***L. erguetae***	*L. audituvelatus*	*L. chiribaya*
L. dorbignyi	*L. fittkaui*	***L. erguetae***	*L. etheridgei*
L. duellmani	*L. forsteri*	*L. erroneus*	*L. evaristoi*
L. eleodori	***L. islugensis***	*L. fabiani*	*L. insolitus*
L. famatinae	***L. jamesi***	*L. foxi*	*L. melanogaster*
L. gracielae	***L. pachecoi***	*L. hajeki*	*L. nazca*
L. griseus	***L. orientalis***	***L. islugensis***	***L. poconchilensis***
L. halonastes	***L. pantherinus***	***L. jamesi***	*L. polystictus*
L. huacahuasicus	***L. pleopholis***	*L. manueli*	*L. robustus*
L. huayra	***L. puritamensis***	*L. molinai*	***L. signifer***
L. inti	***L. schmidti***	***L. nigriceps***	*L. thomasi*
L. montanus	***L. signifer***	*L. omorfi*	*L. victormoralesii*
L. multicolor		***L. pachecoi***	*L. williamsi*
L. nigriceps		***L. pantherinus***	
L. orientalis		*L. patriciaiturrae*	
L. orko		***L. pleopholis***	
L. poecilochromus		***L. poconchilensis***	
L. porosus		***L. porosus***	
L. pulcherrimus		***L. puritamensis***	
L. puritamensis		*L. reichei*	
L. ruibali		*L. robertoi*	
L. scrocchii		*L. rosenmanni*	
L. vallecurensis		***L. schmidti***	
L. vulcanus		***L. signifer***	
		L. stolzmanni	
		L. torresi	

The species distributed in more than one country are shown in bold. The number of species per country is shown in parentheses.

used to reference anatomical and biological character states was compiled from the literature (Etheridge, 1995; Lobo & Espinoza, 1999; Abdala, 2007; Paz, 2012; Quinteros, 2012; Abdala & Juárez Heredia, 2013; among others) (Supporting Information, Appendix S2). We studied 306 morphological characters, including 90 from other authors (Lobo & Quinteros, 2005; Abdala, 2007; Abdala & Juárez Heredia, 2013; Quinteros, 2013; Gutiérrez *et al.*, 2018) and 216 that we used for the first time in a phylogenetic analysis (see Results for details).

Molecular characters

The phylogenetic analyses included five mitochondrial markers. We included 12S and *Cytb* sequences taken from Aguilar *et al.* (2017). We also include sequences of the mitochondrially encoded region spanning *ND1* to *COI* taken from (Schulte *et al.*, 2000, 2003a, b; Schulte, 2013). For newly reported DNA sequences, genomic DNA extraction, polymerase chain reaction conditions, primers used and sequencing were performed following Schulte *et al.* (2003a, b). These

sequences represented the mitochondrially encoded region spanning *ND1* to *COI*. For this analysis, only the protein-coding regions, part of *ND1*, all of *ND2* and part of *COI* were used, given that the intervening tRNA regions were highly variable among sampled taxa, making alignment of these regions unreliable. Base positions inferred to have ambiguous homology at the ends of *ND1* and *ND2* were excluded from phylogenetic analyses. In total, we included 3084 aligned positions (663 from 12S, 643 from *Cytb* and 1751 from *ND1*, *ND2* and *COI*). Sequences were aligned and edited with MEGA v.7.0.26 (Kumar *et al.*, 2016). See the Supporting Information (Appendix S3) for the GenBank accession numbers of specimens.

DATA MATRIX

Three matrices were made: (1) including morphological data only; (2) with molecular characters only; and (3) including both morphological and molecular data. The morphological matrix included 103 terminals and 306 characters, of which 48 were continuous
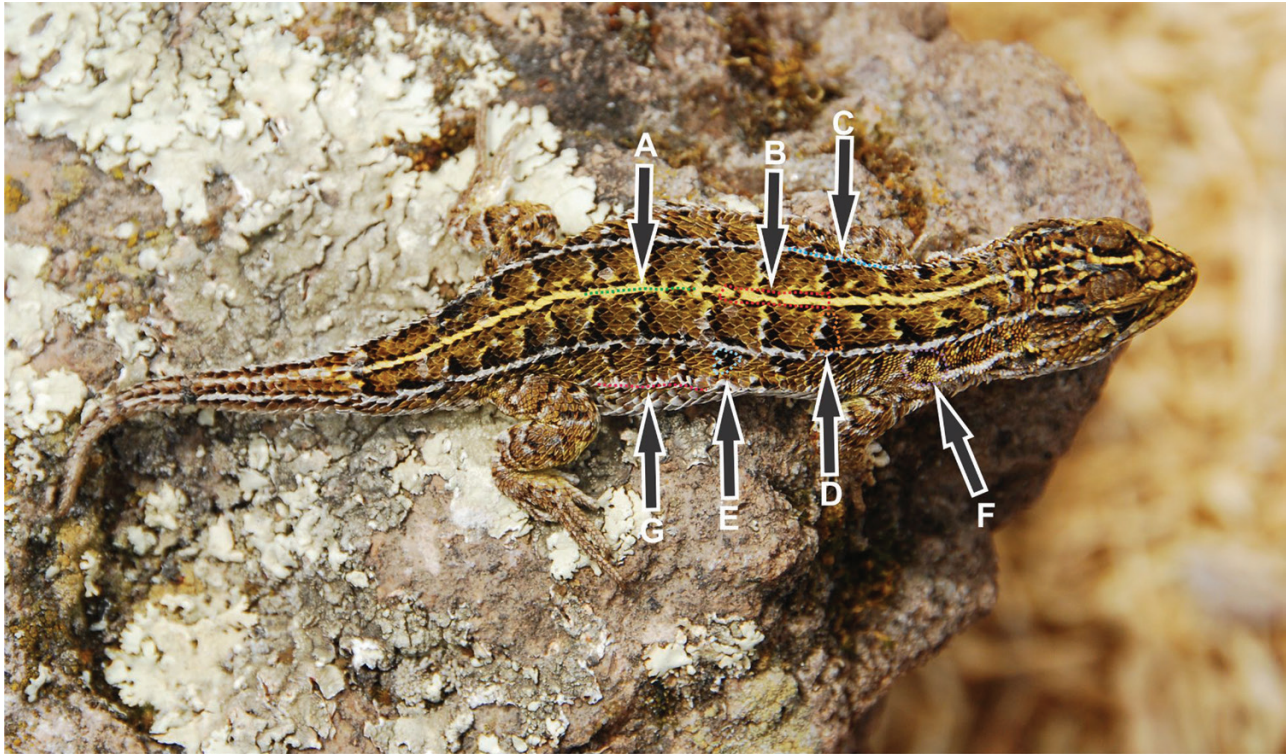
Figure 2. Regions of body of colour pattern used in the present study, modified from Lobo & Espinoza (1999). A, vertebral line. B, vertebral field. C, dorsolateral stripes. D, paravertebral spots. E, lateral spots. F, scapular region. G, ventrolateral line.

and 258 discrete characters. The discrete characters included 143 from coloration, 95 from lepidosis and morphometrics, 16 miscellaneous (osteological, myological and lepidosis) and four ecological or biogeographical. Discrete characters were coded as non-polymorphic binary, polymorphic binary, non-polymorphic multistate or polymorphic multistate. The polymorphic binary characters and polymorphic multistate characters were treated according to Wiens (1995). Characters 33, 42, 45, 46, 48, 49, 53, 55–62, 64, 65, 71–73, 78, 81–83, 87, 88, 107, 121, 122 and 140 were considered additive. Continuous characters were analysed following Goloboff *et al.* (2006), avoiding any discretization. Continuous characters were standardized using the command 'nstates stand' in TNT v.1.5 (Goloboff *et al.*, 2000, 2008; Goloboff & Catalano, 2016). Characters 142 and 306 were discretized under the criterion by Thiele (1993). The molecular matrix included 49 taxa and 3084 bp (Supporting Information, Appendix S3). The total evidence matrix included 103 terminals and 3390 characters, adding 3084 molecular characters to the dataset. The morphological matrix in the total evidence analysis received the same treatment as in the morphological analysis.

CLADISTIC ANALYSIS

To perform the morphological and total evidence analyses, we used TNT v.1.5, with parsimony as the optimality criterion, following Farris (1983). We followed the protocol of Mirande (2008, 2009, 2010) to obtain topologies based on the most stable concavity constant (*K*) values. Group support was estimated using symmetric resampling, with 1000 replicates and a probability of deletion of 0.33.

For the Bayesian analysis, we selected the best-fitting model for each individual gene with JModelTest v.0.1.1 (Guindon & Gausel, 2003; Posadas, 2008), using the corrected Akaike information criterion. We used Bayesian inference (BI) to infer a phylogenetic hypothesis and to estimate nodal support of the concatenated matrix. Bayesian inference analyses were conducted using MrBayes v.3.2 (Ronquist & Huelsenbeck, 2003), and the parameters for all the runs were as follows: mcmc ngen = 50 000 000, printfreq = 1000, samplefreq = 1000, nruns = 2, nchains = 4 and savebrlens = yes. Equilibrium samples (after 25% of burn-in) were used to generate a 50% majority-rule consensus tree; posterior probabilities (Pp) were considered significant when ≥ 0.95 (Huelsenbeck & Ronquist, 2001).

RESULTS

LIST OF CHARACTERS STUDIED

Of the total number of morphological characters used, 216 were new and were derived from the results of this work. They are listed in the Supporting Information (Appendix S4).

TOTAL EVIDENCE HYPOTHESIS

Our total evidence hypothesis (TEH) was based on the combined morphological and molecular matrix. All runs recovered a monophyletic *L. montanus* group. Various hypotheses were obtained with different topologies and clade compositions depending on the *K* values used. Based on the criteria proposed by Mirande (2009), we selected the most stable phylogenetic hypothesis (*K* = 18). This same hypothesis was recovered with *K* values of 16–22. Thus, the proposed hypothesis was highly congruent with the hypotheses obtained when *K* = 9–15, recovering the same groups but with some differences in the composition and relationships among the terminals (Fig. 3).

In the proposed TEH, the *Liolaemus montanus* group was supported by 26 bp and 24 morphological characters, of which 15 were continuous and nine discrete (Supporting Information, Table S1). In the *L. montanus* group, the species were grouped into 12 clades (Fig. 3) that we named as species groups based on the earliest available name within the group and/or following the proposals of Cei (1986, 1993), Díaz Gómez (2007) and Lobo *et al.* (2010a) (Table 4). The following species group clades were recovered (Fig. 3): (*Liolaemus chlorostictus* clade (*Liolaemus andinus* clade (*Liolaemus multicolor* clade (*Liolaemus poecilochromus* clade (*Liolaemus erguetae* clade + *Liolaemus reichei* clade) + (*Liolaemus jamesi* clade (*Liolaemus dorbignyi* clade (*Liolaemus forsteri* clade + *Liolaemus ortizi* clade) + (*Liolaemus robustus* clade + *L. huacahuasicus* clade))))))).

Liolaemus chlorostictus *clade*

This clade is composed of two species: *Liolaemus chlorostictus* Laurent, 1991 and *L. orientalis*. They are medium to large in size [maximal snout–vent length (SVL) > 90 mm]. The dorsal scales of the torso are juxtaposed and weakly keeled; they possess ≤ 70 scales around the midbody, 75 dorsals and 90 ventrals. The species are allopatrically distributed in both northernmost Argentina and southwestern Bolivia (Fig. 4). This clade is supported by six continuous characters and 16 discrete characters (12 lepidosis characters, three coloration characters and one ecological character; Supporting Information, Table S1). This relationship was recovered in all of the TEH runs performed.

Liolaemus andinus *clade*

This clade is composed of 20 terminals, of which 12 correspond to described species and eight represent populations of uncertain taxonomic status (Fig. 3). The majority of these species are distributed in Andean regions, primarily in Argentina and Chile (Fig. 5). It includes medium-sized lizards, but some species reach a SVL of 90 mm [i.e. *Liolaemus nigriceps* (Philippi, 1860) and *Liolaemus patriciaiturrae* Navarro & Núñez, 1993], with smooth to weakly keeled body scales, largely juxtaposed or subimbricate, high scale counts around the midbody (≤ 120), dorsals ≤ 115 and ventrals ≤ 120. This clade is supported by two continuous characters, two lepidosis characters, one colour character and 12 molecular characters (Supporting Information, Table S1). This clade was recovered in all of the runs performed, with variations of the internal topology.

Liolaemus multicolor *clade*

This clade is composed of two described species (*L. multicolor* Koslowski, 1898 and *L. schmidti*) and one terminal from a population of uncertain taxonomic status (*L.* aff. *multicolor*) (Fig. 3). These are medium-sized lizards (maximal SVL = 82 mm) with smooth, juxtaposed dorsal body scales, ≤ 85 scales around midbody and 100 ventrals, with the presence of blue scales on the dorsum, flanks and tail. These species inhabit the Puna of north-western Argentina, south-western Bolivia and north-eastern Chile (Fig. 5). This clade is supported by one continuous character, one discrete character, five colour characters and 19 molecular characters (Supporting information, Table S1). This clade was recovered in all runs performed and in the hypotheses where *K* = 13–15. It is sister to the *L. poecilochromus* clade.

Liolaemus poecilochromus *clade*

This clade is composed of three described species (*Liolaemus pleopholis* Laurent, 1998 (*L. poecilochromus* Laurent, 1986 + *L. halonastes*)) (Fig. 3). They are medium-sized lizards, but *L. pleopholis* exceeds 85 mm (maximal SVL), possessing smooth, juxtaposed dorsals, with ≤ 90 scales around the midbody. These species are distributed in north-western Argentina, north-eastern Chile and adjacent Bolivia (Fig. 5). The clade is supported by six continuous characters and five colour characters (Supporting Information, Table S1). This clade was not recovered in the hypotheses where *K* = 3–11 (only the relationship between *L. poecilochromus* and *L. halonastes* was maintained), but where *K* = 13–15, this clade was recovered as sister to the multicolor clade.
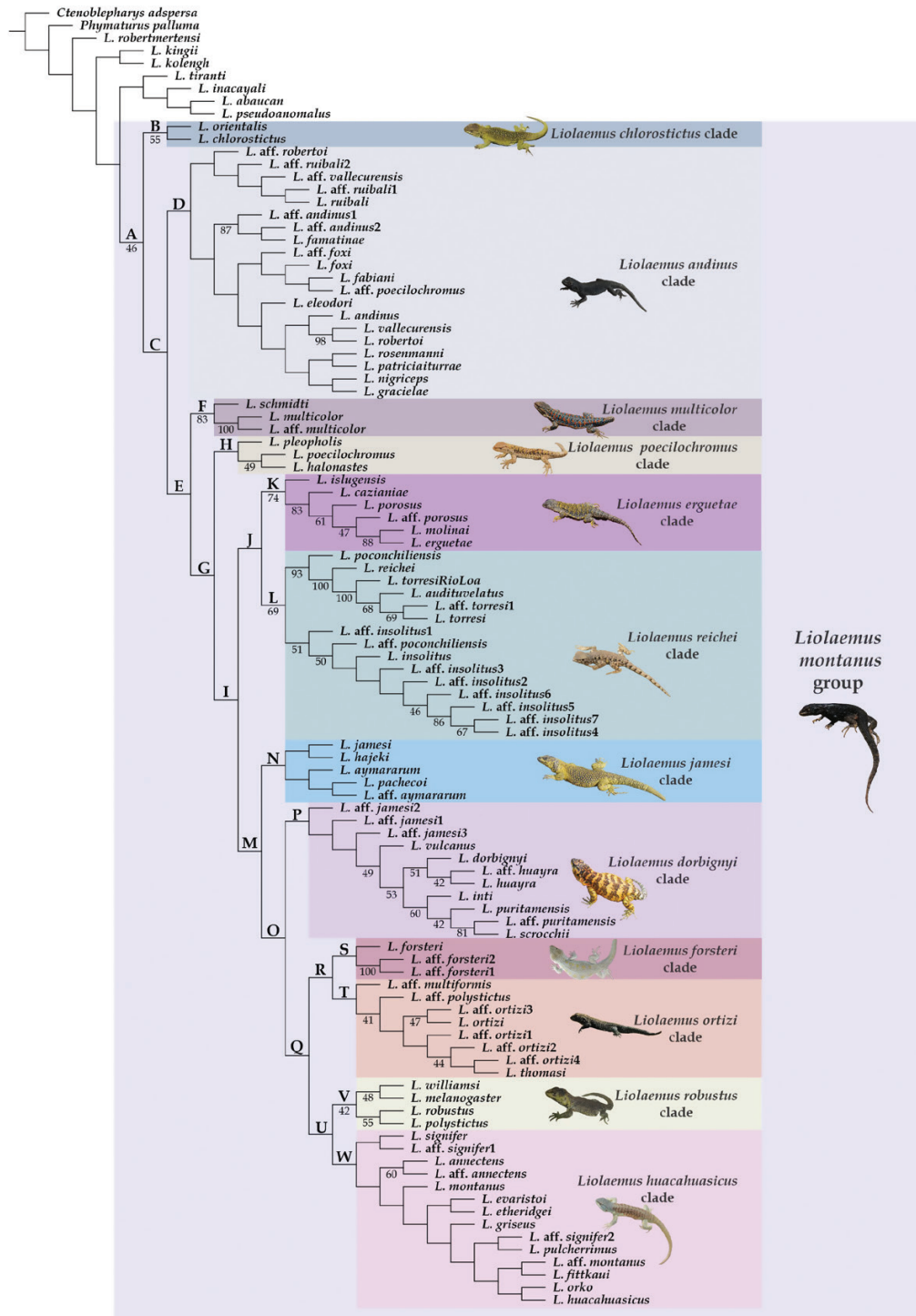
Figure 3. Total evidence hypothesis. Topology recovered by total evidence analysis under parsimony. Numbers below branches correspond to symmetric resampling.

Liolaemus erguetae *clade*

This clade is composed of five described species (*Liolaemus cazianiae* Lobo *et al*., 2010a, *Liolaemus erguetae* Laurent, 1995, *Liolaemus islugensis* Ortiz &

Marquet, 1987, *Liolaemus molinai* Valladares *et al*., 2002 and *L. porosus*) and one terminal from a population of uncertain taxonomic status, *L.* aff. *porosus* (Fig. 3). These lizards are of small to medium size (maximal

Table 4. Indented list of *Liolaemus montanus* group

A. *L. montanus* group
 B. *L. chlorostictus* clade
 C. Unnamed node
   D. *L. andinus* clade
   E. Unnamed node
     F. *L. multicolor* clade
     G. Unnamed node
       H. *L. poecilochromus* clade
       I. Unnamed node
       J. Node: *L. erguetae* clade + *L. reichei* clade
       K. *L. erguetae* clade
       L. *L. reichei* clade
     M. Unnamed node
       N. *L. jamesi* clade
       O. Unnamed node
         P. *L. dorbignyi* clade
         Q. Unnamed node
         R. Node: *L. forsteri* clade + *L. ortizi* clade
         S. *L. forsteri* clade
         T. *L. ortizi* clade
         U. Node: *L. robustus* clade +
       L. huacahuasicus clade
           V. *L. robustus* clade
           W. *L. huacahuasicus* clade

SVL = 77 mm), possessing smooth, juxtaposed dorsals, high counts of scales around the midbody (≤ 105), dorsals (≤ 100) and ventrals (≤ 105), presence of pores in the scales of the neck, venter, groin and tail, and the males generally have a yellow abdomen speckled with small dark spots. These species are distributed in north-western Argentina, south-western Bolivia and north-eastern Chile (Fig. 5). This clade is supported by three continuous characters, eight discrete characters and two coloration characters (Supporting Information, Table S1). This clade was recovered in all hypotheses, with the same composition of terminals and topology and, in most cases, was found as sister to the *L. reichei* clade.

Liolaemus reichei Werner, 1907 *clade*

This clade is composed of 15 terminals, of which five correspond to described species and ten correspond to populations of uncertain taxonomic status (Fig. 3). These are small-bodied lizards (maximal SVL = 65 mm), with short tails in relationship to SVL, heads almost as wide as long, isognathus profiles, between 45 and 75 scales around the midbody, and between 50 and 90 smooth, juxtaposed dorsals. The clade is supported by five continuous characters, four discrete characters and four colour characters (Supporting Information, Table S1). The *L. reichei* clade is recovered in all hypotheses, with the same composition and always divided into

the same two subclades. One subclade includes four described species [*Liolaemus audituvelatus* Núñez & Yáñez, 1983, *Liolaemus poconchilensis* Valladares, 2002, *L. reichei* Werner, 1907 and *Liolaemus torresi* (Núñez *et al.*, 2003)] and two populations of uncertain taxonomic status, all of which are distributed in north-western Chile (Fig. 3). The other subclade is composed of nine terminals, of which only *Liolaemus insolitus* Cei, 1982 has been described formally, evidencing the diversity awaiting description in this subclade. This clade is found in southern Peru, primarily in coastal zones (Fig. 4).

Liolaemus jamesi *clade*

This clade includes four described species [*Liolaemus aymararum* Veloso *et al.*, 1982, *Liolaemus hajeki* Núñez, Pincheira-Donoso & Garín, 2004, *Liolaemus jamesi* (Boulenger, 1891) and *Liolaemus pachecoi* Laurent, 1995] and a terminal representing a population of uncertain taxonomic status (*L.* aff. *aymararum*). These lizards are characterized by their large size (maximal SVL = 100 mm; except *L. hajeki*, maximal SVL = 72 mm), bodies almost as wide as long, with large, juxtaposed dorsals, often with black skin visible between the scales, low numbers of scales around the midbody (mean = 45; except *L. hajeki*, mean = 56), ventral melanism present and conspicuous sexual dichromatism. The *L. jamesi* clade is found in north-eastern Chile and south-western Bolivia (Fig. 4) and is supported by one morphometric character, three coloration characters and 20 molecular characters (Supporting Information, Table S1). This clade was recovered in the majority of the hypotheses, but in the trees where *K* = 7–15 this clade was integrated with the *L. forsteri* clade. The (*L. hajeki* + *L. jamesi*) and (*L. aymararum* (*L. pachecoi* + *L.* aff. *aymararum*)) relationship was recovered in all hypotheses obtained (Fig. 3).

Liolaemus dorbignyi *clade*

This clade includes *L. dorbignyi* Koslowski, 1898, *Liolaemus huayra* Abdala *et al.*, 2008, *Liolaemus aff.* jamesi3, Demangel, 2016, *Liolaemus inti* Abdala *et al.*, 2008, *Liolaemus puritamensis* Núñez & Fox, 1989, *Liolaemus scrocchii* Quinteros *et al.*, 2008, *Liolaemus vulcanus* Quinteros & Abdala, 2011 and four terminals of uncertain taxonomic status: *L.* aff. *huayra*, *L.* aff. *jamesi*1, *L.* aff. *jamesi*2 and *L.* aff. *puritamensis* (Fig. 3). These are large, saxicolous lizards, with maximal SVL = 98 mm, wide bodies, short tails in relationship to SVL, large, smooth to weakly keeled, juxtaposed to subimbricate dorsals, with exposed black skin and numerous heteronote granules between the scales of the dorsum and flanks, a large, dark spot on the dorsal
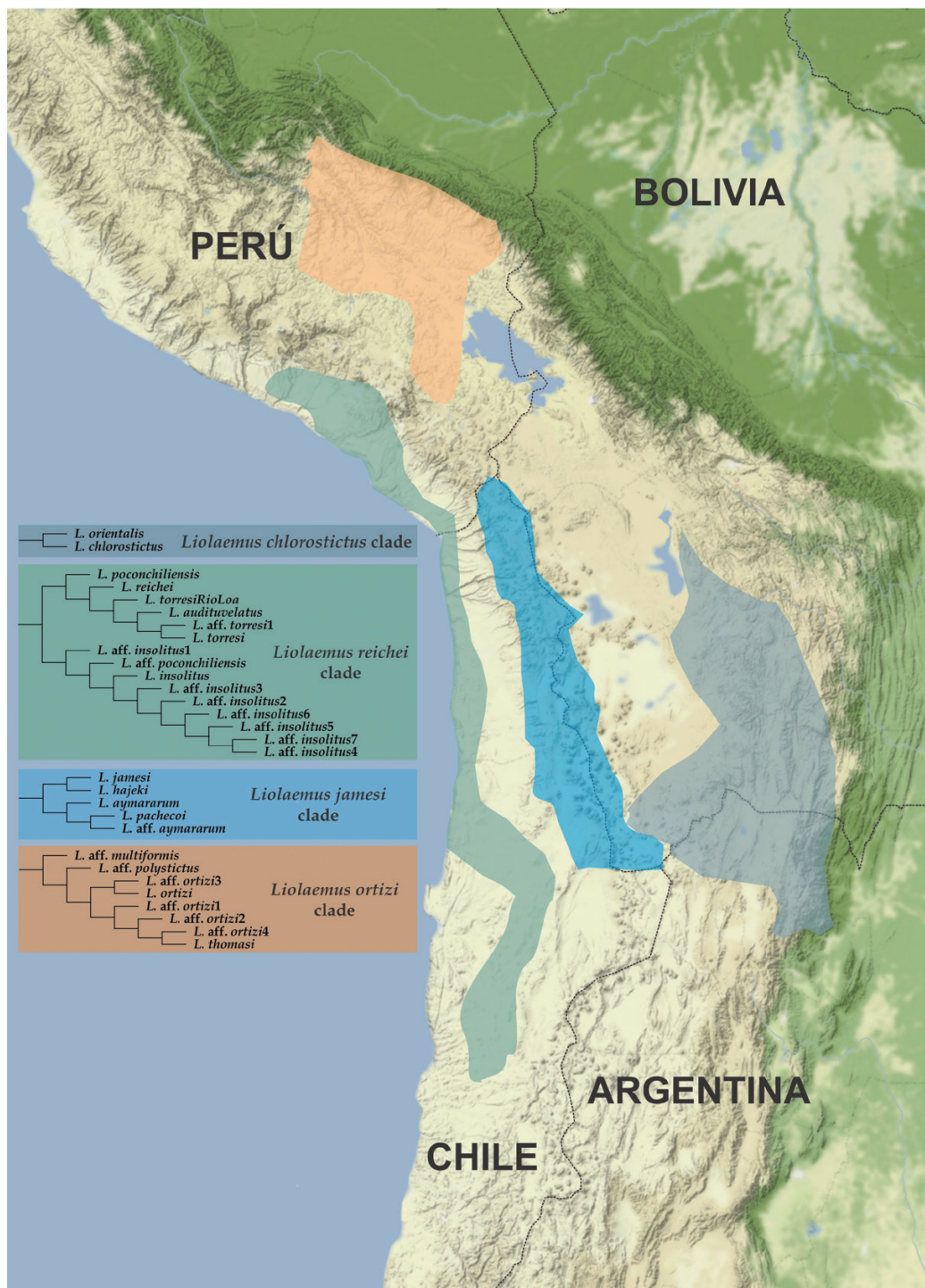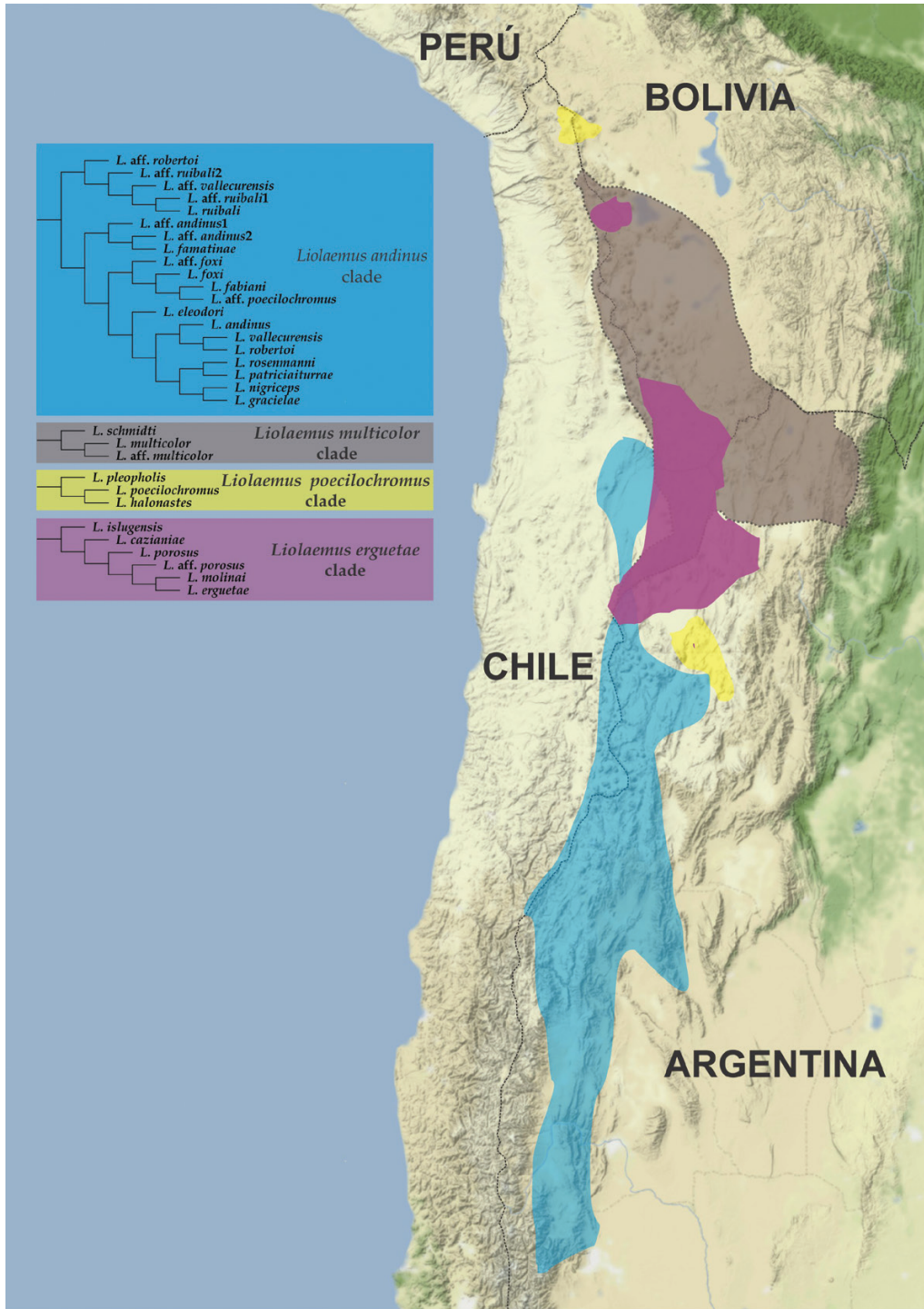
Figure 4. Map showing distribution of the taxa members of the *Liolaemus chlorostictus*, *Liolaemus reichei*, *Liolaemus jamesi* and *Liolaemus ortizi* clades.

surfaces of the head and neck, little evident sexual dichromatism in various species, and a ventral region with a dark reticulate pattern. The *L. dorbignyi* clade occurs in north-western Argentina, north-eastern Chile, south-western Bolivia and extreme south-eastern Peru (Fig. 6) and is supported by one continuous character and 11 coloration characters. This group was recovered in all of the hypotheses obtained.

Figure 5. Map showing distribution of the taxa members of the *Liolaemus andinus*, *Liolaemus multicolor*, *Liolaemus poecilochromus* and *Liolaemus erguetae* clades.

Liolaemus forsteri *clade*

This clade includes three terminals: *L. forsteri*, *L.* aff. *forsteri*1 and *L.* aff. *forsteri*2 (Fig. 3). They are large lizards (maximal SVL = 95 mm), with weakly keeled subimbricate dorsal scales and large, red to yellow blotches on the dorsum of the torso. The *L. forsteri* clade is distributed in southern Peru and northern Andean Bolivia (Fig. 6) and is supported by three continuous

characters, four discrete characters and three coloration characters (Supporting Information, Table S1). Half of the analyses recovered the following relationships: (*L.* aff. *multiformis* (*L. forsteri* (*L.* aff. *forsteri*1 + *L.* aff. *forsteri*2))). This clade was placed as sister to either the *L. ortizi* clade (*K* = 16–22) or the *L. jamesi* clade (*K* = 7–15).

Liolaemus ortizi *clade*

This clade is composed of eight terminals, of which only two correspond to described species: *Liolaemus ortizi* Laurent, 1982 and *Liolaemus thomasi* Laurent, 1998. All other terminals correspond to populations of uncertain taxonomic status (Fig. 3). This group of lizards as characterized by their medium size and low numbers of scales, not exceeding 65 around the midbody, 70 dorsals and 85 ventrals. Dorsal scales of the body and limbs are strongly keeled and imbricate. This clade is supported by two continuous characters, four lepidosis characters and one colour character. In hypotheses where *K* = 3–15, the *L. ortizi* clade is recovered without *L.* aff. *multiformis* and related to *L. huacahuasicus* where *K* = 3–8. In the remaining TEHs, the same composition and topology is recovered as in the proposed hypothesis. The *L. ortizi* group is distributed in high regions of central and southeastern Peru (Fig. 4).

Liolaemus robustus *clade*

This clade consists of (*Liolaemus williamsi* Laurent, 1992 + *Liolaemus melanogaster* Laurent, 1998) + (*Liolaemus polystictus* Laurent, 1992 + *Liolaemus robustus* Laurent, 1992) (Fig. 3). They are medium to large lizards (maximal SVL = 80–95 mm), with subimbricate smooth to weakly keeled dorsal scales on the body. The males are generally of a chestnut colour, with a tendency towards melanism of the pileus. The *L. robustus* clade is distributed in central Peru (Fig. 6) and is supported by three continuous characters, one discrete character and five molecular characters (Supporting Information, Table S1). The composition of this group was recovered in all hypotheses obtained, except where *K* = 3–8, where it was united with the *L. huacahuasicus* clade.

Liolaemus huacahuasicus *clade*

This clade includes 14 terminals (Fig. 3), all medium-sized lizards (maximal SVL = 85 mm) with triangular, imbricate, keeled dorsal body scales, with the dark scales being more strongly keeled than the lighter scales. Body colour in males varies between chestnut and yellow, and there are dark paravertebral blotches with light borders and a generally yellowish venter. This clade is supported by one discrete morphological character, four discrete coloration characters and

eight molecular characters (Supporting Information, Table S1). The lizards of the *L. huacahuasicus* clade are distributed in the extra-Andean sierras of Argentina (*L. montanus*, *L.* aff. *montanus*, *Liolaemus griseus* Laurent, 1984, *L. orko*, *L. huacahuasicus* and *Liolaemus pulcherrimus* Laurent, 1982), Puna and high Amazonian slopes of Bolivia (*L. signifer*, *L. fittkaui* and *L.* aff. *signifer*2), Chilean Puna (*L.* aff. *signifer*1) and the Puna and western ranges of Peru (*Liolaemus annectens* Boulenger, 1901, *L.* aff. *annectens*, *Liolaemus etheridgei* Laurent, 1998, *L. evaristoi* Gutiérrez *et al.*, 2018 and *L. signifer*) (Fig. 6). The composition of the *L. huacahuasicus* clade was recovered in all analyses except the hypotheses where *K* = 3–8, in which *L. annectens*, *L. evaristoi*, *L. signifer*, *L. etheridgei*, *L.* aff. *annectens* and *L.* aff. *signifer1* formed a group separate from the rest of the *L. huacahuasicus* clade and sister to the *L. robustus* clade, whereas the monophyletic group formed by *L. montanus*, *L.* aff. *montanus*, *L. griseus*, *L. fittkaui*, *L. orko*, *L. huacahuasicus*, *L. pulcherrimus* and *L.* aff. *signifer*2 were related to part of the *L. ortizi* clade.

MIXED BAYESIAN HYPOTHESIS

This hypothesis was highly congruent with that obtained with 'parsimony' (Fig. 7). The clades and groups recovered within the *L. montanus* group were the same, with changes in composition in only a few instances. The *L. chlorostictus*, *L. multicolor*, *L. reichei*, *L. forsteri* and *L. robustus* clades had the same species composition, with only some changes in the internal relationships (Fig. 7). The clade with the greatest differences with regard to the 'parsimony' hypothesis was the *L. huacahuasicus* clade, which included members of the *L. andinus* clade (*L. robertoi* Pincheira-Donoso & Nuñez, 2003, *L. vallecurensis* and *L.* aff. *poecilochromus*), the *L. dorbignyi* clade (*L.* aff. *jamesi*3, *L.* aff. *jamesi*1 and *L.* aff. *jamesi*2), the *L. jamesi* clade (*L. aymararum*) and the *L. ortizi* clade (*L.* aff. *multiformis*) (Fig. 7).

MORPHOLOGY-BASED HYPOTHESIS (MH)

In all runs performed with the morphology-only matrix, the *L. montanus* group was never recovered as monophyletic; instead, the outgroup species *L. abaucan*, *L. inacayali*, *L. kingii*, *L. kolengh*, *L. pseudoanomalus*, *L. robertmertensi* and *L. tiranti* were included within the *L. montanus* group, always as terminals of the *L. ortizi* group. Nevertheless, owing to the evidence for monophyly provided by the TEH and molecular hypotheses in the present study and by other authors (Schulte *et al.*, 2000, 2013; Espinoza *et al.*, 2004; Aguilar-Puntriano *et al.*, 2018) and understanding that the outgroup and the characters
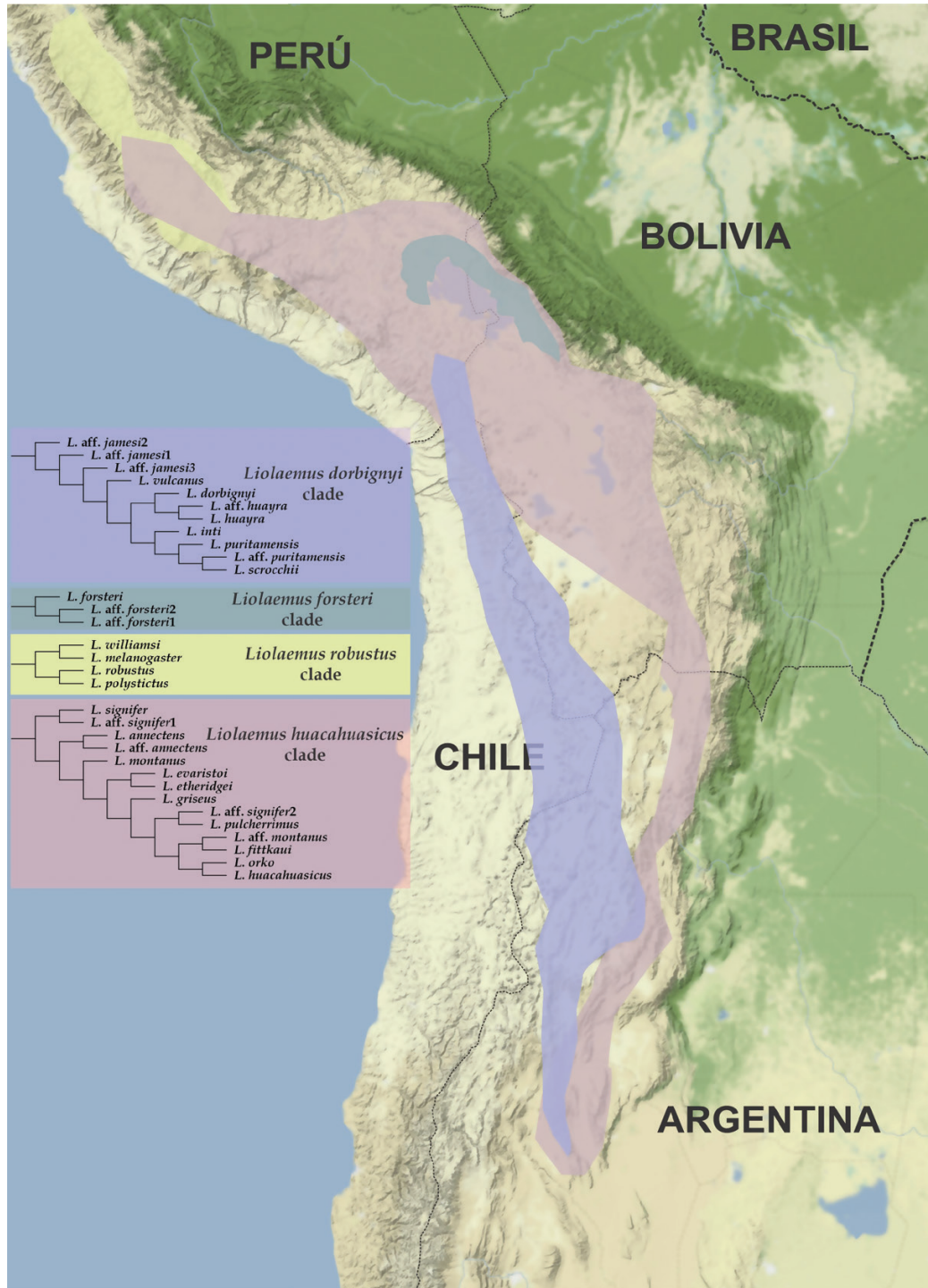
Figure 6. Map showing distribution of the taxa members of the *Liolaemus dorbignyi*, *Liolaemus forsteri*, *Liolaemus robustus* and *Liolaemus huacahuasicus* clades.

proposed to separated them are not sufficient to demonstrate monophyly, we have decided to present only the MH without the conflicting terminals under the assumption of a monophyletic *L. montanus* group.

Various hypotheses with different typologies and compositions were obtained for the clades within the *L. montanus* group, as a function of the *K* values applied. Based on the criteria proposed by Mirande (2009), we
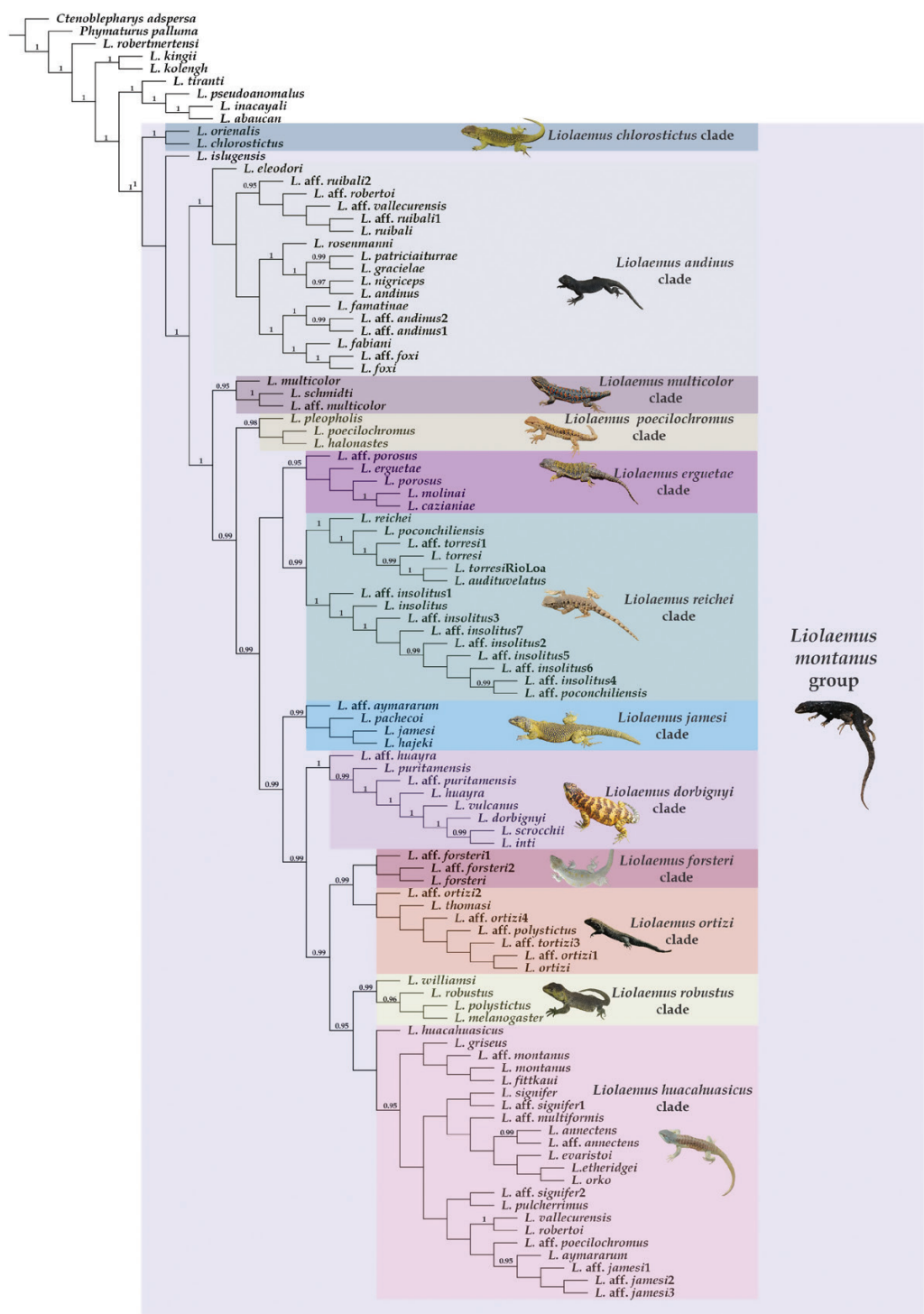
Figure 7. Mixed Bayesian hypothesis.

selected the most stable phylogenetic hypothesis, in which $K = 14$, as our proposed hypothesis (Fig. 8). This same hypothesis was also recovered with $K = 12$–16. Thus, the proposed hypothesis was highly congruent with the hypothesis obtained when $K = 7$–11, recovering

the same groups, albeit with some differences in their relationships and composition. In the proposed MH, the *L. montanus* group was supported by 31 characters, of which nine were continuous, 11 were lepidosis characters and the remaining 11 were miscellaneous.
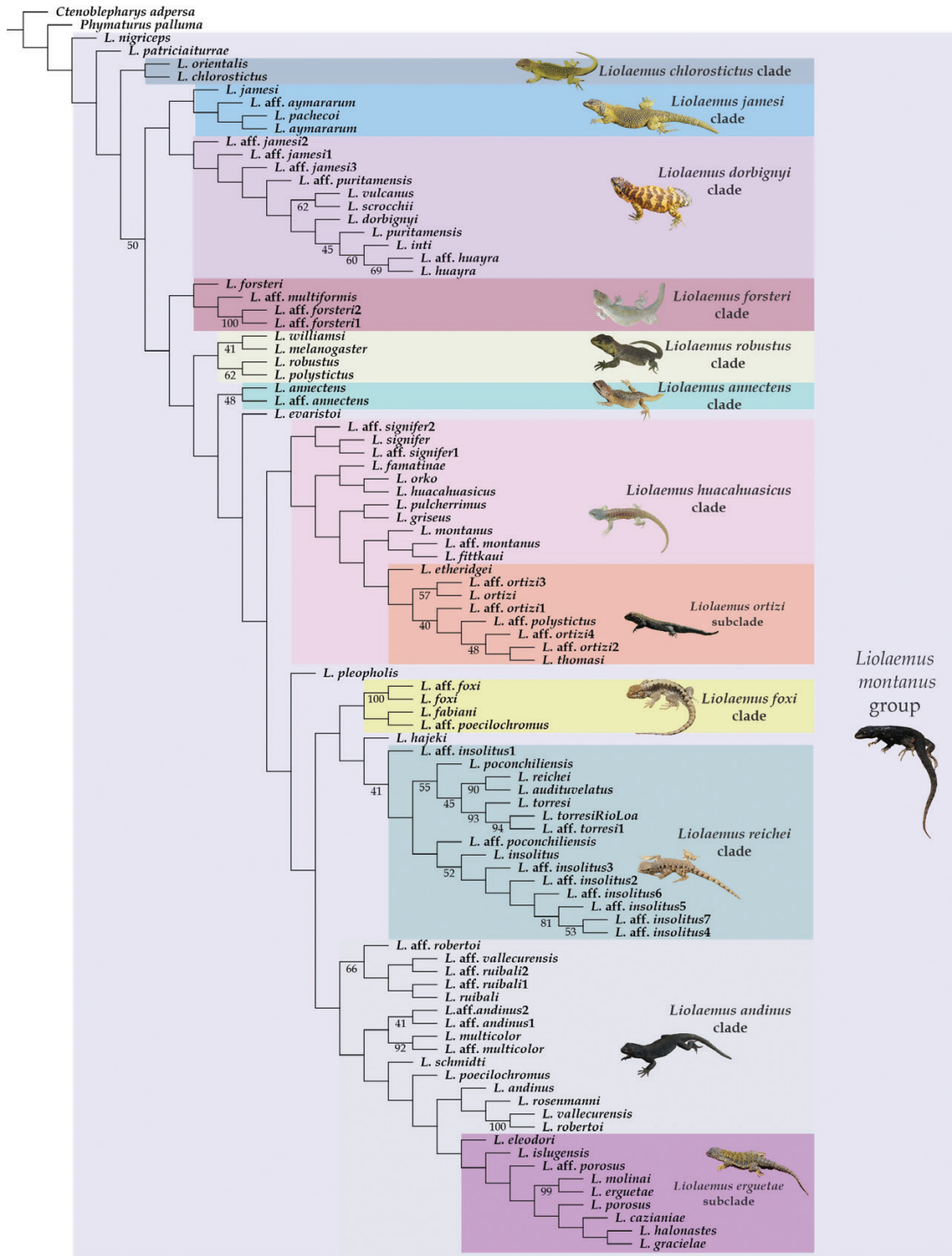
Figure 8. Topology recovered with the morphological hypothesis under parsimony (*K* = 14). Numbers below branches correspond to symmetric resampling.

In the proposed MH, ten clades were recovered, of which eight were congruent with those proposed by the TEH (Fig. 3). The species *L. nigriceps* and *L. patriciaiturrae* were placed basally and outside of the *L. andinus* clade, as also occurred in the TEH. The following clades were recovered (Fig. 8): (*L. nigriceps* (*L. patriciaiturrae* (*L. chlorostictus* clade (*L. jamesi* clade + *L. dorbignyi* clade) + (*L. forsteri* clade

(*L. robustus* clade (*L. annectens* clade (*L. evaristoi* (*L. huacahuasicus* clade (*L. pleopholis* (*L. foxi* clade (*L. hajeki* + *L. reichei* clade) + *L. andinus* clade)))))))))).

This tree recovered two clades not recovered by the TEH: the *L. foxi* clade, present in the TEH as a subclade of the *L. andinus* clade, and the *L. annectens* clade, present as a subclade of the *L. huacahuasicus* clade in the TEH. Also, all members of the TEH *L. multicolor* clade were integrated in the *L. andinus* clade, as was the TEH *L. erguetae* clade, which was recovered as a subclade including *L. halonastes* (Fig. 8). The *L. poecilocromus* clade was not recovered in the MH, and some of its members (*L. poecilochromus* and *L. halonastes*) were included in the MH *L. andinus* clade. The *L. ortizi* clade was recovered but as a subclade of the *L. huacahuasicus* clade. The *L. chlorostictus*, *L. dorbignyi*, *L. robustus* and *L. reichei* clades were recovered in the MH with the same composition as in the TEH. The MH did not recover *L. hajeki* in the *L. jamesi* clade, but instead placed it rather distantly as sister to the *L. reichei* clade. The *L. forsteri* clade included *L.* aff. *multiformis*, which the TEH placed in the *L. ortizi* clade, but this the relationship found by the MH was congruent with various hypotheses obtained with different *K* values in the TEH. The MH *L. huacahuasicus* clade incorporated species of the TEH *L. ortizi* clade and did not recover the species *L. annectens* and *L.* aff. *annectens*, which formed a separate clade. The MH *L. foxi* clade was formed by *L. foxi*, *L. fabiani*, *L.* aff. *foxi* and *L.* aff. *poecilochromus* and was placed as sister to the *L. hajeki* + *L. reichei* clade. The MH *L. reichei* clade presented minor differences from the clade recovered by the TEH, because the terminal *L.* aff. *insolitus*1 was here located basally to the two subclades otherwise recovered by the TEH. The MH *L. andinus* presented various congruent relationships with the TEH, but placed the *L. erguetae* clade as a subclade within the *L. andinus* clade.

MOLECULAR HYPOTHESIS

In order to obtain a molecular evidence-only hypothesis, we generated an agreement subtree (Fig. 9), which discarded conflictive terminal taxa (without sequence), resulting in a highly unresolved topology that might be attributable to the high percentage of missing data in some terminal taxa. The agreement subtree recovered the *L. montanus* group as monophyletic, but formed by only nine of the 12 monophyletic groups recovered by the TEH (Figs 3, 9). The overall topology was similar to that recovered by the TEH and MH, but with fewer taxa owing to the absence of species without molecular data.

The *L. chlorostictus* clade was not recovered as such, because *L. orientalis* was one of the species excluded from the analysis (Fig. 9).

The *L. andinus* clade was recovered as a group formed by 15 terminal taxa, five fewer than in the TEH. The differences between the terminals differed slightly from those recovered by the TEH (Fig. 9).

The *L. multicolor* clade was covered with the same composition and internal relationships as in the TEH (Fig. 9).

The *L. poecilochromus* clade was recovered with a similar composition to that of the TEH, but not including *L. pleopholis*, which was excluded from the analysis (Fig. 9).

The *L. erguetae* clade was recovered with three terminal taxa (out of the six that were included in the TEH). The other three remaining taxa were excluded from the analysis (Fig. 9).

An *L. reichei* clade with four terminal taxa was recovered. Most of the terminal taxa that formed part of this group in the TEH were excluded from the analysis (Fig. 9).

The *L. jamesi* clade was recovered with three terminal taxa. *Liolaemus pachecoi* and *L.* aff *aymararum*, which were part of the TEH, were excluded from the analysis (Fig. 9).

The *L. dorbignyi* clade was recovered with the same relationships as in the TEH. However, only six of the 11 terminals of the TEH were included in the molecular matrix (Fig. 9).

The *L. huacahuasicus* clade was recovered, but only two terminal taxa were included out of the 14 included in the TEH matrix (Fig. 9).

DISCUSSION

The *L. montanus* group (*L. montanus* series *sensu* Schulte *et al.*, 2000), which contains 64 recognized species, is one of the most diverse groups within the *Liolaemus* genus (Abdala & Quinteros, 2014; Gutiérrez *et al.*, 2018; Aguilar *et al.*, 2019), and our TEH recovered an additional 37 candidate species. Despite the importance of this group within *Liolaemus*, the phylogenetic relationships had not been studied in depth. Most of the previous studies including this group were broader phylogenies of the genus (Schulte *et al.*, 2000; Espinoza *et al.*, 2004; Avila *et al.*, 2006; Pyron *et al.*, 2013; Schulte, 2013; Zheng & Wiens, 2016; Esquerré *et al.*, 2019) or based on a particular internal group (Valladares *et al.*, 2002; Olave *et al.*, 2014; Aguilar *et al.*, 2017). Espinoza *et al.* (2004) studied the evolution of herbivory in Liolaemidae and obtained a phylogenetic tree based on 24 morphological characters (plus *ND2* and 12S sequences) but included only eight species (11.9%) of the group. Esquerré *et al.* (2019) studied the evolution of the reproductive modes within Liolaemidae, following a phylogenetic approach using mitochondrial (12S, *Cytb*, *ND2* and
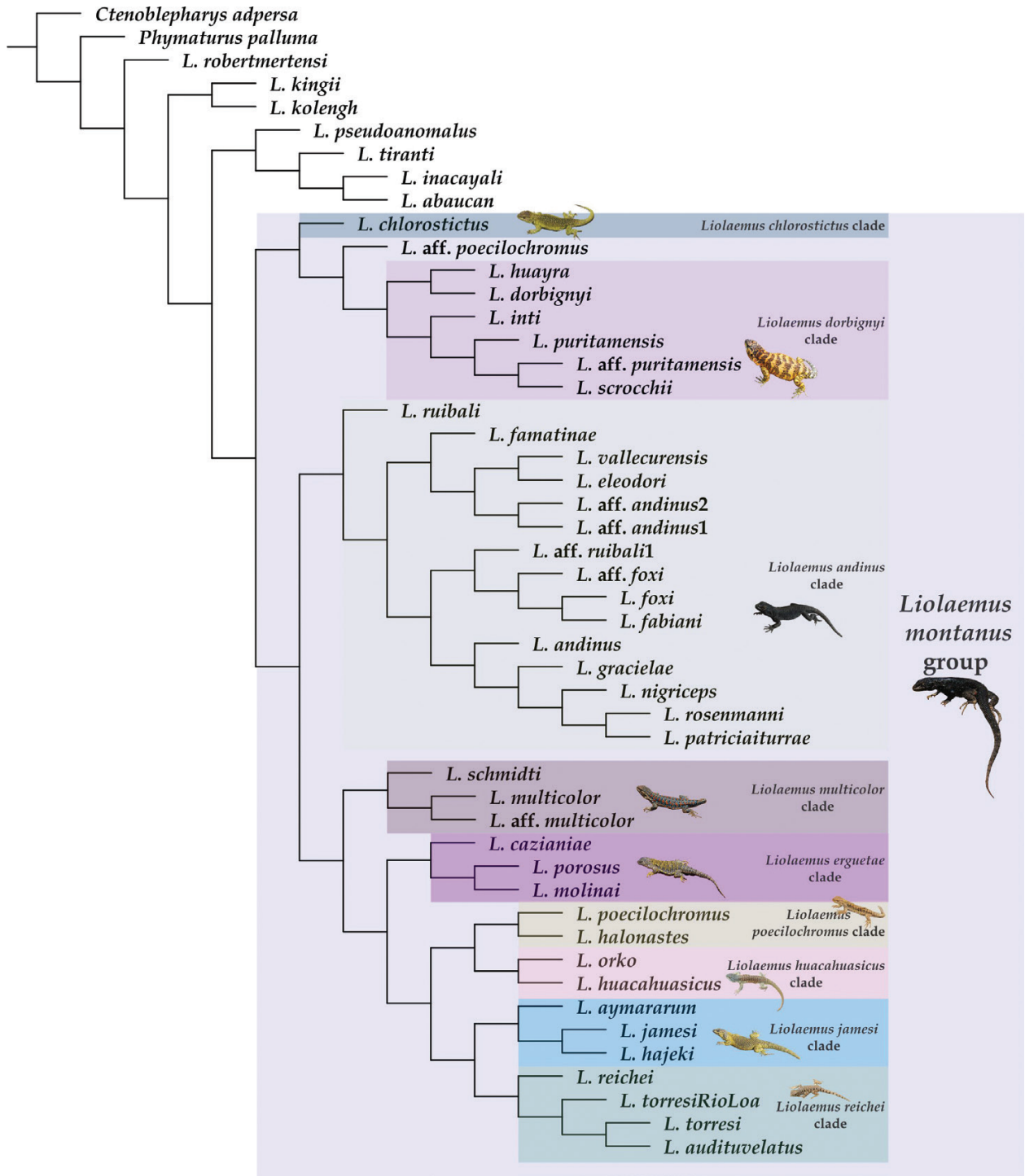
Figure 9. Molecular analysis tree.

ND4) and nuclear (*BID*, *EXPH5*, *KIF24*, *MXRA5*, *PLRL* and *PNN*) loci. The broad taxonomic coverage of their phylogenetic hypotheses is noteworthy and recovered a well-supported *L. montanus* group, but their analyses included only 26 (40.6%) of the 64 recognized species of the group.

A recent work examining the evolution of head shape among species in the *L. montanus* group presented molecular-based phylogenetic estimates based on two mitochondrial (*Cytb*, 12S) and five nuclear (*CMOS*, *EXPH5*, *KIF24*, *MXRA5* and *PRLR*) genes (Aguilar-Puntriano *et al.*, 2018). Although it was

the richest-sampled phylogeny for the *L. montanus* group to date, including 57 terminals, 14 of these were identified as candidate species and one was a 'cf.', resulting in a phylogeny including 43 terminal taxa assigned to species (67.1%) of the 64 recognized species.

To date, no other phylogeny for the species of the *L. montanus* group has included both exhaustive morphological data and molecular evidence. Also, by including 103 terminals, 56 (87.5%) of which belong to recognized species, with the remaining 37 being candidate species, our study presents a more comprehensive phylogeny of the *L. montanus* group by including a considerable number of morphological traits and two or three times more terminal taxa than previous studies.

DIFFERENCES BETWEEN OUR HYPOTHESES

The cladistic analyses performed here resulted in three phylogenetic hypotheses (Fig. 10) based on the three different datasets: (1) morphological characters only; (2) molecular characters only; and (3) the total evidence dataset, including both morphological characters and gene sequences. Most of the previous phylogenies of the *L. montanus* group were based on molecular data only (Schulte *et al.*, 2000; Espinoza *et al.*, 2004; Fontanella *et al.*, 2012; Olave *et al.*, 2014; Aguilar-Putriano *et al.*, 2018; Esquerré *et al.*, 2019). However, our molecular-based phylogeny obtained a hypothesis with a subsampled number of taxa, because of the unavailability of sequences for all terminals. Nevertheless, our morphological-only phylogeny for the *L. montanus* group is the first to include an exhaustive suite of morphological character states, and we consider it necessary to obtain a topology

based only on this dataset for diagnostic purposes. Although the phylogeny of Espinoza *et al.* (2004) included some morphological characters, all of them were synapomorphies of *Ctenoblepharys*, *Liolaemus* and *Phymaturus*, and although useful to diagnose the main groups inside these genera, they were not intended to discriminate between taxonomic groups inside the *L. montanus* group.

The *L. montanus* group was recovered as monophyletic in all the hypotheses we obtained. However, the relationships between the clades and subclades within the *L. montanus* group differed among the three topologies recovered. Despite the incongruence found, Subtree Pruning and Regrafting distances between the three topologies (TEH vs. morphology = 0.6; TEH vs. molecular = 0.82; and morphology vs. molecular = 0.7) showed some congruence between the three topologies recovered (Fig. 10). Despite the lower number of terminal taxa included in the molecular-based phylogeny, there was a high level of congruence between that topology and the other two. The TEH recovered 12 internal clades, of which nine were recovered in the molecular-based phylogeny and ten in the morphology-based phylogeny. From those previous ten recovered in the morphology-based phylogeny, two clades were nested inside other clades, namely the *L. erguetae* and *L. ortizi* subclades (nested within the *L. andinus* and *L. hucahuasicus* clades, respectively). Additionally, the morphology-based topology recovered two more clades that were not recovered in the TEH, the *L. annectens* and *L. foxi* clades (Fig. 10). Species of those clades were members of the *L. huacahuasicus* and *L. andinus* clades, respectively, in the TEH.

Although molecular datasets have been widely used in phylogenetic reconstruction since the 1990s, the use of morphological data has been rejected by some
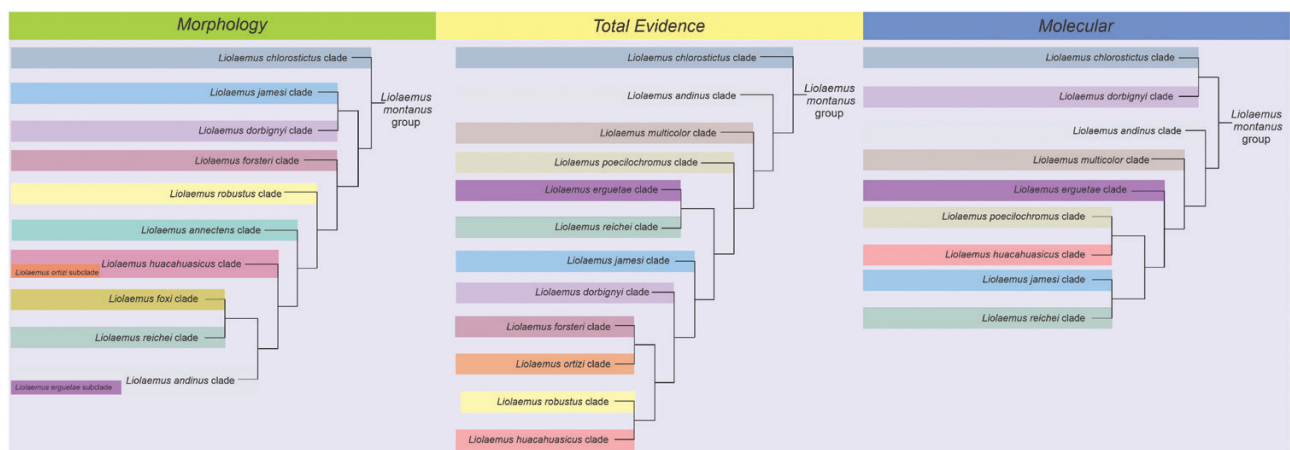

Figure 10. Summarized tree topologies showing the main monophyletic groups recovered under the total evidence, morphological and molecular hypotheses. Shading colours represent the same monophyletic group in each hypothesis.

researchers, who argue that morphology carries a high level of homoplasy (Alvarez *et al.*, 1999; Mueller *et al.*, 2004; Escobar García *et al.*, 2009; Mott & Vieites, 2009). But there is also evidence of homoplasious molecular data (Engstrom *et al.*, 2004; Castoe *et al.*, 2009; Jarvis *et al.*, 2014). Nevertheless, the use of morphological character states has remained widespread for the Liolaemidae (Lobo, 2001, 2005; Lobo & Quinteros, 2005; Abdala, 2007; Quinteros, 2013; Abdala & Juárez Heredia, 2013). Continuous characters analysed as such were used in many different studies (e.g. Abdala, 2007; Quinteros, 2013; Álvarez *et al.*, 2017; Barrionuevo, 2017; Bardin *et al.*, 2017; Portelli & Quinteros, 2018). Moreover, the inclusion of continuous morphological characters reinforces our hypothesis, because many of them are recovered as synapomorphies in the total evidence analysis.

DIFFERENCES FROM OTHER PHENETIC AND PHYLOGENETIC HYPOTHESES

As noted previously, many early hypotheses of relationships between species of the genus *Liolaemus* have been based on phenetic similarity [e.g. the species groups of Cei (1993) and Pincheira-Donoso & Núñez (2005)], not phylogenetic analyses based on the evolution of character states. Table 1 compares our subgroup-level clades against phenetic species groups proposed by previous authors for species of the *L. montanus* group.

Given that the most comprehensive recent phylogenetic hypothesis for the *L. montanus* group is that of Aguilar-Puntriano *et al.* (2018), our discussion focuses on their findings. Although the hypothesis of Esquerré *et al.* (2019) includes 26 of the *L. montanus* group, we are aware of some difficulties with the species names assigned to certain terminals owing to the reliance upon data obtained from GenBank without rigorous review of taxonomic identifications. Also, the work of Esquerré *et al.* (2019) was not focused on the *L. montanus* group. For these reasons, we do not comment further on their findings.

Our TEH recovered the species pair *L. chlorostictus* and *L. orientalis* as basal to remainder of the *L. montanus* group. *Liolaemus chlorostictus* was described as a subspecies of *L. orientalis* by Laurent (1991) and elevated to a full species by Abdala *et al.* (2008); therefore, the close relationship between these two species was expected. The basal position of this clade within the *L. montanus* group is congruent with most previous estimates (Valladares *et al.*, 2002; Espinoza *et al.*, 2004; Pyron *et al.*, 2013; Zheng & Wiens, 2016; Esquerré *et al.*, 2019), all of which used the same molecular sample (GenBank accession AF099247), which corresponds to a nearly topotypic *L. chlorostictus* (although it has been identified as *L. orientalis* by most authors and GenBank). However, Schulte *et al.* (2000)

recovered this specimen as basal to the clade including *L. dorbignyi*, *L. poecilochromus*, *L. multicolor* and '*L. andinus*-Jujuy', which was sister to a clade consisting of *L. ruibali*, '*L. andinus*-La Rioja' and *L. famantinae*. Based on two specimens collected in the Tarija Department of Bolivia, Aguilar-Puntriano *et al.* (2018), recovered *L. orientalis* as a member of a clade including *L. multicolor*, *L. islugensis*, *L.* cf. *schmidti*, *L. pleopholis* and three candidate species. Morphologically, *L. orientalis* is dissimilar to all of the recognized species of that clade in terms of pholidosis and coloration. Furthermore, they recovered *L. chlorostictus* (based on a topotypic specimen not included in GenBank) as sister to their *Liolaemus* sp. 3 (from the Bolivian Altiplano and Andes) within a larger clade including *L. signifer*, *L. forsteri*, *L. annectens*, *L. etheridgei* and various candidate species, a result not expected based on morphology or Laurent's original concept of *L. chlorostictus*. Unfortunately, the molecular data available for *L. orientalis* is limited to that reported by Aguilar-Puntriano *et al.* (2018). Additional geographical sampling of *L. orientalis* genes might clarify its relationships. If the hypothesis of Aguilar-Puntriano *et al.* (2018) is correct, the position of *L. orientalis* within what we could consider the *L. multicolor* group represents either a remarkable case of morphological convergence with members of other species groups or the conservation of a plesiomorphic large-scaled, drab-coloured phenotype within a group of the species that is otherwise characterized by more numerous and smaller dorsal scales and bright colours in males.

Liolaemus andinus Koslowsky, 1895 has a rather contentious taxonomic history owing to the loss of the type series and its vague type locality. However, it has been the prototypical species for the phenetic species group of *L. montanus* group species with numerous, small, juxtaposed dorsal scales and relatively low tail/SVL ratios. Owing to the non-existence of type material and the uncertainties of the type locality, the use of the name *L. andinus* in the literature post-Laurent (1982) must thus be considered provisional in the absence of the designation of a neotype and restriction of the type locality. We note that our assignment of material to *L. andinus* is based on extensive fieldwork and collections in the Catamarca Province and adjacent Chile. The *L. andinus* group of Cei (1986) included *L. andinus*, *L. multicolor* and *L. poecilochromus* and was based on the presence of smooth and juxtaposed dorsal scales, absence of cephalic melanism and marked sexual dimorphism. Our hypotheses recover each of these species in their own unique species groups within the *L. montanus* group. Lobo *et al.* (2010a) included 23 species in their *L. andinus* group based on two character states they identified as synapomorphies: 'between 80–110 scales around midbody' and 'the presence of a particular sexual dichromatism'. However, not all the species

included in the *L. andinus* group of Lobo *et al.* (2010a) are recovered as members of our *L. andinus* clade. Of the 23 species included by Lobo *et al.* (2010a), four of them (*L. griseus*, *L. huacahuasicus*, *L. pulcherrimus* and *L. orko*) are recovered in our *L. huacahuasicus* clade. Lobo *et al.* (2010a) included *L. poconchilensis* in their *L. andinus* group, whereas our phylogenetic hypotheses place *L. poconchilensis* as a member of the *L. reichei* clade. Nevertheless, Lobo *et al.* (2010a) mention that the phylogenetic position of these five species inside the *L. andinus* group is controversial, because the scale counts might be highly variable in comparison with the other members in the group.

The presence of smooth dorsal scales and the absence of cephalic melanism were used by Cei (1986) to define his *L. ruibali* group, including *L. duellmani*, *L. eleodori*, *L. famatinae* and *L. ruibali*. Cei (1986) also envisioned a close relationship between the *L. ruibali* group and *L. andinus*. Our results support this conclusion, because most members of Cei's *L. ruibali* group were recovered nested within the *L. andinus* clade (Fig. 3). However, the position of *L. duellmani* remains unknown, because we could not access specimens of this taxon for our analyses. The close relationship between *L. andinus*, *L. fabiani*, *L. famatinae* and *L. ruibali* obtained in the present study was previously recovered by Valladares *et al.* (2002). Nevertheless, *L. fabiani* was recovered as the sister taxon of *L. audituvelatus* by Valladares *et al.* (2002) using only molecular evidence. In contrast, we recovered *L. audituvelatus* as a member of the *L. reichei* clade (see below, in the paragraph on L. reichei). The species included in the *L. ruibali* group proposed by Pincheira-Donoso & Núñez (2005) were recovered nested in our *L. andinus* group. Pincheira-Donoso & Núñez (2005) applied groups of Cei (1986, 1993) and added the Chilean *L. patriciaiturrae*, *L. robertoi* and *L. rosenmanni* to the *L. ruibali* group. In the present study, we recovered those all those species nested within our *L. andinus* clade. Pincheira-Donoso (2002) also assigned *L. nigriceps* to his *L. ruibali* group, a species we recovered as a member of our *L. andinus* group.

Aguilar-Puntriano *et al.* (2018) recovered the clade (((((*L. patriciaiturrae* + *L. nigriceps*) (*L. rosenmanni* (*L. gracielae* + *L. vallecurensis*)) *L. foxi* + *L. audituvelatus*) *L. andinus* + *L. famatinae*) *L. ruibali*), whose content is consistent with our *L. andinus* clade, with the exception of *L. audituvelatus*, which we recovered in our *L. reichei* clade.

The species included in our *L. multicolor* clade were previously proposed as members of the *L. andinus* group (Cei, 1993; Lobo *et al.*, 2010a) or, in the case of *L. schmidti*, considered a synonym of *L. andinus* (Pincheira-Donoso & Núñez, 2005). The sample identified as *L. andinus* AF099251 by Valladares *et al.* (2002) corresponded to our *L.* aff. *multicolor*, and the

relationships for this taxon recovered here were similar to theirs. As noted above, Aguilar-Puntriano *et al.* (2018) recovered *L.* cf. *schmidti*, *L. multicolor* and other terminal taxa in a clade also including *L. islugensis*, *L. orientalis* and *L. pleopholis* plus some unnamed terminals. As discussed above, we recovered *L. orientalis* as sister to *L. chlorostictus*, which were placed together as basal within the *L. montanus* group. Other authors have recovered *L. multicolor* and *L. poecilochromus* as members of the same clade (Valladares *et al.*, 2002; Espinoza *et al.*, 2004; Esquerré *et al.*, 2019) or even as sister taxa (Schulte *et al.*, 2000). However, we recovered *L. poecilochromus* as a member of its own species group that also included *L. halonastes* and *L. pleopholis*; a clade supported by five continuous characters and six discrete characters related to coloration (Supporting Information, Table S1).

Our *L. erguetae* clade was composed of species with smaller, more numerous dorsal scales and marked sexual dichromatism, including *L. islugensis*, *L. cazianiae*, *L. porosus*, *L. molinai* and *L. erguetae*. Although Aguilar-Puntriano *et al.* (2018) recovered *L. cazianiae* and *L. porosus* as sister taxa, they did not find these to be closely related to *L. islugensis* (and did not include *L. erguetae* or *L. molinai*). Instead, they placed *L. islugensis* as sister to *L. pleopholis* within their clade including *L. multicolor*. Although *L. islugensis* is phenetically rather similar to *L. multicolor*, our TEH recovered it as the basal member of the *L. erguetae* clade, supported by 13 characters (Supporting Information, Table S1), as was also recovered by our morphology-only hypothesis (Fig. 8). The remaining species of the *L. erguetae* clade were supported by 23 morphological characters, including a high number of scales around the midbody, a high number of dorsal scales between the occiput and thighs, a high number of ventrals, males having dark coloration on the pileus, yellow pigmentation of the dorsal surface of the forefeet and hindfeet in both males and females, males with yellow pigmentation of the throat and belly, and dark spots in the centre of the belly and pygal region.

The TEH recovered the *L. erguetae* clade as sister to the *L. reichei* clade based on 15 characters (ten morphological and five molecular), including pores on the base of the tail, number of scale organs in the post rostral scale, number of subdigital lamellae of fourth finger, ratio between trunk width and trunk length, ratio between length of fourth toe and SVL, and dorsal coloration of the forefeet and hindfeet. However, this relationship was not recovered by either the morphology-only or the molecular-only hypothesis.

Our *L. reichei* group included some of the species formerly included in the invalid generic names *Ctenoblepharys* and *Phrynosaura*. In 1891, Steindachner (1891) described *Ctenoblepharys stolzmanni*, a species erroneously placed in the

genus erected for *Ctenoblepharys adspersa* Tschudi, 1845 and unjustifiably emended by Boulenger (1891) when he described *Ctenoblepharys jamesi*. Eight years later, Werner (1907) described the genus *Phrynosaura* and its sole species, *Phrynosaura reichei*. Subsequently, other species were described or reassigned to this genus, including *Phrynosaura marmoratus* and *Phrynosaura werneri* (currently *L. pseudoanomalus* and *L. anomalus*, respectively), *Phrynosaura audituvelatus* (= *L. audituvelatus*) and *C. stolzmanni* (= *L. stolzmanni*). Etheridge (1995) synonymized *Phrynosaura* with *Liolaemus* and left *Ctenoblepharys* Tschudi, 1845 as a monotypic genus. However, Núñez & Veloso (2001) described *Phrynosaura audituvelata* (= *L. audituvelatus*), and Núñez *et al.* (2003) described *Phrynosaura manueli* and *Phrynosaura torresi* (currently, *L. manueli* and *L. torresi*). Pincheira-Donoso & Núñez (2005) used *Phrynosaura* to include the taxa mentioned above and excluded them from the monograph on the Chilean species of *Liolaemus*. Núñez *et al.* (2003) mentioned that the species of the genus *Phrynosaura* show a tibial process, a character state shared by all members of the *L. montanus* group (Etheridge, 1995). Breaking with the tradition of some Chilean workers, Pincheira-Donoso *et al.* (2008) included the species previously encompassed in *Phrynosaura* in the *L. reichei* group (formed by *L. audituvelatus*, *L. erroneous*, *L. manueli*, *L. poconchilensis*, *L. reichei* and *L. torresi*). In the present study, we recovered an *L. reichei* clade formed by two monophyletic groups: one including *L. insolitus* and eight unnamed terminal taxa and the other resembling the *L. reichei* group of Pincheira-Donoso *et al.* (2008). Pincheira-Donoso *et al.* (2008), however, included *L. insolitus* in their *L. montanus* clade. Aguilar-Puntriano *et al.* (2018) explicitly investigated the phylogenetic relationships of the *L. montanus* group species, and their phylogenetic hypothesis distributed species with this morphological syndrome across three clades within the *L. montanus* group and rejected the hypothesis that the 'phrynosauroid' species form a monophyletic group, in contrast to our TEH.

Our TEH recovered *L. jamesi* and *L. dorbignyi* as belonging to their own eponymous clades, which were distinguished morphologically by the presence of spots on the gular region, dorsal region of tail with the same colour pattern as the dorsum, tip of ventral region of tail the same colour as the central belly in the *L. jamesi* group, and dark skin on the dorsum, dark skin on the dorsum of forelimbs, black markings on the chest, belly and pygal region grille-shaped or reticulate, dark markings on the ventral region of the tail grill-shaped or reticulate, and dots on the scapular region in the *L. dorbignyi* group. Aguilar-Puntriano *et al.* (2018) recovered similar clades, but with some differences in their relationships to other clades. First, they recovered

the phrynosauroid *L. stolzmanni* as sister to ((*L. hajeki* + *L. jamesi*) (*L. aymararum* + *L. pachecoi*)). Second, their ((*L. vulcanus* + *L. dorbignyi*) (*L. inti* + *L. scrocchi*)) clade was sister to *L. fittkaui*, and those five species were sister to (*L. huacahuasicus* (*L. cazianiae* + *L. porosus*)). We recovered *L. fittkaui* as a member of our *L. huacahuasicus* clade and placed *L. cazianiae* and *L. porosus* in our *L. erguetae* clade (*L. erguetae* was not included in the analysis by Aguilar-Puntriano *et al.*, 2018).

Liolaemus puritamensis was described from Chilean material by Núñez & Fox (1989), but Núñez & Jaksic (1992) soon synonymized it with the Argentine *L. dorbignyi*. Subsequently, Pincheira-Donoso & Núñez (2005) resurrected *L. puritamensis* as a valid species, but they compared it against specimens from Salta now assigned to *L. scrocchii* (Quinteros *et al.*, 2008), not the true *L. dorbignyi* from Catamarca. In the present study, we recovered *L. puritamensis* as a member of the *L. dorbignyi* clade but clearly distinct from all described species of the group. Moreover, we identified the population assigned to *L. puritamensis* in Argentina as a candidate species, which we will describe in a future paper.

The remaining four clades (*L. forsteri*, *L. ortizi*, *L. robustus* and *L. huacahuasicus* clades) formed a larger clade sister to the *L. dorbignyi* clade and included *L. signifer*, *L. annectens* and related species from Peru, Bolivia and Argentina described almost entirely by Laurent in the 1980s and 1990s. Although we recovered the *L. forsteri* clade as sister to our *L. ortizi* clade, Aguilar-Puntriano *et al.* (2018) placed *L. forsteri* either as sister to *L. signifer* or as the basal member of larger clade sister to *L. ortizi* + *L. thomasi* and including *L. annectens*, *L. chlorostictus*, *L. etheridgei*, *L. signifer*, the members of our *L. robustus* and several candidate species. Our TEH recovered *L. annectens*, *L. etheridgei* and *L. signifer* within the *L. huacahuasicus* clade. These taxa were recovered as closely related by Aguilar-Puntriano *et al.* (2018), but these authors recovered *L. huacahuasicus* as sister to *L. cazianiae* and *L. porosus*, which collectively were sister to species recovered in our *L. dorbignyi* clade. Overall, our hypotheses for these groups were similar to those of Aguilar-Puntriano *et al.* (2018), but those authors did not sample *L. griseus*, *L. montanus*, *L. orko* or *L. pulcherrimus*, which were members of our *L. huacahuasicus* clade. Also, Aguilar-Puntriano *et al.* (2018) recovered *L. fittkaui* as sister to species we recovered in our *L. dorbignyi* group, whereas we recovered it in our *L. huacahuasicus* clade. Laurent (1986) considered *L. fittkaui* as part of his *L. ortizi* group, and we agree that there are significant morphological similarities between these species, and both species are endemic to the humid eastern Amazonian slopes of southern Peru and central Bolivia. However, none of our hypotheses recovered such a relationship.

FINAL CONSIDERATIONS

Our phylogenetic hypotheses are the most complete to date for the *L. montanus* group, including more terminal taxa (56 assigned species and 37 candidate species) than any other previous analysis of the group. Our total evidence hypothesis recovers the *L. montanus* group as monophyletic and formed by 12 major clades, which we name as species subgroup-level clades within the *L. montanus* group. We provide lists of synapomorphies recovered for each one, including morphology, colour pattern, ecology, squamation and molecular character states. Also, we recover a series of terminal taxa that are not assignable to available species names. With the evidence of the phylogenetic results, in addition to the morphological differences found, more than five terminal taxa are currently under description, and many others are considered as candidate species.

We recognize that recent hypotheses for the *L. montanus* group based solely on molecular evidence lead to other conclusions regarding the evolutionary relationships of the species. Here, we base our conclusions on the total available evidence, including our observations of these organisms in their natural environments, their biogeography and ecology, and > 135 collective years of experience with these species. In line with Hillis (2019), we urge that taxonomy must remain open to the consideration of all types of information and the examination of this through different lenses and optics. The consideration of alternative hypotheses of the evolutionary relationships of *Liolaemus* lizards and other organisms, based on multiple bodies of evidence, will lead to advances in our understanding of the infinitely complex evolution of biological diversity. It is precisely the unexpected or contradictory results that most enrich our discovery, debate and, ultimately, understanding.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of specimens studied.
Appendix S2. List of characters used from other studies.
Appendix S3. Accesion numbers of GenBank sequences of the specimens included.
Appendix S4. List of used characters.
Figure 1 S4. Scales of head and ventral regions of body used in this study. A, pink, infralabials; orange, supralabials; red, lorilabials; light blue, nasal; purple, canthal; gold, preocular; blue, subocular; green, postocular; yellow, character 14, number of scales contacting the second infralabial ventrally. B, purple, internasals; yellow, postrostrals; red, rostral; blue, mental (black dashed line, mental pore); green, chin shields; pink, scales between fourth chin shields. C, grey, mental scale; yellow, gular region; light blue, neck (between forelimbs); orange, chest; purple, belly; green, waist; blue, groin; red, tail base; pink, character 27 (number of pygals).
Figure 2 S4. Characters of head scales. A, shape of upper temporals (character 52). *Liolaemus fabiani* (left); *Liolaemus annectens* (centre); *Liolaemus dorbignyi* (right). See text for details. B, lower ciliaries (characters 57–59) and superciliaries (character 60). *Liolaemus* aff. *huayra* (left); *Liolaemus torresi* (right). See text for details. C, postocular scale (character 62). *Liolaemus scrocchii* (left); *Liolaemus multicolor* (right). See text for details.
Figure 3 S4. Some scale shape characters. A, infralabials (character 63). *Liolaemus* aff. *jamesi* (left); *Liolaemus audituvelatus* (right). See text for details. B, scales of occiput (character 64). *Liolaemus patriciaiturrae* (left); *Liolaemus pachecoi* (right). See text for details. C, heteronotes on dorsum (character 82). *Liolaemus montanus* (left); *Liolaemus puritamensis* (centre); *Liolaemus jamesi* (right). See text for details.
Figure 4 S4. Characters of forelimb scales. A, female of *Liolaemus jamesi* (characters 90, 91 and 93) and scales around forelimbs (character 94). B, *Liolaemus huacahuasicus*. Arm and forearm (characters 96–99).

Figure 5 S4. Characters from scales of gular and antehumeral region. A, *Liolaemus* aff. *huayra*. Scales of forelimb (character 93) and antehumeral scales (character 100). B, *Liolaemus molinai*. Enlarged scales on sides of antehumeral fold (character 101) and enlarged central scale on gular region (character 132).

Figure 6 S4. Characters of palmar scales. Palmar scales (characters 102–104). *Liolaemus* aff. *jamesi* (left); *Liolaemus torresi* (right).

Figure 7 S4. Characters of pores on ventral regions. A, ventral region of thigh (character 117). B, gular region (character 126). C, pectoral region (character 133). D, sides of belly (character 135). *Liolaemus porosus*.

Figure 8 S4. Region of body where pores were scored: thighs (character 117); base of tail (character 122); mental region (character 124); gular (character 126); pectoral region (character 133); sides of belly (character 135); waist (character 137). *Liolaemus torresi*.

Figure 9 S4. Characters of pygal region: supernumerary pores (character 138) and scales of pygal region (characters 140 and 141). *Liolaemus* aff. *jamesi* (left); *Liolaemus torresi* (right).

Figure 10 S4. Characters of male coloration. A, *Liolaemus pachecoi* (characters 144, 148, 160, 187, 191, 195, 202 and 209). B, *Liolaemus puritamensis* (characters 145, 146, 180 and 202). C, *Liolaemus molinai* (characters 151, 176, 174, 181 and 197). D, *Liolaemus pulcherrimus* (characters 153–155, 172 and 205). E, *Liolaemus multicolor* (characters 162, 203 and 208).

Figure 11 S4. Characters of male coloration. A, *Liolaemus patriciaiturrae* (characters 156, 157, 168, 177 and 198). B, *Liolaemus* aff. *torresi* (characters 168 and 177). C, *Liolaemus cazianiae* (character 168). D, *Liolaemus porosus* (characters 157 and 168). E, *Liolaemus dorbignyi* (characters 156, 157 and 168). F, *Liolaemus etheridgei* (characters 168, 177 and 195). G, *Liolaemus* aff. *huayra* (characters 168 and 177). H, *Liolaemus andinus* (characters 156, 157 and 168). I, *Liolaemus insolitus* (characters 156, 157 and 168).

Figure 12 S4. Characters of male coloration. A, *Liolaemus jamesi* (characters 159, 161, 191 and 194). B, *Liolaemus islugensis* (characters 164, 171, 179, 181, 197 and 201). C, *Liolaemus cazianiae* (characters 163, 181, 188, 199 and 204). D, *Liolaemus inti* (characters 165, 197 and 199). E, *Liolaemus signifer* (characters 173, 181, 186 and 191). F, *Liolaemus schmidti* (characters 174, 181, 200 and 206). G, *Liolaemus foxi* (characters 183, 184, 193 and 199). H, *Liolaemus ruibali* (characters 192 and 196).

Figure 13 S4. Characters of ventral coloration in males. A, *Liolaemus cazianiae* (characters 211, 213, 219, 226 and 232). B, *Liolaemus* aff. jamesi3 (characters 213, 216, 229 and 232). C, *Liolaemus aymararum* (characters 212, 213, 219, 226, 229 and 232). D, *Liolaemus insolitus* (characters 210, 213, 215, 221, 226 and 232). E, *Liolaemus* aff. *huayra* (characters 215, 216, 219, 226, 228 and 234). F, *Liolaemus nigriceps* (characters 210, 215, 223, 228 and 235).

Figure 14 S4. Sexual dichromatism evident. A, B, male of *Liolaemus gracielae*. C, D, female of *Liolaemus gracielae*.

Figure 15 S4. Character of female coloration. A, specimen without colour pattern (character 238). *Liolaemus multicolor*. B, spots on lateral field (character 261). *Liolaemus montanus*.

Figure 16 S4. Lateral spots on females. Fused lateral spots forming stripes (character 263). A, *Liolaemus fabiani*. B, *Liolaemus multicolor*. C, *Liolaemus* aff. *foxi*.

Figure 17 S4. Character 287. Habitat of the species of *Liolaemus montanus* group.

Table S1. List of synapomorphies for the total evidence hypothesis.