Trabajo

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The identities of *Liolaemus signifer* (Duméril & Bibron 1837), *L. pantherinus* Pellegrin 1909, *L. schmidti* (Marx 1960), and *L. erroneus* (Núñez & Yáñez 1984 "1983-1984") (Squamata: Liolaemidae)

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ABSTRACT

Based on detailed examination of the literature, visits to collections and the field, correspondence with specialists and curators, study of detailed photography of living and preserved specimens, and statistical analysis of meristic data, I propose a number of taxonomic and nomenclatural changes for species of the *Liolaemus montanus* group from the Andes of Bolivia, southern Peru, northern Chile and northwestern Argentina. *Liolaemus signifer* (Duméril & Bibron 1837) is designated a *nomen dubium* and *Liolaemus multiformis* (Cope 1875) and *Liolaemus lenzi* Boettger 1891 are revalidated. *Liolaemus variabilis* Pellegrin 1909 and *Liolaemus bolivianus* Pellegrin 1909 are placed in the synonymy of *L. lenzi*. *Liolaemus pleopholis* Laurent 1998 is considered a *species inquirenda* allied with *L. lenzi*. *Liolaemus annectens* Boulenger 1901 is considered a valid species and *Liolaemus tropidonotus* Boulenger 1902 is considered a junior synonym of *L. multiformis*. *Liolaemus pantherinus* Pellegrin 1909 is recognized as a valid species that includes *L. annectens orientalis* Müller 1924 and *L. multiformis simonsii*—Burt & Burt 1931 are included in its synonymy. *Liolaemus islugensis* Ortiz & Marquet 1987 is removed from the synonymy of *L. pantherinus* and is placed in the synonymy of *L. schmidti* (Marx 1960). *Liolaemus erguetae* Laurent 1995 and *L. molinai* Valladares *et al.* 2002 are placed in the synonymy of *L. erroneus* (Núñez & Yáñez 1984 "1983–1994").

Key Words: Lizards; Taxonomy; Nomenclature; Synonyms; Andes.

RESUMEN

Basado en la revisión detallada de la literatura, visitas a colecciones y el campo, correspondencia con especialistas y curadores, estudio de fotografías detalladas de ejemplares vivos y preservados y análisis estadístico de datos merísticos, se propone varios cambios taxonómicos y nomenclaturales para especies del grupo *Liolaemus montanus* de los Andes de Bolivia, el sur del Perú, norte de Chile y noroeste de Argentina. *Liolaemus signifer* (Duméril & Bibron 1937) se designa *nomen dubium* y se revalidan *Liolaemus multiformis* (Cope 1875) y *Liolaemus lenzi* Boettger 1891. *Liolaemus variabilis* Pellegrin 1909 y *Liolaemus bolivianus* Pellegrin 1909 se consideran sinónimos júniores de *L. lenzi*. *Liolaemus pleopholis* Laurent 1998 se considera una *species inquirenda* aliada a *L. lenzi*. *Liolaemus annectens* Boulenger 1901 se considera especie válida y *Liolaemus tropidonotus* Boulenger 1902 se considera sinónimo júnior de *L. multiformis*. *Liolaemus pantherinus* Pellegrin 1909 se reconoce como especie válida, la cual incluye *L. annectens orientalis* Müller 1924 y *L. multiformis simonsii*—Burt & Burt 1931 en su sinonimia. *Liolaemus islugensis* Ortiz & Marquet 1987 se transfiere de la sinonimia de *L. pantherinus* a la sinónima de *L. schmidti* (Marx 1960). *Liolaemus erguetae* Laurent 1995 y *L. molinai* Valladares *et al.* 2002 se consideran sinónimos júniores de *L. erroneus* (Núñez & Yáñez 1984 "1983–1994").

Palabras claves: Lagartijas; Taxonomía; Nomenclatura; Sinónimos; Andes.

Introduction

The lizard genus *Liolaemus* Wiegmann 1834 is highly diverse with more than 350 published names (including species, subspecies, and varieties), of which over 270 are recognized as valid (Abdala *et al.,* this volume). In addition, there is a growing number of "candidate species" identified by mole-

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cular, morphological, and combined phylogenetic analyses (for example, see Abdala *et al.*, 2020; Aguilar-Puntriano *et al.,* 2018). While modern phylogenetic assessments have clearly demonstrated the monophyly of *Liolaemus*, the genus is generally recognized as included two major clades: *Liolaemus sensu stricto* (the "chileno" group of Laurent, 1983) and *Eulaemus* Girard 1858 (the "argentino" group of Laurent, 1983). Within *Eulaemus,* the monophyletic *L. montanus* group (sensu Etheridge, 1995; Abdala *et al.*, 2020) includes some 60 species (Olave *et al.*, 2014; Aguilar *et al.,* 2017a, Abdala *et al.*, 2020) which are largely restricted to high elevation "puna" environments of the Andes, with the exception of a few lowland species in the Pacific slope deserts and the extra-Andean Sierras of northern and central Argentina (Abdala *et al.,* 2020). As used here, the *L. montanus* group is not equivalent to the *L. montanus* section of *Eulaemus* recovered by Schulte *et al.* (2000), which includes a *L. boulengeri* series characterized by the presence of a patch of enlarged spinose scales on the inner thigh; rather it is equivalent to their *L. montanus* series.

The earliest available name assigned to the *Liolaemus montanus* group is *Proctotretus signifer* Duméril and Bibron 1837, a species based on a single specimen that was lost sometime after it was examined and redescribed by Bell (1843). Cei *et al.* (1980) claimed to have found the lost holotype but Laurent (1984a) noted significant discrepancies in the measurements reported by earlier authors and those reported by Cei *et al.* (1980). Despite his earlier misgivings, Laurent (1992) decided that *L. signifer* is the senior synonym of number of species described from Peru and Bolivia: *L. multiformis* (Cope 1875), *L. lenzi* Boettger 1891, *L. annectens* Boulenger 1901, *L. tropidonotus* Boulenger 1902, *L. pantherinus* Pellegrin 1909*, L. variabilis* Pellegrin 1909, and *L. bolivianus* Pellegrin 1909.

The present paper will explore the taxonomic history of *Liolaemus signifer* and the identity of its purported discovered holotype and then clarify the status of the species included in its synonymy by Laurent (1992), with a special consideration of *L. pantherinus* and a suite of other misunderstood names with intertwined and convoluted histories: *L. schmidti* (Marx 1960), *L. erroneus* (Núñez & Yáñez 1984 "1983-1984"), *L. islugensis* Ortiz & Marquet 1987, *L. erguetae* Laurent 1995, and *L. molinai* Valladares, Etheridge, Schulte, Manríquez, & Spotorno 2002.

Materials and methods

This paper is the result of an analysis of the relevant body of literature (for example, Duméril and Bibron, 1837; Bell, 1843; Cope, 1875; Boettger, 1891; Pellegrin, 1909; Marx, 1960; Cei *et al.,* 1980; Laurent, 1982, 1984a, 1992, 1995); Ortiz and Marquet, 1987; Núñez and Yáñez, 1984 "1983-1984"; Valladares *et al.,* 2002; and Aguilar-Puntriano *et al.*, 2018), review of itineraries of collectors (d'Orbigny 1844, 1846; Créqui Montfort and Sénéchal de la Grange, 1904; Neveu-Lemaire, 1904; Hellmayr, 1932), analysis of unpublished data and notes on type specimens generously provided by Richard E. Etheridge and many other specialists and curators (see Acknowledgements), examination of specimens, including relevant type material during visits to collections including the American Museum of Natural History (AMNH), the Natural History Museum (BMNH), the Colección Boliviana de Fauna (CBF), the Field Museum (FMNH), the Museum of Vertebrate Zoology (MVZ), the Colección de Flora y Fauna Patricio Sánchez Reyes, Pontificia Universidad Católica de Chile (SSUC), and the Smithsonian National Museum of Natural History (USNM) and other material reviewed from detailed digital photographs of additional material from the Academy of Natural Sciences of Philadelphia (ANSP), Carnegie Museum of Natural History (CM), Fundación Miguel Lillo (FML), Monte L. Bean Life Science Museum (BYU), Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA), Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Museo de Zoología de la Universidad de Concepción (MZUC), Museo Nacional de Historia Nacional de Chile (MNHNCL), Museum für Naturkunde (ZMB), Museum of Comparative Zoology (MCZ), Muséum National d'Histoire Naturelle (MNHN), San Diego State University Museum of Biodiversity (SDSU), Senckenberg Museum (SMF), University of Kansas Biodiversity Institute and Natural History Museum (KU), University of Michigan (UMMZ), Zoologische Museum Hamburg (ZMH), and Zoologische Staatssammlung München (ZSM), analysis of counts of dorsal scales between the occiput and the anterior margin of the thighs ("DSOT") of 190 specimens representing 14 species, and consideration of most complete phylogenetic hypotheses and biogeographic patterns for the focal species (Aguilar-Puntriano *et al.*, 2018; Abdala *et al.*, 2020). The complete list of material examined

is presented in Appendix 1.

DSOT counts are a frequently used meristic character in descriptions and diagnoses of *Liolaemus* species, referred to variably as "dorsals", "paravertebrals" or "middorsal scales" in the literature (Etheridge, 1995). The first dorsal row is treated as the first row of scales posterior to the enlarged scales or plates (e.g., postoccipitals) where the scales are not differentiated from those of the dorsal surface of the neck and form a continuous row across the neck. The last row counted is the row intersected by an imaginary line between the anterior margins of the thighs at the insertion of the hind limbs. For specimens with numerous small dorsals or that are otherwise difficult to follow, counts represent the average of 2 or 3 counts. Additional scale counts and comments on specimens were obtained from notes made by Etheridge during his tour of European museums in 1967 (cited as "Etheridge, *in litt.*"). Unpaired two-sample Wilcoxon tests of DSOT counts were performed using *R* (R Core Team, 2016). The DSOT counts of each of the 14 species were compared against those of lizards assigned to *L. pantherinus* and a particular subset of *L. signifer sensu* Laurent (1992) to be discussed later. The results are presented in Table 2 and the data are presented in R format in Appendix 2.

Following Dunn and Stuart (1951) and Smith (1953), information on type localities was investigated using the published itineraries of the stated collectors, gazetteers, and on-line data. Place names mentioned in the text are mapped in Fig. 1. Updated annotated synonymies and partial chresonymies (i.e., cited uses of a name; see Smith and Smith, 1973) and relevant heterochresonymies (i.e., misidentifications or misapplications, sensu Dubois, 2000) are provided in Appendix 3 for the names recognized as valid by the present work. The present contribution is intended to provide taxonomic decisions and nomenclatural acts in accordance with the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) and current best practice in herpetological taxonomy as proposed by Kaiser *et al.* (2013).

Results

Taxonomic history of *Liolaemus signifer* (Duméril & Bibron 1837)

Duméril and Bibron (1837:288) described the genus *Proctotretus* in which they included ten species: two species previously described by Wiegmann (1834) in the subgenus *Tropidurus (Liolaemus)* and eight new species based on material the Muséum National d'Histoire Naturelle (MNHN) in Paris. Their *P. signifer* was based on a single specimen attributed to the collections of d'Orbigny and having the stated locality of simply "Chili" (Duméril and Bibron, 1837:288). Bell (1843:9) borrowed various MNHN specimens to compare against lizards collected by Darwin and provided a redescription and a drawing of the *P. signifer* holotype (Fig, 3). Gray (1845:212) reassigned most species of *Proctotretus* to the doubly misspelled "*Leiolæmus* Weigmann" and included *Leiolæmus signifer*, represented by only a single specimen in Paris. In 1851, Duméril and Duméril (1851:75) reported that the MNHN's sole *Proctotretus signifer* specimen was "manque" (i.e., missing).

Boulenger (1885:154) included *Liolaemus signifer* in his BMNH lizard catalogue and the sole specimen[1] was stated to be from "Chili" and to have 78 scales around midbody. Unfortunately, neither the type description nor Bell's redescription of the holotype include counts of scales around midbody to permit comparison. In his key to the species (p. 140), *L. signifer* was paired against the Peruvian *L. multiformis* (Cope 1875), which he distinguished on the basis of more strongly imbricate dorsals in *L. multiformis* and smaller juxtaposed lateral scales in *L. signifer.*

Koslowsky (1898) included *Liolaemus signifer* in his enumeration of the Argentine reptiles, created the combination *Liolaemus signifer* var. *nigriceps,* and described *L. signifer* var. *zonatus, L. signifer* var. *multicolor*, and *L. signifer* var. *montanus.* None of these taxa have been considered potential synonyms of *L. signifer* or *L. pantherinus* by subsequent authors and they can be excluded from further discussion here. Andersson (1908) commented on lizards collected near Lake Titicaca at "Guaqui, Peru"[2] in 1907 and determined these to belong to *L. signifer*, noting that their scales were "very small and numerous, varying from 78 to 90 around the body". Andersson expressed his doubts about the distinction between *L. signifer* and *L. multiformis* and considered it very probable that the latter is "a more large-scaled variety of the very much varying *L. signifer*", noting that

[1] Presumably BMNH 1851.7.17.76, a specimen that could not be located during my two visits to BMNH.

[2] Guaqui is located in Bolivia near the Peruvian border town of Desaguadero.

Figure 1. Localities mentioned in the text.

Koslowsky (1898) had also tentatively considered *L. multiformis* to be a junior synonym of *L. signifer*. Andersson's paper was the first to assign new material to *L. signifer* and the first to provide a locality from the vicinity of Lake Titicaca.

Pellegrin (1909) found his *Liolaemus variabilis* from Tiahuanaco to be morphologically close to *L. signifer* "from Chile and Argentina" but found it even closer to *L. lenzi* Boettger 1891 from "the Bolivian shores of Lake Titicaca". However, it is unclear on what basis he made his comparison against *L. signifer* and why he believed it was present in Chile and Argentina, other than perhaps a reading of the existing literature (e.g., Koslowsky,

1898). Pellegrin distinguished *L. variabilis* from *L. lenzi* on the basis of slightly higher counts of scales around midbody, i.e., 84–94 in the former vs 74–86 in the latter, presumably based on Boettger's (1891) original description. He did not, however, bother to compare *L. variabilis* against *L. pantherinus*, likely because of the significant gap in the numbers of scales around midbody between the type series of these taxa (84–94 vs 50–52).

Burt and Burt (1931) recognized *Liolaemus signifer* as a valid species but the only specimen in the American Museum of Natural History (AMNH) collections they could assign to it was from Chubut, Argentina, a Patagonian province where no lizards of the *L. montanus* group *sensu* Abdala *et al.* (2020) are known. They also considered *L. multiformis* to be a valid species, within which they included *L. simonsii* Boulenger 1902 as a subspecies. Furthermore, they included *L. annectens orientalis* Müller 1924 as junior synonym of *L. multiformis simonsii*. Shortly thereafter, Burt and Burt (1933:37) recognized *L. signifer* as a valid species with five subspecies: the four Argentine varieties of Koslowsky (1898) and the nominate subspecies *L. signifer signifer* from "Chile, southern Peru, and possibly sections of western Argentina", with no mention of Bolivia.

Hellmich (1962) reviewed the variability of *Liolaemus multiformis* and its possible junior synonyms but made no mention of *L. signifer* even though he discussed at detail all other relevant taxa from Peru and Bolivia that had been described at the time. Similarly, Cope (1875), Boettger (1891), and Boulenger (1901, 1902) also made no mention of *P. signifer* or *L. signifer* in their descriptions of species later included its synonymy by Hellmich (1962) or Laurent (1992).

Donoso-Barros (1966:329) included *Liolaemus signifer* in his *Reptiles de Chile*, mentioning four specimens from the "Altiplano de Antofagasta" and one specimen from "the south of Bolivia", giving the number of scales around midbody as 74. In addition, he also included *L. multiformis* (p. 319) and *L. pantherinus* (p. 327) as valid species of the Chilean reptile fauna.

During his 1967 tour of major European collections, Etheridge examined and briefly characterized the type specimens of numerous species of pleurodont Iguania, including four specimens (MNHN-RA-1905.315–18) labeled at the time as *L. signifer* syntypes (but catalogued as of February 2018 as *L. multiformis multiformis*) and yielding midbody counts of 70 to 82 scales (Etheridge, *in litt.*). However, these specimens were collected at "Bolivia, Stn. 48 Chililayas"[3] in 1903 by Dr. Neveu-Lemaire, the collector of the *L. pantherinus* types, and thus cannot possibly be part of the type series of *L. signifer*, a species described in 1837.

Etheridge also examined the syntypes of *Liolaemus fitzingerii* (Duméril and Bibron 1837:286) and noted that specimen MNHN-RA-0.6860 "compared to *variabilis* (Paris 07.244–50) in all details; frontals paired, 5 expanded supraoculars". This specimen yielded counts of 85 paravertebrals (vs 52 and 56 in the *L. pantherinus* syntypes) and 69 scales around midbody (vs 54 and 60 in the *L. pantherinus* syntypes). Etheridge (*in litt.*) noted that ventrals are "equal or only slightly larger than dorsals" in the *L. pantherinus* syntypes, which he considered to distinguish this species from the so-called "*L. signifer* syntypes" (where ventrals are considerably larger than dorsals), as well as in having far fewer paravertebrals. Etheridge (*in litt.*) also noted that the *L. pantherinus* "are similar to *signifer* type but with larger dorsals and smaller ventrals; paravertebral and midbody scales fewer".

In the *Catalogue of the Neotropical Squamata*, Donoso-Barros (1970:194) recognized *L. signifer* as a species of the Altiplano of Chile, Bolivia, and Argentina and also recognized *L. m. multiformis* and *L. m. simonsii* as valid (p. 187).

Cei *et al.* (1980) reported the rediscovery of the *Liolaemus signifer* holotype in a jar of *L. fitzingerii* types and provided a brief description of this specimen, MNHN-RA-0.6860. Donoso-Barros (1966:295), however, listed MNHN 6859–6860 as collected by d'Orbigny and as types of *L. fitzingerii* var. A, an observation supported by Etheridge's notes on MNHN types (Etheridge, *in litt*), but not mentioned by Cei *et al.* (1980).

In one of his first essays on the northern species of *Liolaemus*, Laurent (1982a) considered *L. signifer, L. multiformis,* and *L. simonsii* to all be valid species, each representing a different morphometric species group. He characterized his "*signifer* group" by their "very small scales and short tail" and also included *L. andinus* Koslowsky 1895, *L. multicolor,* and *L. forsteri* Laurent 1982. His "*simonsii* group" with was comprised of species with "a long tail and larger scales" and his "*multiformis* group" were lizards of "intermediate tail and variable scales, sometimes even larger but

[3] i.e., "Chililaya", presently known as Puerto Pérez.

never very small". Laurent (1982b) described *L. forsteri* from Chacaltaya, Bolivia, and *L. ortizi* from near Cusco, Peru; he compared both species to *L. multiformis*, without mention of *L. signifer*.

After examining the alleged *Liolaemus signifer* holotype of Cei *et al.* (1980), Laurent (1984a) noticed significant discrepancies between the measurements of this specimen and those of the holotype as reported by Duméril and Bibron (1837) and Bell (1843); he also realized that the specimen probably did not belong to the short-tailed group with *L. andinus* because it has relative few scales around midbody and its tail might be regenerated. In his morphometric phenograms, Laurent (1984b) found the purported *L. signifer* holotype to be closest to *L. multiformis* (based on data from BMNH specimens from Capachica, Peru), but found the latter to be even closer to his then-yet-to-published *L. huacahuasicus* Laurent 1985.

In a brief note on the *Liolaemus* known from north of the 22nd parallel, Laurent (1985) stated that "the best known species of the region and the most cited, *L. multiformis,* is a synonym of *L. signifer*" and then restricted the distribution of *L. signifer* to the basin of lakes Titicaca and Poopó, noting that outside of this endorheic basin there are number of isolated valleys with populations that have differentiated to various degrees. Laurent (1986) described *L. fittkaui* from "region de Cochabamba" and "Tiraque", Bolivia, and compared it only to *L. ortizi*, again with no reference to *L. signifer*.

Apparently convinced by the arguments of Cei *et al.* (1980) regarding specimen MNHN-RA-6860, Brygoo (1989:92) claimed that the specimen was erroneously placed with the types of variety A of *Proctotretus fitzingerii* upon its return from Bell, without providing any evidence for this (e.g., mention of correspondence or an annotation indicating the specimen was ever received back at MNHN). Brygoo (1989) also accepted the synonymies of *Liolaemus bolivianus* (p. 16) and *L. variabilis* (p. 33–34, 73, 101–102) under *L. multiformis multiformis* by Donoso-Barros (1970), apparently unaware of Laurent's (1985) synonymy of *L. multiformis* under *L. signifer*. Halloy and Laurent (1988), almost in passing, also mentioned that *L. multiformis* is a synonym of *L. signifer*.

By 1992, after a decade of research on the northern species of *Liolaemus (Eulaemus)*, Laurent had considerably refined his concepts regarding *L. signifer* and related species. Based on his exhaustive morphometric analyses, including the type series of all of the species in question, Laurent (1992) determined that *L. annectens* should be considered a subspecies of *L. signifer* and that *L. multiformis, L. lenzi, L. tropidonotus, L. pantherinus*, *L. variabilis*, and *L. bolivianus* are all junior synonyms of *L. signifer signifer*. The only relevant taxon he did not include in the synonymy of *L. signifer* was *L. annectens orientalis*, a taxon he listed as a full species in an appendix to the paper (Laurent 1992:31) and later redescribed as a polytypic species (Laurent 1993 "1991") comprising the nominate subspecies and the new subspecies *L. orientalis chlorostictus* from Jujuy (Argentina) and Potosí (Bolivia). Laurent (1992, 1995, 1998) continued to describe new taxa of the *L. montanus* group from Bolivia, Chile, and Peru: *L. robustus, L. polystictus,* and *L. williamsi* in 1992, *L. jamesi pachecoi* and *L. islugensis erguetae* in 1995, and *L. melanogaster, L. thomasi, L. pleopholis,* and *L. etheridgei* in 1998.

Valladares et al. (2002) described *Liolaemus molinai* from northern Chile, with tangential comments on *L. signifer* and reference to material of this species from "Cariquima, Provincia de Tarapacá, Chile" (SDSU 1600) and from "Oruro and vicinity", Bolivia (AMNH 90457–60, 90464–6868). Pincheira-Donoso and Núñez (2005:151) recognized a "*signifer* group" including *L. andinus, L. erguetae* Laurent 1995, *L. multicolor, L. pantherinus, L. pleopholis* Laurent 1998, and *L. signifer*. They diagnosed *L. signifer* as having dorsal scales that are "small, rounded, invariably juxtaposed, smooth or gently keeled", possessing 74–80 scales around midbody (p. 173) and found it closest to *L. pleopholis* and *L. annectens,* which they restored to full species status (p. 176). In addition to MNHNCL material from near Tacora (Arica y Parinacota Region), Pincheira-Donoso and Núñez (2005:450) included material assigned to *L. signifer* from "Chili" (BMNH-51.7.17.76) and "Uyuni, Bolivia, 3.600 m" (BMNH.1902.5.29.63–73) in their list of specimens examined.

Troncoso-Palacios (2014) reviewed the geographic distribution of *Liolaemus signifer* and excluded all records from the Potosí Department of Bolivia and all records from Chile outside of the Arica y Parinacota Region (Region XV). He limited the Peruvian range of *L. signifer* to the regions of Puno, Moquegua, and Tacna, recognizing *L. annectens* as the species from the Arequipa Region. Furthermore, he questioned the validity of *L. pleopholis* and considered it to be either a cryptic species morphologically indis-

tinguishable from *L. signifer* or a junior synonym of the same. Demangel-Miranda (2016:461) limited the Chilean range of *L. signifer* to small areas of the Arica y Parinacota Region, with *L. pleopholis* replacing it allopatrically to the south in the Arica y Parinacota Region (p. 403); similar to Troncoso-Palacios, he also noted that these two species are extremely similar to each other (pp. 403, 461).

Aguilar *et al.* (2017a) published the first integrative taxonomic study of the Peruvian species of the *Liolaemus montanus* group, found *L. signifer* to be sister to a clade including *L. annectens* Boulenger 1901 and *L. etheridgei* Laurent 1998, and mapped Peruvian localities of *L. signifer* around Lake Titicaca in the Puno Region and portions of the Moquegua and Tacna regions. Aguilar-Puntriano *et al.* (2018) subsequently included a larger number of terminals representing a broad sampling of lizards of the *L. montanus* group, including material from Bolivia, Chile, and Argentina, in addition to Peru. This expanded molecular study again found *L. signifer* distinct from, but close, to *L. annectens*. The only Bolivian lizards recovered in *L. signifer* were from a small portion the Titicaca basin. Specimens from the Bolivian Altiplano and Andes of La Paz, Oruro, Cochabamba, and Potosí generally assigned to either *L. multiformis* or *L. signifer* were recovered as a clade labeled "*Liolaemus* sp3" that was recovered as sister to *L. chlorostictus*, not to *L. signifer* or *L. annectens*.

In summary, between 1837 and 1992, *Liolaemus signifer* was a name rarely and inconsistently applied in the literature and collections. Following the synonymy of *L. multiformis* and *L. annectens* under *L. signifer* by Laurent (1992), the use of *L. signifer* became more frequent, yet no author has attempted a revision of *L. signifer* and allegedly related species. While work of Aguilar *et al.* (2017a) and Aguilar-Puntriano *et al.* (2018) provides important insights on the northern members of *L. montanus* group, neither paper was intended to be a taxonomic revision, and neither was focused on *L. signifer* per se. Despite the doubts cast by Laurent (1984a), the identity of the alleged *L. signifer* holotype of Cei *et al.* (1980) remained essentially unchallenged until now.

The identity of MNHN-RA-0.6860

In regards to MNHN-RA-0.6860, the specimen believed to be the rediscovered holotype of *Liolaemus signifer* by Cei *et al.* (1980), Laurent (1984a:279) stated that he "was not convinced that it is really the Duméril and Bibron type because there is morphometric discrepancy" (my translation), as evidenced by his comparison of the measurements of the *L. signifer* holotype reported by Duméril and Bibron (1837) and Bell (1843), the measurements of MNHN-RA-6860 reported by Cei *et al.* (1980), and his own measurements of that same specimen. However, this rather well-founded statement did not stimulate any further debate or research on the matter in the literature.

The measurements of the *Liolaemus signifer* holotype reported by Duméril and Bibron (1837:290) yield an SVL of 48 mm and Bell (1843:9) reported head and body lengths totaling 2 inches and 1 line (i.e., 53 mm), a difference not inexplicable as the outcome of different approaches to measuring the same specimen. In contrast, Cei *et al.* (1980) and Laurent (1984a) reported SVLs of 61 and 62 mm for MNHN-RA-0.6860, measurements representing a specimen significantly larger than the one measured by Duméril and Bibron and Bell. However, Etheridge (*in litt.*) found this same specimen to have an SVL of 70 mm in 1967 and Brygoo (1989:92) indicated an SVL of 69 mm (i.e., total length of 130 mm and tail length of 61 mm). Measurements of the specimen by MNHN staff in 2011 (I. Ineich, *in litt.*) obtained an SVL of 71 mm when the specimen was properly extended and a regenerated tail length of 62 mm[4]. This suggests that both Cei *et al.* (1980) and Laurent (1984a) transposed the SVL and tail measurements, as both reported tail length as 69 mm.

Based on the reported measurements of MNHN-RA-0.6860, the specimen believed to be the lost *Liolaemus signifer* holotype by Cei *et al.* (1980) has an SVL of approximately 70 mm and a tail equal to 0.87–0.89% of SVL, which contrasts greatly with measurements of the *L. signifer* holotype, a specimen with an SVL of approximately 50 mm and a tail equal to 143–150% of SVL (Table 1). The notable differences in both SVL and tail/SVL ratio clearly indicate that the two sets of measurements (i.e., those obtained 1837-1843 vs. those obtained 1980-2011) are from two different specimens and that MNHN-RA-0.6860 is not the holotype of *L. signifer*.

A close reading of Duméril and Bibron (1837) reveals other clear discrepancies between their description of the holotype and MNHN-RA-0.6860. It should be noted that Bell's only discrepancy with the original description was that it indicates that the *L.*

[4] Etheridge (*in litt.*) did not include tail length as he considered it to be regenerated, as also suggested by Laurent (1984a).

Table 1. Measurements of *Liolaemus signifer* Holotype and Specimen MNHN-RA-6890.

Author	SVL (mm)	Tail (mm)	Total (mm)	Tail/ SVL
Duméril & Bibron (1837)	48	72	128	1.50
Bell (1843)	53	76	130	1.43
Etheridge (*in litt.*)	70	Regenerated	NA	NA
Cei *et al.* (1980)	69	61	130	0.88
Laurent (1984a)	69	62	131	0.90
Brygoo (1989)	69	61	130	0.88
Ineich (*in litt.*)	71	62	133	0.87

signifer holotype has two series of scales between the subocular and the supralabials (as in *L. wiegmannii* Duméril and Bibron 1837), while Bell (1843) noted that he found only a single series. Duméril and Bibron (p. 289) emphasized that the *L. signifer* holotype had a row of four elongate scales (i.e., "plus longue que large") across the "top of the tip of the snout" as in *L. fitzingerii*, "but they are preceded by four small quadrangular scales, instead of only two, as in *L. fitzingerii*" (my translation). Examination of specimen MNHN-RA-0.6860 reveals that it has four elongate scales between the nasals but only two scales separating these from the rostral (Fig. 2), as noted for *L. fitzingerii*. The description of "Variété A" of *L. fitzingerii* (p. 287) notes that the dorsal pattern includes four series of black spots, bordered posteriorly by white (as in MNHN-RA-0.6860, Fig. 3), while the description of *L. signifer* (p. 290) indicates "black spots, or rather figures, that one would be tempted to take for Arabic characters or letters" (my translation), with no mention of white borders. Also, the drawings provided by Duméril *et al.* (1854) and Bell (1843) do not correspond well with MNHN-RA-0.6860 (Fig. 3). First, the head is much less robust than in MNHN-RA-0.6860. Second, the dorsal pattern depicted certainly fits the description of *L. signifer* but not that of MNHN-RA-0.6860. Both drawings clearly show that the dark dorsal markings are relatively large and U-shaped, with the opening anteriorly, while MNHN-RA-0.6860 shows only short diagonal dark markings bordered poste-

Figure 2. Dorsal view of head of MNHN-RA-0.6860 (photograph courtesy of I. Ineich/MNHN) with the row of four elongate scales across the snout and the two preceding scales highlighted.

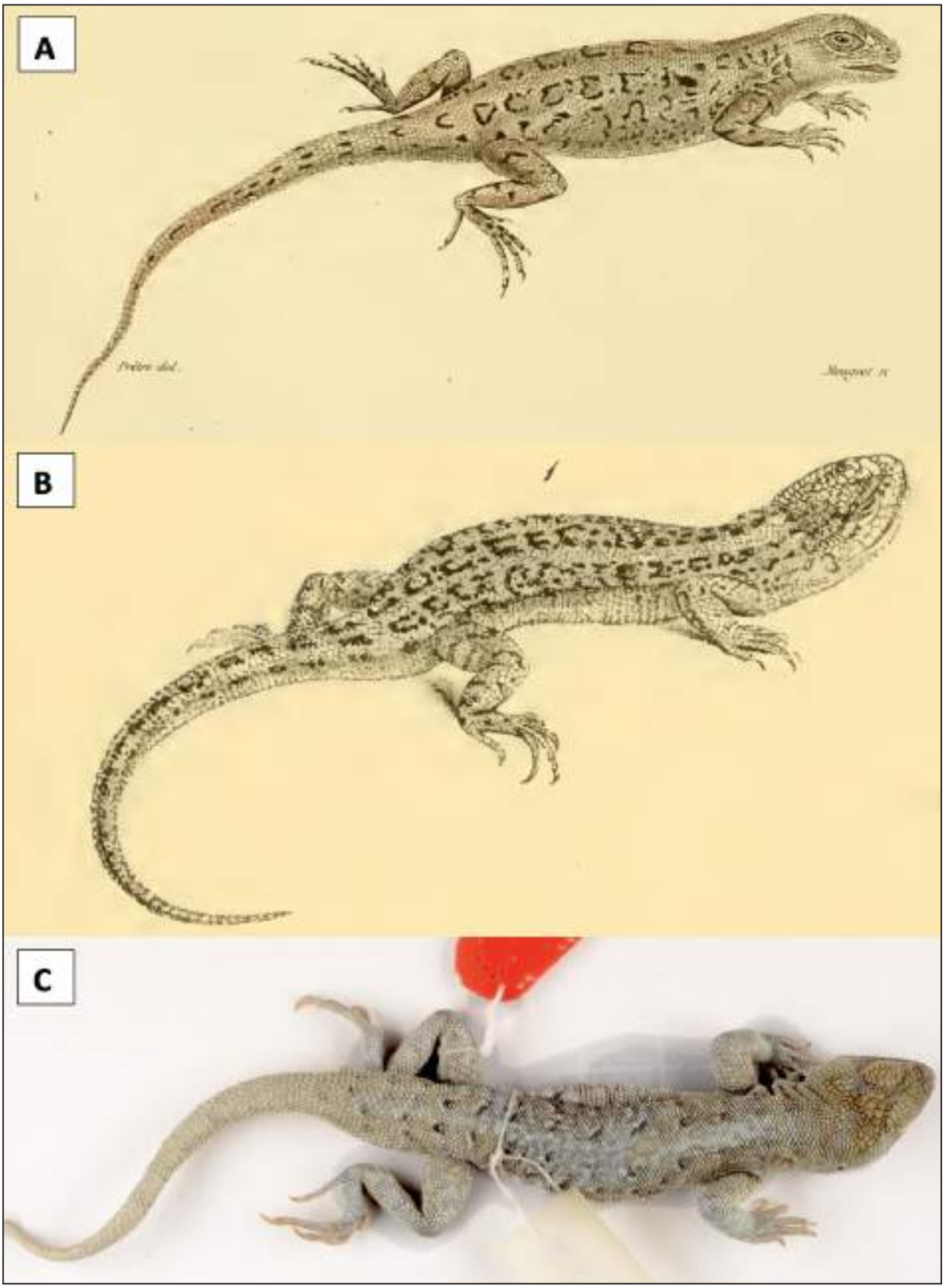

Figure 3. A. *Proctoretus signifer* illustration from Duméril *et al.* (1854); B. *P. signifer* illustration from Bell (1843); C. Photograph of MNHN-RA-0.6860, courtesy of I. Ineich/MNHN.

riorly by light scales. Based on the above, specimen MNHN-RA-0.6860 best matches the description of *L. fitzingerii*, which makes it clear that its residence in the jar of *L. fitzingerii* type specimens was indeed its proper location in 1837, 1851, 1967, 1980, as well as today. Incorrectly identified paratypes

While MNHN-RA-0.6860 was included as a syntype of *Proctotretus fitzingerii* var. A in 1837 and 1851, this specimen clearly does not belong to *Liolaemus fitzingerii,* a Patagonian species with a patch of enlarged spinose scales on the proximal portion of the thigh, a character state typical of species of the *L. boulengeri* group. Laurent's (1992) morphometric analyses found MNHN-RA-6860 to fall closer to the cluster of specimens he assigned to *L. multiformis* than to the *L. annectens* cluster in his and he thus concluded that *L. multiformis* is a junior synonym of *L signifer*, but only because he was reservedly accepting that the specimen was in fact the *L. signifer* holotype, despite his own evidence to the contrary (Laurent, 1984a). The name applicable to this storied specimen will be discussed below.

The Fates of *Liolaemus signifer* (Duméril & Bibron 1837) and its synonyms sensu Laurent (1992)

Given that i) the specimen claimed to be the "rediscovered" holotype of *Liolaemus signifer* by Cei *et al.* (1980) is a paralectotype of *Proctotretus fitzingerii* var. A, ii) its measurements and other characteristics do not match those described for the *L. signifer* holotype, iii) the available information does not permit the meaningful correction or restriction of the locality of the lost *L. signifer* holotype such as to permit the identification of a population corresponding to that name, and, iv) no author has designated a neotype for *L. signifer*, I here recommend that *Liolaemus signifer* (Duméril and Bibron 1837) be considered a *nomen dubium* and I revalidate *Liolaemus multiformis* (Cope 1875) as the name applicable to the populations assigned to *L. signifer* by Aguilar *et al.* (2017a) and Aguilar-Puntriano *et al.* (2018) from the Titicaca basin of Peru, adjacent areas of Puno, Tacna, and Moquegua, and limited areas of the Bolivian Titicaca basin. This nomenclatural act eliminates the unnecessary misapplication of a name that cannot be confidently applied to any known population of lizards and restores the use of Cope's species name that was widely by herpetologists and natural historians between 1875 and 1992.

Despite his own clear evidence, Laurent (1984:280) decided to accept the decision of Cei *et. al.* (1980) while "reserving the right to consider the litigated specimen a neotype". However, Laurent never exercised this right and neither has any other author. There is little to be gained from arbitrarily designating a neotype to conserve a poorly applied species name that has no extant holotype or paratypes, no clear type locality, and an ambiguous morphological description. Rather, it should be both surprising and disconcerting that taxonomists have been describing new species of the *Liolaemus montanus* group from the Andes of southern Peru, Bolivia, and northern Chile for well over a century (e.g., Cope, 1875; Boettger, 1891; Boulenger, 1901, 1902; Pellegrin, 1909; Marx, 1960; Laurent 1982a, 1982b, 1984a, 1992, 1995, 1998; Núñez and Yáñez, 1984 "1983–1984"; Ortiz and Marquet, 1987; Valladares *et al.,* 2002; Gutiérrez *et* al., 2018; Aguilar-Puntriano *et al.*, 2019) without having ever critically examined the identity and validity of *L. signifer*, the earliest available name of the species group.

Now that the situation of *Liolaemus signifer* can be put to rest, our attention can return to the next available names for the lizards of the *L. montanus* group from the Titicaca basin and Altiplano: *L. multiformis*, *L. lenzi*, *L. annectens*, *L. tropidonotus*, *L. pantherinus*, *L. variabilis*, and *L. bolivianus*. Boettger (1891) described *Liolaemus lenzi* from material from the "Bolivian shore of Lake Titicaca", a species he from *L. multiformis* based on the higher number of scales around midbody in the *L. lenzi* types (74–86 vs. 60 –70)[5]. This species was included in the synonymy of *L. multiformis* by Burt and Burt (1931) and subsequent authors such as Hellmich (1962) and Donoso-Barros (1970). Laurent (1992) included *L. lenzi* in the synonymy of *L. signifer*. Boulenger (1901, 1902) described *L. annectens* from Caylloma and Sumbay in the Arequipa Department and then *L. tropidonotus* from Tirapata, Puno, about 40 km northwest of Lake Titicaca. He considered both species allied with *L. multiformis* and the distinguished them based on "larger scales" in *L. annectens* and "strongly keeled dorsals scales" in *L. tropidonotus*; he did not compare either with *L. signifer*. Burt and Burt (1931) placed both species in the synonymy of *L, m. multiformis*, an act followed by Hellmich (1962) and Donoso-Barrros (1970). Laurent (1992) considered *L. annectens* a subspecies of *L. signifer*. Aguilar *et al.*

[5] Based on Boulenger's (1885:153) stated range of 60–70 scales around midbody for *L. multiformis* specimens from "Guascona" (i.e., Huasacona, Puno) specimens.

(2017a) and Aguilar-Puntriano *et al.* (2018) recovered *L. annectens* as sister to *L. etheridgei*, which form an evolutionary lineage clearly distinct from their *L. signifer* clade (=*L. multiformis*), fully supporting *L. annectens* as a valid species.

Núñez (2004) proposed the revalidation of *Liolaemus tropidonotus* after examining the types at BMNH, a decision accepted by Langstroth (2005), Pincheira-Donoso *et al.* (2008) and Etheridge and Frost (2016). While in 2005 I accepted the conclusion of Núñez (2004), I had not yet examined either the *L. tropidonotus* types or the *L. multiformis* types. Rather, my conclusion was based on my familiarity with the small-scaled Bolivian lizards that had been recognized as *L. multiformis* or *L. signifer*. In 2012, I visited BMNH and examined the three *L. tropidonotus* syntypes. The largest male, measuring 70 mm SVL, has 59 scales around midbody and 67 DSOT, strongly keeled and phylloid, not dissimilar from some of the *L. multiformis* paratypes and very similar to *L. multiformis* from 4 km west of Santa Rosa, Puno, some 60 km northwest and upstream of Tirapata (e.g., KU 163536). The two juvenile syntypes, a male and a female, have strongly-defined dorsolateral striping; however, similarly striped specimens are found in *L. multiformis* from the Santa Rosa locality mentioned above (e.g., KU 163549) Furthermore, the DSOT counts of the *L. tropidonotus* type series (67–83) fall entirely within the range of those of *L. multiformis* (62–89). Núñez (2004) based his decision to resurrect *L. tropidonotus* on comparison of its types against those of *L. annectens*, a species Núñez considered to be a synonym of *L. multiformis* fide Laurent (1992). Gutiérrez *et al.* (2018), based on comparison of newly collected material from Tirapata and the range of the Peruvian *L. signifer* (=*L. multiformis*), found the synonymy proposed by Laurent to be justified. Based on my examination of the type series of both species and other *L. multiformis* from the Puno Department, I agree with Gutiérrez *et al.* (2018) and here recognize *L. tropidonotus* as a junior synonym of *L. multiformis*.

Pellegrin (1909) described five species of *Liolaemus* based on specimens he stated generally as "captured in the High Plateaus of the Andes of Perú and of Bolivia, in the Lake Titicaca region, at an altitude of around 4,000 meters" by the 1903 French Expedition. Of these, *L. pulcher* and *L. mocquardi* are generally considered to by junior synonyms of *L. ornatus* (see Laurent, 1982, 1992). Burt and Burt (1931) did not mentions any of Pellegrin's species but recognized them all as valid in their 1933 list of the South American lizards. Mertens (1942, 1952) identified specimens for southern Peru as *L. pantherinus*. Hellmich (1962) placed *L. variabilis* and *L. bolivianus* in the synonymy of *L multiformis* but made no mention of *L. pantherinus*. Donoso-Barros (1966) included *L. mocquardi* and *L. pantherinus* as members of the Chilean fauna. Laurent (1982) considered *L. pantherinus*, *L. pulcher*, and *L. mocquardi* to the juveniles, adult males, and adult females, respectively, of *L. ornatus,* while considering *L. bolivianus* to a member of his "*signifer* group" and *L. variabilis* and each of its varieties to be synonyms of *L. multiformis*. A decade later, Laurent (1992) considered *L. pantherinus*, *L. variabilis*, and *L. bolivianus* to all be synonyms of *L. s. signifer*. Núñez and Jaksic (1992:75) rejected Laurent's (1982;1992) placements of *L. pantherinus* in the synonymies of *L. ornatus* and *L. signifer* and considered a valid Chilean species. In the same work, Núñez and Jaksic (1992:80) considered *L. islugensis* to be a probable junior synonym of *L. pantherinus*, a synonymy affirmed a decade later by Pincheira-Donoso and Núñez (2002). Recently, Ruiz de Gamboa and Ortiz (2020) rejected the synonymy of *L. islugensis* under *L. pantherinus*, recognizing both as valid species and restricting *L. pantherinus* to Peru and Bolivia, without reference to material of this species beyond the syntypes. The identities of *L. lenzi, L. variabilis*, and *L. bolivianus* remained unexamined in the literature after the work of Laurent (1992).

On the Limits of *L. multiformis*

While many workers have commented on *Liolaemus multiformis*, it appears that few have examined the *L. multiformis* type series, which has contributed to a poor understanding of the limits of variability within this species and the relationships of the type series from the Peruvian sector of Lake Titicaca with populations from other regions. Hellmich (1962) did not examine the type series but examined 656 specimens from localities in the Altiplano and Cordillera of La Paz, Bolivia, and just two specimens from Peru (Laguna Umayo, Puno, which likely correspond to *L. multiformis*). Most of the Bolivian specimens examined by Hellmich belong to populations described as *L. lenzi, L. variabilis,* and *L. bolivianus*, and a few may belong to *L. forsteri* from the Cordillera Real.

Donoso-Barros (1966:517–521) provided a rather detailed review of the taxonomy of *Liolaemus multiformis* and assigned specimens from the eastern

sector of the Antofagasta Region to *L. m. multiformis.* However, Núñez and Fox (1989) identified these specimens as *L. puritamensis.* Veloso *et al.* (1982) reported *L. multiformis* from Pampa Chucuyo in the Arica y Parinacota Region, specimens that Laurent (1998) would later describe as *L. pleopholis*.

Laurent (1992) designated ANSP 13064 (Fig. 4) as lectotype of *L. multiformis* but provided no further details about the specimen. My examination of the type series found the lectotype to be a stout female measuring 74 mm SVL with rather smooth but strongly imbricate, phylloid dorsals (DSOT=74) and with a dark dorsal ground color and scattered lighter spots (one or two scales in size), without traces of dorsal blotches. Five of the six type specimens[6] have rather large, imbricate, and keeled dorsal scales (DSOT 62–76), of which ANSP 11370 has exceptionally large, imbricate, and strongly keeled dorsals (DSOT= 62), not unlike the large male syntype of *L. tropidonotus*; ANSP 11369 represents the other extreme among the syntypes, with somewhat smaller (DSOT= 79), more triangular, smooth dorsals that are more similar to individuals from populations from the southern end of Lake Titicaca in Bolivia (e.g., specimens described as *L lenzi, L. variabilis*. or *L. bolivianus*). When I first saw the *L. mutltiformis* type series in December 2016, I was immediately struck by their dissimilarity to my concept of *L. signifer* and *L. multiformis* based on Bolivian specimens. It should be noted that there are no specific locality data for the *L. multiformis* type series although Burt and Burt (1931:277) consider specimens from Juliaca, Puno, be topotypical specimens of *L. m. multiformis*. Curiously, Cope (1877) identified a specimen from Juliaca collected by Orton during his final expedition to Peru (1876–1877) as *Proctotretus fitzingerii,* which he distinguished from his *P. multiformis* on the basis of relatively smaller and smoother lateral scales than in *P. multiformis*, with no mention of a patch of enlarged spinose scales on the inner thigh. In this same paper, Cope assigned as specimen from "La Raia, or the divide which separates the waters of the Ucayali and those of Lake Titicaca" to his *P. multiformis.*

Compared to the lizards described as *Liolaemus multiformis, L. annectens,* and *L. pantherinus*, the lizards from the southern shores of Lake Titicaca and the Altiplano of La Paz and Oruro, including the *L. lenzi* holotype, the *L. bolivianus* syntypes, and the *L. variabilis* syntypes, all recognized as *L. multiformis* or *L. signifer* in the literature of 1970s onwards, tend to have more numerous, smaller, and less imbricate dorsal scales. DSOT counts of *L. multiformis* (n=

[6] It should be noted the Cope (1875) mentioned that there was one specimen of variety I, three specimens of variety II, and one specimen of variety III; this enumeration includes only five specimens. Malnate (1971) included the six specimens examined here.

Figure 4. Lectotype of *Liolaemus multiformis* (ANSP 13064).

18), including the *L. multiformis* type series and MNHN-RA-0.6860, range from 62 to 89 (mean= 75.6, median= 76), while DSOT counts of Bolivian specimens (n= 27) assigned previously to either *L. signifer* or *L. multiformis*, including types of *L. lenzi, L. variabilis*, and *L. bolivianus* (but not including lizards corresponding to *L. forsteri*), range from 74 to 110 (mean= 89.7, median= 87). While there is some overlap, two-sided Wilcoxon rank sum tests permit the rejection of the null hypothesis of equal DSOT count distributions for *L. multiformis* and the southern specimens at $p<0.0001$, a finding which suggests that the lizards of the Bolivian Altiplano with generally smaller and more numerous dorsals, can be reliably distinguished morphologically from those identified here as *L. multiformis* and that the applicability of these names based on the Bolivian specimens now requires reconsideration. This finding is supported by the molecular phylogenetic estimate of Aguilar-Puntriano *et al.* (2018) which included samples of these lizards from localities in the departments of La Paz (e.g., MNCN 34753, 34755, 34757) and Oruro (e.g., MNCN 34762–63, 34775) and recovered them in a clade identified as *Liolaemus* sp3, an independent evolutionary lineage sister to *L. chlorostictus* and quite removed from their *L. signifer* clade (=*L. multiformis*).

The earliest available name for lizards from the southernmost shores of Lake Titicaca and the northern Altiplano and of Bolivia with smaller dorsals and higher DSOT counts is *Liolaemus lenzi* Boettger 1891, a species described from material from the "Bolivian shore of Lake Titicaca" (my translation). Boettger (1891) distinguished *L. lenzi* from *L. multiformis* based on the higher number of scales around midbody in the *L. lenzi* types (74–86 vs. 60–70)[7]. Etheridge (*in litt.*) counted 72 scales around midbody and 87 paravertebrals on the *L. lenzi* holotype and did not mention any paratypes. My examination of the *L. lenzi* holotype (SMF 11110; Fig. 5) finds this specimen to have at least 92 DSOT and the dorsals to be juxtaposed to subimbricate, with very few scales showing development of keels. This evidence suggests that the *L. lenzi* holotype belongs to the southernmost Titicaca-Bolivian Altiplano population, not to *L. multiformis*. While Boettger (1891) made no specific mention of paratypes, he did describe the coloration of at least one juvenile in addition to that of the adult and gave a range of scales around midbody (74–86). Thus, Etheridge's counts of 72 scales around midbody and 87 DSOT

[7] Based on Boulenger's (1885) range of 60–70 for Pentland's "Guascona" specimens.

Figure 5. Holotype of *Liolaemus lenzi* (SMF 11110).

suggest that the *L. lenzi* holotype was at the lower end of Boettger's scale counts and thus DSOT counts for the paratype(s) likely exceed 87–92 given the general positive correlation between scales around midbody and DSOT in the *L. montanus* group, which would only further support the separation of *L. lenzi* from *L. multiformis* based on scales around midbody and DSOT. I here revalidate *Liolaemus lenzi* Boettger 1891 and assign this name to the *Liolaemus* sp3 clade of Aguilar-Puntriano *et al.* (2018), recognizing however that this clade may well represent a species complex and that more work is needed to understand the degrees and patterns of diversification within it. Furthermore, I here place *Liolaemus variabilis* Pellegrin 1909:327 and *Liolaemus bolivianus* Pellegrin 1909:328 in the synonymy of *L. lenzi* Boettger 1891. *Liolaemus lenzi* thus includes lizards from the shores of the southern end of Lake Titicaca, the Altiplano and cordilleras of the La Paz, Oruro, and Cochabamba (and possibly northern Potosí) departments of Bolivia, a small portion of the Desaguadero basin of Puno, Peru, and the Altiplano of Arica y Parinacota (Region XV) in Chile (Fig. 6), lizards which have been largely assigned to *L. multiformis* or *L. signifer*, but also to *L. pleopholis* (see Aguilar-Kirigin *et al.*, 2016 and discussion below). *Liolaemus lenzi* is parapatric with *L. forsteri* on the lower slopes of the Cordillera Real east of the Altiplano in La Paz, with *L. multiformis* in the southern end of the Titicaca basin, and possibly with *L. pleopholis* to the west in the vicinity of Volcán Sajama (but see discussion below).

Based on the characteristics of the populations of lizards now assigned to *Liolaemus multiformis* from the greater Titicaca basin of Peru and a small part of Bolivia and those assigned to *L. lenzi* from the Bolivian Altiplano and adjacent cordilleras, I agree with Laurent that MNHN-RA-6860, a lizard obtained by d'Orbigny during his South American sojourn, can be assigned to *L. multiformis*. Examination of d'Orbigny's detailed travelogue (d'Orbigny, 1834) reveals that he never visited the Peruvian sector of Lake Titicaca, but rather only ventured as far as the vicinity of Achacachi, Bolivia. Being the only place in the range of *L. multiformis* visited by d'Orbigny, we can now correct the locality MNHN-RA-6860 from "Chili" to the vicinity of Achacachi, Bolivia.

On the identity of *Liolaemus pleopholis*

Veloso *et al.* (1982:220–224) reported a series of 55 specimens they collected at "Pampa Chucuyo, (4.240 m s.n.m.)" in the Arica y Parinacota Region of Chile and identified as *Liolaemus multiformis*. These lizards were later described by Laurent (1998) as *Liolaemus (Eulaemus) pleopholis*, which he distinguished from other members of the *L. montanus* group by a combination of characteristics including "the multiplication and fragmentation of scales… in the frontal area and around the interparietal" and "a higher longitudinal count of dorsal scales (87–98 instead of 61–87)" relative to his concept of *L. signifer*, which was a composite of specimens here identified as *L. multiformis*, *L. lenzi*, and *L. annectens*. Pincheira-Donoso and Núñez (2005:168) considered this species valid and distinguished it from their concept of *L. signifer* with *L. signifer* always having juxtaposed dorsals, regularly smooth or weakly keeled, without more strongly keeled scales in the dark dorsal markings, and lower counts of scales around midbody (74–80 vs 80–88). However, the counts around midbody of the type series of *L. pleopholis* are 71–83 (Laurent, 1998), which was not considered diagnostic against *L. signifer*. The range reported

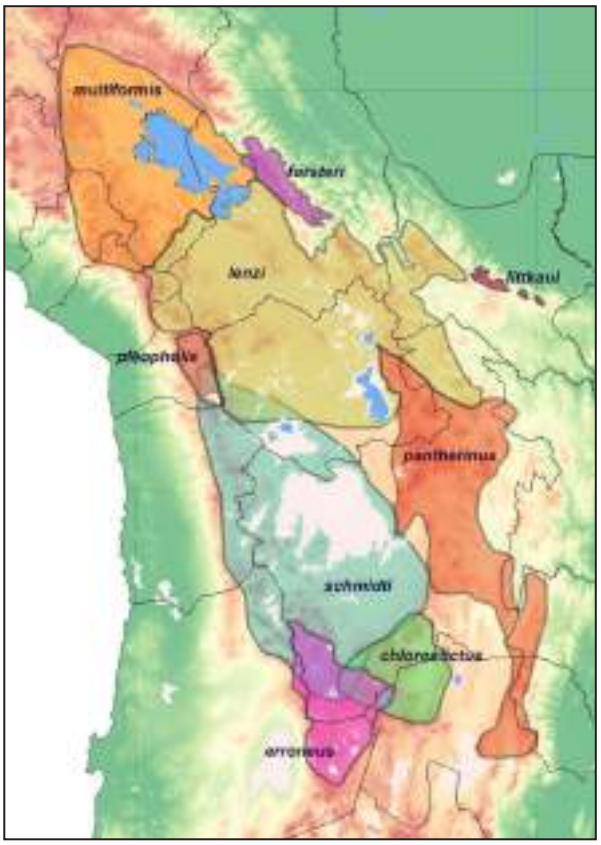

Figure 6. Ranges of focal species: *L. chlorostictus*, *L. erroneus*, *L. forsteri*, *L. lenzi*, *L. multiformis*, *L. pantherinus*, *L. pleopholis*, and *L. schmidti*.

by Pincheira-Donoso and Núñez (2005) for their *L. pleopholis*, 80–88, is exactly the same reported for the *L. bolivianus* type series by Etheridge (*in litt.*), within the range reported by Etheridge for the *L. variabilis* types, 70–94 (Etheridge, *in litt.*), and also within the range (78–88) reported by Rendahl (1937) for specimens he assigned to *L. variabilis* from the Bolivian Altiplano. Furthermore, I have observed the presence of more strongly keeled scales in dark dorsal blotches than in lighter ground areas of the dorsum in Bolivian lizards included here in *L. lenzi*. The "higher longitudinal counts of dorsal scales" reported by Laurent (i.e., 87–98) are entirely within the range of those I include here as *L. lenzi* (74–110 DSOT, x-bar= 89.0). My DSOT counts (76–91 DSOT, x-bar= 82.3) of six putative *L. pleopholis*, including a strict topotype, two Chilean specimens assigned to *L. pleopholis* by Aguilar-Puntriano *et al.* (2018), and three Bolivian specimens assigned to *L. pleopholis* by Aguilar-Kirigin *et al.* (2016), are also within the range of *L. lenzi*. Considering the variation of DSOT and other scale characters within the species assigned here to *L. lenzi* is extensive, I consider that as applied here, *L. lenzi* may well be a complex of cryptic lineages.

While Troncoso-Palacios (2014) counted 96 and 99 DSOT in his sample of two Chilean *Liolaemus pleopholis*, he considered it either a cryptic species or a synonym of *L. signifer*. Demangel Miranda (2016:587–588) also considered the separation of *L. pleopholis* from *L. signifer* to be problematic, based on his examination of new material from various localities in the Arica y Parinacota Region. Based on my examination of relevant material from Chile and Bolivia, I agree with Troncoso-Palacios (2014) and Demangel Miranda (2016) that *L. pleopholis* cannot be distinguished morphologically from lizards they recognized as *L. signifer* from northern Chile (i.e., *L. lenzi*). Aguilar-Kirigin *et al.* (2016) reported various lizards from around Volcán Sajama as the first Bolivian records of *L. pleopholis* due to their overall agreement with Laurent's description, and with topotypic Chilean specimen examined, and their geographic proximity to the Chilean populations in the absence of any geographic barriers or ecological discontinuities. Given the absence of clear morphological or biogeographic limits between Chilean *L. pleopholis* and Bolivian *L. lenzi*, I would not hesitate to place *Liolaemus pleopholis* Laurent 1998 in the synonymy of *L. lenzi*, however, such as decision would be contradicted by the mtDNA-informed phylogenetic estimate of Aguilar-Puntriano *et al.* (2018) or the total evidence hypothesis of Abdala *et al.* (2020).

Aguilar-Puntriano *et al.* (2018) included two terminals identified as *Liolaemus pleopholis* from two localities to the southeast of Pampa Chucuyo and these were recovered as a clade sister to a clade of their *L. islugensis*, which together are sister to *L. orientalis*((*L.* sp1(*L. multicolor*(*L.* cf. *schmidti*+*L.* sp4)))), which together with their *L. pleopholis*+*L. islugensis* form a clade which I refer to here as the *L. multicolor* group. However, the inclusion of *L. pleopholis* and *L. orientalis* in the *L. multicolor* group is quite unexpected morphologically, recalling that *L. pleopholis* has been considered a cryptic species indistinguishable from *L. signifer* (=*L. lenzi*) or conspecific with the same and that *L. orientalis* was described as subspecies of *L. annectens* and has been considered closest to *L. chlorostictus* (originally *L. orientalis chlorostictus*). The inclusion of these taxa within an otherwise morphologically cohesive group could be a rather remarkable convergence between two members of the *L. multicolor* group (*L. pleopholis* and *L. orientalis*) and members of the *L. multiformis* group or perhaps the conservation of a plesiomorphic morphology in either *L. pleopholis* or *L. orientalis*. Alternatively, the recovered phylogenetic hypothesis could result from introgression in an area of contact between *L. pleopholis* and *L. islugensis*.

The *Liolaemus* sp3 clade of Aguilar-Puntriano *et al.* (2018), here referred to the *L. lenzi* complex, includes lizards sampled from Sajama and the Río Cosapilla, Bolivia. Aguilar-Kirigin *et al.* (2016) identified lizards from Sajama as *L. pleopholis*. The specimen assigned to *L. pleopholis* by Aguilar-Puntriano *et al.* (2018), SSUC 569 (Fig 7), is an adult male from the Salar de Surire, Chile, which morphologically is indistinguishable from the *Liolaemus* sp3 specimen from Sajama (MNCN 34763; Fig. 7). The specimen from the Río Cosapilla (4061 masl), MNCN 34757, is from a locality 41 km downstream of Caquena (4460 masl), Chile, a locality where *L. pleopholis* is reported by Troncoso-Palacios (2014). While the Río Cosapilla locality is 400 m lower than Caquena, there are no apparent ecological or geographic barriers to separate these populations and Demangel-Miranda (2016:403) gives an altitudinal range of 4000 to 4600 masl for *L. pleopholis*. The Cosapa, Bolivia, locality where Aguilar-Kirigin *et al.* (2016) reported *L. pleopholis* is at approximately 3930 masl and its type

Figure 7. A. Specimen assigned to *Liolaemus pleopholis* by Aguilar-Puntriano *et al.* (2018) SSUC 569, Chile: Arica y Parinacota: Salar de Surire; B. Specimen assigned to *Liolaemus* sp3 by Aguilar-Puntriano *et al.* (2018), MNCN 34763, Bolivia: Oruro: Sajama.

locality is at 4240 m a.s.l. (Laurent, 1998).

In contrast to Aguilar-Puntriano *et al.* (2018), Abdala *et al.* (2019a) recovered *L. pleopholis* as sister to two Argentine species, *L. poecilochromus* Laurent 1986 and *L. halonastes* Lobo, Slodki, and Valdecantos 2010, in a total evidence phylogenetic estimate including morphological, ecological, and molecular characters. This finding, however, is also not consistent with the observations of Troncoso-Palacios (2014), Demangel Miranda (2016), and those of myself, which find *L. pleopholis* to be either conspecific with *L. lenzi* or that they are closely related cryptic species. While tthe relationship recovered by Abdala *et al.* (2019a) would involve a significant geographic disjunction between *L. pleopholis* and the Argentine species that would require a complex biogeographic history, it may possibly indicate that there are extant or extinct terminals to be described within this geographic gap. The disparate hypotheses regarding *L. pleopholis* stemming from mtDNA analyses (Aguilar-Puntriano *et al.*, 2018), an extensive total evidence approach (Abdala *et al.*, 2019a), and a simpler consideration of geography and morphology (Troncoso-Palacios, 2014; Demangel Miranda, 2016; this work) illustrate how the application of large amounts of data and computational models may

result in unexpected hypothesis that challenge what is deducible from a traditional taxonomic approach and require more complex evolutionary histories resulting in either a remarkable convergence or a major biogeographic disjunction. While I am inclined to simply include it as a member of the *L. lenzi* complex, in light of the contradictory evidence, I will leave *L. pleopholis* as a *species inquirenda*, a species of doubtful identity needing further investigation (International Commission on Zoological Nomenclature, 1999) whose fate remains to be determined by more thorough geographic sampling, morphological, and phylogenetic analyses.

Limits of *L. multiformis, L. lenzi,* and *L. forsteri*

In La Paz Department of Bolivia, in the juncture of Lake Titicaca, the Cordillera Real, and the Altiplano, we find three distinct evolutionary lineages of the *Liolaemus montanus* group: *L. multiformis, L. lenzi,* and *L. forsteri* (Fig. 6). *Liolaemus multiformis* can be distinguished from the other two species by its intermediate-sized dorsal scales that are subimbricate to imbricate, smooth to moderately keeled, and with average DSOT numbers falling between the generally lower counts in *L. annectens* and the generally higher counts in *L. lenzi*. The populations mapped as *L. signifer* by Aguilar *et al.* (2017) correspond to *L. multiformis* and are restricted geographically to the Peruvian Titicaca basin and adjacent parts of Moquegua, Tacna, and Puno, and the northern shores and islands of the main body of Lake Titicaca in Bolivia, but excluding the southern section of the lake (Fig. 6). There is no evidence for the presence of *L. multiformis* in Bolivia outside of the Titicaca basin or anywhere in Chile. All records of *L. multiformis* and *L. signifer* from the Arica y Parinacota Region correspond to *L. lenzi* and all records from the Tarapacá and Antofagasta regions of Chile (e.g., Donoso-Barros, 1966:317–321; Valladares *et al.,* 2002) are based on misidentifications or confused locational data (see also Troncoso-Palacios, 2014).

Liolaemus lenzi, applied here to the population described as *L. bolivianus, L. lenzi,* and *L. variabilis* and included in *Liolaemus* sp3 of Aguilar-Puntriano *et al.* (2018), includes lizards with a great degree of variability in coloration and pholidosis within populations but without known geographic structure (see Hellmich, 1962). The range of *L. lenzi* is mapped in Fig. 6. In Peru, *L. lenzi* is known only from the extreme southwestern portion of the Titicaca-Desaguadero basin (Aguilar-Puntriano *et al.*, 2018), which is also the only part of that country where *L. ornatus*, sensu lato, has been found (R. Gutiérrez Poblete, *in litt.*; C. Aguilar, *in litt.*). In Chile, *L. lenzi* occurs only in Altiplano of the Arica y Parinacota Region. In Bolivia, *L. lenzi* is found in the Altiplano and western Cordillera of the departments of La Paz and Oruro as far south of the southern shores of Lago Poopó, as well as the adjacent Andes to the east in La Paz and Cochabamba.

In the Cordillera Real of Bolivia, *Liolaemus multiformis* and *L. lenzi* are replaced by *L. forsteri* (type locality of "Chacaltaya (4700 m) près de La Paz, Bolivie"), which can generally be distinguished from *L. lenzi* by its tuberculate to conical dorsal scales in adults and distinctive color patterns in both adults and juveniles. Aguilar-Puntriano *et al.* (2018) place *L. forsteri* as sister to *L. multiformis* (i.e., their *L. signifer*) in the 181-terminal maximum likelihood multilocus tree as well as in their Bayesian divergence time tree, while it moves to a position sister to a clade including the *L. robustus* and the *L. multiformis* groups in their maximum likelihood multilocus tree that includes only one sample from each species or candidate species. Based on biogeography and morphology, the sister relationship between *L. forsteri* and *L. multiformis* seems more probable than a more distant evolutionary relationship. In fact, Aguilar-Puntriano *et al.* (2018) report syntopic *L. forsteri* (MNCN 48603) and *L. multiformis* (i.e., their *L. signifer*; MNCN 48602) from the vicinity of Walata on the slope north of Achacachi (Fig.1).

***Liolaemus pantherinus* Pellegrin 1909**

Now that *Liolaemus signifer* is relegated to a *nomen dubium* and the rather divergent *L. multiformis* and *L. lenzi* are revalidated and geographically circumscribed, we can now turn our attention to the enigmatic *L. pantherinus*. Pellegrin (1909) described *L. pantherinus* based on two specimens (MNHN-RA-1905.343–44, Fig. 8) collected in 1903 by the physician Dr. Maurice Neveu-Lemaire somewhere in what Pellegrin referred to as the "Hauts-Plateaux péruviens et boliviens". Pellegrin characterized *L. pantherinus* as having medium-sized dorsal scales, rounded posteriorly and slightly keeled, ventrals just slightly larger than dorsals, 50—52 scales around midbody, and four longitudinal rows of more or less quadrangular blotches along the dorsum.

The subsequent usage of the name *Liolaemus pantherinus* in the literature was sparse for several decades. Burt and Burt (1933) included it in their ca-

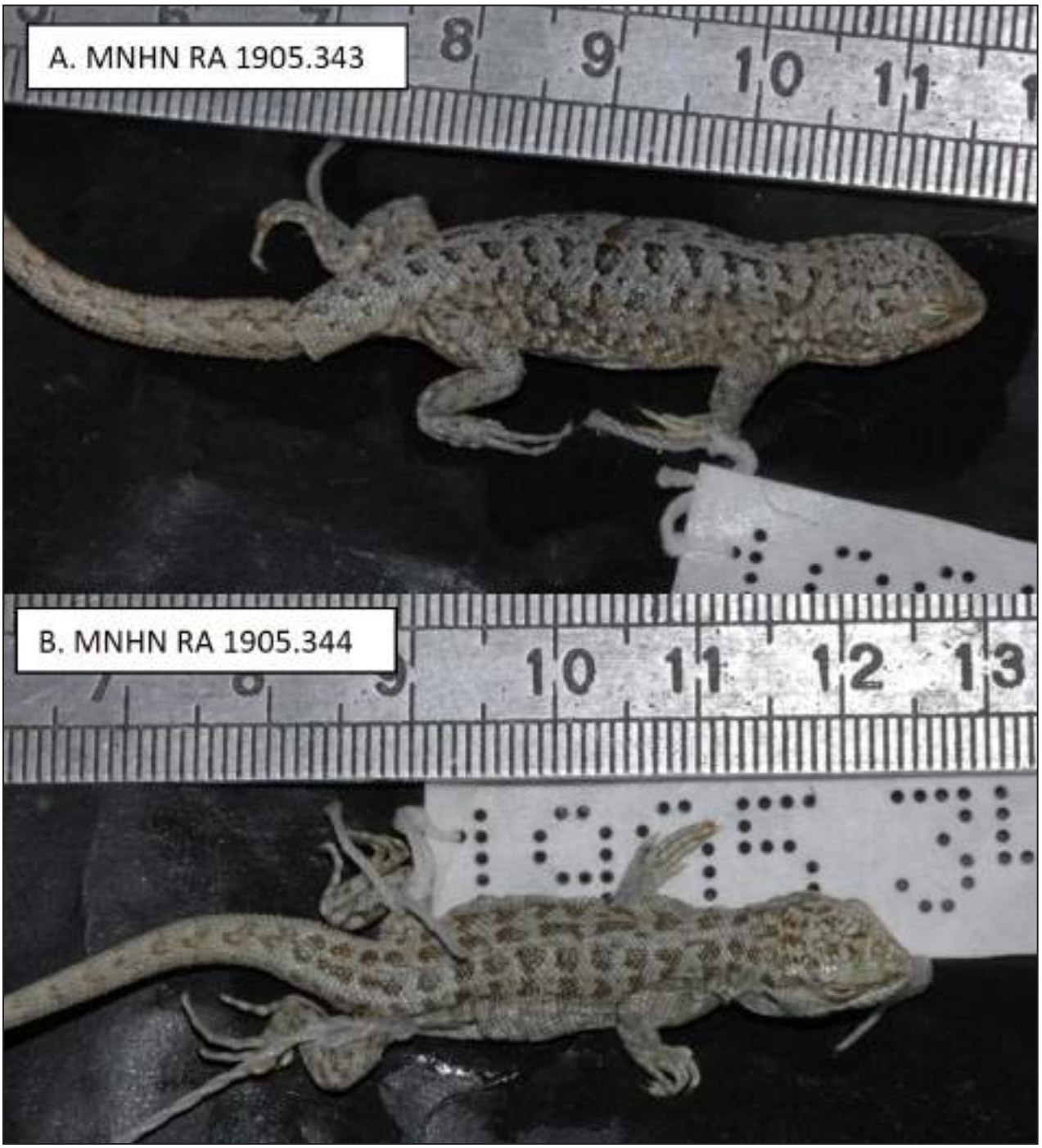

Figure 8. Syntypes of *Liolaemus pantherinus* (MNHN RA 1905.344-45).

talogue of South American lizards without comment or reference to specimens. Mertens (1952) assigned specimens collected by the 1936 Hamburg South Peru Expedition to this species. Donoso-Barros (1961) reported that he collected *L. pantherinus* in the Antofagasta Cordillera of Chile in 1958 and compared *L. constanzae* Donoso-Barros 1961 against those lizards. He later included an account of *L. pantherinus* in his *Reptiles de Chile* (Donoso-Barros 1966:327–329), characterizing specimens from near the Ollagüe volcano and the Tatio geysers in the Antofagasta Region (Region II). Finally, he (1970:192) included *L. pantherinus* as a valid species in the *Catalogue of the Neotropical Squamata* and stated its distribution as "the Altiplano of Peru, Bolivia, and Chile".

Laurent (1982) considered the *Liolaemus pantherinus* syntypes to be juveniles of *L. ornatus* but

later (Laurent, 1992) considered it a junior synonym of *L. s. signifer*. Núñez and Jaksic (1992:75) rejected Laurent's synonymies and considered *L. pantherinus* a valid Chilean species. In the same work, Núñez and Jaksic (1992:80) considered *L. islugensis* a probable junior synonym of *L. pantherinus*, a synonymy affirmed a decade later by Pincheira-Donoso and Núñez (2002) and Pincheira-Donoso and Núñez (2005). While Ruiz de Gamboa and Ortiz (2020) compared the *L. pantherinus* syntypes against *L. islugensis* and concluded that they are distinct and valid species, they did not review the taxonomic status of *L. islugensis* or identify any additional material assignable to *L. pantherinus* beyond the syntypes.

***Liolaemus islugensis* Ortiz & Marquet 1987**

Ortiz and Marquet (1987) described *Liolaemus islugensis* (holotype MZUC 10931; Fig. 9) from the vicinity of Colchane, Tarapacá Region (Region I) of Chile, in the Salar de Coipasa basin, not more than 3 km of the Bolivian border. They characterized *L. islugensis* as having small, smooth, round dorsal scales that are "not imbricate" and diagnosed their new species against just four species: *L. ornatus, L. griseus* Laurent 1984, *L. huacahuasicus*, and *L. pantherinus*. One of these, *L. ornatus,* is not a member of the *L. montanus* group, and two others, *L. griseus* and *L. huacahuasicus*, are restricted range endemics of the Tucumán Province of Argentina. They distinguished their new species from *L. pantherinus* based on a longer tail, a greater number of scales around midbody, and smooth dorsals in *L. islugensis*. However, Ortiz and Marquet did not state the basis for their characterization of *L. pantherinus*, citing neither its original description nor material examined.

My examination of the relevant type material does not support the conspecificity of the lizards described as *Liolaemus islugensis* by Ortiz and Marquet (1987) with the lizards described as *L. pantherinus* by Pellegrin (1909), based on DSOT counts and other general external morphological characters such as the degree of imbrication and development of keels on dorsal scales. Thus, we can safely conclude that *L. pantherinus* is not a senior synonym of *L. islugensis*, in complete agreement with Ruiz de Gamboa and Ortiz (2020). Rather, the lizards described as *L. islugensis* are more similar to those described as *L. multicolor* Koslowsky 1898*, L. schmidti* (Marx 1960), and *L. omorfi* Demangel et al. 2015, of which *L. schmidti* is geographically most proximate. Aguilar-Puntriano *et al.* (2018) included specimens referred to *L. islugensis, L. multicolor,* and *L.* cf. *schmidti* in a molecular phylogenetic estimate of the *L. montanus* group and recovered each of these as distinct lineages within a well-supported clade, which I here refer as the *L. multicolor* group in reference to the earliest available name within this clade (see Figs. S1 and S2 of Aguilar-Puntriano *et al.*, 2018), confirming the relationship implied by morphology. The identities of the specimens analyzed by Aguilar-Puntriano *et al.* (2018) and the status of *L. islugensis*, however, will be clarified below in light of the correction of the

Figure 9. Holotype of *Liolaemus islugensis* (MZUC 10931) from Colchane, by courtesy of J. Troncoso-Palacios.

type locality of *L. schmidti*, the most geographically proximate member of the *L. multicolor* group to *L. islugensis*.

***Liolaemus schmidti* (Marx 1960)**

Marx (1960) described *Ctenoblepharis schmidti* based on two juvenile specimens (FMNH 5759–60; Fig.10) collected in 1923 from "40 miles E of San Pedro, Antofagasta Province, Chile". Donoso-Barros (1966:342–343) included an account of this species in his *Reptiles de Chile* but having not examined the types and not being aware of any other specimens assigned to it at the time of the writing of the account, he provided only a verbatim translation of Marx's description. However, the account ends with the statement: "Terra typica: Oeste de San Pedro de Atacama." This restatement of the type locality is notable in two aspects: first, it reads "west of" the town of reference, not "east" as stated by Marx (1960) and, second, it adds "de Atacama" to the "San Pedro" as reported by Marx. Furthermore, according to Núñez and Yáñez (1984 "1983–1984"), shortly before going to press, Donoso-Barros received a series of eight lizards collected by Luis E. Peña and included a drawing of one of these specimens, a squat, short-tailed lizard with voluminous skin folds and drawn without visible dorsal scales, identified as *C. schmidti*, in Plate XXIV of the book.

In 1969, L.E. Peña collected a series of lizards from Cariquima, Chile (Fig. 1), a town just 20 km south of Colchane, the future type locality of *L. islugensis*. These lizards were originally deposited in the Universidade de São Paulo (MZUSP) and identified by Paulo Emílio Vanzolini as *Ctenoblepharis schmidti* and subsequently distributed to various museums including AMNH (131850-51), BMNH (1977 2277–79), CM (65045-46), MCZ (R-154201-04), and SDSU (1601-03). While Etheridge (1995) included the AMNH and SDSU material among the *L. schmidti* specimens examined and authors such as Valladares *et al.* (2002) and Abdala *et al.* (2008) have referred to these as *Liolaemus schmidti*, my review of the Chilean herpetological literature of the 1970s, 1980s, and 1990s reveals no evidence that these specimens were known to Chilean workers.

In the account of the genus *Ctenoblepharis* in the *Catalogue of the Neotropical Squamata* (Peters and Donoso-Barros, 1970:104), the type locality of *C. schmidti* is given as "40 mi east of San Pedro de Atacama, Antofagasta, Chile", a type locality uncritically restated by subsequent authors, including Yáñez and Núñez (1982), Etheridge (1995), and *The Reptile Database* as of March 2020. Cei (1979) placed *C. schmidti* in *Liolaemus*, a finding later supported by Laurent (1984b) and Etheridge (1995), who included it as a member of the *L. montanus* group. In 1975, L. E. Peña collected two lizards from Julaca, Potosí, Bolivia, a location to just the south of the Salar de Uyuni along the railroad between Ollagüe and Uyuni, and these are cataloged as *L. schmidti* (FMNH 204525–26) and have long been the only Bolivian material referred to this species in the literature (Dirksen and De la Riva, 1999). The second Chilean record for *L. schmidti* was reported by Yáñez and Núñez (1982), 22 years after the description of the species, based on a specimen collected in 1980 from the vicinity of Laguna Lejía, Antofagasta Region, 120 km southeast of San Pedro de Atacama.

In 2003, Núñez (2004) examined the BMNH series catalogued as "*Ctenoblepharis schmidti*" from Cariquima and determined one specimen (BM

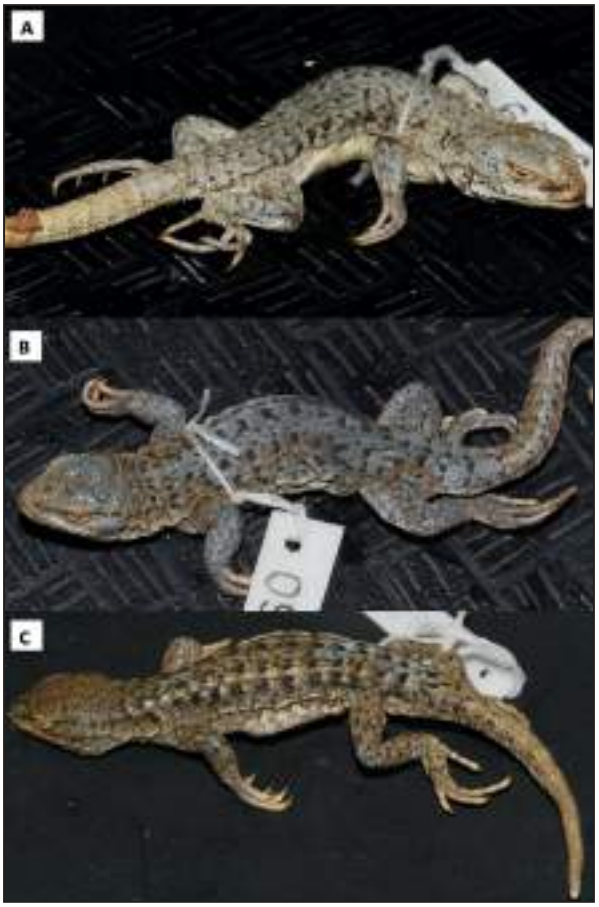

Figure 10. A. Holotype of *Liolaemus schmidti* (FMNH 5759); B. Allotype of *L. schmidti* (FMNH 5760); C. Adult male *L. schmidti* from Ojos de San Pedro (MVZ 66807), an essentially topotypic specimen.

1977 2277; Fig. 11) to be *Liolaemus pleopholis* and the other two (BM 1977 2278–79; Fig. 11) to be *L. andinus*. I examined these specimens in a 2011 visit to London and found all three to be assignable to *L. schmidti.* Furthermore, I found them essentially inseparable from a series collected by P.O. Simons at Uyuni, Bolivia, and identified by Boulenger as *L. signifer* (BMNH 1902.5.29.63–73), lizards also referred to *L. signifer* by Pincheira-Donoso and Núñez (2005:450).

Pincheira-Donoso and Núñez (2005:152) placed *Liolaemus schmidti, L. molinai*, and *L. poecilochromus* Laurent 1986 in the synonymy of *L. andinus*. While there are some similarities between *L. molinai,*

Figure 11. *Liolaemus schmidti* from Cariquima, Region I, Chile: A. BMNH 1977-2277, identified as *L. pleopholis* by Núñez (2004); B. BMNH 1977-2279, identified as *L. andinus* by Núñez (2004).

L. poecilochromus, and the generally accepted concept of *L. andinus* (e.g. Lobo *et al.,* 2010a), a species whose types series is considered to be lost and has no neotype, the type series of *L. schmidti* and the lizards from Cariquima and Julaca cannot be confused with either the original description of *L. andinus* or the general aspect of this rather distinctive phenetic group of small-scaled and short-tailed species. Lobo *et al.* (2010b) rejected these synonymies but without meaningful discussion based on examination of material.

In their description of *Liolaemus porosus*, Abdala *et al.* (2013) included seven specimens identified as *L. schmidti* in the diagnosis*:* FML 1192 and 1197 (Fig. 13), MVZ 66807–08 (Fig. 10), and SDSU 1601–03, which suggests that they considered this species distinct from *L. islugensis, L. erguetae*, and *L. andinus*, as they also referred to material of each these four species. However, their *L. islugensis* were all from the Tarija Department of Bolivia, not type material or other material from Chile. Troncoso-Palacios (2014) made a few tangential comments regarding *L. schmidti*, noting that records of *L. signifer* from the Antofagasta Region and the Potosí Department are probably misidentifications of *L. schmidti* and that the synonymy of *L. schmidti* under *L. andinus* should be rejected, conclusions confirmed by the present paper. Demangel *et al.* (2015) included *L. schmidti* in the diagnosis of their *L. omorfi* and stated that "the only two specimens that can be attributed to *L. schmidti* are the holotype and a paratype". They distinguished between the two species based on lower scale counts around midbody and a relative shorter tail in *L. omorfi* in comparison to the *L. schmidti* types. Demangel-Miranda (2016) did not include an account of *L. schmidti* in his *Reptiles en Chile* but rather provided a discussion (p. 588) about the problems surrounding this species and the fact that he could not find any lizards corresponding it in the area east of San Pedro de Atacama.

As noted above, Aguilar-Puntriano *et al.* (2018) included two specimens the assigned to *Liolaemus* cf. *schmidti* in their molecular phylogenetic estimates of the *L. montanus* group. These specimens are from "the road to San Pedro" some 37 km NW of San Pedro de Atacama, and from "Salar de Aguas Calientes", the same Salar de Aguas Calientes where Demangel *et al.* (2015) reported their *L. omorfi*, some 125 km south-southeast of San Pedro de Atacama. These specimens are recovered as sister to a candidate species "*Liolaemus* sp.4" from Rosario de Lerma Department, Salta Province, Argentina, not sister to *L. islugensis* or *L. multicolor*.

Beyond the type series (FMNH), the Cariquima series (AMNH, BMNH, CM, MCZ, and SDSU), and the Julaca series (FMNH), the only other putative *Liolaemus schmidti* specimens I have identified in collections outside of Chile are FML 1192 and 1197 ("Antofagasta, Atacama" and "Tatio", respectively; Fig. 17 below), MVZ 66807–08 (Fig. 10) from Ojos de San Pedro (Antofagasta Region) and USNM 165639 (Fig. 12) from "Volcán Tatio, Antofagasta Region". Material cataloged as *Ctenoblepharis schmidti* or *L. schmidti* in Chilean collections until 2002 was limited to the specimen from Laguna Lejía (MNHNCL 1074), a series of seven MZUC specimens collected along with the holotype of *L. erroneus*, and specimens from Farellones de Tara (MNHNCL 2162—63) which were later included as paratypes of *L. molinai*.

My examinations and those of colleagues (Valladares *et al.,* 2002; J. Troncoso-Palacio, *in litt.;* M. Ruiz de Gamboa, *in litt.*) reveal that none of the referred specimens in Chilean and Argentine collections correspond to *Liolaemus schmidti*; rather, they all correspond to populations currently recognized as either *L. erguetae* or *L. molinai*. To add to this dismal situation, I recently examined USNM 165639, a specimen collected by Donoso-Barros at Tatio and only the USNM specimen cataloged as *L. schmidti* and found it to be a female *L. hajeki* (Fig. 12). The absence of material correctly assigned to *L. schmidti* in Chilean and Argentine collections in the 1970s, 1980s, and 1990s is likely responsible for the omission of *L. schmidti* in the diagnosis of *L. islugensis* by Ortiz and Marquet (1987), as well as other problematic taxonomic decisions, recalling that in the 1980s there was no Internet and access to foreign museum catalogs and collections was difficult.

The second published record of *Liolaemus schmidti* reported by Yáñez and Núñez (1982) is based on a specimen (MNHNCL HERP 1074) from Laguna Lejía presently cataloged as *L. andinus* (Núñez and Gálvez, 2015:52). Other MNHNCL specimens (4368, 4373) from Laguna Lejía listed as *L. andinus* by Núñez and Gálvez (2015:53) have been identified as *L. molinai* (Troncoso-Palacios, 2014). Similarly, Valladares *et al.* (2002) commented that two of their *L. molinai* paratypes (MNHNCL 2162–63) were originally cataloged as *L. schmidti*; these are also listed as *L. andinus* by Núñez and Gálvez (2015:53). The seven MZUC specimens referred to *L. schmidti*

Figure 12. *Liolaemus hajeki*, USNM 165639, collected by R. Donoso-Barros at Volcán Tatio, Region II, Chile.

by Núñez and Yáñez (1984 "1983–1984") all correspond to *L. molinai* (M. Ruiz de Gamboa, *in litt.*). My examination of the FML specimens referred to *L. schmidti* in the literature (FML 1197 from Tatio, FML 1192 from "Antofagasta, Atacama") finds these specimens to correspond to *L. erguetae* or *L. molinai,* that latter considered a synonym of *L. andinus* by Pincheira-Donoso and Núñez (2005).

Type Locality of *Liolaemus schmidti* (Marx 1960)

Marx (1960) stated the type locality of his *Ctenoblepharis schmidti* as "40 miles east of San Pedro, Antofagasta Province, Chile". As noted above, Donoso-Barros (1966:343), without justification, stated the "terra typica" of this species to be "Oeste San Pedro de Atacama". Subsequent authors have all uncritically accepted that "San Pedro de Atacama" is the proper place of reference for the type locality of *Liolaemus schmidti.* However, there are presently at least five geographic features named "San Pedro" in the Antofagasta Region of Chile: i) "San Pedro de Atacama", a major town near the Salar de Atacama, ii) "Volcán San Pedro", a notable volcano northeast of the city of Calama, iii) "Estación San Pedro", a small town on the railroad along the Loa river near the base of the eponymous volcano, iv) the "San Pedro de Inacaliri" river, a tributary of the Loa, and v) "Ojos de San Pedro", a now-abandoned town located near springs captured for water supply for the copper mining industry. The fact that no lizards corresponding to *L. schmidti* are known from the ranges to the east of San Pedro de Atacama (see Demangel-Miranda, 2016:588) begs for an examination of which "San Pedro" is the point of reference in this species' stated type locality.

Marx (1960) also stated that the type specimens were collected by Colin C. Sanborn on October 3, 1923, which suggests that the itinerary of Mr. Sanborn might reveal valuable insights on the type locality of *Liolaemus schmidti.* A simple online search of the terms "Sanborn", "Chile", San Pedro", and "1923" returns Hellmayr's (1932) *Birds of Chile,* which includes a detailed itinerary of the 1922–24 Marshall Field Expedition to Chile, based largely on the notes of Colin C. Sanborn. This itinerary indicates that between the dates of 01–12 October 1923 Sanborn was collecting between "Ojo de San Pedro-San Pablo and Kilometer 31" and explains that "Kilometer 31" is 31 km upstream along the water pipeline from "San Pedro de Agua Potable up the railroad from Calama", which corresponds to the present-day Estación San Pedro at the confluence of the Loa and San Pedro de Inacaliri rivers, not San Pedro de Atacama. The itinerary also indicates that Sanborn visited "Ojo de San Pedro-San Pablo; Kilometers 31 and 40; Silala, Bolivia" between April 23 and May 5 of 1924, which may well explain Marx's "40 miles". Nowhere in Sanborn's itinerary is there any mention of San Pedro de Atacama. The simple review of the collector's published itinerary reveals

Figure 13. *Liolaemus schmidti*, AMNH R-85773, from "Chili: Rio San Pedro", cataloged as *L. signifer* as of 10 August 2020.

that the type locality of *L. schmidti* is not east of San Pedro de Atacama but rather in the valley of the San Pedro de Inacaliri river, east of the present day Estación San Pedro, in a completely different biogeographic setting than the areas of San Pedro de Atacama. Given that Sanborn reported all distances in kilometers, not miles, we can assume that Marx's "40 miles" is in error; forty miles east of Estación de San Pedro places the locality in Bolivia. I here correct the type locality of *Liolaemus schmidti* (Marx 1960) to "San Pedro de Inacaliri river valley between the localities of Ojos de San Pedro and Inacaliri, Loa Province, Antofagasta Region, Chile". This corrected locality is precise enough, regardless of the exact distance along the pipeline, given that the local ecosystem and *Liolaemus* fauna is reasonably uniform is this area, where *L. schmidti* is generally the most abundant species, followed by *L. pachecoi, L. puna,* and *L. hajeki* (pers. observation).

While the correction of the *Liolaemus schmidti* type locality above was a simple act, resolved by the examination of an itinerary published in 1932, it resolves a 60-year misunderstanding and also has major taxonomic and nomenclatural implications. The lizards from the San Pedro de Inacaliri river valley have been considered to be *L. islugensis* or *L. pantherinus* by contemporary Chilean herpetologists: *L.* cf. *islugensis* (Demangel Miranda, 2016:278–281), *L. islugensis* (J. Troncoso-Palacios in Aguilar-Puntriano *et al.,* 2018), and *L.* cf. *pantherinus* (Núñez and Gálvez, 2015:63). However, AMNH 85773 (Fig. 13) from "Chili: Rio San Pedro" is cataloged as *L. signifer* and clearly corresponds to an adult male *L. schmidti.*

Aguilar-Puntriano *et al.* (2018) included nine specimens identified as *Liolaemus islugensis* in their phylogenetic estimate of the *L. montanus* group: seven specimens from the Potosí Department of Bolivia and two specimens from the Antofagasta Region of Chile. Their Chilean *L. islugensis* were collected at a site "near the San Pedro volcano", approximately 8 km N of the San Pedro de Inacaliri river and 30 km ENE of Estación San Pedro[8], very close to the corrected type locality of *L. schmidti.* One of their

[8] Coordinates for the *L. islugensis* and *L.* cf. *schmidti* specimens generously provided by J. Troncoso-Palacios (*in litt.*) and C. Aguilar-Puntriano (*in litt.*).

L. cf. *schmidti* is from approximately 37 km NW of San Pedro de Atacama and the other is from Salar de Aguas Calientes some 125 km SSE of San Pedro de Atacama, the same site where Demangel *et al.* (2015) reported *L. omorfi*. Thus, the *L. islugensis* of Aguilar-Puntriano *et al.* (2018) are essentially topotypical *L. schmidti* and their *L.* cf. *schmidti* are *L. omorfi* (a species not otherwise sampled by Aguilar-Puntriano *et al.*). The *L. islugensis* clade of Aguilar-Puntriano *et al.* (2018) also includes samples from the around the Salar de Uyuni and Laguna Colorada of Bolivia (Fig. 14). Ruiz de Gamboa and Ortiz (2020) consider lizards from Uyuni to be conspecific with *L. islugensis*.

The discussion above indicates that *Liolaemus islugensis* must be considered a junior synonym of *L. schmidti* and that *L. omorfi* is separate from *L.*

Figure 14. *Liolaemus schmidti*, in life. A. Laguna Colorada, specimen not collected, courtesy of Omar Rocha; B. Uyuni, specimen not collected.

schmidti and phylogenetically closer to the Argentine *L. multicolor. Liolaemus multicolor, L. omorfi*, and *L. schmidti* are generally quite similar in general morphology and coloration in adults and, not surprisingly, the juveniles are essentially indistinguishable morphologically.

Liolaemus schmidti is the name applicable to the Chilean lizards previously considered to be *L. pantherinus* (e.g., Donoso-Barros, 1966; Pincheira-Donoso and Núñez, 2005; Mella Ávila, 2017), to the lizards described as *L. islugensis* from Colchane, as well as to the Bolivian lizards recognized in the literature as *L. schmidti* (e.g., FMNH 204525–26), identified as *L. islugensis* by Aguilar-Puntriano *et al.* (2018), and to the lizards from Uyuni (BMNH 1902.5.29.63–73) cataloged as *L. signifer* by Boulenger and those identified as *L. islugensis* by Ruiz de Gamboa and Ortiz (2020). I also include as *L. schmidti* the lizards from "the altiplano of Antofagasta" and "the south of Bolivia" referred to *L. signifer* by Donoso-Barros (1966:331). However, the lizards referred to *L. islugensis* from "Sama" (Cordillera de Sama, Tarija Department) by Tarifa *et al.* (2007) and "Departamento de Tarija" by Abdala *et al.* (2013) belong to *L. tajzara* Abdala *et al.* 2019, a member of the *L. multicolor* group which was identified by Aguilar-Puntriano *et al.* (2018) as "*Liolaemus* sp2", the basal lineage of the *L. multicolor* group.

While *Liolaemus pantherinus* and *L. schmidti* have little in common morphologically beyond being members of the *L. montanus* group with four rows of dark dorsal blotches (at least in juveniles in the case of *L. pantherinus*), they do have two significant commonalities: each species was based on the description of a pair of juvenile lizards and each was given a vague and misleading type locality which in combination led to great misunderstandings of their identities.

A trilogy of errors: *Liolaemus erroneus, L. islugensis erguetae,* and *L. molinai*

Núñez and Yáñez (1984 "1983–1984") described a single specimen stated as being collected in January 1962 by L. E. Peña from "Antofagasta, Depto. Atacama" as *Ctenoblepharis erroneus*, in honor of Donoso-Barros's erroneous identification of this same specimen as *C. schmidti* in Plate XXIV of his *Reptiles de Chile*. The species was reassigned to *Liolaemus* by Etheridge (1995) but Pincheira-Donoso (2005) considered it a member of *Phrynosaura* Werner 1909. The holotype is considered lost. However, the holotype was part of a series of eight specimens from the same locality and the remaining seven were considered to belong to *C. schmidti* by Núñez and Yáñez.

Laurent (1995) described *Liolaemus islugensis erguetae* based on series of specimens from Laguna Colorada and the nearby Salar de Chalviri (Fig. 15) in the Reserva Nacional de Fauna Andina Eduardo Avaroa in the Sud Lípez Province, Potosí Department, Bolivia. Laurent considered these lizards similar to both *L. islugensis* and *L. multicolor* but ultimately decided to describe them as a subspecies of the former. However, he considered all of these to be quite close to *L. andinus* and ventured that they all might form a single widespread polymorphic species along with *L. fabiani, L. poecilochromus*, and *L. schmidti.* Pincheira-Donoso and Núñez (2002) recommended elevating *L. erguetae* to a full species and formally recognized it as such in their 2005 monograph.

Valladares *et al.* (2002) described *Liolaemus molinai* from a series of specimens (Fig. 16) collected at Farellones de Tara in the eastern part of the Anto-

Figure 15. Lizards recognized as topotypic *Liolaemus erguetae* in life from Sol de Mañana (A), Laguna Colorada (B and C), Potosí Department, Bolivia; specimens not collected.

fagasta Region, approximately 95 km SE of Laguna Colorada, the type locality of *L. erguetae.* However, Valladares *et al.* (2002) did not examine any material corresponding to *L. erguetae* but did include material identified as *L. islugensis* from Enquelga, Chile (lizards now recognized as *L. schmidti*). In fact, they

Figure 16. Specimens SDSU 4012–13, paratypes of *Liolaemus molinai*, courtesy of R. Etheridge.

made no mention of either *L. islugensis erguetae* or *L. erguetae* in their paper, an error analogous to the failure of Ortiz and Marquet (1987) to consider *L. schmidti* when they described *L. islugensis*. Continuing with examples of this type of error, Laurent (1995) did not include any discussion of *L. erroneus* in his description of *L. erguetae*, despite the general similarity of the holotype to specimens of *L. erguetae* and the fact that the description of *L. erroneus* suggests that the holotype possibly could have been collected from Laguna Colorada, Bolivia, the type locality of *L. erguetae.* The failure to examine the holotype of *L. erguetae* was a serious flaw in the description of *L. molinai* and it is quite likely that if the authors had been familiar with *L. erguetae*, they would have simply published the first record of that species for Chile rather than have described a new species. To their credit, Valladares *et al.* (2002) did correctly assign the lizards from Cariquima to *L. schmidti* and noted that MNHNCL specimens from Farellones de Tara cataloged as *L. schmidti* were in fact juveniles of what they described as *L. molinai.* Examination of material of *L. erguetae* and *L. molinai* reveals no meaningful morphometric or meristic differences between these lizards. Furthermore, there are no ecological or geographic barriers separating their known ranges in Bolivia and Chile. While the above indicates the synonymy of *L. molinai* under *L. erguetae,* as suggested by Troncoso-Palacios (2014) and Demangel Miranda (2016), this conclusion must be considered in light of the available information regarding *L. erroneus*, the earliest available name for this triad of species from eastern Antofagasta and southwestern Potosí.

Part of the enigma of *Liolaemus erroneus* is its stated type locality of "Antofagasta, Depto. Atacama". First, there are no "departments" in Chile and, second, Antofagasta and Atacama are mutually exclusive administrative regions. To add to the confusion, the Salar de Atacama is located entirely in the Antofagasta Region, not the Atacama Region. However, examination of the literature (e.g., Abdala and Quinteros 2008; Abdala *et al.*, 2008; Abdala *et. al.*, 2013) reveals that there is another *Liolaemus* specimen with the locality of "Antofagasta: Atacama": FML 1192, a specimen ever-so-coincidentally catalogued as *L. schmidti*. The general morphology of this specimen, a squat, darkened male with lighter colored feet and tail, also corresponds remarkably closely to that of the *L. erroneus* holotype.

The FML 1192 catalogue card information indicates the locality of "Antofagasta – Dep. Atacama – CHILE", that it was collected by Luis Peña in January 1962, and that it was obtained by FML through exchange with the Universidad de Concepción. These three facts indicate that FML 1192 was collected by Peña at the same date and place as the holotype of *Liolaemus erroneus* and that it was later obtained and identified by Donoso-Barros as *Ctenoblepharis schmidti* and cataloged as such at FML. Núñez and Yáñez (1984 "1983–1984") noted that the *L. erroneus* holotype bore tag number 002063 from the Universidad de Concepción; FML 1192 bears a tag reading 002065. Thus, although the *L. erroneus* holotype is considered lost, it is clear that we have a topotype that is remarkably similar to the holotype which was long confused with *L. schmidti.* Therefore, I designate this adult male topotype, FML 1192 (Fig. 17), as the neotype for *Liolaemus erroneus* (Núñez and Yáñez (1984 "1983–1984"). The other FML *L. schmidti* specimen (FML 1197; Fig, 17) from the collections of Donoso-Barros is a female from Tatio, Chile, that is inseparable from typical Bolivian *L. erguetae*. My examination of the types of *L. erroneus, L. erguetae* and *L. molinai* leads to the conclusion that they all represent a single species.

While the present paper was being prepared, M. Ruiz de Gamboa, C. Correa and J.C. Ortiz presented a paper at the VIII Congreso Chileno de Herpetología and published its abstract in an electronic *Libro de Resúmenes*[9] in which they report the discovery of a population of lizards in the Altiplano of Antofagasta that correspond with *L. erroneus* and that these are conspecific with *L. molinai* are conspecific and distinct from *L. schmidti* based on molecular data. This provides an independent line of evidence that supports the arguments I present in this present paper. Furthermore, they discuss the importance of considering intraspecific variations and relationships among species when defining a new species, noting that in the population corresponding to *L. erroneus* only a single individual was found with undifferentiated parietals and supraoculars as described by Núñez and Yáñez (1984 "1983–1984").

Given that *Liolaemus erroneus* is a validly published species with a holotype, a description, and a type locality, it should be recognized as the

[9] Ruiz de Gamboa, M. Correa, C. and Ortiz, J.C. 2017. Nuevos antecedentes sobre especies de *Liolaemus* (Wiegmann, 1834) poco conocidas del norte de Chile. *Libro de Resúmenes.* VII Congreso Chileno de Herpetología. Universidad de Concepción. Concepción, Chile. 22 – 25 de noviembre 2017.

Figure 17. FML specimens originally cataloged as *Ctenoblepharis schmidti*. A. Neotype of *Liolaemus erroneus* (FML 1192); B. Female *L. erroneus* (FML 1197) from Tatio. Photographs courtesy of C. Abdala.

first available name for population of rather unique lizards from the high elevations of the Antofagasta Region of Chile and adjacent southwestern Potosí Department of Bolivia, as well as the Lagunas de Vilama Ramsar Site in Jujuy, Argentina (Sistema de Información de Biodiversidad, n.d.)[10] which have been mistaken for *L. schmidti* by more than one experienced herpetologist and described as *L. islugensis erguetae* 1995 and *L. molinai* Valladares *et al.* 2002. There are no grounds to recognize *L. erroneus* as a

[10] While the web site misidentifies the lizard as *Liolaemus alticolor*, the photographs provided are unequivocally of an *L. erroneus* in life. Also found in the same area, and partially sympatric with *L. erroneus* in parts of Bolivia and Chile, is *L. puritamensis*.

nomen oblitum as it has been repeated mentioned in the literature since its description.

As evidenced by the cases of *Liolaemus schmidti* and *L. erroneus*, the failure of authors to consider all relevant available names and to examine type material of geographically and morphologically proximate species when describing new taxa is unfortunately common practice in *Liolaemus* taxonomic works. Here, we have five interrelated examples of this error: 1) Marx (1960) apparently was unfamiliar with the type species of the genus *Ctenoblepharys* when he named the specimens collected by Sanborn from east of Estación San Pedro; 2) while presumably having seen the photograph in its original description, Donoso-Barros (1966) did not have the opportunity to directly examine the *L. schmidti* types before selecting a specimen to serve as model for a representative illustration of the species; 3) Ortiz and Marquet (1987) did not consider *L. schmidti* in their description of *L. islugensis*; 4) Laurent (1995) did not consider *L. erroneus* (and may not have examined type material of *L. islugensis*) when he described *L. islugensis erguetae*; and 5) Valladares *et al.* (2002) did not consider *L. erguetae* in their description of *L. molinai*. The result of this particular case was the creation of unnecessary, redundant names and six decades of taxonomic confusion which is resolved here by the placement of *L. islugensis* Ortiz and Marquet 1987 in the synonymy of *L. schmidti* (Marx 1960) and the placement of *L. erguetae* Laurent 1995 and *L. molinai* Valladares *et al.* 2002 in the synonymy of *L. erroneus* (Núñez and Yáñez 1984 "1983-1984").

Now that the status of *Liolaemus islugensis* and names associated with the confusing *L. islugensis erguetae*, we shall now return to the clarification of *L. pantherinus*, which requires consideration of lizards from Bolivia identified by Boulenger as *L. annectens*.

Boulenger's Bolivian *Liolaemus annectens*

Examination of bottles of lizards collected by P. O. Simons in the BMNH shelves reveals that, after describing *Liolaemus annectens* in 1901 from Peruvian material, in 1902 Boulenger cataloged numerous other lizards collected by Simons as *L. annectens* but these were from Bolivia. Localities for Boulenger`s Bolivian *L. annectens* include Livichuco (BMNH 1902.5.29.50), Poopó (BMNH 1902.5.29.46–49), Potosí (AMNH 80076, BMNH 1902.5.29.36–45, MCZ 8062), Sucre (AMNH 5241), and Uyuni (BMNH 1902.5.29.50–58). Beyond the description of *L. annectens orientalis* from the Upper Pilcomayo basin of Bolivia by Müller (1924), the only other mention of Bolivian specimens of *L. annectens* in print was a tangential comment by Rendahl (1937:15) regarding a note from BMNH Curator H.W. Parker about BMNH lizards from the "Lake Popo" region that "were referred by Boulenger to his *L. annectens*".

Boulenger (1885) considered *Liolaemus signifer* and *L. multiformis* to be distinct and he continued to consider both species valid and distinct when he described *L. annectens* in 1901, as well as in 1902 when he described *L. tropidonotus* and catalogued the Bolivian lizards collected by P.O. Simons. For example, Boulenger determined lizards from Oruro as *L. multiformis* (BMNH 1902.5.29.30–34), lizards from Uyuni as *L. annectens* (BMNH 1902.5.29.50–58) and others from Uyuni as *L. signifer* (BMNH 1902.5.29.63–73). Boulenger considered *L. annectens* to have larger and fewer dorsal scales and scales around midbody than either *L. multiformis* or *L. signifer*. Despite their geographic proximity, the lizards from Oruro identified by Boulenger as *L. multiformis* are clearly distinct from those he identified as *L. annectens* from the town of Poopó, based on their smaller, more numerous, and subimbricate dorsal scales (77–87 DSOT, N=5) and the presence of more complex and brightly colored patterns in the males (for example, Fig. 18), corresponding to *L. lenzi*. The lizards from Poopó have a more robust build, more subdued coloration, and larger, fewer, imbricate, and keeled dorsal scales (58–62 DSOT, N=3). The town of Poopó is located east of the eponymous lake, along the western foothills of the Cordillera Central, while Oruro is in the plain of the Altiplano proper just north of the lake complex. Based on DSOT, the BMNH *L. annectens* specimens from Livichuco, Poopó, Potosí, and Uyuni (49-62 DSOT) can be readily distinguished from the populations of lizards recognized in this paper as *L. multiformis* and *L. lenzi* (62–110 DSOT, collectively). While there is some overlap with some *L. mutltiformis*, there are other morphological differences that allow the separation of these species, including juvenile and adult coloration, scale morphology, and the more robust build of the Bolivian "*L. annectens*".

During my first visit to London in 2011, I immediately considered the adult specimens identified by Boulenger in 1902 as *Liolaemus annectens*[11]

Figure 18. Male *Liolaemus lenzi* in life, Chiu, near Lago Poopó, Oruro Department, Bolivia. Photo courtesy of Sol Aguilar and Omar Rocha, specimen not collected.

from Potosí and Uyuni (Fig. 19) to correspond to *L. orientalis,* in agreement with Laurent (1993 "1991") who had included Simons' specimens from Potosí (AMNH 80076) and Sucre (AMNH 5251) amongst the material belonging to *L. o. orientalis*. During my second visit in December 2013, I examined the juveniles from Potosí and Uyuni (Fig. 20) and they immediately reminded me of the *L. pantherinus* syntypes (Fig. 8). While neither Müller (1924) nor Laurent (1993 "1991") described the juveniles of *L. orientalis*, Franzen and Glaw (2007) listed four paratypes, of which three are large adults and one, ZSM 0026-1924-2 (Fig. 20), is a juvenile measuring 54 mm SVL. This juvenile paratype of *L. orientalis* clearly agrees with *L. pantherinus* syntype MNHN-RA-1905.343 (44 mm SVL, 51 DSOT) and the BMNH juvenile "*L. annectens*" from Potosí and Uyuni, bearing the typical dorsal and ventral pigmentation and possessing large, keeled, imbricate dorsal scales (49 DSOT).

Comparison of the juvenile specimens identified by Boulenger as *Liolaemus annectens* from Potosí and Uyuni, the juvenile paratype of *L. annectens orientalis*, and the *L. pantherinus* syntypes permits the identification of a morphologically and geographically cohesive population of lizards from the Cordillera Central and Oriental of Bolivia that can readily be distinguished from juveniles belonging to either *L. multiformis, L. lenzi*, or *L. forsteri*, as well as most other species of the *L. montanus* group from Bolivia. Based on the absence of any significant morphological differences between Boulenger's Bolivian *L. annectens* from Potosí and Uyuni, the *L. pantherinus* syntypes, and *L. orientalis*, as well as the biogeographically contiguous distribution of the populations in question, we can safely place *L. annectens orientalis* Müller 1924 in the synonymy of *L. pantherinus* Pellegrin 1909. This is a far more parsimonious and well-supported hypothesis than the unnecessary and contrived assumption that the syntypes of *L. pantherinus* are aberrant juveniles of *L. lenzi* or *L. multiformis* from the Titicaca Basin or northern Altiplano. This finding, however, is not entirely new- The similarity between the holotype of *Liolaemus annectens orientalis* and *L. pantherinus* was also apparent to Etheridge who observed that it "is definitely a member of the *multiformis* group but the scale counts are too low for *multiformis* itself – closer to *pantherinus*" after examining the respective types during his 1967 tour of European museums (Etheridge, *in litt.*).

[11] While the jar labels retain the original determinations as *L. annectens* (which is good practice), the online catalog lists these specimens as *L. multiformis.* A best practice would be to also include the original determinations in online catalogs. A Natural History Museum Data Portal (http://data.nhm.ac.uk) search for "*Liolaemus annectens* Bolivia" finds no records while a search for "*Liolaemus multiformis* Bolivia" returns 24 records.

Correction of the Type Locality of *Liolaemus pantherinus*

Pellegrin (1909:324) stated broadly that the lizards described in his paper were captured in the Lake Titicaca region of the Altiplano (i.e., high plateaus of the Andes) of Peru and of Bolivia, at an altitude of around 4,000 meters, which may explain why Pincheira-Donoso and Núñez (2002) and Ruiz de Gamboa and Ortiz (2020) believed that the *Liolaemus pantherinus* types were from the vicinity of

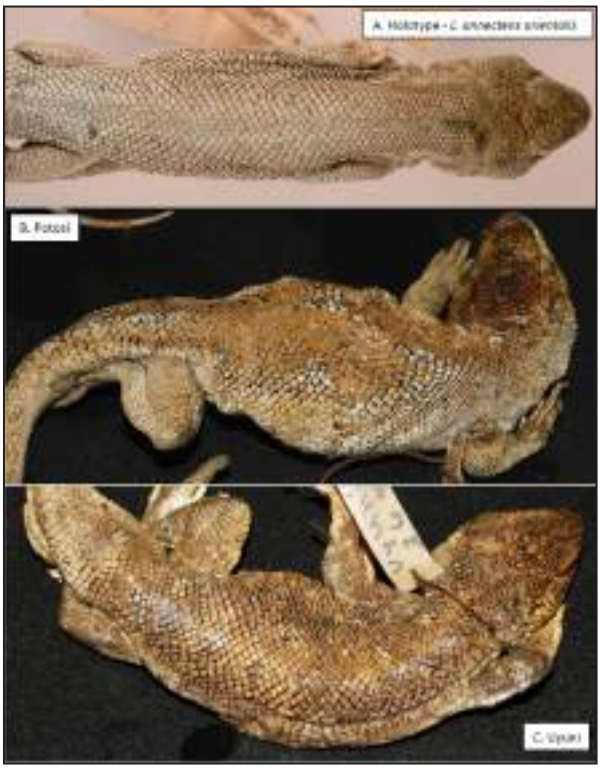

Figure 19. Adult specimens: A. *Liolaemus annectens orientalis*, Holotype ZMB 26405, adult male; B. Adult male "*L. annectens*", Potosí, Bolivia, series BMNH 1902.5.29.36-45, without specific number; C. Adult male "*L. annectens*", Uyuni, Bolivia, series BMNH 1902.5.29.51-58, without specific number.

Lake Titicaca. Regarding the *L. pantherinus* syntypes specifically, Pellegrin (1909:325) provided the following information: "Hauts-Plateaux péruviens et boliviens: Créqui et Sénéchal (récoltés par le Dr Neveu-Lemaire)", information which has led to considerable confusion regarding the type locality and geographic distribution of *L. pantherinus*.

The first confusion is that *Liolaemus pantherinus* might have been collected in Peru. The published itineraries of Dr. Neveu-Lemaire's expedition (e.g., Créqui Montfort and Sénéchal de la Grande, 1904:95–96; Neveu-Lemaire, 1904) do not indicate that he or his team ever entered Peru; thus, there is no evidence to support an assumption that the *L. pantherinus* syntypes were collected in Peru. The second confusion regards the words "Créqui et Sénéchal". Donoso-Barros (1970) stated the type locality of *L. pantherinus* as "Crequi and Sénéchal" and gave the distribution of the species as "Altiplano of Peru, Bolivia, and Chile." Fugler (1989) and Dirksen and De la Riva (1999) similarly stated the type locality of *L. pantherinus* as "Crequi" in the Oruro Department of Bolivia. However, "Créqui et Sénéchal" are not place names; they are the surnames of the directors of the 1903 French expedition: Georges de Créqui-Montfort and Eugène Sénéchal de la Grange. Nevertheless, there is an island in Lake Poopó in the Oruro Department named "Isla Crequi Monfort" but there is no evidence that this island bore this name in 1909 and it was certainly not mentioned by Pellegrin. Furthermore, all *L. montanus* group lizards from Lago Poopó correspond to *L. lenzi*. Thus, the only clear information provided by Pellegrin is that the lizards were collected by Dr. Neveu-Lemaire.

The itineraries of Dr. Neveu-Lemaire indicate that much of his time in Bolivia was spent far from Lake Titicaca and, moreover, beyond the limits of the Altiplano itself. Neveu-Lemaire started his Andean journey at Antofagasta, Chile, on 11 May 1903, traveled by rail to the town of Uyuni, Bolivia, and arrived at Pulacayo, a mining town in the mountains some 15 km east of Uyuni on 20 May 1903 (Neveu-Lemaire, 1904). Neveu-Lemaire and his team spent several weeks in and around Pulacayo in at different times in May, June, and August of 1903, conducting physiological studies on human adaptations to high altitudes but also engaging in zoological collecting expeditions (Neveu-Lemaire, 1904). Menegaux (1909) reported on the birds collected by Neveu-Lemaire from Pulacayo and its environs and Neveu-Lemaire and Grandidier (1911) reported on the mammals. Less than two years before Neveu-Lemaire's work in Pulacayo, P. O. Simons collected mammals, birds, and other fauna around nearby Uyuni in November of 1901 (Chubb, 1919), including the lizards that Boulenger cataloged as *Liolaemus annectens* which I have assigned to *L. pantherinus*. However, despite the large numbers of tourists and biologists passing through Uyuni, no lizards similar to *L. pantherinus* have been reported from the plains around the town of Uyuni itself where *L. puna, L. schmidti* and *L. ornatus* abound or from the Sud Lípez region to the south, where *L. chlorostictus, L. erroneus, L. ornatus, L. pachecoi, L. puna*, *L. puritamensis*, and *L. schmidti* have been collected. However, residents interviewed in Uyuni informed me in October 2017 that larger, robust lizards are found on the nearby hills just to east towards Pulacayo and these particular lizards are collected for sale as medicinal uses in the local markets.

I visited the environs of Pulacayo and Uyuni a second time in May 2018 to search for lizards corresponding to *Liolaemus pantherinus*. Again, interviews with residents indicated that there is a

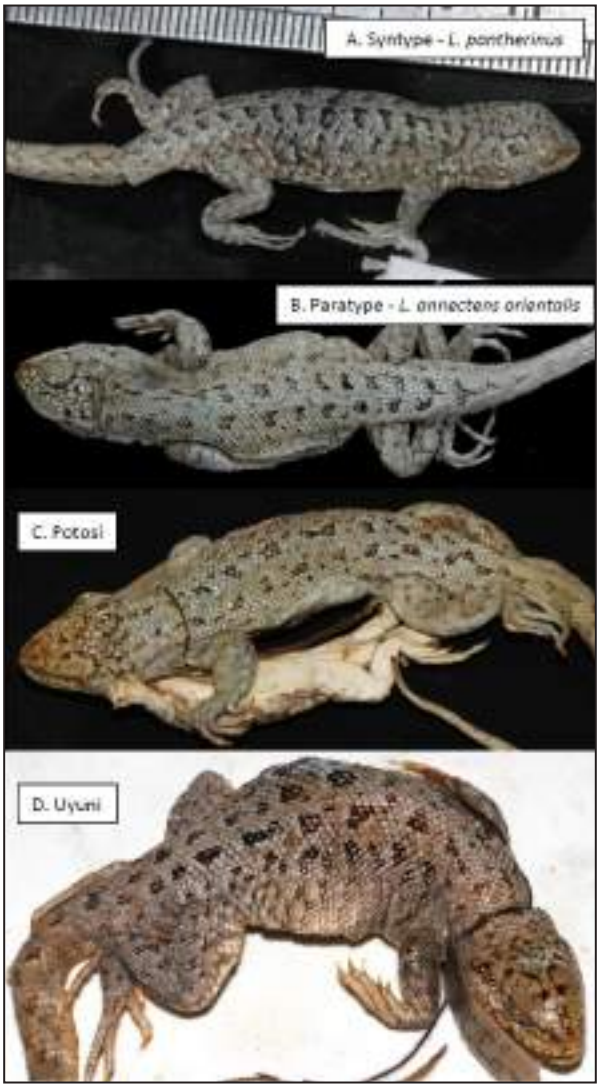

Figure 20. Juvenile specimens: A. *Liolaemus pantherinus*, Syntype MNHN RA 1905.343; B. Juvenile *L. annectens orientalis*, Paratype ZSM 26/1924/2; C. Juvenile "*L. annectens*", Potosí, Bolivia, from series BMNH 1902.5.29.36-45, without specific number (smaller specimen attached is *L. simonsii*); D. Juvenile "*L. annectens*", Uyuni, Bolivia, series BMNH 1902.5.29.51-58, without specific number.

larger species of lizard that is found on the higher hills during the warmer months of the year, generally from November to March or April. We searched the northeastern slopes of Cerro Escara, a 4150-m peak just south of the first summit along the road from Uyuni to Pulacayo, and found a large number of very recently overturned rocks, exactly what one would find in a site where there had been a search for lizards. Furthermore, when we arrived, we encountered a taxi full of people that appeared to be leaving this site and who watched us with great interest as we ascended. While habitats on the hills and ranges east of Uyuni and around Pulacayo are typical of the *L. multiformis* group – shrub-bunch grass steppe with many rocks. the only species we encountered that afternoon was *L. ornatus*[12], which is abundant in the region and not used for medicinal purposes.

In late October 2018, I examined specimens at CBF collected by A. Aguilar-Kirigin, C. Abdala, and associates in March 2017 from the same part of Cerro Escara I searched 2018; these specimens correspond to an adult male (KIRI 552, 50 DSOT) and juvenile (KIRI 553, 56 DSOT) *Liolaemus pantherinus* (Fig. 21). I returned to Pulacayo on 6 November 2018 and found a juvenile lizard (Fig. 22), remarkably similar to the *L. pantherinus* syntypes (Fig. 8), with 52 DSOT, under a rock in somewhat disturbed area of scrubby Puna steppe (Fig. 22) adjacent to the General Cemetery above the town at an altitude of 4209 masl. Thus, the presence of *L. pantherinus* at Pulacayo, the temporary base of Dr. Neveu-Lemaire who collected the type specimens in 1903, and the hills between it and Uyuni, where specimens were collected by P. O. Simons in 1901, is confirmed here by physical and photographic evidence and the type locality of *L. pantherinus* Pellegrin 1909 can now be corrected to "the environs of Pulacayo, Potosí Department, Bolivia, approximately 4200 masl". This is considered to be a correction, not a restriction, as the locality is not on the "high plateaus" or Altiplano, but rather in the western ranges of the Cordillera Central.

Correction of the Type Locality of *Liolaemus annectens orientalis*

Müller (1924) reported the type of locality of *Liolaemus annectens orientalis* as "Oberer Pilcomayo, zwischen Tarija und S. Francisco, Bolivien" and the collector is noted as "Herrmann", which refers to Wilhelm Herrmann, Director of the German Pilcomayo Expedition of 1906–07. At that time, "San Francisco" referred to a mission on the Pilcomayo at the location of the present-day city of Villamontes at the interface of the easternmost Andean foothills

[12] Reviewing Pellegrin (1909), I noticed that some syntypes of both *L. pulcher* and *L. mocquardi* (currently recognized as junior synonyms of *L. ornatus* s.l.) were also collected by Dr. Neveu-Lemaire, with the same vague locality information as the *L. pantherinus* syntypes, in addition to other syntypes said to have been collected by Mr. Courty at Tiahuanaco. Thus, it is quite possible that Dr. Neveu-Lemaire's team may have collected specimens described as *L. pulcher* and *L. mocquardi* from the same areas where they collected the *L. pantherinus* syntypes.

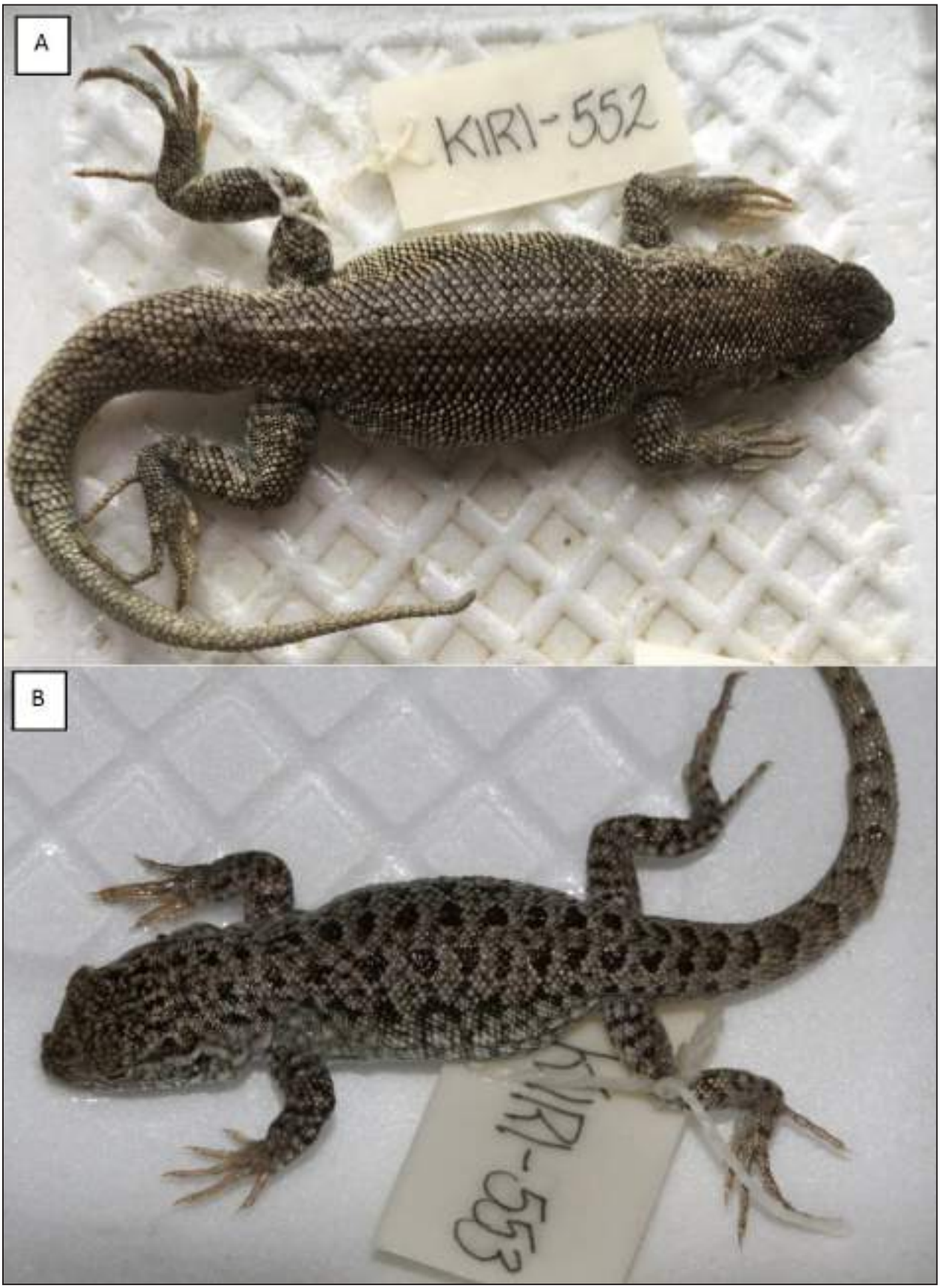

Figure 21. *Liolaemus pantherinus* specimens from Cerro Escara between Uyuni and Pulacayo, Potosí, Bolivia. A. KIRI-552. B. KIRI-553.

Figure 22. Topotypic *Liolaemus pantherinus* in life and habitat adjacent to the Pulacayo General Cemetery, 4209 m a.s.l., 6 November 2018. Specimen not collected.

and the plains of the Gran Chaco (Herrmann, 1906). Herrmann's (1908) hand-drawn map of the route of the Expedition includes neither "S. Francisco" nor "San Francisco" but does include "Villa Montes". In the eastern Bolivian Andes of the Río Grande and Pilcomayo drainages, *Tropidurus* range to approximately 2,800 m (Carvalho *et al.*, 2018) and seem to exclude *Liolaemus* from lower elevations in the mountains (but these genera can be syntopic in the Gran Chaco lowlands). Between the city of Tarija and Villamontes there are no mountain ranges high enough to support puna species of *Liolaemus*, such as *L. pantherinus*. The only documented localities for *L. pantherinus* in the Department of Tarija are in the Cordillera de Sama, to the west of the city of Tarija and almost all above 3,900 m a.s.l (Jiménez Robles and De la Riva, 2019). In the same publication, Müller (1924) gave precisely the same locality given for *L. annectens orientalis* for both *Tropidurus praeornatus* and *T. pictus*, synonyms of *T. melanopleurus* Boulenger 1902, a species of nearly vertical rock-face in habitats subtropical forest of the eastern Andean foothills, for example in road cuts in the gorge of the Pilcomayo river west of present-day Villamontes along the road to Tarija. It is highly unlikely that any *Liolaemus* of the *L. montanus* group would be found in the subtropical forested Subandean ranges inhabited by *T. melanopleurus.* Thus, it appears that the type locality of *T. praeornatus* and *T. pictus* was perhaps transcribed in error by Müller in his description of *L. annectens orientalis*.

Although Müller (1924) explicitly designated a holotype and did not mention paratypes or describe variations in the original description, Laurent (1993 "1991") referred to three "cotipos" for *Liolaemus orientalis orientalis*: an unnumbered male from ZMB and two males from ZSM ("ZSM 26-1924"). Given that Müller (1924) clearly designated the extant ZMB 26405 as holotype, Laurent's designation of syntypes has no bearing. Franzen and Glaw's (2007) catalog of ZSM reptile types included four *L. annectens orientalis* paratypes — ZSM 26/1924/1–2 (i.e., two of Laurent's "cotipos") and ZSM 281/1989/1–2—with the less restrictive locality of "oberer Plicomayo [*sic*], Bolivien", which could be anywhere along Herrmann's route to the city of Potosí in the upper Pilcomayo basin of Bolivia. Herrmann's itinerary indeed included high Andean puna regions of the upper Pilcomayo basin between Tarija and the city of Potosí in the departments of Chuquisaca and Potosí (Herrmann, 1908), areas now known to be inhabited by *L. pantherinus*.

Based on the unlikely presence of species of the *L. montanus* group in the low subtropical ranges between the city of Tarija and the former mission of San Francisco near the actual Villamontes, the presence of *L. pantherinus* along much of the route of Herrmann's expedition towards Potosí and the Altiplano, and the assumption that the lowest known elevation for *L. pantherinus* is not less than approximately 2,800 m a.s.l near Sucre (below which we find *Tropidurus azurduyae* Carvalho, Rivas, Céspedes & Rodrigues 2018), I here correct the type locality of *L. annectens orientalis* to "eastern Andes of the Upper Pilcomayo Basin of Bolivia, above 2,800 m a.s.l".

The Enigma of *Liolaemus multiformis simonsii*

Burt and Burt (1931) created the combination *Liolaemus multiformis simonsii* in their catalogue of the South American lizards at AMNH for lizards from the "Andes of southwestern Bolivia" with "dorsal scales more or less strongly keeled; keels often forming

continuous longitudinal lines; dorsal scales usually only a little smaller than ventrals; general ground color lighter", including *L. simonsii* and *L. annectens orientalis* in its synonymy.

The enigma of this combination is that while *Liolaemus simonsii* Boulenger 1902 is generally considered a junior synonym of *L. ornatus* following Laurent (1992), Burt and Burt (1931) considered a series of *L. simonsii* syntypes obtained by AMNH to be conspecific with a lizard from Sucre (AMNH 5351) they found to agree with Müller's description of *L. annectens orientalis*, a specimen later assigned to *L. orientalis orientalis* by Laurent (1993 "1991"). Furthermore, they considered this group of lizards to be a subspecies of *L. multiformis.* While inclusion of *L. ornatus* and *L. pantherinus* in a single taxon would certainly make the combination *L. multiformis simonsii* a most unusual and unwarranted taxonomic decision, examination of the specimens assigned to *L. multiformis simonsii* by Burt and Burt reveals the soundness of their combination based on the information available to them circa 1931.

Even though most BMNH *Liolaemus simonsii* syntypes I examined in London present patches of enlarged spinose scales on the underside of the inner thigh, Boulenger's (1902) description states "hinder side of thighs uniformly granular". Without having seen the BMNH type series, Burt and Burt (1931) would have had no way to know, or even any reason to suspect, that Boulenger's description was incorrect, as the first mention of this discrepancy did not appear in print until Hellmich (1962). The specimens referred to *L. multiformis simonsii* by Burt and Burt (1931) comprise one specimen (AMNH 13494; Fig. 23) from Uyuni, four specimens (AMNH 13495–98; Fig. 23) from Potosí, and one specimen (AMNH 5251; Fig. 23) from Sucre, all collected by P.O. Simons for BMNH and obtained by AMNH via purchase from W.F.H. Rosenberg. The specimens from Uyuni and Potosí (two of the three localities of the *L. simonsii* types as described by Boulenger) were presumably obtained by AMNH as syntypes of *L. simonsii,* as evidenced by the label on the jar housing these specimens. However, none of these specimens, despite being adults or subadults, show any trace of patches of enlarged spinose scales on the underside of the thigh, nor do they possess lepidosis or pigmentation typical of *L. ornatus*. The Potosí specimens have 46–55 DSOT, the Uyuni specimen has 59 DSOT, and the Sucre specimen has 49 DSOT, with a collective range of 46–59 DSOT (mean= 50.7), encompassing the range of 51–58 DSOT in the *L. pantherinus* syntypes. For comparison, Etheridge (1993) counted 60–83 DSOT (mean= 70.8 in males, 71.4 in females) in his sample of 50 *L. ornatus* from Jujuy and Salta. Based on my examination of the material, I here refer all AMNH specimens referred to *L. multiformis simonsii* by Burt and Burt (1931) to *L. pantherinus.*

Burt and Burt (1931) never had the benefit of examining type material of *Liolaemus signifer* and *L. annectens*; in fact, the only specimen listed as *L. signifer* in their 1931 AMNH catalogue was a certainly misidentified specimen from the Chubut Province of southern Argentina. Their conclusion that the specimen from Sucre and the holotype of *L. annectens orientalis* "are not separable based on scutellation or proportional features" was correct, as later confirmed by Laurent (1993 "1991"). While

Figure 23. Representative *Liolaemus pantherinus* specimens referred to *L. multiformis simonsii* by Burt and Burt (1931): A. AMNH 13494 from Uyuni; B. AMNH 13498 from Potosí; C. AMHN 5251 from Sucre.

Burt and Burt (1931) did not mention having examined the *L. multiformis* type series, they included as *L. m. multiformis* AMNH specimens from Juliaca and Puno, Peru, which certainly correspond to this species. As noted above, the *L. multiformis* type series includes some specimens with larger, fewer, and more strongly keeled dorsal scales that make the inclusion of the AMNH *L. pantherinus* specimens as a subspecies of *L. multiformis* with fewer and larger dorsals a not unreasonable decision. Their concept of *Liolaemus multiformis simonsii* and their decision to include *Liolaemus annectens orientalis* as a junior synonym of *L. m. simonsii* are entirely reasonable when the relevant material and available literature are examined. They were also quite correct in the decision to separate the lizards of southwestern Bolivia from those of the Lake Titicaca region. We can now include the combination *Liolaemus multiformis simonsii* Burt & Burt 1931 as a junior synonym of *Liolaemus pantherinus* Pellegrin 1909.

Examination of other supposed *Liolaemus simonsii* syntypes distributed by W.F.H. Rosenberg to American museums reveals that the AMNH situation is not unique; the MCZ also obtained such specimens. Specimen MCZ R-8056 was collected by P.O. Simons at Uyuni, purchased by MCZ from Rosenberg in 1911, and cataloged as a syntype of *L. simonsii*, sharing a jar with much smaller specimen cataloged as a juvenile *L. simonsii* syntype from Challapata (MCZ R-189412), the third locality of the syntypes described by Boulenger. While the Challapata specimen clearly possesses a femoral patch and pigmentation patterns broadly agreeing with the concept of *L. ornatus* and thus can be considered a syntype of *L. simonsii,* MCZ R-8056 from Uyuni in fact corresponds to *L. pantherinus.* Specimen MCZ R-8062 from Potosí, part of the accession from Rosenberg, is cataloged as *L. annectens* and is identified here as *L. pantherinus*. Specimens MCZ R-14351 from Uyuni, received by exchange with BMNH in 1921, corresponds to *L. simonsii*.

The case of *Liolaemus multiformis simonsii* represents yet another artefact of a series of errors, starting with Boulenger's flawed description of *L. simonsii*, followed by the mislabeling or misidentification of the specimens sent to AMNH by Rosenberg, and finally the Burts' erroneous assumption that the available information was correct.

Diagnosis of *Liolaemus pantherinus*

Liolaemus pantherinus Pellegrin 1909 can be distinguished from all other species of the *L. montanus* group found north of the Tropic of Capricorn by the following combination of characters: 1) adults with robust body and reaching SVL of greater than 95 mm (maximum adult SVL less than 90 mm in *L. audituvelatus, L. chiribaya, L. erroneus, L. evaristoi, L. fittkaui, L. hajeki, L. insolitus, L. manueli, L. multicolor, L. nazca, L. poconchilensis, L. pulcherrimus, L. stolzmanni, L. schmidti, L. torresi,* and *L. victormoralesii*); 2) absence of contrasting blue, cyan, green, yellow, orange, or red scales on the flanks or dorsum of adult males (present in *L. annectens, L. chiribaya, L. erroneus, L. etheridgei, L. evaristoi, L. fittkaui, L. forsteri, L. lenzi, L. multicolor, L. multiformis, L. nazca, L. poconchilensis, L. pulcherrimus, L. schmidti*)[13]; 3) absence of light dorsolateral lines or stripes in juveniles or adults (often present in *L. fittkaui, , L. multicolor, L. multiformis, L. pulcherrimus, L. schmidti*); 4) DSOT fewer than 70 (typically greater than 70 in *L. erroneus, L. fabiani, L. forsteri, L. lenzi, L. multicolor, L. multiformis, L. pleopholis, L. schmidti*) and greater than 40 (often fewer than 40 in *L. jamesi* and *L. pachecoi*); 5) absence of palpebral fringes (notable in *L. audituvelatus, L. insolitus, L. manueli, L. poconchilensis, L. stolzmanni, L. torresi*); and 8) geographically restricted to Cordillera Central and Cordillera Oriental of Bolivia (Oruro, Potosí, Chuquisaca, and Tarija departments) and eastern Jujuy Province of Argentina (all Peruvian endemics including *L. annectens, L. chiribaya, L. etheridgei, L. melanogaster, L. nazca, L. ortizi, L. polystictus, L. robustus, L. thomasi, L. victormoralesii* and *L. williamsi,* are separated by the northern Altiplano, the Cordillera Real, and the ranges of *L. lenzi*).

DSOT counts of 44 specimens (41 from Bolivia and 3 from Argentina) here assigned to *L. pantherinus,* yield a range of 45–67 and mean of 54.7, including the MNHN syntypes (DSOT of 51 and 58), all examined BMNH *L. annectens* from Bolivia, the *L. annectens orientalis* type series, and others from collections and field photographs. As noted above, Laurent's (1993 "1991") sample of 50 *L. orientalis orientalis* (11 from Bolivia and 39 from Argentina) yielded a range of 48–68 DSOT, which corresponds remarkably well with the counts reported here.

[13] These brightly colored scales are in contrast to the ground or base color of the dorsum and flanks, which some *L. pantherinus* may be interspersed yellowish to greenish scales among dark brown to black scales as in *L. chlorostictus* and some *L. multiformis* and *L. lenzi.*

Abdala *et al.* (2008) reported 56–70 dorsals from a sample of 21 Argentine specimens identified as *L. orientalis*; this could be an indication that Laurent's (1993 "1991") earlier suspicions regarding the conspecifity of Bolivian and Argentine populations may have been warranted. Table 2 summarizes DSOT count data from a total of 190 individuals from 14 relevant species of the *L. montanus* group (i.e., those documented from Bolivia as of December 2018: *L. chlorostictus, L. erroneus, L. fittkaui, L. forsteri, L. jamesi, L. lenzi, L. multiformis, L. pachecoi, L. puritamensis,* and *L. schmidti,* plus *L. annectens* and the *L. tropidonotus* syntypes), including *W* and p-values for comparisons of each against *L. pantherinus* and *L. multiformis*. The only Bolivian species of the *L. montanus* group that cannot be reliably separated from *L. pantherinus* based on DSOT count distributions is *L. fittkaui* (p= 0.1503).

Of the Peruvian species of the *Liolaemus montanus* group, *L. melanogaster* Laurent 1998 is morphologically most similar to *L. pantherinus* and *L. victormoralesii* considering their low DSOT counts, robust form of the adults, and dorsal pigmentation patterns. However, *L. melanogaster* possesses a distinctive ventral melanism (i.e., black pigmentation vs. darker grey in some *L. pantherinus*) in most adults and is geographically restricted to a small area of the Pacific drainage of the Ayacucho Department, very remote from the range of *L. pantherinus*. *Liolaemus melanogaster* belongs to a well-supported clade consisting of species endemic to Peru, including *L. polystictus, L. robustus*, and *L. williamsi*, but not *L. annectens* or *L. multiformis* (Aguilar *et al.*, 2017). My examination of the specimens (ZMH R10990–91) reported from southern Peru ("Puna, between Ajno and Tayapampa") by Mertens (1952) as *L. pantherinus* reveal that they in fact belong to *L. melanogaster*[14]. *Liolaemus victormoralesii* differs from *L. pantherinus* its smaller known maximum SVL (89 mm vs >100 mm in *L. pantherinus*), the absence of strongly keeled dorsal scales, the absence of vestigial cloacal pores in females and its restricted range in the Ayacucho Region of Peru.

As noted above, the only Bolivian species of the *Liolaemus montanus* that cannot be distinguished from *L. pantherinus* solely based on DSOT is *L. fittkaui* (Table 2). However, these two species are otherwise very distinctive morphologically and ecologically. While *L. pantherinus* is typically drab, large-bodied (e.g., ZMB 26405 measures 101 mm SVL, Etheridge, *in litt.*) lizard of the drier interior ranges of Oruro, Potosí, Chuquisaca, Tarija, and Jujuy, *L. fittkaui* lives in humid puna on the north slope of the Cordillera Oriental in Cochabamba (Fig. 6) and is a small-bodied species (50-65 mm SVL; Jiménez-Robles *et al.*, 2016) with distinctive male and female color patterns and strongly keeled, mucronate, lanceolate scales, suggestive of species of the *alticolor* group of the subgenus *Liolaemus*. Amongst the members of the *L. montanus* group, *L. fittkaui* is most similar morphologically to *L. ortizi*, as originally noted by Laurent (1986), which both seem to occur similar humid puna environments on the Amazonian fringes of the eastern Andes.

Other robust-bodied and large-scaled species of the *Liolaemus montanus* group from Bolivia, northern Chile, and northwestern Argentina such as *Liolaemus jamesi, L. aymararum, L. puritamensis, L. pachecoi,* and *L. scrocchii* have been assigned to a putative *L. dorbignyi* group (Díaz Gómez, 2007; Lobo *et al.*, 2010a; Abdala *et al.*, 2020). Most of these species are relatively robust and can reach SVL at least 90 mm but tend to have even larger and fewer dorsal scales than *L. pantherinus* (see Abdala *et al.*, 2008). The members of the "*L. jamesi* group" can be distinguished from *L. pantherinus* by a combination of external morphological characters such as generally less imbricate (in adults), larger, and fewer dorsals, distinctive coloration patterns, and by their mutually exclusive geographic ranges[15]. No species of the *L. jamesi* group are known to be sympatric with *L. pantherinus* but the geographically closest species are *L. pachecoi* and *L. puritamensis*, which are found to the west of the known range of *L. pantherinus.*

Despite having been originally described by Laurent (1993 "1991") as a subspecies of *Liolaemus orientalis, L. chlorostictus* is rather distinct from most *L. pantherinus* based on general morphology and coloration of the adults, particularly in males. However, the juveniles of *L. pantherinus* and *L. chlorostictus* are very similar. While the trunk scales of *L. chlorostictus* tend to be smaller and smoother than in *L. pantherinus*, the DSOT distributions shows considerable overlap—56–65 (median= 62)

[14] Tayapampa is approximately 40 km south of Puquio, Ayacucho Region.

[15] However, *L. pachecoi* and *L. puritamensis* are sympatric in some areas of the southwestern Potosí Department, Bolivia, such as around Laguna Colorada.

Table 2. Dorsal scale rows between occiput and anterior margin of thigh (DSOT) for fourteen species of the *L. montanus* group from the Bolivian Andes and adjacent regions, ordered by DSOT means. W= Wilcoxon value from unpaired two-sample tests. Data are presented in Appendix 2.

						vs. *L. pantherinus*		vs. *L. multiformis*	
Species	N	Range	Mean	Median	SD	W	p-value	W	p-value
L. pachecoi	9	31–42	38	38	2.94	396	<0.00001	162	<0.0001
L. jamesi	5	37–43	39.8	38	2.64	220	0.0003	90	0.0009
L. puritamensis	7	46–52	48.7	48	2.43	260	0.0038	126	0.0002
L. fittkaui	6	47–56	51.2	50.5	3.34	180.5	0.1505	108	0.0004
L. pantherinus	44	45–67	54.7	54	5.27	--	--	784.5	<0.00001
L. annectens	13	49–72	60.1	61	7.51	174.5	0.0343	221.5	<0.0001
L. chlorostictus	11	56–65	61.5	62	2.39	63.5	0.0002	192.5	<0.0001
L. tropidonotus	6	67–84	74.2	74	5.34	1	<0.0001	65	0.4826
L. multiformis	18	62–89	75.6	76	6.58	7.5	<0.00001	--	--
L. schmidti	22	75–91	81.8	84	4.68	0	<0.00001	295	0.1218
L. pleopholis	6	76–91	82.3	82.5	5.31	0	<0.00001	25	0.0565
L. forsteri	6	77–89	84	84	5.44	0	<0.00001	15.5	0.011
L. lenzi	26	74–110	88.8	86.5	9.88	0	<0.00001	55.5	<0.0001
L. erroneus	11	83–101	92.7	94	5.53	0	<0.00001	5	<0.0001

in *L. chlorostictus* vs. 45–67 (median= 54) in *L. pantherinus.* Also, some *L. chlorostictus* have keeled dorsals (e.g., topotype SDSU 3518), but not as strongly keeled as in some *L. orientalis.* However, double-sided Wilcoxon tests permit rejection of the null hypothesis of the equal DSOT distributions (W= 63.5, p= 0.0002) among *L. pantherinus* and *L. chlorostictus*. Adult male *L. chlorostictus* are dominated by yellow to greenish scales with varying degrees of black scales interspersed, sometimes weakly patterned (in younger individuals), quite distinct from male *L. pantherinus*. Adult female *L. chlorostictus* can be essential unicolor as many adult *L. pantherinus* but often retain distinctive dorsal blotches, and may be similar to some *L. schmidti* or *L. multiformis* at first glance, often showing reddish orange markings or reddish gravid coloration. As typical within the *L.* montanus group, juvenile *L. pantherinus* and juvenile *L. chlorostictus* are quite similar in general aspect and pigmentation. While considered a subspecies of *L. orientalis* by Pincheira-Donoso *et al.* (2008) and Etheridge and Frost (2016), I consider *L. pantherinus* and *L. chlorostictus* to clearly be separate species, in agreement with Díaz Gómez (2007), Lobo *et al.* (2010b), and Avila *et al.* (2013). Abdala *et al.* (2019) recover *L. orientalis* and *L. chlorostictus* as sister species.

Redescription of *Liolaemus pantherinus*

Liolaemus pantherinus Pellegrin 1909 is a medium to large-sized species of the *L. montanus* group, with a robust build in adults, with some individuals exceeding 100 mm SVL; tail is moderately long, 1.41–1.43 times SVL in syntypes, gradually tapering. Upper head scales smooth, convex in fronto-nasal region, with 15–17 scales from rostral to occipitals in syntypes. Rostral wider than tall, in contact with six scales, separated from nasals by a pair of postrostrals. Internasals four, but three in one syntype. Frontonasals (11–15) and prefrontals (3–4) in syntypes. Frontal divided longitudinally and transversely into four scales in most specimens (3 in one syntype). Frontoparietals four. Interparietal smaller than adjacent pair of posterior parietals, in contact with 6–7 scales, parietal eye evident. Three rows of occipitals between parietals and dorsal nuchals. Supraoculars may be rather irregular, in three rows, 4–7 transversely expanded; circumorbital semicircles imperfect. Subocular entire, in contact with five lorilabials. Single row of loribials between subocular and supralabials. Supralabials 7–8, wider than high, 5 or 6 to center of eye. Temporals smooth but may be convex. Auricular lobules not prominent, auditory meatus as large as eye, rectangular, taller than wide. Lateral neck and axillary scales juxtaposed, granular to conical, Y-shaped lateral neck folds well

developed. Dorsal scales 45–67 (mean= 54.7; 51–58 in syntypes), between occiput and anterior margin of thighs, subimbricate to imbricate, smooth or weakly to strongly keeled, rarely with weak mucron, not tuberculate or conical, may present heteronotes laterally. Scales around midbody 54–60 in syntypes. Ventral scales 88-90 from mental to cloaca in syntypes. Mental wider than high, in contact with four scales. Infralabials six. Chin shields four on each side, two scales between second pair. Gulars 21-24 in syntypes; gular fold absent. Ventrals subequal to dorsals, smooth, imbricate; Precloacal pores 4–11 well developed in males, supernumerary pores sometimes present, 0–6 vestigial to moderately developed precloacal in females (none in the syntypes). Scales of posterio-ventral surface of thighs granular. Lamellae of fourth finger 15–16 and of fourth toe 22–23 in syntypes. Tail verticillate, scales imbricate and keeled dorsally, smooth ventrally, no mucron.

Dorsum in older adult males generally uniform, drab olive to beige in preservation, pileus may be darker. Juveniles and subadults in both sexes with strong darker dorsal blotches in four rows, sometimes forming irregular transverse bands. Females retain stronger traces of juvenile pattern. The dorsal blotches found in females and juveniles are indeed not unique to *L. pantherinus* but are a characteristic of many species in the *L. montanus* group, which has led to much confusion in the past. Some populations with specked dorsal pattern formed by scales with lighter-colored posterior portion of dorsal scales. Venter spotted brownish or grey in juveniles, developing diffuse dark grey (not black) in some adults while others speckled to nearly immaculate in belly; however, gular region almost always with dark grey or brown lines or spots in individuals of all ages.

Variations in Form

Despite its relatively large geographic range, *Liolaemus pantherinus* has been rarely photographed in life compared to other Bolivian species, perhaps due to its drab coloration, perhaps due to its range in areas less frequented by tourists and biologists, and perhaps to relatively low population densities compared to other species, as suggested by Jiménez Robles and De la Riva (2017). William E. Duellman photographed an adult male (KU 160198), and adult female (KU 160201) in life (Fig. 24) from 7 km S of Potosí, 4220 m a.s.l, belonging to a series identified as *L. orientalis* by Laurent (1993 "1991").

While generally recognizable as robust, drab lizards with rather large, keeled, imbricate dorsal scales, some individuals have somewhat smaller and smoother scales or have more contrasting pigmentation patterns (at least in preservation), a degree of variability in pigmentation and pholidosis certainly typical of species of the *Liolaemus montanus* group. Laurent (1993 "1991") remarked that "the Argentine populations of *L. orientalis* at first appeared different" and that he had considered describing them as a new species. He noted that the northern (i.e., Bolivian) populations possess lower numbers of longitudinal scales and lower Hellmich indices (number of dorsal scales equivalent to length of head) than the Argentine populations, which indicates shorter and more numerous dorsals. In contrast to Burt and Burt's (1931) observation of "dorsal scales more or less strongly keeled; keels often forming continuous longitudinal lines" in *L. multiformis simonsii,* Cei (1993:244) stated that the dorsals of Argentine *L. orientalis* are "weakly keeled or smooth, broad and short, subimbricate or juxtaposed" and that the laterals are "smaller, sometimes granular and largely juxtaposed". Abdala *et al.* (2008) considered Argentine *L. orientalis* to have weak keels on dorsals (versus "absent" or "distinct"). AMNH specimens from Potosí and Sucre have rather strongly keeled dorsals, as does *L. annectens orientalis* paratype ZSM 0026-1924-1. While Laurent (1993 "1991") stated that *L. o. orientalis* can be distinguished from *L. annectens* due to "the more evident contrast between the dorsal rows (15-21 scales) and the lateral scales in *L. orientalis* while in *annectens* there is a very progressive transition between the large scales of the back and the small ones of the sides", uniformity in the size of the dorsal scales around the midbody is typical of most Bolivian *L. pantherinus*, exactly the opposite of what Cei and Laurent described based their examination of presumably largely Argentine material. Despite these differences, the Argentine lizards recognized as *L. orientalis* in the literature are tentatively included here in *L. pantherinus* but future work may well find Laurent's (1993 "1991") suspicions to be warranted.

Comment on the Phylogenetic Position of *Liolaemus pantherinus*

The lizards we recognize now as *L. pantherinus* have been variously presumed to be:

i) conspecific with *L. annectens* (Boulenger's unpublished determinations circa 1902);

ii) a subspecies of *L. annectens* (Mülller, 1924); a

Figure 24. *Liolaemus pantherinus* in life, 7 km south of Potosí, 4220 masl. A. Male, KU 160198. KUDA 9518; B. Female, KU 160201, KUDA 9519. © William E. Duellman/University of Kansas.

subspecies of *L. multiformis* (Burt & Burt 1931);
iii) closely allied to *L. multiformis* (Cei *et al.* 1980);
iv) close to *L. signifer* (Laurent 1992; Cei 1993);
v) a sister taxon to *L. chlorostictus* (Laurent, 1993 "1991"); and
vi) a member of the *L. dorbignyi* group (Díaz Gómez, 2007; Lobo *et al.,* 2010a).

Prior to Aguilar-Puntriano *et al.,* (2018), all molecular phylogenetic estimates that included *Liolaemus orientalis* (e.g., Schulte *et al.*, 2000; Valladares *et al.*, 2002; Harmon *et al.*, 2003; Espinoza *et al.*, 2004) were based on genetic material from the same specimen, SDSU 3517, which is fact belongs to *L. chlorostictus*. All of these prior studies recovered this specimen as the basal member of the *L. montanus* series, which agrees with the morphological phylogenetic estimate of Abdala *et al.* (2019a) which placed *L. chlorostictus* as sister to *L. pantherinus* (their *L. orientalis*) in a clade with no morphological synapomorphies shared with other members of the *L. montanus* group.

Using new Bolivian material for the Cordillera de Sama in Tarija, the molecular phylogenetic estimate of Aguilar-Puntriano *et al.* (2018) recovers *Liolaemus pantherinus* (their *L. pantherinus*) within the clade I identify as the *L. multicolor* group, a clade that did not include *L, chlorostictus*. This relationship contrasts sharply with all previous hypotheses, especially Laurent's hypothesis that *L. chlorostictus* was best considered as subspecies of *L. orientalis*. Aguilar-Puntriano *et al.* (2018) recovered *L. chlorostictus* as sister to *L. lenzi* (their *Liolaemus* sp3) in a larger clade also including *L. multiformis* (their *L. signifer*) and *L. annectens,* a clade we can consider the *L. multiformis* group. Figure 25 presents the proposed phylogenetic relationships of *L. pantherinus* and most closely related species based on the findings of this paper and the hypotheses of Aguilar-Puntriano *et al.* (2018), following taxonomy of the present paper.

The "*Liolaemus orientalis*" samples used by Aguilar-Puntriano *et al.* (2018) were collected in an area with an established presence of *L. orientalis* in the literature (see Jiménez-Robles and De la Riva, 2019, for example). Specimens from this population are clearly identifiable as *L. pantherinus* (e.g. uncatalogued MNCN material with field numbers 8315, 8389, 8392). As in the case of their *L. pleopholis* samples, if Aguilar-Puntriano *et al.* (2018) are correct, their estimate could be another rather remarkable case of either convergence of *L. pantherinus* with members of the *L. multiformis* group or the conservation of a plesiomorphic morphology in *L. pantherinus.* However, it could also represent a case of introgression between *L. pantherinus* and the sympatric *L. tajzara* (their *Liolaemus* sp2).

Based on the available evidence, I find the sister relationship between *Liolaemus pantherinus* and *L. chlorostictus* to a far more plausible evolutionary scenario than membership in the *L. multicolor* group recovered by Aguilar-Puntriano *et al.* (2018). However, in agreement with Aguilar-Puntriano *et al.* (2018), these two species are likely to be most closely related to *L. lenzi* and members of the *L. multiformis* group, not the *L. multicolor* group. As evident in Fig. 6, there is a contact zone between *L. pantherinus* and *L. lenzi* in the northern part of the *L. pantherinus* range along the eastern edge of the Altiplano and in the Cordilleras of northern Potosí.

Conservation and Legal Implications of the Proposed Taxonomic Decisions

Given that one of the arguments frequently used in favor of maintaining taxonomic stability is that unnecessary changes have implications on conservation and legislation (Padial and De la Riva, 2006; Morrison *et al.*, 2009; Kaiser *et al.*, 2013), I provide

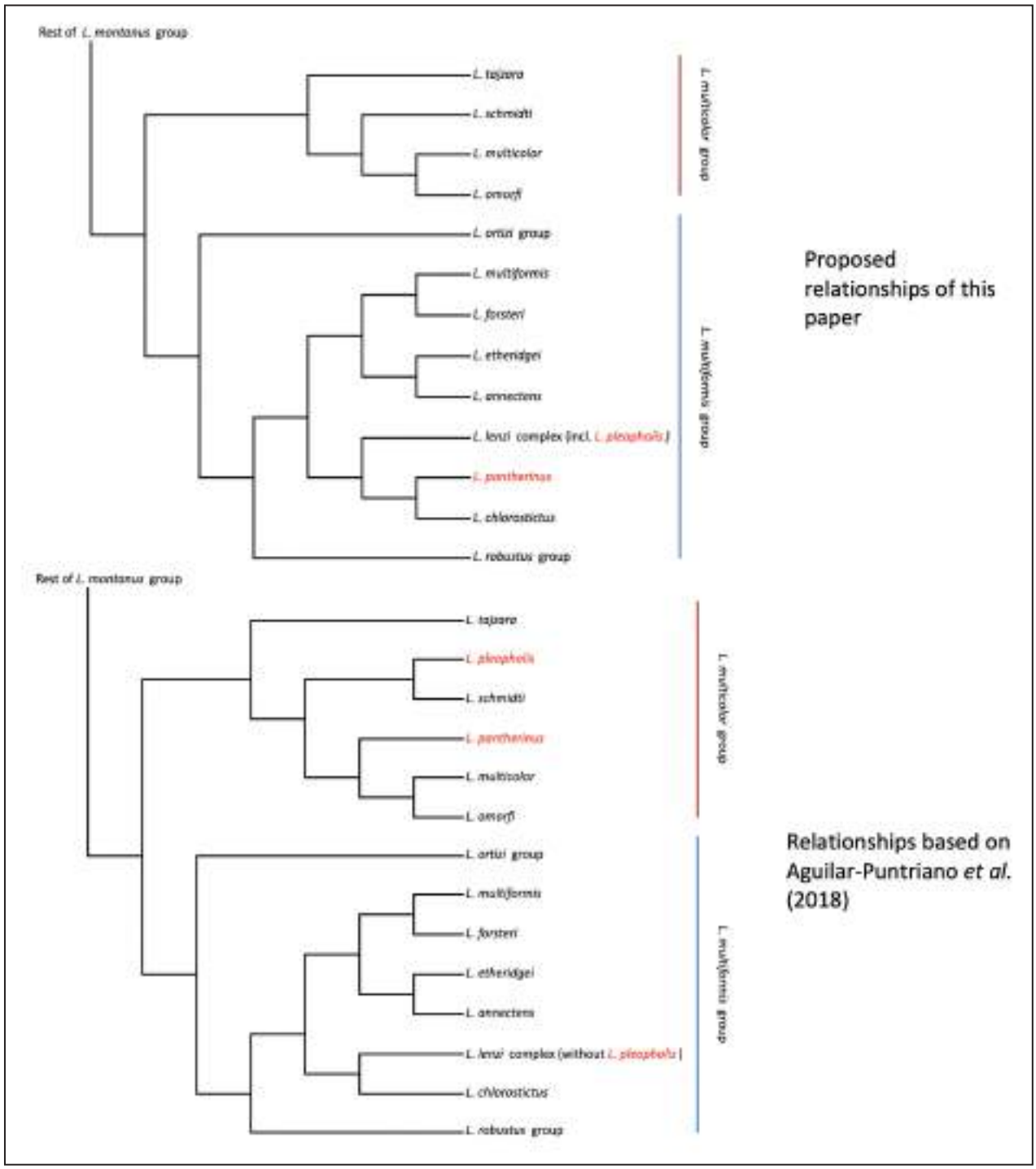

Figure 25. Schematic representation of proposed phylogenetic relationships of *Liolaemus pantherinus*, *L. pleopholis*, and nearest relatives based on findings of this paper and hypothesis of Aguilar-Puntriano *et al.* (2018), following taxonomy of the present paper.

here a discussion of the effects of the taxonomic decisions proposed here on IUCN and national conservation categories.

Liolaemus pantherinus has not been assessed by the IUCN and is not mentioned by the Bolivian Red Book. The Chilean Species Classification Process currently recognizes *L. pantherinus* as a species that has never been shown to be present in Chile and which is not presumed to be a senior synonym of *L. islugensis* (Ministerio del Medio Ambiente, 2019a). *Liolaemus orientalis* is listed as Vulnerable in Argentina by Resolución No. 1055/2013 (Secretaría de Ambiente y Desarrollo Sustentable, 2013) and as Least Concern globally by the IUCN (Ávila and Abdala, 2016). It

was not included in the Bolivian Red Book. Based on the extent of its range (Fig. 6, approximately 50,500 km^2), the absence of widespread impacts to its habitats, and its only localized use for medicinal purposes, I recommend the global category of Least Concern for *L. pantherinus*.

Liolaemus signifer is listed as Near Threatened by the IUCN Red List (Aguilar *et al.* 2017b). The IUCN assessment and range map for this species includes *L. multiformis* and *L. lenzi* collectively but does not include the populations recognized as *L. pleopholis*. The estimated range of *L. multiformis* likely does not exceed 50,000 km^2 and that of *L. lenzi* is approximately 94,000 km^2 (Fig. 6). *Liolaemus signifer* has not been included in the Bolivian (Ministerio de Medio Ambiente y Agua, 2009) or Peruvian Servicio Nacional Forestal y de Fauna Silvestre, 2018) Red Books, but has been classified as Near Threatened by the Chilean Species Classification Process (Ministerio del Medio Ambiente, 2019b) due its small range and habitat loss from mining activities. Based on the relatively widespread conversion of habitats for crop production and the relatively high levels of use for medicinal purposes (De la Gálvez Murillo and Pacheco, 2009), I recommend that both *L. multiformis* and *L. lenzi* should be classified as Near Threatened.)

Liolaemus pleopholis is listed as Least Concern by the IUCN Red List (Lobos *et al.*, 2016), which considers it endemic to Chile. However, the Chilean Ministry of the Environment recommends national category of Endangered for *L. pleopholis* (Ministerio de Medio Ambiente, 2019c).

Liolaemus schmidti is listed as Least Concern by the IUCN Red List (Núñez *et al.*, 2017) and their concept included *L. omorfi* as a junior synonym. The IUCN Red List should recognize *L. omorfi* as a valid species and species experts should provide an assessment of its status, and the Chilean Species Classification Process currently proposes the category of Least Concern for *L. omorfi* (Ministerio de Medio Ambiente, 2019d). *Liolaemus islugensis* has not been assessed by the IUCN and is not mentioned by the Bolivian Red Book. The Chilean Species Classification Process currently proposes the category of Least Concern for *L. islugensis* (Ministerio de Medio Ambiente, 2019e). The Chilean Species Classification Process considers *L. schmidti* a synonym of *L. andinus* (Ministerio del Medio Ambiente, 2013a. Based on the extent of its range (Fig. 6, approximately 84,300 km^2) and the absence of widespread impacts to its habitats and the absence of any significant use of these lizards by humans, I recommend the global status of Least Concern for *L. schmidti*.

Liolaemus erroneus has been listed as Data Deficient by the IUCN Red List (Núñez *et al.*, 2016). It was considered a junior synonym of *L. andinus* by the Chilean Ministry of the Environment (Ministerio del Medio Ambiente, 2013b) but is presently listed as Data Deficient (Ministerio del Medio Ambiente, 2018d). *Liolaemus erguetae* is listed as Least Concern by the IUCN Red List (Ruiz de Gamboa *et al.*, 2017) and is presently proposed as Vulnerable by the Chilean Species Classification Process (Ministerio del Medio Ambiente, 2019f). *Liolaemus molinai* is listed as Least Concern by the IUCN Red List (Mella *et al.*, 2016) and the Chilean Species Classification Process proposes the national category of Data Deficient and only recognizes it from its type locality (Ministerio del Medio Ambiente, 2019g). Given the extent of its range (Fig. 6, approximately 17,300 km^2) and the absence of widespread impacts to its habitats and the absence of any significant use of these lizards by humans, I recommend the global status of Least Concern for *L. erroneus*.

Discussion

The extraordinarily convoluted and confused taxonomic history of lizards of the *Liolaemus montanus* group from the Bolivian Andes illustrates the importance of applying good taxonomic and nomenclatural practice in research on any group of organisms. The misuse or misapplication of names leads to potentially significant misunderstandings and misinterpretations of evolutionary, ecological, and biogeographic information, as well as considerable unnecessary efforts and resources.

While taxonomic stability is certainly desirable, I argue here that it is only desirable when based on correct use of names, when it accurately communicates evolutionary relationships, and when it properly reflects and respects the history of the research and researchers (see Padial and De la Riva, 2006). Retaining the use of names that do not meet these criteria is counterproductive to our understanding and stewardship of biodiversity (see Morrison, *et al.*, 2009). The decision to relegate *Liolaemus signifer* to the status of *nomen dubium* and to resurrect *L. multiformis* and *L. lenzi* restores order rather than creates instability and furthermore recognizes hidden diversity and allows for its conservation. If taxonomy is

to continue to be a science, and not merely an art, taxonomic decisions and nomenclatural acts must be subject to hypothesis testing and refutation, not be taken as absolute truths, even when based on hypothesis generated by morphological or molecular models of evolution, and examined in the absence of truly total evidence, not just morphological and molecular, but also ecological, biogeographic, and literature-based evidence. The interpretation (or lack thereof) of models based on a subset of evidence without consideration of insights from other sources of evidence can lead to erroneous inferences The case of the placement of *Liolaemus pleopholis* and *L. orientalis* (= *L. pantherinus*) in a major clade otherwise corresponding to a morphologically-congruent *L. multicolor* group by Aguilar-Puntriano *et al.* (2018) based on molecular data alone may appear reasonable to readers unfamiliar with the organisms in question but is a very unexpected finding to those familiar with these animals and their biogeography. Likewise, these authors applied the names *L. islugensis* and *L.* cf. *schmidti* to material without a proper understanding of the relationship of their specimens to the real type locality of *L. schmidti.*

Disregarding or simply "ignoring" validly published names (i.e., "available names" per the ICZN) is a not good taxonomic practice, even if the species is based on now-lost single specimen with a somewhat vague type locality as in the case of *Liolaemus erroneus*. It should be the responsibility of subsequent authors to deal with relevant available names they believe are of doubtful application or validity *before* creating new names that may apply to the same group of organisms. The omission (whether intentional or unintentional) relevant (i.e., geographically and morphologically proximate) species from the diagnosis of a new species can result in the needless creation of names for previously named species, as in the case of *L. islugensis* which did not include *L. schmidti*.

While we have made significant advances in recent decades on our understanding of the diversity, systematics, and taxonomy of *Liolaemus*, we still have challenges ahead. However, we must not lose sight of the past. Taxonomy as a practice and science has evolved over time and it is crucial to frame our critiques and revisions with consideration of the practices and limitations of authors in the past, even as recently as the 1980s and early 1990s. This paper has examined various cases of taxonomic problems in the *L. montanus* group in the spirit of advancing our understanding of these lizards and preparing the way for future workers by eliminating confusing and redundant names and properly assigning valid names to their intended lineages within the group. Table 3 below provides a summary of the taxonomic and nomenclatural conclusions made throughout this paper and Table 4 provides details on the more

Table 3. Summary of proposed taxonomic and nomenclatural conclusions.

Original name	Current name	Status	Comments
Proctotretus signifer Duméril & Bibron 1837	*Liolaemus signifer* (Duméril & Bibron 1837)	Nomen dubium	Holotype remains lost. Specimen identified as such by Cei *et al.* (1980) is a syntype of *Proctotretus fitzingerii* Variété A Duméril & Bibron 1837 which is actually a specimen of *L. multiformis* collected by A. d'Orbigny in Bolivia near Lake Titicaca.
Proctotretus multiformis Cope 1875	*Liolaemus multiformis* (Cope 1875)	Valid name	Applied here to clade identified as *Liolaemus signifer* in Aguilar-Puntriano *et al.* (2018).
*Liolaemus lenz*i Boettger 1891	*Liolaemus lenzi* Boettger 1891	Valid name	Applied here to clade identified as *Liolaemus* sp3 in Aguilar-Puntriano *et al.* (2018). While *L. lenzi* is applied broadly here, this clade is likely a complex including a number of undescribed species.
Liolaemus annectens Boulenger 1901	*Liolaemus annectens* Boulenger 1901	Valid name	Endemic to southern Peru.
Liolaemus tropidonotus Boulenger 1902	*Liolaemus multiformis* (Cope 1875)	Junior subjective synonym	New synonymy
Liolaemus pantherinus Pellegrin 1909	*Liolaemus pantherinus* Pellegrin 1909	Valid name	Type locality is corrected to "environs of Pulacayo, Potosí Department, Bolivia".

Liolaemus variabilis Pellegrin 1909	*Liolaemus lenzi* Boettger 1891	Junior subjective synonym	New synonymy
Liolaemus variabilis Var. *crequii* Pellegrin 1909	*Liolaemus lenzi* Boettger 1891	Junior subjective synonym	New synonymy
Liolaemus variabilis Var. *neveui* Pellegrin 1909	*Liolaemus lenzi* Boettger 1891	Junior subjective synonym	New synonymy
Liolaemus variabilis Var. *courtyi* Pellegrin 1909	*Liolaemus lenzi* Boettger 1891	Junior subjective synonym	New synonymy
Liolaemus annectens orientalis Müller 1926	*Liolaemus pantherinus* Pellegrin 1909	Junior subjective synonym	New synonymy. Populations referred to *L. orientalis* in Argentina and adjacent areas of Tarija (Bolivia) require further assessment and not presumed to belong to population at type locality of *L. a. orientalis*.
Ctenoblepharis schmidti Marx 1960	*Liolaemus schmidti* (Marx 1960)	Valid name	Applied here to clade identified as *L. islugensis* by Aguilar-Puntriano *et al.* (2018). Type locality is corrected to "San Pedro de Inacaliri river valley between the localities of Ojos de San Pedro and Inacaliri, Loa Province, Antofagasta Region, Chile".
Liolaemus forsteri Laurent 1982	*Liolaemus forsteri* Laurent 1982	Valid name	Locally sympatric with *L. multiformis* and perhaps *L. lenzi* in Bolivia along lower western slopes of the Cordillera Real.
Ctenoblepharis erroneus Núñez & Yáñez 1984 "1983-1984"	*Liolaemus erroneus* (Núñez & Yáñez 1984 "1983-1984")	Valid name	Specimen FML 1192 is designated as neotype
Liolaemus islugensis Ortiz & Marquet 1987	*Liolaemus schmidti* (Marx 1960)	Junior subjective synonym	New synonymy
Liolaemus orientalis chlorostictus Laurent 1993 "1990"	*Liolaemus chlorostictus* Laurent 1993 "1990"	Valid name	Allopatric sister species to *L. pantherinus*. Specimen SDSU 3517 has been used as source of genetic material referred to *L. orientalis* on the literature but belongs to *L. chlorostictus*.
Liolaemus islugensis erguetae Laurent 1995	*Liolaemus erroneus* (Núñez & Yáñez 1984 "1983-1984")	Junior subjective synonym	New synonymy
Liolaemus (*Eulaemus*) *pleopholis* Laurent 1998	*Liolaemus pleopholis* Laurent 1998	Species inquirenda	May be a member of the *L. lenzi* species complex but major conflicts exist between molecular and morphological phylogenetic hypotheses.
*Liolaemus molina*i Valladares, Etheridge, Schulte, Manríquez & Spotorno 2002	*Liolaemus erroneus* (Núñez & Yáñez 1984 "1983-1984")	Junior subjective synonym	New synonymy
Liolaemus omorfi Demangel, Sepúlveda, Jara, Pincheira-Donoso & Núñez 2015	*Liolaemus omorfi* Demangel, Sepúlveda, Jara, Pincheira-Donoso & Núñez 2015	Valid name	Applied here to clade identified as *Liolaemus* cf. *schmidti* by Aguilar-Puntriano *et al.*(2018).

important collections made by 19th and early 20th century travelers and collectors: Charles Darwin, Alcide d'Orbigny, Perry O. Simons, and Maurice Neveu-Lemaire.

Acknowledgments

I thank my wife Susy for her patience with me during this odyssey. I thank the following people/institutions for providing access to collections and/or photographs of material studied during the many

Table 4. Summary of *Liolaemus* species described from collections by relevant 19th and early 20th century collectors.

Collector	Years	Countries (where *Liolaemus* were collected)	Key Worker/ Museum and References	*Liolaemus* species described from collections	Comments
Alcide d'Orbigny	1830-1832	Argentina, Bolivia, Chile	Gabriel Bibron/ MNHN Duméril & Bibron (1837)	*L. pictus, L. wiegmannii, L. fitzingerii, L. signifer, L. multimaculatus*	Duméril & Bibron (1837) erroneously attributed many of d'Orbigny's specimens to Chile when in fact they were collected in Bolivia or Argentina.
Charles Darwin	1832-1836	Argentina, Chile	Thomas Bell/ BMNH Bell (1843)	*L. gracilis, L. bibronii, L. kingii, L. darwinii*	When describing Darwin's material, Bell examined specimens described by Bibron from MNHN, including the now-lost *L. signifer* holotype.
Perry O. Simons	1900-1901	Peru, Bolivia	George Boulenger/ BMNH Boulenger (1901, 1902)	*L. annectens, L. simonsii.*	Simons was killed by his Chilean guide in Argentina, December 1901. The squamate reptiles collected by Simons have not been fully enumerated and revised.
Maurice Neveu-Lemaire	1903	Bolivia	Jacques Pellegrin/ MNHN Pellegrin (1909)	*L. pantherinus, L. pulcher, L. mocquardi, L. variabilis, L. bolivianus*	The material collected by Neveu-Lemaire and fellow expedition members has not been fully enumerated and revised.

years that led to this paper (in alphabetical order by institution): Darrell Frost/David Kizirian/AMNH, Ned Gilmore/ANSP, Patrick Campbell/Barry Clark/ BMNH, James Aparicio/Álvaro Aguilar-Kirigin/CBF, Cristian Abdala/FML, Alan Resetar/FMNH, William E. Duellman/KU, Herman Núñez/MNHN-C, Ivan Ineich/Nicolas Vidal/MNHN-P, Michelle Koo/MVZ, Margarita Ruiz de Gamboa/MZUC, Richard Etheridge/SDSU, Jaime Troncoso-Palacios/SSUC, Kenneth Tighe/Addison Wynn/USNM, Jakob Hallermann/ ZMH, and Michael Franzen/ZSM. Special thanks to the late Richard Etheridge for access to his invaluable notes and data on type specimens of *Liolaemus* in European collections but moreover for his support, feedback, advice, and openness over the years of my development as a liolaemologist, to William Duellman for providing the first known photographs of *L. pantherinus* in life as well his patient mentoring and support in my early days, to César Aguilar Puntriano for his insights into the relationships of the Peruvian members of the *montanus* group and his constructive criticisms of my approaches and assumptions, and to Margarita Ruiz de Gamboa for sharing her work and insights on *L. pantherinus, L. schmidti,* and *L. erroneus.* Finally, I am indebted to the anonymous peer reviewers whose comments and queries greatly improved the quality of this work.

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Appendix 1. Material Examined

Liolaemus annectens: PERU: Arequipa: Caylloma: BMNH 1946.8.12.1–3 (Syntypes); BYU-CAP 1184, 1195–96, 1202;

Arequipa: Sumbay: BMNH 1946.8.12.4 (Syntype), BYU-CAP 1198, 1198–99, 1204–05.

Liolaemus cf. *aymararum:* BOLIVIA: Oruro: Parque Nacional Sajama: CBF 1913; Peru: Tacna: Tarata: MVZ 99650–51.

Liolaemus chlorostictus: ARGENTINA: Jujuy: Rinconada: Cuesta de Fundiciones: FML 2284 (Holotype); Jujuy: Rinconada: 15.5 km E Orosmayo: SDSU 3517–19; Bolivia: Potosí: Khastor: Photograph in Life; Potosí: Laguna Coruto: Photographs in Life (3 individuals).

Liolaemus erroneus: BOLIVIA: Potosí: Laguna Cachi CBF 512, Potosí: Laguna Colorada: CBF 732, 1293–95, 1298–99, 1934, FML 3208; Potosí: Salar de Chalviri: CBF 1300; CHILE: Antofagasta: Atacama: FML 1192 (Neotype); Antofagasta: Salar de Tala: SDSU 4012–13; Antofagasta: Tatio: FML 1192, USNM 165640.

Liolaemus etheridgei: PERU: Arequipa: BYU 50493, 50495, KU 163564–65

Liolaemus fittkaui: BOLIVIA: Cochabamba: UMMZ 68143, 17931–33, 224325–28; Cochabamba: Tiraque: MVZ 36458.

Liolaemus forsteri: BOLIVIA: La Paz: Chacaltaya ZSM 646/1979 (Holotype); La Paz: Millipaya: 48603–04; La Paz: Warisata: MNCN 48584; La Paz: Zongo: MNCN 34747, 34749–50.

Liolaemus hajeki: CHILE: Antofagasta: Tatio: MVZ 66810, USNM 165639; Antofagasta: Salar de Ascotán: SSUC 0362; Antofagasta: El Abra Mine: SSUC 0484.

Liolaemus jamesi: CHILE: Tarapacá: Holotype BMNH 1946.8.12.39, BMNH 91.7.3.1; Tarapacá: Alto Camiña: MVZ 66805–06.

Liolaemus lenzi: BOLIVIA: Cochabamba: Challa: KU 160049, 160122–23; Cochabamba: La Cumbre: MNCN 48540–41; La Paz: Caxata: MNCN 48569; La Paz: Cerro Gigante, 5 km SW: MNCN field tags NGR 8278 – 8282; La Paz: Charaña: MNCN 34753, 34755; La Paz: Chililaya: MNHN 1905-0345–47 (Syntypes of *L. bolivianus*); La Paz: Colquiri: MNCN 48557–58, 48560–61; La Paz: Río Cosapilla: MNCN 34757; La Paz: Shore of Lake Titicaca: Holotype SMF 1110; La Paz: Tiahuanaco: MNHN 1907-247, 1907-249–51 (Syntypes of *L. variabilis*); La Paz: CBF 1557–58, 3479; Oruro: Cosapa: CBF 3716; Oruro: Curahuara de Carangas: MNCN 34775; Oruro: Oruro: AMNH 90458, 90460, 90462, 90464–68, 12813; BMNH 1902.5.29.30–34; Oruro: Sajama: MNCN 34762–63; CHILE: Arica y Parinacocha: Chivatambo: SSUC 570; Arica y Parinacocha: Surire: SSUC 569; PERU: Puno: Desaguadero: Santa Ana: MUSM 29110.

Liolaemus melanogaster: PERU: Ayacucho: Lucanas: BYU 57388–92, MVZ 57834, ZMH R10990–91.

Liolaemus multicolor: ARGENTINA: Jujuy: BMNH 1922.290–91.

Liolaemus multiformis: BOLIVIA: La Paz: Achacachi: MNHN-P 6080 (Syntype of *L. fitzingerii* Var. A); La Paz: Lago Titicaca: Cerro Iutane: MNCN 48506–07; La Paz: Millipaya: MNCN 48602; PERU: Puno: Capachica: BMNH 1971.450–468, BYU-CAP 085; Puno: Lake Titicaca: ANSP 13064 (Lectotype of *L. multiformis*), ANSP 13104, 13065, 13098, 11368–70 (Paralectotypes of *L. multiformis*); Puno: Lake Titicaca: Isla Amantani: BYU 50353, 50356, 50361, 50444; Puno: Tincopalta: KU 163591, 163593; Puno: Santa Rosa: KU 163535–36, 16348–49; Puno: Tirapata: BMNH 1946.8.12.30-32 (Syntypes of *L. tropidonotus*).

Liolaemus omorfi: CHILE: Antofagasta: Salar de Aguas Calientes: SSUC 0134–41

Liolaemus ornatus (sensu lato): BOLIVIA: La Paz: Calamarca: KU 183458; Oruro: Caracollo: KU 160034, 160035; Oruro: Challapata: BMNH 1946.8.1.10.45-49 (Syntypes of *L. simonsii*), KU 183459–60, MCZ R-189412 (Syntype of *L. simonsii*); Potosí: Potosí: BMNH 1946.8.12.24–26 (Syntypes of *L. simonsii*), Potosí: Tupiza: KU 160211; Potosí: Uyuni: BMNH 1946.8.12.20–23 (Syntypes of *L. simonsii*); PERU: Puno: BYU-CAP 072–73, MUSA 1064–65

Liolaemus pachecoi: BOLIVIA: Potosí: Laguna Colorada: Allotype FML 2788; Potosí: Desierto de Siloli: Photograph in Life; Potosí: Reserva Eduardo Abaroa: Photograph in Life; CHILE: Antofagasta: Salar de Alconcha: Photograph in Life (SGA, 2007); Antofagasta: Salar de Carcote: MNHN-CL; Antofagasta: Portezuelo: Photograph in Life (SGA, XXXX).

Liolaemus pantherinus: ARGENTINA: Jujuy: Departamento Humahuaca: Photographs CSA5404, 5413, 5420; BOLIVIA: Chuquisaca: Sucre: AMNH 5251; Oruro: Livichuco: BMNH 1902.5.29.50, Oruro: Poopó: BMNH 1902.5.29.46–49; Potosí: Potosí: AMNH 13495–98, BMNH 1902.5.29.36–45, KU 160198–208, MCZ 8062; Potosí: Paso Mazo Cruz ("Abra de Macho Cruz"): MCZ R-101275, Potosí: Portugalete: AMNH 80076; Potosí: Pulacayo: MNHN RA 1905.344–45 (Syntypes of *L. pantherinus*); Potosí: Uyuni: AMNH 13494, BMNH 1902.5.29.51–58, MCZ R-8056; Potosi: Uyuni: Cerro Escalona: CBF KIRI-552–53; Tarija: Cordillera de Sama: Department Unknown: Upper Pilcomayo Basin: ZMB 26405 (Holotype of *L. annectens orientalis*); ZSM 26/1924/1–2 (Syntypes of *L. annectens orientalis*), ZSM 281/1989/1–2 (Syntypes of *L. annectens orientalis*).

Liolaemus pulcherrimus: ARGENTINA: Jujuy: Mudana: FML 2202 (Holotype).

Liolaemus puritamensis: CHILE: Antofagasta: Paratypes OSUS R5124-25; BOLIVIA: Potosí: Campamento Khastor: CBF 0736.

Liolaemus schmidti: BOLIVIA: Potosí: Julaca: FMNH 204525–26; Potosí: Laguna Colorada: CBF 0715–l6, 296–97 (Paratypes of *L. islugensis erguetae*), CBF 3495, FML 3207 (Paratype of *L. islugensis erguetae*); Potosí: Uyuni: BMNH 1902.5.29.63–73; Potosí: Nor Chichas: MCZ 101277; CHILE: Antofagasta: San Pedro de Inacaliri valley: Holotype FMNH 5759, Allotype FMNH 5760, AMNH 85773, MVZ 66807–08; Tarapacá: Colchane: MZUC 10931–32 (Holotype and Allotype of *L. islugensis*), 10935, 10944, 23699–700; Tarapacá: Cariquima: AMNH 131850-51, BMNH 1977 2277-279, SDSU 1601-03.

Liolaemus williamsi: PERU: Ayacucho: BYU 50143–44, 50463–65.

Appendix 2. R Data used in Wilcoxon Tests for Dorsal Scales Comparisons

Annectens <- c(63, 72, 61, 66, 49, 53, 51, 50, 70, 61, 59, 69, 57)
Chlorostictus <- c(65, 59, 61, 63, 61, 64, 63, 60, 62, 56, 62)
Erroneus <- c(91, 90, 83, 86, 101, 94, 99, 98, 87, 95, 96)
Fittkaui <- c(55, 56, 51, 50, 48, 47)
Forsteri <- c(89, 84, 79, 91, 77, 84)
Jamesi <- c(43, 43, 37, 38, 38)
Lenzi <- c(87, 86, 77, 74, 84, 98, 103, 104, 110, 102, 106, 87, 99, 87, 88, 77, 92, 82, 81, 85, 88, 83, 82, 83, 79, 84)
Multiformis <- c(83, 73, 67, 77, 72, 77, 73, 76, 77, 89, 80, 86, 74, 76, 75, 65, 79, 62)
Pachecoi <- c(39, 37, 38, 38, 42, 41, 31, 37, 39)
Pantherinus <- c(62, 62, 58, 54, 49, 53, 51, 54, 54, 62, 62, 54, 60, 52, 55, 58, 56, 51, 49, 60, 67, 62, 54, 58, 51, 50, 59, 52, 53, 45,

49, 50, 49, 54, 53, 54, 52, 55, 67, 49, 55, 46, 46, 59)
Pleopholis <- c(76, 82, 82, 86, 83, 91)
Puritamensis <- c(46, 50, 52, 46, 47, 52, 48)
Schmidti <- c(76, 84, 76, 80, 77, 84, 80, 86, 78, 89, 77, 84, 76, 76, 86, 84, 75, 86, 84, 85, 85, 91)
Tropidonotus <- c(67, 84, 73, 70, 75, 76)

Appendix 3. Annotated Synonymies, Partial Chresonymies, and Referred Material

Liolaemus multiformis (Cope)

1837 *Proctotretus Fitzingerii* Duméril & Bibron (*partim*), Type locality: "Chili". Specimen MNHN-RA-6860 was a syntype of *L. fitzingerii* "Variété A" but is a *L. multiformis* collected by d'Orbigny in Bolivia and misidentified by Cei *et al.* (1980) as the holotype of *L. signifer*.

1875 *Proctotretus multiformis* Cope, *J. Acad. Nat. Sci. Philadelphia*, Ser. 2, 8: 173. Type locality: "the elevated Lake of Titicaca, Peru". Lectotype: Acad. Nat. Sci. Philadelphia No. 13064, designated by Laurent (1998).

1885 *Liolaemus multiformis*—Boulenger, *Catalogue of the Lizards of the British Museum (Natural History), Vol. 2*:153. First use of combination.

1902 *Liolaemus tropidonotus* Boulenger, *Ann. Mag. Nat. Hist.* 7(10):397. Type locality: "Tirapata, Peru". Syntypes: BMNH Synonymy by Burt & Burt (1931).

1931 *Liolaemus multiformis multiformis*—Burt & Burt (*partim*), *Bull. Am. Mus. Nat. Hist* 61:276. The Burts included a composite of specimens referable to *L. annectens, L. forsteri, L. lenzi*, *L. multiformis*, *L. tropidonotus*, and a probable new species (e.g., from "Potone") under this name.

1954 *Liolaemus multiformis multiformis*—Pearson, *Copeia* 1954(2):111.

1970 *Liolaemus multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:186. Donoso-Barros included *L. annectens, L. lenzi*, *L. multiformis*, and *L. pantherinus* under this name.

1970 *Liolaemus multiformis multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:187. Donoso-Barros included included *L. annectens, L. lenzi*, and *L. multiformis* under this name.

1992 *L*[*iolaemus*] *s*[*signifer*] *signifer*—Laurent (*partim*), *Breviora* 495:31. First use of this combination. Laurent included a composite of specimens referable to *L. lenzi* and *L. multiformis* in this name.

2002 *Liolaemus signifer*—Valladares *et al.* (*partim*), *Rev. Chil. Hist. Nat*. 73:489. Specimen SDSU 1600 is *L. multiformis* from Tincopalta, Puno, Peru, not from Cariquima, Chile as indicated. AMNH 90457-60, 90464-6868 from Oruro and vicinity are *L. lenzi.*

2005 *L*[*iolaemus*] *s*[*signifer*] *signifer* —Langstroth (*partim*), *Kempffiana* 1(1):124. Langstroth included both *L. lenzi* and *L. multiformis* in this name.

2014 *Liolaemus signifer*—Troncoso-Palacios (*partim*), *Check List* 10(1):221, Troncoso-Palacios included both *L. lenzi* and *L. multiformis* in this name.

2016 *Liolaemus signifer signifer*—Etheridge & Frost (*partim*), Liolaemidae:59. Etheridge & Frost included both *L. lenzi* and *L. multiformis* in this name.

2017 *L*[*iolaemus*] *signifer*—Aguilar *et al. Biol. J. Linn. Soc.* 120:456. Aguilar *et al.* did not include specimens referable to *L. lenzi* from their *L. signifer* clade.

2018 *L*[*iolaemus*] *signifer*—Aguilar-Puntriano *et al.* 2018. *Ecol. Evol.* 8(23):11403. Aguilar-Puntriano *et al.*'s *L. signifer* clade does not include lizards referable *L. lenzi*, which corresponds to their *L.* sp3 clade.

Referred material:

Lectotype: ANSP 13064, PERU: Puno: Lake Titicaca. Paralectotypes: ANSP 13104, 13065, 13098, 11368–70, same locality as lectotype. Others: BOLIVIA: La Paz: Achacachi: MNHN-RA-6860 (Syntype of *L. fitzingerii* Variété A); La Paz: "Camino a montañas en Millipaya. Sorata": MNCN 48602; La Paz: Cerro Iutane: MNCN 48506–07; PERU: Puno: Capachica: BMNH 1971.450–468, CAP-BYU 085; Puno: Isla Amantani: BYU 50353, 50356, 50361, 50444; Puno: Tincopalta: KU 163591, 163593; Puno: Santa Rosa: KU 163535–36, 16348–49; Puno: Tirapata: BMNH 1946.8.12.30-32 (Syntypes of *L. tropidonotus*).

Liolaemus lenzi Boettger

1891 *Liolaemus Lenzi* Boettger, *Zool. Anzeiger* 14: 344. Type locality: "Bolivianisches Ufer des Titicaca-Sees". Holotype: SMF 11110

1893 *Liolaemus lenzi*—Boettger, *Kat. Rept. Samml. Mus. Senck. Naturf. Gesell.* Pt. 1: 61.

1908 *Liolaemus signifer*—Andersson, *Jahrb. Nass. Vereins. Naturk.* 61:302.

1909 *Liolaemus variabilis* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15:327. Type locality: None specified, but all material collected at "Tiahuanaco, département de La Paz", Bolivia. Syntypes: Mus. Natl. Hist. Nat. 07-244–251. New synonymy.

1909 [*Liolaemus variabilis*] Var. *Crequii* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15:327. Type locality: "Tiahuanaco, département de La Paz", Bolivia. Syntypes: Mus. Natl. Hist. Nat. 07-244–246, by original designation. New synonymy.

1909 [*Liolaemus variabilis*] Var. *Neveui* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15:327. Type locality: "Tiahuanaco, département de La Paz", Bolivia. Syntypes: Mus. Natl. Hist. Nat. 07-247–250, by original designation. New synonymy.

1909 [*Liolaemus variabilis*] Var. *Courtyi* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15:328. Type locality: "Tiahuanaco, département de La Paz", Bolivia. Holotype: Mus. Natl. Hist. Nat. 07-251 by original designation. New synonymy.

1909 *L*[*iolaemus*] *Lenzi*—Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris,* 328.

1909 *Liolaemus bolivianus* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15:328. Type locality: "Hauts-Plateaux péruviens et boliviens", restricted to Chililaya, Departamento de La Paz, Bolivia. Holotype: Mus. Natl. Hist. Nat. 05-345–347 by original designation. New synonymy.

1931 *Liolaemus multiformis multiformis*—Burt & Burt (*partim*), *Bull. Am. Mus. Nat. Hist* 61:275. Burt & Burt included both *L. lenzi* and *L. multiformis* in this name.

1937 *Liolaemus variabilis*—Rendahl, *Arkiv för Zool.* 29A(13):7.

1962 *Liolaemus multiformis*—Hellmich (*partim*), *Opusc. Zool.* 67:4. Hellmich included *L. annectens, L. lenzi*, and *L. multiformis* in this name.

1970 *Liolaemus multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:186. Donoso-Barros included included *L. annectens, L. lenzi*, *L. multiformis*, and *L. pantherinus* under this name.

1970 *Liolaemus multiformis multiformis*—Donoso-Barros

(*partim*), *U.S. Nat. Mus. Bull.* 297:187. Donoso-Barros included included *L. annectens, L. lenzi*, and *L. multiformis* under this name.

1982 *L*[*iolaemus*] *lenzi*—Laurent, *Neotrópica* 28:88.

1982 *Liolaemus multiformis*—Veloso *et al.*, Ambiente natural y las poblaciones humanas de los Andes del norte grande de Chile: 220.

1989 *Liolaemus multiformis*—Fugler (*partim*), *Ecol. Bolivia* 13:61. Fugler included *L. ornatus,* sensu lato, *L. lenzi,* and *L. multiformis* under this name.

1989 *Liolaemus signifer*—Fugler, *Ecol. Bolivia* 13:62.

1999 *Liolaemus signifer*—Dirksen & De la Riva (*partim*), *Graellsia* 55:206. Dirksen & De la Riva included material assignable to *L. forsteri, L. lenzi, L. multiformis*, and *L. pantherinus* under this name.

2002 *Liolaemus signifer*— Valladares *et al.* (*partim*), *Rev. Chil. Hist. Nat*. 73:489. AMNH 90457-60, 90464-6868 from Oruro and vicinity are *L. lenzi.* Specimen SDSU 1600 is actually *L. multiformis* from Tincopalta, Puno, Peru, not from Cariquima, Chile as indicated.

2005 *Liolaemus (Eulaemus) signifer*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:172. In their referred material (p. 450), BMNH-1902.5.29.63–73 are *L. schmidti.*

2005 *Liolaemus signifer signifer*—Langstroth (*partim*), *Kempffiana* 1(1):124. Langstroth included both *L. lenzi* and *L. multiformis* in this name.

2014 *Liolaemus signifer*—Troncos-Palacios (*partim*), *Check List* 10(1):221. Troncoso-Palacios included both *L. lenzi* and *L. multiformis* under this name.

2016 *Liolaemus signifer*—Demangel Miranda, Reptiles en Chile:461.

2016 *Liolaemus pleopholis*—Aguilar-Kirigin *et al.*, *Cuad. Herp.* 30(2):89.

2018 *L*[*iolaemus*] sp3 Aguilar-Puntriano *et al.* 2018. *Ecol. Evol.* 8(23):11403.

2019?

Referred material: Holotype SMF 1110, BOLIVIA: La Paz: Shore of Lake Titicaca; Others: BOLIVIA: Cochabamba: Challa: KU 160049, 160122–23; Cochabamba: La Cumbre: MNCN 48540–41; La Paz: Caxata: MNCN 48569; La Paz: Cerro Gigante, 5 km SW: MNCN field tags NGR 8278 – 8282; La Paz: Charaña: MNCN 34753, 34755; La Paz: Chililaya: MNHN 1905-0345–47 (Syntypes of *L. bolivianus*); La Paz: Colquiri: MNCN 48557–58, 48560–61; La Paz: Río Cosapilla: MNCN 34757; La Paz: Tiahuanaco: MNHN 1907-247, 1907-249–51 (Syntypes of *L. variabilis*); La Paz: CBF 1557–58, 3479; Oruro: Cosapa: CBF 3716; Oruro: Curahuara de Carangas: MNCN 34775; Oruro: Oruro: AMNH 90458, 90460, 90462, 90464–68, 12813; BMNH 1902.5.29.30–34; Oruro: Sajama: MNCN 34762–63; PERU: Puno: Desaguadero: Santa Ana: MUSM 29110.

Liolaemus annectens Boulenger

1901 *Liolaemus annectens* Boulenger, *Ann. Mag. Nat. Hist* 7(7):546. Type locality: "Caylloma and Sumbay", Peru. Syntypes: Brit. Mus. Nat. Hist. 1900.11.27.20–23 (now 1946.8.12.1–4)

1931 *Liolaemus multiformis multiformis*—Burt & Burt (*partim*), *Bull. Am. Mus. Nat. Hist* 61:276. The Burts included a composite of specimens referable to *L. annectens, L. forsteri, L. lenzi*, *L. multiformis*, *L. tropidonotus*, and a probable new species (e.g., from "Potone") under this name.

1962 *Liolaemus multiformis*—Hellmich (*partim*), *Opusc. Zool.*67:4. Hellmich considered *L. annectens* type specimens to correspond perfectly with *L. multiformis* but his concept of the latter included proper *L. multiformis* as well as Bolivian *L. lenzi.*

1970 *Liolaemus multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:186. Donoso-Barros included included *L. annectens, L. lenzi*, *L. multiformis*, and *L. pantherinus* under this name.

1970 *Liolaemus multiformis multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:187. Donoso-Barros included included *L. annectens, L. lenzi*, and *L. multiformis* under this name.

1992 *L*[*iolaemus*] *s*[*ignifer*] *annectens*—Laurent, *Breviora* 494:31. First use of combination.

2008 *Liolaemus annectens*—Pincheira-Donoso, Scolaro, & Sura, *Zootaxa* 1800:42.

2016 *Liolaemus signifer annectens*—Etheridge & Frost, Liolaemidae:59.

2017 *L*[*iolaemus*] *annectens*—Aguilar *et al. Biol. J. Linn. Soc.* 120:456.

2018 *L*[*iolaemus*] *annectens*—Aguilar-Puntriano *et al.* 2018. *Ecol. Evol.* 8(23):11403.

Referred material: Syntypes: PERU: Arequipa: Caylloma: BMNH 1946.8.12.1–3, Arequipa: Sumbay: BMNH 1946.8.12.4. Others: PERU: Arequipa: Caylloma: BYU-CAP 1184, 1195–96, 1202; Arequipa: Sumbay: BYU-CAP 1198, 1198–99, 1204–05.

Liolaemus pantherinus Pellegrin

1909 *Liolaemus pantherinus* Pellegrin, *Bull. Mus. Natl. Hist. Nat. Paris*, 15: 324. Type locality: "Hauts-Plateaux péruviens et boliviens", corrected to environs of Pulacayo, Potosí Department, Bolivia. Locality is not on the Altiplano. Syntypes: Mus. Natl. Hist. Nat. Paris No. 05-344 and 05-345.

1924 *Liolaemus annectens orientalis* Müller, *Mitt. Zool. Mus. Berlin*, 11: 81. Type locality: "Oberer Pilcomayo, zwischen Tarija und S. Francisco, Bolivien" (Upper Pilcomayo, between Tarija and San Francisco, Bolivia), corrected here to Upper Pilcomayo basin of Bolivia, above 2,800 masl. Holotype: Zool. Mus. Berlin 26405. New synonymy.

1931 *Liolaemus multiformis simonsii*—Burt & Burt, not *Liolaemus simonsii* Boulenger, 1902. These authors based this combination on specimens from Potosí, Uyuni, and Sucre, all corresponding to *L. pantherinus* and applied the name *simonsii* due to a series of misidentified specimens believed to represent Boulenger's *L. simonsii*. New synonymy.

1970 *Liolaemus multiformis*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:186. Donoso-Barros included included *L. annectens, L. lenzi*, *L. multiformis*, and *L. pantherinus* under this name.

1970 *Liolaemus multiformis simonsii*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:187. Donoso-Barros included *L. montanus*, *L. ornatus* (sensu lato), and *L. pantherinus* under this name.

1970 *Liolaemus pantherinus*—Donoso-Barros (*partim*), *U.S. Nat. Mus. Bull.* 297:192. Donoso-Barros both *L. pantherinus* and *L. schmidti* under this name.

1989 *Liolaemus pantherinus*—Brygoo, *Bull. Mus. Natn. Hist. Nat.* 4th Ser., 11, Sect. A, (3) Suppl.:76.

1989 *Liolaemus orientalis*—Fugler, *Ecol. Bolivia* 13:62. First use of the binomial.

1989 *Liolaemus pantherinus*—Fugler, *Ecol. Bolivia* 13:62.

1989 *Liolaemus simonsii*—Fugler (*partim*), *Ecol. Bolivia* 13:62. Fugler included both *L. ornatus* (sensu lato) and *L. pantherinus* under this name.

1992 *L*[*iolaemus*] *s*[*ignifer*] *signifer*—Laurent (*partim*), *Breviora* 494:31. Laurent placed *L. pantherinus* in the synonymy of *L. signifer.*

1992 *L*[*iolaemus*] *orientalis*—Laurent, *Breviora* 494:31

1993 *Liolaemus orientalis orientalis*—Laurent, *Acta Zool. Lilloana*, 40:98. ("1991"). New synonymy.

1999 *Liolaemus signifer*—Dirksen & De la Riva (*partim*), *Graellsia* 206. These authors included KU specimens from 7 km S of Potosí but these are in fact *L. pantherinus.*

1999 *Liolaemus simonsii*—Dirksen & De la Riva (*partim, non* Boulenger, 1902), *Graellsia* 206. These authors included the AMNH specimen from Sucre and the *L. annectens orientalis* holotype but these are in fact *L. pantherinus.*

2002 *L*[*iolaemus*] *orientalis*—Valladares *et al.* (partim), *Rev. Chil. Hist. Nat.* 73:475. The specimen referred to as *L. orientalis* that was utilized for the molecular analysis, GenBank AF099247 (SDSU 3517) from "15.5 km E Orosmayo on Ruta Prov. 70, Dpto. Rinconada, Prov. Jujuy", is *L. chlorostictus.* However, the specimen examined for morphological comparison (p. 489), AMNH 80076 from Portugalete, Bolivia, is *L. pantherinus.*

2007 *L*[*iolaemus*] *orientalis*—Díaz Gómez, *Check List* 3(2):117

2008 *Liolaemus orientalis orientalis*—Pincheira-Donoso, Scolaro, & Sura, *Zootaxa* 1800:42.

2016 *Liolaemus orientalis*—Etheridge & Frost (partim), *Liolaemidae* 43. These authors included *L. chlorostictus* as a subspecies of *L. orientalis,* following Laurent (1993 "1991").

2016 *Liolaemus orientalis orientalis*—Etheridge & Frost, *Liolaemidae* 43.

2016 *Liolaemus pantherinus*—Etheridge & Frost (partim), *Liolaemidae* 46. These authors included *L. islugensis* in the synonymy of *L. pantherinus,* following Pincheira-Donoso & Núñez (2005).

2020 *Liolaemus pantherinus*—Ruiz de Gamboa & Ortuz, *Gayana* 84(1):86.

Heterochresonymy:

1942 *Liolaemus pantherinus*—Mertens, *Beiträge von Fauna Perus* 269. The referred specimens belong to *L. melanogaster* Laurent 1992.

1966 *Liolaemus pantherinus*—Donosos-Barros, *Reptiles de Chile* 327. Misidentification of lizards belonging to *L. schmidti* (Marx 1960).

1992 *Liolaemus pantherinus*— Núñez & Jaksic, *xxx* 80. These authors followed the tradition of Donoso-Barros (1960) and considered *L. islugensis* Ortiz & Marquez 1987 a probable junior synonym of *L. pantherinus, sensu* Donoso-Barros1960 *non* Pellegrin 1909.

1999 *Liolaemus pantherinus*—Dirksen & De la Riva (*partim*), *Graellsia* 206. These authors included UMMZ specimens from Tiraque, Cochabamba, which are *L. fittkaui.*

2000 *Liolaemus pantherinus*—Ramírez *et al.*, *Bull. Inst. Français Études Andines* 29(2):237. These authors erroneously identified a lizard mandible in an owl pellet from Tacna, Peru, as belonging to *L. pantherinus.*

2005 *Liolaemus pantherinus*—Pincheira-Donoso & Núñez, *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:157. These authors followed the tradition of Donoso-Barros (1966) in misapplying the name to lizards belonging to *L. schmidti* (Marx 1960).

2008 *Liolaemus pantherinus*—Pincheira-Donoso, Scolaro, & Sura (partim), *Zootaxa* 1800:42. These authors followed the tradition of Donoso-Barros (1966) in misapplying the name to lizards belonging to *L. schmidti* (Marx 1960).

2016 *Liolaemus pantherinus*—Etheridge & Frost (partim), *Liolaemidae* 46. These authors included *L. islugensis* in the synonymy of *L. pantherinus,* following Pincheira-Donoso & Núñez (2005).

2016 *Liolaemus pantherinus*—Ruiz de Gamboa, *Bol. Chil. Herp.* 3:10. Author did not refer to material or populations, but *L. pantherinus* Pellegrin 1909 is not applicable to any lizards occurring in Chile.

2017 *Liolaemus pantherinus*—Mella Ávila, *Guía de Campo, Reptile de Chile, Vol. 2, Zona Norte* 136. Following Donoso-Barros (1966), this author misapplied the name to lizards belonging to *L. schmidti* (Marx 1960).

Referred material: Syntypes: Bolivia: Potosí: Pulacayo: MNHN RA 1905.344–45. Others: ARGENTINA: Jujuy: Departamento Humahuaca: Photographs CSA 5404, 5413, 5420; BOLIVIA: Chuquisaca: Sucre: AMNH 5251; Oruro: Livichuco: BMNH 1902.5.29.50, Oruro: Poopó: BMNH 1902.5.29.46–49; Potosí: Potosí: AMNH 13495–98, BMNH 1902.5.29.36–45, KU 160198–208, MCZ 8062; Potosí: Paso Mazo Cruz ("Abra de Macho Cruz"): MCZ R-101275, Potosí: Portugalete: AMNH 80076; Potosí: Uyuni: AMNH 13494, BMNH 1902.5.29.51–58, MCZ R-8056; Potosi: Uyuni: Cerro Escalona: CBF KIRI-552–53; Tarija: Cordillera de Sama: MNCN uncataloged, field numbers 8315, 8389, 8392; Department Unknown: Upper Pilcomayo Basin: ZMB 26405 (Holotype of *L. annectens orientalis*); ZSM 26/1924/1–2 (Syntypes of *L. annectens orientalis*), ZSM 281/1989/1–2 (Syntypes of *L. annectens orientalis*).

Liolaemus schmidti (Marx)

1960 *Ctenoblepharis schmidti* Marx, *Fieldiana Zool.* Type locality: Stated as "40 miles east of San Pedro, Antofagasta Province, Chile" by Marx and corrected in this work to "San Pedro de Inacaliri river valley between the localities of Ojos de San Pedro and Inacaliri, Loa Province, Antofagasta Region, Chile". Holotype: FMNH 5759, by original designation.

1966 *Liolaemus pantherinus*—Donosos-Barros (*partim, non* Pellegrin 1909), Reptiles de Chile:327. The author applied this name to *L. schmidti* from Ollagüe and the vicinity of Tatio in the Antofagasta Region of Chile. The lizard in his Plate 21 representing *L. pantherinus* is *L. schmidti.*

1966 *Liolaemus signifer*—Donoso-Barros (*partim*), Reptiles de Chile:329. The author applied this name to *L. schmidti* from the Altiplano of the Antofagasta Region of Chile and southern Bolivia. The lizard in his Plate 21 representing *L. signifer* is *L. schmidti.*

1966 *Ctenoblepharis schmidti*—Donoso-Barros (*partim*), Reptiles de Chile:342. The author included a verbatim translation of the Marx's (1960) description but in his Plate 24 depicted a specimen later to become the holotype of *L. erroneus.*

1970 *Ctenoblepharis schmidti*—Peters & Donoso-Barros, *U.S. Nat. Mus. Bull.* 297:104.

1984 *Liolaemus schmidti*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". First use of combination. Cei (1979) placed *Ctenoblepharis schmidti* in *Liolaemus* but

did not use this combination in the paper. Yáñez & Núñez (1982) used the new combination but for a specimen now assignable to *L. erroneus.*

1987 *Liolaemus islugensis* Ortiz & Marquet, *Gayana, Zool.* 51(1–4):59, Type locality: "Colchane a 3.850 m, Provincia de Iquique, Chile (19°42'S, 68°53'W)", Holotype: MZUC 10931. New synonymy.

1989 *Liolaemus islugensis*—Marquet *et al.*, *Oecologia* 81:16.

1995 *Liolaemus islugensis erguetae* Laurent (*partim*), Type locality: "Laguna Colorada"; *L. erguetae* paratypes CBF 1296–98 and FML 3207 are specimens of *L. schmidti*.

1999 *Liolaemus islugensis*—Dirksen & De la Riva (*partim*), *Graellsia,* 55:206. These authors included the type series of *L. islugensis erguetae* as *L. islugensis*, which includes specimens of *L. schmidti*, from Laguna Colorada and Salar de Chalviri but did not mention *L. islugensis erguetae.*

1999 *Liolaemus schmidti*—Dirksen & De la Riva, *Graellsia,* 55:206. These authors correctly included the FMNH series from Julaca as the first record of *L. schmidti* for Bolivia.

2002 *Liolaemus schmidti*—Pincheira-Donoso, *Not. Mens. Mus. Nac. Hist. Nat. Chile* XX:20. Included *L. schmidti* as part of the Bolivian reptile fauna.

2002 *L*[*iolaemus*] *islugensis*—Valladares *et al.*, *Rev. Chil. Hist. Nat*. 73:474.

2002 *L*[*iolaemus*] *schmidti*—Valladares *et al.*, *Rev. Chil. Hist. Nat*. 73:474. These authors (p. 489) correctly included the SDSU series from Cariquima, Chile and the FMNH series from Julaca, Bolivia.

2004 *Liolaemus andinus*—Núñez, *Not. Mens. Mus. Nac. Hist. Nat. Chile*. :29. Núñez assigned BMNH 2277–79 to *L. andinus* but both are in fact *L. schmidti.*

2004 *Liolaemus pleopholis*—Núñez, *Not. Mens. Mus. Nac. Hist. Nat. Chile*. :30. Núñez assigned BMNH 2277 to *L. pleopholis* but it is in fact *L. schmidti.*

2005 *Liolaemus (Eulaemus) andinus*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:152. These authors unjustifiably included *L. schmidti, L. poecilochromus* Laurent 1986, and *L. molinai* in the synonymy of *L. andinus.* Specimens in their Figure 22 are *L. erroneus*.

2005 *Liolaemus (Eulaemus) erguetae*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:157. Specimen in their Figure 23 is *L. schmidti.*

2005 *Liolaemus (Eulaemus) pantherinus*—Pincheira-Donoso & Núñez, *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:164.

2005 *Liolaemus (Eulaemus) signifer*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:172. In their list of material examined for *L. signifer* (their p. 450), these authors included BMNH 1902.5.29.63–73 from Uyuni, Bolivia, which are all *L. schmidti*.

2005 *Liolaemus multicolor*—Ramírez Leyton & Pincheira-Donoso (*partim*), *Fauna del Altiplano y Desierto de Atacama,* 135. Lizard in photograph on their p. 136 is *L. schmidti*.

2005 *Liolaemus pantherinus*—Ramírez Leyton & Pincheira-Donoso

2016 *Liolaemus pantherinus*—Etheridge & Frost (*partim*), *Liolaemidae* 46. These authors included *L. islugensis* in the synonymy of *L. pantherinus,* following Pincheira-Donoso & Núñez (2005).

2016 *Liolaemus schmidti*—Etheridge & Frost, *Liolaemidae* 56.

2016 *Liolaemus islugensis*—Ruiz de Gamboa, *Bol. Chil. Herp.* 3:9.

2016 *Liolaemus schmidti*—Ruiz de Gamboa, *Bol. Chil. Herp.* 3:10.

2016 *Liolaemus islugensis*—Demangel Miranda, *Reptiles en Chile*, 274.

2016 *Liolaemus* cf. *islugensis* Demangel Miranda, *Reptiles en Chile*, 278.

2016 *Liolaemus* cf. *pantherinus* Demangel Miranda, *Reptiles en Chile*, 378.

2017 *Liolaemus pantherinus*—Mella Ávila, *Guía de Campo, Reptile de Chile, Vol. 2, Zona Norte*, 136. Following Donoso-Barros (1966), this author misapplied the name to lizards belonging to *L. schmidti* (Marx 1960).

2018 *L*[*iolaemus*] *islugensis*—Aguilar-Puntriano *et al. Ecol. Evol.* 8(23):11403.

2020 *Liolaemus islugensis*—Ruiz de Gamboa & Ortuz, *Gayana* 84(1):86.

Heterochresonymy:

1966 *Ctenoblepharis schmidti*—Donoso-Barros, *Reptiles de Chile,* cxx. The illustration in his Plate 24 was based on the future holotype of *L. erroneus* Núñez & Yánez 1984 "1983-1984".

1982 *Liolaemus schmidti*—Yáñez & Núñez, *Not. Mens. Mus. Nac. Hist. Nat. Chile* 303–304: 12. The specimen identified as the second record of *L. schmidti* for Chile has been subsequently identified as *L. molinai* Valladares *et al.* by J. Troncoso-Palacios (*in litt.*).

1984 *C[tenoblepharis] schmidti*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". The seven MZUC specimens referred to as *C. schmidti* are in fact *L. erroneus* (Ruiz de Gamboa, *in litt.*).

1984 *Liolaemus schmidti*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". The seven MZUC specimens referred to as "*C. schmidti* (actualmente *Liolaemus schmidti – sensu* Cei 1979 –)" are in fact *L. erroneus* (Ruiz de Gamboa, *in litt.*).

1992 *Liolaemus schmidti*—Núñez (*partim*), *Smith. Herp. Info. Serv.* 91:13. *Liolaemus schmidti* from Salar de Tara (i.e., type locality of *L. molinai*) and Laguna Lejía are *L. erroneus.*

2008 *Liolaemus schmidti*—Abdala *et al.* (*partim*), *Herpetologica* 64(4):471. Specimens FML 1192 and FML 1197 were included as *L. schmidti* in list of material examined but these correspond to *L. erroneus*.

2018 *L*[*iolaemus*] cf. *schmidti* Aguilar-Puntriano *et al. Ecol. Evol.* 8(23):11403. These lizards correspond to *L. omorfi* Demangel *et al.* 2015.

Referred material: Holotype: CHILE: Antofagasta: Río San Pedro de Inacaliri valley, between Ojos de San Pedro and Inacaliri: FMNH 5759; Others: BOLIVIA: Potosí: Julaca: FMNH 204525–26; Potosí: Uyuni: BMNH 1902.5.29.63–73; Potosí: Laguna Colorada: CBF 0715–l6, 296–97 (Paratypes of *L. islugensis erguetae*), CBF 3495, FML 3207 (Paratype of *L. islugensis erguetae*), MNCN 48666–67; Potosí: Nor Chichas: MCZ R-101277; Potosí: road between Polulos and Cerrillos: MNCN 48647; Potosí: Salar de Uyuni: Cerro Isla Chica: MNCN 39912–13; Potosí: Salar de Uyuni: Isla del Pescado: MNCN 39894–95; CHILE: Antofagasta: Río San Pedro de Inacaliri valley, between Ojos de San Pedro and Inacaliri: FMNH 5760 (allotype); Antofagasta: near San Pedro Volcano: SSUC 328–27; Antofagasta: Ojos de San Pedro: MVZ 66807–08; Antofagasta: Río San Pedro:

AMNH 85773; Tarapacá: Cariquima: AMNH 131850–51, BMNH 1977 2277–278, CM 65045–46, MCZ R-154201–04, SDSU 1601–1603; Tarapacá: Colchane: MZUC 10931–32 (Holotype and Allotype of *L. islugensis*), 10935, 10944, 23699–700.

Liolaemus erroneus (Núñez & Yáñez)

1966 *Ctenoblepharis schmidti*—Donoso-Barros (*partim*). The illustration of the lizard representing *C. schmidti* in his Plate XXIV was based on the future holotype of *L. erroneus*.

1982 *Liolaemus schmidti*—Yáñez & Núñez, *Not. Mens. Mus. Nac. Hist. Nat. Chile* 303–304: 12. The referred specimen, now MNHNCL HERP 1074, is presently cataloged as *L. andinus* (Núñez & Gálvez, 2015:52).

1984 *Ctenoblepharis erroneus* Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". Type locality: "Antofagasta, Depto. Atacama", Chile. Holotype: Universidad de Concepción 002063, by original designation.

1984 *C[tenoblepharis] schmidti*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". The seven MZUC specimens referred to *C. schmidti* are in fact juvenile *L. erroneus* (M. Ruiz de Gamboa, *in litt.*).

1984 *Liolaemus schmidti*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 40:91, "1983–1984". The seven MZUC specimens referred to as "*C. schmidti* (actualmente *Liolaemus schmidti – sensu* Cei 1979 –)" are in fact *L. erroneus* (M. Ruiz de Gamboa, *in litt.*).

1992 "*Ctenoblepharys" erroneus*—Núñez & Yáñez, *Bol. Mus. Nac. Hist. Nat. Chile* 43:80.

1992 *Liolaemus schmidti*—Núñez (*partim*), *Smith. Herp. Info. Serv.* 91:13. The *Liolaemus schmidti* specimens from Salar de Tara (i.e., type locality of *L. molinai*) and Laguna Lejía are *L. erroneus*.

1995 *Liolaemus erroneus*—Etheridge, *Am. Mus. Novit.* 3142:32. First use of combination.

1995 *Liolaemus (Eulaemus) islugensis erguetae* Laurent, *Cuad. Herp.* 9(1):2. Type locality: "Laguna Colorada (22º 17'S, 67º 47' W)", Potosí Department, Bolivia. Holotype: CBF 1293. Paratypes CBF 1296–98 and FML 3207 are *L. schmidti*.

1999 *Liolaemus islugensis*—Dirksen & De la Riva (*partim*), *Graellsia*. These authors included the type series, which includes specimens of *L. schmidti,* from Laguna Colorada and Salar de Chalviri but did not distinguish between *L. islugensis* and *L. islugensis erguetae*.

2000 *Liolaemus islugensis erguetae*—Etheridge & Espinoza, *Smith. Herp. Info. Serv.* 126:6.

2001 *Liolaemus erroneus*—Núñez & Veloso,

2002 *Liolaemus erroneus*—Valladares, Etheridge, Schulte, Manríquez & Spotorno, *Rev. Chil. Hist. Nat*. 73:474.

2002 *Liolaemus molinai* Valladares, Etheridge, Schulte, Manríquez & Spotorno, *Rev. Chil. Hist. Nat*. 73:477. Type locality: Not explicitly designated, however, localities are stated as "Salar de Tara, ubicado en el altiplano de la Región de Antofagasta, Chile (25º 50'S, 67º 16'O)" and "Farellones de Tara, Provincia del Loa, Segunda Región de Antofagasta, Chile". The given latitude of "25º 50'S" is in error and the correct latitude is approximately 23º 00' S. Holotype: MNHNC 3174.

2002 *Liolaemus erguetae*—Pincheira-Donoso & Núñez, *Not. Mens. Mus. Nac. Hist. Nat. Chile* 59:41. These authors recognized *L. erguetae* as a valid species after placing *L. islugensis* in the synonymy of *L. pantherinus*.

2005 *Liolaemus (Eulaemus) andinus*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:152. These authors unjustifiably included *L. schmidti, L. poecilochromus* Laurent 1986, and *L. molinai* in the synonymy of *L. andinus*. Specimens in their Figure 22 are *L. erroneus*.

2005 *Liolaemus (Eulaemus) erguetae*—Pincheira-Donoso & Núñez (*partim*), *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:157. Specimen in their Figure 23 is *L. schmidti.*

2005 *Liolaemus (Eulaemus) multicolor*—Pincheira-Donoso & Núñez, *Pub. Ocas. Mus. Nac. Hist. Nat. Chile* 350:161. Specimen in their Figure 23 is *L. erroneus.*

2005 *Phrynosaura erronea*—Ramírez Leyton & Pincheira-Donoso, *Fauna del Altiplano y Desierto de Atacama,* 147. First use of combination.

2008 *Liolaemus schmidti*—Abdala & Quinteros, *Cuad. herpetol.* 22(1):47. These authors included FML 1192 and FML 1197 as *L. schmidti* in list of material examined, but both are *L. erroneus*.

2008 *Liolaemus erroneus*—Pincheira-Donoso, Scolaro, & Sura, *Zootaxa* 1800:46.

2013 *Liolaemus schmidti*—Abdala *et al.* (*partim*), Rev. Biol. Trop. 61(4):1583. These authors included FML 1192 and FML 1197 as *L. schmidti* in list of material examined, but both are *L. erroneus*.

2016 *Liolaemus erroneus*—Etheridge & Frost, *Liolaemidae,* 20.

2016 *Liolaemus erroneus*—Ruiz de Gamboa, *Bol. Chil. Herp.* 3:9.

2016 *Liolaemus erguetae*—Demangel Miranda, *Reptiles en Chile,* 214.

2016 *Liolaemus molinai*—Demangel Miranda, *Reptiles en Chile,* 338.

2016 *Liolaemus erroneus*—Demangel Miranda, *Reptiles en Chile,* 588.

Referred material:

Holotype: CHILE: Antofagasta: "cacerío, camino a Tumbe" (road to the settlement of Tumbre, a locality east of the Salar de Atacama): MZUC 002063 (presumed lost), topotypes: MZUC 0020XX-XX, FML 1192; Antofagasta: Between Aguas Calientes and Cortaderal: BMNH 92.4.19.8; Antofagasta: Farellones de Tara: MNHNC 2162–63, 3174–75, 3423–28, SDSU 4012–3; Antofagasta: Volcán Tatio: FML 1197, USNM 165640; BOLIVIA: Potosí: Laguna Colorada: CBF 1293–95, 1296–98, 1300; FML 3208; Potosí: Salar de Chalviri: CBF 1299

Liolaemus chlorostictus Laurent 1993 "1991"

1993 *Liolaemus orientalis chlorostictus* Laurent, *Acta Zool. Lilloana* 40(2):98. Type locality: "Cuesta de Fundiciones, a 42 km al este de Minas Pirquitas (22° 41' S, 66° 31' W), Dpto. Rinconada, 4150 m", Jujuy Province, Argentina. Holotype: FML 02284. Printed date of issue was 1991, but not published until early1993 (Cei, 1993:745).

1993 *Liolaemus orientalis chlorostictus*—Cei, *Reptiles del Noroeste, Nordeste y Este de la Argentina* 746.

1995 *Liolaemus (Eulaemus) orientalis chlorostictus*—Laurent, *Cuad. Herp.* 9(1):1.

2000 *L*[*iolaemus*] *orientalis*—Schulte *et al.*, *Biol. J. Linn. Soc.* 69:78.

2002 *L*[*iolaemus*] *orientalis*—Valladares et al. (partim), *Rev. Chil. Hist. Nat*. 73:475. The specimen referred to as *L. orientalis* that was utilized for the molecular analysis,

GenBank AF099247 (SDSU 3517) from "15.5 km E Orosmayo on Ruta Prov. 70, Dpto. Rinconada, Prov. Jujuy", is *L. chlorostictus.* However, the specimen examined for morphological comparison (p. 489), AMNH 80076 from Portugalete, Bolivia, is *L. pantherinus.*

2005 *L*[*iolaemus*] *orientalis chlorostictus*—Langstroth, *Kempffiana* 1(1):110.

2007 *L*[*iolaemus*] *chlorostictus*—Díaz Gómez, *Check List* 3(2):117. First use of the binomial.

2008 *L*[*iolaemus*] *chlorostictus*—Abdala & Quinteros, *Cuad. Herp.* 22(1):39.

2008 *Liolaemus orientalis chlorostictus* —Pincheira-Donoso, Scolaro, & Lura, *Zootaxa* 1800:42.

2013 *Liolaemus chlorostictus*—Avila, Martinez, & Morando, *Zootaxa* 3616(3):206.

2016 *Liolaemus orientalis chlorostictus*—Etheridge & Frost, *Liolaemidae,* 20.

Referred material:

Holotype: ARGENTINA: Jujuy: Rinconada: Cuesta de Fundiciones: FML 02284. ARGENTINA: Jujuy: Rinconada: 15.5 km E Orosmayo: SDSU 3517–19.