

## TWO NEW SPECIES OF *LIOLAEMUS* (IGUANIA: LIOLAEMIDAE) FROM THE PUNA OF NORTHWESTERN ARGENTINA

CRISTIAN SIMÓN ABDALA<sup>1</sup>, ANDRÉS SEBASTIÁN QUINTEROS<sup>2</sup>, AND ROBERT E. ESPINOZA<sup>3,4</sup>

<sup>1</sup>Instituto de Herpetología, Fundación Miguel Lillo, CONICET and Cátedra de la REHM, Facultad de Ciencias Naturales and IML, Miguel Lillo 251, Tucumán 4000, Argentina

<sup>2</sup>Cátedra de Anatomía Comparada and IBIGEO-CONICET, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Avenida Bolivia 5150, Salta 4400, Argentina

<sup>3</sup>Department of Biology, California State University, Northridge, Northridge, CA 91330-8303, USA

**ABSTRACT:** We describe two new species of *Liolaemus* belonging to the *montanus* series. The new species are closely related to *L. dorbignyi*, but are disjunctly distributed with respect to this taxon. Both new species exhibit unique color patterns, which, along with differences in squamation, differentiate the two new taxa from the other species in the series. Both new species are saxicolous and inhabit rocky hills in the Puna regions of northwestern Argentina. One occurs in the Cerro de la Virgen, Nevados de Cachi and Nevados de Palermo of Salta Province. The other is known only from its type locality in the Cerro El Pichao of Tucumán Province.

**RESUMEN:** Describimos dos nuevas especies de *Liolaemus* pertenecientes a la serie *montanus*. Las nuevas especies están cercanamente relacionadas a *L. dorbignyi*, pero presentan una distribución disjunta respecto a este taxón. Las nuevas especies presentan un patrón de coloración único, con diferencias en escamación, lo que las distingue de las otras especies de la serie. Ambas son saxícolas y habitan zonas rocosas en regiones de la Puna del Noroeste de Argentina. Una habita en el Cerro de la Virgen, Nevados de Cachi y Nevados de Palermo de la Provincia de Salta. La otra es conocida solo de su localidad tipo en el Cerro El Pichao en la Provincia de Tucumán.

**Key words:** Argentina; *Eulaemus*; Liolaemidae; *Liolaemus*; Lizard; New species; Puna; Taxonomy

THE GENUS *Liolaemus* includes approximately 200 species of lizards that are distributed in southern South America from the Andes of central Perú to Tierra del Fuego in southern Argentina. Over this vast landscape *Liolaemus* species inhabit a diversity of semiarid to arid habitats ranging from the hot sandy beaches of Rio de Janeiro to the cool bunchgrass-dominated Altiplano or Puna region of the Andes. The Puna is a high-elevation (2700–4400 m) plateau of the Andean cordillera in northwestern Argentina, southern Bolivia, northeastern Chile, and southern Perú (21° 45'–26° 45' S). The climate of the Puna is characterized as arid and cool, with high winds, intense solar radiation by day, and subfreezing temperatures possible throughout the year (Martínez Carretero, 1995; Piacentini et al., 2003). Despite these challenging environmental conditions, the Puna is home to many species of *Liolaemus*, including numerous endemics (Díaz Gómez, 2007),

and a number of recently described species (e.g., Abdala and Díaz Gómez, 2006; Abdala and Lobo, 2006; Lobo and Espinoza, 2004; Lobo et al., 2007; Martínez Oliver and Lobo, 2002; Quinteros et al., 2008; Valladares et al., 2002). These new discoveries, however, may be just the tip of the iceberg. Indeed, with an average of nearly five new species described annually for the past 10 y (1998–2007), the known diversity of *Liolaemus* is growing at the fastest rate in its history (Fig. 1).

One of the consequences of the large number of species and broad geographic distribution of *Liolaemus* is that its taxonomic history is long and complex (see Etheridge, 1995; Etheridge and Espinoza, 2000); however, recent research on the relationships among the major lineages of this genus (and its many aliases) has provided some stability. Laurent (1983, 1985) split *Liolaemus* into two subgenera: *Liolaemus* (grupo Chileno) and *Eulaemus* (grupo Argentino). Cei (1993) also recognized a “super-grupo Argentino,” whose content included species belonging to Laurent’s (1983, 1985) *Eulaemus*. Subsequently, Etheridge

<sup>4</sup> CORRESPONDENCE: e-mail, robert.e.espinoza@csun.edu

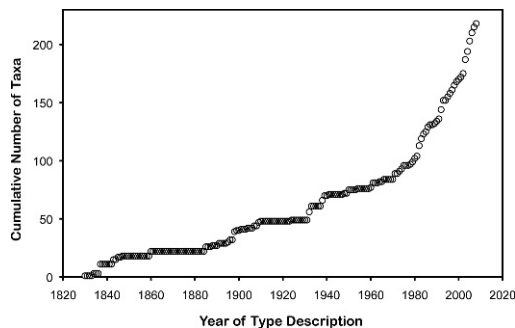


FIG. 1.—Cumulative growth curve of currently recognized *Liolaemus* species and subspecies (revised and updated from Etheridge and Espinoza, 2000). The rate of descriptions of new *Liolaemus* species increased substantially starting in the early 1980s, and within the last 10 yr (1998–2007) has averaged 4.9 per year.

(1995) revised *Liolaemus* and two closely related genera (*Ctenoblepharys* and *Phymaturus*) and proposed a morphologically based phylogenetic taxonomy for this clade (currently recognized as Liolaemidae, sensu Frost et al., 2001 or Liolaemini, sensu Schulte et al., 2003). Rather than erecting a traditional classification based on Linnean ranks, Etheridge (1995) proposed informal group names—most of which were already in use—for the major clades of *Liolaemus*. The composition of one of the major *Liolaemus* clades recognized by Etheridge (1995), the *montanus* group, closely resembled that of the subgenus *Eulaemus* of Laurent (1983, 1985). Schulte et al. (2000) conducted the first molecular phylogenetic analysis of the genus, which included 60 species of *Liolaemus* representing most of the previously recognized major lineages. With a few exceptions, the relationships among the major *Liolaemus* clades recovered by Schulte et al. (2000; see also Espinoza et al., 2004) are largely congruent with the taxonomies proposed by Laurent (1983, 1985) and Etheridge (1995). Schulte and coworkers (2000) proposed a new classification, which included Laurent's subgenera *Liolaemus* and *Eulaemus* and sequentially nested subclades: genus (subgenus (section (series))). Within *Eulaemus*, Schulte et al. (2000) recognized two clades: the *lineomaculatus* section and the *montanus* section, the latter closely corresponding to Etheridge's *montanus* group. Within the *montanus* section, Schulte et al. (2000) further recognized

the *montanus* series and the *boulengeri* series, the latter equivalent to Etheridge's (1995) *boulengeri* group (see also Abdala, 2007; Avila et al., 2006, 2008; Espinoza et al., 2004).

The *montanus* series includes more than 50 species of small-to-large-bodied (maximum snout–vent length [SVL] 55–108 mm) *Liolaemus*, most of which are distributed along the Andean cordillera in Argentina, Bolivia, Chile, and Perú. Accordingly, almost all of the species belonging to this clade live at high elevations (reaching 5000 m) and are viviparous (Espinoza et al., 2004). Members of the *montanus* series can be morphologically distinguished from all other *Liolaemus* by three character states: (1) presence of a bladelikey process on the distal posterior tibia (Etheridge, 1995), which is associated with (2) a greatly hypertrophied *M. tibialis anticus* (Abdala et al., 2006), and (3) absence of an enlarged patch of scales on the posterior thighs. Presence of the latter is a synapomorphy of the *boulengeri* series (Abdala, 2005a,b, 2007; Etheridge, 1995).

Recently, *L. dorbignyi* Koslowsky 1898, one of the oldest known species in the *montanus* series, was redescribed and its type locality was restricted to the Sierra de Fiambalá, Catamarca Province, Argentina (Quinteros et al., 2008). Redefining this polymorphic species and its distribution facilitated the recognition of *L. scrocchii*, a morphologically similar yet undescribed species (Quinteros et al., 2008). Additionally, Quinteros and coworkers (2008) noted that other populations currently ascribed to *L. dorbignyi* required reexamination, as they, too, might prove to be new species. Based on our study of several “*L. dorbignyi*” populations from the provinces of Salta and Tucumán in northwestern Argentina, we describe two additional new species of *Liolaemus* that were previously confused with *L. dorbignyi*. Like *L. scrocchii*, the two species described herein are allopatric with respect to known populations of *L. dorbignyi*, and differ from that species in color pattern and squamation.

#### MATERIALS AND METHODS

We studied the morphological characters traditionally used in *Liolaemus* taxonomy including those of Laurent (1985), Cei

(1986, 1993), Etheridge (1993, 1995, 2000), Lobo (2001), and Abdala (2002, 2003, 2007). Unless otherwise specified, we followed Smith's (1946) terminology for our descriptions of squamation and Frost (1992) for neck-fold terminology. Descriptions of body-color patterns followed Lobo and Espinoza (1999). Descriptions of color in life for the new species were based on observations made in the field or from photographs of specimens taken soon after capture. Sexual maturity was assessed via examination of gonads (for previously dissected specimens) or a combination of body size and the presence of secondary sexual characteristics (see Valdecantos and Lobo, 2007; Valdecantos et al., 2007). Tissue (liver) samples were collected from paratypes of each new species (MCN 2183 and 2184), minced, flushed with 95% ethanol, and stored in 95% ethanol in 1.5 ml cryovials. Measurements and scale counts were recorded from specimens that were fixed in 10% formalin and preserved in 70% ethanol. Body and scale measurements were taken with digital calipers to the nearest 0.02 mm. When necessary, a binocular dissecting microscope (10–40×) was used to count and characterize scales. Where bilateral, scale counts and mensural data were taken from the right side of the lizards.

For purposes of diagnosing the new species described herein, we examined the type series or topotypes of other members of the *montanus* series whenever possible (Appendix I). However, because this clade includes more than 50 species (many known only from type material) that are distributed over a vast area in four countries, not all of the taxa in the *montanus* series were available to us for study. Consequently, we relied secondarily on the type descriptions (e.g., those cited Etheridge and Espinoza, 2000) and recent redescriptions (e.g., Pincheira-Donoso and Núñez, 2005) of the following taxa: *L. audituvelatus*, *L. aymararum*, *L. disjunctus*, *L. erroneus*, *L. fabiani*, *L. filiorum*, *L. foxi*, *L. hajeki*, *L. insolitus*, *L. islugensis arguetae*, *L. i. islugensis*, *L. jamesi pachecoi*, *L. juanortizi*, *L. manueli*, *L. melanogaster*, *L. molinai*, *L. ortizi*, *L. pantherinus*, *L. patriciaturrae*, *L. pleopholis*, *L. poconchilensis*, *L. polystictus*, *L. robertoi*, *L. robustus*, *L. rosenmanni*, *L. thomasi*, *L. torresi*, and *L.*

*williamsi*. These unexamined taxa are distributed far out of the range of the species described herein (most are from Chile or Perú), and are thus unlikely to be confused with the new taxa. We included subspecies in our comparisons because some of these are diagnosable and disjunct from the nominal form and thus may prove to be independent lineages in the future. In total, we examined 624 specimens from nine institutions (Appendix I). Institutional abbreviations follow Leviton et al. (1985) with the addition of the Museo de Ciencias Naturales, Salta (MCN) and the Museo de la Plata, Buenos Aires (MLP.S), both of which are in Argentina.

#### SPECIES DESCRIPTIONS

##### *Liolaemus huayra* sp. nov.

*Holotype*.—FML 18069. Adult male. Cerro el Pichao, Sierra de Quilmes, Departamento Tafí del Valle, Provincia de Tucumán, Argentina (26° 22' 26.7" S, 66° 04' 54.2" W; 3545 m). Collected by C. S. Abdala and A. S. Quinteros, 21 November 2006.

*Paratypes*.—MCN 2184. Adult male. Same data as holotype. FML 1219-1-7. Two adult males, two adult females, and three juveniles. Puesto Pacheco, climbing [by horse] from Pichao, Sierra de Quilmes, Departamento Tafí del Valle, Provincia de Tucumán, Argentina. Collected by O. Pagaburo and E. Teran, 8 March 1982.

*Diagnosis*.—*Liolaemus huayra* is a member of the *montanus* series (sensu Schulte et al., 2000), or the non-*boulengeri* group members of the *montanus* group (sensu Etheridge, 1995), which are characterized as possessing a bladelike process on the distal posterior tibia (Etheridge, 1995) that is associated with a greatly hypertrophied *M. tibialis anticus* (Abdala et al., 2006), and lacking an enlarged patch of scales on the posterior thighs (Etheridge, 1995). *Liolaemus huayra* is most similar to *L. dorbignyi*, but differs from this species and all other members of the *montanus* series in its unique dorsal color pattern of orange-brown background with irregular dark orange transverse paravertebral bars (Fig. 2a). *Liolaemus huayra* also has keeled, slightly imbricate dorsals, whereas the dorsals of *L. dorbignyi* are slightly keeled and

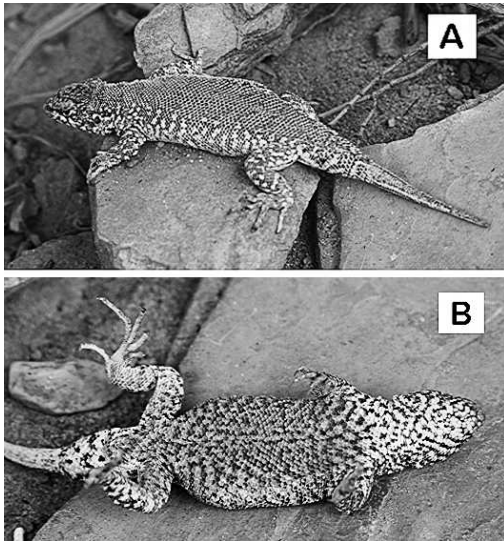


FIG. 2.—(A) Dorsal and (B) ventral views of the holotype of *Liolaemus huayra* (FML 18069).

imbricate. *Liolaemus huayra* has keeled dorsals differing from *L. inti* sp. nov. (described below), which has slightly keeled dorsals; *L. huayra* has supernumerary pores, which are not present in *L. inti*, also the dorsal color patterns are different between these two taxa. Among other members of the *montanus* series, *L. huayra* is a robust, large-bodied lizard (maximum SVL 94.3 mm), which distinguishes most adult specimens of this new species from *L. andinus*, *L. audituvelatus*, *L. eleodori*, *L. erroneus*, *L. etheridgei*, *L. fabiani*, *L. famatinae*, *L. filiorum*, *L. fittkai*, *L. griseus*, *L. hajeki*, *L. huacahuasicus*, *L. insolitus*, *L. islugensis*, *L. manuela*, *L. molinai*, *L. montanus*, *L. multicolor*, *L. orko*, *L. ortizi*, *L. pantherinus*, *L. poconchilensis*, *L. poecilochromus*, *L. pulcherrimus*, *L. reichei*, *L. rosenmanni*, *L. ruibali*, *L. torresi*, and *L. vallecurensis*, which are smaller (maximum SVL 50–85 mm). *Liolaemus huayra* has flat, slightly imbricate, keeled dorsals, unlike *L. andinus*, *L. audituvelatus*, *L. islugensis arguetae*, *L. filiorum*, *L. forsteri*, *L. insolitus*, *L. islugensis*, *L. molinai*, *L. patriciaturrae*, *L. poecilochromus*, *L. robertoi*, *L. rosenmanni*, *L. scrocchii*, *L. schmidti*, and *L. stolzmanni*, which have smooth juxtaposed dorsals, from *L. manuela* (smooth and slightly imbricate), and *L. aymararum*, *L. etheridgei*, *L. fittkai*,

*L. huacahuasicus*, *L. montanus*, *L. ortizi*, and *L. thomasi*, which have imbricate, strongly keeled, mucronate dorsals. *Liolaemus chlorostictus*, *L. eleodori*, *L. jamesi*, *L. juanortizi*, *L. orientalis*, *L. poconchilensis*, *L. robustus*, *L. scrocchii*, *L. signifer annectens*, *L. s. signifer*, and *L. stolzmanni* have slightly keeled, juxtaposed dorsals. Number of scales around midbody in *L. huayra* ranges 53–64, which distinguishes this new species from *L. andinus*, *L. disjunctus*, *L. duellmani*, *L. eleodori*, *L. foxi*, *L. islugensis arguetae*, *L. i. islugensis*, *L. molinai*, *L. multicolor*, *L. nigriceps*, *L. patriciaturrae*, *L. pleopholis*, *L. poecilochromus*, *L. pulcherrimus*, *L. robertoi*, *L. rosenmanni*, *L. ruibali*, *L. s. signifer*, and *L. vallecurensis*, which have 64–110 midbody scales, and from *L. juanortizi*, which have fewer scales around midbody (39–53). Both of the adult female *L. huayra* examined have preloacal pores, in contrast to female *L. andinus*, *L. audituvelatus*, *L. aymararum*, *L. duellmani*, *L. fabiani*, *L. griseus*, *L. hajeki*, *L. i. islugensis*, *L. jamesi*, *L. melanogaster*, *L. polystictus*, *L. puritamensis*, *L. robertoi*, *L. rosenmanni*, *L. ruibali*, *L. s. signifer*, *L. stolzmanni*, and *L. vallecurensis*, which lack preloacal pores.

*Description of the holotype*.—SVL 94.3 mm. Trunk length 43.4 mm. Head longer (18.8 mm) than wide (17.2 mm). Head height 11.6 mm. Eye diameter 4.4 mm. Interorbital distance 9.6 mm. Orbit–auditory meatus distance 8.2 mm. Auditory meatus height 4.3 mm high, 2.4 mm wide. Orbit–commis-sure of mouth distance 3.0 mm. Internares 3.7 mm. Subocular scale 4.9 mm. Femur length 15.0 mm, tibia 13.0 mm, and foot 23.4 mm. Humerus length 10.2 mm. Tail length 56.4 mm, approximately 40% autotomized.

Dorsal surface of the head smooth, with 18 scales. Rostral wider than tall, bordered by six scales. Mental larger than rostral, trapezoidal, bordered by four scales. Nasal not in contact with rostral. Two internasals. Nasal surrounded by eight scales, separated from canthal by one scale. Six scales between frontal and supercilliaris. Nine scales between frontal and rostral. Frontal divided horizontally into three scales. Two postrostrals. Interparietal smaller than parietals, in contact with seven



scales. Orbital semicircles complete. Preocular separated from lorilabial row by one scale. Two scales along anterior margin of auditory meatus and none along the upper margin. Six smooth temporals. Five lorilabials in contact with subocular. Eleven supralabials, none in contact with subocular. Five supraoculars. Nine lorilabials. Six infralabials, second in contact ventrally with two scales. Five chinshields, second pair separated by two scales.

Sixty-three scales around midbody. Fifty-four round, slightly imbricate, keeled dorsals from occiput to hind limbs. Twenty-nine scale rows along dorsum. Scales of flank same size and shape as dorsals. Ventrals same size as dorsals, flat, juxtaposed. Thirty-four smooth weakly imbricate gulars. Eight preloacal and four supernumerary pores. Antehumeral scales flat, larger or equal in size to dorsals. Postauricular, rectal, and longitudinal folds present. Scales on longitudinal fold granular and smooth. Fourth finger with 20 subdigital lamellae; fourth toe with 27. Infracarpals and infratarsals flat, imbricate, trifid.

*Color in life.*—Fig. 2. Head darker than body, dorsally bluish-green, with scattered dark gray to black scales. First two lorilabials bright orange, third and fourth lorilabials share an overlapping orange spot. Trunk orange-brown with nine diffuse, dark orange, paravertebral bars aligned transverse to the body axis (Fig. 2a). Vertebral region dark orange (same as paravertebral bars). Posterior margins of dorsals light blue. Fore- and hind limbs variegated with grey and light bluish-green markings dorsally. Lateral region of body same general color as fore- and hind limbs, but with some white or orange scales. Dorsal tail same color as limbs. Throat pale yellow, with variegated black markings. Gular region with variegated black and white scales. Chest to cloacal region with scattered black scales on bright orange background (Fig. 2b). Thighs light orange. Ventral tail with black spots on light blue background.

*Variation.*—Based on eight paratypes. Head longer (16.7–21.1 mm; mean = 18.1 mm) than wide (13.8–18.6 mm; mean = 15.8 mm). Head height 9.1–12.4 mm (mean = 10.4 mm). Neck wider than head. SVL 73.0–94.3 mm (mean = 84.0 mm), averaging 2.2 times longer than trunk. Tail length 98.8 mm (FML 1219-6).

Width of tail base 8.5–13.4 mm (mean = 11.4 mm). Humerus length 6.7–10.5 mm (mean = 9.0 mm). Tibia length 11.2–15.0 mm (mean = 12.5). Foot length 20.7–25.2 mm (mean = 22.7 mm). Fourth finger length 9.0–10.3 mm (mean = 9.7 mm). Fourth toe length 12.8–15.6 mm (mean = 14.6 mm). Dorsal surface of head smooth or slightly rugose, with 15–18 scales. Seven to eight supercilliaris. Thirteen to 14 upper cilliaris. One row of lorilabials, same size as supralabials. Seven to nine lorilabials. Eight to 11 supralabials. Frontal divided horizontally into two or three scales. Interparietal always smaller than parietals, surrounded by 7–8 scales. Nasal surrounded by 8–9 scales. Six infralabials. Mental in contact with four scales. Six to eight smooth round temporals. Longitudinal, postauricular, and antehumeral folds present. Horizontal fold Y-shaped between the shoulder and the auditory meatus.

Scales around midbody 53–64 (mean = 58.5). Gulars 28–39 (mean = 32.0). Dorsal scales between occiput and hind limbs 52–57 (mean = 54.7). Ventrals 83–92 (mean = 87.3). Males with 7–8 (mean = 7.3) preloacal pores. Aside from the holotype, one male (FML 1219-2) with four supernumerary pores. Females with 3–5 (mean = 4.0) preloacal pores. Dorsals flat, slightly imbricate, keeled. Seventeen to 21 infradigital lamellae on fourth finger and 23–27 on fourth toe.

*Variation in color pattern.*—Only males were observed in life. Only modest variation in color pattern was observed, with differences varying primarily in intensity of color. Females (preserved specimens) have more conspicuous paravertebral spots and a brown background. Juveniles (three preserved specimens) are brown or gray dorsally with numerous tiny black and white spots. Ventrally juveniles are similar to adults.

*Distribution.*—*Liolaemus huayra* is known only from the type locality in the Sierra de Quilmes, near Pichao, Departamento Tafí del Valle, Tucumán, Argentina (Fig. 3, 4).

*Natural history.*—Because only two adult males were collected in nature, we have little natural history information on this new species. *Liolaemus huayra* is a rock-dwelling lizard, which was encountered while basking



FIG. 3.—Habitat at Cerro el Pichao, Sierra de Quilmes, Departamento Tafi del Valle, Provincia de Tucumán, Argentina ( $26^{\circ} 22' 26.7''$  S,  $66^{\circ} 04' 54.2''$  W; 3545 m), the type locality of *Liolaemus huayra*.

from  $\sim 1330$ – $1530$  h approximately two-thirds of the way up a hill on large basaltic rock outcrops at the type locality (Fig. 4). The dominant plant in the area is the bunchgrass *Festuca*, which occurs in virtually a monoculture at the type locality. This species is sympatric with the colubrid *Tachymenis peruviana*.

*Etymology*.—“Huayra” is a Quechuan word, attributable to the indigenous peoples of present-day northern Argentina and southern Bolivia, which means wind or windy. *Liolaemus huayra* inhabits rocky places on the tops of mountains of the Sierra de Quilmes, which is a windy region.

*Liolaemus inti* sp. nov.

*Holotype*.—FML 18399. Adult male. Near 15th station of Via Crucis, Cerro de la Virgen, Cachi Adentro, Departamento Cachi, Provincia de Salta, Argentina ( $25^{\circ} 03' 07.6''$  S,  $66^{\circ} 17' 29.4''$  W; 3938 m). Collected by C. S. Abdala and A. S. Quinteros, 18 November 2006.

*Paratypes*.—MCN 2183. Adult male. Same data as holotype. FML 1669-1-7. One adult male, five adult females, and one juvenile. Cerro de la Virgen, Cachi Adentro, Departamento Cachi, Provincia de Salta, Argentina (3700–3860 m). Collected by O. Pagaburo and E. Pereyra, 21 January 1985.

*Diagnosis*.—*Liolaemus inti* is a member of the *montanus* series (sensu Schulte et al., 2000), or the non-*boulengeri* group members of the *montanus* group (sensu Etheridge,

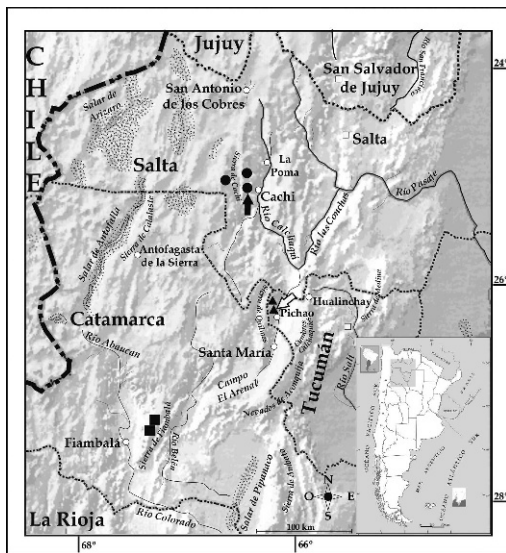


FIG. 4.—Distribution of *Liolaemus huayra* (triangles), *L. inti* (circles), and *L. dorbignyi* (squares). The white arrow indicates the type locality of *L. huayra* and the black arrow indicates the type locality of *L. inti*.

1995), which are characterized as possessing a bladelike process on the distal posterior tibia (Etheridge, 1995) that is associated with a greatly hypertrophied *M. tibialis anticus* (Abdala et al., 2006), and lacking an enlarged patch of scales on the posterior thighs (Etheridge, 1995). The dorsal color pattern of *L. inti*—a bold chain-link fence pattern of irregular black transverse stripes on a bright yellow background (Fig. 5)—distinguishes the new species from all other members of the *montanus* series (and all other *Liolaemus*), and is the principal difference between this new species and *L. chlorostictus* (green with small black spots), *L. disjunctus* (dark dorsum with small light-colored spots), and *L. williamsi* (black with oblique and transverse bands and marks). Furthermore, among members of the *montanus* series, *L. inti* is a robust, large-bodied lizard (maximum SVL 90.4 mm), which distinguishes most adults of this new species from *L. andinus*, *L. audituvelatus*, *L. eleodori*, *L. erroneus*, *L. etheridgei*, *L. fabiani*, *L. famatinae*, *L. fililorum*, *L. fittkaii*, *L. griseus*, *L. hajeki*, *L. huacahuasicus*, *L. insolitus*, *L. islugensis*, *L. manuely*, *L. molinai*, *L. montanus*, *L. multicolor*, *L. ortizi*, *L. orko*, *L. pantherinus*, *L. pleopholis*, *L. poconchilensis*, *L. poecilochromus*, *L. pulcher-*

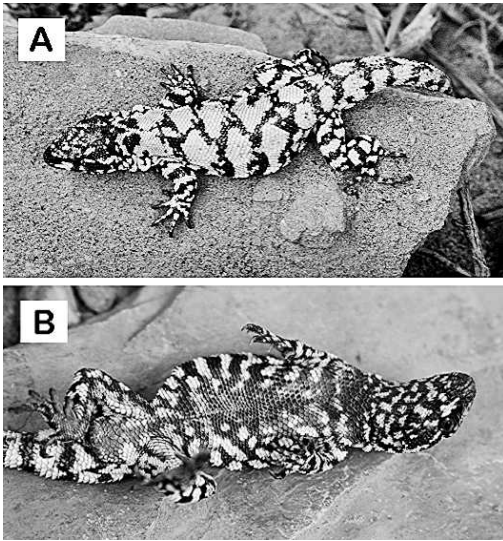


FIG. 5.—(A) Dorsal and (B) ventral views of the holotype of *Liolaemus inti* (FML 18399).

*rimus*, *L. reichei*, *L. rosenmanni*, *L. ruibali*, and *L. vallecurensis*, which are smaller (maximum SVL 50–85 mm). *Liolaemus inti* has flat, weakly imbricate to imbricate and slightly keeled dorsals, which distinguishes this new species from *L. andinus*, *L. audituvelatus*, *L. eleodori*, *L. erroneus*, *L. fililorum*, *L. forsteri*, *L. insolitus*, *L. islugensis erquetae*, *L. i. islugensis*, *L. manueli*, *L. molinai*, *L. patriciaturrae*, *L. poecilochromus*, *L. robertoi*, *L. rosenmanni*, *L. scrocchii*, *L. schmidti*, *L. stolzmanni*, and *L. torresi*, which have smooth dorsals, from *L. huayra*, which have keeled weakly imbricate dorsals, from *L. signifer annectens*, which have slightly keeled and juxtaposed dorsals, and from *L. aymararum*, *L. etheridgei*, *L. fittkawi*, *L. huacahuasicus*, *L. montanus*, *L. ortizi*, and *L. thomasi*, which have imbricate, strongly keeled, and mucronate dorsals. The number of scales around midbody in *L. inti* is 61–76, which distinguishes this new species from *L. andinus*, *L. duellmani*, *L. eleodori*, *L. foxi*, *L. molinai*, *L. multicolor*, *L. nigriceps*, *L. patriciaturrae*, *L. robertoi*, *L. rosenmanni*, and *L. vallecurensis*, which have 77–110 midbody scales, and from *L. aymararum*, *L. dorbignyi*, *L. etheridgei*, *L. fililorum*, *L. fittkawi*, *L. insolitus*, *L. juanortizi*, *L. melanogaster*, *L. ortizi*, *L. robustus*, and *L. stolzmanni*, which have 40–60 midbody scales. Five of seven adult female *L. inti* examined

have 1–6 precloacal pores, in contrast to female *L. andinus*, *L. audituvelatus*, *L. aymararum*, *L. duellmani*, *L. fabiani*, *L. griseus*, *L. hajeki*, *L. islugensis*, *L. jamesi*, *L. melanogaster*, *L. polystictus*, *L. puritamensis*, *L. robertoi*, *L. rosenmanni*, *L. ruibali*, *L. s. signifer*, *L. stolzmanni*, and *L. vallecurensis*, which lack precloacal pores. The absence of supernumerary pores in *L. inti* distinguishes this new species from *L. huayra* sp. nov. and *L. orientalis*.

*Description of the holotype*.—SVL 89.6 mm. Trunk length 44.2 mm. Head longer (19.9 mm) than wide (16.4 mm). Head height 10.7 mm. Eye diameter 5.3 mm. Interorbital distance 10.2 mm. Orbit–auditory meatus distance 7.8 mm. Auditory meatus height 3.5 mm, wide 2.1 mm. Orbit–commissure of mouth distance 2.2 mm. Internares 3.5 mm. Subocular 5.6 mm. Femur length 14.2 mm, tibia 11.4 mm, and foot 22.8 mm. Humerus length 9.5 mm. Tail complete, 117.8 mm.

Dorsal surface of the head smooth, with 17 scales. Rostral wider than tall, bordered by six scales. Mental shorter than rostral, trapezoidal, bordered by four scales. Nasal not in contact with rostral. Two internasals. Nasal surrounded by eight scales, separated from canthal by one scale. Five scales between frontal and supercilliaris. Nine scales between rostral and frontal. Frontal divided horizontally into three scales. Two postrostrals. Interparietal smaller than parietals, in contact with five scales. Orbital semicircles complete. Preocular separated from lorilabials by one scale. Two scales along anterior margin of auditory meatus and two along the upper margin. Eight smooth temporals. Two lorilabials in contact with subocular. Seven supralabials, none in contact with subocular. Five supraoculars. Nine lorilabials. Five infralabials, the second ventrally in contact with two scales. Five chinshields, second pair separated by two scales.

Sixty-six scales around midbody. Fifty-four, round, weakly keeled, slightly imbricate dorsals from occiput to hind limbs. Thirty-three dorsal scale rows. Scales of flanks same size and shape as dorsals. Ventrals same size as dorsals, flat, juxtaposed. Forty-three smooth slightly imbricate gulars. Six precloacal pores. Antehumeral scales flat, smaller than dorsals.



Postauricular, rictal, and longitudinal folds present. Scales of longitudinal fold granular, smooth. Fourth finger with 17 subdigital lamellae; 23 on the fourth toe. Infracarpals and infratarsals flat, imbricate, trifid.

*Color in life.*—Fig. 5. Head darker than rest of body, dorsally black, with some yellow spots and scales. Lateral fields of head with yellow and black spots. Trunk bright yellow, with six irregular black stripes dorsally forming a chain-link fence pattern (Fig. 5a). Stripes fork in the lateral field and cross in the vertebral region. Lateral region of body, fore-, and hind limbs with similar design as dorsum. Tail similar color as body dorsally and ventrally, but yellow color less vibrant. Ventrally, variegated black markings on intense yellow background from mental to cloacal region (Fig. 5b). Gular region black.

*Variation.*—Based on eight paratypes, and four additional specimens. Head slightly longer (14.5–19.1 mm; mean = 16.7 mm), than wide (13.6–17.6 mm; mean = 15.3 mm). Head height 7.5–11.2 mm (mean = 9.3 mm). Neck wider than head. SVL 69.1–90.0 mm (mean = 80.4 mm). SVL averaging 2.1 times longer than trunk. Tail length 87.5–117.8 mm (mean = 102.6 mm). Width of tail base 8.5–12.6 mm (mean = 10.6 mm). Humerus length 8.8–12.9 mm (mean = 10.9 mm). Tibia length 11.4–17.6 mm (mean = 15.0). Foot length 19.8–25.1 mm (mean = 22.2 mm). Fourth finger length 6.3–8.3 mm (mean = 7.6 mm), fourth toe 11.3–14.5 mm (mean = 13.0 mm).

Dorsal surface of head, smooth or slightly rugose, with 13–18 scales. Seven to eight supercilliaris. Thirteen to 16 upper cilliaris. One row of lorilabials same size as supralabials. Six to nine lorilabials. Seven to 10 supralabials. Frontal divided horizontally into 2–4 scales. Interparietal always smaller than parietals, surrounded by 5–8 scales. Nasal surrounded by 6–7 scales. Five to six infralabials. Mental in contact with four scales. Nine to 12 smooth round temporals. Longitudinal, postauricular, and antehumeral folds present. Horizontal fold is Y-shaped between shoulder and auditory meatus. Scales around midbody 61–76 (mean = 67.3). Gulars 29–43 (mean = 34.3). Dorsal scales between occiput and hind limbs 54–66 (mean = 59.5). Ventrals

83–96 (mean = 90.7). Males with 5–7 (mean = 6) precloacal pores. Five of seven females have 1–6 precloacal pores. Dorsals flat, slightly imbricate to imbricate, slightly keeled. Fifteen to 22 infradigital lamellae on fourth finger and 23–30 on fourth toe.

*Variation in color pattern.*—Only adult males were observed in life. Sexually dichromatic. In males the dorsal pattern is similar to that of the holotype, varying in the distribution of the irregular black transverse stripes. One male paratype (FML 1669-4) has five small round spots in each paravertebral field. Gular melanism is incomplete in this paratype, the black gular band is narrower than in holotype. Heads of females (preserved specimens) vary from brown to black dorsally. Dorsally females have 5–6 transverse gray stripes with well-defined black margins on their trunks. In some individuals, the stripes on either side of the paravertebral field join at midline to form a single band. Two paratypes (FML 1669-3, 1669-6) have same paravertebral spots as male paratype FML 1669-4. In these paratypes, the dorsal surface of the limbs is similar in color to dorsum, with irregular black lines and the dorsal tail has the same transverse stripes as body, but these narrow toward the tail tip, forming irregular rings. Ventral color of these paratypes is like that of male paratype FML 1669-4, with gular melanism intense laterally, yet always incomplete. Two females from Nevado de Palermo have same dorsal pattern as paratypes, but in one (FML 1432-1) the background color is black, and the irregular stripes are narrower. Ventrally, the Nevado de Palermo paratypes are similar to the other paratypes. Specimens from Nevado de Cachi (FML 952) have the same pattern, but the irregular stripes are wider and have some light gray scales and spots. Ventrally these specimens are similar to the others.

*Distribution.*—*Liolaemus inti* is known from the type locality in the Cerro de la Virgen, and from Nevados de Cachi (Fig. 6), and Nevados de Palermo, Departamento Cachi, Provincia de Salta, Argentina (Fig. 3).

*Natural history.*—Little natural history information is available for this new species. *Liolaemus inti* is saxicolous, having been observed at the type locality basking during





FIG. 6.—Habitat at Via Crucis, Cerro de la Virgen, Cachi Adentro, Departamento Cachi, Provincia de Salta, Argentina (25° 03' 07.6" S, 66° 17' 29.4" W; 3938 m), the type locality of *Liolaemus inti*.

midday on granite rocks or hiding in rock crevices of large rock outcrops near the top of a hill (Fig. 6). The dominant plant in the area is the bunchgrass *Festuca*. This new species is sympatric with *L. lavillai*.

*Etymology*.—"Inti" is a Quechuan word, attributable to the indigenous peoples of present-day northern Argentina and southern Bolivia, which means sun. The epithet of this new species refers to the bright golden-yellow dorsal and ventral color of *Liolaemus inti*.

#### DISCUSSION

*Liolaemus dorbignyi*, *L. huayra*, *L. inti*, *L. puritamensis*, and *L. scrocchii* occur in the Puna region (3500–4900 m) of Argentina and adjacent Chile and occupy rocky habitats (Núñez and Fox, 1989; Pincheira-Donoso and Núñez, 2005; Quinteros et al., 2008), but other aspects of their natural history are poorly understood. We offer predictions about the biology of these species based on data for *L. puritamensis* and *L. scrocchii*, and the assumption that, given their shared saxicolous habits, other aspects of their biology may also be phylogenetically conserved. Espinoza et al. (2004) studied the evolution of herbivory in liolaemids and found that *L. dorbignyi* (locality data corresponding to *L. scrocchii*; Quinteros et al., 2008) is omnivorous. O'Grady et al. (2005) also analyzed the diet of *L. dorbignyi* (unspecified provenance), and reported that the species is herbivorous. Likewise, pollen, whole flowers, and insect

wings were reported from the scats of *L. puritamensis* (Núñez and Fox, 1989). In light of this information, we predict that *L. dorbignyi*, *L. huayra*, and *L. inti* are omnivorous and likely include a high proportion of plants in their diets. We also predict that these species are viviparous based on their high-elevation distribution and apparently close relationship with *L. puritamensis* and *L. scrocchii*, which are known to be viviparous (Espinoza et al., 2004; Pincheira-Donoso and Núñez, 2005; Schulte et al., 2000).

In recent years, researchers have discovered that many widespread "species" of *Liolaemus* actually constitute complexes of numerous cryptic species. For example, four species have been discriminated from the polymorphic *L. dorbignyi*: *L. huayra*, *L. inti*, *L. puritamensis*, and *L. scrocchii*, and at least one more awaits description. Similar findings have resulted for *L. alticolor* (Lobo and Espinoza, 1999, 2004; Martínez Oliver and Lobo, 2002; Lobo et al., 2007), *L. bibronii* and *L. gracilis* (Morando et al., 2007; Vega et al., 2008), *L. boulengeri* (Abdala, 2002, 2003, 2005a,b, 2007; Avila et al., 2006, 2008), *L. darwinii* (Abdala, 2005c; Abdala and Díaz Gómez, 2006; Abdala and Lobo, 2006; Cabrera and Monguillot, 2006; Cei and Scolaro, 1999; Etheridge, 1992, 1993, 2001; Lobo and Kretzschmar, 1996; Morando et al., 2004; Monguillot et al., 2006), and *L. elongatus* (Avila et al., 2003, 2004; Espinoza et al., 2000; Espinoza and Lobo, 2003; Morando et al., 2003). We predict a similar fate for several other geographically widespread and polymorphic *Liolaemus*: *L. andinus*, *L. chiliensis*, *L. cayanus*, *L. multicolor*, *L. ornatus*, *L. ruibali*, *L. signifer*, and *L. wiegmannii*.

Prior to the revision of Quinteros et al. (2008), *Liolaemus dorbignyi* was considered a geographically widespread and polymorphic species. Indeed, most of the museum specimens that we examined from northwestern Argentina that fit the description of large robust body, variegated ventral pattern, well-developed neck folds, yellow to orange dorsal color, dorsal scales lacking mucrons, and inhabiting rocky places from 3000–4500 m, were assigned to *L. dorbignyi*. This broad characterization, coupled with the uncertain type locality of *L. dorbignyi*, has hindered the

TABLE 1.—Comparison of characters among large-bodied members of the *Liolaemus montanus* series.

Character	<i>L. chlorostictus</i> (n = 18)	<i>L. dorbignyi</i> (n = 25)	<i>L. huayra</i> sp. nov. (n = 9)	<i>L. jamesi</i> (n = 3)	<i>L. inti</i> sp. nov. (n = 13)	<i>L. nigriceps</i> (n = 26)	<i>L. orientalis</i> (n = 21)	<i>L. puritamensis</i> (n = 13)	<i>L. scroochii</i> (n = 25)
Scales around midbody	61–72	48–59	53–64	47–60	61–76	90–98	56–70	47–57	55–68
Dorsals <sup>1</sup>	56–71	45–56	52–57	38–42	54–66	95–104	54–74	40–52	42–53
Ventrals	80–86	77–94	82–93	73–78	83–96	92–109	78–88	80–85	72–98
Gulars	27–31	32–52	28–39	26–31	29–43	36–44	25–34	33–39	34–46
Keels on dorsal scales	Weak	Weak	Distinct	Absent	Weak	Absent	Weak	Absent	Absent
Preloateal pores in males	6–7	5–8	7–8	6–7	5–7	5–6	4–8	4–5	2–10
Preloateal pores in females	2–6	0–6	3–5	0	1–6	0–5	0–3	0	3–6
Maximum SVL (mm)	85.0	98.3	94.3	97.5	90.4	98.0	99.2	91.0	95.0
Maximum tail length (mm)	109.6	117.4	98.8	119.3	117.8	108.9	101.5	95.7	101.3

<sup>1</sup> Counted from occiput to the midline of the thighs.

recognition of undescribed species and apparently caused taxonomic confusion among closely related taxa. For example, Núñez and Fox (1989) described *L. puritamensis* from Baños de Puritama, Chile. Thereafter, Núñez and Jaksic (1992) synonymized *L. puritamensis* with *L. dorbignyi*, but this finding was based (unwittingly) on specimens corresponding to *L. scroochii* (Quinteros et al., 2008). Recently, Pincheira-Donoso and Núñez (2005) revalidated the specific status of *L. puritamensis*, but their comparisons were also made with the same specimens of *L. scroochii*. Since then, specimens ascribed to *L. puritamensis* have been reported from Argentina, ca. 100 km northeast of the type locality in Chile (Quinteros and Abdala, 2007). Thus, *L. puritamensis* may be a trans-Andean species, which is relatively rare among *Liolaemus*, or the population in Argentina represents yet another undescribed species. Additional fieldwork in northwestern Argentina and adjacent Chile, coupled with molecular analyses, may resolve the ranges and discriminate the species boundaries among *L. dorbignyi* and its close relatives.

Several primarily molecular phylogenetic analyses have included members of the *montanus* series (Cruz et al., 2005; Espinoza et al., 2004; Schulte et al., 2000; Valladares et al., 2002). In these studies *L. dorbignyi* (now known to be *L. scroochii*; Quinteros et al., 2008) was grouped as the sister taxon of species or clades including *L. andinus*, *L. multicolor*, and *L. poecilochromus*. These relationships are likely more indicative of limited taxon sampling (i.e., only a single large-bodied *montanus* series species, *L. scroochii*, was included) than the actual relationships among these taxa. More likely, *L. dorbignyi*, *L. puritamensis*, *L. scroochii*, and the two new species described herein, are more closely related to other morphologically similar members of the *montanus* series (e.g., *L. jamesi*, *L. nigriceps*, *L. orientalis*, *L. robustus*, *L. signifer*, and *L. williamsi*), than to *L. andinus*, *L. multicolor*, and *L. poecilochromus*. A phylogenetic analysis with broader sampling among members of the *montanus* series is needed.

*Acknowledgments.*—We are grateful to J. M. Díaz Gómez, R. Etheridge, F. Lobo, and two anonymous

referees for comments on early drafts of this manuscript. We thank A. Leviton and J. Vindum (CAS), E. Lavilla and S. Kretzschmar (FML), B. Duellman and J. Simmons (KU), K. Beaman and D. Kizirian (LACM), F. Lobo (MCN), J. Williams (MLP), D. Wake and B. Stein (MVZ), and R. Etheridge (SDSU) for giving us access to collections under their charge. We appreciate the field assistance of E. Derlindati, R. Guanuco, G. Scrocchi, J. C. Stazonelli, and E. Yampa. We acknowledge the provincial Departments of Fauna of Salta and Tucumán for providing collecting permits (Expediente N° 119-11390/06). ASQ was supported by a graduate fellowship from CONICET. REE was supported by a sabbatical leave from California State University, Northridge, the Universidad Nacional de Salta, and a Fulbright Fellowship. Portions of this study were supported by grants from the Consejo de Investigaciones de la Universidad Nacional de Salta to F. Lobo (CIUNSA, 1236), and from the Consejo Nacional de Investigaciones Científicas y Técnicas to F. Lobo (PIP 5982), F. Cruz (PIP 6287), and E. Lavilla (PIP 5780), and the Consejo de Investigaciones de la Universidad Nacional de Tucumán to R. Montero (CIUNT G315).

#### LITERATURE CITED

- ABDALA, C. S. 2002. Nuevo *Liolaemus* (Iguania: Liolaemidae) perteneciente al grupo *boulengeri* de la provincia de Neuquén, Argentina. Cuadernos de Herpetología 16:3–13.
- ABDALA, C. S. 2003. Cuatro nuevas especies del género *Liolaemus* (Iguania: Liolaemidae), pertenecientes al grupo *boulengeri*, de la Patagonia Argentina. Cuadernos de Herpetología 17:3–32.
- ABDALA, C. S. 2005a. Sistemática y filogenia del grupo de *L. boulengeri* (Iguania: Liolaemidae, *Liolaemus*) en base a caracteres morfológicos y moleculares. Tesis Doctoral, Universidad Nacional de Tucumán, Tucumán, Argentina.
- ABDALA, C. S. 2005b. Dos nuevas especies del género *Liolaemus* (Iguania: Liolaemidae) y redescipción de *Liolaemus boulengeri* (Koslowky, 1898). Cuadernos de Herpetología 19:3–33.
- ABDALA, C. S. 2005c. Una nueva especie del género *Liolaemus* perteneciente al complejo *darwinii* (Iguania: Liolaemidae) de la provincia de Catamarca, Argentina. Revista Española de Herpetología 19:5–17.
- ABDALA, C. S. 2007. Phylogeny of the *boulengeri* group (Iguania: Liolaemidae, *Liolaemus*) based on morphological and molecular characters. Zootaxa 1538:1–84.
- ABDALA, C. S., AND J. M. DÍAZ GÓMEZ. 2006. A new species of the *Liolaemus darwinii* group (Iguania: Liolaemidae) from Catamarca Province, Argentina. Zootaxa 1317: 21–33.
- ABDALA, C. S., AND F. LOBO. 2006. Nueva especie para el grupo de *Liolaemus darwinii* (Iguania: Liolaemidae) del noroeste de Argentina. Cuadernos de Herpetología 19:3–18.
- ABDALA, V., C. ABDALA, AND M. J. TULLI. 2006. Muscular characters in the phylogeny of *Liolaemus* (Squamata: Iguania: Liolaemidae): a reappraisal. Zootaxa 1205: 55–68.
- AVILA, L. J., M. MORANDO, AND J. W. SITES, JR. 2006. Congeneric phylogeography: hypothesizing species limits and evolutionary processes in Patagonian lizards of the *Liolaemus boulengeri* group (Squamata: Liolaemini). Biological Journal of the Linnean Society 89:241–275.
- AVILA, L. J., M. MORANDO, AND J. W. SITES, JR. 2008. New species of the iguanian lizard genus *Liolaemus* (Squamata, Iguania, Liolaemini) from central Patagonia, Argentina. Journal of Herpetology 42:186–196.
- AVILA, L. J., C. H. PEREZ, AND M. MORANDO. 2003. A new species of *Liolaemus* (Squamata: Iguania: Liolaemidae) from northwestern Patagonia (Neuquén, Argentina). Herpetologica 59:532–543.
- AVILA, L. J., M. MORANDO, C. H. PEREZ, AND J. W. SITES, JR. 2004. Phylogenetic relationships of lizards of the *Liolaemus petrophilus* group (Squamata: Liolaemidae), with a description of two new species from western Argentina. Herpetologica 60:187–203.
- CABRERA, M. R., AND J. C. MONGUILLOT. 2006. A new Andean species of *Liolaemus* of the *darwinii* complex (Reptilia: Iguanidae). Zootaxa 1106:35–43.
- CEI, J. M. 1986. Reptiles del Centro, Centro-oeste y Sur de la Argentina. Museo Regionale di Scienze Naturali, Torino: Monografie 4:1–527.
- CEI, J. M. 1993. Reptiles del Noroeste, Nordeste y Este de la Argentina. Museo Regionale di Scienze Naturali, Torino: Monografie 14:1–946.
- CEI, J. M., AND J. A. SCOLARO. 1999. Speciation of the “*darwinii* complex” (genus *Liolaemus*, “patch group”) in the southernmost area of its distribution (Reptilia: Tropicuridae). Revue Frances Aquariologie 26:79–82.
- CRUZ, F. B., L. A. FITZGERALD, R. E. ESPINOZA, AND J. A. SCHULTE, II. 2005. The importance of phylogenetic scale in tests of Bergmann’s and Rapoport’s rules: lessons from a clade of South American lizards. Journal of Evolutionary Biology 18:1559–1578.
- DÍAZ GÓMEZ, J. M. 2007. Endemism in *Liolaemus* (Iguania: Liolaemidae) from the Argentinian Puna. South American Journal of Herpetology 2:59–68.
- ESPINOZA, R. E., AND F. LOBO. 2003. Two new species of *Liolaemus* lizards from northwestern Argentina: speciation within the northern subclade of the *elongatus* group (Iguania: Liolaemidae). Herpetologica 59: 89–105.
- ESPINOZA, R. E., F. LOBO, AND F. B. CRUZ. 2000. *Liolaemus heliodermis*, a new lizard from northwestern Argentina with remarks on the content of the *elongatus* group (Iguania: Tropicuridae). Herpetologica 56: 235–244.
- ESPINOZA, R. E., J. J. WIENS, AND C. R. TRACY. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. Proceedings of the National Academy of Sciences, USA 101:16819–16824.
- ETHERIDGE, R. 1992. A new psammophilus lizard of the genus *Liolaemus* (Squamata: Tropicuridae) from northwestern Argentina. Bolletino del Museo Regionale di Scienze Naturali, Torino 10:1–19.
- ETHERIDGE, R. 1993. Lizards of the *Liolaemus darwinii* complex (Squamata: Iguania: Tropicuridae) in northern Argentina. Bolletino del Museo Regionale di Scienze Naturali, Torino 11:137–199.
- ETHERIDGE, R. 1995. Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolae-



- minae (Reptilia: Squamata: Tropiduridae). American Museum Novitates 3142:1–34.
- ETHERIDGE, R. 2000. A review of lizards of the *Liolaemus wiegmanni* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand-dwelling species. Herpetological Monographs 14: 293–352.
- ETHERIDGE, R. 2001. A new species of *Liolaemus* (Reptilia: Tropiduridae) from Mendoza Province, Argentina. Cuadernos de Herpetología 15:3–15.
- ETHERIDGE, R., AND R. E. ESPINOZA. 2000. Taxonomy of the Liolaeminae (Squamata: Iguania: Tropiduridae) and a semi-annotated bibliography. Smithsonian Herpetological Information Service 126:1–64.
- FROST, D. R. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). American Museum Novitates 3033:1–68.
- FROST, D. R., R. ETHERIDGE, D. JANIES, AND T. A. TITUS. 2001. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). American Museum Novitates 3343:1–38.
- KOSLOWSKY, J. 1998. Enumeración sistemática y distribución de los reptiles Argentinos. Revista Museo La Plata 8:161–200.
- LAURENT, R. F. 1983. Contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). Boletín de la Asociación Herpetológica Argentina 1:16–18.
- LAURENT, R. F. 1985. Segunda contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). Cuadernos de Herpetología 1:1–37.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.
- LOBO, F. 2001. A phylogenetic analysis of lizards of the *Liolaemus chiliensis* group (Iguania: Tropiduridae). Herpetological Journal 11:137–150.
- LOBO, F., AND R. E. ESPINOZA. 1999. Two new cryptic species of *Liolaemus* (Iguania: Tropiduridae) from northwestern Argentina: resolution of the purported reproductive bimodality of *Liolaemus alticolor*. Copeia 1999:122–140.
- LOBO, F., AND R. E. ESPINOZA. 2004. Two new *Liolaemus* from the Puna region of Argentina and Chile: further resolution of purported reproductive bimodality in *Liolaemus alticolor* (Iguania: Liolaemidae). Copeia 2004:850–866.
- LOBO, F., AND S. KRETZSCHMAR. 1996. Descripción de una nueva especie de *Liolaemus* (Iguania: Tropiduridae) de la provincia de Tucumán, Argentina. Neotrópica 42:33–40.
- LOBO, F., S. QUINTEROS, AND J. M. DÍAZ GÓMEZ. 2007. Description of a new species of the *Liolaemus alticolor* group (Iguania: Liolaemidae) from Cuzco, Perú. Herpetologica 63:537–543.
- MARTINEZ CARRETERO, E. 1995. The Puna vegetation in the valley of Río Cazaderos, Catamarca province, Argentina. Candollea 52:497–508.
- MARTINEZ OLIVER, I., AND F. LOBO. 2002. Una nueva especie de *Liolaemus* del grupo *alticolor* (Iguania: Liolaemidae) de la Puna Salteña, Argentina. Cuadernos de Herpetología 16:47–64.
- MONGUILLOT, J. C., M. R. CABRERA, J. C. ACOSTA, AND J. VILLAVICENCIO. 2006. A new species of *Liolaemus* (Reptilia: Iguanidae) from San Guillermo National Park, western Argentina. Zootaxa 1361:33–43.
- MORANDO, M., L. J. AVILA, AND J. W. SITES, JR. 2003. Sampling strategies for delimiting species: genes, individuals, and populations in the *Liolaemus elongatus-kriegi* complex (Squamata: Liolaemidae) in Andean–Patagonian South America. Systematic Biology 52:159–185.
- MORANDO, M., L. J. AVILA, J. BAKER, AND J. W. SITES, JR. 2004. Phylogeny and phylogeography of the *Liolaemus darwini* complex (Squamata: Liolaemidae): evidence for introgression and incomplete lineage sorting. Evolution 58:842–861.
- MORANDO, M., L. J. AVILA, C. R. TURNER, AND J. W. SITES, JR. 2007. Molecular evidence for a species complex in the Patagonian lizard *Liolaemus bibronii* and phylogeography of the closely related *Liolaemus gracilis* (Squamata: Liolaemini). Molecular Phylogenetics and Evolution 43:952–973.
- NÚÑEZ, H., AND S. FOX. 1989. A new species of iguanid lizard previously confused with *Liolaemus multififormis* (Squamata: Iguanidae). Copeia 1989:456–460.
- NÚÑEZ, H., AND F. JAKSIC. 1992. Lista comentada de los reptiles terrestres de Chile continental. Boletín del Museo Nacional de Historia Natural, Chile 43:63–91.
- O'GRADY, S., M. MORANDO, L. J. AVILA, AND M. D. DEARING. 2005. Correlating diet and digestive tract specialization: examples from the lizard family Liolaemidae. Zoology 108:201–210.
- PIACENTINI, R. D., A. CEDE, AND H. BÁRCENA. 2003. Extreme solar total and UV irradiances due to cloud effect measured near the summer solstice at the high-altitude desertic plateau Puna of Atacama (Argentina). Journal of Atmospheric and Solar-Terrestrial Physics 65:727–731.
- PINCHEIRA-DONOSO, D., AND H. NÚÑEZ. 2005. Las Especies Chilenas del Género *Liolaemus* Wiegmann, 1834 (Iguania: Tropiduridae: Liolaeminae). Taxonomía, Sistemática y Evolución. Publicación Ocasional del Museo Nacional de Historia Natural, Chile 59:7–486.
- QUINTEROS, A. S., AND C. S. ABDALA. 2007. *Liolaemus puritamensis* Núñez y Fox, 1989 (Iguania: Liolaemidae). Cuadernos de Herpetología 21:117.
- QUINTEROS, A. S., C. S. ABDALA, AND F. J. LOBO. 2008. Redescription of *Liolaemus dorbignyi* Koslowsky, 1898 and description of a new species of *Liolaemus* (Iguania: Liolaemidae). Zootaxa 1717:51–67.
- SCHULTE, J. A., II, J. P. VALLADARES, AND A. LARSON. 2003. Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. Herpetologica 59:399–419.
- SCHULTE, J. A., II, J. R. MACEY, R. E. ESPINOZA, AND A. LARSON. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. Biological Journal of the Linnean Society 69:75–102.
- SMITH, H. M. 1946. Handbook of Lizards: Lizards of the United States and of Canada. Comstock, Ithaca, New York, U.S.A.

- VALLADARES, J. P., R. ETHERIDGE, J. A. SCHULTE, II, G. MANRIQUEZ, AND A. SPOTORNO. 2002. Nueva especie de lagartija del norte de Chile, *Liolaemus molinae* (Reptilia: Liolaeminae). Revista Chilena de la Historia Natural 75:473–489.
- VALDECANTOS, M. S., AND F. LOBO. 2007. Dimorfismo sexual en *Liolaemus multicolor* y *L. irregularis* (Iguania: Liolaemidae). Revista Española de Herpetología 21:55–69.
- VALDECANTOS, S., F. LOBO, AND V. MARTINEZ. 2007. Estimación de edades, tamaño corporal y adquisición de la madurez sexual en dos especies de *Liolaemus* (Iguania: Liolaemidae). Cuadernos de Herpetología 21:31–44.
- VEGA, L., P. J. BELLAGAMBA, AND F. LOBO. 2008. A new endemic species of *Liolaemus* (Iguania: Liolaemidae) from the mountain range of Tandilia, Buenos Aires province, Argentina. Herpetologica 64:81–91.
- L. eleodori* (5).—ARGENTINA: Provincia de San Juan: Departamento Iglesia, Llano de los Hoyos, Río San Guillermo: FML 1703 [4]; Llano de los Hoyos, Cordillera de San Guillermo: SDSU 1610.
- L. etheridgei* (1).—PERÚ: Departamento Arequipa: Provincia de Arequipa, 3 km NE Yura: SDSU 1622.
- L. famatinae* (35).—ARGENTINA: Provincia de La Rioja: Departamento Famatina, Cerro de Famatina: FML 232 [2]; Cueva de Perez, Nevados de Famatina: FML 1720 [32], SDSU 1624 (paratype).
- L. fittkaui* (2).—BOLIVIA, Departamento Cochabamba: Tiraque: FML 1612 [2].
- L. forsteri* (1).—BOLIVIA: Departamento La Paz: Chacaltay: FML 2211.
- L. griseus* (9).—ARGENTINA: Provincia de Tucumán: Departamento Tañi del Valle, Vega Mataderos, Vacahuasi: FML 1354 [4]; SW of Cerro Lomo Ballena, Cumbres Calchaquíes: FML 1582; Cerro Negro, Cumbres Calchaquíes: FML 1586 [4].
- L. huacahuasicus* (39).—ARGENTINA: Provincia de Catamarca: Departamento Andalgalá, Filo los Heladitos, climbing from Capillitas: FML 1224 [18]; Departamento Santa María, El Cerrillo: FML 486–87; 1 km S of Cerro El Overo, Nevados del Aconquija: FML 665; Filo Colorado, 2–3 km W Cerro El Overo, Nevados del Aconquija: FML 674–75; 5 km W of Nevado del Candado: FML 677; Nevado de las Animas: FML 885 [7]; Provincia de Tucumán: Departamento Tañi del Valle, Laguna de El Negro: FML 66 [3] (paratypes); Cerro El Negro: FML 203 [2], 469–70 (paratypes), SDSU 1623.
- L. huayra* sp. nov. (9).—ARGENTINA: Provincia de Tucumán: Departamento Tañi del Valle, Cerro el Pichao, Sierra de Quilmes (26° 22' 26.7" S, 66° 04' 54.2" W; 3545 m): FML 18069 (holotype), MCN 2184 (paratype); Puesto Pacheco, climbing [by horse] from Pichao, Sierra de Quilmes: FML 1219 [7] (paratypes).
- L. inti* sp. nov. (13).—ARGENTINA: Provincia de Salta: Departamento Cachi, Near 15<sup>th</sup> station of Via Crucis, Cerro de la Virgen, Cachi Adentro (25° 03' 07.6" S, 66° 17' 29.4" W; 3938 m): FML 18399 (holotype), MCN 2183 (paratype); Cerro de la Virgen, Cachi Adentro: FML 1669 [7] (paratypes); Mina Santa Elena, Nevados de Palermo (4000 m): FML 1432 [2]; Ladera SW of Nevado de Cachi (3500 m): FML 9652 [2].
- L. jamesi* (3).—CHILE, Región I, Tarapacá: Punta Arica: FML 1193; Parinacot, Arica: FML 1775 [2].
- L. montanus* (36).—ARGENTINA: Provincia de Catamarca: Departamento Ambato, El Rodeo: FML 279 [7], 289; Cerro El Manchao: FML 908–10, 981–82, 1723 [16], 2141 [5]; Falda, E base of Cerro El Manchao: SDSU 1621.
- L. multicolor* (79).—ARGENTINA: Provincia de Jujuy: Departamento Cochinota, Abra Pampa: FML 259, 272 [3], 1873 [9], 2065 [18], 2098 [4], 2349 [2], 2592; 3 km NW of Abra Pampa: FML 1464 [13], 1539 [16]; 3 km NW Abra Pampa on Ruta Provincial 7: SDSU 1314–19; 4.2 km W Abra Pampa on Ruta Provincial 71 (22° 42' 24.4" S; 65° 43' 12.4" W): SDSU 3589–91; Provincia de Salta: Departamento Los Andes, 11.1 km E Olacapato on Ruta Nacional 51 (24° 10' 10.9" S; 66° 39' 05.8" W): SDSU 3592, 3595–96.
- L. nigriceps* (70).—ARGENTINA: Provincia de Salta: Departamento Los Andes, Cono aluvial al S Volcán Socompa: FML 1633 [3], 1635 [31]; Quebrada de ladera

Accepted: 24 November 2008

Associate Editor: Christopher J. Raxworthy

#### APPENDIX I

*Specimens Examined*.—Numbers in parentheses following each taxon name are the number of individuals examined. Note that some specimen numbers from FML represent lots of more than one individual. In such cases, the number of individuals in the lot is indicated in brackets following the catalog number.

*Liolaemus andinus* (27).—ARGENTINA: Provincia de Catamarca: Departamento Tinogasta, Aguas Calientes: FML 1409 [17]; Las Grutas, 20 km from Paso San Francisco: FML 1913, 2025; Near Río Chaschuil, 42 km SE of Paso San Francisco: FML 2545; 68 km NW of Río San Francisco: FML 2546; Cazadero Grande: MCN 1648–53.

*L. chlorostictus* (25).—ARGENTINA: Provincia de Jujuy: Departamento Rinconada, Cuesta de Fundiciones, Mina Piriquitas: FML 1515 [14]; Laguna Vilama: FML 2706 [2]; Cuesta de Fundiciones, 47 km NW Mina Piriquitas: SDSU 1613–18; 15.5 km E Oros mayo on Ruta Provincial 70 (22° 29' 26.7" S; 66° 16' 16.6" W): SDSU 3517–19.

*L. dorbignyi* (24).—ARGENTINA: Provincia de Catamarca: Cordillera de Catamarca: MLP.S 57 (lectotype), 844–45, 991–92 (paralectotypes); Departamento Tinogasta, Puesto la Lagunita, 35–38 km NE of Medanitos, climbing from Medanitos, Sierra de Fiambalá: MCN 2119–21; Los Aujeritos, 34–36 km NE of Medanitos, 2 km SW of Puesto la Lagunita, climbing from Medanitos, Sierra de Fiambalá: MCN 2132–33; Saujil, Ruta 60: FML 1855 [7]; Puesto la Lagunita, 35–38 km NE of Medanitos, climbing from Medanitos, Sierra de Fiambalá: FML 17230–36.

*L. duellmani* (6).—ARGENTINA: Provincia de Mendoza: Departamento Malargüe, Paso el Choique, 50 km SSW El Manzano: KU 161127–28 (paratypes); 48 km S intersection Ruta Provincial 221 and Ruta Nacional 40 on Ruta 221 (36° 21' 12.0" S; 69° 48' 08.7" W): SDSU 3389–91; 19 km N intersection Ruta Provincial 221 and Ruta Nacional 40 on Ruta 221 (36° 21' 12.0" S; 69° 48' 8.7" W): SDSU 3424.

del cerro Socompa: FML 1632 [4]; 3 km E estación Socompa: FML 1634 [2], SDSU 3687–88; N slope of hill S of cerro Socompa: FML 1635 [21], 1680 [2]; CHILE: *Región II, Antofagasta*: Socompa, 8 km from border: FML 923–24; Portezuelo Socompa: FML 1636; Socompa: SDSU 1620.

*L. orientalis* (38).—ARGENTINA: *Provincia de Jujuy*: Departamento Humahuaca, Road to Laguna Blanca: FML 928 [4], 949 [2]; Chorcán: FML 930, 938–39, 944; Camino a Laguna Blanca: FML 949 [2]; Laguna Leandro, W of Chorcán: FML 1456 [4]; Mina Aguilar, SE exposure FML 1537 [2]; Quebrada Tonocote: FML 2035 [14]; Tablayo, W of Chaupi Rodeo: FML 2104 [6].

*L. orko* (13).—ARGENTINA: *Provincia de Catamarca*: Departamento Tinogasta, Puesto La Lagunita, Sierra de Fiambalá: FML 18416 (holotype); FML 18417–21 (paratypes); MCN 2130–31 (paratypes); Las Pampas, Campo Potreritos: FML 1911 [5].

*L. poecilochromus* (40).—ARGENTINA: *Provincia de Catamarca*: Departamento Antofagasta de la Sierra, Salar de Antofalla: FML 878; Los Nacimientos: FML 1171 [12] (paratypes); Volcanes de Los Nacimientos: FML 1173; Ojo de Calalaste: FML 3068 [2]; Las Quinuas, Salar de Antofalla: FML 369–71; 4–5 km N of Antofagasta de la Sierra: MCN 249–51; 288–91; Paycuqui: MCN 278–79, 298–301; 3 km N of Antofagasta de la Sierra: MCN 280–82; Cuesta de Randolpho: MCN 285–87; Departamento Tinogasta, Aguas Calientes: SDSU 1597; *Provincia de Salta*: Departamento Los Andes, 7 km SW Huatiquina: SDSU 1598–99.

*L. pulcherrimus* (17).—ARGENTINA: *Provincia de Jujuy*: Departamento Humahuaca, Mudana: FML 1961 [2], 2184 [15] (paratypes).

*L. puritamensis* (12).—ARGENTINA: *Provincia de Jujuy*: Departamento Rinconada, Rocks on W bank of Laguna Vilama: MCN 2498; Road between intersection of road to Laguna Cerro Negro and road to Laguna Isla Grande: MCN 2500; Rocks on east bank of Laguna Vilama: MCN 2505; Peñón on SE bank of Laguna Vilama: MCN 2507–08; Road to Laguna Isla Grande, E of Vilama on the road to Cerro Granada and Mina Pirquitas: MCN 2509–13; Around Laguna Cerro Negro: MCN 2517–19.

*L. reichei* (2).—CHILE: *Región I, Tarapacá*: Pampa Chaca: LACM 9312; PERÚ: *Departamento Tacna*: Provincia Tacna, 6.4 km N Tacna: MVZ 99663.

*L. ruibali* (54).—ARGENTINA: *Provincia de La Rioja*: Departamento Vinchina, Agua Quemada, 47 km E of Alto Jagüe: FML 2975–76; *Provincia de Mendoza*: Departamento Las Heras, Paramillo de Uspallata: FML 1076, 1104; Ruta Nacional 7, Paramillo, Uspallata: FML 2549 [7]; 24 km SE of Uspallata: FML 3462–63; 25 km W of Uspallata, on Ruta Provincial 7: FML 3730 [5]; 20 km NE Uspallata: SDSU 1604–05; *Provincia de San Juan*: Departamento Iglesia, gravel flats just S Tocota (30° 41'

0.25° S; 69° 26' 38.1" W): FML 3461 [12], SDSU: 3436–39, 3454–58, 3502–14.

*L. schmidti* (7).—CHILE: *Región II, Antofagasta*: Atacama: FML 1192; Volcán Tatio: FML 1197; Ojos San Pedro, 88.5 km NE Calama: MVZ 66807–08; *Región I, Tarapacá*: Tarapacá, Cariquima: SDSU 1601–03.

*L. scrocchii* (26).—ARGENTINA: *Provincia de Jujuy*: Departamento General Belgrano, Around base of Cerro Paño, Serranía de Chañi: FML 992 [4] (paratypes); Casa Mocha, climbing from NW of Nevado del Chañi: MCN 714, 898, 961 (paratypes); Departamento Humahuaca, Abra del Cerro Toro, Sierra de Aguilar: MCN 899 (paratype); Departamento Susques, 2 km SE of Susques on Ruta Nacional 52: FML 17228 (holotype), 17229 (paratype); Departamento Tumbaya, El Quemado, Abra de Pives: FML 1817–1 (paratype); Susques Pueblo: FML 976, 978 [2]; *Provincia de Salta*: Departamento La Poma, La Mesada, 64 km from La Poma to Abra del Acay: FML 6481 (paratype); Departamento Los Andes, Olacapato, Quebrada de Los Berros: 1365 [3]; Santa Rosa de los Pastos Grandes: FML 1763 (paratype); Agua de los Sapos (Puesto de Cruz Soriano), 20 km from Mina Tincalcayo: FML 1759 [2] (paratypes); road to Abra del Acay from Ruta Nacional 51: MCN 964 (paratype); km marker 210, Ruta Nacional 51, 0.6 km from Ruta Nacional 51, 6.4 km to S of Olacapato (24.2411475 °S, 66.69711 °W): MCN 1922–25 (paratypes).

*L. signifer annectens* (4).—PERÚ: *Departamento Tacna*: Provincia de Tacna, Sierra de Tacna: FML 340; River crossing the road 150 m from Arequipa (road Arequipa–Puno): FML 15431–33.

*L. signifer signifer* (24).—BOLIVIA: *Departamento Cochabamba*: Provincia Tapacari, Confital, road La Paz–Cochabamba: FML 1562 [2]; PERÚ: *Departamento Apurímac*: Provincia de Aymaraes, 40 km SW Chalhuanca: MVZ 57832–33; *Departamento Arequipa*: Provincia de Caylloma: Vincocaya: CAS 80901–02, 80904; *Departamento Ayacucho*: Provincia de Lucanas, 35 km ENE Puquio: MVZ 57834; *Departamento Moquegua*: Pampa Huatire: MVZ 57811; *Departamento Puno*: Provincia de Puno, Lago Titicaca: FML 1434 [2]; Lago Titicaca road to Puno: FML 1557; 82 km W Puno: MVZ 57827; Pichupichuin, 8 km NW Huacallani: MVZ 57830; Caccahara: MVZ 57837; 12.9 km SSW Limbani: MVZ 57843; 4 km NNW of Juliaca: MVZ 83692; Huaylarco, 88.5 km ENE Arequipa: MVZ 92871; 5 km W Tincopalca: SDSU 1600; *Departamento Tacna*: Provincia Tacna, 5 km E Lago Sucho: MVZ 57823; Provincia de Tarata, 16 km S Tarata: MVZ 99650–53.

*L. stolzmanni* (2).—CHILE: *Región II, Antofagasta*: Alta Camina, 177 km NE Iquique: MVZ 66805–06.

*L. vallecurensis* (1).—ARGENTINA: *Provincia de San Juan*: Departamento Iglesia, Valle de Cura: FML 2404.