# Two New *Liolaemus* from the Puna Region of Argentina and Chile: Further Resolution of Purported Reproductive Bimodality in *Liolaemus alticolor* (Iguania: Liolaemidae)

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We provide descriptions for two new cryptic species belonging to the *Liolaemus alticolor* group from northern Argentina and northeastern Chile. The new species were previously considered conspecific with either *Liolaemus walkeri* in northeastern Chile or *L. alticolor* in northwestern Argentina and adjacent Chile. However, the new species differ from these taxa, and all other members of the *alticolor* group, in a number of characteristics. *Liolaemus chaltin* n. sp. differs from *L. alticolor* from the type locality (Tiahuanaco, Bolivia) in the following ways: this new species has a larger body size; a fragmented vertebral stripe; and a pigmented subocular (white in *L. alticolor*), and is one of just three members of the *alticolor* group that is oviparous. *Liolaemus puna* n. sp. differs from all other members of the *alticolor* group in that male *L. puna* lack paravertebral markings and dorsolateral and vertebral stripes. Females, however, are similar to other members of the *alticolor* group but can be distinguished from them by several meristic characters. *Liolaemus puna* is widely distributed throughout the high-elevation (3680–4400 m) Puna regions (a flat or gently sloping steppe dominated by perennial bunch grasses and small shrubs) in northwestern Argentina and northeastern Chile. *Liolaemus chaltin* is known only from the Puna of central Jujuy Province, Argentina (3400–3750 m). Based on examinations of the type series of *L. alticolor* and *L. walkeri*, we determined that virtually all northern Chilean populations of *Liolaemus* previously considered to belong to either of these two species should be assigned to *L. puna*. Thus, the range of *L. alticolor* is restricted to Bolivia and southern Perú, and the range of *L. walkeri* is restricted to central and southern Andean Perú. *Liolaemus chaltin* is oviparous, and *L. puna* is viviparous, and because both are morphologically similar to *L. alticolor*, some investigators have suggested that some populations of *L. alticolor* may be reproductive bimodal. Our studies, however, indicate that these populations represent sympatric populations of the cryptic species described herein. A diagnostic key is provided for the currently recognized members of the *alticolor* group.

En este trabajo presentamos la descripción de dos nuevas especies pertenecientes al grupo *Liolaemus alticolor* del norte de Argentina y nordeste de Chile. Las nuevas especies fueron consideradas previamente como conespecíficas con *Liolaemus walkeri* en el noreste de Chile, o *L. alticolor* en el noroeste de Argentina y areas limitantes de Chile. En efecto, las nuevas especies difieren de estos taxa y de todos los otros miembros del grupo *alticolor* en varios caracteres morfológicos y biológicos. *Liolaemus chaltin* n. sp. difiere de *L. alticolor* de la localidad tipo (Tiahuanaco, Bolivia) de la siguiente forma: es de mayor tamaño, la línea vertebral fragmentada, la subocular pigmentada, y es uno de los tres miembros del grupo que es ovíparo. *Liolaemus puna* n. sp. difiere de todos los otros miembros del grupo *alticolor* en que los machos de esta especie carecen de bandas dorsolaterales, manchas paravertebrales, y de linea vertebral. Las hembras son similares a las de las restantes especies del grupo aunque pueden diferenciarse mediante diferentes caracteres meristicos. *Liolaemus puna* está ampliamente distribuido en las regiones de considerable elevación (3680–4400) de la Puna (una estepa carente de arboles y caracterizada por la presencia de pastizales perennes y pequeños arbustos) en el norte de Argentina y noreste de Chile. *Liolaemus chaltin* es conocido solamente en la Puna de la región central y norte de la provincia de Jujuy, Argentina (3400–3750 m). Basados en el estudio de las series tipo de *L. alticolor* y *L. walkeri*, hemos determinado que casi todas las poblaciones del norte de Chile de *Liolaemus* previamente consideradas como una u otra de esas dos especies deberían ser asignadas a *L. puna*. De este modo el rango de *L. alticolor* se limita a Bolivia y sur del Perú, y el rango de *L. walkeri* esta limitado a los Andes del sur y centro de Perú. *Liolaemus chaltin* es

**ovíparo y *L. puna* es vivíparo, y debido a que ambas especies son morfológicamente similares a *L. alticolor*, algunos investigadores han sugerido que *L. alticolor* podría ser reproductivamente bimodal. Nuestros estudios indican, de todos modos, que estas poblaciones representan especies crípticas, las cuales son descriptas en este trabajo. Se provee de una clave diagnóstica de las especies reconocidas actualmente como miembros del grupo *alticolor*.**

*The beginning of wisdom starts with calling things by their right names.*(Chinese proverb cited in Wilson, 1992:44)

RECENT interest in lizards belonging to the *Liolaemus alticolor* group (Qualls et al., 1997; Blackburn, 1998; Lobo and Espinoza, 1999) has been stimulated by reports of reproductive bimodality in *L. alticolor* from northwestern Argentina (Ramírez Pinilla, 1989, 1991; Ramírez Pinilla and Laurent, 1996). The most provocative aspect of these reports was the suggestion that there might exist at least two reproductively bimodal populations of this single species, a previously undocumented phenomenon for vertebrates. Indeed, intraspecific reproductive bimodality is exceedingly rare among squamate reptiles (Shine, 1985; Blackburn, 1995; Shine and Lee, 1999) and is limited to cases in which the oviparous and viviparous populations are allopatric (e.g., Qualls et al., 1995; Heulin et al., 1997; Smith et al., 2001). Hence, confirmation of reproductive bimodality within populations of *L. alticolor* would be both unprecedented and of great scientific value insofar as a bimodal population would provide an ideal system for investigating the factors that influence the evolution of viviparity in nature (Guillette, 1993). Recent studies of one of these purportedly reproductively bimodal populations in Tucumán Province, Argentina, resulted in the recognition of two undescribed, cryptic species—one oviparous (*Liolaemus ramirezae*) and the other viviparous (*Liolaemus pagaburoi*)—thereby resolving the case of reproductive bimodality for this population (Lobo and Espinoza, 1999). However, an additional report of a reproductively bimodal population of *L. alticolor* in Salta Province, Argentina (Ramírez Pinilla and Laurent, 1996), was not adequately investigated in our previous study. Nevertheless, cursory observations led us to suggest that these populations also represented cryptic species (Lobo and Espinoza, 1999), and comparisons and analyses presented elsewhere (Martínez Oliver and Lobo, 2002) and herein support those initial findings.

In addition to reports of reproductive bimodality, many systematic issues remain unresolved for the *alticolor* group. First, monophyly has not been established, and the content of the group is uncertain (Lobo and Espinoza, 1999). Ortiz (1981) assigned three species to this group (*L. alticolor*, *Liolaemus tacnae*, and *Liolaemus walkeri*), whereas Cei (1993) included only two (*L. alticolor* and *L. walkeri*). However, neither investigator provided a definitive diagnosis for their respective group. Lobo and Espinoza (1999) recently suggested that as many as 14 species belonging to the more inclusive *chiliensis* group (sensu Etheridge, 1995; Lobo, 2001) are morphologically similar to *L. alticolor* and could, therefore, be assigned to this group based on the diagnoses provided by either Ortiz (1981) or Cei (1993). Thus, the goals of this investigation were to (1) provide a diagnosis of the *alticolor* group based on shared, derived characteristics; (2) determine the content of the group; (3) reexamine specimens from the purportedly reproductively bimodal population in Salta Province, Argentina (Ramírez Pinilla and Laurent, 1996), to assess their taxonomic status; and (4) provide a key for species belonging to this group. The phylogenetic relationships among members of the *alticolor* group are currently under investigation.

MATERIALS AND METHODS

*Taxonomy.*—To provide a diagnosis and key for the *alticolor* group, as well as a diagnosis for the species described herein, we examined a series of virtually all taxa belonging to the more inclusive *chiliensis* group (approximately 80 taxa, sensu Etheridge, 1995; Lobo, 2001). After an initial survey, we focused on species that are morphologically similar to *L. alticolor* and those previously considered potential members of the *alticolor* group (Lobo and Espinoza, 1999; Martínez Oliver and Lobo, 2002). Included in this analysis were more than 75 populations previously or currently assigned to *L. alticolor* from Argentina, Bolivia, Chile, and Perú and the type series of species that are geographically most proximate and morphologically most similar to *L. alticolor* (*L. alticolor*, *Liolaemus bitaeniatus*, *L. pagaburoi*, *L. ramirezae*, *L. tacnae*, *Liolaemus variegatus*, and *L. walkeri*). In total, we examined more than 300 specimens of these taxa (see Material Examined). For the taxonomic analyses, we con-

TABLE 1. DISTRIBUTION OF THE 10 SPECIES RECOGNIZED AS MEMBERS OF THE *alticolor* GROUP INCLUDING THE TWO NEW TAXA DESCRIBED HEREIN. See text for a diagnosis of the group.

| Species | General distribution |
| --- | --- |
| *Liolaemus alticolor* | Bolivia and S Perú |
| *L. bitaeniatus* | NW Argentina |
| *L. chaltin* n. sp. | NW Argentina |
| *L. pagaburoi* | NW Argentina |
| *L. puna* n. sp. | NW Argentina and NE Chile |
| *L. ramirezae* | NW Argentina |
| *L. tacnae* | SW Perú |
| *L. variegatues* | N Bolivia |
| *L. walkeri* | SC Perú |
| *L. yanalcu* | NW Argentina |

sidered external morphology (i.e., squamation, coloration, color patterns) and reproductive mode. When possible, live specimens were examined to record color in life. Additional specimens were examined after fixation in 10% formalin and preservation in 70% ethanol. Some character states were determined with the aid of a binocular dissecting microscope (10–40×), and measurements were taken with electronic calipers to the nearest 0.01 mm. Terminology for the description of squamation is after Smith (1946), and for neck-fold terminology, we followed Frost (1992). Definitions and detailed descriptions of body patterns found in members of the *alticolor* group (and species similar to them) can be found in Lobo and Espinoza (1999). Institutional abbreviations follow Leviton et al. (1985) with the addition of the Museo de Zoología de la Universidad de Concepción, Chile (MZUC).

*Ecology.*—We searched for and collected *L.* "*alticolor*" in January (midsummer) 1995 and 1996 in Jujuy Province. Included in our survey were localities known to have either oviparous or viviparous populations of *L.* "*alticolor*" (Ramírez Pinilla and Laurent, 1996). The surveys also coincided with the time of parturition for oviparous and viviparous *L.* "*alticolor*" populations in northwestern Argentina (Ramírez Pinilla, 1989, 1991; Ramírez Pinilla and Laurent, 1996). Individuals from some populations were returned to the laboratory and either immediately sacrificed or retained until reproductive modes could be ascertained at the time of parturition. This enabled us to adopt the strictest criteria set by Blackburn (1993) for determining the reproductive modes of individuals from most populations. While in the field, we recorded gravid-female coloration (yellow or orange along sides of the head and/or belly), habitat selection, and behavior. We also searched for evidence of clin-

al variation or hybridization (i.e., morphologically intermediate individuals) between the lizards exhibiting the two reproductive modes especially near potential zones of sympatry (based on museum records). At each site, we collected environmental temperatures (air, substratum perpendicular to sun, and deep shade) and body temperatures of the lizards (measured at a depth of approximately 1 cm in the cloaca) with a digital thermometer (Omega 871A, Stamford, CT).

RESULTS

*Diagnosis of the alticolor group.*—Members of the *alticolor* group (Table 1), as defined here, were found to share a suite of derived morphological characteristics (based on reanalysis of published data; Lobo, 2001) that collectively unite this group to the exclusion of other members of the more inclusive *chiliensis* group (sensu Etheridge, 1995; Lobo, 2001) with the exception of members of the *bibronii* group (Cei, 1986; see below). The synapomorphies for the *alticolor* group include small body size (rarely > 60 mm SVL; Appendix 1), a distinct pattern of dorsal stripes as described previously (Lobo and Espinoza, 1999), fine gray to black markings (line segments or spots) diffusely marking the ventral tail. Species of the *alticolor* group (as defined here) share a general terrestrial lifestyle and exhibit body patterns that are similar to those found among species belonging to the *bibronii* group (*Liolaemus bibronii, Liolaemus exploratorum, Liolaemus gracilis, Liolaemus sanjuanensis*, and *Liolaemus saxatilis*), which are morphologically similar, yet geographically distributed farther south (Cei, 1986; Lobo, 2001). Subsequent analyses may find that these two species groups form a single clade within the more inclusive *chiliensis* group, as suggested by the limited sampling of these groups in Schulte et al. (2000; note that

Fig. 1.    *Liolaemus chaltin* (holotype; FML 9874). Male, 51.8 mm SVL.

the *L. alticolor* sampled by these authors is one of the new species described below). However, for the purpose of describing the new species below, we limit our comparisons to the northern species belonging to the *alticolor* group.

Our analysis of 61 morphological characters and reproductive mode also suggest that populations assigned to *L. alticolor* or *L. walkeri* in northern Argentina and northeastern Chile represent at least three additional cryptic species. One of these species, *Liolaemus yanalcu*, was described recently (Martínez Oliver and Lobo, 2002), and the other two are described below.

### *Liolaemus chaltin* n. sp.
### Figures 1–3, Table 1, Appendix 1

*Holotype.*—FML 9874 (field tag: REE 341), adult male collected from off Ruta Provincial 71, 4.2 km west of Abra Pampa, Departamento Cochinoca, Provincia de Jujuy, Argentina (22°42′24.4″S, 65°43′12.4″W; 3360 m), on 5–6 January 1995 by R. E. Espinoza, R. Etheridge, E. Lavilla, F. Lobo, and J. C. Moreta (Fig. 1).

*Paratypes.*—FML 9875–9913 (field tags: REE 342–53, 355–59, 361–62, 364–65, 367–68, 370–74, 376–77, 379–81, 383, 385–89) same data as holotype.

*Etymology.*—The specific epithet *chaltin* is a vernacular name used by local inhabitants to specifically refer to these small striped lizards. At the type locality, *L. chaltin* is distinguished by people who work in the field from two larger syntopic species, *Liolaemus multicolor* and *Liolae-*

*mus ornatus*, which are referred to as *lagartijas* (''lizards'' in Español). The precise origin of ''chaltin'' is unknown, but the word is probably Quechuan and, therefore, attributable to the indigenous peoples of present-day northern Argentina and southern Bolivia.

*Diagnosis.*—A small (58.7 mm maximum SVL) slender *Liolaemus* belonging to the *alticolor* group (as defined above) with a variable dorsal pattern (Fig. 2). Within the *alticolor* group, *L. chaltin* differs from *L. alticolor* in its larger body size (SVL of *L. chaltin* mean = 54.7 mm vs mean = 46.9 mm in *L. alticolor*), a fragmented midvertebral line (rarely fragmented in *L. alticolor*), a pigmented subocular scale (white in *L. alticolor*), and the new species is oviparous, whereas *L. alticolor* is viviparous (Lobo and Espinoza, 1999). The new species lacks paravertebral markings, whereas these are distinct in *L. bitaeniatus*, *L. pagaburoi*, and *L. variegatus*. *Liolaemus chaltin* also has smooth dorsal head scales in contrast to the rugose head surface of *L. bitaeniatus*. Female *L. chaltin* lack precloacal pores, whereas some female *L. bitaeniatus* (41%) and *L. yanalcu* (19%), and most female *L. ramirezae* (94%) have precloacal pores (Lobo and Espinoza, 1999; Martínez Oliver and Lobo 2002). Male *L. chaltin* are immaculate cream-white ventrally, whereas male *L. tacnae* and *L. walkeri* have ventral melanism. This new species has dorsolateral stripes in both sexes, which are absent in *L. tacnae* and *L. yanalcu*. Compared to *L. walkeri*, *L. chaltin* is larger in body size (SVL: mean = 54.7 mm vs mean = 48.3 mm in *L. walkeri*), and
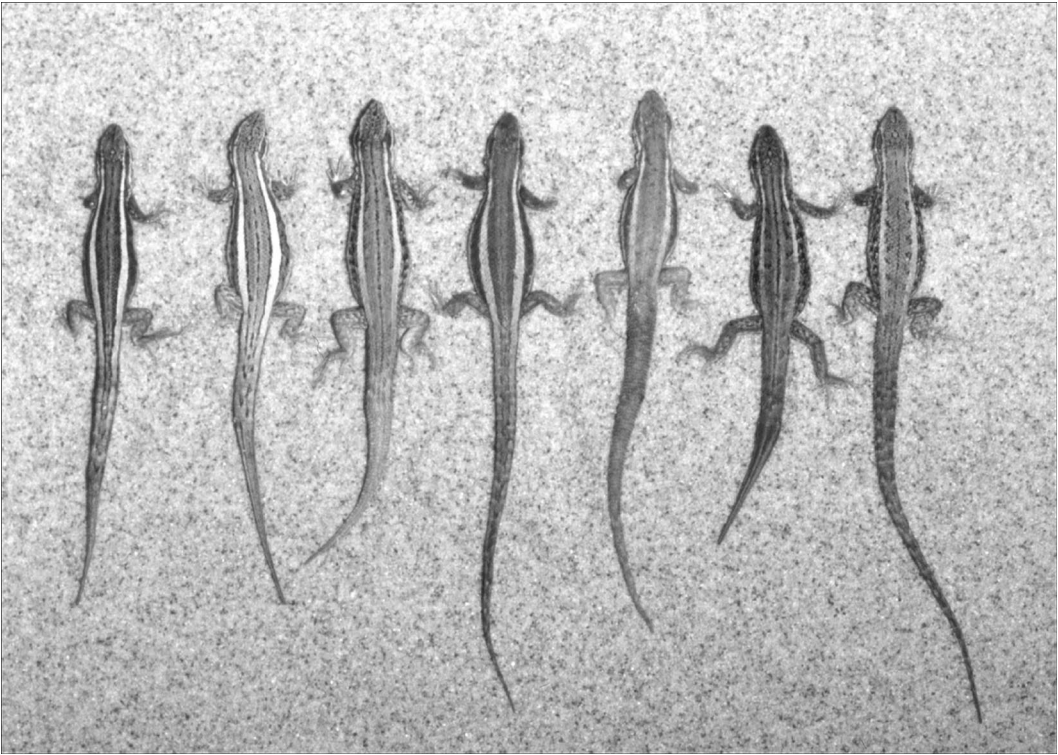
Fig. 2. Variation in dorsal pattern of *Liolaemus chaltin* from the type locality.

this new species has fewer scales around the midbody (mean = 47.7 vs mean = 52.7 in *L. walkeri*). *Liolaemus puna* n. sp. (described below) is also smaller in body size than *L. chaltin* (*L. puna* mean = 47.9 mm), and males of the former species lack the distinct dorsal stripes found in both sexes of *L. chaltin*. Additionally, *L. puna* has nearly twice as many scale organs (mean = 5.1; $n = 50$) in the postrostral scale than recorded for *L. chaltin* (mean = 2.6; $n = 20$). Fifty percent of the *L. puna* examined ($n = 40$) have a preocular scale that is in contact with the lorilabials, a character state also observed in *L. alticolor*, *L. tacnae*, and *L. walkeri* but never observed in *L. chaltin*. All male and most female *L. puna* have fine gray to black irregular spots on the sides of the posterior throat and neck, whereas both sexes of *L. chaltin* have an immaculate cream-white throat. The two new species also differ in reproductive mode: *L. chaltin* is oviparous and *L. puna* is viviparous. Female *L. chaltin* exhibit gravid coloration, whereas the viviparous members of the *alticolor* group, as far as known, do not (Appendix 1).

*Description of holotype.*—Male (Fig. 1). Snout—vent length 51.8 mm. Head length (measured from snout to anterior border of auditory me-atus) 11.4 mm. Head width (at widest point over posterior mandibles) 8.6 mm. Head height (at parietal) 6.5 mm. Axilla–groin distance (between the posterior insertion of forelimb and anterior insertion of thigh) 23.9 mm (46.1% of SVL). Foot length (ankle to tip of the fourth toe including claw) 16.3 mm (31.5% of SVL). Tail length (complete, not regenerated) 89.6 mm (1.7 times SVL).

Twelve dorsal head scales (from a line drawn horizontally between anterior margin of external auditory meatus to anterior margin of rostral). Dorsal head scales smooth, with scale organs most abundant in prefrontal and internasal regions. Three scale organs in each postrostral. Nasal scale in contact with rostral, separated from first supralabial by one scale. Nasal bordered by six scales. Canthal separated from nasal by one scale. Loreal region flat. Six supralabials (counting only the "enlarged" series of the main row) with fourth upturned posteriorly and contacting subocular on both sides of head. Four enlarged infralabials. Auditory meatus oval shaped (height 2.1 mm; width 1.4 mm). Auricular scale differentiated on left side, with two small projecting scales on anterior margin of auditory meatus (both sides). Eight convex, imbricate, keeled temporals (counting

vertically from buccal commissure to posterior corner of orbit). Orbit–auditory meatus distance: 4.5 mm. Orbit–anterior margin of rostral distance: 3.9 mm. Rostral almost three times wider than high (width: 2.7 mm; height: 1.0 mm). Mental subpentagonal, about two times as wide as high (width: 2.5 mm; height: 1.2 mm). Interparietal pentagonal with an elongated posterior apex. Interparietal bordered by six scales, the parietals being largest. Frontal elongate. Supraorbital semicircles incomplete posteriorly on right side. Semicircles formed by 10 scales on both sides. Three/four (left/right) enlarged supraoculars. Five/six distinctly imbricate supercilliaries. Thirteen upper and 11 lower ciliaries (right side). Subocular elongate (3.8 mm), longer than eye diameter (2.0 mm; measured between anterior and posterior commissure of ciliaries), separated from supralabials by a single, but interrupted row of lorilabials. Fourth supralabial elongate (2.1 mm), about same length as eye diameter. Six lorilabials with single row of scale organs. Third/fourth through sixth lorilabial contacting subocular. Preocular small, separated from lorilabial row by one scale. Postocular same length as preocular, located above fifth supralabial. Mental in contact with four scales: first infralabials (on each side) and two enlarged chinshields. Chinshields form a longitudinal row of three enlarged scales separated one from the other by nine smaller scales. Scales of throat round, flat, and imbricate. Thirty gulars between auditory meatus. Lateral nuchal folds well developed, with flat slightly keeled scales over longitudinal fold that are smaller than dorsals. Antehumeral pocket well developed. Twenty-nine scales between auditory meatus and shoulder (counting along postauricular and longitudinal fold), 18 scales between auditory meatus and antegular fold. Supernumerary, gular, and oblique folds absent.

Dorsal scales lanceolate, moderately keeled, imbricate. Dorsal scales between occiput and groin: 42. Scales around midbody: 45. Twenty-two rows of keeled scales on dorsum at midtrunk. Scales become smooth along flank and toward belly. Ventral scales about the same size as dorsals. Ventral scales between mental and precloacal pores: 86. Four precloacal pores. Brachial and antebrachial scales keeled and imbricate with round posterior margins. Supracarpals laminar, round, smooth. Subdigital lamellae of fingers with three keels, in number I: 8; II: 13; III: 16; IV: 20; V: 12. Claws moderately long. Supradigital lamellae convex, smooth, imbricate. Infracarpals and infratarsals keeled, distinctly imbricate. Supracarpals and supratarsals smooth, with round posterior margins. Subdi-

gital lamellae of toes I: 9; II: 14; III: 19; IV: 26; V: 14.

*Color in ethanol.*—Background coloration of dorsum from occiput to base of tail dark gray–brown, darkest over shoulders (Fig. 1). Dorsal tail gray proximally, fading to light brown distally with numerous paravertebral, dorsolateral, and lateral black markings or line segments. Lateral field dark brown dorsolaterally with small black markings, fading to gray ventrolaterally. Off-white ventrolateral stripe distinct anteriorly, becoming diffuse posteriorly, fading completely into the background coloration just posterior to the level of the cloaca. Throat and belly charcoal gray, except faint peach near insertion of hind limbs and adjacent posterior belly. Ventral tail and hind limbs immaculate cream-white. Precloacal pores cream-yellow.

*Variation.*—Based on 12 paratypes (seven females and five males). Snout—vent length 48.9–58.7 mm (mean = 54.7 mm; SD = 2.7). Head length 18–31% (mean = 21.0%; SD = 3.0) of SVL. Auditory meatus 1.2–1.5 (mean = 1.4; SD = 0.1) times higher than wide. Tail length 1.5–2.0 (mean = 1.7; SD = 0.2) times SVL. Scales around midbody 40–54 (mean = 47.7; SD = 3.7). Scales from occiput to thighs 40–48 (mean = 43.7; SD = 2.3). Dorsal head scales 11–13 (mean = 11.9; SD = 0.9). Ventrals 79–87 (mean = 82.6; SD = 2.6). Precloacal pores in males 4–5 (mean = 4.2; SD = 0.4), absent in females. Scales surrounding interparietal 5–9 (mean = 6.7; SD = 1.1). Scales of neck along posterior border of auditory meatus to shoulder 25–35 (mean = 28.6; SD = 2.7). Scales from posterior border of auditory meatus to antehumeral fold 16–20 (mean = 17.4; SD = 1.2). Gulars 28–34 (mean = 31.0; SD = 2.5). Relationship between length of subocular/diameter of eye 1.3–1.9 (mean = 1.5; SD = 0.2). Relationship between fourth supralabial/diameter of eye 0.8–1.1 (mean = 1.0; SD = 0.1). Ratio of width of nasal at nares to width of nasal in contact with rostral 1.4–7.9 (mean = 3.3; SD = 2.0). Scales between rostral and frontal 4–5 (mean = 4.5; SD = 0.5). Subdigital lamellae of fourth finger 14–20 (mean = 16.7; SD = 1.8). Subdigital lamellae of fourth toe 21–25 (mean = 23.3; SD = 1.1). Temporals smooth to weakly keeled. Scales of longitudinal fold of neck smaller than dorsals, weakly keeled, laminar. Fourth supralabial curved posteriorly, usually (67%) in contact with subocular. One to three enlarged scales projecting over anterior border of auditory meatus, some individuals (33%) with a distinct auricular scale. Vertebral stripe absent (50%) or

fragmented (50%). Paravertebral field without distinctive markings. Females with distinct dorsolateral stripes, same stripes in males fade at mid trunk. Dorsolateral stripes in females bordered on both sides by fine black lines that run length of dorsolateral stripes, these lines absent or fragmented posterior of shoulders in males. Subocular almost always (92%) pigmented, rarely white. Throat immaculate in both sexes.

*Color in life.*—Dorsal background color of head, trunk, and limbs light gray to dark brown (Fig. 2). Head with short black segments or markings in frontal and parietal regions, sometimes surrounding parietal scale. Subocular white with black border dorsally. Dorsolateral stripes varying in color from cream-white, gray, golden or greenish yellow, or golden brown, most vibrant at midbody. In females, dorsolateral stripe bordered on both sides with fine black line (one scale wide), but in males dorsolateral stripes appear less well defined relative to background because they either lack fine black lines, especially posterior to the shoulder, or these lines form only short fragmented segments. Ventral field same as background color with thin (one scale wide), black, usually fragmented, sometimes inconspicuous (especially in males) vertebral line. Background color of flanks brown to gray. Lateral field light gray to dark brown, occasionally pinkish orange or brick red–orange, with small, irregular black or dark brown, occasionally white (males only) markings. Dorsal limbs also with small dark brown to black irregular marks. Ventrolateral line white, usually inconspicuous in males. Base of tail striped as trunk, fading posteriorly to uniform gray or brown with small, irregular, middorsal black markings. Ventrally usually immaculate cream-white to charcoal gray, darker on head and lighter toward cloacal region and tail. Rarely, small dark brown to black markings appear on margins of throat. Adult males with light yellow color on abdomen, femoral and cloacal regions, and ventral tail. Gravid coloration in females appears as yellow to orange highlights along the flanks extending to and covering the belly.

*Distribution.*—*Liolaemus chaltin* is known from the eastern Puna region of Jujuy Province, Argentina (Fig. 3) where it occurs at elevations ranging 3400–3750 m.

*Natural history.*—*Liolaemus chaltin* is a terrestrial lizard that usually seeks refuge in clumps of dense bunchgrass (*Festuca* sp.) or a short, spiny shrub (*Adesmia* sp., Fabiaceae) when disturbed. The center of the bunchgrass clumps are pri-
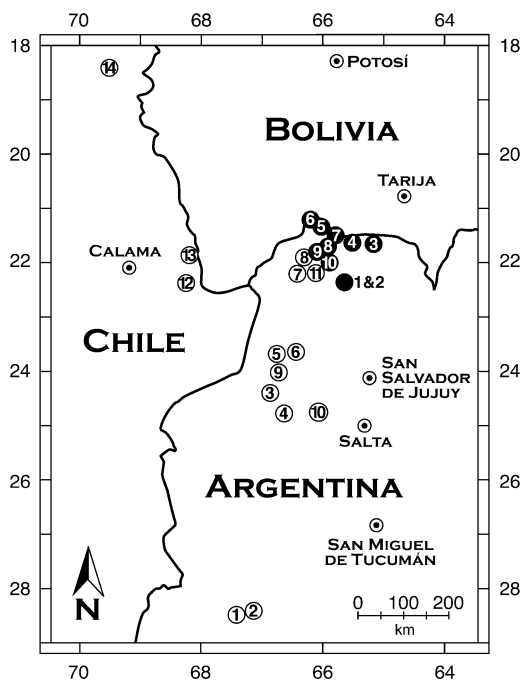


Fig. 3. Distribution of *Liolaemus chaltin* (black circles) (all Jujuy Province, Argentina): 1. Abra Pampa (type locality); 2. Arbolito; 3. 22 km east of de Yavi; 4. 12 km south of de La Quiaca; 5. Santa Catalina; 6. El Angosto; 7. Cieneguillas; 8. Entre Rodeo and Pasaje; 9. west of Laguna Pozuelos; 10. Laguna Pozuelos. Distribution of *Liolaemus puna* (white circles) (Catamarca, Salta, and Jujuy Provinces, Argentina and Atacama Region, Chile): 1. Tambería, Catamarca; 2. Cerro El Mojón, Catamarca; 3. Olacapato, Salta (type locality); 4. Santa Rosa de los Pastos Grandes (Salta); 5. Susques (Jujuy); 6. Abdón Castro Tolay, Jujuy; 7. Fundiciones, Jujuy; 8. Rinconada, Jujuy; 9. Sur de Sey, Jujuy; 10. Cuesta del Acay, Salta; 11. Entre Pampa de los Pozuelos and Abra Pampa, Jujuy; 12. San Pedro de Atacama, Chile; 13. Volcán Tatío, Chile; 14. Chiapa, Tarapacá, Chile.

marily dead straw that varies in color from brown–gray to golden yellow. Thus, the background color and distinct golden-yellow stripes of these lizards make them remarkably cryptic in this microhabitat. When we visited the region of type locality (3360–3636 m) in midsummer (5–6 and 18–21 January 1995 and 1996, respectively), lizards were active from approximately 1000–1800. Body temperatures of active *L. chaltin* (mean SVL = 48.8 mm; SD = 4.3) during this season ranged from 25.3–36.9 C (mean = 31.3 C; SD = 2.7; $n = 40$). The diet of *L. chaltin* (as inferred from examinations of feces produced by approximately 25 adults collected in midsummer) included small insects and, to a lesser extent, seeds of *Festuca*.

Interestingly, the reproductive mode of *L. chaltin*, which was not known to us at the time we collected the first specimens (January 1995), was described to us as oviparous by a local woman (Mrs. Mamanî) who lived near the type locality. Her information was confirmed when two captive females deposited eggs in March 1996. An oviparous reproductive mode was unexpected for *L. chaltin* for two reasons. First, only three other species in the *alticolor* group are oviparous (*L. bitaeniatus, L. ramirezae,* and *L. yanalcu*). Second, in *Liolaemus* (Ramírez-Pinilla, 1991; Etheridge and Espinoza, 2000; Schulte et al., 2000), as in other squamate lineages (Tinkle and Gibbons, 1977; Shine, 1985; Guillette, 1993), species inhabiting high elevations tend to be viviparous. The adaptive explanation for this distributional pattern—termed the ''cold-climate'' hypothesis (Shine, 1983, 1985; Guillette, 1993)—is that gravid females of viviparous taxa can select thermal niches (via behavioral thermoregulation) that benefit their developing offspring (e.g., Beuchat, 1986; Shine and Harlow, 1993; Andrews, 2000). In contrast, oviparous species typically deposit their eggs in subterranean nests where the developing embryos are subjected to the vagaries of the nest environment (see Packard et al., 1977; Packard and Packard, 1988; Overall, 1994). *Liolaemus chaltin* is distributed at elevations (3400–3750 m) exceeding those achieved by most oviparous *Liolaemus*. Indeed, most *Liolaemus* that are distributed above 3000 m are viviparous (Schulte et al., 2000; REE, unpubl. data). For example, over much of its range, *L. chaltin* is syntopic with *L. multicolor* and *L. ornatus*, both of which are viviparous (Schulte et al., 2000). *Liolaemus chaltin* produces from 4–5 asymmetrically ovoid eggs during spring (REE, unpubl. data), which is similar to clutch sizes recorded for other members of the *alticolor* group (Ramírez Pinilla, 1991; Espinoza and Lobo, 1996; Lobo and Espinoza, 1999).

### *Liolaemus puna* n. sp.
### Figures 3–5, Table 1, Appendix 1

*Holotype.*—FML 1364 (formerly of FML 1364, a lot containing 15 specimens), adult male collected at Quebrada Los Berros, approximately 5 km east of Olacapato, Departamento Los Andes, Provincia de Salta, Argentina (24°08.35′S, 66°42.05′W; approximately 4200 m), on 9–11 January 1983 by E. Terán and O. Pagaburo (Fig. 4).

*Paratypes.*—FML 9914–9927 (the remaining specimens in FML 1364; see above). Four females and 10 males. Same data as holotype.
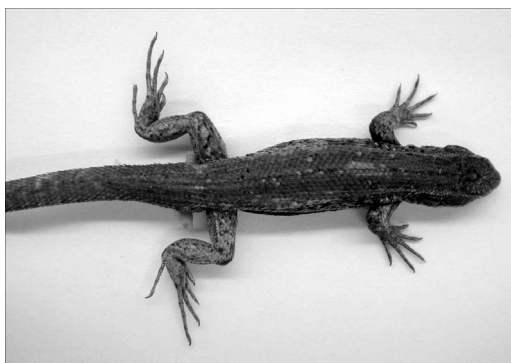


Fig. 4. *Liolaemus puna* (holotype; FML 1364–1). Male, 54.0 mm SVL.

*Etymology.*—The specific epithet *puna* is a noun in apposition and is attributable to the phytogeographic province known as the Puna—the only known habitat of this species. The origin of the word is Quechuan and is attributable to the indigenous people known as the Kollas who lived in this region. ''Puna'' is also a colloquial term for the high-elevation sickness (i.e., dizziness, headache, nausea) often experienced by unacclimatized visitors of Puna habitats. *Liolaemus puna* shares its etymological roots with another liolaemid lizard, *Phymaturus punae* (Cei et al., 1983).

*Diagnosis.*—*Liolaemus puna* is a member of the *alticolor* group (as defined above) but differs from other members of that group in the following ways. In *L. puna*, the nasal is in limited contact with the rostral (height of nasal more than two times the height of the area in contact with rostral) compared to the broad contact between these two scales in *L. alticolor, L. pagaburoi,* and *L. walkeri. Liolaemus puna* usually (90.5%; $n = 42$) have 13 or fewer dorsal head scales, whereas *L. tacnae* and *L. walkeri* have 13–15. Scales of the dorsal head surface are smooth in *L. puna*, slightly rugose in *L. alticolor* and distinctly rugose in *L. bitaeniatus* and *L. variegatus.* The upper temporals are keeled in *L. bitaeniatus, L. pagaburoi,* and *L. variegatus*, whereas the temporals are smooth or only slightly keeled in *L. puna*, and smooth in *L. tacnae* and *L. walkeri.* The majority of *L. puna* examined (61.9%; $n = 42$) have six scales in contact with the interparietal versus seven in *L. alticolor, L. bitaeniatus,* and *L. walkeri.* The new species has 40–50 scales around the midbody compared to 50–60 in *L. tacnae* and *L. walkeri.* Infradigital lamellae of the fourth finger number 17–18 in *L. puna*, 19–20 in *L. ramirezae*, and 16 or fewer in *L. alticolor, L. bitaeniatus,* and *L. pagaburoi.* In most *L. puna*

(85.7%; $n = 42$), the subocular is pigmented (i.e., same as background color), whereas in *L. alticolor*, *L. bitaeniatus*, *L. pagaburoi*, *L. ramirezae*, *L. variegatus*, and *L. walkeri*, this scale is white. The chest and belly region is immaculate in both sexes of *L. puna* but black in all males of *L. walkeri* and some males (66%) of *L. tacnae*. Paravertebral markings are absent in *L. puna* but present in *L. bitaeniatus*, *L. pagaburoi*, *L. variegatus* (Laurent, 1984) and in some (36%; $n = 9$) females of *L. walkeri*. The paravertebral fields of *L. ramirezae* occasionally have irregular rows of short line segments (as seen in *L. bibronii* and *L. exploratorum*; Cei, 1986), but these are absent in *L. puna*. In *L. puna*, the throat is marked with irregularly shaped spots or small line segments in both sexes, but in *L. pagaburoi*, *L. variegatus*, and *L. walkeri*, usually only males have spotted throats, and in *L. alticolor*, *L. bitaeniatus*, *L. ramirezae*, and *L. yanalcu*, the throat is immaculate in both sexes. The vertebral line is absent or highly fragmented in male *L. puna* but nearly complete in females. In both sexes of *L. alticolor*, *L. pagaburoi*, and *L. walkeri*, this line is well differentiated (or, very rarely, slightly fragmented). In *L. bitaeniatus*, *L. tacnae*, *L. variegatus*, and *L. yanalcu*, this line is always absent, and in *L. ramirezae*, the vertebral line is usually absent or, when present, highly fragmented. Dorsolateral stripes are almost always absent in male *L. puna* (rarely these are reduced to the region between the head and shoulders, but fade posteriorly), usually well developed in females (infrequently females resemble males), and increase in width posteriorly to the shoulders and near the base of the tail. In *L. pagaburoi* (both sexes), these stripes are of constant width the length of the torso, but in all other species of the *alticolor* group, these are present in both sexes and become wider posteriorly to the tail. Male *L. puna* have 3–5 precloacal pores, whereas *L. alticolor*, *L. bitaeniatus*, *L. pagaburoi*, *L. ramirezae*, and *L. tacnae* have only 1–3. In *L. bitaeniatus*, *L. ramirezae*, and *L. yanalcu*, a notable proportion of females have precloacal pores (41, 94, and 19%, respectively; Lobo and Espinoza, 1999; Martínez Oliver and Lobo, 2002), but females of other species of the *alticolor* group, including *L. puna*, lack these pores. Female *L. puna* lack gravid coloration, whereas the oviparous members of the *alticolor* group (*L. bitaeniatus*, *L. chaltin*, *L. ramirezae*, and *L. yanalcu*) exhibit this coloration from 2–3 weeks before and after parturition (FL and REE, pers. obs.).

*Description of holotype.*—Male (Fig. 4). Snout—vent length 54.0 mm. Head length 10.8 mm. Head width 9.2 mm. Head height 6.1 mm. Axilla–groin distance 25.6 mm. Foot length 16.7 mm. Tail length 93.8 mm. Scales of the dorsal head smooth, slightly convex. Twelve scales between rostral and occiput. Nasals in broad contact with rostral (nasal height at nares 0.8 mm; at level of contact with rostral 0.3 mm), surrounded by six scales. Nares in posterior half of nasal scale. Six enlarged supralabials, more slender than infralabials. Fourth supralabial (length 1.8 mm) of left side curved upward posteriorly, not in contact with subocular. Four large infralabials. Second infralabial in contact with two sublabials. Seven lorilabials forming a single row between supralabials and subocular. Fourth/fifth (left/right) through the seventh (both sides) lorilabials in contact with subocular. Subocular white, elongate (length 3.4 mm), with pigmented dorsal keel. Canthal separated from nasal by one scale. One preocular, separated from nasal by 2/3 scales. Eleven/13 laminar superior palpebrals and 10/11 inferior palpebrals. Eye diameter 2.2 mm. Temporals smooth, 9/10 from auditory meatus to posterior eye (eight scales, counted vertically between commissure of mouth and parieto-temporal region). Supercilliaries 6/7, all but two posterior-most elongate. Loreal region slightly concave. Two postrostrals each with 5/6 scale organs. Four internasals. Ten prefrontals. Frontal large, undivided. Five scales between rostral and frontal. Supraorbital semicircles complete, formed by 11 small scales. Five/six scales between supercilliaries and frontal. Interparietal large, subpentagonal, surrounded by six scales. Two postparietals, both larger than interparietal. Mental in contact with four postmentals, the latter larger than first infralabials. Two noncontacting rows of three chinshields. Four/five enlarged supraoculars. Openings of auditory meatus oval shaped (right side: height 1.9 mm; width 1.2 mm). One enlarged scale at anterior border of meatus and no differentiated auricular scales. Thirty-three gulars between auditory meatus.

Twenty-six scales between posterior border of auditory meatus and shoulder (counted along a mid line over longitudinal fold). Most scales posterior to auditory meatus small, flat, imbricate. Sixteen larger (near size of dorsals), flat, imbricate, unkeeled scales between posterior border of auditory meatus and antehumeral fold (counted over longitudinal fold). Antehumeral fold nearly forming a pocket, scales within small and granular toward shoulders and surrounding insertion of forelimbs. Longitudinal, postauricular, and postrictal folds indistinct.

Dorsal scales principally lanceolate, keeled, imbricate. Midbody scales 47. Twenty-three dorsal keeled scale rows at midbody. Seventeen dor-

sal scale rows at shoulders. Forty-six dorsal scales from occiput to anterior border of thighs. Dorsal scales of tail larger and imbricate with more prominent keels. Eleven keeled dorsal scale rows at cloaca, 4/5 over dorsal surface of thighs, 6/8 on each tibia. Scales along flanks of trunk small, flat, and distinctly imbricate, smaller and granular in forelimb axillae. Eighty-seven ventral scales between rostral and cloaca. Four precloacal pores with yellow–orange exudate. Hemipenes everted, however, preparation not adequate to record details of lobes or ornamentation.

Brachials and superior antebrachials (dorsals), large, flat, smooth, imbricate. Inferior antebranchials (ventral) smaller, keeled; strongly keeled closest to palms of forelimbs. Scales of palms small, keeled, oriented along longitudinal axis of fingers. Nine scales between insertion points of fingers one through five. Sixteen infradigital lamellae on fourth finger.

Most scales of thighs very small, flat, or granular, posterior thighs with very large, flat, smooth scales. Only dorsal scales of thighs keeled. Tibial scales large, flat, smaller and strongly imbricate in area of articulation with foot, only keeled on dorsal surface. Foot with large scales, flat on dorsal side, slightly keeled between toes five and four, much smaller, and keeled on ventral foot surface, oriented almost perpendicular to longitudinal axis/orientation of toes. Eight scales between insertion points of toes one through five. Twenty-five infradigital lamellae on fourth toe. Claw length of fourth toe 1.2 mm.

*Color in ethanol.*—Background coloration of dorsum from occiput to base of tail olive green (Fig. 4). Tail dark brown dorsally. Lateral field with small black markings. Ventrolateral stripe indistinct, bordered dorsally and laterally by a series of black markings. Ventral field of flanks with small, irregular, dark brown to black marks becoming more diffuse toward belly. Throat gray with fine, darker gray diffuse marks more evident below mandibles.

*Variation.*—Meristic data are from the paratype series and additional specimens (15 females and 19 males: FML 1364—1–15, 1761; MNHNC 583, 585, 588; MZUC 19392; SDSU 3579–82). Snout–-vent length 31.4–55.6 mm (mean = 47.9 mm; SD = 5.8). Head length 19–24% (mean = 21.0; SD = 1.0) of SVL. Auditory meatus 1.2–3.1 (mean = 1.7; SD = 0.4) times higher than wide. Tail length 1.6–1.9 (mean = 1.7; SD = 0.1) times SVL. Scales around midbody 43–54 (mean = 47.2; SD = 2.8). Dorsal scales from occiput

to thighs 40–51 (mean = 44.7; SD = 2.7). Dorsal head scales 9–14 (mean = 11.1; SD = 1.1). Ventrals 74–94 (mean = 83.9; SD = 4.9). Precloacal pores in males 3–5 (mean = 3.6; SD = 0.9), absent in females. Scales surrounding interparietal 6–8 (mean = 6.5; SD = 0.7). Scales of neck between posterior borders of auditory meatus 27–38 (mean = 31.9; SD = 3.0). Scales between auditory meatus and antehumeral fold 16–24 (mean = 20.3; SD = 2.1). Gulars 28–41 (mean = 33.8; SD = 2.7). Ratio of length of subocular/diameter of eye 1.3–1.9 (mean = 1.5; SD = 0.1). Ratio of fourth supralabial/diameter of eye 0.4–1.1 (mean = 0.8; SD = 0.1). Ratio of width of nasal at level of nares/width of nasal in contact with rostral 1.0–5.3 (mean = 2.1; SD = 0.8). Scales between rostral and frontal 4–6 (mean = 4.8; SD = 0.6). Subdigital lamellae of fourth finger 15–20 (mean = 16.9; SD = 1.4). Subdigital lamellae of fourth toe 19–25 (mean = 22.5; SD = 1.4). Fourth supralabial curved with posterior extremity in contact with subocular in 43.6% of specimens. Subocular usually pigmented like background color, but white in a few specimens. Most (70.6%) males lack dorsal pattern. Dorsolateral stripes, dorsal markings (vertebral line, paravertebral markings, etc.) absent (71.6%), or reduced and fragmented in males between head and shoulders. In remaining males (29.4%), these stripes reach the base of tail, but are barely evident or diffuse. Rarely, dorsolateral stripes are reduced to varying degrees in females. Temporals usually smooth, in some specimens a few temporals are slightly keeled. Scales of longitudinal fold of neck smaller than dorsals, smooth (slightly keeled in a few individuals), laminar. Throat darker or more distinctly marked in males than in females, in some females these markings are very fine and/ or diffuse and less evident below the mandibles. Usually 1–3 enlarged scales projecting over anterior border of auditory meatus, very rarely with a differentiated auricular scale. In some females dorsolateral stripes bordered on dorsal margin by fine solid or fragmented black line. Paravertebral field occasionally with a series of slender, short, black parallel segments, forming patterns similar to those in *L. bibronii, L. exploratorum,* and *L. ramirezae.* Vertebral line fragmented (56%) or absent (44%) in males, but almost always present (88%; albeit fragmented) in females.

*Color in life.*—Dorsal background color of males (SDSU 3579–82) brown to olive green, without patterns or conspicuous dorsolateral stripes, except where scarcely discernable stripes appear as faint color fading posteriorly along shoulders
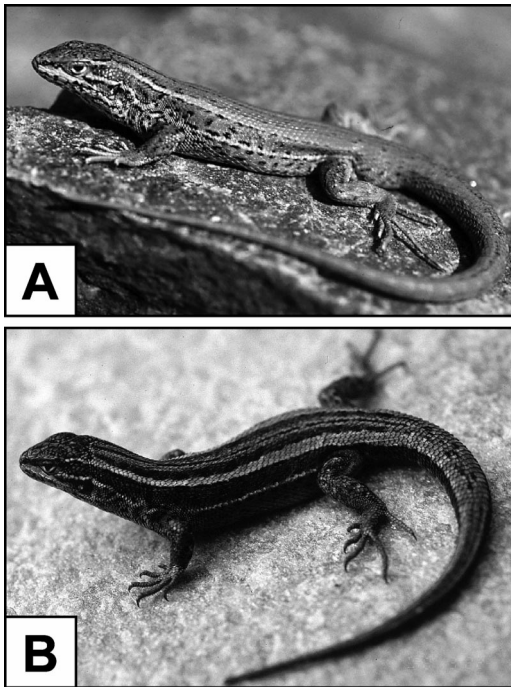
Fig. 5. Male (A) and female (B) *Liolaemus puna* in life from the type locality.

(Fig. 5A). Limbs olive green, slightly lighter in color than dorsal trunk and tail. Brownish-red stripe (approximately four scales wide) with very small black markings originating from between eye and shoulder extends posteriorly along lateral field of flanks to thighs. Brownish-pink below lateral field on flanks, fading ventrally along flanks to light orange. Small black markings in ventral field of flanks become larger and more distinct anterior to forelimbs on flanks and on upper forearm. Base of tail light brown dorsally, grading to orange–pink laterally. Ventral region of throat, chest, and abdomen light lead gray. Throat with small gray or darker marks, especially below jaws. Subocular and loreal regions lighter than background. Faint orange–yellow on posterior abdomen to anterior ventral thighs and from cloaca to most of ventral tail.

Dorsal background coloration golden brown to chocolate brown in females (Fig. 5B). Vertebral line black, fragmented into line segments on trunk, more segmented and slender on tail. Dorsolateral stripes (extending from posterior border of eye to thighs) brown, lighter and brighter than brown background color of dorsum, bordered by a fine black usually fragmented line from eye to shoulders. Small, widely scattered black markings on flanks of trunk. Ven-

trolateral line white-cream to tan, very slender. Flanks and dorsal tail same color as dorsal trunk. Ventrally light lead gray. Throat heavily marked with black elongate marks running direction of longitudinal axis of the body. Gray of ventral trunk fades to cream on ventral thighs.

*Distribution.*—*Liolaemus puna* is distributed over much of the Puna region of northwestern Argentina and northeastern Chile at elevations ranging 3680–4400 m (Fig. 3). This species occurs as far south as the Sierra de Fiambalá (Catamarca Province), north to Santa Rosa de los Pastos Grandes, Cuesta del Acay, and Olacapato in Salta Province, and Abdón Castro Tolay, Pampa de los Pozuelos, and along the road to Laguna Blanca, Jujuy Province (Fig. 3). *Liolaemus puna* appears to have a western distributional limit near 66°W longitude. In northern Chile, this species is known from San Pedro de Atacama and the Volcán Tatío region to Chiapa, Tarapacá. Records from the west at Las Pampas (around Medanitos) and from the east at Tambería and Cerro El Mojón (around Condor Huasi) in the Sierra de Fiambalá, Catamarca Province (FML 1852, 1915) mark the southernmost population of this species. There are 340 km (straight line) between Las Pampas, Catamarca Province and the next-closest locality recorded for this species at Santa Rosa de los Pastos Grandes, Salta Province. More field work is needed to determine whether this species is present, as we presume, in the intermediate, high-elevation mountainous areas of the Sierra de Culampajá, Sierra Laguna Blanca, and the Puna habitats of Antofagasta de la Sierra, Catamarca Province.

*Natural history.*—At the type locality, *L. puna* is usually found near clumps of bunch grass (*Festuca* sp.) or in small spiny shrubs (*Adesmia* sp.) on low-lying sand dunes or in rocky areas on the periphery of the dunes. Here *L. puna* is sympatric with three other species of *Liolaemus* (*Liolaemus dorbignyi*, *Liolaemus ornatus*, and *Liolaemus* cf. *andinus poecilochromus*).

Our limited data and information from the literature suggest that *L. puna* is omnivorous. Studies conducted in northern Chile found a sample of 24 individuals to have nearly 60% plant matter in their diet (Valencia et al., 1982).

*Liolaemus puna* is viviparous. We examined embryos dissected from females from Olacapato (FML 1364, 2779) and Cuesta del Acay (FML 1663), Salta Province that were collected on 22 January 1985. One lot from Olacapato (FML 2779) includes a female with two embryos and two oviductal eggs (12.7 × 7.3 mm and 14.2 ×

7.1 mm). Of the four females dissected from Cuesta del Acay, only one had embryos in advanced stages of development, whereas the other three had inactive ovaries with 5–6 tiny (approximately 1 mm) ovarian follicles, suggesting that parturition had already taken place. The yolk sacs of embryos from a female collected at Cuesta del Acay (FML 1663) were nearly completely absorbed and the embryos were positioned in the distal oviduct with their heads near the cloacal aperture (one on each side), suggesting that the time of parturition was imminent.

DISCUSSION

Members of the *alticolor*, as defined here, include 10 species that are widely distributed in the Puna and cordilleran regions of Argentina, Bolivia, Chile, and southern Perú. The taxonomic status of many of these populations has been, and continues to be, the focus of research because they exhibit noteworthy polymorphism in color and pattern, interesting ecological characteristics (e.g., high-elevation distributions), and oviparous and viviparous reproductive modes. In the past, investigators had reported cases of reproductive bimodality in *L. alticolor*, with two populations exhibiting both oviparous and viviparous individuals (Laurent and Noriega, 1988; Ramírez Pinilla and Laurent, 1996). Recently, we reexamined populations from the provinces of Tucumán and Catamarca and found them to be two cryptic species (*L. pagaburoi* and *L. ramirezae*; Lobo and Espinoza [1999]). *Liolaemus pagaburoi* (viviparous) is found at a slightly higher elevation than *L. ramirezae* (oviparous). However, both species were collected in a zone of sympatry (km marker 88) along Ruta Provincial 307 that connects Tafí del Valle in the east, to Amaicha in the west. Because they are morphologically similar, the two species were cataloged as a single lot (i.e., the same jar), which subsequently misled future workers who investigated their reproductive modes (Lobo and Espinoza, 1999). The contact zone at km marker 88 is a transition zone wherein the cooler, moister habitat to the east, which is dominated by bunchgrass (*Festuca*), and the warmer, drier scrub vegetation of the south meet along the sloping hillsides and steep valleys (Lobo and Espinoza, 1999). Both species of *Liolaemus* were found to be habitat specialists: *L. pagaburoi* in the bunchgrass and *L. ramirezae* associated with a spindly shrub (*Parastrephia*), yet both maintained their strong microhabitat preferences and are, therefore, not syntopic

even in this zone of sympatry (Lobo and Espinoza, 1999).

The suspected presence of females with different reproductive modes from the same locality at Olacapato, Salta Province (FML 1364; Ramírez Pinilla and Laurent, 1996) apparently represents similar taxonomic circumstances. We have determined that female specimens that had been separated to a different collection number (FML 2779, but with the same collection data as FML 1364), are two distinct species: one viviparous (*L. puna*), and the other oviparous (*L. ramirezae*). However, this oviparous species is not known from Olacapato because its distribution only reaches north of the Valle Calchaquí (western Tucumán, eastern Catamarca, and west-central Salta; Lobo and Espinoza, 1999). Another example of this type of confusion is found in a lot (FML 1852) that includes specimens of *L. bitaeniatus* (oviparous) and *L. puna* (viviparous), at a reported elevation of 3700–4000 m (Tambería, Cerro Mojón, around Condor Huasi). This elevation far exceeds that known for *L. bitaeniatus* (2800 m; Schulte et al., 2000). On a recent visit to this locality, *L. bitaeniatus* was found no higher than 2600 m at Condor Huasi, but to reach the population of *L. puna*, one has to climb from Condor Huasi to Cerro Mojón at an elevation of almost 4000 m (FL, unpubl. data). There is a possible contact zone for *L. chaltin* and *L. puna* south of Laguna Pozuelos, Jujuy, and another on Ruta Provincial 11 between Cochinoca, a *L. chaltin* locality, and Abdón Castro Tolay, a *L. puna* locality. The *L. "alticolor"* reported in Schulte et al. (2000) was collected from the type locality of *L. chaltin* and is referable to this species.

Donoso-Barros (1966) reports *Liolaemus alticolor walkeri* from the cordilleran region of Antofagasta, Catamarca to Calama and San Pedro de Atacama, Chile at similar latitudes (22–24°S) and along the border of the provinces of Salta and Jujuy. We examined specimens from the Museo de Concepción (MZUC 19392) from Antofagasta, Volcán Tatío, additional material from the Museo Nacional in Santiago, Chile (MNHNC 583, 585, 588), from San Pedro de Atacama, and specimens from Tarapacá, Chiapa (MCZ 149852, 149854–56; SDSU 1697–99), and assign these to *L. puna*. We also compared the materials of *L. puna* from various museums with the type series of *L. walkeri*, in addition to other material from Perú. Our observations indicate that *L. walkeri* is restricted to Perú, whereas the form found in northern Chile, parts of Bolivia, and the Puna of Argentina is *L. puna*. Specimens collected along the cordilleran zone adjacent to Calama suggest that there may be an

elevational replacement between *L. puna* and *Liolaemus paulinae* (the latter restricted to the zone of Calama and at lower elevations [2000–2500 m], and *L. puna* from approximately 3700 m and higher) similar to the one described for *L. ramirezae* and *L. pagaburoi* (Lobo and Espinoza, 1999). In Chile, *L. alticolor* may be found in the region of Arica at Putre to 3500 m (Codoceo, 1950) and in Caquena and Parinacota (Donoso-Barros, 1966). Populations assigned to *L. alticolor* from eight high-Andean localities in northern Chile have been studied ecologically (Marquet Iturriaga, 1985). Unfortunately, materials from this region were not available to us, but they may prove informative for determining the overlap (if any) of the distributions of *L. alticolor* and *L. puna.*

*Liolaemus alticolor* is widely distributed in Bolivia from areas near the type locality (Tiahuanaco) to just south of Potosí. To the west, the region of extensive dry, saline basins (e.g., Salar de Uyuni, Salar de Empexa, Salar de Coipasa, etc.) may function as natural barriers separating *L. puna* in Chile (and possibly in western Bolivia) from *L. alticolor* in the Puna and cordilleran areas of Bolivia. In the north, *L. alticolor* reaches southern Perú at Sicuani (AMNH 38068–70).

Morphological data suggest that several of the northernmost-distributed species in the *alticolor* group (*L. alticolor, L. puna, L. tacnae,* and *L. walkeri*) form a subclade. For example, in these species, the preocular is often (30–50%) in direct contact with the lorilabials. In contrast, the other members of the *alticolor* group have a very low frequency (≤ 5%) of this character state, and in all other species of the more-inclusive *chiliensis* group, the preocular and lorilabial row is separated by one scale (Lobo, 2001). Within this northern subclade, *L. tacnae* and *L. walkeri* may be sister taxa because males of these species share ventral melanism. Studies are currently underway to test these hypotheses using a combination of morphological and molecular data.

KEY TO THE SPECIES OF THE *alticolor* GROUP

The following key was developed for use with either preserved or live adult specimens. Some of the characteristics described in the couplets refer to specific body patterns (or lack thereof) that have been defined and illustrated elsewhere (Lobo and Espinoza, 1999:fig. 1). Although members of the *alticolor* group can be distinguished based on morphological characteristics alone, we provide additional information (i.e., distribution, color in life, reproductive mode, natural history) for some species to assist in confirming their identities.

1a. Opposing paravertebral markings (short, usually paired, black transverse bars or spots) in the paravertebral fields ........ 2
1b. Paravertebral markings absent ........ 4
2a. Vertebral line complete. Head scales smooth or slightly rugose. Males with spotted throats. Northwest Argentina. Viviparous ...... *pagaburoi*
2b. Midvertebral line absent or incomplete. Head scales distinctly rugose ........ 3
3a. Light-colored dorsolateral stripes slender but distinct. Tail length more than twice SVL. Northwest Argentina. Oviparous ...... *bitaeniatus*
3b. Dorsolateral stripes absent. Mountains near Cochabamba, Bolivia ........ *variegatus*
4a. Ventral surface of tail spotted ........ 5
4b. Ventral surface of tail immaculate ........ 6
5a. Males with ventral melanism. Perú ........ 7
5b. Males lacking ventral melanism ........ 8
6a. Both sexes with same pattern of light, dorsolateral stripes. Throat of males immaculate (no spots or dark pigmentation). Females with gravid coloration. Oviparous. Northwest Argentina ........ *chaltin*
6b. Males without dorsal pattern (or occasionally present only on neck), background color olive to brown. Females with well-defined light, dorsolateral stripes and gravid coloration. Throat of males uniformly dark. Viviparous. Northwest Argentina and northeast Chile ...... *puna*
7a. Midvertebral line and dorsolateral stripes present. Viviparous. South and central Andean Perú ........ *walkeri*
7b. Midvertebral line and dorsolateral stripes absent. Frontal scale fragmented. Viviparous. Southwest Perú ........ *tacnae*
8a. Temporal scales slightly keeled. Paravertebral field always immaculate. Throat of males spotted. Females lack precloacal pores. Viviparous. Andean Bolivia and south Perú ...... *alticolor*
8b. Temporal scales smooth. Paravertebral field with small and longitudinal scattered markings (line segments). Throat of males immaculate. Some females with precloacal pores. Oviparous. Northwest Argentina ........ 9
9a. Dorsolateral stripes present, sometimes slightly differentiated from paravertebral field coloration, but never bordered by fine black lines. General coloration of dorsum brown to gray, lateral field (of flank) brown to light brown. Oviparous. Northwest Argentina ...... *ramirezae*
9b. Dorsolateral stripes absent, background coloration dark brown (almost black), lateral field darker than dorsum. Oviparous. Puna regions of Salta, Argentina ........ *yanalcu*

MATERIAL EXAMINED

With the exception of the new species described herein, specimens listed in our previous studies (Lobo and Espinoza, 1999; Lobo, 2001; Martínez Oliver and Lobo, 2002) are not listed

below. This includes members of the *alticolor* group: *L. alticolor*, *L. bitaeniatus*, *L. pagaburoi*, *L. ramirezae*, *L. tacnae*, *L. variegatus*, *L. walkeri*, and *L. yanalcu*, as well as species in the more-inclusive *chiliensis* group that were used for comparative purposes: *L. bibronii*, *L. exploratorum*, *L. gracilis*, *L. robertmertensi*, *L. sanjuanensis*, and *L. saxatilis*. Some numbers 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. Specimens are from Argentina unless otherwise noted.

*Liolaemus chaltin*: FML 9874 (holotype), FML 9875–9913 (paratypes), off Ruta Prov. 71, 4.2 km W Abra Pampa, Dpto. Cochinoca, Jujuy (22°42′24.4″S, 65°43′12.4″W; 3360 m). FML 1459 [4], Inti Cancha, 22 km E of Yavi, Dpto. Yavi, Jujuy. FML 1460 [5], 12 km S La Quiaca, Dpto. Yavi, Jujuy. FML 1521, Road to Santa Catalina, El Angosto, 5 km from Santa Catalina, Dpto. Santa Catalina, Jujuy (3700 m). FML 1524 [4], El Angosto, Dpto. Santa Catalina, Jujuy (3400 m). FML 1531 [3], Ladera NW Cerro Santa Catalina and on right bank of Río Santa Catalina, Dpto. Santa Catalina, Jujuy (3750 m). FML 1527 [8], 3 km Cieneguillas, road to Santa Catalina, Jujuy (3450 m). FML 973, Laguna Pozuelos, Jujuy. FML 3428 [2], near the shore of Laguna Pozuelos, Dpto. Rinconada, Jujuy (22°28′S, 65°57′W; 3720 m). FML 1528 [16], planicie W of Laguna Pozuelos (within 100–900 m of lakeshore), Dpto. Rinconada, Jujuy (3500 m). FML 2351, Laguna Pozuelos, Dpto. Yavi, Jujuy. FML 1878 [5], Zona entre Rodeo-Pasaje cerca (Este) Laguna Pozuelos, Jujuy (3650 m). FML 1538 [2], 3 km W Abra Pampa, Dpto. Cochinoca, Jujuy (3460 m). FML 1871 [4], Abra Pampa, Dpto. Cochinoca, Jujuy (3440 m). FML 1461 [5], 3 km NW Abra Pampa, Dpto. Cochinoca, Jujuy. FML 2074 [5], Abra Pampa, Jujuy. FML 2477, Abra Pampa, Jujuy. FML 2513 [2], Abra Pampa, Dpto. Cochinoca, Jujuy. FML 3487 [2], Arbolito, Ruta Prov. 7, Dpto. Cochinoca, Jujuy. FML 3492, Abra Pampa, Dpto. Cochinoca, Jujuy (3660 m).

*Liolaemus puna*: FML 1364 (holotype), FML 9914–27 (paratypes), Quebrada Los Berros, approximately 5 km E of Olacapato, Dpto. Los Andes, Salta (24°08.35′S, 66°42.05′W; ca. 4200 m). FML 929, road to Laguna Blanca, Jujuy. FML 1265, Susques, Dpto. Susques, Jujuy. FML 1512, Camino Rinconada (3800 m), Laguna Larga, Dpto. Rinconada, Jujuy. FML 1517, Cuesta de Fundiciones, road to Mina Pirquitas, entre 35–37 km antes de población.

Ladera exposición W-SE-NE, Dpto. Rinconada, Jujuy. FML 1519, 5 km from Rinconada, Dpto. Rinconada, Jujuy (3800 m). FML 1533, Pampa de los Pozuelos a Abra Pampa (40 km from Abra Pampa), Dpto. Rinconada, Jujuy. FML 1661, 1663 Cuesta del Acay, Dpto. La Poma, Salta (4100 m). FML 1761, Santa Rosa de los Pastos Grandes, Dpto. Los Andes, Salta (3800 m). FML 1874, Abdón Castro Tolay, Jujuy, Dpto. Cochinoca, Jujuy (3680 m). FML 2779, Quebrada Los Berros, Olacapato, Dpto. Los Andes, Salta. FML 3647, Campo Amarillo, at N base of Cerro Verde, Dpto. Los Andes, Salta. FML 3348, Ruta Prov. 74, road to Sey, Dpto. La Poma, Salta. FML 3649, W of base of Cerro Verde, Dpto. Los Andes, Salta (4440 m). SDSU 3579–82, 5.2 km E Olacapato on Ruta Nac. 51, Dpto. Los Andes, Salta (24°08′21.3″S, 66°42′3.71″W; 4230 m). FML 1852, Tambería, Cerro El Mojón (climbing mountain from Condor Huasi), Dpto. Belén, Catamarca, (3700–4000 m). FML 1915, Las Pampas, Campo Potreritos (climbing from Medanitos), Tinogasta, Dpto. Tinogasta, Catamarca (3900 m). MNHNC 583, 585, 588, San Pedro de Atacama, II Región, Chile. MZUC 19392 [3], Volcán Tatío, Antofagasta, Chile Chiapa, Tarapacá, II Región, Chile.

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APPENDIX 1. VARIATION IN CHARACTER STATES AMONG MEMBERS OF THE *alticolor* GROUP (REVISED FROM LOBO AND ESPINOZA, 1999; MARTÍNEZ OLIVER AND LOBO, 2002). Sample sizes are based on specimens used for meristic characters. In most cases, additional specimens were examined for the pattern descriptions. Unless otherwise indicated, numbers are means (followed by SD and range below) with the exception of that for scales contacting the nasal, which is expressed as the number (and percentage) of individuals exhibiting a particular state. Some data for *Liolaemus variegatus* were taken from Laurent (1984).

| Character | alticolor n = 23 | bitaeniatus n = 25 | chaltin n. sp. n = 12 | pagaburoi n = 33 | puna n. sp. n = 34 | ramirezae n = 30 | taenae[a] n = 5 | variegatus n = 2 | walkeri n = 36 | yanalcu n = 41 |
|---|---|---|---|---|---|---|---|---|---|---|
| Dorsal head scales | 12.2 (1.6) (10–15) | 12.6 (1.1) (10–14) | 11.9 (0.9) (11–13) | 11.3 (1.0) (9–13) | 11.1 (1.1) (9–14) | 10.8 (0.9) (9–13) | 13.5 (0.6) (13–14) | 12 (1.4) (11–13) | 13.3 (1.2) (11–16) | 12.8 (1.0) (10–16) |
| Head surface | smooth | rugose | smooth | slightly rugose | smooth | smooth | smooth | rugose | smooth | smooth |
| Nasal-rostral contact[b] | 2.0 (0.7) (1.2–4.4) | 2.2 (0.6) (1.3–3.5) | 3.3 (2.0) (1.4–7.9) | 1.6 (0.4) (1.1–3.0) | 2.1 (0.8) (1.0–5.3) | 4.8 (2.6) (1.5–12.7) | 8.7 (7.9) (2.4–20.2) | 4.3 (2.9) (2.3–6.4) | 4.3 (3.7) (1.3–17.2) | 2.5 (0.7) |
| Scales contacting nasal | 7 (65.0%) 6 (35.0%) | 7 (71.8%) 8 (18.7%) | 7 (55.0%) 6 (45.0%) | 7 (82.8%) 6 (14.3%) | 6 (57.5%) 7 (42.5%) | 6 (59.0%) 7 (33.3%) | 7 (80.0%) 6 (20.0%) | 7 (66.6%) 6 (33.4%) | 7 (66.6%) 6 (33.4%) | 7 (73.8%) 6 (26.2%) |
| Temporals | weakly keeled | keeled | smooth to weakly keeled | keeled | smooth to weakly keeled | weakly keeled | smooth | weakly keeled | smooth | weakly keeled |
| Number of neck scales | 30.9 (4.0) (24–41) | 27.2 (3.6) (21–36) | 28.6 (2.7) (25–35) | 25.1 (3.2) (20–32) | 31.9 (3.0) (27–38) | 26.9 (3.0) (20–34) | 32 (2.7) (28–34) | 28 — | 34.8 (3.5) (29–43) | 32.8 (2.6) (26–37) |
| Number of gulars | 29.4 (2.5) (25–34) | 28.7 (2.7) (22–34) | 31.0 (2.5) (28–34) | 28.4 (2.6) (24–33) | 33.8 (2.7) (28–41) | 30.4 (3.0) (24–35) | 30.7 (0.9) (30–32) | 31.5 (0.7) (31–32) | 31.2 (3.6) (25–38) | 33.2 (2.5) (26–39) |
| Throat in males | spotted | immaculate | immaculate | spotted | irregular marks | immaculate | dark with white spots | immaculate | spotted | immaculate |
| Lateral folds of neck | inconspicuous | inconspicuous | distinct | inconspicuous to absent | distinct | distinct | distinct | inconspicuous to absent | distinct | distinct |
| Scales around midbody | 44.1 (3.1) (40–51) | 41.8 (2.9) (37–48) | 47.7 (3.7) (40–54) | 42.0 (2.9) (36–48) | 47.2 (2.8) (43–54) | 42.1 (2.8) (38–48) | 45.5 (1.7) (44–47) | 41.8 (1.4) (37–49) | 52.7 (3.2) (47–59) | 45.3 (2.4) (40–50) |
| Vertebral line | complete | absent | absent or fragmented | complete | absent or fragmented | absent | absent | absent | complete | fragmented |
| Paravertebral markings | absent | present | absent | present | absent | absent or inconspicuous | inconspicuous | present | absent or inconspicuous | absent |
| Dorsolateral stripes[c] | wide | slender | wide | slender | wide in females, absent in males | wide | absent | absent | slender | absent |

APPENDIX 1. CONTINUED.

| Character | *alticolor* n = 23 | *bitaeniatus* n = 25 | *chaltin* n. sp. n = 12 | *pagaburoi* n = 33 | *puna* n. sp. n = 34 | *ramirezae* n = 30 | *tacnae*[a] n = 5 | *variegatus* n = 2 | *walkeri* n = 36 | *yanalcu* n = 41 |
|---|---|---|---|---|---|---|---|---|---|---|
| Male precloacal pores | 3.6 (1.3) (2–6) | 2.1 (0.8) (2–4) | 4.2 (0.4) (4–5) | 3.6 (1.4) (2–6) | 3.6 (0.9) (3–5) | 3.2 (0.6) (3–5) | absent | 5 (3.5) (3–8) | 4.0 (0.8) (3–6) | 2.9 (0.8) (2–5) |
| Females with precloacal pores | 0% | 41% | 0% | 0% | 0% | 94.1% | 0% | 0% | 0% | 19% |
| Maximum SVL (mm) | 55.1 | 61.3 | 58.7 | 57.2 | 55.6 | 57.6 | 48.8 | 60 | 63.4 | 61.4 |
| Reproductive mode | viviparous | oviparous | oviparous | viviparous | viviparous | oviparous | viviparous? | viviparous? | viviparous | oviparous |
| Gravid-female coloration | unknown | present | present | absent | absent | present | unknown | unknown | unknown | present |
| Elevation (m) | 3000–4700 | 700–2800 | 3400–3750 | 3000–4700 | 3680–4400 | 2820–3200 | 2438–4080 | 1800–4000 | 3048–4755 | 3730–4305 |

[a] A recent examination of the type series of *Liolaemus tacnae* (MCZ 45806–08) indicates that the *L. "tacnae"* examined in our previous study (FML 1544; SDSU 1924; Lobo and Espinoza, 1999) are not referable to this species.
[b] Maximum heigt of the nasal scale in relation to the width that is in contact with the rostral.
[c] Dorsolateral stripes may become wider posteriorly toward the shoulders or remain slender. These stripes are absent occasionally.