Two New Cryptic Species of *Liolaemus* (Iguania: Tropiduridae) from Northwestern Argentina: Resolution of the Purported Reproductive Bimodality of *Liolaemus alticolor*

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The *Liolaemus alticolor* group (Iguania: Tropiduridae) currently includes two or three species of morphologically similar, small-bodied lizards distributed from southern Perú and Bolivia to northern Argentina and Chile. Recently, a few populations of *L. alticolor* from northwestern Argentina were reported to be reproductively bimodal—having both oviparous and viviparous females at the same locality. We reexamined lizards from these putatively bimodal populations and found evidence that these populations include two sympatric yet distinct species—one oviparous, the other viviparous. These species can also be distinguished from *L. alticolor* sensu stricto from the type locality (Tiahuanaco, Bolivia). Here we describe the two new species, *L. ramirezae* and *L. pagaburoi*, from the province of Tucumán, Argentina. *Liolaemus ramirezae* differs from *L. alticolor* in having distinct neck folds, precloacal pores in females, and an oviparous reproductive mode, and in lacking both spots on the throat in males and a vertebral line. *Liolaemus pagaburoi* differs from *L. alticolor* in having distinct paravertebral markings, slender dorsal stripes, and more rugose head scales. Recognition of these new species as distinct resolves the paradox of reproductive bimodality in *L. alticolor*. Interestingly, both of the new species appear to be microhabitat specialists that associate with a single species of plant in their respective habitats. As predicted by the cold-climate hypothesis, the oviparous species is distributed in a warmer climate than is the viviparous species.

El grupo *Liolaemus alticolor* (Iguania: Tropiduridae) actualmente incluye unas dos a tres especies morfólogicamente similares. Se trata de lagartos pequeños distribuídos desde el sur de Perú y Bolivia hasta el norte de Argentina y Chile. Recientemente, unas pocas poblaciones de *L. alticolor* del noroeste de Argentina fueron reportadas por exhibir bimodalidad reproductiva, es decir, contar tanto con hembras ovíparas como hembras vivíparas en la misma localidad. En este trabajo se revisaron esas poblaciones y encontramos evidencia que las mismas incluyen dos especies simpátricas, una vivípara y la otra ovípara. Estas especies se diferencian asimismo de *L. alticolor* sensu stricto de la localidad tipo (Tiahuanaco, Bolivia). Aquí se describen las dos nuevas especies, *L. ramirezae* y *L. pagaburoi* de la provincia argentinas de Tucumán. *Liolaemus ramirezae* difiere de *L. alticolor* por tener más marcados los pliegues laterales del cuello, presentar poros precloacales en las hembras, por ser una especie ovípara, carecer (los machos) de un manchado característico en la garganta, y carecer de línea vertebral. *Liolaemus pagaburoi* se diferencia de *L. alticolor* por contar con manchas paravertebrales, escamas del dorso de la cabeza mas rugosas y con las bandas dorsolaterales no ensanchadas más allá de los hombros. El reconocimiento de estas nuevas especies como distintas resuelve la paradoja de la bimodalidad reproductiva en *L. alticolor*. Ambas especies parecen ser especialistas en cuanto al microhabitat preferido, estarían asociadas a una sola especie de planta en sus respectivos habitats. Como lo predice la hipótesis del clima frío, la especie ovípara se distribuye en un clima más cálido que la especie vivípara.

THE *Liolaemus alticolor* group (Iguania: Tropiduridae) is poorly defined and has never been formally described. Ortiz (1981) considered the *alticolor* group to be comprised of *L. alticolor*, *L. tacnae*, and *L. walkeri*, whereas the *alticolor* group of Cei (1993) included only *L. alticolor* and *L. walkeri*. Neither author, however, provided a definitive diagnosis of their respective group, and as a consequence, neither definition excludes similar-looking but clearly unrelated species. Indeed, at least 14 additional species of the more inclusive *chiliensis* group (Etheridge, 1995) share several of the morphological affinities used to define the *alticolor* groups of Ortiz (1981) and Cei (1993; unpubl. data; Table 1). For the purpose of diagnosing

TABLE 1. MEMBERS OF THE *chiliensis* GROUP (ETHERIDGE, 1995) SHARING MORPHOLOGICAL AFFINITIES WITH SPECIES OF THE *alticolor* GROUP (SENSU ORTIZ, 1981; CEI, 1993) USED FOR DIAGNOSING THE NEW SPECIES DESCRIBED IN THIS STUDY. Members of the *alticolor* group sensu Ortiz (1981) are indicated with an *, and those sensu Cei (1993) with a †. Note the monophyly of, and the relationships among, these species has not been determined.

Species	General Distribution
Liolaemus "alticolor"*†	NW Argentina, S Bolivia, NE Chile, and S Perú
L. bibronii	C to S Argentina and into WC Chile
L. bitaeniatus	NW Argentina
L. fuscus	N Chile
L. gracilis	C and S Argentina
L. gravenhorstii	C Chile
L. hernani	C Chile
L. lemniscatus	C to S Chile and WC Argentina
L. paulinae	NC Chile
L. robertmertensi	N Argentina
L. sanjuanensis	N Argentina
L. saxatilis	N Argentina
L. schroederi	NC Chile
L. tacnae*	SE Perú
L. variegatus	SC Bolivia
L. walkeri*†	E Perú

the new species described herein, we tentatively recognize species in the *alticolor* group by their keeled, lanceolate dorsal scales and a distinct pattern including dorsal and/or lateral stripes (Fig. 1) which have been embellished or lost by a few species in the group. Lizards belonging to this group are small (50–70 mm SVL), slender, elongate, and generally terrestrial (see Table 2). Most are distributed exclusively in Argentina or Chile, but a few have ranges that extend into Bolivia and southern Perú. They are generally found in semiarid to arid regions from sea level to elevations up to 4800 m (Donoso-Barros, 1966; Cei, 1986, 1993; REE, unpubl. data). As is true for the majority of the species in the genus, most aspects of the natural history of these lizards are unknown. However, recently, the reproductive biology of *L. alticolor* was studied in northwestern Argentina, and some provocative results were reported. Investigators found that some populations of *L. alticolor* (*L. alticolor alticolor* of Laurent and Noriega, 1988) were oviparous, whereas in other populations, the same species was viviparous (Ramírez Pinilla, 1989, 1991a; Ramírez Pinilla and Laurent, 1996). Aside from their differing reproductive modes,

females from oviparous and viviparous populations were found to be morphologically indistinguishable by phenetic cluster analyses (Ramírez Pinilla and Laurent, 1996). In addition, both oviparous and viviparous females were collected from a **single** population in the province of Tucumán (Ramírez Pinilla and Laurent, 1996). These results led these investigators to conclude that *L. alticolor* may be either reproductively bimodal or polytypic and comprised of two or more cryptic species.

The existence of a single population of squamate reptiles exhibiting alternative reproductive modes is noteworthy, both because it is unprecedented and because of its potential value for testing predictions regarding the evolution of viviparity. Among squamate reptiles, intraspecific reproductive bimodality is exceedingly rare (Shine, 1985; Shine and Lee, 1999), and in all reported cases, the oviparous and viviparous populations are allopatric (e.g., Qualls et al., 1995; Heulin et al., 1997; Smith and Shine, 1997). Recent reports of a single reproductively bimodal population of *Sceloporus bicanthalis* (Mink and Sites, 1996; Benabib et al., 1997; Creer et al., 1997) appear to be the result of an error in classifying reproductive modes (M. Benabib and J. S. Sites, pers. comm.). Few studies have provided detailed taxonomic analyses of the taxon (or taxa) reported to be reproductively bimodal (but see Qualls et al., 1995; Mink and Sites, 1996; Benabib et al., 1997). Hence, the taxonomic status of most reproductively bimodal squamates is uncertain. Nevertheless, investigators have suggested that, if viviparity evolves in a gradualistic fashion (for a recent discussion, see Blackburn, 1995, 1998; Qualls et al., 1997), we would expect to find populations with both oviparous and viviparous individuals (Guillette, 1993; Andrews and Rose, 1994; Qualls et al., 1995). Indeed, if a reproductively bimodal population of *L. alticolor* did exist, it would provide an ideal system for studying numerous aspects of the evolution of viviparity in squamate reptiles (Guillette, 1993). As a first step toward studying the evolution of viviparity in the *alticolor* group, we reexamined specimens ascribed to *L. alticolor*—including those from the reportedly reproductively bimodal population—to revisit the taxonomic status of the oviparous and viviparous individuals.

We were also interested in examining aspects of the thermal environment experienced by these lizards because investigators have long implicated environmental correlates as factors selecting for the evolution of viviparity in squamate reptiles (see e.g., Tinkle and Gibbons, 1977; Shine, 1985; Guillette, 1993). Specifically,
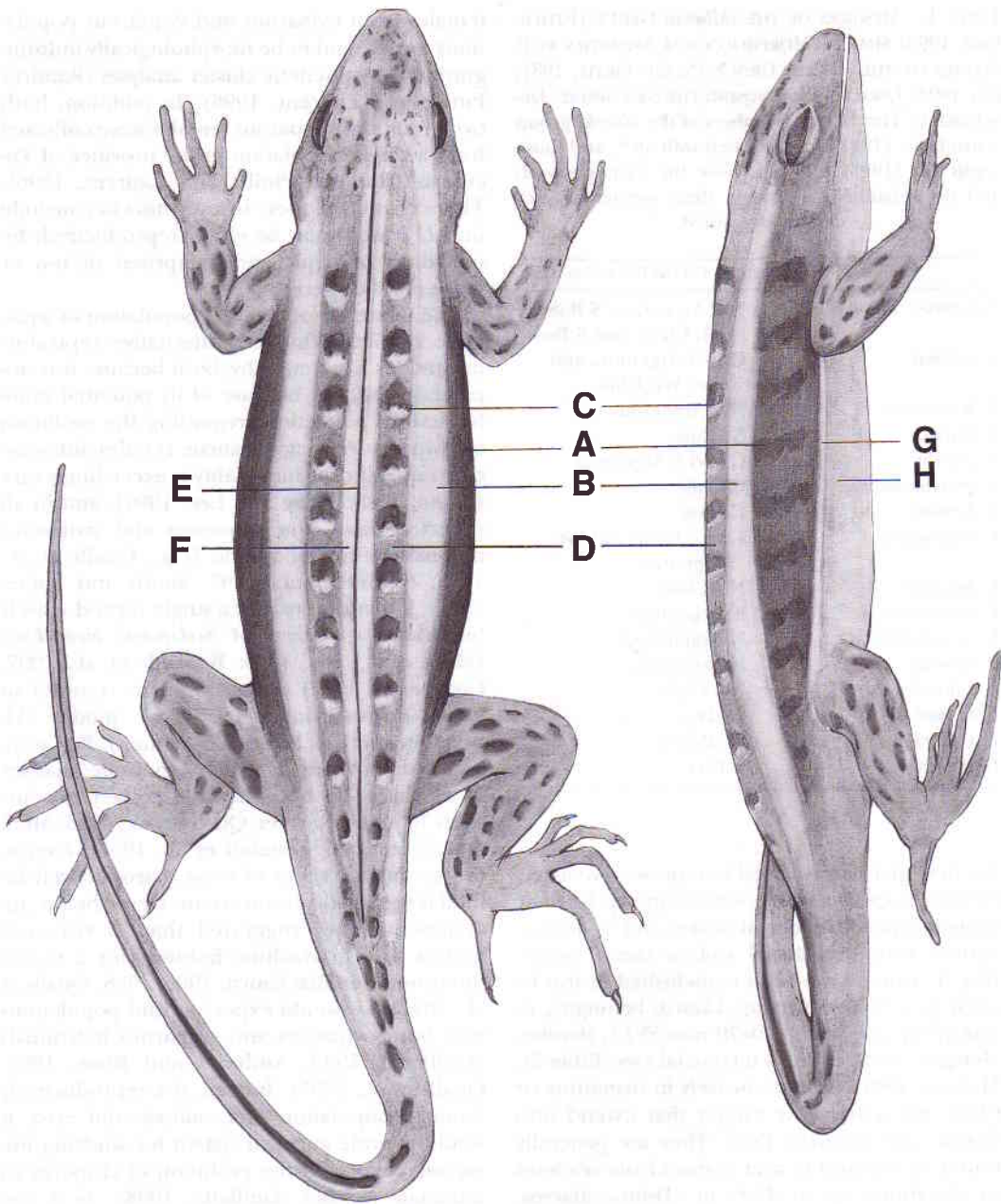
Fig. 1. Schematic representation of the features of the body patterns commonly found in potential members of the *alticolor* group and used in this analysis. (A) Lateral field; (B) dorsolateral stripe; (C) paravertebral markings; (D) paravertebral field; (E) vertebral line; (F) vertebral field; (G) ventrolateral stripe; and (H) ventral field. Refer to the text for descriptions of variation.

viviparity is thought to provide a selective advantage in cool environments (e.g., high latitudes and elevations) because viviparous lizards can regulate the body temperatures of their developing embryos via behavioral thermoregulation (e.g., Beuchat, 1986; Shine and Harlow, 1993). In contrast, oviparous species deposit their eggs in the substratum, where the developing embryos are subjected to the vagaries of the nest environment (see Packard et al., 1977; Packard and Packard, 1988). Such conditions may include nest temperatures that are too cool for normal or optimal development (Vinegar, 1974; Shine, 1983; Shine and Harlow, 1996). Indeed,

TABLE 2. VARIATION IN CHARACTER STATES AMONG MEMBERS OF THE *chiliensis* GROUP THAT ARE MOST MORPHOLOGICALLY SIMILAR TO THE TWO SPECIES DESCRIBED HEREIN. Unless otherwise indicated, numbers are means (followed by SD and the range below) with the exception of that for scales contacting the nasal, which is expressed as the number (and percentage) of the majority of individuals examined exhibiting a particular state. Some of the data for *Liolaemus variegatus* were taken from Laurent (1984).

Character	*alticolor* n = 14	*bitarniatus* n = 25	*pagaburoi* n. sp. n = 33	*ramirezae* n. sp. n = 30	*tacnae* n = 1	*variegatus* n = 2	*walkeri* n = 24
dorsal head scales	11.3 (1.2) (10–15)	12.6 (1.1) (10–14)	11.3 (1.0) (9–13)	10.8 (0.9) (9–13)	13	12 (1.4) (11–13)	13.3 (1.2) (12–16)
dorsal surface of head	smooth	rugose	slightly rugose	smooth	smooth	rugose	smooth
surface of temporals	slightly keeled	keeled	keeled	slightly keeled	smooth	slightly keeled	smooth
nasal-rostral contact[a]	1.7 (0.2) (1.2–2.1)	2.2 (0.6) (1.3–3.5)	1.6 (0.4) (1.1–3.0)	4.8 (2.6) (1.5–12.7)	4.6	4.3 (2.9) (2.3–6.4)	4.3 (4.1) (1.3–17.2)
scales contacting nasal	7 (58.8%) 6 (17.6%)	7 (71.8%) 8 (18.7%)	7 (82.8%) 6 (14.3%)	6 (59.0%) 7 (33.3%)	7	7 (66.6%) 6 (33.3%)	7 (61.5%) 6 (30.8%)
number of neck scales	28.8 (2.4) (24–33)	27.2 (3.6) (21–36)	25.1 (3.2) (20–32)	26.9 (3.0) (20–34)	41	28	35.7 (3.7) (29–43)
number of gulars	30.3 (2.2) (26–33)	28.7 (2.7) (22–34)	28.4 (2.6) (24–33)	30.4 (3.0) (24–35)	34	31.5 (0.7) (31–32)	32.5 (3.3) (27–38)
lateral folds of neck	inconspicuous	inconspicuous/distinct	inconspicuous/absent	distinct	inconspicuous	inconspicuous/absent	distinct
throat in males	spotted	immaculate	spotted	immaculate	?	immaculate	spotted
scales around midbody	41.5 (3.0) (40–51)	41.8 (2.9) (37–48)	42.0 (2.9) (36–48)	42.1 (2.8) (38–48)	58	41.8 (1.4) (37–49)	53.8 (3.2) (47–59)
paravertebral markings	absent	present	present	absent/inconspicuous	absent	present	absent/inconspicuous
vertebral line	present	absent	present	absent	absent	absent	present
dorsolateral stripes[b]	wide	slender	slender	wide	absent	absent	slender
male precloacal pores	3.3 (1.2) (2–5)	2.1 (0.8) (2–4)	3.6 (1.4) (2–6)	3.2 (0.6) (3–5)	absent	5.5 (3.5) (3–8)	4.5 (1.0) (4–6)
females with precloacal pores	0%	41%	0%	94.1%	0%	0%	0%
maximum SVL (mm)	55.1	61.3	57.2	57.6	42.5	60	63.4
reproductive mode	viviparous	oviparous	viviparous	oviparous	?	?	viviparous
elevational range (m)	3000–4700	700–2800	3000–4700	2820–3200	4080	1800–4000	3048–4755

[a] Maximum height of the nasal scale in relation to the width in contact with the rostral.
[b] Dorsolateral stripes may become wider posteriorly toward the shoulders, or remain slender. Occasionally these stripes are absent.

as predicted by the "cold-climate hypothesis," viviparous squamates tend to be distributed in cooler environments (Tinkle and Gibbons, 1977; Shine, 1985; Guillette, 1993). Hence, we also expected the oviparous and viviparous populations of *L. "alticolor"* to be distributed as predicted by the cold-climate hypothesis.

MATERIALS AND METHODS

Taxonomy.—To determine the taxonomic status of the oviparous and viviparous lizards assigned to *L. alticolor*, we reexamined the specimens studied by Ramírez Pinilla and Laurent (1996, their table 2). We also examined more than 70 additional populations that had been referred to *L. alticolor*. Because the content and monophyly of the *alticolor* group has not been established, we extended our examination to include other members of the *chiliensis* group (approximately 70 taxa)—the next known, most inclusive clade (Etheridge, 1995). In total, we examined more than 800 specimens representing 69 species of the *chiliensis* group (including the type series of *L. alticolor* and several other species). Although the definition and diagnosis of the *alticolor* group is beyond the scope of this study, for the purpose of diagnosis, the species described below were compared with those species of the *chiliensis* group that are morphologically most similar (see Table 1). In our taxonomic analysis, we considered external morphology (lepidosis, coloration, and color patterns), as well as 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×). Measurements were taken with electronic calipers to the nearest 0.01 mm. Terminology for the description of squamation follows Smith (1946), and for neckfold terminology, we followed Frost (1992). Institutional abbreviations follow Leviton et al. (1985).

Ecology.—We searched for and collected *L. "alticolor"* in mid-November (late Austral spring) 1996 along Ruta Provincial 307 (between kilometer markers 82 and 98) in the province of Tucumán, Argentina. This region includes the site (km 95) where both the oviparous and viviparous individuals were reported to coexist (Ramírez Pinilla and Laurent, 1996). This season also coincides with the time of parturition for both the oviparous and viviparous individuals (Ramírez Pinilla, 1989, 1991a; Ramírez Pin-

illa and Laurent, 1996). This enabled us to confirm reproductive modes following the strictest criteria suggested by Blackburn (1993) and to record gravid female coloration and behavior. We also looked for evidence of clinal variation or hybridization (i.e., morphologically intermediate forms) between the lizards exhibiting the two reproductive modes at the reportedly bimodal population (Ramírez Pinilla and Laurent, 1996) and at other potential zones of sympatry (based on museum records). Lizards were collected at 0.5–1.0 km intervals and within 0.5 km of the road (Ruta Prov. 307) until the entire 10-km potential zone of sympatry for the oviparous and viviparous individuals had been thoroughly surveyed. At each site, we collected environmental (air and substratum in direct sun and deep shade) and body temperatures (measured at a depth of 1 cm in the cloaca) of the lizards with a digital thermometer (Omega 871A, Stamford, CT).

RESULTS

Our analysis of 16 morphological characters and reproductive mode (Table 2) suggests that *L. alticolor* sensu lato is a composite of at least four diagnosable species—three of which are undescribed. Here we describe the two species that were previously considered a single taxon (*L. alticolor alticolor*) that exhibited reproductive bimodality (Ramírez Pinilla, 1989, 1991b; Ramírez Pinilla and Laurent, 1996). The new species are first differentiated from other members of the putative *alticolor* group (sensu Ortiz, 1981; Cei, 1993; Table 1) and two additional species (*L. bitaeniatus* and *L. variegatus*), which share numerous morphological similarities with this group. Following these comparisons, a diagnosis is provided that includes comparisons with 11 other species in the *chiliensis* group that, because of their general morphological similarity, might be confused with the two species described herein. Figure 1 provides a key to the general body patterns described and referred to in the text. The determination of the content and monophyly of the *alticolor* group, as well as the description of additional species, are the subjects of ongoing studies.

Liolaemus ramirezae n. sp.
Figures 2–4, 6, Table 2

Holotype.—FML 06071, adult female collected at km 95 on Ruta Provincial 307, Departamento Tafí del Valle, Provincia de Tucumán, Argentina (26°40.82′S, 65°48.74′W; 2820 m), on 11–13 March 1993 by O. Pagaburo (Fig. 2).
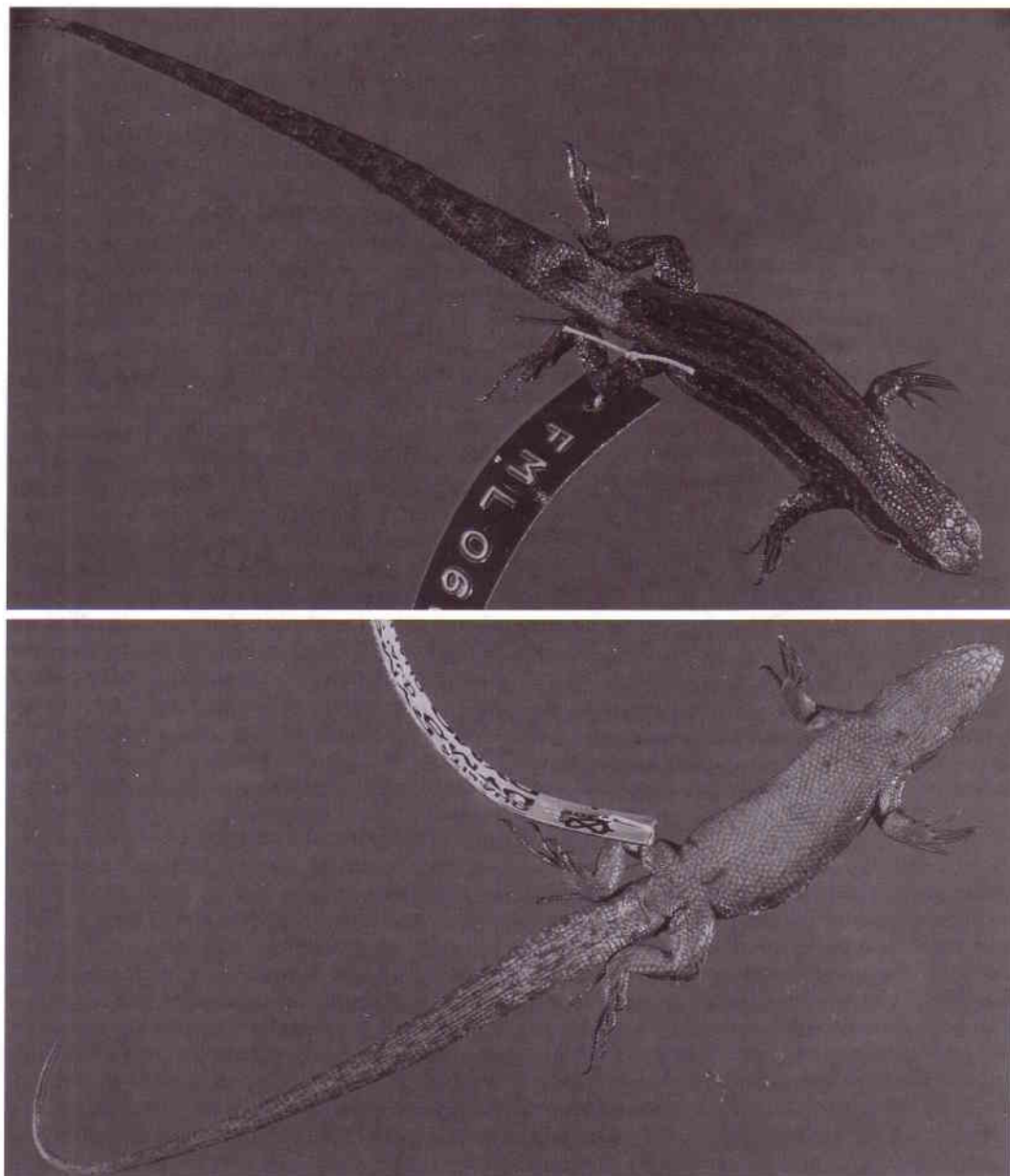
Fig. 2. Dorsal and ventral views of *Liolaemus ramirezae* (holotype; FML 06071). From km 95 (Ruta Provincial 307), Depto. Tafí del Valle, Tucumán, Argentina.

Paratypes.—FML 02921, 3 females. Same data as holotype. FML 02248, 2 males. Same locality as holotype. Collected 20 December 1988 by O. Pagaburo.

Diagnosis.—A small, slender *Liolaemus* that is similar in body proportion, pattern, and color to other members of the *alticolor* group (sensu Ortiz, 1981; Cei, 1993). However, *L. ramirezae* lack the black paravertebral marks found in *L.* *bitaeniatus*, *L. pagaburoi* n. sp. (see description below), and *L. variegatus*. The new species has strongly rugose dorsal head scales unlike the smooth head scales of *L. bitaeniatus* and *L. variegatus*. Male *L. ramirezae* have an immaculate cream-white throat unlike the black-spotted throats found in male *L. alticolor* sensu stricto, *L. pagaburoi*, and *L. walkeri*. *Liolaemus ramirezae* lack the bold black vertebral line of *L. alticolor*, *L. pagaburoi*, and *L. walkeri*. Unlike most of the
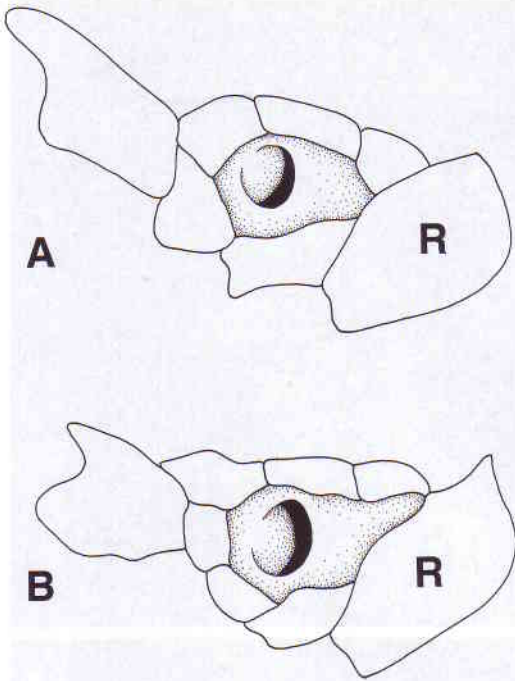
Fig. 3. Nasal regions (stippled) in (A) *Liolaemus ramirezae* and (B) *L. pagaburoi*. In *L. ramirezae*, the nasal is only in slight contact with the rostral (R) and is surrounded by five other scales. In *L. pagaburoi*, the nasal is in broad contact with the rostral and surrounded by six other scales.

otherwise similar-looking members of the *chiliensis* group (Table 1), most female *L. ramirezae* have precloacal pores (94.1%; n = 17), which are otherwise known only in females of *L. bitaeniatus* (41%; n = 9). *Liolaemus ramirezae* exhibit gravid-female coloration (yellow to ferrous orange highlights along the flank extending to and covering the belly) unlike *L. pagaburoi*. Unlike most other members of the *alticolor* group (sensu Ortiz, 1981; Cei, 1993) for which reproductive mode is known, *L. ramirezae* is oviparous, whereas *L. alticolor, L. pagaburoi,* and *L. walkeri* are viviparous. In contrast to that seen in *L. alticolor, L. bitaeniatus, L. pagaburoi,* and *L. tacnae, L. ramirezae* has narrow nasals that are in slight contact with the rostral (Table 2, Fig. 3A). *Liolaemus ramirezae* has fewer, larger scales around the midbody than *L. tacnae* and *L. walkeri* (mean: 42.1 vs 58 and 53.8, respectively), and differs from *L. tacnae* in having substantially smaller and, therefore, a greater number temporal scales (8.1 vs 9.0 in *L. tacnae*).

Description of holotype.—Female. Snout–vent length 48.9 mm. Head width 8.1 mm, head length 9.8 mm (1.2 times longer than wide).

Thirteen dorsal head scales (from a line drawn horizontally between anterior margin of external auditory meatus to anterior margin of rostral). Nasal scales not in contact with rostral, separated from first supralabial by one scale. Nasal bordered by six scales. Canthal not projecting ventrally and separated from nasal by one scale. Loreal region flat or slightly concave. Six enlarged supralabials, with the fourth upturned posteriorly and contacting the subocular on the left side. Four enlarged infralabials. Auditory meatus slightly oval shaped (height 1.6, width 1.5 mm) with a small, white, posteriorly projecting scale along its anterior margin. Eight convex, imbricate temporal scales between the upper anterior corner of auditory meatus and posterior margin of orbit. Upper temporals slightly keeled; lower temporals smooth. Eight temporals (counting vertically from the buccal commisure to posterior corner of orbit). Scales of anterior margin of auditory meatus large; scales of the posterior margin smaller, flat, some almost granular. Orbit-auditory meatus distance (4.0 mm) about equal to orbit-rostral distance (4.1 mm, or 41.7% head length). Rostral scale about three times wider than high (2.3 and 0.8 mm, respectively). Mental scale subpentagonal, about twice as wide as high (2.1 and 1.1 mm, respectively). Interparietal scale hexagonal shaped with an elongated, posteriorly directed apex. Interparietal bordered by six scales, the parietals being the largest. Frontal region with two azygous scales. Supraorbital semicircles complete, formed by 10 scales. Three or four enlarged supraoculars. Dorsal head scales smooth, flattened, with scale organs most apparent on the prefrontal and internasal regions (9–10 per scale), and over anterior supraoculars. Superciliaries 5–6, strongly imbricate. Thirteen to 15 upper ciliaries, weakly projecting, and square shaped; 11 to 12 lower ciliaries of similar shape. Subocular elongate (3.3 mm), 1.7 times longer than orbit diameter (2.0 mm from anterior to posterior margin of ciliaries). Subocular separated from supralabials by a single (but interrupted) row of lorilabials. Fourth supralabial elongated (2.1 mm), slightly longer than orbit diameter. Four enlarged infralabials. Inner ciliaries (7–8) larger and fewer than outer ciliaries. Six lorilabials, with the fourth through sixth contacting the subocular. A row of scale organs located along lorilabials. Preocular scale small, in restricted contact with canthal. Postocular elongated, level with fifth supralabial scale. Mental in contact with first infralabials (on each side) and two enlarged chinshields. Chinshields forming two longitudinal rows of three enlarged scales separated one from the

other by five smaller scales. Scales of throat round, flat, imbricate. Twenty-nine gulars between auditory meatus. Four types of folds found along the lateral neck region: postauricular, rictal, longitudinal, and antegular. The first three form a "Y" between auditory meatus and shoulder. Postauricular, rictal, and longitudinal folds not well developed, almost absent or inconspicuous on right side of neck. Antegular fold deep, well delimited by large, flat scales along its anterior margin, and very small scales in pocket. Longitudinal fold interrupted by antegular fold. Antehumeral fold reduced, formed by very small scales. Scales over longitudinal, postauricular, and rictal folds medium to large, laminar, keeled, imbricate. Neck scales between auditory meatus and shoulder 30 (counted over postauricular and longitudinal folds). Scales between auditory meatus and antegular fold 19. Antegular folds separated medially by 15 scales. Supernumerary antegular folds and oblique folds absent.

Dorsal scales lanceolate, moderately keeled, imbricate. Scales around midbody 43. Seventeen rows of keeled scales on dorsum at midtrunk. Scales become smooth with round posterior margins along flank and toward the belly. Ventral scales about same size as dorsals. Dorsal scales between occiput and groin 44. Ventral scales between mental and precloacal pores 87. Three small precloacal pores. Axilla-groin distance 23.2 mm (47.4% of SVL).

Brachial and antebrachial scales keeled and imbricate, slightly smaller than dorsals, with round posterior margins. Supracarpals laminar, round, smooth. Subdigital lamellae of fingers with three blunt keels, in number: I: 8; II: 12; III: 17; IV: 19; V: 11. Claws moderately long. Supradigital lamellae convex, smooth, imbricate. Infracarpals and infratarsals small, strongly imbricate, keeled. Supracarpals and supratarsals larger, fewer in number, smooth or slightly keeled, round. Scales of ventral surfaces of thighs and tibia of the same shape and size as ventrals. Number of subdigital lamellae on toes: I: 9; II: 15; III: 19; IV: 23; V: 13. Hind-foot length 14.3 mm (29.2% of SVL).

Tail length 88.9 mm (1.8 times SVL). Proximal third of tail thick, flattened; width 1.4 times greater than height (width 5.9; height 4.1 mm) becoming increasingly cylindrical distally. Dorsal caudal scales similar to those of trunk. Scales of ventral caudal surface similar to those of posterior fourth of trunk ventrals. Distal to this point, ventral caudal scales become elongate and keeled like those of dorsals.

Dorsal pattern with a light brown vertebral field 2–3 scales wide at midbody. Vertebral line nearly absent, remaining only as two or three small, diffuse segments in the posterior third of trunk. Paravertebral field slender, two scales wide, slightly darker brown than vertebral field. Paravertebral markings dark brown, diffuse, almost inconspicuous, elongate line segments, situated laterally in paravertebral field and in contact with dorsolateral stripes. Dorsolateral stripes golden yellow, one scale wide between auditory meatus and shoulder, increasing in width posteriorly to two scales wide on posterior third of trunk. Lateral field darker than dorsal field, with small, black markings irregularly scattered along flank. Lateral line absent on left side and diffuse but present on right. Ventrolateral field light brown, becoming lighter toward belly. Brown coloration in fields described above tinged with a varying degree of bronze hue. Lateral line follows anteriorly beyond shoulder, along longitudinal and postauricular folds of neck, across temporal region, and terminates at postocular scale. Dorsolateral stripes become diffuse on head at posterior corner of orbit. Subocular white. Tail brown with diffuse transverse markings, lacking a vertebral line. Throat immaculate cream-white. Throat, chest, belly, and ventral surfaces of the thighs with light yellow tinge.

Variation.—*Liolaemus ramirezae* is similar in size to other similar-looking members of the *chiliensis* group (Table 1) with adults from 45.9–57.6 mm SVL ($\bar{x} = 51.5$; SD = 2.8). No apparent body-size dimorphism (males $\bar{x} = 51.8$; SD = 3.0; range = 45.9–57.6; n = 12; females $\bar{x} = 51.3$; SD = 2.6; range = 46.3–55.5; n = 18). Tail length (from intact, nonregenerated tails) ranges 1.5–1.9 times SVL ($\bar{x} = 1.8$; SD = 0.1; n = 9).

Dorsal scales usually lanceolate, moderately keeled, imbricate, but less distinctly lanceolate and more nearly rhomboidal in some individuals. Scales around midbody range 38–48 ($\bar{x} = 42.1$; SD = 2.8). Dorsal scales (between occiput at the anterior margin of auditory meatus and anterior surface of thighs) range 38–47 ($\bar{x} = 42.6$; SD = 2.5). Head scales range 9–13 ($\bar{x} = 10.8$; SD = 0.9). Ventral scales smooth, round, slightly larger than dorsals, wider than longer, 73–86 in number ($\bar{x} = 80$; SD = 4.9). Precloacal pores conspicuous, with an orange exudate at the opening, numbering 3–5 ($\bar{x} = 3.3$; SD = 0.6) in males, and 2–3 ($\bar{x} = 2.2$; SD = 0.4) in females. Precloacal pores almost always present in females (94.1%). Interparietal scale usually pentagonal shaped, bordered by 5–8 scales ($\bar{x} = 6.3$; SD = 0.9). Temporal scales usually smooth,

may become slightly keeled dorsally. Temporals range 7–9 ($\bar{x} = 8.1$; SD = 0.5).

Scales along neck (from postauricular and longitudinal folds to shoulder) vary from 20–34 ($\bar{x} = 26.9$; SD = 3.0). Fifteen to 23 scales ($\bar{x} = 18.5$; SD = 1.9) between auditory meatus and antegular fold. Gular scales between both auditory meatus range from 24–35 ($\bar{x} = 30.4$; SD = 3.0). Nasals usually in limited contact with rostral but contact lacking in some individuals. Nasal (at nostril level) 1.5–12.8 times the width of the scale in contact with the rostral ($\bar{x} = 4.8$; SD = 2.6). Nasal usually bordered by six scales (range 5–7; $\bar{x} = 6.3$; SD = 0.6). Development of subdigital lamellae keels varying individually. Number of subdigital lamellae on fourth finger varies from 15–20 ($\bar{x} = 17.6$; SD = 1.4), and from 19–26 ($\bar{x} = 22.4$; SD = 1.5) along fourth toe.

Dorsal pattern in *L. ramirezae* more variable than noted for similar-looking species in the *chiliensis* group. Complete vertebral line absent, although thin black "remnants" of a line present in some individuals. Paravertebral markings usually absent but, when present, highly variable: often appearing as small, elongate markings irregularly distributed in the paravertebral field or as thick black lines distributed throughout this field. Small black, occasionally white, flank markings common in lateral field. Flank markings occasionally reduced to margins of lateral field as fine, interrupted black lines. Lateral line usually absent or nearly so but in some specimens may appear as poorly defined or diffuse segments.

Color in life.—Dorsally gray, with dorsolateral stripes lighter, sometimes yellow or cream, or light brown. In some individuals, margins of dorsolateral stripes bordered by a fine black line. Lateral field usually gray-brown but varying from gray to completely dark brown. Flank markings black, irregularly scattered, never forming large marks associated in tandem with the paravertebral marks (as occurs in *L. pagaburoi*; see below). Females exhibit gravid coloration along flanks and on to belly which varies from yellow to ferrous-orange. This color fades a week or two following oviposition.

Color in ethanol.—Similar to color in life, but darker brown coloration may become somewhat subdued, and lighter ventral region may darken to gray. Gravid-female coloration usually lost within six months.

Etymology.—We name this species in honor of Martha Ramírez Pinilla in recognition of her

contribution toward our understanding of the reproductive biology of this and other species of Argentinian *Liolaemus.*

Natural history.—We collected *Liolaemus ramirezae* in mid-November 1996 at km 88–95 Ruta Provincial 307, Departmento Tafí del Valle, Provincia de Tucumán where it occurs along the gentle slopes, valleys, and washes of the Nevados del Aconquija. The habitat is the typical scrub of the Prepuna region (Cabrera and Willink, 1980), but this region is only sparsely vegetated. The dominant shrubs of the valleys and dry washes are the spindly woody shrub *Parastrephia phyllicaeformis* (Asteraceae) and creosote bush (*Larrea* sp.). To the east, and at slightly higher elevations, *Parastrephia* and another small, spiny shrub (*Adesmia* sp.) coexist with the bunch grass, *Festuca hieronymi*, and pampas grass (*Coraderia* sp.).

At this site, *L. ramirezae* appears to be associated almost exclusively with *P. phyllicaeformis*. When active, the lizards move about the base of these shrubs where dead twigs, leaves, and other dry litter accumulate. When disturbed, *L. ramirezae* typically will remain motionless among the litter, where it is remarkably cryptic. If further disturbed, the lizards usually retreated to the nearest *Parastrephia* or, on occasion, entered the burrow of a small rodent (probably *Ctenomys* sp.) at the base of the shrubs or took refuge under rocks. Although generally terrestrial, on several occasions this species was seen climbing up to 0.4 m into the canopy of the *Parastrephia* shrubs.

Based on analyses of fecal samples obtained in the field and via observations under captive conditions, *L. ramirezae* appears to feed on a variety of insects and other small arthropods, but occasionally may eat vegetation (i.e., soft leaves and flowers). Unlike most members of the *alticolor* group, this species is oviparous. Gravid females that recently had oviposited (as evidenced by their extremely saccate bodies) were collected in mid-November. Gravid females contained 4–6 ovate eggs (see also Espinoza and Lobo, 1996). Gravid-female coloration fades following parturition and is usually undetectable about 7–10 days thereafter. Body temperatures collected for 17 active adults averaged 32.2 C (SD = 2.1).

In this region *L. ramirezae* is commonly found syntopically with the oviparous *L. quilmes*, and sympatrically with a rare and undescribed saxicolous member of the *L. elongatus* group (sensu Cei, 1974). An adult, road-killed *Philodryas* sp., a racerlike colubrid, was found near the type locality and could be considered a potential
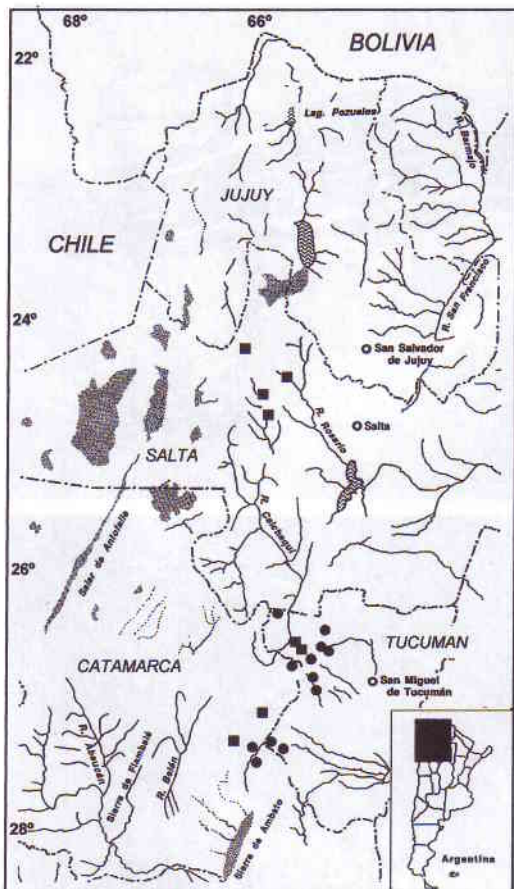
Fig. 4. Distribution of *Liolaemus ramirezae* (squares) and *Liolaemus pagaburoi* (circles) based on specimens examined in this study.

predator, as may be the burrowing owl (*Athene cunicularia*) and other predatory birds.

Distribution.—*Liolaemus ramirezae* is distributed in northwestern Argentina (Fig. 4), where it is found at lower elevations (2800–3200 m) than are most other members of the *alticolor* group (3400–4800 m; sensu Ortiz, 1981; Cei, 1993). The species occurs west of the Nevados del Aconquija, from km 88–98 on Ruta Provincial 307, Depto. Tafí del Valle, Provincia de Tucumán. It can be found in sympatry with another, morphologically similar, but viviparous species also assigned to *L. alticolor* (described below) at km 88 and probably to the northwest at other locations. In Catamarca province, *L. ramirezae* is known from the steep hills of Mina Capillitas (up to 3200 m) and Morro El Ingenio. To the north, the species has been collected at La Poma and near San Antonio de los Cobres (the northern range limit) in the province of Salta.

To the east, *L. ramirezae* can be found at Quebrada del Toro and Santa Rosa de Tastil, Salta. This species may also be distributed along the slopes of several mountain ranges to the north of the type locality including: Cumbres Calchaquíes, Sierra de Carahuasi, and along the eastern and western slopes of the Cumbres del Obispo.

Liolaemus pagaburoi n. sp.
Figures 3–6, Table 2

Holotype.—Male. FML 06069. Abra de El Infiernillo, Ruta Provincial 307, Departamento Tafí del Valle, Provincia de Tucumán, Argentina (26°44'S, 65°45'W; 3042 m), on 26 January 1997 by C. Terán, J. M. Lefebvre, and F. Lobo (Fig. 5).

Paratype.—FML 06070. Same data as holotype.

Diagnosis.—A small, slender *Liolaemus* morphologically similar to other members of the *alticolor* group (sensu Ortiz, 1981; Cei, 1993), but unlike *L. alticolor* (sensu stricto), the new species has paravertebral markings, slightly rugose dorsal head scales, keeled temporals, and dorsolateral stripes that taper in width posterior to the shoulders. *Liolaemus pagaburoi* differs from *L. bitaeniatus* in having a vertebral line, males with spotted throats, females lacking precloacal pores and gravid coloration, and a viviparous reproductive mode. In contrast to *L. walkeri*, *L. pagaburoi* has fewer scales around the midbody (range 36–48; $\bar{x}$ = 42.0; vs 47–59; $\bar{x}$ = 53.8), fewer head scales (9–13; $\bar{x}$ = 11.3 vs 12–16; $\bar{x}$ = 13.3), rugose dorsal head scales, keeled temporals, a nasal scale that is in much broader contact with the rostral, fewer scales along the neck (20–32; $\bar{x}$ = 25.1 vs 29–43; $\bar{x}$ = 35.7; from the auditory meatus to the shoulder), fewer gulars (24–33; $\bar{x}$ = 28.4 vs 27–38; $\bar{x}$ = 32.5), with the exception of the antegular fold, the lateral nuchal folds are reduced or absent, and males usually have fewer precloacal pores (2–6; $\bar{x}$ = 3.5 vs 4–6; $\bar{x}$ = 4.5). Unlike *L. variegatus*, *L. pagaburoi* has slightly fewer dorsal head scales, more strongly keeled temporals, a nasal scale that is in broader contact with the rostral, males with black-spotted throats, a distinct black vertebral line, and gray or cream dorsolateral stripes. Males of *L. tacnae* lack precloacal pores (Shreve, 1938), whereas *L. pagaburoi* have, on average, 3.7.

Description of holotype.—Male. Snout–vent length 50.5 mm. Head width 8.9 mm, head length 10.8 mm (length 1.2 times width). Fifteen dorsal
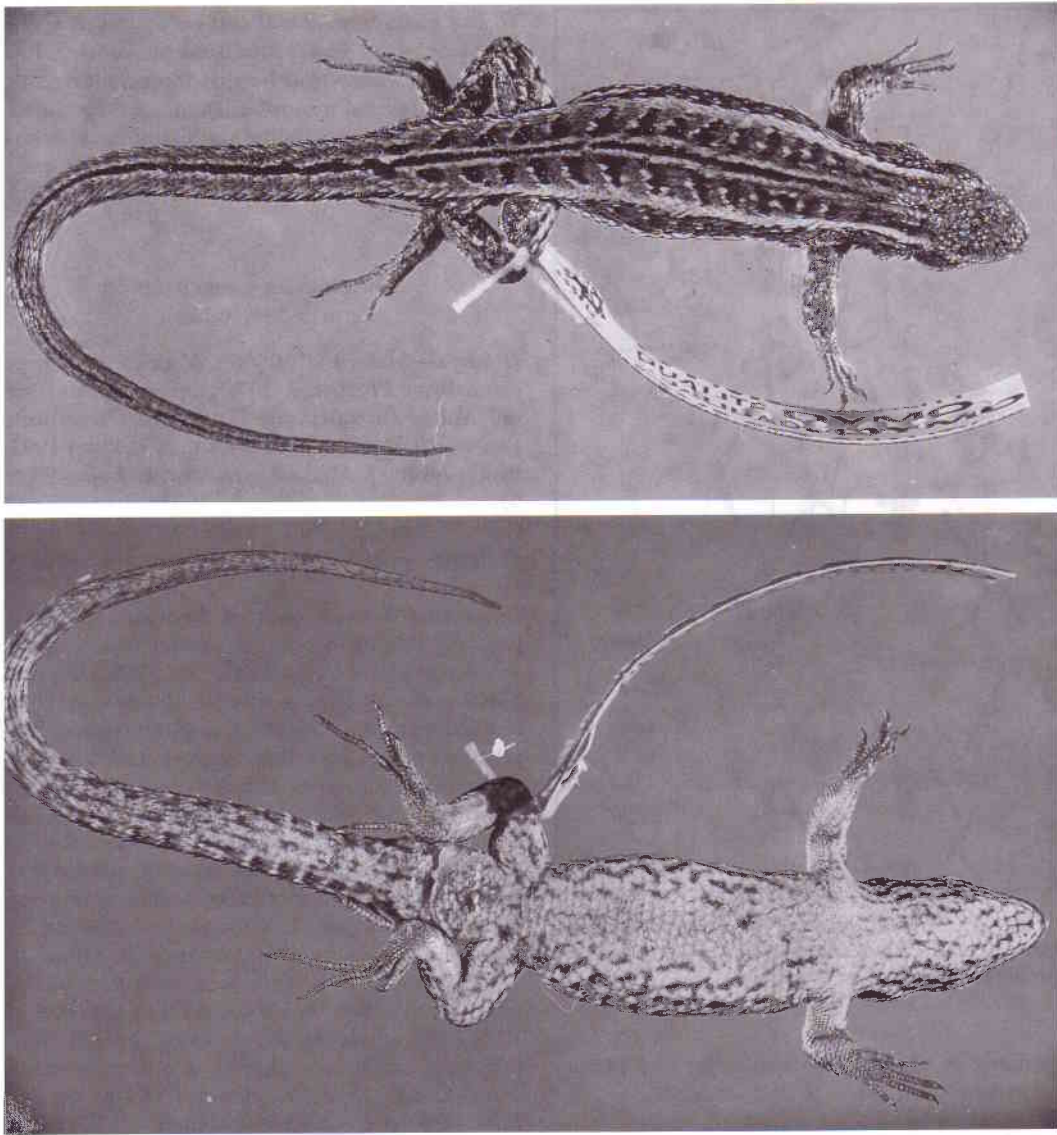
Fig. 5.   Dorsal and ventral views of *Liolaemus pagaburoi* (holotype; FML 06069). From El Infiernillo, Depto. Tafí del Valle, Tucumán, Argentina.

head scales at midline. Head scales convex, slightly rugose, especially scales of parietal and supraocular regions. Nostrils oriented laterally. Nasal scale contacting rostral (2.7 times wider at the nostril than at the point of contact; Fig. 3B) separated from first supralabial by one scale. Nasal bordered by seven scales. One scale separates nasal from canthal, the latter elongated anteriorly with a straight ventral margin. Loreal region slightly concave. Six enlarged supralabials, the fourth being longest with its posterior tip upturned but not in contact with subocular. Subocular elongate (3.5 mm), 1.8 times longer than orbit diameter (1.9 mm), separated from supralabials by only one scale row. Fourth supralabial elongated. Four enlarged infralabials. Third or fourth through the sixth lorilabials contacting subocular. Preocular scale same size as postocular. Frontal region with azygous anterior scale and paired posterior scales. Supraorbital semicircles incomplete along their posterior half. Three to four enlarged supraoculars. Scale organs on dorsal surface of head 3–4 per scale along prefrontal and internasal areas. Five to six elongate, strongly imbricate superciliaries on upper margin of orbit. Thirteen upper and lower outer ciliaries. Nine weakly separated inner ciliaries. Auditory meatus oval shaped (1.5

times higher than wide), scales of anterior margin projecting over the opening. Temporals keeled, eight between orbit and auditory meatus. Scales along anterior margin of auditory meatus laminar, large, those along posterior margin small, almost granular. Orbit-auditory meatus distance (4.0 mm) shorter than length of snout(4.6 mm; measured from angle formed by upper and lower outer ciliaries to anterior margin of rostral). Rostral scale 2.8 times wider than high. Mental subpentagonal shaped, 1.9 times wider than high. Mental in contact with four scales: first two infralabials, and two enlarged chinshields. Chinshields form a pair of rows of three to four enlarged scales that become smaller posteriorly along throat. Second chinshields of each row separated by two scales. Margin of interparietal scale irregular, bordered by nine scales.

Lateral wall of neck convex, inflated, with postauricular, rictal, and longitudinal folds absent. Lateral neck scales laminar, imbricate, keeled, slightly smaller than those along dorsal neck region. Antegular fold deep.

Vertebral field 2.5–3.0 scales wide, light gray, with a single-scale wide vertebral line. Paravertebral markings wide, short, 3.0–3.5 scales wide, one scale long. Posterior half or third of these scales white, giving a whitish appearance to margins of paravertebral marks. Eleven paravertebral markings between shoulder and thighs. Width of paravertebral field equal to that of paravertebral markings. Dorsolateral stripes cream yellow, 1.5 scales wide, with same width from neck to end of trunk. Lateral field three scales wide, with black flank markings forming vertical bars in paired association with paravertebral markings. White lateral line one scale wide separates lateral from ventrolateral field. Ventrolateral field light gray, with many black-and-white scales scattered throughout.

Variation.—Vertebral line sometimes broken into segments but always present. Flank markings usually arranged in transverse vertical bars and arranged in tandem with paravertebral markings. Some individuals regularly spotted with small black markings along flank, including along lateral and lateroventral fields. Markings may be extended onto limbs and along tail base.

Dorsal scales lanceolate, moderately to strongly imbricate, sharply keeled. Keels forming longitudinal rows over the dorsum. Scales around midbody range 36–48 ($\bar{x} = 42.0$; SD = 2.9). Dorsals (at midline from the occiput at anterior margin of auditory meatus to anterior surface of thighs) 34–43 ($\bar{x} = 38.7$; SD = 2.3). Head scales 9–13 ($\bar{x} = 11.3$; SD = 1.0). Ventrals

with rounded posterior margins, same size or slightly larger than dorsals. Ventrals 70–89 ($\bar{x} = 77.6$; SD = 5.0; from mental to precloacal pores in males, or anterior margin of cloacal aperture in females). Precloacal pores absent in females, 2–6 ($\bar{x} = 3.7$; SD = 1.2) in males. Scales bordering interparietal 5–10 ($\bar{x} = 6.3$; SD = 1.1), with the two posterior parietals commonly larger than interparietal. Temporal scales large, imbricate, keeled, ranging 7–9 ($\bar{x} = 7.9$; SD = 0.6). Subocular elongate, 1.3–1.8 times length of eye diameter ($\bar{x} = 1.5$; SD = 0.1), conspicuous from side of head. Fourth supralabial elongate, slightly smaller to about diameter of eye (0.7–1.2 times; $\bar{x} = 0.9$; SD = 0.1). Nasal bordered by 6–8 scales ($\bar{x} = 6.9$; SD = 0.4). Nasal in broad contact with rostral with maximum height of the latter 1.1–3.1 times width of rostral ($\bar{x} = 1.6$; SD = 0.4; Fig. 3B). Lateral folds of neck, with exception of antegular, usually absent or inconspicuous. Scales around neck (from auditory meatus to shoulder) 20–32 ($\bar{x} = 25.1$; SD = 3.2). Scales between auditory meatus and antegular fold 11–19 ($\bar{x} = 15.7$; SD = 1.6). Gulars 24–33 ($\bar{x} = 28.4$; SD = 2.6). Scales of throat laminar, slightly imbricate to moderately imbricate along neck. Subdigital lamellae along fingers 13–18 ($\bar{x} = 15.7$; SD = 1.3) and 18–23 ($\bar{x} = 19.9$; SD = 1.1) along toes.

Liolaemus pagaburoi is a small member of the *chiliensis* group, with adults 41.6–57.2 mm SVL ($\bar{x} = 48.7$; SD = 4.3). The species lacks obvious body-size dimorphism: female SVL 41.6–55.4 ($\bar{x} = 49.7$; SD = 4.4; n = 16); male SVL: 42.4–57.2 ($\bar{x} = 47.8$; SD = 4.2; n = 17). Tail length 1.5–1.9 times SVL ($\bar{x} = 1.7$; SD = 0.2; n = 8).

Color in life.—Background color brown. In most individuals, dorsolateral stripes gray or cream, occasionally light gold. Paravertebral field brown. Paravertebral markings black with a white posterior margin. Vertebral line black, often segmented. Lateral field brown. Subocular white. Females lack gravid coloration: pregnant females that gave birth in captivity retained their immaculate off-white belly.

Color in ethanol.—Similar to color in life, but overall coloration becomes less vibrant, particularly the cream to golden-yellow color of the dorsolateral stripes. The off-white ventral region has darkened to gray in a few individuals.

Etymology.—We name this new *Liolaemus* in honor of Omar Pagaburo who has collected extensively throughout Argentina for over 20 years. The richness of the herpetological collection at the Fundación Miguel Lillo—particularly the

Liolaemus collection—is a reflection of Pagaburo's collecting expertise and many years of service.

Natural history.—We collected *L. pagaburoi* in mid-November 1996 from Abra de El Infiernillo (at km 84) to km 88 along Ruta Provincial 307, Tucumán province. Here, this species can be commonly found along the gentle slopes and higher valleys of the Nevados de Aconquija. To the east, the habitat is nearly monotypic stands of the dense, golden (in midspring) bunchgrass, *Festuca hieronymi*. At some locations, the bunchgrass is occasionally interspersed with patches of a small spiny shrub (*Adesmia* sp.), which rarely reach a height of 0.5 m. The region is heavily grazed primarily by goats, but also by cattle, equids, and llama. There are few rocks or other surface refugia. Consequently, the only cover in the area is the bunchgrass and the abundant rodent burrows (*Ctenomys* sp.).

At this site, *L. pagaburoi* was found nearly exclusively in association with *Festuca*. Active lizards were found along the bases and in the occasionally open centers of the bunchgrass. When disturbed, *L. pagaburoi* typically remains motionless in the bunchgrass where it is remarkably cryptic. If pursued, these lizards usually retreated to the next nearest clump of *Festuca* or, on occasion, entered rodent burrows. Feces produced by *L. pagaburoi* within 24 h of capture contained a variety of small insects—similar to those seen in feces collected from *L. ramirezae*. However, unlike *L. ramirezae*, *L. pagaburoi* is viviparous, and in mid-November we collected several neonates and four pregnant females. The latter were so near parturition that they appeared disfigured. Dissected females contained 4–6 well-developed embryos. Body temperatures collected for 34 active adults averaged 31.7 C (SD = 2.8), which is not statistically distinguishable from the body temperatures recorded for *L. ramirezae* ($P = 0.57$). Yet despite the lack of differences between body temperature during activity, the length of diel activity for *L. pagaburoi* appeared to be substantially shorter than that noted for *L. ramirezae* (REE, unpubl. data). This may be a function of the cooler ambient temperatures experienced by *L. pagaburoi*. Mean air temperatures are 10 C cooler over the range of *L. pagaburoi* (Ramírez Pinilla, 1991a). In the spring, at least, these lower temperatures are the result of dense morning fog that moves in from a humid valley (Tafí del Valle) some 21 km to the southeast. This thick fog deposited appreciable amounts of dew along the southeastern hillsides. In mid-November, the fog did not dissipate until early after-

noon (1300–1400 h). Following fog dissipation, air temperatures rapidly rose from 8–12 C to 17–22 C at which time *L. pagaburoi* became active and could be seen basking in clumps of *Festuca*.

Distribution.—Populations of *L. pagaburoi* are known only from the Cumbres Calchaquíes, Cumbre del Cajón, and Nevados del Aconquija mountain ranges which span the provinces of Catamarca and Tucumán (Fig. 4). This species has been collected from 3000–4700 m above sea level. Despite considerable effort (more than 60 person hours over three years), we have not found *L. pagaburoi* with the oviparous *L. ramirezae* at their originally described site of sympatry (km 95, Ruta Prov. 307, Tucumán; Ramírez Pinilla and Laurent, 1996). In this region, the furthest northwest record for *L. pagaburoi*, and the current site of sympatry with *L. ramirezae*, is km 88.

Comparisons with similar taxa.—Because the content and monophyly of the *alticolor* group has not been formally established, we provide brief comparisons with other members of the *chiliensis* group that are morphologically similar and may therefore be confused with the new species described above.

In *L. bibronii* (n = 23), the background color is brown, the vertebral line is present, sometimes broken, and the dorsal pattern is one of longitudinal rows of irregularly separated markings. Scale counts are higher than those recorded for both new species: midbody 47–55 ($\bar{x} = 51.2$; SD = 2.6), ventrals 84–92 ($\bar{x} = 88.2$; SD = 2.5), between auditory meatus and shoulder 30–37 ($\bar{x} = 33.2$; SD = 2.5), between auditory meatus and antegular fold 18–24 ($\bar{x} = 20.1$; SD = 2.1), and gulars 31–40 ($\bar{x} = 36.0$; SD = 2.9). The contact between the nasal and the rostral scales is intermediate with respect to the new species (1.9–4.2; $\bar{x} = 2.8$; SD = 0.8). *Liolaemus bibronii* has more subdigital lamellae than *L. pagaburoi* (fingers $\bar{x} = 17$; toes $\bar{x} = 22.1$).

The similarity between some features of the dorsal pattern of *L. alticolor* and *L. fuscus* and *L. lemniscatus* have long been recognized (Burt and Burt, 1931; Hellmich, 1961). However, unlike *L. ramirezae*, *L. fuscus* (n = 14) has an unfragmented vertebral line, and the subocular scale lacks the white highlights seen in *L. pagaburoi*. *Liolaemus fuscus* has differentiated scales along the anterior margin of the auditory meatus, more scales around the midbody ($\bar{x} = 47.8$ vs 42.1 in *L. ramirezae* and 42.0 in *L. pagaburoi*), more ventrals ($\bar{x} = 91$ vs 80 in *L. ramirezae* and 77.6 in *L. pagaburoi*), more scales in the auditory

meatus-antegular fold ($\bar{x}$ = 19.6 vs 15.7 in *L. pagaburoi*), more gulars ($\bar{x}$ = 35.8 vs 30.4 in *L. ramirezae*), and more subdigital lamellae on the fingers and toes ($\bar{x}$ of fingers = 18.1, $\bar{x}$ of toes = 22.8 vs 15.7 and 19.9, respectively, in *L. pagaburoi*). The contact between the nasal and the rostral is broader in *L. fuscus* than in *L. ramirezae* ($\bar{x}$ = 1.7 vs 4.8, respectively).

Liolaemus gracilis (n = 22) lacks paravertebral marks which are distinct in *L. pagaburoi* and can be distinguished from *L. ramirezae* by its well-differentiated dorsolateral stripes and the presence of distinct black lines bordering the lateral stripes. In *L. gravenhorstii* (n = 15), the lateral nuchal folds are absent, but in *L. ramirezae* these are well developed, and in *L. pagaburoi* the antegular fold is deep and always distinct. *Liolaemus gravenhorstii* has a slightly rugose to rugose dorsal head surface, a white subocular, lacks paravertebral markings (distinct in *L. pagaburoi*), and lacks a vertebral line (present in *L. pagaburoi*). The dorsolateral stripes, when visible, increase in width beyond the shoulders (these remain slender in *L. pagaburoi*).

Liolaemus hernani (n = 12) is more robust with a longer SVL than either *L. pagaburoi* or *L. ramirezae*. *L. hernani* lacks dorsolateral stripes and has a distinct auricular scale, and deeper neck folds than both new species. Unlike *L. pagaburoi*, *L. hernani* has a fragmented vertebral line.

Liolaemus lemniscatus (n = 16) can be differentiated from *L. ramirezae* because the former has paravertebral markings, a rugose dorsal head surface, and white highlights on the suboculars. Unlike *L. pagaburoi*, *L. lemniscatus* lacks a vertebral line and has a slender auricular and an elongate scale along the anterior margin of the auditory meatus. *Liolaemus lemniscatus* also has two small scales projecting slightly over the auditory meatus—similar to those seen in *L. fuscus* (these scales are undifferentiated in *L. pagaburoi* and *L. ramirezae*), fewer precloacal pores in males ($\bar{x}$ = 2.2 vs 3.2 in *L. ramirezae* and 3.6 in *L. pagaburoi*), and slightly fewer gulars than in *L. pagaburoi* ($\bar{x}$ = 28.4 vs $\bar{x}$ = 32.2 in *L. lemniscatus*). The contact between the nasal and rostral is intermediate in *L. lemniscatus* relative to the new species ($\bar{x}$ = 2.8 vs 1.6 in *L. pagaburoi* and 4.8 in *Liolaemus ramirezae*). Unlike either of the new species, *L. lemniscatus* has small, powder-blue spots scattered throughout the dorsal and lateral fields.

Liolaemus paulinae (n = 15) shares many of the morphological characteristics with the species listed in Table 1 but lacks the basic dorsal pattern described here for the other species in the group including dorsolateral stripes, a vertebral line, and paravertebral markings (all present in *L. pagaburoi*). Although *L. ramirezae* and *L. pagaburoi* have only one scale between the nasal and canthal, *L. paulinae* (and *L. sanjuanensis*) exhibit variation in this character (1–2 scales).

Liolaemus robertmertensi (n = 8) has fewer scales around the midbody ($\bar{x}$ = 32.5) than that recorded for either *L. ramirezae* or *L. pagaburoi*. Lateral nuchal folds are absent in *L. robertmertensi*. Males of *L. robertmertensi* lack dorsolateral stripes, have a longer tail length relative to SVL [2.2 times longer than SVL vs. 1.9 in both new species (maximum ratio recorded for all three species)]. *Liolaemus robertmertensi* has conspicuous black spots in the lateral field that, in some specimens, becomes fused forming a solid black band.

With the exception of some females (Cei, 1982), *L. sanjuanensis* (n = 2) lacks a vertebral line and dorsolateral stripes—both of which are present in *L. pagaburoi*. Unlike *L. ramirezae*, the nasal scale of *L. sanjuanensis* is in broad contact with the rostral, and male *L. sanjuanensis* have more precloacal pores (4 vs 3.2 in *L. ramirezae*).

Liolaemus saxatilis (n = 12) has a distinct pattern of paravertebral markings (absent in *L. ramirezae* and smaller than those found in *L. pagaburoi*), the lateral nuchal folds are absent, and, relative to both new species, there are fewer scales between the auditory meatus and the shoulder ($\bar{x}$ = 22.6). *Liolaemus saxatilis* also tend have more precloacal pores ($\bar{x}$ = 4). *Liolaemus schroderi* (n = 12) shares the character states listed above for *L. gravenhorstii* with the exception of the paravertebral markings, which are present in this species, and lacking in *L. ramirezae*.

DISCUSSION

Contact zones.—At the eastern portion of its range, *L. pagaburoi* is not known to occur with any other species of lizard. However, fewer than 5 km northwest (at km 88), we identified a contact zone for *L. pagaburoi* and *L. ramirezae* (and also *L. quilmes*). In this region as well, the populations of *Parastrephia* and *Festuca* also interdigitate—especially on the hilltops and in the upper stretches of the valleys. This vegetational ecotone presumably permits these habitat specialists to coexist. Interestingly, during mid- November, km 88 was also the northwestern limit of fog penetration (as discussed above). The coincidental limit of fog penetration, coupled with that of the distribution of the two plants used by these *Liolaemus*, further suggests that *Festuca* and *Parastrephia* may be limited by some climatic variable (i.e., temperature, precipitation), which in turn appears to be a limiting factor for

the distribution of these two lizards. Alternatively, it could be argued that these lizards may simply be associated with their respective "host" plants because these species are the dominant cover in their respective habitats. However, at the contact zone (km 88) where both plant species appeared to be roughly equally distributed, we found *L. ramirezae* only under *Parastrephia*, and *L. pagaburoi* only in *Festuca*.

One record from the FML collection (FML 02921) contained both of the newly described species 7 km west of the zone of sympatry recorded by us—well past the western distribution of *Festuca* noted above. This anomalous record can be explained by the fact that the *L. ramirezae* were collected in the lower valleys along the road, whereas the *L. pagaburoi* were collected at higher elevations in *Festuca* (O. Pagaburo, pers. comm.). Additional contact zones are likely to occur in this general region providing the appropriate microhabitats (i.e., *Parastrephia* and *Festuca*) are available. Unfortunately, verifying the location of additional zones of sympatry will be difficult because these mountainous regions are vast, rugged, and, because of a lack of roads, accessible only by foot or pack animal.

Environmental correlates of reproductive modes.—Correlative evidence has long suggested that temperature plays an important role in selecting for the evolution of viviparity in many lineages of squamate reptiles (e.g., Tinkle and Gibbons, 1977; Guillette et al., 1980; Shine, 1985). More recently, empirical evidence has been offered to support this contention (Shine, 1983; Shine and Harlow, 1996). Our expectation that the viviparous *L. pagaburoi* would be found in cooler environments than would the oviparous *L. ramirezae* was also confirmed. Moreover, these differences are greatest about the time when both taxa experience peak reproductive activity (Fig. 6). Such conditions may have either selected for the in situ evolution of viviparity in *L. pagaburoi* or, if the species had evolved viviparity prior to colonizing this environment, provided this species with a fitness advantage in this cooler climatic region. Testing these alternative hypotheses will require first having a robust estimate of phylogeny for these and related taxa. This is the subject of studies now in progress.

In addition, the data gathered for *L. pagaburoi* suggest that this species may reproduce only biennially, as has been determined for other *Liolaemus* with high-elevation distributions (e.g., *L. huacahuasicus*: Halloy and Laurent, 1988; Ramírez Pinilla, 1991c; *L. pictus*: Ibargüengoytía and Cussac, 1996). The fact that parturition was occurring from mid- to late spring, coupled with

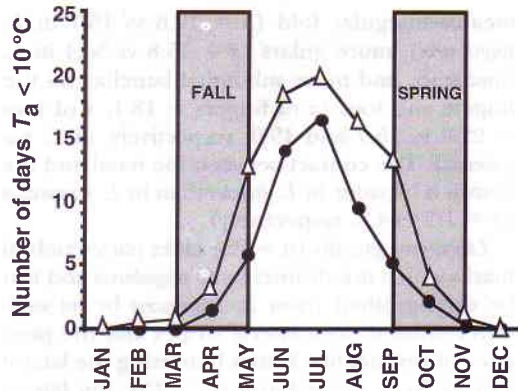

Fig. 6. Number of days per month over which air temperatures (T_a) fell below 10 C at sites near the extreme western distribution of *Liolaemus ramirezae* (circles; at Amaicha del Valle, 1960–1976) and near the eastern limit for *L. pagaburoi* (triangles; at Tafí del Valle, 1943–1972) in Tucumán province (Ramírez Pinilla, 1991a). Gray bars correspond to periods of peak reproductive activity (Ramírez Pinilla, 1989, 1991a; Ramírez Pinilla and Laurent, 1996). Note in times of peak reproductive activity, populations of *L. pagaburoi* may experience as many as seven aditional days of temperatures below 10 C.

the known length of gestation for related viviparous *Liolaemus* [70–90 days; Lemus, 1967; Ramírez Pinilla, 1991a (see her table 3); Ibargüengoytía and Cussac, 1996], suggests that females probably reproduce during summer or fall, overwinter while pregnant, and complete gestation the following spring. This hypothesis is supported further by the absence of oviductal eggs or developing embryos in adult female *L. pagaburoi* collected after January (midsummer).

Resolution of taxonomic confusion.—The previously unrecognized composite nature of *L. alticolor* has resulted in notable taxonomic confusion. In the recent past, the two species described herein were confused with the presumably wide-ranging *L. alticolor* (see Ramírez Pinilla, 1991b; Cei, 1993; Lavilla et al., 1993). The manifestation of this confusion has ranged from simple errors in nomenclature to invoking exceptional reproductive anomalies. To cite a few examples of the former, the third photo on Lám. 35 in Cei's (1993) monograph on reptiles from northern Argentina, lists a *L. alticolor* from Cerro Muñoz. This specimen is actually a *L. pagaburoi*, whereas the other two *Liolaemus* (same page) from the Province of Jujuy appear to be *L. alticolor* sensu stricto. The communally nesting lizards considered to be *L. alticolor* in Espinoza and Lobo (1996), are the oviparous *L. ramirezae*.

Of greater consequence was the suggestion that *L. alticolor* might be reproductively bimodal (Ramírez Pinilla, 1989, 1991a; Ramírez Pinilla and Laurent, 1996). As noted above, very few squamate reptiles are thought to be reproductively bimodal (Shine, 1985; Qualls et al., 1995; Heulin et al., 1997). Moreover, evidence for a sympatric population of oviparous and viviparous females is unprecedented. Hence, the possibility that *L. alticolor* was reproductively bimodal was indeed a noteworthy discovery—especially the report of the bimodal populations. But Ramírez Pinilla and Laurent (1996) also considered the alternative possibility that *L. alticolor* might represent a composite of cryptic species. Indeed, rather than a reproductively unique population of *L. alticolor*, our reexamination of the same lizards studied by Ramírez Pinilla and Laurent (1996, table 2) resulted in the identification of the two cryptic species described above. Specifically, specimens from Amaicha del Valle, Tucumán (FML 02225, 02248) were determined to be *L. ramirezae*. Specimens from Quebrada del Alazán, Cumbres Calchaquíes (FML 00849), Quebrada del Barón, Tafí del Valle (FML 00658), and Puesto de Arriba de Bordón, Lindero Blanco, Hualinchay, Trancas (FML 01048) are *L. pagaburoi*. Finally, FML 01314 from Quebrada Peña La Horqueta, Espinillo, Andalgalá, Catamarca is a *L. bitaeniatus*. A few other Argentinian populations of *L. "alticolor"* have been reported to have lizards with differing reproductive modes. Among these is a population at Olacapato, Salta province, which also has been reported to have sympatric oviparous and viviparous *L. alticolor* (Ramírez Pinilla, 1989, pers. comm.). We are currently examining these populations as well as others from the provinces of Salta and Jujuy which also appear to be undescribed species.

Following this revision, *L. alticolor* sensu stricto appears to have a more limited distribution in northern Argentina than considered previously. Currently, the species appears to be restricted to the province of Jujuy and to a few isolated populations in Salta. However, because these areas (in addition to those in Bolivia, southern Perú, and northern Chile) form a vast region—most of which is unexplored—clearly more work is needed before the taxonomic status of all populations currently referred to *L. alticolor* can be resolved.

MATERIAL EXAMINED

Liolaemus alticolor: AMNH 169004; 7287, Tiahuanaco, Bolivia (cotypes). AMNH 38068–70, Sicuani, Perú. AMNH 13501, Potosí, Potosí, Bolivia. AMNH 13499–500, 81401–03, Oruro, Bolivia. AMNH 77622–23; 77631, Oruro, Playa Verde, Bolivia. MCZ 128518–25, Tiahuanaco, not far from Lake Titicaca, Bolivia. MCZ 12409, Río Huarocondo, Perú.

Liolaemus bibronii: AMNH 80046; 80051, 95 mi SE of Puerto Aysén, Chile. MCZ 14923–24, Huanulan, Argentina. SDSU 1805, 2 mi S Laguna Blanca, Dpto. Zapala, Prov. Neuquén, Argentina. SDSU 1810–13, Puerto Deseado, Dpto. Deseado, Prov. Santa Cruz, Argentina.

Liolaemus bitaeniatus: FML 00822, Sierra de Medina, Prov. Tucumán, Argentina (paratypes). FML 02455; 02918, Dique La Angostura, Dpto. Tafí del Valle, Tucumán. MCZ 149865–66, Iturbe, Prov. Jujuy, Argentina. MCZ 169547, El Maray, San Fernando de Escoipe, Dpto. Chicoana, Prov. Salta, Argentina.

Liolaemus fuscus: AMNH 131833–34, Los Cristales (Huilmo), Coquimbo, Chile. CM 64725, Las Trancas, Prov. Numble, Chile. CM 64736, Ovalle, Prov. Coquimbo, Chile. MCZ 38621–26, Valparaíso, Chile. MCZ 165149–50, Aconcagua, Calera, Chile. MCZ 65395, El Cerezo, Cordillera Santiago, Chile. MCZ 165146, Coquimbo, Coquimbo, Chile. MCZ 165147, Valparaíso, Dunas de Mantagua, Chile. MCZ 165148, Valparaíso, Viña del Mar, Chile. SDSU 1866, Parque Nacional de Campana, Chile.

Liolaemus gracilis: SDSU 1869, Puerto Madryn, Prov. Chubut, Argentina. SDSU 3409, SE beach of Embalse Nihuil, Dpto. San Rafael, Prov. Mendoza, Argentina.

Liolaemus gravenhorstii: MCZ 154184–85; 65396–97; 38627–28, Polpaico, Santiago, Chile.

Liolaemus hernani: AMNH 80054–55, Santiago, Chile. SDSU 1873–76, Termas de Flaco, Sixth Region, Chile.

Liolaemus lemniscatus: AMNH 21145, Concepción, Chile. AMNH 18335, Cerro Caracol, Cordillera de la Costa, Prov. Concepción, Chile. AMNH 37556, Santiago, Chile. AMNH 21142–43, Talcahuano, Chile. CM 64727; 64730, Concepción, Prov. de Concepción, Chile. CM 64728, Escuadrón, Prov. de Concepción, Chile. CM 64729, Curanilahue (Villa Alegre), Prov. Arauco, Chile. MCZ 164037–38; 164041; 164045; 164047; 164049; 164056; 164059; 164060; 164062–64, Concepción, Prov. Concepción, Chile.

Liolaemus pagaburoi: FML 00057, Cumbre del Cajón, Colalao del Valle, Dpto. Tafí del Valle, Prov. Tucumán, Argentina. FML 00477, Camino al Co. Negrito, Cumbres Calchaquíes, Prov. Tucumán. FML 00537, "Cerros Calchaquíes," Tucumán. FML 00632, Lag. Huaca Huasi, km 83, Ruta Prov. 307, Tafí del Valle, Tucumán. FML 00648, Pendiente N, al S del Río Cochuna,

Dpto. Chicligasta, Tucumán. FML 00658, Quebrada del Barón, Dpto. Tafí del Valle, Tucumán. FML 00667, El Negrito, Cumbres Calchaquíes, Tucumán. FML 00816, "Nevados del Aconquija," Dpto. Chicligasta, Tucumán. FML 00849, Quebrada del Alazán, Cumbres Calchaquíes, Tucumán. FML 00861; 02238, Hombro de las Pegmatitas, Camino a Huaca Huasi, Cumbres Calchaquíes, Tucumán. FML 00879, Mo. del Bernardo, Co. Muñoz, Dpto. Tafí del Valle, Tucumán. FML 00886, Cumbre del Co. Muñoz, Depto. Tafí del Valle, Tucumán. FML 00997; 01048, Puesto de Arriba de Bordón (approximately de Lindero Blanco), Hualinchay, Dpto. Trancas, Tucumán. FML 01264, Puesto González, Co. Muñoz, Dpto. Tafí. Tucumán. FML 01337, Cerro Muñoz, Sa. del Aconquija (approximately de Puesto Gonzalez), Tucumán. FML 01829, Camino a Huaca Huasi. FML 02225, Amaicha del Valle, Ruta Prov. 307, km 98, Dpto. Tafí del Valle, Tucumán. FML 02248, km 95, Ruta Prov. 307, Dpto. Tafí del Valle, Tucumán. FML 00889; 00891; 02435; 02446; 02454; 02456; 02464, Puesto El Muñoz, 90, Ruta Prov. 307, Dpto. Tafí del Valle, Tucumán. FML 02746, Hualinchay, Dpto. Trancas, Tucumán. FML 02921, km 95, Ruta Prov. 307, Dpto. Tafí del Valle, Tucumán. FML 00108, Corralito, Prov. Catamarca, Argentina. FML 00208, Quebrada de los Cazadores, Catamarca. FML 00676, Cerro El Overo, Catamarca. FML 00913, Valle Tinajas, Co. Manchao, Catamarca. FML 00914, Portezuelo del Co. Bayo-Co. Manchao, Catamarca. FML 01074, Nevados del Aconquija, lado S. del R'o Chiflón. Dpto. Santa María, Catamarca. FML 01226, Vega Filo "La Banderita" subiendo desde Capillitas. Dpto. Andalgalá, Catamarca. FML 01234, Filo "Los Heladitos," Dpto. Andalgalá, Catamarca.

Liolaemus paulinae. FML 01341, no data. IZUC 19362–71, Calama, Chile. SDSU 1909–11, S shore of Loa River, Chile.

Liolaemus ramirezae. FML 01215; 02196; 02240; 02269; 02275; 02279; 02288; 02299; 02306; 02330; 02383; 02386; 02394; 02402; 02436; 02444; 02450; 02463; 02468; 02473; 02481; 02486; 02498; 02569; 02575; 02944, km 98, Ruta Prov. 307, Tafí del Valle, Amaicha del Valle, Dpto. Tafí, Prov. Tucumán, Argentina. FML 01367, km 98 to 95, Ruta Prov. 307, Tafí del Valle-Amaicha del Valle, Dpto. Tafí, Tucumán. FML 02715, Ruta Prov. 307, al O. del Infiernillo, Dpto. Tafí del Valle, Tucumán. FML 02921, km 95, Ruta Prov. 307, Tafí del Valle-Amaicha del Valle, Dpto. Tafí, Tucumán. FML 01228, 03431; 03612, Mina Capillitas, Dpto. Andalgalá, Prov. Catamarca, Argentina (27°21′S, 66°22′W). FML 02561, Morro El Arenal (El Ingenio), Dpto. An-

dalgalá, Catamarca. FML 01361, San Antonio de los Cobres, Dpto. Los Andes, Prov. Salta, Argentina. FML 01658, La Poma, Dpto. La Poma, Salta. FML 03006, 26.1 km al N de La Poma, sobre Ruta Nac. 40, Dpto. La Poma, Salta. FML 03333; 03335, Santa Rosa de Tastil, Dpto. Rosario de Lerma, Salta. FML 03339; 03345; 03346, Ruta Nac. 51, km 158 (2 km SW San Antonio de los Cobres), Dpto. La Poma, Salta.

Liolaemus robertmertensi. FML 01706, Puesto Río Blanco, Andalgalá, Catamarca, Argentina.

Liolaemus sanjuanensis. FML 01016 (paratypes), approximately Mgte. Corralitos, Sierra Pie de Palo, San Juan, Argentina.

Liolaemus saxatilis. AMNH 65193–99; 126616, Achiras, Córdoba, Argentina. SDSU 1736–37, El Chacay, Dpto. Río Cuarto, Córdoba, Argentina.

Liolaemus schroederi. AMNH 131847–48, Curicó, Las Tablas, Chile. MCZ 51948-49 (paratypes), Los Queñes, Chile. MCZ 14904, Alhué, Santiago, Chile. MCZ 65404, Peyuhue Prov. Maule, Chile. MCZ 126712-13, Alto Vilches, Prov. Talca, Chile.

Liolaemus tacnae. FML 1544, Ruta Arequipa, Puno, Perú. SDSU 1924, 3 km E Portezuelo Chapiquina, Prov. Tarapaca, Chile.

Liolaemus variegatus. FML 01210, Cochabamba, Bolivia.

Liolaemus walkeri. AMNH 63389–90, Llocllapampa, Dpto. Junín, Perú (paratypes). AMNH 88324–26, Acolla, near Jauja, Dpto. Junín, Perú. MCZ 43770–75; 43777; 43779, Llocllapampa, Dpto. Junín (type and paratypes). MCZ 45850, Rapi, Dpto. Ayacucho, Perú. MCZ 157221, Tarata, Prov. Tarata, Dpto. Tacna, Perú. MCZ 43780– 81, Mina Janchiscochas, Dpto. Junín, Perú. MCZ 43783–86, Ticlio, Dpto. Luna, Perú. MCZ 45813–19, Dpto. Junín, Perú. MCZ 157222, Pampa Galera, Prov. Lucanar, Dpto. Ayacucho, Perú. MCZ 157219, Acolla, Prov. Jauja, Dpto. Junín, Perú. MCZ 157220, Ticlio, Prov. Yauli, Dpto. Junín, Perú. MCZ 100111, Dpto. Junín, Perú. MCZ 45887–89, Maraynioc, EN of Tarma, Dpto. Junín, Perú. SDSU 1937, 6 km ENE Paccha, Prov. Junín, Perú.

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