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TWO NEW SPECIES OF *LIOLAEMUS* LIZARDS FROM NORTHWESTERN ARGENTINA: SPECIATION WITHIN THE NORTHERN SUBCLADE OF THE *ELONGATUS* GROUP (IGUANIA: LIOLAEMIDAE)

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ABSTRACT: The *Liolaemus elongatus* group currently includes eight species (including the species described herein) of mid-sized, long-tailed, primarily saxicolous lizards. Members of this lineage are distributed in northwestern Argentina along the Andean Cordillera south to the Patagonian Steppe (27–44° S) and over a wide range of elevations (350–3900 m). Here we describe two new species belonging to the northern radiation of the *elongatus* group. The four currently recognized members of this northern subclade (including the two species described herein) have fewer midbody scales than other members of the *elongatus* group, brown to black heads, and lack the distinct dorsal body or tail patterns found in adults of other species belonging to the *elongatus* group. Additionally, pregnant and recently spent females exhibit crimson red color in the cloacal region—a trait known only for members of this northern lineage and *L. buergeri.* The first new species, *L. dicktracyi* from the Sierra de Famatina of La Rioja Province, differs from all other members of the *elongatus* group in several meristic characters and in its unique dorsal coloration: black heads, shoulders, and tails, with blue torsos and hind limbs. The second new species, *L. umbrifer* from the Quebrada de Randolfo in northeastern Catamarca Province, is morphologically similar to *L. capillitas,* but differs from this and other species in the *elongatus* group in several meristic characters, the presence of black shoulders and upper arms, and crimson red coloration of the cloacal region in both males and females. The natural history of both of the new species is similar in many respects to *L. capillitas* and *L. heliodermis,* which further supports the phylogenetic affinities of members of this subclade within the *elongatus* group. Finally, we provide comparisons of recent phylogenetic hypotheses and discuss the content of the *elongatus* group.

Key words: Argentina; Liolaemidae; *Liolaemus dicktracyi* sp. nov.; *Liolaemus elongatus* group; *Liolaemus umbrifer* sp. nov.; Lizard; New species; Taxonomy

THROUGHOUT the arid and semiarid regions of South America, *Liolaemus* lizards reign as the dominant components of most reptile communities. Members of this clade are widely distributed from the high Andes of central Perú to the shores of Tierra del Fuego and over a broad range of climates and habitats (Cei, 1986, 1993; Donoso-Barros, 1966; Etheridge and Espinoza, 2000). Several species of *Liolaemus* even hold records among squamates for their latitudinal (54° S; *L. magellanicus*) or elevational distributions (≥5000 m; *L. irregularis, L. nigriceps,* and *L. signifer*) (R. E. Espinoza, unpublished data). This remarkably large genus of lizards—second only to *Anolis* in number of species—includes >160 recognized taxa and has continued to grow at a rate of nearly four new species per year over the last decade (Etheridge and Espinoza, 2000).

Recent phylogenetic analyses of mitochondrial DNA sequences for 60 species of *Liolaemus* (Schulte et al., 2000) indicate a well supported basal split dividing the lineage into two, similarly sized clades that largely correspond to groups defined previously from morphological evidence (Etheridge, 1995). One of these lineages, the *chiliensis* group (sensu Etheridge, 1995; Lobo, 2001; = subgenus *Liolaemus* sensu Laurent, 1985; see also Schulte et al., 2000), includes approximately 75 species

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TABLE 1.—Maximum body sizes (SVL) and geographic distributions of the eight *Liolaemus* species currently recognized as belonging to the *elongatus* group (including the two new species described herein). Data for *L. thermarum* are from Videla and Cei (1996) and Espinoza et al. (2000) with the inclusion of a northern range extension for *L. elongatus* (Avila and Lobo, 1999) and new elevation records for *L. petrophilus*. The four species belonging to the northern subclade of the *elongatus* groups are indicated with an asterisk.

Species	Maximum SVL (mm)	Latitude range (degrees S)	Elevation range (m)
Liolaemus austromendocinus	103	34–37	900–2310
*L. capillitas**	93	27	2500–3900
L. dicktracyi sp. nov.*	91	29	2600–2800
L. elongatus[1]	89	28–45	700–3000
*L. heliodermis**	81	27	2820
L. petrophilus	100	41–44	350–1400
L. thermarum	85	35	2400–2500
L. umbrifer sp. nov.*	89	27	3190–3490

[1] See Discussion for comments on the distribution of *L. elongatus*.

that share two derived morphological characteristics: a fused Meckel's groove and four or fewer precloacal pores. Within the *chiliensis* group, several informal group names have been applied to morphologically similar species (Cei, 1986, 1993; reviewed in Lobo, 2001). One of these, the *elongatus* group as originally defined by Cei (1974; see also Cei, 1975, 1986; Hulse, 1979), was recently diagnosed and redefined to include six species: *L. austromendocinus, L. capillitas, L. elongatus, L. heliodermis, L. petrophilus,* and *L. thermarum* (Espinoza et al., 2000).

The six currently recognized species of the *elongatus* group are distinguished from other species in the *chiliensis* group by their moderate to large body size (approximately 80–100 mm snout–vent length: SVL); moderately slender to robust, elongate bodies; small, nonoverlapping to subimbricate body scales (>55 around midbody) that do not terminate in a spine; and tails that are longer than 1.5 times the SVL and round in cross section (Espinoza et al., 2000). Members of this lineage are distributed from near the intersection of the Cumbres Calchaquíes and the Sierra del Aconquija of western Tucumán Province (27° S), southward to the Patagonian Steppe of Chubut Province (44° S), and over a wide range of elevations (350–3900 m; Table 1). Species in the *elongatus* group usually inhabit arid environments, including the eco-regions known as Prepuna, Patagonian Forests, and Patagonian Steppe (Burkart et al., 1999; Cabrera and Willink, 1980). Most are moderately to exclusively saxicolous, insectivorous to omnivorous, and all species for which reproductive mode has been determined are viviparous (Cei, 1974, 1986; Espinoza et al., 2000; Hulse, 1979; Videla, 1983).

Within the *elongatus* group are two closely related, geographically isolated species, *L. capillitas* (Hulse, 1979) and *L. heliodermis* (Espinoza et al., 2000), which are distributed far north of most other species in the *elongatus* group, with the exception of a few disjunct northern populations of *L. elongatus* (Avila and Lobo, 1999; but see Discussion). We refer to the subclade including *L. capillitas* and *L. heliodermis* as the northern radiation of the *elongatus* group. Members of this subclade, which currently includes the two species listed above plus the two new species described below, differ from other species in the *elongatus* group in the following ways: usually fewer midbody scales 58–76 (versus 71–90 in other species of the group), a uniformly brown to black head (dorsal head is irregularly marked in other species of the group), a torso and tail that lack distinct patterns (no stripes, bars, or rings) in adults, a darkly pigmented (usually black) area surrounding the insertion of the forelimbs that is speckled with light colored spots, and crimson red coloration in the cloacal region of pregnant and recently spent females (Table 2). Here we describe two new species, one from La Rioja Province and another from Cata-

TABLE 2.—Diagnostic character states for currently recognized members of the *Liolaemus elongatus* group. Data for all but the new species are from Videla and Cei (1996; for *L. thermarum*) or Espinoza et al. (2000) with minor revisions. Precloacal pores are for males only. Descriptions of body color (except red coloration of the cloacal region) and patterns were taken from preserved adult lizards, but the traits listed below are also discernable in live specimens.

Character	*austromendocinus* (n = 10)	*capillitas* (n = 16)	*dicktracyi* sp. nov. (n = 10)	*elongatus* (n = 10)	*heliodermis* (n = 3)	*petrophilus* (n = 3)	*thermarum* (Videla and Cei, 1996)	*umbrifer* sp. nov. (n = 16)
Midbody scales	76–82	58–67	60–73	74–89	62–69	71–95	84–89	58–76
Keels on dorsal scales	weak	distinct	weak/distinct	moderate/distinct	weak	distinct	weak	weak
Precloacal pores	2–3	0–4	3–4	3–6	3–4	3	0	3–4
Head color	brownish gray	black	black	brown	black	brownish gray	light brown/gray	dark brown/black
Background body color	brownish gray	brown/black	indigo/light blue	brown	sulfur yellow	dark brown/ ochre yellow	brownish gray	brown/black
Dorsal body pattern	indistinct	indistinct	indistinct	irregularly striped[1]	indistinct	transverse bars	indistinct	indistinct
Tail rings	usually distinct[2]	absent	absent	usually distinct	absent	distinct	absent	absent
Red in cloacal region[3]	absent	females	females	absent	unknown	absent	absent	both sexes

[1] Irregular black stripes in lateral or dorsolateral field usually distinct and increase in width at midbody.

[2] In our previous work (Espinoza et al., 2000, their table 2, p. 510), *L. austromendocinus* was listed as not possessing a ringed tail (in error), but was correctly noted as often possessing this trait in the text (see Diagnosis of *L. heliodermis* in Espinoza et al. [2000], p. 510).

[3] A patch of crimson red in the cloacal region, abdomen, ventral thighs, and proximal ventral tail, previously known only from pregnant and recently spent females of species belonging to the northern clade of the *elongatus* group, both sexes in *L. buergeri* (M. Christie, personal communication; Hulse, 1979; F. Lobo and R. E. Espinoza, personal observations), and both sexes of *L. umbrifer* (see Discussion for further comments).

marca Province, that belong to this northern radiation of the *elongatus* group.

Materials and Methods

For purposes of diagnosing the new species and defining the northern clade of the *elongatus* group, we examined a series of each of the six species currently considered to be members of the *elongatus* group (sensu Espinoza et al., 2000; Table 1; Appendix I). Specimens examined, including the new species described herein, are deposited in the herpetological collections of the Museo Ciencias Naturales (MCN); Universidad Nacional de Salta, Argentina; the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, USA; the Fundación Miguel Lillo (FML), Tucumán, Argentina; and the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, California, USA. All specimens examined had been collected either at their type localities or within 100 km thereof. In our taxonomic analysis, we considered external morphology, including squamation, coloration, and color patterns. We examined live specimens of all species belonging to the *elongatus* group to record color in life (except for *L. thermarum* for which we used information in Videla and Cei, 1996). A Scout™ global-positioning device (Trimble Navigation Systems, Sunnyvale, California, USA) was used to record the latitude, longitude, and elevation of lizards collected in the field. 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 digital calipers to the nearest 0.01 mm. Terms for the description of scales are those of Smith (1946); the distribution of body patterns is after Lobo and Espinoza (1999); and for neck-fold terminology we follow Frost (1992).

Species Description

Liolaemus **dicktracyi** sp. nov.

Holotype.—FML 9928 (field tag: REE 184), an adult male from Portezuelo Blanco, 26.5 km west of Famatina on road to Cueva de Perez, Sierra de Famatina, Departamento Famatina, Provincia de La Rioja, Argentina (28° 54′ 30″ S, 67° 41′ 30″ W; 2800 m); collected by F. B. Cruz and R. E. Espinoza, 16–17 February 1998 (Fig. 1).

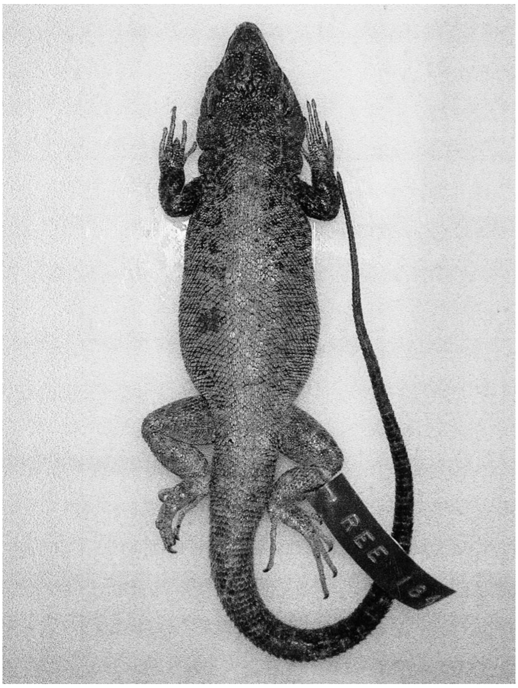

FIG. 1.—Holotype of *Liolaemus dicktracyi* (FML 9928; SVL = 88.4 mm).

Paratypes.—CM 147716–17 (field tags: PT 3291; REE 201), FML 9929–33 (field tags: PT 3286–89, 3292), and MCN 461–62 (field tags: PT 3285, 3290) same data as holotype.

Diagnosis.—A moderate to large bodied, robust lizard belonging to the *Liolaemus elongatus* group (sensu Espinoza et al., 2000) that can be distinguished from all other members of that group (and all other *Liolaemus*) in possessing the following characteristics: black heads (reviewed by Cei, 1998) and shoulders, indigo to light blue torsos, and charcoal gray to black ventral coloration (Table 2; Fig. 2). *Liolaemus dicktracyi* also differs from other members of the *elongatus* group, except those in the northern radiation (*L. capillitas, L. heliodermis,* and *L. umbrifer* sp. nov., see description below), in possessing

FIG. 2.—Upper: adult male *Liolaemus dicktracyi* in life; lower: adult male *Liolaemus umbrifer* in life.

larger and, therefore, usually fewer midbody scales (Table 2): *L. dicktracyi*: 60–73; versus 76–82 in *L. austromendocinus*; 72–90 in *L. elongatus*; 74–89 in *L. petrophilus* (Donoso-Barros and Cei, 1971); 84–89 in *L. thermarum* (Videla and Cei, 1996), and presence of red coloration in the cloacal region of pregnant and recently spent females. *Liolaemus capillitas, L. elongatus,* and *L. petrophilus* have dorsal scales that are more distinctly imbricate than those of *L. dicktracyi. Liolaemus elongatus* have dark brown, irregular, longitudinal stripes (6–12 scales wide) that extend along the vertebral and lateral fields, whereas *L. dicktracyi* lack stripes or similar body patterns (Table 2). *Liolaemus petrophilus* have a distinct dorsal pattern of transverse dark bars that form a "tigroid" pattern (Cei, 1975; Donoso-Barros and Cei, 1971) that is lacking in the new species. Unlike *L. dicktracyi, L. elongatus* (southern populations; see Discussion), *L. petrophilus,* and most *L. austromendocinus* have distinctly ringed tails (Table 2). The temporals of *L. umbrifer* sp. nov. (described below) are only slightly keeled; the head is dark brown, not black; and both males and females of this species have red coloration in the cloacal region. In *L. dicktracyi,* the temporals are usually distinctly keeled, the head is always black, and only females possess red coloration in the cloacal region. In contrast to *L. dicktracyi,* which lack dorsal body patterns and possess 3–4 precloacal pores, *L. thermarum* have dark, wide stripes on the lower flanks and lack precloacal pores (Videla and Cei, 1996, 1998).

Description of the holotype.—Adult male (Fig. 1), 88.4 mm SVL; tail length 152.1 mm, complete, not regenerated. Axilla–groin distance 39.6 mm. Head 19.6 mm long (from anterior border of auditory meatus to tip of snout), 15.4 mm wide (at anterior border of auditory meatus), 9.0 mm high. Snout length 6.8 mm (posterior margin of canthal to tip of snout). Interorbital distance (between arcs of circumorbitals) 1.4 mm. Eye–nostril distance 4.3 mm. Tibial length 19.4 mm. Foot length 25.2 mm (ankle to tip of claw on fourth toe).

Dorsal head scales smooth, 17 between rostral and anterior border of auditory meatus. Ten keeled temporals (left side), all but those closest to auditory meatus with 1–2 scale organs along their posterior margins. Interparietal subpentagonal, smaller than parietals in size, surrounded by seven scales. Frontal scale azygous. Six scales between frontal and rostral. Two postrostrals with 8–9 scale organs each. Circumorbitals complete. Five enlarged supraoculars (both sides). Five scales between frontal and supercilliaries. Six/seven (left/right) flat, elongate, imbricate supercilliaries. Canthal separated from nasal by two scales (both sides). Loreal region flat. Seven scales surrounding nasals (both sides). Nasals not in contact with rostral. Seven/eight lorilabials, fourth through seventh/sixth through eighth in contact with subocular. Six/five enlarged supralabials. Fourth supralabial (both sides) curved upward posteriorly but not in contact with subocular. Five infralabials (both sides), slightly taller than supralabials. Four internasals. Orbit with 15 upper and 13 lower ciliaries (left side). Orbit diameter 3.6 mm (measured between upper and lower ciliaries on left side). Subocular scale elongate. Preocular unfragmented. Longitudinal ridge along upper margin of the three ocular scales. Rostral scale twice as wide (3.9 mm) as high (1.9 mm). Mental twice as wide (3.8 mm) as high (1.8 mm), followed posteriorly by two rows of 5/4 chinshields. First chinshield in contact with first infralabial. Scales of throat between chinshields juxtaposed in first two rows, imbricate posteriorly. Fifty-seven gulars between auditory meatus. Two outward projecting laminar scales along anterior border of auditory meatus. Auditory meatus higher (4.3 mm) than wide (2.9 mm). Lateral scales of neck granular. Subdermal fat bodies give slightly inflated appearance to neck region. Antehumeral fold distinct. Rictal, postauricular, and longitudinal folds present but less conspicuous than antehumeral. Thirty-six scales between auditory meatus and antehumeral fold (counted along postauricular and longitudinal folds).

Fifty-eight dorsal scales between occiput and anterior surface of thighs. Dorsal body scales with round posterior margin, slightly imbricate, weakly keeled. Twenty-five longitudinal keeled scale rows over dorsum of trunk. Scales of neck region smaller than dorsals. Sixty-five scales around midbody. Ventral scales of similar size to dorsals, 110 between mental and precloacal pores. Three precloacal pores, each with a waxy exudate. Ventral surface of thighs with enlarged, laminar, imbricate scales anteriorly, abruptly changing to smaller granular scales on posterior third of ventral thigh.

Fourth finger with 23 keeled, tridentate, subdigital lamellae. Claw of fourth finger 1.8 mm, curved, sharp tipped, opaque brown. Fourth toe with 28 keeled subdigital lamellae. Claw of fourth toe 2.2 mm, similar to that of fourth finger.

Variation.—Based on an additional seven adult males and two adult females. SVL 72.0–91.2 mm. Head length 16.0–20.1 mm, width 12.4–16.9 mm. Axilla–groin distance 31.0–45.1 mm. Tail length 138.3–152.1 mm. Midbody scales 60–73. Dorsal scales round to rhomboidal, occasionally pointed, weakly to distinctly keeled, subimbricate, 56–66 between occiput and anterior surface of thighs. Some individuals with interstitial granules along posterior flanks. Dorsal head scales 12–17, variable in size but usually small, some irregular in shape, most convex. Ventrals 104–113. Scales around interparietal 5–8. Three to six enlarged supraoculars. Preocular not divided, not fused to subocular. Temporals 8–10, weakly to distinctly keeled. Scales between auditory meatus and antehumeral fold 30–36. Gulars 48–57, smooth, imbricate, circular to elliptical. Supralabials 5–7. Infralabials 4–6. Posterior tip of fourth or fifth through seventh supralabial upturned. Scales around nasals 6–8. Nasals in slight (60%) or lacking contact (40%) with rostral. Four internasals. Rostral barely visible from above. Scales between rostral and frontal 5–7. Postrostrals 2 (90%) to 3 (10%), with 5–13 scale organs each. Six to nine lorilabials, fourth, fifth, or sixth through ninth in contact with subocular. Supercilliaries 6–8. Subdigital lamellae on fourth finger 20–24; on fourth toe 26–30. Precloacal pores 3–4 in males, not present in females.

Color in life.—Head black, abruptly fading posteriorly to indigo, light blue in nuchal region at about the level of the posterior border of the auditory meatus (Fig. 2). Trunk (at shoulder level) to first third of tail indigo to light blue, most uniform in coloration in the mid-vertebral field. Light blue and black scales occasionally speckle the dorsal trunk, but these markings are most abundant in the dorsolateral fields. Flanks slightly darker than dorsal field. Ventrolateral field speckled with irregular light blue spots in most specimens. Insertion of forelimbs and antehumeral and posthumeral regions speckled with small blue markings (6–8 scales) on a dark indigo to black background. Tail fades from indigo to light blue in anterior third to dark brown indigo posteriorly. Regenerated portions of tails are black. Ventrally charcoal gray to black. Ventral side of the tail darkens from about mid-tail to the tip. Precloacal pores yellow orange. Adult fe-

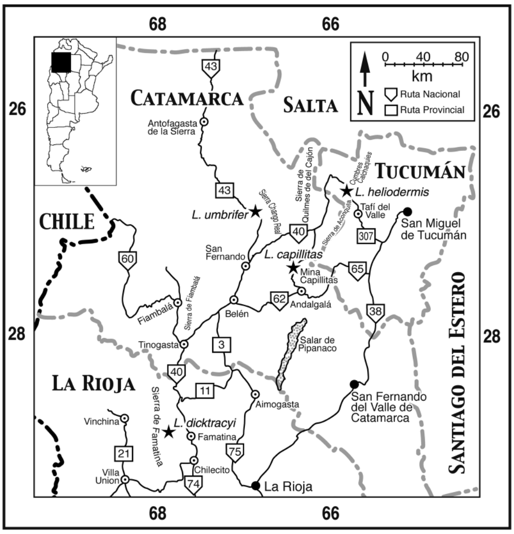

FIG. 3.—Type localities (stars) of species belonging to the northern radiation of the *Liolaemus elongatus* group in northwestern Argentina. *Liolaemus heliodermis* in Tucumán Province, *L. capillitas* and *L. umbrifer* sp. nov. in Catamarca Province, and *L. dicktracyi* sp. nov. in La Rioja Province. Insert = Argentina. Some mountain ranges have been excluded for clarity.

FIG. 4.—Eroded white cliffs of Portezuelo Blanco, Sierra de Famatina, Departamento Famatina, La Rioja Province (28° 54′ 30″ S, 67° 41′ 30″ W; 2800 m), the type locality of *Liolaemus dicktracyi.*

males had crimson red coloration in the cloacal region and at the base of the thighs and tail when collected in mid-February, otherwise sexual dichromatism is absent.

Color in preservative.—Bright blue color of torso in life fades and darkens to brownish blue in alcohol and overall color darkens slightly on trunk and ventrally. Red coloration in cloacal region of females fades almost completely after approximately 6 mo. Precloacal pores fade from yellow orange to cream yellow.

Etymology.—The specific name is a noun in the genitive case formed in honor of Dr. C. Richard (“Dick”) Tracy, currently Professor of Biology and Director of the Biological Resources Research Center at the University of Nevada, Reno, for his numerous contributions to the understanding of the biology of lizards generally and for inspiring, supporting, and collaborating with us on our research with *Liolaemus* specifically. With the addition of *L. dicktracyi,* this brings the number of *Liolaemus* named after various investigators of *Liolaemus* and their supporters to 60 (approximately 30% of the currently recognized taxa; Etheridge and Espinoza, 2000).

Distribution.—*Liolaemus dicktracyi* is known only from the immediate vicinity of the type locality (Fig. 3): Portezuelo Blanco, Sierra de Famatina, La Rioja (28° 54′ 30″ S, 67° 41′ 30″ W; 2600–2800 m), a geologically well studied exposed cliff face with strata representing Permo-Triassic and Quaternary deposits (Cei, 1982; Fig. 4). Two specimens were also collected from 8.4 km southeast of the type locality along an unnamed dirt road that runs along the Río Amarillo and leads to Cueva de Perez in the Sierra de Famatina. With the addition of *L. dicktracyi,* three species of Liolaemidae [*L. famatinae* and *Phymaturus mallimaccii*; Cei (1980)] are now known to be endemic to the Sierra de Famatina. Currently, *L. dicktracyi* and *L. elongatus* (Avila and Lobo, 1999; but see Discussion) are the only species in the *elongatus* group known from La Rioja; however, we have examined two additional isolated, montane populations of *L.* cf. *capillitas* from that province that also appear to be undescribed species.

Natural history.—Specimens of *L. dicktracyi* were found primarily on the steep and eroded cliffs and hillsides of Portezuelo Blanco (Fig. 4). The two additional specimens were found along basaltic rock walls that project out along the Río Amarillo and along more open, gentle slopes just southeast of the type locality. The habitat at the type locality (2600–2800 m) is classified as Prepuna (Burkart et al., 1999; Cabrera and Willink, 1980). Dominant plants species include the small spiny shrub *Adesmia* (Fabiaceae) and a spindly, sparsely vegetated *Baccharis* (Asteraceae) that grows to 1 m. Large metamorphic rock outcrops are common along the road cut that follows along the Río Amarillo. When we visited the type locality in late summer (mid-February) 1998, the lizards were active from 0930 to approximately 1800 and were most often seen basking from 1–10 m above the road cut on either sedimentary deposits (at the type locality) or on large outcrops of basaltic rock (along dirt road). Body temperatures of two adult male (76 and 85 mm SVL) *L. dicktracyi* collected on different days as they were basking in the afternoon on the steep cliffs of the type locality averaged 35.9 C (35.8–36.0 C) despite variable weather conditions (sunny versus overcast and windy). The predominantly saxicolous lifestyle (although not always on consolidated rock) of *L. dicktracyi* is consistent with the microhabitat selection of other members of the *elongatus* group (Cei, 1974, 1986; Espinoza et al., 2000), and particularly that of *L. capillitas, L. heliodermis,* and *L. umbrifer* sp. nov. (described below), which are strictly saxicolous (Espinoza et al., 2000; Hulse, 1979; see below) and appear to be closely related to the new species (Lobo, 2001; R. E. Espinoza and F. Lobo, unpublished data). We encountered no other species of lizards in syntopy with *L. dicktracyi.* However, at a slightly lower elevation (Los Corrales, 28° 49′ 50″ S, 67° 38′ 20″ W; 2200 m), we encountered *L. koslowskyi,* and the type locality for *L. famatinae* and *Phymaturus mallimaccii* is Cueva de Perez [>4000 m; Cei (1980)], <20 km by road south of the type locality of *L. dicktracyi.*

Members of the *elongatus* group are viviparous (as far as is known) and live at moderate to high latitudes or elevations (Cei, 1986; Espinoza et al., 2000; Hulse, 1979; Schulte et al., 2000). This correlation is consistent with the hypothesis that viviparity is an adaptation to reproducing in cold climates (e.g., Guillette, 1993; Shine, 1985; Tinkle and Gibbons, 1977). We were unable to determine the reproductive mode of *L. dicktracyi* because the lizards were collected in late summer, past the time when other members of the *elongatus* group are known to give birth (Hulse, 1979; Ibargüengoytía and Cussac, 1998). However, because *L. dicktracyi* lives at a relatively high elevation (2600–2800 m) and because its closest relatives are viviparous, we predict that this species is also live bearing. Female *L. dicktracyi* collected in mid-February, although no longer pregnant, exhibited pregnant-female coloration as described above and for *L. capillitas* (Hulse, 1979; R. E. Espinoza and F. Lobo, personal observation; see also description below of *L. umbrifer* sp. nov.). The red color faded after the lizards were in captivity for approximately 3 wk.

Other members of the *elongatus* group are primarily insectivorous (Cei, 1986; Hulse, 1979; Videla, 1983) but may periodically include some plant matter in their diets (R. E. Espinoza, unpublished data). Feces produced by *L. dicktracyi* (n = 10) within 3 d of capture from the field contained the remains of insects, with ants appearing to constitute a substantial portion of the diet. Hence, the diet of *L. dicktracyi* is similar to that of *L. capillitas,* which also feeds primarily on ants (Hulse, 1979).

Liolaemus ***umbrifer*** sp. nov.

Holotype.—FML 9934 (field tag: ACUNSa 52), an adult male from Quebrada de Randolfo, Ruta Provincial 43, 60.3 km northwest of intersection of Ruta Provincial 4 and Ruta Provincial 43, 166 km southeast of Antofagasta de la Sierra, Departamento Antofagasta, Provincia de Catamarca, Argentina (26° 51.456′ S, 66° 44.804′ W; 3192 m); collected by C. Abdala, R. E. Espinoza, F. Lobo, and M. I. Martínez Oliver, 18 January 2001 (Fig. 5).

Paratypes.—FML 9935–45 (field tags: ACUNSa 50, 53–55, 57, 82–89) and MCN 463–64 (field tags: ACUNSa 51, 56) same

FIG. 5.—Holotype of *Liolaemus umbrifer* (FML 9934; SVL = 88.8 mm).

data as holotype. CM 147714–15 (field tags: ACUNSa 58–59) 2 km southeast Peña Fria, Ruta Provincial 43, 32 km northwest of Quebrada de Randolfo, 105 km southeast of Antofagasta de la Sierra, Departamento Antofagasta, Provincia de Catamarca, Argentina (26° 43.19′ S, 66° 57.66′ W; 3487 m); collected by C. Abdala, R. E. Espinoza, F. Lobo, and M. I. Martínez Oliver, 18 January 2001.

Diagnosis.—A moderate to large-bodied, elongate lizard belonging to the *L. elongatus* group (sensu Espinoza et al., 2000) that can be distinguished from all other members of that group (and all other *Liolaemus*) in possessing the following traits: black arms (distinct from light to dark brown background color of dorsum) and red coloration in the posterior abdomen, cloacal region, ventral thighs, and ventral base of the tail in both sexes (Table 2). The new species can be distinguished from all other members of the *elongatus* group, except the northern radiation (*L. capillitas, L. dicktracyi,* and *L. heliodermis*) by its larger and usually fewer midbody scales: *L. umbrifer*: 58–76; versus 76–82 in *L. austromendocinus*; 72–90 in *L. elongatus*; 74–89 in *L. petrophilus* (Donoso-Barros and Cei, 1971); 84–89 in *L. thermarum* (Videla and Cei, 1996) (Table 2). *Liolaemus capillitas, L. elongatus,* and *L. petrophilus* have dorsal scales that are more distinctly imbricate than those of *L. umbrifer,* and the former three species have keels that occupy the entire scale, whereas the scales of *L. umbrifer* are only weakly keeled (Table 2). *Liolaemus elongatus* have dark brown, irregular, longitudinal stripes (6–12 scales wide) that extend along the vertebral and lateral fields, whereas *L. umbrifer* lack stripes or similar body patterns (Table 2). *Liolaemus petrophilus* have a distinct dorsal pattern of transverse dark bars that form a “tigroid” pattern (Cei, 1975; Donoso-Barros and Cei, 1971), which are lacking in this new species. Unlike *L. umbrifer, L. elongatus* (southern populations; see Discussion), *L. petrophilus,* and most *L. austromendocinus* have distinctly ringed tails (Table 2). The temporals of *L. umbrifer* are only slightly keeled, the head is dark brown with irregular black markings, and both males and females of this species have red coloration in the cloacal region, whereas in *L. dicktracyi* the temporals are usually distinctly keeled, the head is black, and only females possess red coloration in the cloacal region. Adult *L. dicktracyi* and male *L. heliodermis* have blue or yellow torsos, respectively, whereas *L. umbrifer* have a light to dark brown trunk. In contrast to *L. umbrifer,* which lack dorsal body patterns and possess 3–4 precloacal pores, *L. thermarum* have dark, wide stripes on the lower flanks and lack precloacal pores (Videla and Cei, 1996, 1998).

Description of the holotype.—Adult male (Fig. 5), 88.8 mm SVL; tail length 102.4 mm, 71.1 mm (69.4%) regenerated. Axilla–groin distance 41.5 mm. Head 19.2 mm long (from anterior border of auditory meatus to tip of snout), 15.9 mm wide (at anterior border of auditory meatus), 10.2 mm high. Snout length 6.3 mm (posterior margin of canthal to tip of snout). Interorbital distance (between arcs of circumorbitals) 1.7 mm. Eye–nostril distance

3.3 mm. Tibial length 18.4 mm. Foot length 24.9 mm (ankle to tip of claw on fourth toe).

Dorsal head scales smooth, 18 between rostral and anterior border of auditory meatus. Ten keeled temporals (left side), all with one scale organ on their posterior margins. Interparietal subpentagonal, slightly smaller than parietal, surrounded by seven scales. Frontal divided into two pairs of scales. Six scales between frontal and rostral. Two postrostrals with 8/10 (left/right) scale organs each. Supraorbital semicircles complete. Three enlarged supraoculars (both sides). Five scales between frontal and supercilliaries. Six/seven flat, elongate, imbricate supercilliaries. Canthal separated from nasal by two scales (both sides). Loreal region flat. Seven/eight scales surrounding nasals. Nasals in slight contact with rostral. Eight lorilabials (both sides), fifth through eighth in contact with subocular. Eight/nine enlarged supralabials. Fifth and sixth supralabial (both sides) curved upward posteriorly and in contact with subocular. Five/six infralabials slightly taller than supralabials. Four internasals. Orbit with 15 upper and 14 lower cilliaries (left side). Orbit diameter 4.0 mm (measured between upper and lower ciliaries on left side). Subocular scale elongate. Preocular unfragmented. Longitudinal ridge along upper margin of the three ocular scales. Rostral scale more than twice as wide (3.9 mm) as high (1.5 mm). Mental nearly twice as wide (3.9 mm) as high (2.2 mm), followed posteriorly by two rows of four chinshields (both sides). First chinshield in contact with first infralabial. Scales of throat between chinshields slightly imbricate posteriorly. Sixty-six imbricate gulars between auditory meatus. Four outward-projecting (virtually perpendicular) laminar scales along anterior border of auditory meatus. Auditory meatus oval shaped: 4.1 × 2.6 mm. Lateral scales of neck granular. Subdermal fat bodies give slightly inflated appearance to neck region. Antehumeral fold distinct. Rictal, postauricular, and longitudinal folds present but less conspicuous than antehumeral. Thirty-six scales between auditory meatus and antehumeral fold (counted along postauricular and longitudinal folds).

Sixty-six dorsal scales between occiput and anterior surface of thighs. Dorsal body scales round, slightly imbricate, weakly keeled. Thirty-one longitudinal keeled scale rows over dorsum of trunk. Scales of neck region smaller than dorsals. Scales become increasingly rounded laterally and along flanks. Sixty-four scales around midbody. Ventral scales of similar size to dorsals, 115 between mental and precloacal pores. Three precloacal pores, each with a waxy exudate. Ventral surface of thighs with enlarged, laminar, imbricate scales anteriorly, abruptly changing to smaller granular scales on posterior third of thigh.

Fourth finger with 23 tridentate, subdigital lamellae. Claw of fourth finger 2.0 mm, curved, sharp tipped, opaque dark brown. Fourth toe with 29 subdigital lamellae. Claw of fourth toe 2.3 mm, similar to that of fourth finger. Hemipenes everted but lobes inadequately preserved for describing details of ornamentation.

Variation.—Based on an additional six adult males and eight adult females. SVL 69.0–89.0 mm. Head length 14.6–19.5 mm, width 11.6–16.6 mm. Axilla–groin distance 28.7–45.5 mm. Tail length 110.9–142.2 mm. Midbody scales 58–76. Dorsal scales round, not pointed, weakly keeled, subimbricate, 60–74 between occiput and anterior surface of thighs. Some individuals with interstitial granules and/or posteriorly notched scales along posterior flanks. Dorsal head scales 13–18, smooth, variable in size but usually small, some irregular in shape, most convex. Ventrals 98–122. Scales around interparietal 6–9. Three to six enlarged supraoculars. Preocular not divided, not fused to subocular. Temporals 8–10, smooth to weakly keeled. Scales between auditory meatus and antehumeral fold 32–42. Gulars 47–66, smooth, round, imbricate. Supralabials 5–8. Infralabials 4–7. Posterior tip of fourth through sixth supralabial upturned. Scales around nasals 7–8. Nasals always in slight contact with rostral. Internasals 4 (93%) to 5 (7%). Rostral barely visible from above. Scales between rostral and frontal 5–7. Two postrostrals with 4–19 scale organs each. Six to nine lorilabials, fourth, fifth, or sixth through ninth in contact with subocular. Supercilliaries 6–8. Subdigital lamellae on fourth finger 21–24; on fourth toe 25–31. Precloacal pores 2–4 in males, not present in females.

Color in life.—Background color of body dark brown to brown with light brown to beige scales often forming irregular clusters of 2–4 scales on trunk (especially in the dorsolateral field) giving the appearance of faint spots (Fig. 2). Small, black (≤1 scale in size) marks also dispersed over the dorsum. Rarely, black scales congregate posteriorly forming an irregular rectangle-shaped black field mid-dorsally. Head brown to dark brown with diffuse, irregular black marks sometimes reaching the level of the shoulders. Parietal and temporal regions of head dark brown to black. Forelimbs black at the point of insertion with the trunk to the forearms. On forearms, brown flecks increase in density towards toes. Along flanks of trunk and surrounding the insertion of forelimb, black areas are speckled with cream white scales giving the appearance of a dark night sky with stars. Dorsal hind limbs and tail same color as trunk in most individuals. Distal third of tail in a few individuals becomes dark brown to black dorsally. Ventrally light to charcoal gray with irregular darker gray markings scattered on belly and tail. Throat usually lighter gray than ventral torso. Cloacal region, lower belly, ventral thighs, and ventral base of tail with crimson red coloration in females (pregnant or recently spent). Males of this species also exhibit this ventral coloration (Table 2), although it is usually restricted to the cloacal region and ventral thighs, and the color is generally less vibrant, and sometimes orange yellow rather than crimson red. In adult males, the posterior margins of the ventral thighs are sulfur yellow. Precloacal pores yellow-orange. In one male (ACUNSa 82), the torso is entirely black dorsally from just posterior to the shoulders to the base of the tail. In this individual, the forelimbs are also entirely black to the digits and the hind limbs are black to half the length of the tibia. The melanism on the dorsum of this individual extends to the flanks and most of the belly, but fades slightly to charcoal gray mid-ventrally. In juveniles, the torso is brown with irregular, dark brown transverse bands and lacks the distinct black pigmentation seen in adults. The shoulders of juveniles are dark brown to nearly black, but the black coloration, when present, is not as widely distributed on the arms, suggesting the black-arm coloration may be acquired ontogenetically. Ventrally, juveniles are light gray, almost white, with a few small, diffuse, darker gray markings. Juveniles also lack the red coloration seen in the cloacal region of adults.

Color in preservative.—As in life, overall background color darkens slightly on head, trunk, and ventrally. Red coloration in cloacal region fades to a pale rosy pink after approximately 6 mo in preservative. Precloacal pores fade from yellow orange to cream yellow.

Etymology.—The specific epithet *umbrifer* is derived from the Latin word *umbra* (shade) and the Latin suffix *-ifer* (from the verb *fero,* meaning to carry or bear). The literal translation "shade bearer" refers to the distinctly black upper arms and shoulders that are distinguishing characteristics of this species (Fig. 2).

Distribution.—*Liolaemus umbrifer* is known primarily from the type locality (Fig. 3): Quebrada de Randolfo, along Ruta Provincial 43, Departamento Antofagasta, Catamarca, Argentina (26° 51.456′ S, 66° 44.804′ W; 3192 m). Two additional specimens were collected 2 km southeast of Peña Fria on Ruta Provincial 43, 32 km northwest of the type locality (26° 43.19′ S, 66° 57.66′ W; 3487 m). Aside from the recent discovery of a population of *L. elongatus* (Avila and Lobo, 1999; but see Discussion), *L. umbrifer* and *L. capillitas* are the only members of the *elongatus* group known from Catamarca Province. Quebrada Randolfo lies along the northern limit of the drainage of the Río El Bolsón and west of the Sierra Chango Real, approximately 70 km (straight line) from the type locality of *L. capillitas* [Mina Capillitas, Departamento Andalgalá, Catamarca; Hulse (1979); Fig. 3]. Although the distance sep-

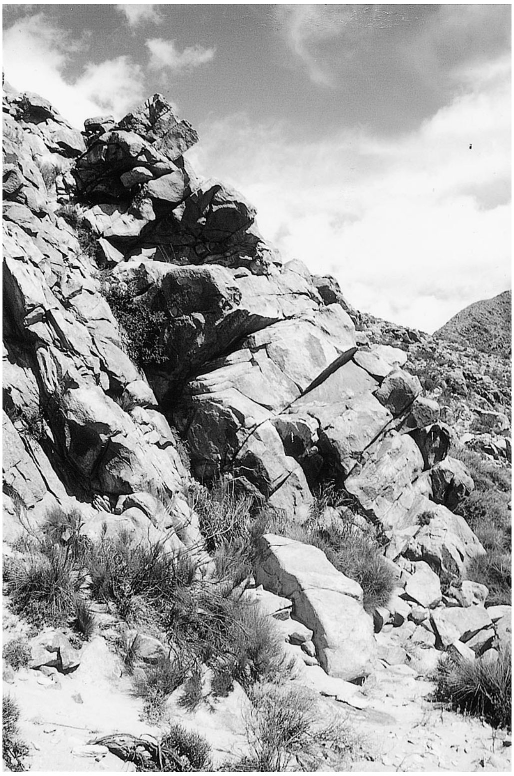

FIG. 6.—Granite hillsides of Quebrada Randolfo, Departamento Antofagasta, Catamarca Province (26° 51.456′ S, 66° 44.804′ W; 3192 m), the type locality of *Liolaemus umbrifer.*

arating these two species is relatively short, there is a vast, low elevation valley (Monte habitat) in the watershed of the Río Belén that lacks suitable habitat and runs in a southwest–northeast direction between the mountain ranges separating *L. capillitas* and *L. umbrifer.*

Natural history.—Specimens of *L. umbrifer* were most commonly encountered basking along the steep, rocky hillsides of Quebrada Randolfo just below the road cut of Ruta Provincial 43 (Fig. 6). The habitat at the type locality (approximately 3500 m) is characterized as Puna (Burkart et al., 1999; Cabrera and Willink, 1980). Dominant plant species include the spiny shrub *Adesmia,* the bunch grass *Festuca, Senecio* sp. (Asteraceae), lupines, and additional unidentified spiny shrubs to 1-m high. Large outcrops of light gray, brown, maroon, or black granite boulders cover the sides of the gorge. These rocky hillsides provide ample habitat for *L. umbrifer,* which are agile saxicolous lizards that, when pursued, move quickly from boulder to boulder or retreat temporarily into crevices or under large rocks. Body temperatures of surface-active adults (n = 9) collected in the afternoon (1215–1445) ranged from 31.2–35.1 C ($\bar{x}$ = 33.1 C, SD = 1.4). At the type locality, *L. umbrifer* is syntopic with *Phymaturus antofagastensis* and sympatric with an undescribed species belonging to the *L. andinus* group that lives among large *Adesmia* shrubs in the wind-blown sand dunes at the bottom of the gorge. Two additional specimens of *L. umbrifer* were found basking in the late afternoon (approximately 1800) sun on small, black, basaltic rocks (approximately 0.5 × 0.3 × 0.3 m) along Ruta Provincial 43 in a region of rolling hills covered with small pebbles, *Adesmia,* and sparse clumps of *Festuca* some 32 km (by road) northwest of the type locality.

We were unable to determine the reproductive mode of *L. umbrifer* because the lizards were collected in late summer, past the time when other members of the *elongatus* group are known to give birth (Hulse, 1979; Ibargüengoytía and Cussac, 1998). However, because *L. umbrifer* lives at relatively high elevation (approximately 3200–3500 m) and because its closest relatives are viviparous, we predict that this species is also live bearing. Most of the adult female *L. umbrifer* we collected in mid-January, although no longer pregnant, exhibited pregnant-female coloration as described above. Interestingly, males of this species also exhibit this ventral coloration (Table 2), although the color was generally less vibrant and appeared to be less widely distributed ventrally.

Feces produced by *L. umbrifer* (n = 11) within 3 d of capture contained the remains of insects and, occasionally, parts of flowers (probably *Senecio* sp.).

DISCUSSION

Distribution of pregnant-female coloration.—A number of *Liolaemus* exhibit gravid- or pregnant-female coloration (e.g., Etheridge, 2000; R. E. Espinoza and F.

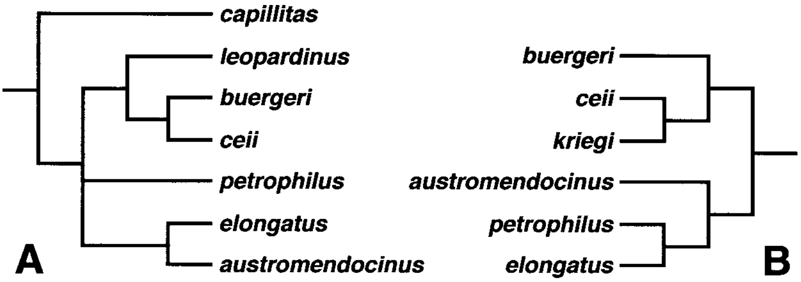

FIG. 7.—Phylogenetic affinities of the *elongatus* group following (A) the molecular phylogeny of Schulte et al. (2000) and (B) Cei (1975). There is much congruence between the hypothesized relationships despite their different data sources (mitochondrial DNA versus blood serum, respectively) and methods of analysis (cladistic versus phenetic, respectively). However, the tree of Schulte et al. (2000) has members of the *kriegi* group [*L. buergeri, L. ceii,* and *L. kriegi*; sensu Cei (1986)] nested within the *elongatus* group and posits different relationships among *L. austromendocinus, L. elongatus,* and *L. petrophilus* than that of Cei (1975). See text for further discussion.

Lobo, personal observation; Lobo and Espinoza, 1999). In most species, this consists of bright yellow to orange or salmon color along the sides of the head, throat, and neck, which sometimes extends along the flanks or belly. In members of the northernmost clade of the *elongatus* group, this color consists of a patch of crimson red in the cloacal region that extends to the lower belly and, in some species, along the thighs and onto the proximal quarter of the tail. Within this group, this coloration is known from pregnant and recently spent female *L. capillitas* (Hulse, 1979; F. Lobo and R. E. Espinoza, personal observation), recently spent female *L. dicktracyi* (described above), males and recently spent females of *L. umbrifer* (described above), and suspected but not confirmed for pregnant and recently spent female *L. heliodermis* (Table 2). Additionally, this coloration was recently observed in male and pregnant female *L. buergeri* (M. Christie, personal communication; F. Lobo and R. E. Espinoza, personal observation), a species that may be nested within the *elongatus* group (Schulte et al., 2000; and see below). When we collected *L. dicktracyi* and *L. umbrifer,* females were no longer pregnant but still exhibited this coloration. We hypothesized that, owing to the timing of reproduction among members of the *elongatus* group (Hulse, 1979; Ibargüengoytía and Cussac, 1998; F. Lobo and R. E. Espinoza, unpublished data), the females were collected soon after parturition and simply retained the coloration for several days thereafter as is typical of *L. capillitas* (F. Lobo and R. E. Espinoza, personal observation) and other iguanians (Cooper and Greenberg, 1992; Cooper and McGuire, 1993). However, the presence of this trait in male *L. umbrifer* poses either an exception or an interesting challenge to linking this coloration with pregnancy. Moreover, it is not known how, or even whether, this coloration is used for communication among species of *Liolaemus.* In other iguanian lizards, gravid-female coloration is usually distributed along the flanks, head, or neck and is thought to provide a visual signal which, when coupled with aggressive behavior, deters males from attempting to court or copulate with females (Cooper and Greenberg, 1992). In contrast, the ventral distribution of this coloration seems less conspicuous in members of the northern radiation of the *elongatus* group, which would suggest the need for specialized behaviors associated with exhibiting the red patches. Behavioral studies are sorely needed to test these predictions.

Phylogenetic relationships within the elongatus *group.*—A recent cladistic analysis of mitochondrial DNA gene sequences for 60 species of *Liolaemus* (Schulte et al., 2000) found strong bootstrap support (100%) for a clade including the *elongatus* group members (sensu Cei, 1974, 1986) plus *L. buergeri, L. ceii,* and *L. leopardinus* (Fig. 7A). In a phenetic analysis based on serological evidence, Cei (1975) also considered the *elongatus* group (which, at that time, consisted only of *L. austromendocinus, L. elongatus,* and *L.* [*elongatus*] *petrophilus*) to be closely related to the *kriegi* group (see also Cei, 1986), which includes *L. buergeri, L. ceii,* and *L. kriegi* (Fig. 7B). It is worth noting that these two hypotheses of relationships are remarkably similar despite the difference in the kinds of data used and types of analyses conducted. The only incongruence between the hypotheses that cannot be attributed to differences in taxon sampling lies in the determination of the sister species of *L. elongatus.* Cei (1975) allied this species with *L.* [*elongatus*] *petrophilus* (Fig. 7B), whereas Schulte et al. (2000) found *L. elongatus* to be most closely related to *L. austromendocinus* (bootstrap 100%; Fig. 7A). However, the *L. elongatus* used in the Schulte et al. (2000) analysis was collected near Uspallata, in Mendoza Province, and the type locality of this species is Chubut Province (although not precisely identified; Koslowsky, 1896), at least 1300 km south. Other researchers have noted the variability in size, squamation, body patterns, and color among populations of the widely distributed *L. elongatus* (L. Avila, personal communication; Cei, 1986; R. E. Espinoza and F. Lobo, unpublished data; Espinoza et al., 2000; Quatrini et al., 1998). Some of these populations are allopatric and readily diagnosable; in fact, our preliminary examination of specimens assigned to *L. elongatus* suggests that there are at least three cryptic species within the complex (R. E. Espinoza and F. Lobo, unpublished data). Hence, the taxon in the tree of Schulte et al. (2000) most likely represents an undescribed species rather than *L. elongatus* sensu stricto. Indeed, recent morphological and molecular analyses, which include specimens of *L. elongatus* from Chubut, support Cei's (1975) sister grouping of *L. elongatus* and *L. petrophilus* (R. E. Espinoza and F. Lobo, unpublished data).

Schulte et al. (2000) also identified *L. capillitas* as the sister taxon to the remaining members of their more inclusive *elongatus* group (i.e., including the *kriegi* group; Fig. 7A). Thus, if *L. dicktracyi* and *L. umbrifer* form a clade with *L. capillitas* and *L. heliodermis,* as is supported by our morphological and molecular evidence (R. E. Espinoza and F. Lobo, unpublished data), then this northern radiation constitutes the sister lineage of the more inclusive *elongatus* group. Additionally, *L. leopardinus,* a species from moderate elevations (1800–2750 m) in north central Chile (33–34° S) was placed as the outgroup of *L. buergeri* + *L. ceii* [the *kriegi* group of Cei (1986), less *L. kriegi*] (Schulte et al., 2000; Fig. 7A). Given that *L. ramonensis* and *L. valdesianus* are both morphologically similar to, and were originally described as, subspecies of *L. leopardinus* (Hellmich, 1950; Müller and Hellmich, 1932), future analyses of the *elongatus* group should consider these taxa as well. Finally, *L. coeruleus, L. cristiani, L. isabelae,* and *L. neuquensis* share a number of morphological traits in common with species in the *elongatus* group (e.g., elongate body and long tail, small body scales, lack of precloacal pores) and may, therefore, represent additional members of this lineage (Lobo, 2001; F. Lobo, unpublished data; Videla and Cei, 1998). Determining the taxonomic status of the various morphs of *L. "elongatus"* and the phylogenetic relationships among the numerous putative members of the *elongatus* group are the subjects of detailed molecular and morphological analysis currently under investigation (L. Avila, personal communication; R. E. Espinoza and F. Lobo, unpublished data).

RESUMEN

El grupo de especies de *Liolaemus elongatus* actualmente incluye ocho especies (incluyendo las especies que aquí se describen) de lagartos de mediano tamaño, con colas largas, y primariamente saxícolas. Los miembros de este linaje se distribuyen desde el noroeste de Argentina hacia el sur, a lo largo de la Cordillera de los Andes hasta la estepa Patagónica (27–44° S) y sobre un amplio rango de elevación (350–3900 m). Aquí nosotros describimos dos especies nuevas que pertenecen a la radiación norteña del grupo *elongatus.* Los cua-

tro miembros actualmente reconocidos de este subclado norteño (incluyendo las dos especies que aquí se describen) se diferencian de los otros miembros del grupo *elongatus,* por contar con un menor número de escamas alrededor del cuerpo, cabezas marrón a negras, y por carecer de los distintos patrones dorsales de cola o cuerpo encontrados en adultos de otras especies que pertenecen al grupo *elongatus.* Además, las hembras que recientemente han parido exponen color rojo vivo en la región cloacal, una característica única conocida para miembros de este linaje norteño y *L. buergeri.* La primera especie nueva que se describe, *L. dicktracyi,* de la Sierra de Famatina de la Provincia de La Rioja, difiere de todo los otros miembros del grupo *elongatus* en varios caracteres merísticos y en su coloración dorsal única: posee cabeza, hombros y cola negros, y el torso y extremidades posteriores azules. La segunda de las especies nuevas que se describen, *L. umbrifer* de la Quebrada de Randolfo en el noreste de la Provincia de Catamarca, es morfológicamente parecido a *L. capillitas,* pero difiere de ésta y otras especies en el grupo *elongatus* en varios caracteres merísticos, la presencia de brazos y hombros negros, y en la coloración roja viva de la región cloacal en ambos, machos y hembras. La historia natural de ambas especies nuevas es similar en muchos aspectos a *L. capillitas* y *L. heliodermis* debido a sus afinidades filogenéticas de los miembros de este subclado dentro del grupo *elongatus.* Finalmente, nosotros proveemos comparaciones de recientes hipótesis filogenéticas y discutimos el contenido del grupo *elongatus.*

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Appendix I

Specimens Examined

Liolaemus austromendocinus (10).—ARGENTINA: Provincia de Mendoza: Departamento Malargüe, on Ruta Nacional 40, 47 km S Malargüe (35° 46′ 10.4″ S, 69° 38′ 46.8″ W; 1920 m): FML 3432 (1–7); Laguna Niña Encantada (35° 09′ 37.4″ S, 69° 52′ 09.0″ W; 1680 m): FML 7189–91 (erroneously identified as *L. thermarum* in Espinoza et al. [2000]).

L. capillitas (16).—ARGENTINA: Provincia de Catamarca: Departamento Andalgalá, Mina Capillitas (3000–3600 m): FML 1229 (1, 2, 4, 6, 7, 11, 12, 16, 18–21); Morro El Arenal (El Ingenio) (3100 m): FML 2029 (1–4).

L. dicktracyi (10).—ARGENTINA: Provincia de La Rioja: Departamento Famatina, 26.5 km W of Famatina on road to Cueva de Perez, Portezuelo Blanco (28° 54′ 30″ S, 67° 41′ 30″ W; 2800 m): FML 9928 (holotype); CM 147716–17 (paratypes); FML 9929–33 (paratypes); MCN 461–62 (paratypes).

L. elongatus (10).—ARGENTINA: Provincia de Neuquén: Departamento Alumine, along Arroyo Rucaco, SE end of Lago Choroi, 3.5 km E and 6.5 km N Cerro Ruca Choroi (39.12° S, 71.17° W; 1250 m): MVZ 188764. Provincia de Río Negro: Departamento Bariloche, ridge above Refugio Neumeyer, 15 km S Bariloche (41.26° S, 71.31° W; 1600 m): MVZ 188781. Departamento Ñorquinco, along Río Chenqueniyen, 10 km E and 3 km S Cerro Pico Quemada (41.53° S, 71.00° W; 1150 m): MVZ 188732–33, 188739; rimrock, 4 km S and 1 km E Alto del Escorial (41.59° S, 70.76° W; 1100 m): MVZ 188743; Laguna de Los Junco, Escorial de Chenqueniyen, 5 km N Alto de Escorial (41.51° S, 70.78° W; 1150 m): MVZ 188758. Departamento Pilcaniyeu, 1.5 km N Estación Perito Moreno, approximately 28 km ENE Bariloche (41.05° S, 71.01° W; 900 m): MVZ 180069; Cañadon Bonito, 23 km NE Pilcaniyeu (40.98° S, 70.42° W): MVZ 188727–28.

L. heliodermis (3).—ARGENTINA: Provincia de Tucumán: Departamento Tafí del Valle, Ruta Provincial 307, approximately 32 km (by road) from Tafí del Valle at km marker 95 (26° 40.82′ S, 65° 48.74′ W; 2820 m): FML 6006–07 (paratypes), FML 7196 (holotype).

L. petrophilus (3).—ARGENTINA: Provincia de Chubut: Ruta Nacional 25, 10 km S Puesto Espinal (350 m): FML 793 (1–3).

L. umbrifer (16).—ARGENTINA: Provincia de Catamarca: Departamento Antofagasta, Quebrada de Randolfo, Ruta Provincial 43, 60.3 km north of intersection of Ruta Provincial 4 and Ruta Provincial 43, 166 km southeast of Antofagasta de la Sierra (26° 51.456′ S, 66° 44.804′ W; 3192 m): FML 9934 (holotype), FML 9935–45 (paratypes), MCN 463–64 (paratypes); 2 km southeast Peña Fria, Ruta Provincial 43, 32 km northwest of Quebrada de Randolfo, 105 km southeast of Antofagasta de la Sierra (26° 43.19′ S, 66° 57.66′ W; 3487 m): CM 147714–15 (paratypes).