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Author(s): Cristián S. Abdala , Diego Baldo , Ricardo A. Juárez , and Robert E. Espinoza

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# The First Parthenogenetic Pleurodont Iguanian: A New All-female *Liolaemus* (Squamata: Liolaemidae) from Western Argentina

Cristián S. Abdala<sup>1</sup>, Diego Baldo<sup>2</sup>, Ricardo A. Juárez<sup>3</sup>, and Robert E. Espinoza<sup>4</sup>

**Vertebrate taxa with entirely unisexual populations are composed of females that reproduce without fertilization and are generally of hybrid origin. At least 23 vertebrate families have unisexual lineages. Within squamate reptiles, >40 uniparental species have been described from five major lineages: acrodont iguanians, Gekkota, Serpentes, Scincomorpha, and Varanidae. Pleurodont iguanians include >1100 species, all of which have gonochoristic reproduction. Here we report the discovery of a new unisexual lizard from the liolaemid genus *Liolaemus*, a species-rich (~260 species) clade distributed over most of southern South American. The new species, *Liolaemus parthenos*, is the only known all-female triploid pleurodont iguanian. The structural chromosome heteromorphisms of the karyotypes support the hypothesis that *L. parthenos* is the product of a hybrid origin. Based on morphology, the new species is assignable to the *L. boulengeri* group (*sensu* Abdala, 2007), and phylogenetic analyses of mitochondrial DNA indicate that *L. parthenos* is nested within *L. darwinii*, suggesting that the latter is the maternal ancestor of this species. Additional data are needed to identify the patrilineal ancestor.**

**Los taxones de vertebrados con poblaciones totalmente unisexuales se componen de hembras que se reproducen sin fecundación y son generalmente de origen híbrido. Al menos 23 familias de vertebrados tienen linajes unisexuales. Dentro de los reptiles escamosos, se han descrito >40 especies uniparentales pertenecientes a cinco grandes linajes: iguanios acrodontes, Gekkota, Serpentes, Scincomorpha y Varanidae. Los iguanios pleurodontes incluyen >1100 especies, las cuales todas tienen reproducción gonocórica. Aquí presentamos el descubrimiento de un nuevo lagarto unisexual del género *Liolaemus*, clado con gran riqueza específica (~260 especies) distribuido en casi todo el sur de América del Sur. La nueva especie, *Liolaemus parthenos*, es la única conocida con hembras triploides entre los iguanios pleurodontes. Los heteromorfismos cromosómicos estructurales de sus cariotipos apoyan la hipótesis de que *L. parthenos* es producto de un origen híbrido. Basado en la morfología, la nueva especie es asignable al grupo de *L. boulengeri* (*sensu* Abdala, 2007) y el análisis filogenético de ADN mitocondrial indica que *L. parthenos* está anidada dentro de *L. darwinii*, lo que sugiere que este último es el antepasado matrilineal de esta especie. Se necesitan más datos para identificar su antepasado patrilineal.**

**O**F the more than 67,000 recognized species of vertebrates, unisexual taxa that reproduce without fertilization are very rare and generally of hybrid origin. Although it is estimated that only 0.1% of vertebrate species are unisexual, this mode of reproduction is phylogenetically widespread, particularly among fishes, amphibians, and reptiles (Avisé, 2008; Neaves and Baumann, 2011). Squamate reptiles (lizards and snakes) provide the only known examples of unisexual vertebrates that reproduce with all-female clones via parthenogenesis—a process in which females reproduce without males or male gametes (Avisé, 2008). Of the more than 6000 species of lizards currently recognized (Uetz and Hošek, 2015), <1% are known to be parthenogenetic (Dawley, 1989). Most parthenogenetic lizard species or populations occur within two major lizard clades: Gekkota (solely in Gekkonidae) and Scincomorpha (reported in: Gymnophthalmidae, Lacertidae, Scincidae, Teiidae, and Xantusiidae; Vrijenhoek et al., 1989; Adams et al., 2003; Malysheva et al., 2006; Avisé, 2008; Kearney et al., 2009); however, isolated cases of facultative parthenogenesis have been reported in other lineages of captive squamates (reviewed by Avisé, 2008; Lampert, 2008; Kearney et al., 2009; Booth et al., 2011; Neaves and Baumann, 2011).

Unlike Gekkota and Scincomorpha, few parthenogenetic species have been reported from the large lizard clade Iguania. Iguania includes two well-defined groups characterized by dental implantation: Acrodonta (Agamidae and Chamaeleonidae) and Pleurodonta (12 families, *sensu* Townsend et al., 2011; Wiens et al., 2012; Pyron et al., 2013; Reeder et al., 2015). Within Acrodonta, a small number of agamid and chamaeleonid species have been reported to be parthenogenetic (Malysheva et al., 2006; Kearney et al., 2009; Grismer and Grismer, 2010; Grismer et al., 2014). Within the pleurodont iguanians, unisexuality is confined to a single incident of presumed facultative parthenogenesis in a long-term captive liolaemid, *Phymaturus patagonicus* (Chiszar et al., 1999). However, the alternative hypothesis of extended sperm retention could not be rejected for this case. Pleurodonta is a diverse group composed of 12 families and more than 1100 species (Uetz and Hošek, 2015). One of the pleurodont families, Liolaemidae, includes the second most species-rich genus of lizards in the world (*Liolaemus*) with nearly 260 currently recognized species (Abdala and Quinteros, 2014). *Liolaemus* has one of the broadest latitudinal and elevational distributions of any lizard genus and occupies most arid and semi-arid habitats in southern South America (Etheridge, 1995; Lobo et al., 2010). Here we

<sup>1</sup> Instituto de Herpetología, Fundación Miguel Lillo (CONICET) and Universidad Nacional de Tucumán, Miguel Lillo 251, 4000 Tucumán, Argentina; Email: samiryjazmin@gmail.com.

<sup>2</sup> Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical (CONICET-UNaM), Facultad de Ciencias Exactas, Universidad Nacional de Misiones, Félix de Azara 1552, CPA N3300LQF, Posadas, Misiones, Argentina; Email: diegobaldo@gmail.com.

<sup>3</sup> Laboratorio de Zoología, Museo de Ciencias Naturales e Antropología, Antonio Serrano, Gardel 62, 3100 Entre Ríos, Argentina; Email: ricardoj73@hotmail.com.

<sup>4</sup> Department of Biology, California State University, Northridge, Northridge, California 91330-8303; Email: robert.e.espinoza@csun.edu. Send reprint requests to this address.

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describe a new species of *Liolaemus* from western Argentina that all evidence indicates is unisexual and parthenogenetic.

We had four principal goals for this study: (1) describe a new parthenogenetic species in the lizard genus *Liolaemus*, which is the first known unisexual species of pleurodont iguanian; (2) characterize the karyotype of this new species; (3) provide a phylogenetic hypothesis for the new species and closely related congeners to determine its phylogenetic position and attempt to identify its maternal ancestor; and (4) propose a hypothesis for the origin of unisexuality in the new species based on morphological, cytogenetic, and DNA-sequence data.

## MATERIALS AND METHODS

**Morphology.**—For the description of the new species, we scored morphological character states of specimens of the new species and 60 of the 64 currently recognized species belonging to the *L. boulengeri* group (*sensu* Abdala, 2007). In total, we examined more than 1500 specimens (see Material Examined). For the six species unavailable for study (*L. arambarensis*, *L. azarai*, *L. cinereus*, *L. enigmaticus*, *L. rabinoi*, and *L. riojanus*), we relied on information from their type descriptions and data from subsequent taxonomic revisions. We studied characters traditionally included in taxonomic studies of *Liolaemus* lizards, as described in detail by Etheridge (1995) and Abdala (2003, 2005, 2007). Terminology for the description of squamation follows Smith (1946) and neck-fold terminology is after Frost (1992). Terminology for body patterns and coloration follows Lobo and Espinoza (1999) and Abdala (2007). When characters were bilateral, data were taken from the right side of the specimen. Scale characteristics and counts were made with the aid of a stereomicroscope (10–40 $\times$ ) and measurements were made with digital calipers ( $\pm 0.05$  mm). Colors in life were based on observations made in the field and from digital photographs taken immediately after capture. Specimens of the new species have been deposited in the following Argentine collections: Fundación Miguel Lillo, Tucumán (FML), Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical, Misiones (LGE), Museo de Historia Natural de San Rafael, Mendoza (MHNSR), and Museo de La Plata (MLP, including MLP.S).

**Natural history.**—We made field observations and collected lizards assignable to the new species at or near the type locality (see below) on 24 occasions over an 18-year period (1995–2012). Over this period, 26 individuals spent an estimated 650 combined person hours searching for and collecting lizards. All searches took place during the activity season (austral summer), during daylight hours, and under favorable conditions for lizard activity (i.e., air temperatures  $> 25^{\circ}\text{C}$ ; low to moderate wind and cloud cover).

We collected environmental and field body temperatures ( $T_b$ ) of active lizards on 11 February 1995 from 1842–1915 hr.  $T_b$  was measured with a digital thermometer (Omega 871A, type-K thermocouple; Stamford, CT). Lizards were handled by their head and one of their limbs to minimize heat exchange with the investigator and a 30-AWG (0.5 mm diameter, tip polished smooth) thermocouple was inserted  $\sim 2$  mm into the cloaca. Only  $T_b$ s recorded within 10 s of the time the lizard was captured were included in analyses. Lizard body sizes (snout–vent length, SVL) were measured with a transparent ruler following  $T_b$  measurement.

**Cytogenetic analyses.**—Chromosome preparations were obtained from ten adults of the new species (see Material Examined) from samples of bone marrow and intestines after the specimens were treated with *in vivo* injections of colchicine and processed following methods described by Schmid et al. (2010). Chromosome number and morphology were studied on conventional stained preparations with Giemsa solution (10%). We followed the methods of Howell and Black (1980) for silver-nucleolus organizer region (Ag-NOR) staining. Images were observed under an Olympus BX50F-3 photomicroscope and photomicrographs were taken with a Sony ExwaveHAD videocamera. Karyotypes were arranged and chromosomes were classified following the methods of Levan et al. (1964). We followed common nomenclatural conventions for describing the chromosomes of pleurodont iguanian lizards (Gorman et al., 1967; Paull et al., 1976; Bickham, 1984), where  $2n$  and  $3n$  were used to designate diploid and triploid karyotypes, respectively, and chromosomes were characterized as macro- (M) or micro-chromosomes (m) based on their size and morphology.

**Phylogenetic analyses.**—Sequences used for the molecular analyses were obtained from GenBank and new samples using previously published protocols for genomic DNA extraction, amplification, and sequencing reactions (Schulte et al., 2000). Briefly, DNA was extracted from liver or thigh muscle and mitochondrial DNA (mtDNA) was obtained for 34 taxa of *Liolaemus*, focusing on taxa that have been shown to be closely related to the new species in previous analyses (reviewed in Abdala, 2007; and see Results). For phylogenetic analysis, molecular data representing the coding regions ND1, tRNAIle, tRNAGln, tRNAMet, ND2, tRNATrp, tRNAAla, tRNAAsn, tRNACys, tRNATyr, and COI were aligned as described by Schulte et al. (2000), resulting in 1776 characters.

Trees were reconstructed from aligned sequences using Bayesian inference and maximum parsimony. For the Bayesian analyses, we followed the methods described by Schulte (2013), which are summarized below. We used jModelTest v. 2.1.6 (Posada, 2008) and Akaike information criterion (AIC) to simultaneously select the best-fit nucleotide substitution model and partitioning scheme. Phylogenetic analyses were performed using MrBayes v. 3.2.0 (Ronquist et al., 2011) and consisted of two independent runs of 20 million generations each, starting with random trees and ten Markov chains (one cold), which were sampled every 1000 generations. To ensure that Bayesian analyses reached stationarity, the first 5000 trees were discarded as “burn-in.” We assessed stationarity by plotting the  $-\ln L$  per generation in Tracer v. 1.5 (Rambaut and Drummond, 2007) and from the mean standard deviation of split frequencies from MrBayes. If the two runs converged on the same tree, the mean standard deviation of split frequencies would be expected to approach zero. After we determined that each run appeared to reach stationarity, the 30,000 trees (15,000 per run after burn-in) were used to calculate Bayesian credibility values (BC) for each node in a 50% majority-rule consensus tree. Clades with  $\text{BC} \geq 95\%$  were considered strongly supported, although we acknowledge that BC may overestimate nodal confidence (Alfaro et al., 2003; Douady et al., 2003; Lewis et al., 2005).

Maximum parsimony, which reconstructs the shortest tree(s) with the least homoplasy, was implemented in TNT v. 1.1 (Goloboff et al., 2003). A heuristic search with tree bisection reconnection (TBR) was applied to the character

matrix with equal weighting of characters and nonadditive steps. The consistency index (CI; Kluge and Farris, 1969) and retention index (RI) were calculated for each tree(s). Branch support was estimated by bootstrapping and jackknifing (deletion probability = 36 with 500 replicates) using absolute frequencies.

### *Liolaemus parthenos*, new species

urn:lsid:zoobank.org:act:53CC2C59-2E4D-41AA-8804-462B90ABAEC

Figures 1–5; Table 1

*Liolaemus boulengeri* Cei (1973:464, in part).

*Liolaemus boulengeri* Cei and Roig (1976:71, 87, Map 5, in part).

*Liolaemus boulengeri* Cei and Castro (1978:9, 21, Map 16, in part).

*Liolaemus boulengeri* Cei (1986:220–221, in part).

*Liolaemus boulengeri* Schulte et al. (2000:79, 87; table 1; figs. 4–6).

*Liolaemus* sp. nov. Morando et al. (2004:845; table 1–3; figs. 2, 8).

*Liolaemus* sp. Abdala and Díaz Gómez (2006:29; fig. 3).

*Liolaemus* sp. 3. Abdala (2007:51, 55, 57, 60, 77; figs. 32–36).

*Liolaemus* cf. *darwinii* Pincheira-Donoso et al. (2007:32; fig. 3).

*Liolaemus* cf. *darwinii* Schulte (2013:5; fig. 1).

*Liolaemus* sp. 3 Olave et al. (2014:329, 331; figs. 4, 6).

**Holotype.**—FML 16221, adult female, Argentina, Mendoza Province, San Rafael Department, collected on the dunes next to El Nihuil Dam on Provincial Route 180, 35°2'19.77"S, 68°40'12.60"W, 1305 m, C. Abdala, J. Abdala, and E. Malovini, January 2001 (Fig. 1).

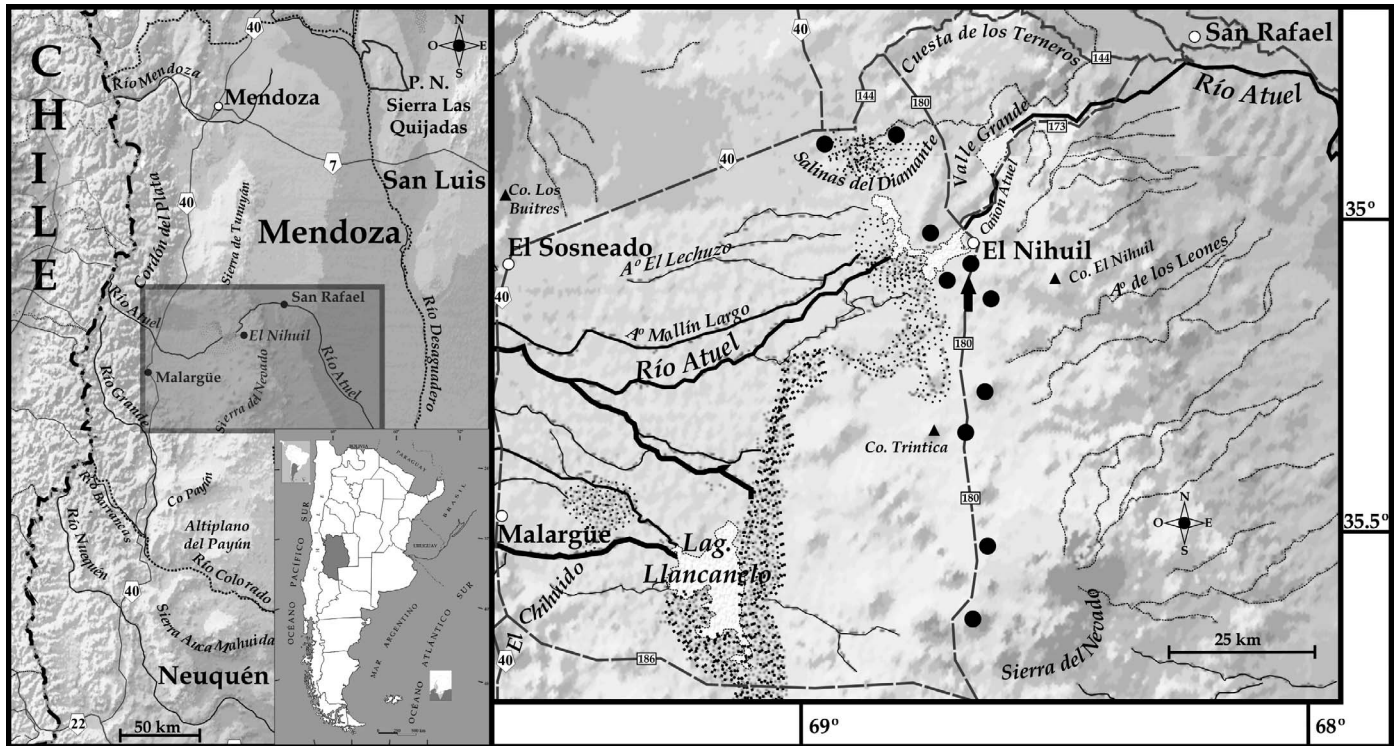
**Paratypes.**—FML 16222–24, same data as holotype; IBAUNC 9772–73, 9775–77, Argentina, Mendoza Province, San Rafael

Department, 10 to 60 km S of El Nihuil, 35°7'0.71"S, 68°41'4.28"W to 35°33'49.47"S, 68°41'15.14"W, 1400–1600 m, 25 November 1973; IBAUNC 11431–35, Argentina, Mendoza Province, San Rafael Department, Pampa del Diamante, 34°54'44.39"S, 68°51'38.58"W, 1400 m, 17 February 1975; MHNSR 78–82, Argentina, Mendoza Province, San Rafael Department, Club de Pescadores, El Nihuil, 35°2'10.54"S, 68°42'33.84"W, 1325 m, 1 January 1975.

**Diagnosis.**—*Liolaemus parthenos* is the only known triploid unisexual iguanian lizard with the karyotype  $3n = 49$  (19M + 30m). The new species is a member of the *L. boulengeri* group (Etheridge, 1995; Abdala, 2007), with which it shares a femoral patch of enlarged scales on the posterior thigh. The *L. boulengeri* group includes the following subclades (Abdala, 2007): *L. anomalus*, *L. darwinii*, *L. wiegmanni*, and *L. melanops* (= *L. telsen* group + *L. goetschi* group), each of which includes several species as described below. Within the *L. boulengeri* group, *L. parthenos* is a member of the *L. darwinii* group (Abdala, 2007), with which it shares the following eight synapomorphies: (1) 14–18 dorsal head scales; (2) 24–28 gulars; (3) tail length/SVL ratio: 1.40–1.65; (4) femur length/SVL ratio: 0.16–0.20; (5) 1–3 differentiated scales along the lower half of the anterior border of the external auditory meatus; (6) weakly developed longitudinal fold; (7) dark line passing vertically through superciliaries, eye, and subocular; and (8) small prescapular spots. *Liolaemus parthenos* can be distinguished from species in the *L. anomalus* group (*L. acostai*, *L. anomalus*, *L. ditadai*, *L. lentus*, *L. millcayac*, *L. pipanaco*, and *L. pseudoanomalus*) because the new species has a tail that is longer than its body, a head that is longer than wide, and lacks both a palpebral “comb” and pterygoid teeth. *Liolaemus parthenos* can be distinguished from species in the *L. wiegmanni* group (*L. arambarensis*, *L. azarai*, *L. cuyumhue*, *L. lutzae*, *L. multimaculatus*, *L. occipitalis*, *L. rabinoi*, *L. riojanus*, *L. salinicola*, *L. scapularis*, and *L. wiegmanni*) because the new species has a single row of lorilabials between the subocular and the supralabials (2–3 rows in members of the *L. wiegmanni* group) and four scales around the mental (6 scales in the *L. wiegmanni* group species). The new species, can be distinguished from species of the *L. goetschi* group (*L. camarones*, *L. canqueli*, *L. casamiquelai*, *L. chehuachekenk*, *L. cuyanus*, *L. dumerili*, *L. fitzingerii*, *L. goetschi*, *L. mapuche*, *L. melanops*, *L. morenoi*, *L. puelche*, *L. rothi*, *L. sagei*, *L. shehuen*, *L. tromen*, and *L. xanthoviridis*) based on its shorter SVL (maximum SVL 63.4 mm vs. 77–106 mm for the aforementioned taxa) and considerably less ventral melanism (except *L. rothi* and *L. sagei*). The new species also lacks the cephalic melanism typical of *L. canqueli* and *L. melanops*. With respect to *L. casamiquelai*, *L. chehuachekenk*, *L. fitzingerii*, *L. morenoi*, *L. tromen*, and *L. xanthoviridis*, the new species lacks the gular and antihumeral melanic collar that is typical of the aforementioned species. *Liolaemus parthenos* is distinct from *L. cuyanus*, *L. goetschi*, *L. josei*, *L. mapuche*, and *L. puelche* because the new species has four scales in contact with the mental, whereas *L. cuyanus* has six scales and *L. goetschi*, *L. josei*, *L. mapuche*, and *L. puelche* have from 4–6 scales in contact with the mental. The new species differs from *L. donosobarrosi* because the former has fewer scales around the midbody (mean = 57.1; range = 53–61 vs. mean = 85.4; range = 79–95, respectively). Also, the new species has a distinct dorsal pattern of quadrangular paravertebral markings, which distinguishes it from *L. rothi*, which has irregular markings that are not quadrangular. The new species also has pre- and postscapular spots that are not present in *L. rothi*.



**Fig. 1.** Dorsal (A) and lateral (B) views of the holotype (FML 16221) of *Liolaemus parthenos*, new species, from the type locality in San Rafael Department, Mendoza Province, Argentina.

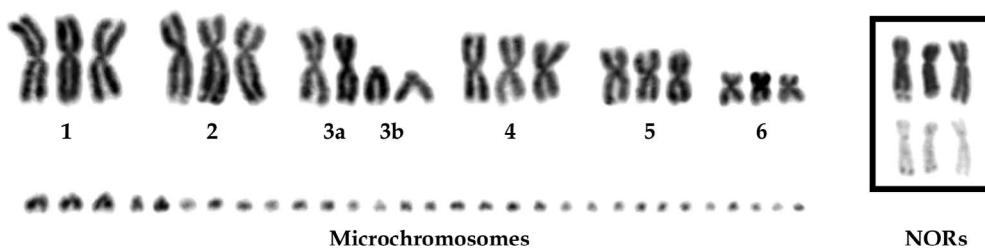


**Fig. 2.** Map showing known localities of *Liolaemus parthenos*, new species (black circles), in San Rafael Department, Mendoza Province, Argentina. Arrow indicates the type locality.

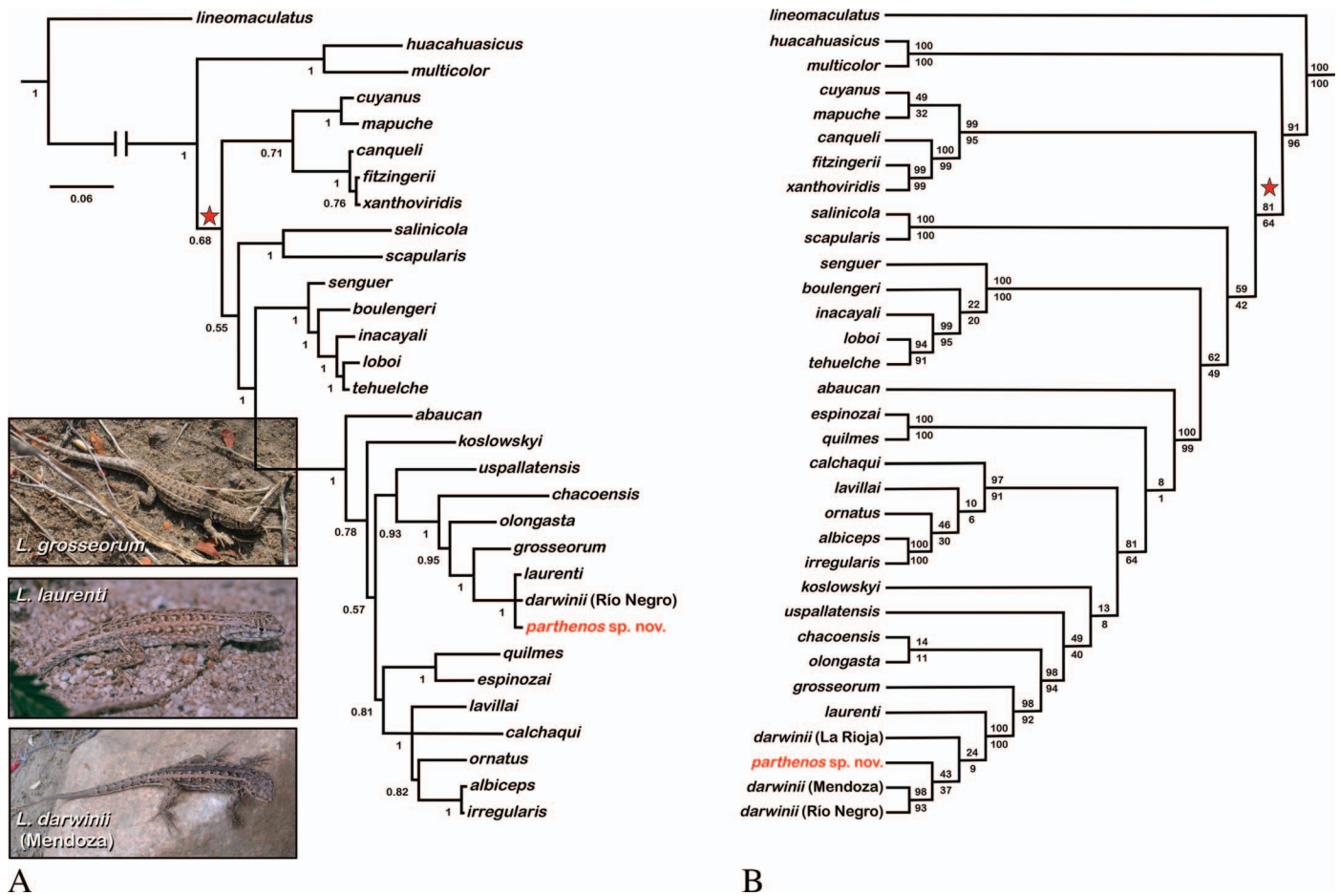
*Liolaemus parthenos* can be distinguished from species in the *L. telsen* group (*L. boulengeri*, *L. hermannunezi*, *L. inacayali*, *L. lobo*, *L. martorii*, *L. purul*, *L. senguer*, *L. sitesi*, and *L. tehuelche*) by its lack of gular melanism and dorsolateral bands that are more well defined. The new species differs from *L. telsen* because the former has less gular melanism, paravertebral markings are more well defined, well-defined dorsolateral bands, and fewer middorsal scales on the trunk (counted from occiput to anterior thigh: mean = 65; range = 61–68 vs. mean = 88.8; range = 83–96, respectively). The new species also differs from *L. boulengeri*, *L. hermannunezi*, *L. lobo*, *L. martorii*, *L. purul*, and *L. tehuelche* because the former has less conspicuous scapular spots. Within the *L. darwini* group, *L. parthenos* is the only species with strongly cuspidate coronas and distally expanded cheek teeth, as well as a unique color pattern for the group. The new species can be further distinguished from members of the *L. darwini* group (*L. abaucan*, *L. albiceps*, *L. calchaqui*, *L. chacoensis*, *L. cinereus*, *L. crepuscularis*, *L. darwini*, *L. diaguaita*, *L. espinozai*, *L. grosseorum*, *L. irregularis*, *L. koslowskyi*, *L. laurenti*, *L. lavillai*, *L. montanezi*, *L. olongasta*, *L. ornatus*, *L. pacha*, *L. quilmes*, and *L. uspallatensis*) because *L. parthenos* has a unique pattern of large dark brown or black quadrangular or subquadrangular paravertebral and lateral markings, white dorsolateral stripes, and a white abdomen with small dark spots. *Liolaemus*

*parthenos* can be further distinguished from *L. albiceps*, *L. calchaqui*, *L. crepuscularis*, *L. irregularis*, *L. lavillai*, and *L. ornatus* because females of the latter three species possess preloacal pores and adult *L. albiceps* and *L. irregularis* are considerably larger than *L. parthenos* (*L. parthenos*: maximum SVL 63.4 mm vs. 82.5–86.1 mm, respectively). Finally, *L. parthenos* can be differentiated from *L. darwini* because the new species lacks an antehumeral arch and abdominal and femoral melanism.

**Description of holotype.**—Adult female (Fig. 1). SVL: 59.8 mm. Tail complete, not regenerated: 92.7 mm. Rostral surrounded by 6 scales. Nasal dorsolateral in orientation. Supraoculars: 8. Interparietal smaller than parietals. Lorilabials: 7. Supralabials: 8. Mental surrounded by 4 scales. Infralabials: 5. Temporals: 8, not keeled. Posterior teeth with expanded cusps. Anterior border of auditory meatus with one differentiated scale. Snout blunt in lateral view. Midbody scales: 58. Dorsal scales: 68 from occiput to anterior thigh, laminar, imbricate, and keeled. Lateral neck folds well developed. Gulars: 27. Ventrals: in 21 rows, imbricate, same size as dorsals. Infratarsals and infracarpals imbricate and trifold. Femoral patch well developed. No preloacal pores. Head light brown with two rows of quadrangular dark brown paravertebral marks with white posterior margins. Back-



**Fig. 3.** Karyotype (left) and pair carrier of nucleolus organizer regions (right) for *Liolaemus parthenos*, new species.



**Fig. 4.** Phylogenetic hypotheses for 31 species of *Liolaemus* emphasizing species in the *L. boulengeri* group (stars) based on 1776 aligned base pairs of mtDNA sequence data. (A) Phylogeny based on Bayesian inference showing branch lengths proportional to evolutionary change and branch support represented as Bayesian credibility values below each node. (B) Cladogram based on a maximum parsimony analysis showing bootstrap and jackknife values above and below each clade, respectively. Retention index (RI): 0.796, consistency index (CI): 0.490. Photos show species of *Liolaemus* inferred by both analyses to be closely related to *L. parthenos*, new species.

ground of vertebral region dark brown with four lateral markings of same color. Anterior and posterior limbs same color as dorsum. Ventrally, throat variegated with dark brown or black spots; spot density increases posteriorly toward chest, abdomen, limbs, and tail.

**Measurements of holotype.**—Head 1.2 times longer (11.9 mm) than wide (9.6 mm). Head height: 8.2 mm. Eye diameter: 2.9 mm. Subocular: 3.7 mm. Auditory meatus height: 2.2 mm; width: 1.8 mm. Torso length: 26.8 mm; width: 12.9 mm. Thigh length: 9.9 mm. Upper arm length: 8.2 mm; width: 2.1 mm. Forearm length: 8.3 mm. Hand length: 9.2 mm. Tail length: 92.7 mm.

**Variation.**—Data from 70 females, unless otherwise noted. Mental in contact with four scales. Infralabials: 5–6. Lorilabials: 6–7, in one row. Interparietal smaller than parietal. Temporals: 8–12. Auditory meatus with 1–3 scales on anterior edge and 0–2 on posterior edge. Neck folds well developed. Gulars: 23–28. Head narrow, longer (mean = 12.1 mm) than wide (mean = 9.4 mm). Neck narrower than head and trunk. Body slender, SVL 36.1–63.4 mm (mean = 56.7 mm). Scales around midbody: 53–61 (mean = 57.1). Dorsal scales between occiput and anterior thigh: 61–68 (mean = 65.0). Dorsal scales laminar, keeled, and imbricate. Infratarsals and infracarpals with imbricate, trifid scales. Femoral

patch with 23–30 cone-shaped, mucronate scales. Ventrals: 91–105 (mean = 97.6), larger than dorsals. Precloacal pores absent. Complete tail: 64.3–92.7 mm long ( $n = 48$ ; mean = 83.3 mm); 1.4–1.6 times longer than SVL.

**Color variation in life.**—Dorsal head light brown or gray with small black, irregularly distributed scales. Background dorsal color of body usually light brown, but light gray specimens not uncommon. Paravertebral markings square or rectangular, arranged longitudinally to long axis of body and dark brown or dark gray with white posterior margins. Lateral markings same color and form as paravertebral markings, but smaller than paravertebrals in some specimens. Vertebral region dark gray or light brown. Prescapular or postscapular spots less well defined, generally darker than lateral markings, but sometimes indistinguishable from them. Throat, abdomen, and cloaca region white with small irregularly shaped black spots. Ventral spots usually most dense along sides of abdomen. Mental and shield scales usually dark brown, but occasionally dark green. Longitudinal line extending along lateral tail (25–50% total tail length) splits into small black or dark brown rectangular bars. Color becomes less vibrant, but otherwise does not change appreciably after >6 mo in preservative (70% ethanol).

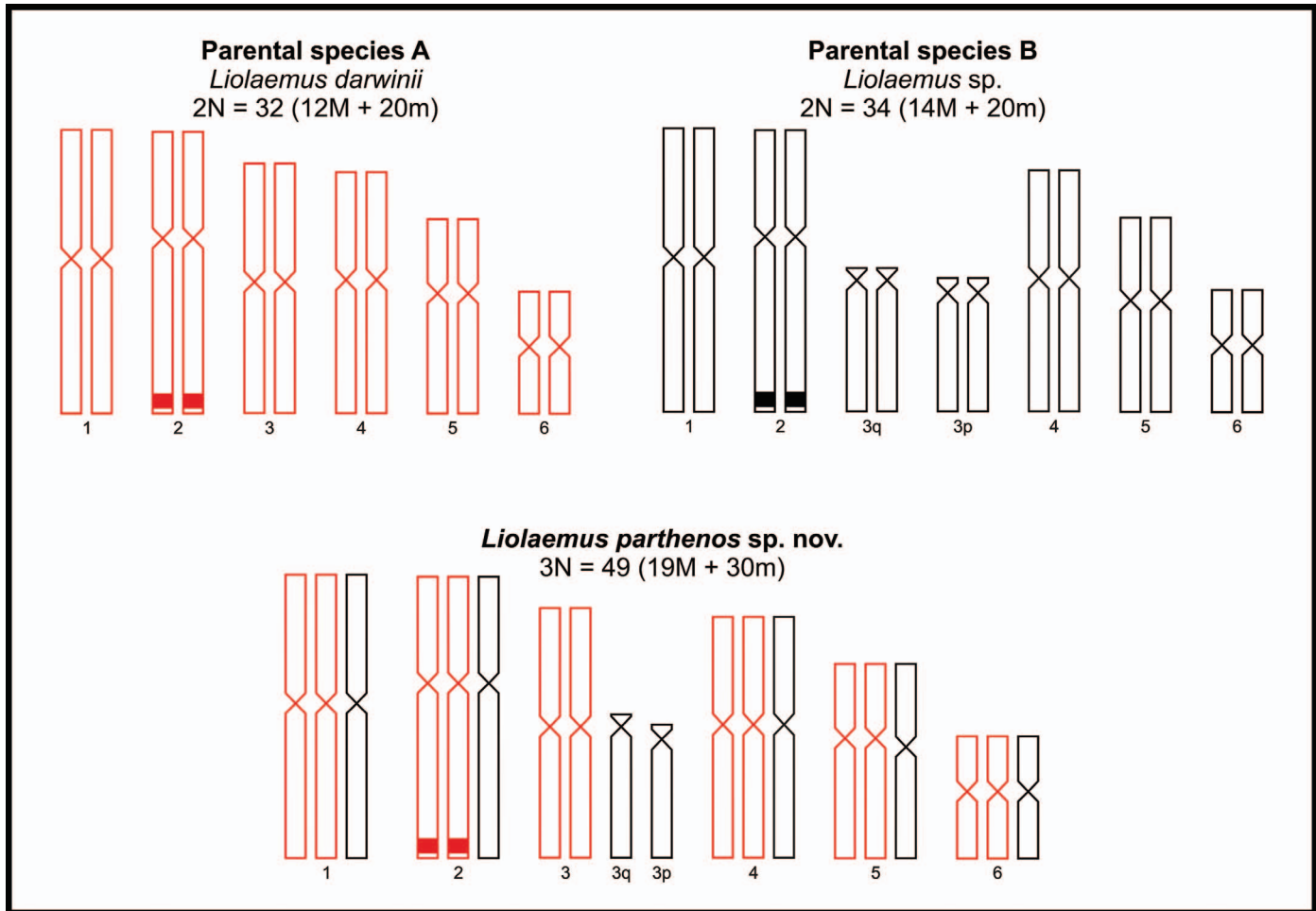


Fig. 5. Macrochromosome idiograms for *Liolaemus parthenos*, new species, and its hypothetical parental species.

**Etymology.**—The specific epithet *parthenos* is a Greek noun meaning “virgin” or “maiden,” in reference to the presumed reproductive strategy of this all-female species.

**Distribution.**—*Liolaemus parthenos* is known only from the outskirts of El Nihuil, Salinas del Diamante, and from south of El Nihuil on Provincial Route 180 near Sierra El Nevado, San Rafael Department, Mendoza Province, Argentina (1305–1600 m; Fig. 2).

**Natural history.**—*Liolaemus parthenos* is apparently an all-female parthenogenetic species. Despite 24 collecting expeditions since 1995 for a total of approximately 650 combined person hours of observing and collecting this species in nature, and after examining more than 300 specimens (note only 65 specimens were collected and preserved because of restrictions imposed by collecting permits), no males were encountered. Thus, the probability of not encountering a male, if this was a bisexual species with an equal population sex ratio, would be  $0.5^{65}$  or  $2.7^{-20}$ , an infinitesimally small likelihood.

Field observations of active *L. parthenos* were made from October through February, and again in April. During summer months (December to February), lizards were active only in the morning and afternoon. The shift to bimodal activity apparently helps them avoid the extreme heat of midday. In April (fall), only juveniles were active at midday, indicating seasonal or ontogenetic variation in diel activity. Body temperatures ( $T_b$ s) from four adult *L. parthenos* (SVL =

$51.8 \pm 3.4$  mm) collected in the late afternoon of 11 February 1995 along the sandy shore of El Nihuil reservoir averaged  $34.6 \pm 3.4^\circ\text{C}$ , which is similar to the field  $T_b$ s reported for other low-elevation *Liolaemus* lizards (Espinoza et al., 2004).

*Liolaemus parthenos* is oviparous and reproduces in summer. Reproductively active females (well-developed eggs in oviducts) were observed in January ( $n = 5$ ), and non-reproductive females were found in December and February ( $n = 13$ ). However, in a different year, we found females with oviducts full of developing eggs in December ( $n = 11$ ). These observations suggest that the reproductive period begins in November and lasts until late January.

*Liolaemus parthenos* is sympatric with the lizards *Aurivela longicauda* (Teiidae), *Diplolaemus sexcinctus* and *Leiosaurus bellii* (Leiosauridae), and two congeneric species: *L. gracilis*

**Table 1.** Percentage of uncorrected pairwise distances between partial sequences of the mitochondrial ND1 gene of *Liolaemus parthenos*, new species, and the other species belonging to the *L. gosseorum* clade of the more inclusive *L. boulengeri* group. GenBank accession numbers appear in parentheses.

	1	2	3	4	5
1 <i>L. laurenti</i> (AF099273.1)	—				
2 <i>L. gosseorum</i> (AF099272.1)	4.91	—			
3 <i>L. darwinii</i> (AF099274.1)	1.04	5.16	—		
4 <i>L. darwinii</i> (DQ002490.1)	1.21	4.97	0.86	—	
5 <i>L. parthenos</i> (AF099275.1)	1.39	4.97	1.27	1.44	—

and *L. grosseorum*. Several species of snakes, which are potential predators of the new species, have also been observed in the area: the dipsadine colubrid snakes *Oxyrhopus rhombifer*, *Philodryas trilineata*, and *Xenodon semicinctus*, as well as the viperid *Bothrops ammodytoides*.

**Cytogenetic analysis.**—*Liolaemus parthenos* has a triploid karyotype with  $3n = 49$  chromosomes (19 macrochromosomes + 30 microchromosomes): 17 of the macrochromosomes are biarmed metacentric or submetacentric and two are acrocentric. All the microchromosomes appear to be acro- or telocentric (Fig. 3). Because of their size and morphology, the macrochromosomes clustered into four groups: (1) the two largest pairs almost equal in size, but differing in centromere position (the first metacentric and the second submetacentric); (2) pairs 3 and 4 almost equal in size and morphology (with a centric fission in the haploid homologue of pair 3); (3) pair 5 (submetacentric in two homologues and metacentric in the third); and (4) pair 6, the smallest of the macrochromosomes with metacentric morphology. Only two of the homologous regions of chromosome pair 2 show secondary constrictions and areas with NORs in the telomere of their long arms.

**Phylogenetic analysis.**—The trees based on Bayesian inference and maximum parsimony were topologically very similar, with sources of conflict occurring solely at nodes that were weakly supported in one or both analyses (Fig. 4). With respect to the new species, both trees strongly supported the placement of *L. parthenos* in the *L. grosseorum* clade of the *L. boulengeri* group: *L. boulengeri* group (*L. chacoensis* group (*L. laurenti* group (*L. darwinii* group (*L. grosseorum* clade)))) (Fig. 4). The *L. grosseorum* clade is also supported by nine morphological synapomorphies (Abdala, 2007). Within the *L. grosseorum* clade, *L. parthenos* is in a well-supported yet unresolved clade with *L. darwinii* (Río Negro Province) and *L. laurenti* (Fig. 4A) or nested within a weakly supported clade containing populations of *L. darwinii* from the more southern provinces of Mendoza and Río Negro and those occurring farther north in La Rioja Province, with *L. laurenti* strongly supported as sister to these four lineages (Fig. 4B).

## DISCUSSION

Based on previous studies (Schulte et al., 2000; Morando et al., 2004; Pincheira-Donoso et al., 2007; Schulte, 2013) and the phylogenetic hypotheses presented here (Fig. 4), *L. parthenos* is closely related to *L. darwinii* and *L. laurenti*, species that are morphologically typical of the *L. darwinii* group (Etheridge, 1993; Abdala, 2007). The closest known locality for *L. laurenti* is approximately 300 km to the north of the type locality of *L. parthenos*, whereas *L. darwinii* has a much wider distribution (Abdala, 2007) including a small population that is sympatric with *L. parthenos* at the type locality of the latter species. It is noteworthy that a similarly proximate distributional association has been reported for a parthenogenetic species of *Leiolepis* and its matrilineal ancestor (Grismer and Grismer, 2010; Grismer et al., 2014). A close phylogenetic association between *L. parthenos* and *L. darwinii* has been reported in previous phylogenetic analyses based on mtDNA. Schulte et al. (2000) recovered *L. parthenos* (as "*L. boulengeri*") in the clade: *L. grosseorum* (*L. darwinii* (*L. parthenos* (*L. laurenti*))). A phylogeographic analysis of the *L. darwinii* group conducted by Morando et al. (2004) recovered *L. parthenos* (as "*L. sp. nov.*") as the sister taxon to *L. laurenti* +

*L. darwinii*. Finally, Pincheira-Donoso et al. (2007) recovered *L. parthenos* (as *L. cf. darwinii*; SDSU 3469, AF099275) as the sister taxon to *L. darwinii* in the clade (*L. grosseorum* (*L. darwinii* (*L. parthenos* + *L. darwinii* from Chubut))). Although *L. parthenos* is superficially similar to *L. boulengeri*, these three molecular studies each strongly support the relationships among *L. parthenos*, *L. darwinii*, *L. laurenti*, and *L. grosseorum*.

The most parsimonious interpretation of the triploid karyotype of *L. parthenos* (Fig. 5) is that the species arose via hybridization. The karyotype of *L. parthenos* (Fig. 4) has a clear diploid component (12M + 20m) contributed by one parental species and an additional haploid set (7M + 10m) provided by the other parental genome (Fig. 5). In the haploid component the two acrocentric macrochromosomes are interpreted as homologs of the two arms (3p and 3q) of pair 3 (3a) in the 2n set. The 30 microchromosomes of *L. parthenos* are best interpreted as ten pairs from the diploid genome (2n = 20), and 10m from the haploid genome.

The low levels of genetic distance between *L. parthenos* and *L. darwinii* and *L. laurenti* (Table 1; Schulte et al., 2000; Morando et al., 2004; Pincheira-Donoso et al., 2007) suggest that one or both of these two species, or one or more closely related undescribed or extinct taxa, are the maternal ancestor(s). This conclusion is further supported if we assume a hybrid origin and that the number and morphology of the chromosomes are the same as the inferred parental species, *L. darwinii* (Fig. 5), which has the chromosomal complement  $2n = 32\text{--}34$  (12M + 20–22m; Aiassa et al., 2005). Unfortunately, no cytogenetic data are currently available for *L. laurenti*. Although analyses based on mtDNA (Schulte et al., 2000; Morando et al., 2004; Pincheira-Donoso et al., 2007; this study) have provided clues of the identity of the maternal ancestor of *L. parthenos*, studies including nuclear gene sequences are needed to identify the paternal ancestor, which is likely *L. grosseorum* or *L. laurenti* based on genetic and morphological similarity and geographic proximity.

We detected structural heteromorphisms in the chromosomes of *L. parthenos*, which supports the hypothesis that this species is the product of a hybrid origin with two or three parental species, as is the case for most other triploid unisexual vertebrates (Vrijenhoek et al., 1989; Kraus, 1995; Schmidt, 1996; Avise, 2008; Lamborot, 2008; Neaves and Baumann, 2011). The species of *Liolaemus* examined to date have gonochoristic reproduction, and the 79 species studied cytogenetically have diploid karyotypes with 28–44 chromosomes (Aiassa et al., 2005; Lamborot, 2008). The variation in chromosome number among species of *Liolaemus* results from chromosomal fusions and fissions. Natural triploids have been reported in Chilean populations of *L. chiliensis* and *L. gravenhorstii*, each of which has  $3n = 48$  chromosomes (Lamborot and Vásquez, 1998; Lamborot et al., 2006), and although Lamborot (2008) suspected that some populations of these species might be or eventually evolve unisexuality, to date, no such populations have been reported.

Early ecological studies of parthenogenetic whiptail lizards (*Aspidoscelis*) from southwestern North America described their niches as "weed habitats," which were considered intermediate to those occupied by their parental species (Wright and Lowe, 1968). The adaptive explanation for this shift in habitat was, although sympatric (at least initially), interspecific competition would be reduced by a lack of syntopy between the parthenogen and its ancestors. Darevsky et al. (1985) extended this idea, asserting that the habitats occupied by parthenogenetic species should exceed that of their individual parental species because parthenogens



possess the genotypes of two or more parental species. In the case of *L. parthenos*, there appears to be little habitat segregation between the new species and its potential parental species. For example, *L. parthenos* occurs syntopically with *L. darwini* and *L. grosseorum*. In fact, most low-elevation members of the *L. darwini* group have the same microhabitat preferences and several have overlapping distributions (Ceï, 1986; Etheridge, 1993; Abdala, 2007). Thus, *L. parthenos* may not conform to the expected niche segregation with its parental species because of historical contingency.

We provide strong evidence for the first unisexual species belonging to the large lizard clade Pleurodonta, extending the occurrence of this rare cytogenetic and reproductive anomaly among vertebrates generally, and for squamate reptiles specifically. Although the mechanism of unisexual reproduction in this species remains to be determined, all known unisexual reptiles species are apparently parthenogenetic (meiotically unreduced ova developed in the absence of sperm) with no records of gynogenesis (sperm-dependent unisexuality) or hybridogenesis (Beukeboom and Vrijenhoek, 1998). Examination of additional molecular markers, detailed field studies, high-resolution cytogenetic techniques, and studies of congeneric species will allow us to establish the type of unisexuality, mechanistic origin, and evolutionary history of unisexuality in this unique lizard species.

#### MATERIAL EXAMINED

We examined more than 1560 specimens (276 in list below + 1284 in Abdala, 2007) of *Liolaemus* focusing primarily on 60 of the currently recognized species in the *L. boulengeri* group. Specimens examined previously and listed in Abdala (2007) are not included here. The list below includes members of the *L. boulengeri* group described after the publication of Abdala (2007), plus specimens of other species examined since 2007. Specimens are from Argentina unless otherwise noted. Institutional abbreviations follow Sabaj Pérez (2014), with the following additions: Colección del Consejo Regional de Investigaciones Científicas y Técnicas de Mendoza (CRYCIT) and Museo Patagónico de Ciencias Naturales, General Roca, Río Negro (MPCN). Some FML lots include more than one individual.

*Liolaemus acostai* ( $n = 20$ ): FML 690, San Juan Province, Caucete Department, 20 km from Caucete; FML 3734, San Juan Province, Jachal Department, Posta el Balde, km 241 on Ruta Nacional 40; FML 16336–37, 18398, 24118–26, San Juan Province, Albardón Department, La Laja; FML 22437–43, San Juan Province, Albardón Department, La Laja, Baños de Salado, 20 km N of San Juan capital; FML 24127, San Juan Province, Zonda Department, bed of Río San Juan; FML 24128, San Juan Province, Zonda Department, Barreal de Matagusanos.

*Liolaemus camarones* ( $n = 10$ ): FML 13052, Chubut Province, Florentino Ameghino Department, Bahía Camarones, Lola Beach; FML 13965, Chubut Province, Florentino Ameghino Department, 18 km S of Camarones; FML 23301–08, Chubut Province, Florentino Ameghino Department, Bahía Camarones, 3 km S of Camarones.

*Liolaemus chehuachekenk* ( $n = 2$ ): MLPS 2535 (holotype), 2536 (paratype), Chubut Province, Cushamen Department, SW

slope of Calcatapul Mountains, 8 km N of El Molle on Provincial Route 13, 900 m.

*Liolaemus cuyumhue* ( $n = 7$ ): MACN 38981 (holotype), Neuquén Province, Añelo Basin, 28.7 km NW Añelo, 38°11'S, 69°01'W, 259 m; FML 17592–94, MACN 38982–84 (paratypes), Neuquén Province, southern edge of Ruta Provincial 7, 38°13'S, 68°57'W, 260 m.

*Liolaemus diaguia* ( $n = 16$ ): MCNI 3247 (holotype), Salta Province, Guachipas Department; FML 23821–25 (paratypes), MCNI 3145–50, 3243, 3248–50 (paratypes), Salta Province, Guachipas Department, Quebrada de las Conchas, 61 km N of Cafayate, 400 m S of Río Las Conchas, 25°47'07.1"S, 65°41'26.1"W, 1328 m.

*Liolaemus dumerili* ( $n = 20$ ): FML 24169 (holotype), FML 24170–88 (paratypes), Río Negro Province, 9 de Julio Department, Sierra Colorada, km marker 23 of Provincial Route 212 on route to Los Menucos, 40°32'54.5"S, 67°37'10.4"W.

*Liolaemus goetschi* ( $n = 20$ ): FML 21501–07, 21511, MPCN 57–65, Río Negro Province, General Roca Department, Laguna Playa, ca. 20 km N of General Roca, 30°52'59"S, 67°34'08"W; FML 21508, Río Negro Province, General Roca Department, 20 km S of Catriel on National Route 151; FML 21509–10, Río Negro Province, General Roca Department, 50 km S of Catriel, on National Route 151.

*Liolaemus lutzae* ( $n = 7$ ): FML 1287, Brazil, Rio de Janeiro Province, Cabo Frio.

*Liolaemus mapuche* ( $n = 10$ ): FML 17005, Neuquén Province, Zapala Department, 13 km S of Paso de Los Indios; FML 17150–58, Neuquén Province, Zapala Department, 4 km before Ramón Castro.

*Liolaemus millcayac* ( $n = 16$ ): FML 28600 (holotype), 28601–03 (paratypes), Mendoza Province, Lavalle Department, N of Mendoza 1 km from National Route 40 on detour to Lagunas del Rosario; FML 22434–36, San Juan Province, 25 de Mayo Department, National Route 141, 46 km NW of El Encón; FML 24129–32, La Rioja Province, Rosario Vera Peñalosa Department, S of Macasin; MLP 86–87, San Luis Province, Belgrano Department, Sierra del Gigante; MLP 88–90, San Luis Province, Belgrano Department, Alto Pencoso.

*Liolaemus morenoi* ( $n = 14$ ): FML 17020–28, Neuquén Province, Collon Curá Department, 2 km N of Cerrito Piñon; FML 22206–10, Neuquén Province, Zapala Department, 20 km SW to Zapala on National Route 40.

*Liolaemus occipitalis* ( $n = 9$ ): FML 1288–89, 2618–20, Brazil, Rio Grande do Sul Province, Tramandai.

*Liolaemus parthenos* ( $n = 70$ ): FML 16221 (holotype), FML 16222–24 (paratypes), Mendoza Province, San Rafael Department, dunes next to El Nihuil Dam on Provincial Route 180, 35°2'19.77"S, 68°40'12.60"W; FML 23485–88, Mendoza Province, San Rafael Department, 37 km S of El Nihuil on Provincial Route 180, near Cerro Trintrica, 35°21'35.29"S, 68°42'26.38"W; FML 24480–84, LGE 9376–77 (seven karyotyped specimens), LGE 9378–79, Mendoza Province, San Rafael Department, near El Nihuil Dam; IBAUNC 9772–73, 9775–77 (paratypes), Mendoza Province, San Rafael Depart-

ment, 10 to 60 km S of El Nihuil, 35°7'0.71"S, 68°41'4.28"W to 35°33'49.47"S, 68°41'15.14"W, 1400–1600 m; IBAUNC 11431–35 (paratypes), Mendoza Province, San Rafael Department, Pampa del Diamante, 34°54'44.39"S, 68°51'38.58"W, 1400 m; LGE 9380–82 (3 karyotyped specimens), Mendoza Province, San Rafael Department, Salinas del Diamante, Provincial Route 144 at km marker 728, 34°54'40.23"S, 68°50'9.39"W; MHNSR 78–82 (paratypes), Mendoza Province, San Rafael Department, Club de Pescadores, El Nihuil, 35°2'10.54"S, 68°42'33.84"W.

*Liolaemus pipanaco* ( $n = 7$ ): FML 1480, 1501–02, Catamarca Province, Andalgalá Department, Salar de Pipanaco; FML 18396, Catamarca Province, Andalgalá Department, pass through Río Blanco, W of entrance to Salar de Pipanaco, 27°49'23.9"S, 65°14'38.2"W; FML 19225, Catamarca Province, Andalgalá Department, Salar de Pipanaco, entrance to Río Blanco, 36 km S of Andalgalá, 737 m.

*Liolaemus purul* ( $n = 25$ ): FML 24153 (holotype), FML 24154–63 (paratypes), Neuquén Province, La Rinconada Department, 6 km N of San Ignacio on National Route 40 on way to Zapala, 39°50'54.4"S, 70°39'52.6"W, 1071 m; FML 21473–74, Neuquén Province, Zapala Department, Parque Nacional Laguna Blanca, near park ranger station, 39°02'38.5"S, 70°19'36.4"W, 1272 m; FML 21482, Neuquén Province, Zapala Department, Parque Nacional Laguna Blanca; FML 21499, 21534–35, Neuquén Province, Zapala Department, Parque Nacional Laguna Blanca entrance gate on Provincial Route 46, 39°02'55.8"S, 70°16'36.2"W, 1306 m; FML 22187–88, Neuquén Province, Collón Curá Department, 35 km S of Collón-Curá; FML 22211, Neuquén Province, Collón Curá Department, 2 km S of Collón Curá bridge; FML 24164–65, Neuquén Province, Zapala Department, on Provincial Route 13 on way to Primeros Pinos, 38°52'16.1"S, 70°19'17.9"W, 1275 m; FML 24166–68, Neuquén Province, Zapala Department, 1 km S of Provincial Route 13 and 41 km W of Zapala, 38°51'14.4"S, 70°30'22.3"W, 1288 m.

*Liolaemus shehuen* ( $n = 8$ ): FML 22191–95, Chubut Province, Telsen Department, 60 km W of Telsen; FML 22217–19, Chubut Province, Telsen Department, 80 km W of Telsen.

*Liolaemus tromen* ( $n = 8$ ): FML 17735 (holotype), FML 17731–34, 17736 (paratypes), Neuquén Province, El Cholar Department, km marker 140 on Provincial Route 21, 7 km N of El Huecú; FML 22386–87, Neuquén Province, Chos Malal Department, near Tromen Volcano, 37°04'56.8"S, 70°06'15.5"W, 2189 m.

*Liolaemus xanthoviridis* ( $n = 7$ ): FML 21259–65, Chubut Province, Florentino Ameghino Department, 22 km NE of Dos Pozos on Provincial Route 75.

**GenBank accession numbers.**—Only individuals not included in previous studies (and previously accessioned in GenBank) are listed here. Museum acronyms follow those listed above.

*Liolaemus boulengeri* (FML 15733): KP190030

*Liolaemus calchaqui* (FML 17019): KP190031

*Liolaemus canqueli* (MCN 1294): KP190032

*Liolaemus darwini* (FML 17104): KP190033

*Liolaemus espinozai* (MCN 213): KP190034

*Liolaemus inacayali* (FML 13233): KP190035

*Liolaemus lavillai* (MCN 1730): KP190036

*Liolaemus lobo* (FML 13254): KP190037

*Liolaemus mapuche* (FML 11462): KP190038

*Liolaemus senguer* (FML 23679): KP190039

*Liolaemus tehuelche* (FML 13218): KP190040

*Liolaemus xanthoviridis* (FML 17033): KP190041

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