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A New Andean Species of Leaf-toed Gecko (Phyllodactylidae:*Phyllodactylus*) from Ecuador

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Abstract

We describe a new species of *Phyllodactylus* from a xerophytic forest in the Andes of southern Ecuador. The new species differs from other mainland species of *Phyllodactylus* from South America by the combination of the following characters: preanal scales similar in size to other ventral scales, well-defined longitudinal rows of tubercles dorsally, a medial longitudinal row of enlarged caudal scales ventrally, tubercles on dorsal surface of tibia present, enlarged postanal scale absent, tubercles on dorsal surface of forearm absent, interorbital scales homogeneous in size, enlarged scales on proximal one-fourth of tail absent, gular scales granular, and maximum snout–vent length of 55 mm. Even though morphological similarity suggests a close relationship between the new species and *Phyllodactylus reissii*, phylogenetic analyses of 10 nuclear and mitochondrial genes contradict this hypothesis. We also report the first records of *Phyllodactyluskofordi* for Ecuador.

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The New World nocturnal gecko genus, *Phyllodactylus* Gray 1828, includes approximately 47 currently recognized species occurring from southern North America to southern South America

and the Caribbean (Dixon and Huey, 1970; Murphy et al., 2009). South American species of *Phyllodactylus* occur in arid or semiarid regions along the Pacific versant of the Andes from Ecuador to Chile, the Galápagos Archipelago, the upper Amazon basin of northwestern Peru, and the Caribbean lowlands from eastern Colombia to central Venezuela (Dixon and Huey, 1970). Eight species of *Phyllodactylus* are known from Ecuador; one (*Phyllodactylus pumilus*) from the mainland, six (*Phyllodactylus barringtonensis*, *Phyllodactylus bauri*, *Phyllodactylus darwini*, *Phyllodactylus galapagoensis*,*Phyllodactylus gilberti*, *Phyllodactylus leei*) endemic to the Galápagos islands, and one (*Phyllodactylus reissii*) occurring both in the mainland and the Galápagos (Dixon and Huey, 1970; Torres-Carvajal, 2001).

Species delimitation of South American *Phyllodactylus* is problematic in most cases because of morphological similarity among putative species and the lack of molecular taxonomic approaches. This is reflected in the low number of taxonomic publications. Dixon and Huey (1970) provided a broad taxonomic revision of South American*Phyllodactylus* in which they reported 19 mainland species. The only other taxonomic paper focusing on South American taxa, published roughly four decades later, described two new species of *Phyllodactylus* from Peru (Venegas et al., 2008). Herein we describe a new species of Leaf-toed Gecko from the Andes of southern Ecuador based on morphological characters and report the first country records of *Phyllodactylus kofordi*. In addition, we test for exclusivity (sensu Rieppel, 2010) of the new species and of *P. reissii*, a morphologically similar species, by performing phylogenetic analyses of 10 mitochondrial and nuclear genes.

Materials and Methods

Morphological Data

All type specimens of the new species described in this paper are listed in the type series below and were deposited in the Museo de Zoología, Pontificia Univeridad Católica del Ecuador, Quito (QCAZ), Ecuador. Specimens of other species of *Phyllodactylus* examined in this study are listed in Appendix 1. We follow previously proposed terminology (Dixon, 1964; Dixon and Huey, 1970) for measurements and squamation. Snout–vent length (SVL) and tail length (tL) measurements were taken with a ruler and recorded to the nearest millimeter. All other measurements were made with digital calipers and recorded to the nearest 0.1 mm. Clutch size was determined from digital x-ray radiographs (QCAZ 4464, 4466, 9923, 9925) taken in a Thermo Kevex X-ray Imaging System. Egg volume was calculated with the prolate spheroid formula: $V = 4/3\ \pi\ (\text{length}/2)*(\text{width}/2)^2$. Sex was determined by noting the presence of hemipenes or by dissection.

DNA Sequence Data

Total genomic DNA was digested and extracted from liver or muscle tissue using a guanidinium isothiocyanate extraction protocol. Tissue samples were first mixed with Proteinase K and lysis buffer and digested overnight prior to extraction. DNA samples were quantified using a NanoDrop® ND-1000 (NanoDrop Technologies, Inc), resuspended, and diluted to 25 ng/µl in ddH_2O prior to amplification.

Using primers and amplification protocols from Gamble et al. (2008) and Blair et al. (2009), we obtained 5,025 nucleotides (nt) encompassing six nuclear genes and four mitochondrial genes from one individual of *P. kofordi*, seven of *P. reissii*, and three of the new species described herein. Additionally, we used sequences of *Gekko gecko*from GenBank as the outgroup. Nuclear genes included brain-derived neurotrophic factor (BDNF, 617 nt), oocyte maturation factor MOS (c-mos, 387 nt), recombination-activating gene 1 (RAG1, 310 nt), recombination-activating gene 2 (RAG2, 430 nt), acetylcholinergic receptor M4 (ACM4, 324 nt), and phosducin (PDC, 410 nt). Mitochondrial loci included NADH dehydrogenase subunit 4 (ND4, 596 nt) and a continuous fragment of 12S rRNA-tRNA^{Val}-16S rRNA (1,951 nt). Gene regions of taxa included in phylogenetic analyses along with their GenBank accession numbers are shown in Table 1.

Phylogenetic Analyses

Editing, assembly, and alignment of sequences were performed with Geneious Pro^{TM} 5.3 (Drummond et al., 2010). Phylogenetic relationships were assessed under a Bayesian approach in MrBayes 3.2.0 (Ronquist and Huelsenbeck, 2003). The model of character evolution for each gene or partition was obtained in jModeltest (Posada, 2008) under the Akaike information criterion. Genes were combined into a single dataset with eight partitions, one per gene, with the continuous fragment 12S rRNA-tRNA^{Val}-16S rRNA as a single partition. In addition, both the mitochondrial and nuclear datasets were analyzed separately as single partitions. For each dataset, four independent analyses were performed to reduce the chance of converging on a local optimum. Each analysis consisted of five million generations and four Markov chains with default heating values. Trees were sampled every 1,000 generations resulting in 5,000 saved trees per analysis. Stationarity was confirmed by plotting the −ln *L* per generation in the program Tracer 1.2 (Rambaut and Drummond, 2003). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman and Rubin, 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. Adequacy of mixing was assessed by examining the acceptance rates for the parameters in MrBayes and the effective sample sizes in TRACER. After analyzing convergence and mixing, 500 trees were discarded as “burn-in” from each run. We then confirmed that the four analyses reached stationarity at a similar likelihood score, and that the topologies were similar, and used the resultant 18,000 trees to calculate posterior probabilities (BPP) for each bipartition on a 50% majority rule consensus tree.

Systematics

The taxonomic conclusions of this study are based on the observation of morphological features and color patterns as well as on inferred phylogenetic relationships. We consider this information as species delimitation criteria following the general species concept of de Queiroz (1998, 2007).

Phyllodactylus leoni sp. nov.

Holotype

QCAZ 9924 (Figs. 1, 2), an adult male from the upper valley of Río León (3.450°S, 79.1667°W, 1,855 m) near the Río León bridge on the old Oña-Cuenca road, Provincia Azuay, Ecuador, collected on 11 October 2009 by O. Torres-Carvajal, P. Mafla, and S. Báez.

Paratypes

Ecuador: Provincia Azuay: QCAZ 9923, 9925–9928, same collection data as the holotype; QCAZ 8652–8653, type locality, collected on 27 June 2008 by O. Torres-Carvajal, E. Arbeláez, A. Carvajal-Campos, and D. Salazar-Valenzuela; QCAZ 4464–4466, 4487, type locality, collected on 8 July 2011 by D. Salazar-Valenzuela, P. Loaiza, M. Read, E. Arbeláez, and J. M. Falcón. Provincia Loja: QCAZ 11122–11124, La Papaya, 3°31.789′S, 79°16.585′W, 1,971 m, collected on 20 December 2010 by D. Salazar-Valenzuela, P. Loaiza, and L. Bustamante.

Diagnosis

Together with *P. pumilus* and *P. reissii*, the new species can be distinguished from other species of *Phyllodactylus*from mainland South America by the combination of the following characters: preanal scales similar in size to other ventral scales, well-defined longitudinal rows of tubercles dorsally, a medial longitudinal row of enlarged caudal scales ventrally, tubercles on dorsal surface of tibia present, enlarged postanal scale absent, and tubercles on dorsal surface of forearm absent. From *P. pumilus* (character states in parentheses) the new species differs in having interorbital scales homogeneous in size (Fig. 1; supraoculars largest of interorbital series; Dixon and Huey, 1970) and in lacking enlarged scales on proximal one-fourth of the tail (at least two rows of enlarged scales; Dixon and Huey, 1970). From *P. reissii* the new species differs in having granular gular scales (flat and juxtaposed or subimbricate in *P. reissii*) and in being smaller (55 mm vs. 75 mm maximum SVL).

Description of Holotype

Male (Figs. 1, 2); SVL = 55 mm; tL = 59 mm; maximum head width = 10.96 mm; head length = 14.1 mm; head height = 6.7 mm; distance between eye and tympanum = 4.9 mm; rostral 2.32 mm wide, 1.18 mm high, with a shallow median cleft along its posterior third; internasals two, separated medially by two small scales; nostril surrounded by rostral anteriorly, first supralabial laterally, internasal medially, and two postnasals; loreals from the eye to nostril 13; scales in posterior loreal region as large as interorbital scales; snout scales concave; temporal and posterior dorsal surface of head with granular scales and scattered enlarged, round and smooth scales; interorbitals at level of center of eyes 23; scales across the snout at the level of the third labial 25, 17 at the level of the second labial; supralabials between rostral and center of eye 6; infralabials between mental and center of eye 5 (right)–6 (left); ear opening elliptical, posterodorsally oriented, its maximum length 0.49 times the maximum eye diameter, its anterior and posterior borders strongly denticulate; mental trapezoidal, maximum width = 2.49 mm, maximum length = 2.26 mm; postmentals two, in contact with first infralabials laterally and five scales posteriorly; gulars granular; dorsum with projecting granular scales and larger trihedral tubercles disposed in 13 dorsal longitudinal rows; tubercles in paravertebral row (i.e., first row of tubercles next to vertebral line) between tympanum

and cloaca 56, between axilla and groin 36; ventrals from posterior gular region to vent 63; longitudinal rows of ventrals at midbody 27; scales of thighs flat, imbricate, and homogeneous in size anterodorsally, heterogeneous in size posterodorsally, and granular posteriorly; dorsal scales of shanks heterogeneous in size, with a few scattered large tubercles; dorsal scales of arms homogeneous in size, flat, imbricate; lamellae on Fingers I, II, III, IV, and V 8, 11, 10, 8, and 6, respectively; lamellae on Toes I, II, III, IV, and V 6, 8, 12, 12, and 12, respectively; caudals flat, smooth, and imbricate, with an enlarged medial row ventrally; tail 1.07 times SVL.

Color in Life of Holotype

Background color of head, body, limbs, and tail almond; dorsal surface of head, body, and limbs with a dark brown irregular reticulation which is discontinuous on body middorsally; distinct, dark brown stripe extending laterally on each side from snout to midbody, through ventral aspect of eye, dorsal aspect of tympanum, scapular region, and flanks; tail with 11 dark brown crossbands, 2–3 scales wide, that reach ventral aspect only laterally; ventral surface of head, body, limbs, and tail uniformly pinkish-cream, with fingers and toes dark grey; iris copper with a fine, dark brown reticulation.

Variation

Scale counts in *Phyllodactylus leoni* vary as follows (mean, standard deviation, and sample size in parentheses): longitudinal rows of dorsal tubercles 11–14 (12.31, 0.85, 13); paravertebrals between tympanum and cloaca 48–57 (51, 2.97, 13); paravertebrals between axilla and groin 26–36 (29.62, 2.87, 13); scales from nostril to eye 10–13 (11.20, 0.86, 15); scales across snout at level of second labials 12–19 (15.46, 2.07, 13); scales across snout at level of third labials 18–25 (22.69, 1.97, 13); supralabials between rostral and center of eyes 5–7 (6.31, 0.63, 13); infralabials between mental and center of eyes 5–6 (5.38, 0.51, 13); interorbitals at level of center of eyes 16–23 (19.47, 1.92, 15); postmentals 2–3 (2.08, 0.28, 13); longitudinal rows of ventrals 22–27 (24.86, 1.75, 14); transverse row of ventrals 52–68 (59.08, 4.50, 12); lamellae on Finger IV 6–11 (7.77, 1.24, 13); lamellae on Toe IV 9–13 (10.85, 1.14, 13). Maximum SVL in males and females is 55 mm and 51 mm, respectively. Morphological variation in *P. kofordi*, *P. leoni* sp. nov., *P. pumilus*, and *P. reissii* is summarized in Table 2.

An adult male (QCAZ 9926) is similar in color pattern to the holotype (Fig. 3). An adult female (QCAZ 9923) differs from both males in having a lighter dark stripe from snout to approximately midbody and in having lighter reticulations on the head, body, and limbs (Fig. 3).

Hemipenial Morphology (QCAZ 8653, right organ)

Maximum length 3.35 mm; maximum width 2.28 mm; basal and medial portions similar in width; apical portion with two short but distinct semispherical lobes; body smooth, without ornamentations; sulcus spermaticus single, recurved, extending medially between lobes; asulcate and lateral sides of lobes calyculate; sulcate side of lobes calyculate peripherally, smooth and wrinkled centrally (Fig. 4).

Natural History

All specimens of *Phyllodactylus leoni* were found sleeping during the day under rocks or in rock crevices. Similar to*P. reissii* (Goldberg, 2007), clutch size in *P. leoni* varies between 1–2 eggs. Females (QCAZ 9923, 9925) collected in October 2009 had only one shelled egg in one of their oviducts. Size and volume of these eggs was 0.70–0.78 mm × 1.12–1.16 mm and 0.29–0.35 mm^3, respectively. On the other hand, females (QCAZ 4464, 4466) collected in July 2011 contained one shelled egg in each oviduct. Size and volume of these eggs was 0.79–0.81 mm × 1.11–1.19 mm and 0.38–0.39 mm^3, respectively. Females containing one egg were smaller than those containing two eggs, suggesting that clutch size is related to body size. During collecting trips in July and October 2009, broken pieces of several egg shells were found under single rocks; even though an exact count was not possible, this suggests that this species has communal nests. The smallest individual examined (SVL = 21 mm; QCAZ 11122) was captured on 20 December 2010.

Phyllodactylus leoni exhibits at least two defense mechanisms. First, when threatened in the lab, several specimens coiled up their tails presumably mimicking a scorpion. Second, 53% of the collected specimens had broken or regenerated tails, indicating that tail autotomy is frequent.

Distribution

Phyllodactylus leoni occurs in southern Ecuador in the upper basin of the León River, a tributary of the Jubones River (Pacific drainage, Fig. 5). It occurs at elevations between 1,855–1,971 m in xeric, inter-Andean, montane shrubland (Cuesta et al., 2009). This species is not known to occur in sympatry with other species of *Phyllodactylus*.

Etymology

The specific epithet *leoni* is a noun in apposition and refers to the León River. All type specimens of *Phyllodactylus leoni* were collected in the León River valley close to the Pan American highway, Provincias Azuay and Loja.

Phylogenetics

Selected models of the evolution of gene regions used in phylogenetic analyses are shown in Table 3. With 93% constant sites, the nuclear regions included in this study are poorly informative; 91% of the parsimony informative characters from all genes are included in the mitochondrial gene regions (Table 3). All three datasets (i.e., combined, mitochondrial, and nuclear) strongly support the exclusivity (Rieppel, 2010) of both *Phyllodactylus reissii*and the new species described in this paper (Fig. 6). However, these taxa are not recovered as sister species as suggested by morphology. Instead, a strong sister taxon relationship (BPP = 1.00) is inferred for *P. leoni* and *P. kofordi* (Fig. 6, but see below).

Discussion

Recent collections of reptiles and amphibians in southern Ecuador have resulted in the discovery of new records for this country as well as new species to science, suggesting that the diversity of

reptiles, amphibians, and possibly other taxa from this region is currently underestimated (Torres-Carvajal and Carvajal-Campos, 2009; Torres-Carvajal et al., 2009; Ayala-Varela and Torres-Carvajal, 2010; Ron et al., 2010; Ayala-Varela et al., 2011). Two species of *Phyllodactylus*, *P. pumilus* and *P. reissii*, had been reported from mainland Ecuador (Dixon and Huey, 1970; Torres-Carvajal, 2011). In this paper we describe a new species of *Phyllodactylus* and provide the first records of *P. kofordi* (Fig. 5; Appendix 1), both from southern Ecuador. These discoveries increase the number of species of Leaf-toed Geckos from Ecuador to 10, of which six are endemic to the Galápagos.

Morphological similarity among species of *Phyllodactylus* makes species recognition and taxonomy within this clade difficult. We did not recover any specimens of *P. pumilus* even though we examined material from near its type locality (Appendix 1). At least one of the character states used by Dixon and Huey (1970) to diagnose *P. pumilus*, scales on supraocular region largest of midorbital series, was also seen in several specimens of *P. reissii* from throughout its distribution range. Further collections and analyses of DNA sequence data are needed to better assess the taxonomic status of the populations currently circumscribed as *P. pumilus*. In contrast, monophyly of seven individuals from several localities supports *P. reissii* as a distinct species. Phylogeographic studies of *P. reissii* are currently ongoing and will be presented elsewhere.

In this paper we show that some of the traditional external morphological characters used to characterize species of*Phyllodactylus* (e.g., tubercles on tail) seem to be homoplastic. The new species is most similar morphologically to*P. reissii* instead of to its closer relative, *P. kofordi* (Fig. 6), from which it differs significantly in morphology (e.g., the new species lacks the dorsal tubercles on tail, characteristic of *P. kofordi*). However, the phylogenetic tree presented in this paper should be interpreted with caution. The sister taxon relationship between *P. leoni* and *P. kofordi* might be an artifact resulting from poor taxon sampling. Inclusion of other species of *Phyllodactylus* from South America in a larger phylogenetic analysis might yield a different sister taxon for *P. leoni*. Additionally, a larger taxon–specimen sampling could also reveal that *P. leoni*, *P. reissii*, or both are not exclusive (Rieppel, 2010), as shown in this paper.

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Appendix 1

Specimens examined

Phyllodactylus kofordi

ECUADOR: Provincia Loja: Comuna Numbiaranga, Barrio Canguraka, Reserva Natural Laipuna, 220–638 m, QCAZ 3074, 7954–7955, 10238–10239; Quebrada El Faique, 256 m, QCAZ 10381, 10355, 10366; Zapallal slope, 234 m, QCAZ 10352, 10340.

P. reissii

ECUADOR: Provincia El Oro: Santa Rosa, QCAZ 5540; Bosque Protector Puyango, QCAZ 6390; Reserva Ecológica Militar Huaquillas, QCAZ 7912–7915. Provincia Manabí: Portoviejo, QCAZ 3037, 6110; Santa Teresa, km 13 on road to Bahía, QCAZ 6099; Isla de la Plata, QCAZ 2849–2851, 2874, 642; Jipijapa, QCAZ 3605; Manta, Picoazá, QCAZ 1669–1670; 1 km W Manta, QCAZ 130, 2006; Puerto Cayo, 10 m, QCAZ 4091–4092; San Vicente, 3 m, QCAZ 3786; Pedernales, 3 m, QCAZ 8968; Crucita, QCAZ 6113; Cabo Pasado, QCAZ 3331. Provincia Loja: Zapotillo, Quebrada de las Lajas, QCAZ 3072–3073; Quebrada El Faique, 256 m, QCAZ 10358, 10341, 10346–10348, 10351, 10359–10365, 10367; Zapallal slope, 234 m, QCAZ 10353; Macará, QCAZ 5296; access road to Macará-Zapotillo highway, QCAZ 5294–5295; Reserva Natural Laipuna, 638 m, QCAZ 7955, 10236; Catamayo, San Antonio, QCAZ 9603–9604. Provincia Esmeraldas: Esmeraldas, QCAZ 2239; Hostería el Andaluz, QCAZ 4191, 4194. Provincia Guayas: La Troncal, QCAZ 1105–1106; Isla Puná, Nueva Puná, 10 m, QCAZ 3528–3529; Guayaquil, QCAZ 3946; El Mango, Cerro Mansalve, QCAZ 6357–6358, 6386, 6973; Bosque Protector Cerro Blanco, 237 m, QCAZ 9096–9097, 9099, 9101, 9105, 9135, 9137; on road El Palmar-Balsas, QCAZ 6359.

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FIG. 1. Head of holotype (QCAZ 9924) of *Phyllodactylus leoni* sp. nov. in dorsal (left), ventral (top right), and lateral (bottom right) views. Scale bar = 2 mm.

enlarge figure

FIG. 2. Views of holotype (QCAZ 9924) of *Phyllodactylus leoni* sp. nov. Pelvic region in dorsal view (left), proximal aspect of tail in ventral view (center), and right hind foot in ventral view (right). Scale bar = 2 mm (left, center), 1 mm (right).

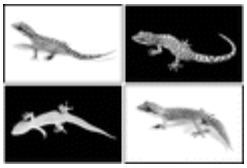

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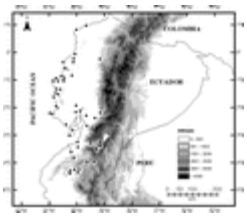
FIG. 3. *Phyllodactylus leoni* sp. nov. Adult female (SVL = 40.80 mm, QCAZ 9923, top left), adult male (SVL = 46.91 mm, QCAZ 9926, top right), and subadult male (SVL = 38.15 mm, QCAZ 8653, bottom left and right).

enlarge figure

FIG. 4. Right hemipenis of *Phyllodactylus leoni* sp. nov. (QCAZ 8653) in asulcate (left) and sulcate (right) views. Scale bar = 2 mm.



enlarge figure

FIG. 5. Distribution of *Phyllodactylus kofordi* (triangles), *P. leoni* sp. nov. (squares), and *P. reissii* (circles) in mainland Ecuador. White arrow points at type locality of *P. leoni* sp. nov.

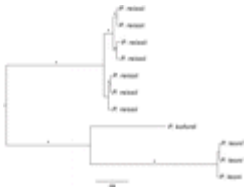


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FIG. 6. Majority rule (50%) consensus tree of 18,000 trees obtained from a Bayesian analysis of 10 genes and 12 specimens. The outgroup used to root the tree (*Gecko gecko*) is not shown. Asterisks correspond to posterior probability values of 1.00.

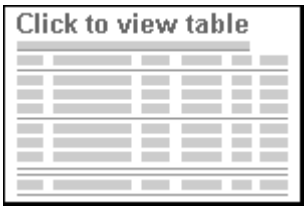

TABLE 1. GenBank accession numbers of taxa and gene regions included in this study.

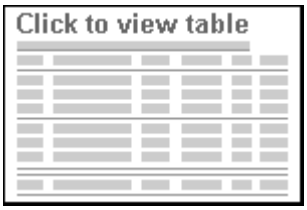

TABLE 2. Morphological characters of the four species of *Phyllodactylus* occurring in mainland Ecuador. Data are from Dixon and Huey (1970) except for*P. leoni* sp. nov.

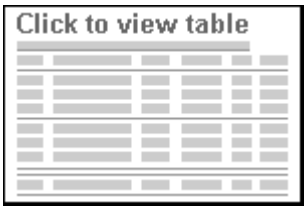

TABLE 3. Gene regions used in this study. For each region, the number of nucleotide positions (nt), parsimony informative sites (pi), constant sites (cs), and the model of evolution used in phylogenetic analyses are shown.