

A NEW SPECIES OF LEAF-TOED GECKO, GENUS *PHYLLODACTYLUS* (SQUAMATA: GEKKOTA: PHYLLODACTYLIDAE) FROM GUERRERO, MEXICO

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ABSTRACT. A new, miniaturized species of *Phyllodactylus* Gray from Guerrero, Mexico is described. The species appears to be the smallest American species of leaf-toed gecko. The diploid karyotype consists of a graded series of 36 acrocentric and 2 subtelocentric chromosomes; the telocentric pair is the second largest. The new form is morphologically very similar to *P. duellmani*, but is electrophoretically quite distinctive having a genetic distance of 0.839. The new population is also meristically quite similar to allopatric *P. bordai*, but can be distinguished by its small size at which reproductive maturity is attained and by the number of transverse ventrals.

KEYWORDS. Reptilia; Gekkota; Phyllodactylidae; Guerrero; Mexico; *Phyllodactylus* karyotypes; *Phyllodactylus papenfussi* sp. nov.

INTRODUCTION

Geckos of the family Phyllodactylidae (Gamble *et al.*, 2008) encompass a trans-Atlantic distribution with representatives distributed throughout the New World and northern Africa. The leaf-toed gecko genus *Phyllodactylus* Gray contains approximately 47 species distributed throughout the New World tropics and subtropics. In North America and Middle America, *Phyllodactylus* is known on the west coast of Panama in the south to northern Sonora, Mexico, throughout the Peninsular Ranges of Baja California including southern California, on islands in the Gulf of California, including the Islas Las Tres Marias, and on the eastern seaboard in Belize. Representatives also occur throughout the Antilles, the Caribbean coasts of Colombia and Venezuela, and along the Pacific versant of the Andes including the Galapagos archipelago (Dixon 1962; Dixon and Huey, 1970; Wright, 1983). Dixon (1962, 1964, 1966, 1973) and Dixon and Huey (1970) reviewed the taxonomy of *Phyllodactylus* and described many new species based chiefly on features of squamation. However, as Dixon (1964) noted, squamation characteristics of the genus are highly variable and have been responsible for a significant amount of taxonomic confusion.

There have been few attempts to unravel the systematics of this widespread genus on characteristics other than squamation. Dixon and Anderson (1973), Dixon and Kluge (1964), and Dixon and Kroll (1974) studied osteological characters and removed three species groups from the genus *Phyllodactylus*, one

each from Madagascar, Australia and Iran. Further, Bauer *et al.* (1997) used allozymic data to erect several new genera of Old World geckos previously designated as *Phyllodactylus*. Karyological analysis has been applied to the Australian species *Christinus marmoratus*, formerly classified as *Phyllodactylus* (King and Rofe, 1976). In the Americas, there is a single cytotaxonomic application to the systematics of *Phyllodactylus*; Murphy and Papenfuss (1980) utilized biochemical methods to show that the population of *P. unctus* reported in Michoacan, Mexico (Dixon, 1964) was actually *P. paucituberculatus*. Both karyological and allozymic data suggest that solutions to many systematic problems within *Phyllodactylus* may be found utilizing karyological and molecular techniques.

During additional field excursions in Guerrero, Mexico, Ted Papenfuss collected a single, small *Phyllodactylus* at the junction of the Rio Balsas and Mexico Highway 95. Subsequently, three series of tiny leaf-toed geckos were collected adjacent to the highway near Mezcala at night on rocks while lantern walking. In the first series, collected in 1977, three of five specimens were gravid females. The second series of seven individuals, including one gravid female, were obtained in 1978 and the third series of two female specimens was made in 2001. Dixon (1960) described the smallest known species, *P. duellmani*, from Michoacan, Mexico about 320 km from the collecting site of the tiny Guerrero geckos. The maximum snout-vent length (SVL) of adult *P. duellmani* was 43 mm whereas the maximum observed SVL of the

Guerrero specimens was 36 mm, the gravid females averaging 31.8 mm. The discrepancy in body lengths signaled the possibility of a new species of gecko and provided the impetus for further evaluation.

Because a significant amount of taxonomic confusion has resulted from studies of the genus *Phyllodactylus*, an objective approach to the determination of the taxonomic status of the new form was desired. Before the investigation was initiated a null hypothesis to be tested was formed: the new population is not genetically isolated from any other population of leaf-toed geckos and therefore does not represent a new species. The null hypothesis must be rejected to show that the new population is an undescribed species.

MATERIALS AND METHODS

Abbreviations for all specimens reported herein are: ROM – Royal Ontario Museum; TCWC – Texas Cooperative Wildlife Collection, Texas A & M University; CAS – California Academy of Sciences, San Francisco; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley; LACM – Los Angeles County Museum of Natural History. Field numbers and UCLA lab numbers (now in the ROM) are given for tissue and chromosome slide numbers.

Karyological preparations were made from meiotic and mitotic suspensions by colchicine/hypotonic citrate techniques of Patton (1967) except that the animals were injected with colchicine 12 hr in advance of euthanasia. Centromeric position classification follows that of Levan *et al.* (1964). For karyological comparisons the following taxa (and number of specimens) were examined: *Phyllodactylus* new species (1); *P. bugastrolepis* (3); *P. delcampi* (1); *P. duellmani* (2); *P. lanei* (1); *P. unctus* (9); *P. paucituberculatus* (3); *P. nocticolus* (4); *P. nocticolus sloani* (3); *P. xanti* (3). The localities and museum deposition are given in Appendix 1.

The allozyme comparison utilized four specimens each of *P. duellmani*, (CAS 146358, 147360, 147362, and 147363) and the new population of *Phyllodactylus* (CAS 147354-56; TCWC 55124). Tails were autotomized from living specimens within two weeks of capture and immediately stored frozen in deionized water at -25°C. Tissues were thawed, refrozen, and maintained at -25°C. Subsequently, tissue samples were individually thawed, minced, and refrozen in fresh deionized water at -25°C for 18 hr. Preparations were thawed and centrifuged at 30,000 g for 30 min.

Horizontal starch gel electrophoresis (Murphy *et al.*, 1996) was used to separate the products of 14 presumptive gene loci including L-lactate dehydrogenase (Ldh-A, Ldh-B; EC 1.1.1.27), malate dehydrogenase (Mdh-1, Mdh-2; EC 1.1.1.37), glutamate dehydrogenase (Gtdh-A; EC 1.4.1.2), phosphoglucosmutase-1 (Pgm-1; EC 5.4.2.2), nonspecific dipeptidases using L-leucyl-L-alanine as substrate (Pep-1, Pep-2; EC 3.4.-.-), glycerol-3-phosphate dehydrogenase (G3pdh-A; EC 1.1.1.8), non-specific esterases (Es-1), creatine kinase (Ck-A; EC 2.7.3.2), adenylate kinase (Ak-1; EC 2.7.4.3), and general proteins resolved using Amido Black (Gp-1, Gp-2). The following gel and electrode bath buffer systems (given as “gel/electrode”) were used in the electrophoretic analysis to separate the various gel products: lithium borate/tris-citrate (ES); tris-HCl acid/tris (GP, PEP); tris-citrate/borate (pH 8.7) (LDH, PGM); tris-citrate II/tris-citrate II (G-3-PDH); tris-citrate-EDTA (CK, AK, and MDH). Enzyme and locus nomenclature follow Murphy *et al.* (1996).

Scale counts, measurements, and description follow that of *P. duellmani* (Dixon, 1960) to a great extent. However, additional measurements and counts are given along with standard deviations to allow comparison of the new population with other forms.

RESULTS

Eleven populations of leaf-toed geckos have been karyotypically examined (Appendix 1). All populations of *Phyllodactylus* were found to have a diploid complement of 38 chromosomes, except *P. paucituberculatus*, which has a 2N of 32. Relative to centromeric position, all chromosome pairs were recorded as being acrocentric, with exceptions found in *P. bugastrolepis* and the new form of *Phyllodactylus*. In the new form the second largest pair of chromosomes was found to be subtelocentric whereas in *P. bugastrolepis* two of the smaller pairs were determined to be metacentric. In all taxa, there is no distinct break between macro- and microchromosomes. The karyotypes consist of a graded series and are consistent with the definition of a gekkonid karyotype (Gorman, 1973).

An electrophoretic comparison was made between the new form and *P. duellmani*. Products of 14 presumptive gene loci were resolved. Five (Mdh-2, G3pdh-A, Ck-A, Gp-1, and Gp-2) were found to be monoallelic for both populations. The products of six loci (Ldh-A, Ldh-B, Mdh-1, Pep-1, Es-1, and Ak-1)

were monoallelic within species, but fixed for different alleles between species. Gtdh-A and Pgm-1 were found to be polymorphic in the new population with the rare Gtdh-A allele and the common Pgm-1 allele being shared by *P. duellmani*. Polymorphism at Gtdh-A was detected by the presence of a single heterozygote. No heterozygotes were found at Pgm-1. A single heterozygote was found at the Pep-2 locus in *P. duellmani* although neither allele was shared with the new population. Quantification of the electrophoretic data (Nei, 1972) yields a genetic distance (*D*) of 0.839 (standard error [SE] of ± 0.306) and a genetic identity (*I*) of 0.432.

Table 1 summarizes the morphological characteristics of the new form and compares them to the other species of *Phyllodactylus*. Only two meristic characteristics would serve to separate juvenile *P. bordai* from the new form: 1) the number of scales across the venter, 26-31 and 20-25, respectively, and 2) the percent of lower labials juxtaposed with the premental which is 22% in *P. bordai* and 100% in the new form.

DISCUSSION

Molecular and cytological comparisons were limited by available tissue samples. In particular, no samples of *P. bordai* were available for allozymic and karyological comparison. Ideally, the species description should be based on phylogenetic relationships and this analysis is currently in progress using DNA sequence data for most of the described Mexican taxa. Although the new form is morphologically very similar to *P. duellmani* (Table 1), it is very distinct genetically. No gene flow occurs between the two populations. Insight into the extent of genetic distinctiveness can be gleaned from *D* values. If gene flow were occurring, we would expect to find a very low *D* (*D* < 0.1). Generalizations about *D* values between populations have been made and these values provide a relative base comparison to examine genetic distinctiveness between *P. duellmani* and the new form. Most local populations of reptiles appear to be separated by a *D* value of 0.0 to 0.1, most subspecies by around 0.1 to 0.2, and most species by 0.2 or greater (e.g., Adest, 1977; Avise, 1976). The genetic distance between the new population and *P. duellmani* (*D* = 0.839) is substantial. It could be argued that this estimation of *D* is high because of the relatively small number of loci surveyed. However, if the number of loci surveyed were doubled (*n*₁ = 28)

TABLE 1. The mean values of 12 characters for 12 species of *Phyllodactylus* from Dixon (1964) compared to the new species.

	<i>P. unctus</i>	<i>P. paucituberculatus</i>	<i>P. duellmani</i>	<i>P. delcampi</i>	<i>P. bordai</i>	<i>P. davisi</i>	<i>P. muralis</i>	<i>P. homolepidurus</i>	<i>P. xanti</i>	<i>P. lanei</i>	<i>P. tuberculatus</i>	<i>P. insularis</i>	new species
% First labial-postmental contact	74%	0%	25%	36%	22%	43%	50%	82%	50%	4%	19%	100%	100%
Scales bordering postmentals	7.0	7.0	7.0	6.3	5.6	7.1	8.0	6.7	8.3	5.0	5.9	7.1	6.4
Scales bordering internasals	6.0	5.3	6.6	5.7	5.1	6.6	7.0	0.5	0.1	5.4	6.8	7.4	5.1
Scales bordering nostril and eye	11.4	10.2	10.8	13.8	10.9	11.6	13.1	11.9	10.8	11.6	12.3	13.7	9.8
Interorbital scales	19.3	17.5	15.6	20.2	15.2	19.2	21.4	20.5	19.2	15.1	18.9	23.7	17.5
Third labial-snout scales	21.7	19.5	19.9	21.0	19.4	23.7	26.1	22.5	16.5	21.3	24.1	29.4	17.8
Rows of tubercles across dorsum	0.0	10*	11.2	14.6	14.9	15.7	13.6	13.2	13.6	15.8	15.2	15.4	14.5
Tubercles from head to tail	0.0	28.7*	37.1	63.4	32.9	41.6	33.1	35.9	37.0	34.1	35.6	49.5	33.2
Tubercles from axilla to groin	0.0	14.7*	24.0	37.0	18.0	22.9	17.0	20.2	24.1	17.9	19.3	28.0	18.9
Scales across venter	29.4	25.2	23.6	30.0	28.8	30.8	29.6	30.3	34.4	30.1	30.1	30.3	24.6
Lamellae of fourth toe	12.8	13.5	11.5	15.0	12.6	12.2	12.3	14.1	11.2	15.2	13.6	13.7	10.1

* Murphy and Papenfuss (1980) report that some specimens of *P. paucituberculatus* are totally void of tubercles.

without detecting any additional allelic differences between both populations, then D would be about 0.3, still well within the values of D calculated between species, and not between subspecies or populations. These electrophoretic data strongly support the recognition of the new population as being distinct from *P. duellmani*.

The new form was found to be morphologically distinct from all North American species of *Phyllodactylus* (Table 1). The most similar species include *P. bordai*, *P. davisii*, *P. lanei*, and *P. tuberculatus*. Of these species *P. davisii* is extralimital in its geographic distribution, being found in the Mexican states of Colima and coastal Michoacan. The maximum SVL of both *P. lanei* and *P. tuberculatus* (> 100 mm and > 78 mm, respectively [Dixon, 1964]) is greater than twice that of the tiny gravid females of the new population. Thus, we are left with the null hypothesis that *P. bordai* and the new population are one and the same. Only two scale characteristics serve to separate juvenile *P. bordai* and the new population: the number of scales across the venter and the percent of first lower labials juxtaposed with the mental scale.

Perhaps the most compelling evidence that *P. bordai* and the new population represent genetically isolated populations comes from data on the body size at which reproductive maturity is first attained. Three of the paratypes are gravid females, each containing a single egg, although two eggs are typical for most *Phyllodactylus* (Dixon and Huey, 1970). A male paratype was histologically determined to have meiotically active testes. Female *Phyllodactylus* may reach sexual maturity before gaining maximum adult body size, as evidenced by the presence of eggs in small females (Dixon, personal communication; Murphy, unpublished data). However, it is difficult to assess the analogous situation in males. Indeed, there are no data on the minimum body size at which male *Phyllodactylus* attain sexual maturity.

Dixon (personal communication) reported a single gravid female (one egg) of *P. paucituberculatus* that had a SVL of 33.5 mm; this is identical to the body length of the largest gravid female of the new population (TCWC 55124). However, *P. paucituberculatus* is a relatively small species having a maximum body size of only 42 mm (Dixon, 1960). Further, *P. paucituberculatus* can be easily distinguished from the new form by its reduced number of tubercles from axilla to groin and the lack of infralabial/postmental contact. The small, gravid female *P. paucituberculatus* reached sexual maturity at about 80% of the maximum adult size. And Dixon (1964) noted that

sexually mature individuals of one of the smallest known species, *P. duellmani*, had a SVL of 32 mm; the maximum SVL was reported to be 43 mm. Thus, *P. duellmani* apparently reaches sexual maturity at about 75% of the maximum adult size. This value is very close to the minimum adult SVL that Dunham *et al.* (1978) report for insular populations of *Uta* in which individuals reached sexual maturity at 77-88% of adult SVL. In addition, Maisano (2001) provides data on size at maturity and maximum SVL for 14 species of lizards. Most of these species attain sexual maturity at 70-93% maximum SVL, the exception being the viviparous *Xantusia riversiana*, which can attain maturity at 62%; two gekkotans attained maturity at 77% (*Coleonyx variegatus*) and 84% (*Gonatodes albogularis*). Further, Regaldo (2006) concluded that seven species of *Sphaerodactylus* reach sexual maturity at approximately 88% maximum SVL (range = 85-90). If females of the new form were early-maturing *P. bordai*, then they would have attained sexual maturity at a minimum of 50% adult SVL (the smallest gravid female of the new form has a SVL of 30.3 mm and the largest known adult *P. bordai* has a SVL of 60 mm; Dixon, 1964). Within the new population, maturity appears to be attained at 88% maximum SVL. This ratio of minimal SVL for reproductive maturity to maximum body size is twice as low as that observed for other species of small lizards. If the reproductively mature specimens of the new population were young adults, the expected maximum SVL for the species would only be 41 mm. Specimens of the new form were collected on three separate occasions, and at different months of the year (June, November and January). All individuals were approximately the same, small size. Thus, it seems highly unlikely that the estimates of body size represented an artifact of collecting. These data strongly support the recognition of the new population as a distinctive population, genetically isolated from all other populations of leaf-toed geckos. Thus, the null hypothesis is rejected.

Species Account

Phyllodactylus papenfussi sp. nov.
(Fig. 1)

Holotype – ROM 45098 (Field No. ROM 35313), an adult female from 10.8 km (by road) south of Mezcala on old Hwy 95 (17°50'44"N, 99°34'36"W, 594 m elevation) Guerrero, Mexico, collected 22 June 2001

by Johan Lindell, Fausto R. Méndez de la Cruz, and Francisco Rodríguez.

Paratypes – IHB 21957 (ROM 45099; Field No. ROM 35314), an adult female from 10.8 km (by road) south of Mezcala on old Hwy 95 (17°50'44"N, 99°34'36"W, 594 m elevation) Guerrero, Mexico, collected 22 June 2001 by Johan Lindell, Fausto R. Méndez de la Cruz, and Francisco Rodríguez; TCWC 55123 (adult male; CSL 4177 and UCLA Lab No. 77-1006), TCWC 55124 (adult female, gravid with one egg; original numbers CSL 4176 and UCLA Lab No. 77-1007), TCWC 55125 (CSL 4178, UCLA Lab No. 77-1005), TCWC 55126 (CSL 4179) all taken from 24.9 km south of Mezcala (by Mex. Hwy. 95), 780 m elevation, west side of an abandoned road tunnel on the west side of Mexico Highway 95, Guerrero, Mexico, taken 24 November 1977 by Robert W. Murphy, Carl S. Lieb, and John E. Cadle; CAS 145358, 145359 (adult female, gravid with one egg), and 147353-57 (UCLA Lab No. 78-78 to 78-82, respectively) from 12 km south of Mezcala (by Mex. Hwy. 95), taken 20 January 1978 by Theodore J. Papenfuss and John E. Cadle; MVZ 112381 (TJP 10206), Rio Balsas at Mexico Highway 95, collected 31 July 1974 by Theodore J. Papenfuss.

Diagnosis – *Phyllodactylus papenfussi* can be separated from all other North American species of *Phyllodactylus* by its small size. It can also be distinguished from all North American and Middle American species, except *P. duellmani*, in having a low mean value of loreal scales from eye to snout (9.6) and from all species except *P. duellmani* and *P. paucituberculatus*



FIGURE 1. Photograph of a living specimen of a paratype of *Phyllodactylus papenfussi* in defensive posture.

in having a low mean value of scales across the venter (23.6); from *P. duellmani* and *P. paucituberculatus* it can be distinguished by a larger mean value of transverse tubercle rows (13.8) and from *P. duellmani* in having a lower mean value of a) tubercles from head to tail (31.8), b) tubercles from axilla to groin (18.9) and c) six transverse rows of tubercles across the tail base (including juveniles).

Description of holotype – (All bilateral counts are given as left/right). Adult female, head not greatly flattened, neck slightly constricted, canthal ridges distinct, slightly depressed between; slight depression in frontal region; rostral twice as wide as high, upper half divided medially; nostril bordered by a single supranasal, first labial, rostral, and two postmentals; supranasals slightly wider than long, separated by a single granular; 8 scales between anterior edge of orbits; 14 scales across snout at second labial, 20 at third; 11/11 loreal scales between eye and nostril; 7/7 enlarged supralabials; 1st supralabial with anterior, dorsal projection in contact with nostril; 6/6 enlarged infralabials; scales bordering supralabials somewhat rounded, not imbricate; supercillaries weakly pointed; diameter of eye contained in snout length slightly less than twice; auricular opening elongate, small; occipital scales approximately equal to interorbital scales, with intermixed, larger rounded tubercles; mental longer than wide, “V” shaped when viewed from below; two postmentals, narrowly in contact with each other and contacting first infralabials, postmentals followed by a transverse row of six rounded scales, laterally decreasing in diameter; body granular above with fourteen longitudinal rows of distinctly enlarged, strongly keeled tubercles; dorsally inter-tuberculate space rarely greater than diameter of tubercles; eight of these rows extend from anterior to insertion of arm to base of tail; 30 tubercles in a median dorsal row from rear of head to base of tail, 21 between mid-arm and leg insertion; 23 rows of flat, cycloid scales across venter, 39 from mid-arm insertion to mid-leg insertion, 57 from gular region to anus; ventral abdominal scales about two times larger than lateral body scales, four times larger than gular scales.

Upper arm with flat imbricate scales on anterior and posterior surfaces; lower arm similar anteriorly, dorsally and ventrally granules non-imbricate with interspaced rounded tubercles. Femur scales similar to arm with a single row of tubercles dorsally and granular on posterior surface; lower leg with four longitudinal rows of keeled tubercles intermixed with granular and imbricate scales.

Sub-digital lamellae formula for hand 6/6-7/7-9/9-10/9-7/8, fourth finger longest; foot lamellae formula 6/5-8/8-9/10-9/10-8/9; terminal pads slightly longer than wide, tips rounded; claw usually completely hidden between terminal pads; lateral claw sheath scales extended slightly beyond toe pad; fourth toe longest.

Tail autotomized near base.

Measurement of holotype – In mm: SVL 33.78; axilla-groin 16.19; head length 12.11; head width 7.07; snout length (to eye) 2.88; eye diameter 1.6; auricular opening (maximum) 0.3; length of fourth finger 2.19; length of fourth toe 2.3; width between eye superciliaries 3.34; ear-snout length 8.28; internarial 1.01; upper arm length 2.64; lower arm length (to end of third toe) 5.81; upper leg length 5.06; lower leg length (to end of third toe) 8.51.

Karyotype of single paratype – Karyotype is a diploid complement of 38 chromosomes consisting of a graded series of 26 acrocentric and 2 subtelocentric chromosomes. The subtelocentric chromosome pair is the second largest pair.

These data represent chromosome complements analyzed from 40 meiotic cells taken from the paratype TCWC 55123 (CSL 4177 and UCLA Lab No. 77-1006). Reproductive maturity of the tiny male was confirmed by the presence of numerous Anaphase II and Metaphase II cells.

Pattern and color (in life) – Light brown above with seven faint, but darker pairs of spots; pairs separated by a light mid-dorsal vertebral stripe; legs and arms with dark brown spots except ventrally; dark stripe from nostril through eye to base of head; whitish below.

Distribution – The new form is restricted in distribution, found only in the Plan de las Liebres valley in the Cañon del Zopilote region south of Mezcala in the state of Guerrero.

Variation – All meristic and morphometric data are given below to provide a base for statistical comparisons; the data are represented as follows: range, mean \pm one standard deviation (SD; N-1 weighting). Sample size (n) is 14 for all characteristics except adult SVL where n = 12.

Measurements and ratios – In mm: SVL of adults 30.3-36.6, 33.95 ± 2.1 ; SVL of juveniles 22.5 and

28.9; axilla-groin/SVL 0.37-0.48, 0.44 ± 0.02 ; head length/SVL 0.30-0.36, 0.33 ± 0.02 ; head width/SVL 0.19-0.23, 0.20 ± 0.01 ; snout length/SVL 0.09-0.13, 0.11 ± 0.01 ; eye diameter/SVL 0.05-0.08, 0.06 ± 0.004 ; ear diameter/SVL 0.02-0.05, 0.03 ± 0.01 ; fourth finger length/SVL 0.05-0.08, 0.06 ± 0.004 ; fourth toe length/SVL 0.07-0.09, 0.08 ± 0.01 ; distance between eyes/SVL 0.09-0.12, 0.10 ± 0.01 ; distance from ear to snout/SVL 0.23-0.32, 0.25 ± 0.02 ; internarial distance/SVL 0.03-0.04, 0.04 ± 0.002 .

Counts – Bilateral meristic data given left/right: canthal ridge 8-11, $9.9 \pm 0.9/8-11, 9.7 \pm 1.1$; scales across snout between second labials 12-15, 13.5 ± 0.9 ; scales across snout at third labial 17-21, 18.5 ± 1.3 ; granules in contact with nasal series 5-8, $6.8 \pm 0.9/5-7, 6.7 \pm 0.9$; supralabials 7-10, $7.6 \pm 1.0/7-10, 7.6 \pm 0.7$; infralabials 6-9, $7.4 \pm 0.8/6-8, 6.8 \pm 0.5$; no granules in contact with mental; granules in contact with first infralabial 1-2, $1.1 \pm 0.5/1-2, 1.1 \pm 0.5$; scales across venter 20-26, 24.3 ± 1.6 ; ventrals between mid-arm and mid-leg 35-41, 37.7 ± 2.0 ; supralabial below center of eye 6-8, $6.6 \pm 0.8/6-7, 6.7 \pm 0.5$; infralabial below center of eye 5-8, $5.9 \pm 0.7/5-6, 5.5 \pm 0.5$; tubercles between mid-arm and mid-leg 22-25, 23.3 ± 1.1 ; transverse tubercles 14-16, 14.5 ± 0.8 ; scales between middle of orbits 14-19, 17.2 ± 1.5 ; scales between anterior edge of orbits 9-12, 11.1 ± 0.9 ; tubercles from base of head to tail 32-37, 33.2 ± 1.6 ; tubercles from axilla to groin 18-21, 19.9 ± 0.8 ; tubercles across base of tail 6; scales bordering postmentals 5-7, 6.1 ± 0.8 ; scales bordering internasals 4-6, 5.1 ± 0.7 ; lamellae on fourth finger 7-10, $8.9 \pm 0.9/8-10, 9.0 \pm 0.9$; lamellae on fourth toe 9-11, $10.1 \pm 0.7/7-12, 10.4 \pm 1.3$.

Variation in color pattern (in 70% ethanol) – Typical of *Phyllodactylus*, color pattern varies considerably. Holotype has relatively little pigmentation; most other specimens have a pronounced dark stripe from snout over shoulder to past arm insertion and considerable pigmentation on head (Fig. 1, in life); dark body patterns appear both as transverse rows and random, interrupted in 9 of 12 by a light mid-dorsal stripe; ventral pigmentation varies from very light to moderate.

Etymology – The species is named for Theodore J. Papenfuss, who collected the first known specimen (MVS 112381), and in recognition of his outstanding worldwide collecting efforts and his openly assisting the research efforts of others.

RESUMEN

Se describe una nueva especie diminuta de *Phyllodactylus* Gray procedente de Guerrero, Mexico. La especie parece ser la más pequeña del geco dedos de hoja. El cariotipo diploide consiste de una serie graduada de 36 cromosomas acrocéntricos y 2 subtelo-céntricos; el par telocéntrico es el segundo de los más grandes. La forma nueva es morfológicamente muy similar a *P. duellmani*, pero es muy diferente electroforéticamente con una distancia genética de 0.839. Además, la nueva población es merísticamente muy similar a *P. bordai*, distinguiéndose por el tamaño pequeño que presenta durante la madurez sexual y por el número de escamas ventrales transversales.

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APPENDIX 1

Specimens examined

The following is a list of Leaf-toed geckos, genus *Phyllodactylus*, examined in the karyotypic analysis. The Mexican states where the specimens were collected are listed. Numbers in parentheses refer to the number of individuals (n) examined per species. Precise localities are available from the museums where the voucher specimens are deposited.

Phyllodactylus papenfussi (1). Mexico: Guerrero (TCWC 55123).

Phyllodactylus duellmani (3). Mexico: Michoacan (CAS 147358-147360).

Phyllodactylus lanei (1). Mexico: Guerrero (LACM 127453).

Phyllodactylus delcampi (1). Mexico: Guerrero (LACM 127449).

Phyllodactylus unctus (6). Mexico: Baja California del Sur (CAS 147371-147376).

Phyllodactylus xanti (2). Mexico: Baja California del Sur (CAS 147377-147378).

Phyllodactylus nocticolus (7). Mexico: Baja California (Norte) (CAS 147364-147370).

Phyllodactylus nocticolus sloani (5). Mexico: Baja California (Norte) (CAS-KS 17-21).

Phyllodactylus bugastrolepis (1). Mexico: Isla Santa Catalina, Baja California del Sur (CAS 139698).

Phyllodactylus paucituberculatus (5). Mexico: Michoacan (CAS 147203-147208).