



Taxonomic changes and description of two new species for the *Phyllodactylus lanei* complex (Gekkota: Phyllodactylidae) in Mexico

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Abstract

An integrative taxonomy approach was implemented based on analysis of genetic, phylogenetic, morphological and ecological data to identify the cryptic diversity within the *Phyllodactylus lanei* complex. At least six species can be identified, of which four are currently considered subspecies: *Phyllodactylus lanei*, *Phyllodactylus rupinus*, *Phyllodactylus isabelae*, *Phyllodactylus lupitae* and two corresponding to undescribed taxa, which are identified and described in this contribution. These differ from other Mexican geckos in several characters: genetic distance (DNAmt), position in molecular phylogeny (concatened data DNAmt+DNAnu), species tree, morphological characters such as snout-vent length, longitudinal scales, tubercles from head to tail, interorbital scales, scales across venter, third labial–snout scales and rows of tubercles across dorsum; there are also differences in their bioclimatic profiles (temperature and precipitation) and geographical distribution. The most recent studies on taxonomy and evolution of Mexican geckos (*Phyllodactylus*) show that the diversity of this group of reptiles is currently underestimated, suggesting that more research and conservation efforts are should be addressed at these lizards.

Key words: molecular phylogenetics, endemic geckos, diversity, species validation, morphology, bioclimatic profiles, integrative taxonomy, species tree

Resumen

Se implementó un enfoque de taxonomía integrativa con base en análisis de datos genéticos, filogenéticos, morfológicos y ecológicos para identificar la diversidad críptica dentro del complejo *Phyllodactylus lanei*. Al menos seis especies pueden ser identificadas, de las cuales, cuatro actualmente son consideradas subspecies: *Phyllodactylus lanei*, *Phyllodactylus rupinus*, *Phyllodactylus isabelae*, *Phyllodactylus lupitae* y dos corresponden a taxones no descritos aun, mismos que son identificados y descritos en la presente contribución. Éstos se diferencian de otros geckos mexicanos a partir de distancia genética (DNAmt), posición en la filogenia molecular (datos concatenados DNAmt+DNAnu), en el árbol de especies, caracteres morfológicos tales como longitud hocico-cloaca, escamas longitudinales, tuberculos cabeza-cola, escamas a través del vientre, escamas interorbitales, numero de escamas a través de la tercer escama labial, filas de tuberculos a través del dorso; también muestran diferencias en sus perfiles bioclimáticos (temperatura y precipitación) y distribución geográfica. Los estudios más recientes sobre taxonomía y evolución de los geckos mexicanos (*Phyllodactylus*) demuestran que la diversidad de este grupo de reptiles se encuentra actualmente subestimada, por lo tanto, sugerimos que se requieran mayores esfuerzos en investigación y conservación para este tipo de lagartijas.

Palabras clave: filogenia molecular, geckos endémicos, diversidad, validación de especies, morfología, perfiles bioclimáticos, taxonomía integrativa, árbol de especies

Introduction

The family Phyllodactylidae includes 10 genera and 130 species of geckos widely distributed in Africa, the

Mediterranean region, Central and South America and the Caribbean Islands. They inhabit diverse ecosystems, although most species occur in dry regions or desert climates (Murphy *et al.* 2009). The genus *Phyllodactylus* Gray, 1828 is the largest group, with 48 species of nocturnal geckos that are typically found in rocky habitats (Vitt & Caldwell 2014; Uetz & Hošek 2016). In Mexico 15 species of *Phyllodactylus* geckos are distributed of which 13 are endemic; this highlights the importance of the genus for herpetofaunal richness of Mexico.

The Lane's leaf-toed gecko, *Phyllodactylus lanei* Smith, 1935, is a medium-sized gecko which is morphologically similar to *P. tuberculatus* Wiegmann but differs because it has a smaller number of interorbital scales, a white ventral coloration and a smaller number of scales across the snout at the level of the third labial scales (Dixon 1964). In a review of the genus *Phyllodactylus*, Dixon (1964) described two subspecies for *P. lanei* based on morphological character analysis and geographical distribution, in order to generate "natural" classifications and contribute more precise knowledge in the fields of systematics and taxonomy in this group of geckos. As a result of his analysis, he recognized the nominate subspecies *P. l. lanei* for the populations of the state of Guerrero and *P. l. rupinus* Dixon for the populations of the states of Michoacan and Jalisco. Later, Castro-Franco & Uribe-Peña (1992) described two new subspecies based on a study of morphological characters of specimens collected in Mexican Pacific islands, *P. l. isabelae* Castro-Franco & Uribe-Peña collected on the Marietas Islands and *P. l. lupitae* Castro-Franco & Uribe-Peña endemic to the island El Coral (also known as La Peña Island). Both islands are along the coast of Nayarit. It is necessary to highlight that these studies did not fully resolve the systematics of the *P. lanei* complex and several authors have commented on the taxonomic problem of this group of geckos, as well as the great intra and interspecific morphological variation, and they affirm that it is necessary to incorporate more data to fully resolve the systematics of the genus *Phyllodactylus* in Mexico (Dixon 1964; Murphy *et al.* 2009; Blair *et al.* 2015; Ramírez-Reyes *et al.* 2017).

Few studies have been performed on the molecular systematics of the genus *Phyllodactylus* in Mexico to date. Blair *et al.* (2009) performed the first study of systematics and taxonomy based on molecular data and determined the phylogenetic relationships between insular and continental species of the genus *Phyllodactylus* in Mexico. Their findings demonstrated genetic evidence of the validity of *P. nocticolus* Dixon as a distinct species and sister of *P. xanti* Cope and *P. unctus* Cope. The genetic studies developed by Blair *et al.* (2009; 2015) and Ramírez-Reyes *et al.* (2017) show that geckos of the genus *Phyllodactylus* in Mexico possess a high molecular cryptic diversity, since these geckos maintain very conserved morphologies, which contrast deeply with the genetic variation that is present in some species and populations. In particular, the study of molecular systematics and species delimitation of the *P. lanei* complex elaborated by Ramírez-Reyes *et al.* (2017) evidenced the existence of cryptic lineages, which evolve independently and should be considered as species, and also supports taxonomic changes for the four subspecies currently recognized within the *P. lanei* complex. The main objective of the present contribution is to formally propose taxonomic changes within the *P. lanei* complex, as well as present the description of two new continental species through of analysis of genetic, morphological and ecological characters.

Materials and methods

Sampling. Between 2013 and 2014 tissue samples were collected from 73 individuals and 31 reference specimens from populations of the four subspecies of the *P. lanei* complex (*P. l. lanei*, *P. l. rupinus*, *P. l. lupitae*, *P. l. isabelae*) through their geographic range (Fig. 1), including the type localities of each taxon (Dixon 1964; Castro-Franco & Uribe-Peña 1992). We obtained tail tips less than 3 cm in length of each individual captured, which were maintained in 96% ethanol and preserved at the Institute of Ecology (IE-UNAM). Once the tissue samples were obtained, we measured the snout-vent length (SVL) and later most of the individuals were released at the same collection site. Voucher specimens that were kept (*P. isabelae*: MZFC 28709–28713, *P. lupitae*: MZFC 28714–28718, *P. lanei*: MZFC 28725–28732, *P. krobotkini* **sp. nov.** MZFC 28735–28739, *P. rupinus* 28767–28771, *P. benedettii* **sp. nov.** MZFC 28773–28774) were fixed in 96% ethanol and preserved in 70% ethanol, later deposited in the herpetological collection of the Museum of Zoology "Alfonso L. Herrera" at the Faculty of Sciences (MZFC-UNAM). In addition, tissue samples from two species of geckos were requested from the herpetological collection of MZFC: *P. bordai* Taylor from a population of Cuicatlán Valley, Oaxaca and a sample of *P. tuberculatus* from Chihuahua, the information generated was incorporated into the analysis (Appendix I).

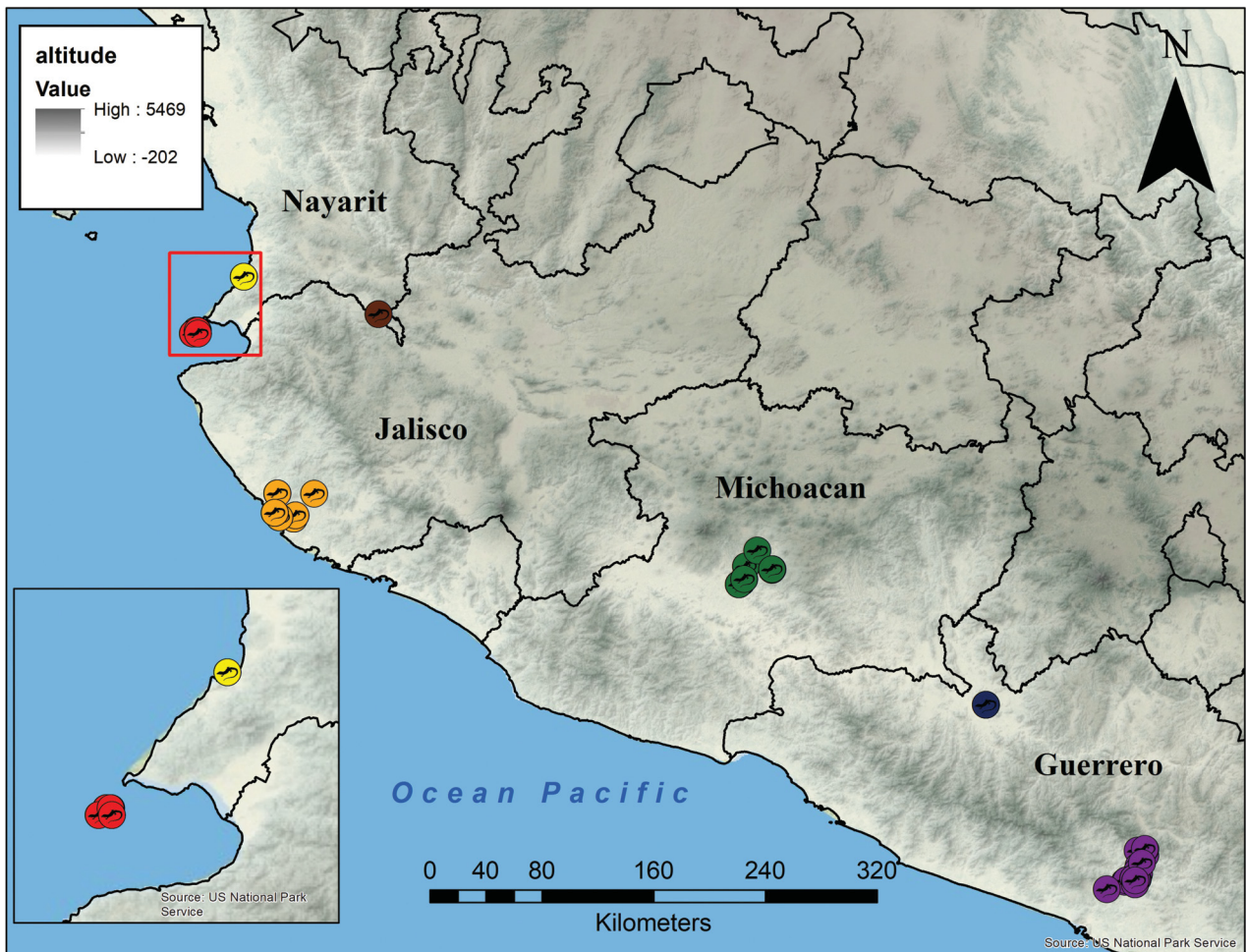


FIGURE 1. Map of geographical distribution of the species of the *P. lanei* complex. The colored circles represent populations of each species of the *P. lanei* complex and are congruent with the species tree (see results): *P. lanei* (violet), *P. kropotkini* sp. nov. (blue), *P. rupinus* (green), *P. benedettii* sp. nov. (orange), *P. isabelae* (red), *P. lupitae* (yellow). *Phyllodactylus* sp. a genetically distinct undescribed population, is shown in dark brown. Localities from museum specimens and tissue from collections not shown.

Sequences and genetic divergence. We obtained genomic DNA from tissues with QIAGEN DNeasy Blood and Tissue Kit, following the suggested protocols. For more information about DNA extraction, sequencing and molecular biology see Ramírez-Reyes *et al.* (2017). Sequence chromatograms were visualized with ChromasPro v1.7.6 (2012) and edited with BioEdit v7.2.5 (Hall, 1999). Correct identification of the amplified fragments was performed with BLAST (<http://www.ncbi.nlm.nih.gov>). Next, sequences were aligned using the online version of MAFFT (<http://www.ebi.ac.uk/Tools/msa/mafft/>) and visualized with Mesquite v3.04 (Maddison & Maddison, 2015). Coding genes were translated into amino acids to verify for stop codons and confirm the absence of pseudogenes. Heterozygous alleles were identified using Phase (Stephens *et al.* 2001) implemented in DnaSP v5.10 (Librado & Rozas, 2009; Unmack *et al.* 2012). Final sequences were deposited in GenBank (Appendix I). Considering that evolutionary distances are fundamental to study molecular evolution and are widely used in phylogenetic reconstruction and divergence time estimation, we estimated nucleotide distances for Cyt b, using the Tamura-Nei model, implementing rate variation and pattern heterogeneity, with MEGA 6 (Tamura *et al.*, 2013). In addition, we estimated mitochondrial DNA genetic differentiation with F_{ST} with DnaSP v5.10 (Librado & Rozas, 2009), for more values of genetic diversity and divergence see Ramírez-Reyes *et al.* (2017).

Concatenated gene trees. We amplified mitochondrial DNA (DNAm) sequences of the cytochrome b (Cyt b, 310 bp) and 16S rRNA (16S, 530 bp) genes and nuclear DNA (DNAnu) of the C-mos (proto-oncogene, 420 bp) and Brain-Derived Neurotrophic Factor (BDNF, 420 bp) genes (Carranza 2002; Carranza *et al.* 2006; Blair *et al.* 2009; Šmid *et al.* 2013a; Ramírez-Reyes *et al.* 2017); amplification conditions were standardized from Blair *et al.*

(2009). The best evolution models for each gene obtained with jModelTest v2.1.6 (Darriba *et al.* 2012) under AIC were: Cyt b (TIM2+G, $\Delta=0.0$), 16S rRNA (TIM2+I+G, $\Delta=0.0$), BDNF (TrN+I, $\Delta=0.0$), C-mos (TPM3uf+I+G, $\Delta=0.0$); for concatenated mitochondrial (16S+Cyt b) and nuclear genes (C-mos + BDNF) were GTR+I+G, $\Delta=0.0$ under AIC for both. Maximum likelihood analyses were implemented in RaxmlGUI v1.3 (Silvestro & Michalak 2012). Support of branches was assigned by a bootstrap analysis with 1000 pseudoreplics. Bayesian Inference analyses were implemented in MrBayes v3.2.5 (Ronquist *et al.* 2012). We used two runs of four Markov chains for 20 million generations, with sampling intervals every 5000 generations. 25% of sampled trees were discarded as burn-in and a majority consensus tree was generated; this consensus tree presents the values of posterior probabilities (pp) of support for each branch. In both cases, branches with bootstrap (ML $\geq 70\%$) and pp (BI $\geq .95$) were considered highly supported (Šmid *et al.* 2013b). Adequate sampling for all parameters in Bayesian analyses were evaluated with Tracer v1.6 (Rambaut *et al.* 2014) with ESS values greater than 200.

Species tree. A species tree was estimated using a multispecies coalescence approach implemented in *BEAST (Heled & Drummond 2010) with BEAST 2 (Bouckaert *et al.* 2014). Mitochondrial genes and phased nuclear alleles were used in *BEAST resulting in six independent partitions. For this analysis we did not incorporate the haplotypes recovered from Nayarit and Oaxaca as independent lineages (identified as III, IV and X in the gene trees, see results) since only one individual was analyzed by population, therefore we considered it pertinent to exclude haplotypes from these lineages to infer the species tree. We performed two independent runs of 20 million generations sampling every 5000 generations, of which 10% were discarded as burn-in. Models and specifications of priors were as follows: we used a GTR substitution model for each partition with frequencies of all nucleotides and proportion of invariant sites, these were indicated as empirical to be estimated by the program. We used a lognormal relaxed clock for the species tree (estimated), and for the population size we used a linear model with constant root. We used a Yule speciation process and random starting tree. Convergence for all model parameters was assessed by examining Trace plots and histograms in Tracer v1.4 (Rambaut *et al.* 2014) and obtaining an effective sample size (ESS) >200 . Runs were combined using LogCombiner, and maximum credibility trees with divergence time means and 95% highest probability densities (HPDs) were produced using Tree Annotator through their respective modules implemented in BEAST 2 (Bouckaert *et al.* 2014).

Species delimitation. Species delimitation and validation was implemented in BP&P 3.3 (Yang 2015) with the total data set (DNAnu + DNAm) and analysis A10 was specified, that is, species delimitation using a fixed guide tree. For this analysis we consider the species tree recovered by *BEAST as a robust hypothesis of candidate species and phylogenetic relationships among them, due mainly to the high posterior probability values in most branches (Yang & Rannala 2010; Rannala & Yang 2013; Yang 2015). Each analysis was repeated at least twice, using 200,000 rjMCMC generations, with a burnin of 20,000 (10%), with algorithm 1 ($\alpha = 2$ and $\mu = 1$). Because the posterior probabilities of the resulting models can be affected mainly by the values of the priors (θ and τ) (Yang & Rannala 2010), in the present study we implemented four combinations of prior settings for these parameters. We used a Gamma distribution (α , β) for each model and the four respective models: (I) small effective population size and shallow divergences $\theta=G(2, 1000)$ and $\tau=G(2, 2000)$, (II) small effective population size and deep divergences $\theta=G(2, 1000)$ and $\tau=G(2, 10)$, (III) large effective population size and shallow divergences $\theta=G(2, 10)$ and $\tau = G(2, 2000)$ and finally (IV) large effective population size and deep divergences $\theta=G(2, 10)$ and $\tau=G(2, 10)$. The priors selected also constitute a close approximation to previous hypotheses of historical population sizes in the geckos of the genus *Phyllodactylus* in Mexico (Ramírez-Reyes *et al.*, 2017).

Morphological analyses. A total of 130 specimens of the *P. lanei* complex were examined for morphological analysis (morphometric and meristic characters), representative of the populations that inhabit the type localities of the taxa under study (Appendix II). It is very important to mention that the selection of the specimens under review was strictly careful, since previous studies suggest that for some taxa "each population may represent a distinct species" in some species of *Phyllodactylus* (Blair *et al.* 2015; Ramírez-Reyes *et al.* 2017); therefore, the selection of populations that conform to a species in this group of geckos should be careful and preferably be supported by molecular phylogenetic and genetic analysis to avoid increasing the taxonomic uncertainty in this group of geckos. The analyzed specimens are deposited in three national scientific collections: Colección Nacional de Anfibios y Reptiles at Instituto de Biología (CNAR-UNAM), Museo de Zoología de la Facultad de Ciencias (MZFC-UNAM) and the Colección de Anfibios y Reptiles at Escuela Nacional de Ciencias Biológicas (ENCB-IPN). Morphological characters were counted and measured by the first author (T.R.R.) using a vernier caliper; the measurements are in millimeters. The characters registered for all taxa were snout-vent length (SVL), head length (HL), digital lamellae

of fourth finger and toe (LFT), for which we count the digital lamellae from the base up, to where we find a differentiated scale (longer than wide), scales across venter (SAV) these scales were counted from the lateral scales that differ from the dorsal scales, from side to side in the middle position of the body approximately, tubercles from head to tail (THT) from the first distinguishable tubercle of the head to the last distinguishable at the level of the cloacal opening approximately, tubercles from axilla to groin (TAG), rows of tubercles across dorsum (TAD), interorbital scales (IS), scales bordering internasals (SBI), third labial–snout scales (TLS), scales bordering nostril and eye (SBNE), scales bordering postmentals (SBP) and longitudinal ventral scales (LVS) in an imaginary horizontal line that crosses the anterior legs, the medium scale towards the posterior region until cloacal opening. Additionally we measured some morphometric characters in seven species of *Phyllodactylus*: axilla-groin length (LAG), head width (HW), snout length (SL), eye diameter (ED), auricular opening (AO), length of fourth finger (LFF), length of fourth toe (LFT), width between eye supercilliaris (WES) and internasal length (LI).

We conducted multivariate analyses with morphological characters using PCA and MANOVA to determine significant differences among species of the *P. lanei* complex and between the two new proposed species. One-way ANOVA was performed to compare the mean SVL of all the species of the *P. lanei* complex. All statistical analyzes (morphometric, meristic and bioclimatic profiles) were implemented in PAST 3.13 (Hammer *et al.* 2001). In addition we used the table of characters proposed by Murphy *et al.* (2009) for the purpose of having a frame of reference on average differences for 17 species of *Phyllodactylus* in Mexico (Appendix III).

Bioclimatic Profiles. We obtained 980 occurrence records of *P. lanei* from the Global Biodiversity Information Facility database (GBIF), to which were annexed records collected by the first author of collections and databases from national scientific collections (MZFC and CNAR). The records were carefully selected to represent the populations that conform the four continental species of the *P. lanei* complex; in total 339 records were selected to elaborate the climatic profiles for each species. It is important to mention that due to the absence of meteorological stations at the islands inhabited by *P. isabelae* and *P. lupitae*, these two species were discarded for this analysis. To characterize and compare parts of the realized ecological niche for the continental species, we compiled information for 19 bioclimatic variables associated to each georeferenced record with the maximum spatial resolution of 30 arc seconds (~ 1km) from the Worldclim climate database. The geoprocessing of the data was implemented in ArcGIS 10. Multivariate analyzes by PCA and MANOVA were implemented to determine if there is any type of overlap in part of the realized niche of the species in terms of temperature and precipitation (bioclimatic profiles).

Results

Genetic differentiation. The Tamura-Nei distances demonstrated a clear pattern of genetic distance related to geographical distance. The southernmost species, *P. lanei*, showed a differentiation of more than 20% with respect to the species of the Balsas basin (*P. rupinus*), western Pacific coast (*P. benedettii* **sp. nov.**, *Phyllodactylus* sp.) and insular species (*P. isabelae* and *P. lupitae*) while from the nearest species (*P. kropotkini* **sp. nov.**) it showed a distance of 14%. The lowest genetic distances (< 10%) were obtained between the western Pacific coast and insular species. On the other hand, the paired distances F_{ST} showed high values of genetic differentiation with most species above 0.9 (Table 1).

Concatenated gene trees. Mitochondrial and concatenated gene trees (DNAnu + DNAm) recovered by ML and BI are highly congruent because they recovered the same topology with most nodes with high support values (bootstrap ML > 75% and IB pp > 0.95). The concatenated nuclear gene tree showed low resolution of the clades recovered by the mitochondrial gene tree and complete data (DNAm+DNAnu) previously reported by Ramírez-Reyes *et al.* (2017). The resolved concatenated gene trees recovered a single clade of sibling species, the insular clade is comprised of two sibling species (*P. isabelae* + *P. lupitae*), these are closely related to continental species of Western Mexico, in the state of Nayarit (clades III and IV) and with populations of the coast of Jalisco (clade V), which differs clearly from *P. rupinus* in Michoacán (clade VII). This species is related to *P. kropotkini* **sp. nov.**; both species inhabit the Balsas Basin, but the second is restricted to Tlapachuala in the state of Guerrero (clade VIII). At the base of the gene trees is *P. lanei* (clade IX), restricted to the type locality (Tierra Colorada) and also some populations of Chilpancingo, both in the state of Guerrero. *Phyllodactylus lanei* is related to an undescribed species that is distributed on the coast of Oaxaca (clade X) and the sister species of the whole complex is *P. bordai*

(Fig. 2). All recovered clades are closely related and demonstrate the monophyly of the *P. lanei* complex (clades I–X). The recovered lineages identified as *Phyllodactylus* sp. in samples from Oaxaca and Nayarit (clades III, IV and X) are not described in the present contribution due to the small sample size of specimens included in our analyses. These haplotypes were discarded for the elaboration of the species tree in *BEAST.

TABLE 1. Matrix of mitochondrial DNA (Cyt b) genetic distances between populations of the *Phyllodactylus lanei* complex from Mexico. Paired F_{ST} and Tamura-Nei distances below and above the diagonal, respectively.

	<i>P. isabelae</i>	<i>P. lupitae</i>	<i>P. benedettii</i> sp. nov.	<i>Phyllodactylus</i> sp.
<i>P. isabelae</i>	-	0.06	0.06	0.08
<i>P. lupitae</i>	0.89	-	0.09	0.12
<i>P. benedettii</i> sp. nov.	0.84	0.94	-	0.08
<i>Phyllodactylus</i> sp.	0.94	0.98	0.96	-
<i>P. rupinus</i>	0.97	0.99	0.98	1.00
<i>P. lanei</i>	0.97	0.99	0.98	0.99
<i>P. krotokini</i> sp. nov.	0.92	0.94	0.92	0.94

continued.

	<i>P. rupinus</i>	<i>P. lanei</i>	<i>P. krotokini</i> sp. nov.
<i>P. isabelae</i>	0.15	0.25	0.24
<i>P. lupitae</i>	0.15	0.25	0.22
<i>P. benedettii</i> sp. nov.	0.14	0.25	0.21
<i>Phyllodactylus</i> sp.	0.14	0.25	0.21
<i>P. rupinus</i>	-	0.22	0.19
<i>P. lanei</i>	0.99	-	0.14
<i>P. krotokini</i> sp. nov.	0.95	0.92	-

Species tree and Bayesian species delimitation. Similar to the trees solved by the concatenation method, the mitochondrial and "species" gene trees recovered the same topology by using the multispecies coalescent model, with the discarded individuals as previously mentioned (Fig 3). Posterior probabilities obtained with *BEAST showed that individuals assigned as different species have high probabilities of being metapopulation lineages that evolve independently and recovered seven candidate species within the *P. lanei* complex, which also are differentiated in the topologies of the phylogenies with concatenated data. The only difference in the resolved topology elaborated with the multispecies coalescent model with respect to the concatenated matrix is that the trees recovered two clades of sibling species. The insular clade is represented by two endemic species of the Marietas Islands and Coral Island (*P. isabelae* and *P. lupitae* respectively) and at the base of the species tree we recovered a clade composed by two sibling species *P. krotokini* sp. nov. and *P. lanei*, which are distributed in the southern part of Mexico, both in the state of Guerrero. The Bayesian delimitation of species showed that the models with higher values of posterior probability and congruence with the tree of species were the models I and II, which clearly suggest that the effective population size in this group of geckos has been historically small, as suggested Blair *et al.* (2014) in previous studies, while in the case of depth of the branches (deep and shallow) there is no significant variation in the recovery of the real number of species (Fig. 4).

Morphological analyses. The multivariate analysis by PCA (bootstrap $N=1 \times 10^5$) of meristic data for nine species of the *P. tuberosus* group (Table 2), showed that 98% of the variance is explained by the first three components, the first component (54%) is primarily loaded with the number of longitudinal scales, tubercles from head to tail and interorbital scales, the second component (26%), is loaded with the number of scales across venter in addition to the previous ones and finally the third component (18%) is mainly represented by the number of third labial-snout scales and rows of tubercles across dorsum. The graphic of the first two components (PC1 and PC2) showed a clear separation in the space of meristic variables between *P. isabelae* and *P. lanei* and a partial overlap among *P. muralis* Taylor, *P. tuberosus magnus* Taylor and *P. tuberosus*; and total overlap in *P. lupitae*, *P.*

rupinus and *P. benedettii* **sp. nov.** at least in a bidimensional space of PCA (Fig. 5). All the meristic characters are highly variable among individuals of different ages or sizes and sex, despite this, trends on average were observed in values that show taxonomic signal. For example, average values of longitudinal scales place species in two clearly differentiated groups, species with less than 60 scales, in ascending order: *P. t. magnus* (54.66), *P. isabelae* (56.2), *P. tuberculosus* (57.7), *P. muralis* (59) and the other group of species with more than 60 scales *P. lupitae* (61.8), *P. benedettii* (62.6), *P. rupinus* (63.6), *P. lanei* (66), *P. kropotkini* (67.6). In the number of scales across venter we can observe a group with less than 30 scales, in ascending order: *P. lupitae* (24.6), *P. rupinus* (26.5), *P. t. magnus* (27.3), *P. isabelae* (27.8), *P. benedettii* (29.1) and another group with more than 30 scales: *P. lanei* (30), *P. tuberculosus* (30.2), *P. kropotkini* (30.6), *P. muralis* (33). The third labial–snout scales have two groups, a group of less than 25 scales: *P. kropotkini* (20.2), *P. rupinus* (20.6), *P. lanei* (21.2), *P. isabelae* (21.4), *P. benedettii* (22.3), *P. tuberculosus* (24.2), *P. t. magnus* (24.6); and only two species of more than 25 scales *P. lupitae* (25.5) and *P. muralis* (33). The number of tubercles from head to tail obtains two groups, one with less than 30: *P. benedettii* (27.4), *P. rupinus* (28), *P. kropotkini* (28.4), *P. lupitae* (28.8), while the group of more than 30 contains *P. isabelae* (32.2), *P. muralis* (33), *P. lanei* (33.2), *P. tuberculosus* (36.4), *P. t. magnus* (37). In combination, these characters give a first approximation to the taxonomic identity of some of the species of the *P. tuberculosus* group.

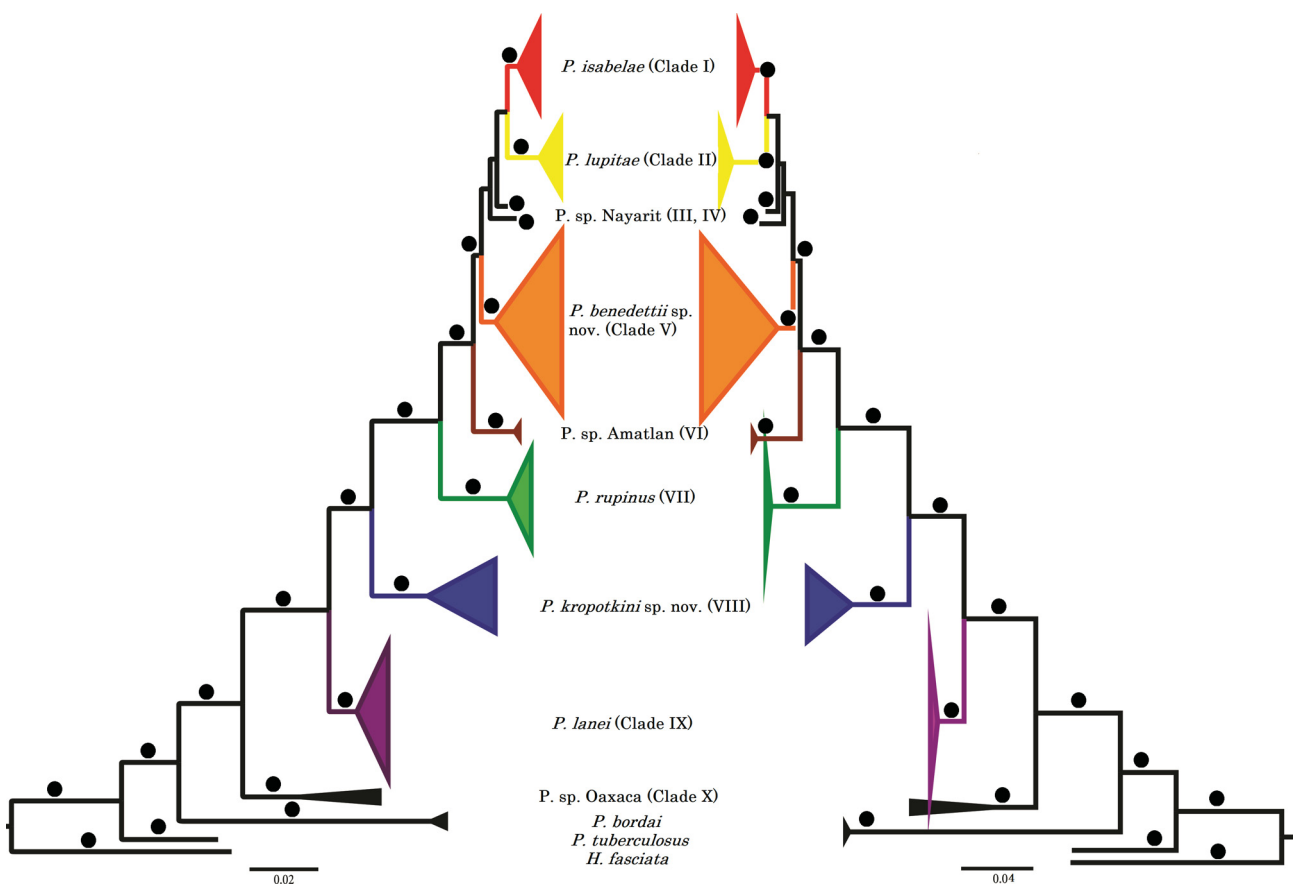


FIGURE 2. Concatenated genes tree (DNAnu + DNAm; left) and mitochondrial concatenated gene tree (right) for the *P. lanei* complex. *Phyllodactylus bordai*, *P. tuberculosus* and *Homonota fasciata* represent the outgroups. Black circles represent branch support values (posterior probability > 95% and bootstrap > 70%). The clades are colored according to their geographical distribution on the distribution map (Fig. 1).

To determine if there are statistical differences in meristic characters among species of the *P. tuberculosus* group, we performed one-way analysis of variance (ANOVA) for the three main characters: tubercles from head to tail, interorbital scales and number of longitudinal scales. Additional non-parametric tests (Kruskal-Wallis) were included as well. If the ANOVA showed significant inequality of the means, we made paired comparisons with Tukey test and Mann-Whitney pairwise test.

For the first character (THT), the ANOVA test showed that there are significant differences among species ($F=14.82$, $df=8$, $P=1.19 \times 10^{-10}$) supported by the non-parametric Kruskal-Wallis test, which showed significant

TABLE 2. Mean, standard deviation and range of meristic variables examined for species of the *P. tuberculosis* group.

Variable	Code	<i>P. isabellae</i>			<i>P. lupitae</i>			<i>P. lanei</i>			<i>P. rupinus</i>		
		Mean±SD	range	Range	Mean±SD	range	Range	Mean±SD	range	Range	Mean±SD	range	Range
4th lamellae of anterior toe right	4ATR	12±0.81	11–13	13–14	13.16±0.4	11–13	13–14	12.15±1.28	10–14	10–14	11.87±0.64	11–13	
4th lamellae of anterior toe left	4ATL	12.28±0.75	11–13	13–14	13.33±0.51	11–13	13–14	12.75±0.86	11–14	11–14	12.12±0.64	11–13	
4th lamellae of posterior toe right	4PTR	12±0.81	11–13	13–14	13.2±0.44	11–13	13–14	13.16±1.02	11–15	11–15	12.25±0.88	11–13	
4th lamellae of posterior toe left	4PTL	12.71±0.95	11–14	12–14	13.16±0.75	11–14	12–14	12.92±1.18	11–14	11–14	12.25±1.03	11–13	
Scales across venter	SAV	27.8±0.92	26–29	23–26	24.6±1.03	26–29	23–26	30±1.4	29–32	29–32	26.5±1.51	24–28	
Tubercles from head to tail	THT	32.28±1.79	30–35	27–31	28.8±2.04	30–35	27–31	32.4±1.81	30–34	30–34	28±1.51	26–30	
Tubercles from axilla to groin	TAG	22.57±2.29	20–26	20–22	20.8±0.83	20–26	20–22	18.6±1.94	17–22	17–22	19.62±1.68	17–22	
Rows of tubercles across dorsum	RTD	16.71±1.11	15–18	14–15	14.83±0.4	15–18	14–15	15.14±0.69	14–16	14–16	14±0.53	13–15	
Interorbital scales	IS	15±0.57	14–16	14–20	16.83±2.04	14–16	14–20	16±1.29	15–18	15–18	15.5±0.92	14–17	
Scales bordering internasals	SBI	5.42±0.53	5–6	6–7	6.33±0.51	5–6	6–7	5.76±0.72	5–7	5–7	6.25±0.88	5–7	
Third labial–snout scales	TLS	21.14±1.57	19–24	23–28	25.5±2.07	19–24	23–28	21.61±1.55	20–25	20–25	20.62±1.59	18–22	
Scales bordering nostril and eye	SNE	12±0.81	11–13	10–14	11.5±1.37	11–13	10–14	11.69±1.10	10–13	10–13	10.5±1.51	9–13	
Scales bordering postmentals	SBP	5.85±0.37	5–6	4–5	4.66±0.51	5–6	4–5	4.76±0.83	4–6	4–6	6.37±1.4	4–8	
Longitudinal scales (Gular–anus)	LS	56.22±2.01	52–58	60–64	61.8±1.83	52–58	60–64	66±5.88	60–74	60–74	63.6±3.70	56–67	

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TABLE 2. Mean, standard deviation and range of meristic variables examined for species of the *P. tuberculosus* group (continued)

Variable	Code	<i>P. benedictii</i> sp. nov.		<i>P. kropotkini</i> sp. nov.		<i>P. i. magnus</i>	
		Mean±SD	range	Mean±SD	range	Mean±SD	range
4th lamellae of anterior toe right	4ATR	11.9±0.85	10–13	13.2±0.44	13–14	11±1.4	10–12
4th lamellae of anterior toe left	4ATL	12.09±0.97	10–14	13.4±0.54	13–14	11.5±0.7	11–12
4th lamellae of posterior toe right	4PTR	12.08±0.84	11–14	13±0.7	12–14	11.3±0.57	11–12
4th lamellae of posterior toe left	4PTL	11.95±0.8	10–13	12.8±0.83	12–14	11.5±0.07	11–12
Scales across venter	SAV	29.1±2.08	25–32	30±1.86	29–33	27.3±1.5	26–29
Tubercles from head to tail	THT	29±2.32	24–33	28.4±2.19	25–31	37±2.6	35–40
Tubercles from axilla to groin	TAG	21.08±2.04	17–25	19.8±1.92	17–22	23.6±2.08	22–26
Rows of tubercles across dorsum	RTD	14.12±0.79	13–16	13.4±0.89	12–14	14.3±1.15	13–15
Interorbital scales	IS	15.25±1.39	13–18	14.6±0.54	14–15	22.3±1.15	21–23
Scales bordering intermasals	SBI	6.08±0.77	5–7	5.4±0.54	5–6	7±0	7–7
Third labial–snout scales	TLS	22.04±1.23	20–25	20.2±0.83	19–21	24.6±1.5	24–26
Scales bordering nostril and eye	SNE	10.7±0.85	9–12	11.4±1.51	10–13	12±0	12–12
Scales bordering postmentals	SBP	5.16±0.96	4–7	5.2±0.44	5–6	7.6±1.5	6–9
Longitudinal scales (Gular–anus)	LS	62.6±3.1	60–69	67.6±4.4	63–73	54.6±3.05	52–58

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TABLE 2. Mean, standard deviation and range of meristic variables examined for species of the *P. tuberculosus* group (continued)

Variable	Code	<i>P. tuberculosus</i>		<i>P. muralis</i>	
		Mean±SD	range	Mean±SD	range
4th lamellae of anterior toe right	4ATR	10.5±0.57	10–11	10.25±1.5	8–11
4th lamellae of anterior toe left	4ATL	11.2±0.44	11–12	11.6±0.57	11–12
4th lamellae of posterior toe right	4PTR	12.6±0.89	12–14	11±1.41	10–13
4th lamellae of posterior toe left	4PTL	11.75±0.95	11–13	11±1	10–12
Scales across venter	SAV	30.2±2.58	27–33	33±0	33–33
Tubercles from head to tail	THT	36.4±3.20	33–41	33.6±5.50	30–40
Tubercles from axilla to groin	TAG	20.8±1.78	18–22	22.3±3.21	20–26
Rows of tubercles across dorsum	RTD	14±1.87	12–17	12.25±0.5	12–13
Interorbital scales	IS	19.2±2.68	16–22	23.2±2.62	21–27
Scales bordering internasals	SBI	6.6±0.54	6–7	7.25±0.5	7–8
Third labial–snout scales	TLS	24.2±1.92	21–26	25.25±1.89	24–28
Scales bordering nostril and eye	SNE	11.8±1.09	10–13	14±0.81	13–15
Scales bordering postmentals	SBP	7±0.70	6–8	6.2±0.95	5–7
Longitudinal scales (Gular–anus)	LS	57.75±6.70	51–64	59±2.82	57–61

TABLE 3. Paired tests of Tukey (on the diagonal) and Mann-Whitney (under diagonal) for tubercles from head to tail among nine species of the *P. tuberculosus* group.

	<i>P. isabeale</i>	<i>P. lupitae</i>	<i>P. lanei</i>	<i>P. rupinus</i>	<i>P. benedettii</i>	<i>P. kropotkini</i>	<i>P. t. magnus</i>	<i>P. muralis</i>	<i>P. tuberculosus</i>
					sp. nov.	sp. nov.			
<i>P. isabeale</i>		0.2731	0.9979	0.082	0.03056	0.156	0.02997	0.9795	0.0884
<i>P. lupitae</i>	0.02015		0.05508	0.9997	0.9869	1	0.0001476	0.02523	0.0001811
<i>P. lanei</i>	0.153	0.003602		0.0117	0.003699	0.02606	0.1737	1	0.3789
<i>P. rupinus</i>	0.000776	0.596	0.0007568		1	1	0.0001404	0.004872	0.0001441
<i>P. benedettii</i> sp. nov.	0.0002073	0.4902	0.0002831	0.8327		0.9988	0.0001398	0.001521	0.0001405
<i>P. kropotkini</i> sp. nov.	0.008414	0.915	0.00365	0.5966	0.4475		0.0001422	0.0113	0.0001535
<i>P. t. magnus</i>	0.0195	0.03466	0.01577	0.01577	0.01158	0.03577		0.3055	1
<i>P. muralis</i>	0.8502	0.2188	0.4625	0.0264	0.01434	0.09698	0.5066		0.57
<i>P. tuberculosus</i>	0.01844	0.01167	0.05795	0.003699	0.002028	0.01193	0.8808	0.3711	

Values in bold highly significant ($P < 0.05$)

TABLE 4. Paired tests of Tukey (on the diagonal) and Mann-Whitney (under diagonal) for interorbital scales among nine species of the *P. tuberculosus* group.

	<i>P. isabeale</i>	<i>P. lupitae</i>	<i>P. lanei</i>	<i>P. rupinus</i>	<i>P. benedettii</i>	<i>P. kropotkini</i>	<i>P. t. magnus</i>	<i>P. muralis</i>	<i>P. tuberculosus</i>
					sp. nov.	sp. nov.			
<i>P. isabeale</i>		0.5489	0.9999	0.9999	0.9974	0.9996	0.000138	0.000138	0.0006579
<i>P. lupitae</i>	0.04905		0.826	0.826	0.1518	0.2139	0.0001389	0.000138	0.1564
<i>P. lanei</i>	0.3345	0.1413		1	0.9492	0.979	0.000138	0.000138	0.002457
<i>P. rupinus</i>	0.341	0.1627	0.9545		0.9492	0.979	0.000138	0.000138	0.002457
<i>P. benedettii</i> sp. nov.	0.2371	0.01888	0.09667	0.09433		1	0.000138	0.000138	0.000176
<i>P. kropotkini</i> sp. nov.	0.1588	0.05029	0.04443	0.0864	0.7234		0.000138	0.000138	0.0002044
<i>P. t. magnus</i>	0.009992	0.02688	0.01335	0.01653	0.01039	0.03033		0.9766	0.01707
<i>P. muralis</i>	0.004446	0.01392	0.006241	0.007582	0.004116	0.01745	1		0.0007435
<i>P. tuberculosus</i>	0.003331	0.1621	0.00785	0.01092	0.003611	0.01042	0.129	0.1039	

Values in bold highly significant ($P < 0.05$)

TABLE 5. Paired tests of Tukey (on the diagonal) and Mann-Whitney (under diagonal) for longitudinal ventral scales among nine species of the *P. tuberculosus* group.

	<i>P. isabeale</i>	<i>P. lupitae</i>	<i>P. lanei</i>	<i>P. rupinus</i>	<i>P. benedettii sp. nov.</i>	<i>P. kropotkini sp. nov.</i>	<i>P. t. magnus</i>	<i>P. muralis</i>	<i>P. tuberculosus</i>
<i>P. isabeale</i>	0.136	0.00277	0.006174	0.0276	9.40x10⁻⁰⁵	0.9994	0.9885	0.9988	
<i>P. lupitae</i>	0.001531	0.7305	0.9926	1	0.2448	0.1796	0.9901	0.7508	
<i>P. lanei</i>	0.005891	0.2293	0.98	0.8627	0.9993	0.008325	0.4529	0.07437	
<i>P. rupinus</i>	0.003449	0.1524	0.7979	0.9998	0.6443	0.02656	0.82	0.2365	
<i>P. benedettii sp. nov.</i>	0.0005473	0.8946	0.2987	0.3145	0.3512	0.07041	0.9466	0.4733	
<i>P. kropotkini sp. nov.</i>	0.002855	0.05358	0.9021	0.2102	0.05196	0.0008761	0.1664	0.009348	
<i>P. t. magnus</i>	0.4379	0.02688	0.05183	0.0317	0.01757	0.03577	0.9354	0.9744	
<i>P. muralis</i>	0.273	0.3085	0.2472	0.189	0.2873	0.07864	0.3865	1	
<i>P. tuberculosus</i>	0.9373	0.5883	0.1465	0.1048	0.4382	0.1054	0.8597	0.817	

Values in bold highly significant ($P < 0.05$)

TABLE 6. Paired tests of Tukey (on the diagonal) and Mann-Whitney (under diagonal) for snout-vent length (SVL) among six species of the *P. lanei* complex.

	<i>P. isabealae</i>	<i>P. lupitae</i>	<i>P. lanei</i>	<i>P. rupinus</i>	<i>P. benedettii sp. nov.</i>	<i>P. kropotkini sp. nov.</i>
<i>P. isabealae</i>		0.000207	0.1615	0.0007366	2.76x10⁻⁰⁸	0.1551
<i>P. lupitae</i>	0.0005862		0.08289	0.8099	0.9883	0.3983
<i>P. lanei</i>	0.05204	0.06724		0.4558	0.01258	0.9949
<i>P. rupinus</i>	0.0001242	0.1047	0.2589		0.8947	0.9301
<i>P. benedettii sp. nov.</i>	2.57x10⁻⁰⁷	0.5367	0.02767	0.09713		0.3952
<i>P. kropotkini sp. nov.</i>	0.001792	0.03832	0.9438	0.06837	0.00976	

Values in bold highly significant ($P < 0.05$)

TABLE 7. Mean, standard deviation and range of morphometric variables examined for six species of *Phyllodactylus*.

Variable	<i>P. isabelae</i>			<i>P. lupitae</i>			<i>P. lanei</i>		
	Code	Mean±SD	Range	Mean±SD	range	Mean±SD	range	Mean±SD	Range
Snout-vent length	SVL	45.91±5.91	36.6–55.2	64.25±7.6	51–72.1	60.2±7.09	52.2–71		
Axilla-groin	AG	18.14±3	14.3–22.2	27.93±3.91	21.6–31.7	24.7±3.82	19.9–30.4		
Head length	HL	12.45±1.49	9.6–13.7	16.86±1.89	13.7–19	15.62±1.40	14.5–18.4		
Head width	HW	8.91±1.02	7.3–10.2	12.08±1.48	9.8–13.8	11.22±1.29	9.6–13.4		
Snout length (to eye)	SLE	8.18±0.88	6.6–9	11.63±1.3	9.7–13.2	10.61±0.94	9.4–12		
Eye diameter	ED	2.8±0.43	2–3.3	3.83±0.53	3–4.4	3.57±0.30	3.2–4		
Auricular opening	AO	1.51±0.3	1–2	2±0.31	1.4–2.3	1.95±0.15	1.7–2.1		
Length of fourth finger	LF	3.55±0.36	3–4.1	5.26±0.57	4.5–6	4.68±0.45	4.1–5.4		
Length of fourth toe	LT	4.3±0.51	3.5–5.1	6.28±0.58	5.3–7	5.6±0.85	4.6–7		
Width between eye supercillaries	WBE	5.94±0.81	4.4–6.8	8.3±1.17	6.4–9.4	7.25±0.65	6.2–8		
Length intermaral	LI	1.55±0.15	1.4–1.7	2.08±0.27	1.6–2.3	2.08±0.44	1.6–2.7		
Continued.									
Variable	<i>P. rupinus</i>			<i>P. benedettii</i> sp. nov.			<i>P. kropotkini</i> sp. nov.		
	Code	Mean±SD	range	Mean±SD	range	Mean±SD	range	Mean±SD	range
Snout-vent length	SVL	62.85±2.65	59.3–66.6	66.58±6.67	44.1–75.2	55.26±5.59	49.1–62.2		
Axilla-groin	AG	26.1±0.95	24.8–27.7	28.4±3.97	18.9–35.8	22.54±2.07	20–25.7		
Head length	HL	16.56±0.88	15.3–18	17.91±1.89	12–21.3	15.02±1.22	13.9–16.9		
Head width	HW	11.78±0.78	11–13.4	12.85±1.47	8.7–15	10.98±0.95	10–12.3		
Snout length (to eye)	SLE	11.07±0.5	10.3–12	11.95±1.24	8.7–13.9	9.34±1.16	7.5–10.6		
Eye diameter	ED	3.48±0.17	3.2–3.7	3.96±0.45	2.7–4.6	3.26±0.15	3–3.4		
Auricular opening	AO	1.9±0.27	1.5–2.3	2.35±0.54	1.4–3.2	1.78±0.13	1.7–2		
Length of fourth finger	LF	4.68±0.39	4–5.1	5.25±0.68	3.7–6.3	4.44±0.36	4.1–5		
Length of fourth toe	LT	5.86±0.53	5.4–7	6.12±0.64	4.4–7.4	5.5±0.66	4.6–6.1		
Width between eye supercillaries	WBE	7.21±0.85	6–8.7	8.53±0.99	6–9.9	7.4±0.46	7–8.1		
Length intermaral	LI	1.83±0.140	1.6–2	2.06±0.2	1.6–2.5	1.54±0.11	1.4–1.7		

differences among sample medians ($\text{Chi}^2=39.42$; $P=3.61 \times 10^{-6}$). The Tukey and Mann-Whitney paired test (Table 3) showed significant differences as well. The Tukey test showed that *P. lanei* differs from *P. rupinus*, *P. benedettii* and *P. krotokini* and showed high differences among *P. t. magnus*, *P. muralis*, *P. tuberculosis* and the species from the *P. lanei* complex. The Mann-Whitney test showed significant differences among *P. isabelae* and the others 6 species of *P. tuberculosis* group, also among *P. lanei*, *P. rupinus* and *P. benedettii*. The ANOVA for interorbital scales showed that there are significant differences among species ($F=25.21$, $\text{df}=8$, $P=4.94 \times 10^{-15}$), supported by the Kruskal-Wallis test, which showed significant difference among sample medians ($\text{Chi}^2=33.51$; $P=2.73 \times 10^{-5}$) and the Tukey and Mann-Whitney paired tests (Table 4). Significant differences for the Tukey test were found among *P. t. magnus*, *P. tuberculosis* and *P. muralis* and the species from the *P. lanei* complex, supported by the Mann-Whitney paired test which added *P. isabelae*, *P. lupitae* and *P. lanei* as significant species. Finally, the ANOVA for number of longitudinal scales showed that there are significant differences among species ($F=6.848$, $\text{df}=8$, $P=1.22 \times 10^{-5}$) supported by the nonparametric Kruskal-Wallis test. This test showed significant difference among sample medians ($\text{Chi}^2=19.19$; $P=0.013$). Finally, the Tukey and Mann-Whitney paired tests showed differences for this characteristic however only *P. isabelae* is clearly differentiated from the rest of species (Table 5).

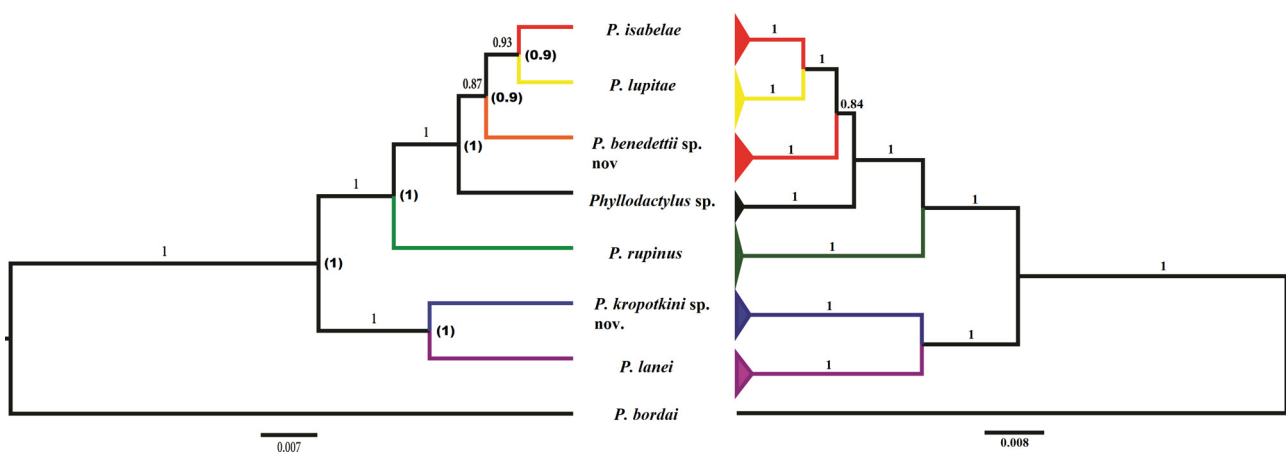


FIGURE 3. Trees obtained with the multispecies coalescent model with *BEAST: species tree obtained with total dataset (DNAnu + DNAm; left) and mitochondrial gene tree (right). The values on the branches indicate the posterior probability, the values in parentheses indicate the probability of speciation recovered from analysis A10 implemented in BP&P.

To determine statistically significant differences among the SVL of six species of *Phyllodactylus*, we performed one-way analysis of variance (ANOVA) with SVL values of adult specimens from scientific collections and collected in field. The ANOVA showed that there are significant differences between SVL means in six species ($F=10.06$, $\text{df}=5$, $P=4.44 \times 10^{-8}$) ($P<0.05$) supported by the Kruskal-Wallis test, which showed that there are significant differences among medians ($\text{Chi}^2=36.89$; $P=6.3 \times 10^{-7}$) ($P<0.05$). Paired Tukey and Mann-Whitney tests showed that most species within the *P. lanei* complex are distinct in size with significant statistical differences (Table 6). *Phyllodactylus isabelae* is the smallest species of the *P. lanei* complex with a registered maximum SVL of 57.5 mm, followed by *P. krotokini* with a maximum SVL of 62.3 mm; the largest species are *P. lupitae*, *P. benedettii* and *P. lanei* with SVL maximum of 73.3, 74.2 and 71 mm respectively; *P. rupinus* is a medium-sized species with a maximum SVL of 69.4 mm (Fig. 6).

Finally, the multivariate analysis by PCA (bootstrap $N=1 \times 10^5$) of morphometric data for six species of the *P. lanei* complex (Table 7) showed that about 98% of the variance was explained by the first component (PC1), mostly represented by snout-vent length (SVL) and axilla-groin length (AGL). The graphic of two principal components (PC1 and PC2) showed two species clearly differentiated in the space of morphometric variables: *P. isabelae* and *P. benedettii* (Fig. 7). From PCA analysis were selected the variables that most explain the variance and with them we performed a multivariate analysis (MANOVA). MANOVA rejected that the species of the *P. lanei* complex show the same multivariate mean ($P<0.05$). The statistics Wilk's lambda ($\lambda=0.17$, $\text{df}=5$, $F=31.17$, $P=1.36 \times 10^{-11}$) and Pillai trace (Trace= 0.896, $\text{df}=5$, $F=58.86$, $P=2.91 \times 10^{-15}$) showed that there are significant differences among the species. The multivariate paired test of Hotelling supported difference between the two new species ($P=3.40 \times 10^{-8}$). Hotelling's multivariate paired tests widely support the distinction of species of the *P. lanei*

complex, only non-significant multivariate differences were obtained between *P. benedettii* and *P. lupitae* ($P=0.05$), between *P. kropotkini* and *P. lanei* ($P=0.11$) and among *P. rupinus* with *P. lanei* ($P=0.28$) and *P. lupitae* ($P=0.05$) (Table 8).

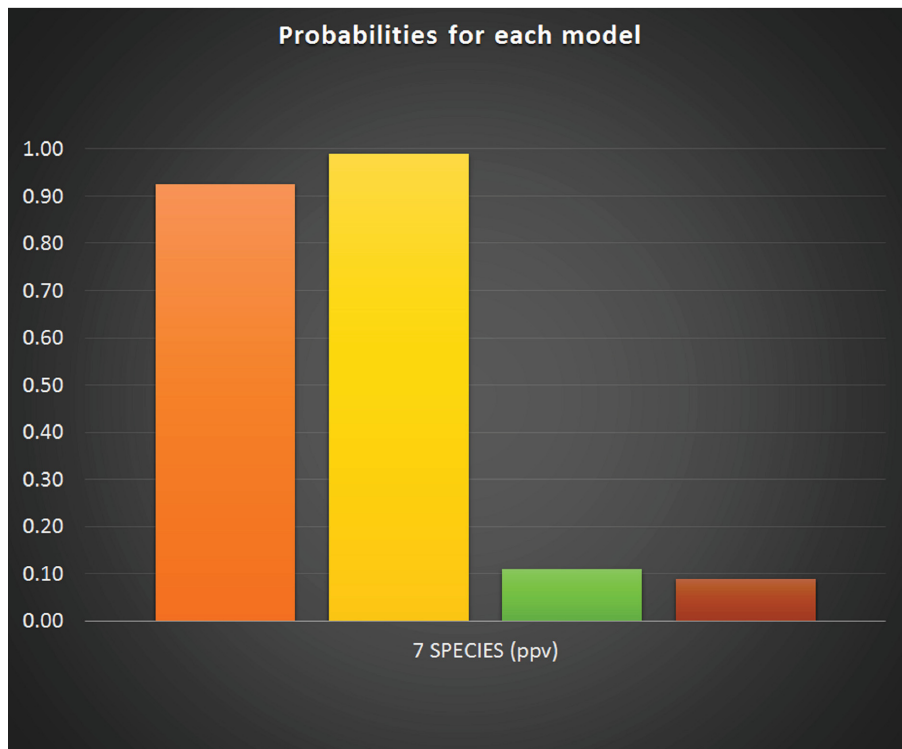


FIGURE 4. Values of Bayesian species validation analysis (analysis A10) of the multispecies coalescent model for seven candidate species of the *P. lanei* complex. The colors of each bar represent the four models analyzed (I–IV), the highest probabilities correspond to the models that incorporated small effective population sizes as priors in the Bayesian analysis, models I (small effective population size and shallow divergences) and II (small effective population size and deep divergences). Note the low probability values recovered to models III (large effective population size and shallow divergences) and IV (large effective population size and deep divergences).

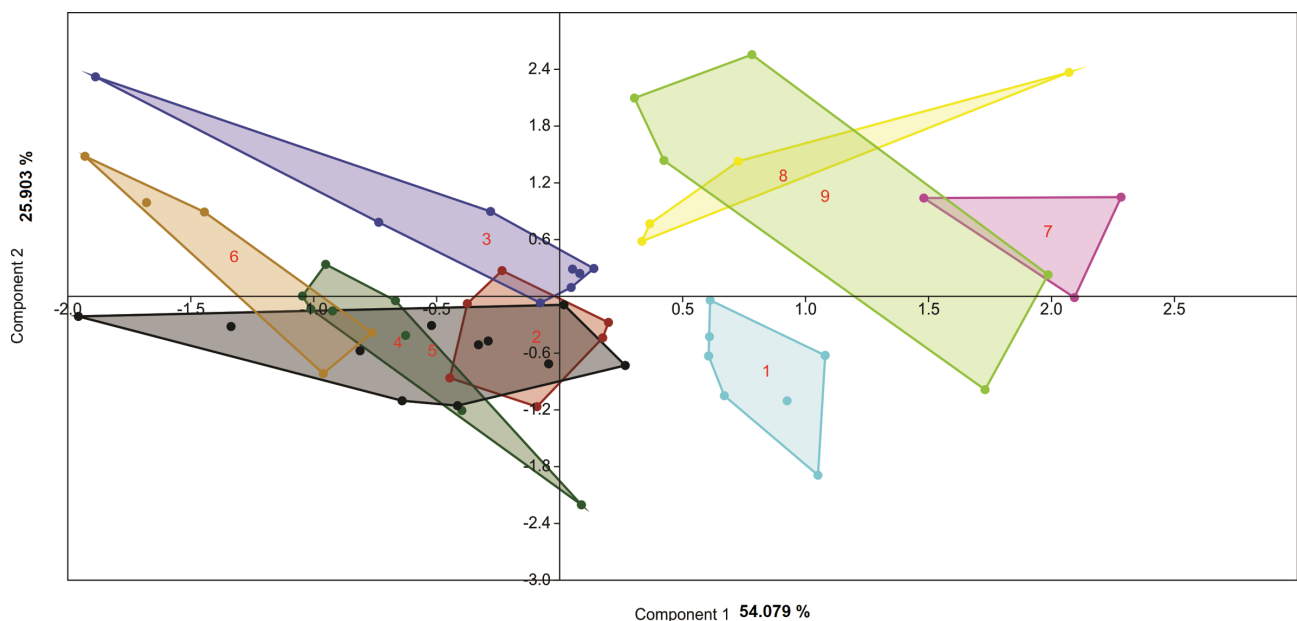


FIGURE 5. Scatter plot of 14 meristic variables for 9 species of the *P. tuberculosis* group: *P. isabelae* (Blue aqua, group 1), *P. lupitae* (Brown, group 2), *P. lanei* (Blue, group 3), *P. rupinus* (Green, group 4), *P. benedettii* (Black, group 5), *P. kropotkini* (Darkgolden, group 6), *P. t. magnus* (Fuchsia, group 7), *P. muralis* (Yellow, group 8), *P. tuberculosis* (Yellow-green, group 9). The first two components are shown with the percentage of variance shown in the axes.

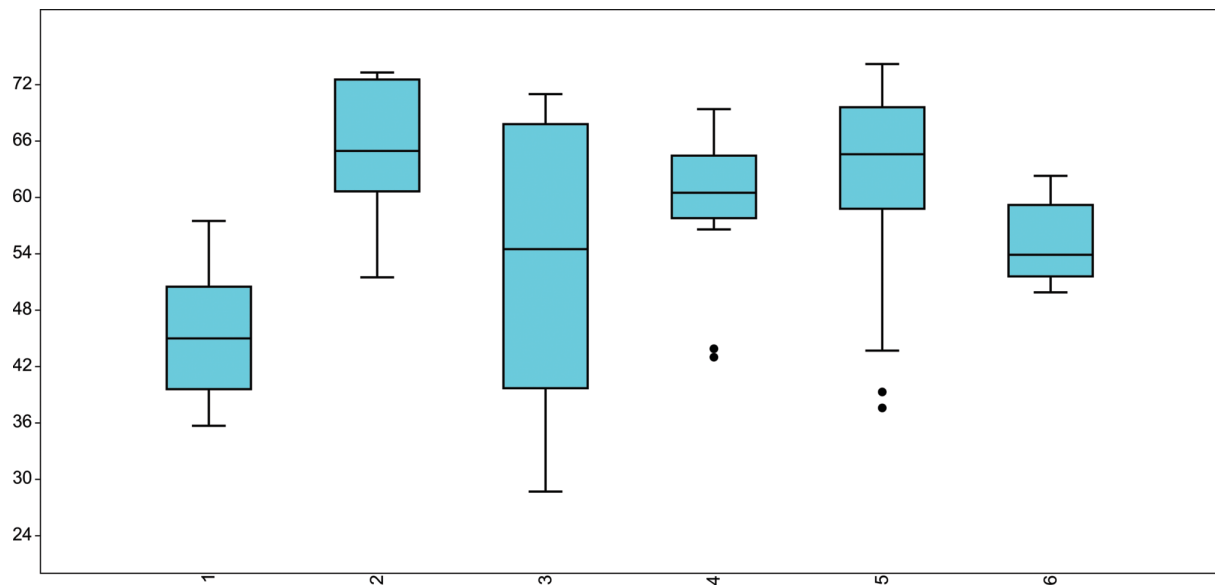


FIGURE 6. Box plot of SVL for six species of *Phyllodactylus*, on the horizontal axis: *P. isabelae* (1), *P. lupitae* (2), *P. lanei* (3), *P. rupinus* (4), *P. benedettii* (5), *P. krotokini* (6), the vertical axis indicates the length in mm. The medians are indicated by horizontal lines inside the boxes, the black dots indicate outliers.

TABLE 8. Hotelling's paired test of morphometric variables for 6 species of *Phyllodactylus*, in bold significant values are shown ($P < 0.05$).

	<i>P. benedettii</i> sp. nov.	<i>P. krotokini</i> sp. nov.	<i>P. rupinus</i>	<i>P. lanei</i>	<i>P. lupitae</i>	<i>P. isabelae</i>
<i>P. benedettii</i> sp. nov.						
<i>P. krotokini</i> sp. nov.	5.24×10^{-05}					
<i>P. rupinus</i>	0.00040391	0.017862				
<i>P. lanei</i>	0.00011247	0.11213	0.28298			
<i>P. lupitae</i>	0.056787	0.002864	0.051115	0.012501		
<i>P. isabelae</i>	1.36×10^{-07}	0.0075299	1.19×10^{-05}	0.00012442	1.42×10^{-05}	

Bioclimatic profiles. The multivariate analysis by PCA showed that about 87% of the variance is explained by the first two components, the PC1 (70.51%) showed that the variables that contribute most to the variance were BIO17 (Precipitation of Driest Quarter), BIO19 (Precipitation of Coldest Quarter) and BIO4 (Temperature Seasonality), while the Precipitation of Warmest Quarter (BIO18) mainly explains the variance of PC2 (16.81 %) (Appendix IV). The graphic of the first two components did not show any overlap between bioclimatic variables and showed a clear separation among the four groups (Fig. 8). MANOVA multivariate analysis showed a clear separation of bioclimatic variables for the four continental species of the *P. lanei* complex (Wilks $\lambda = 2.69 \times 10^{-13}$ y Pillai trace = 3.978). There was no overlap in this part of the ecological niche for the populations that representing continental species. The paired tests of Hotelling widely support the differences in bioclimatic profiles of *P. lanei*, *P. rupinus*, *P. benedettii* and *P. krotokini* (Table 9).

Taxonomy. Based on the results of phylogenetic, morphological and ecological analyses of the *P. lanei* complex, we propose four taxonomic changes, which consist of elevating two subspecies to species level, as well as the description of two new species. Our taxonomic proposal is necessary to avoid paraphyletic groups among previously recognized taxa (*sensu* Dixon, 1964) and to avoid the use of infraspecific categories, since lineages that evolve independently (species) are widely recognized by all analyzes in the present contribution and previously by other studies (Castiglia *et al.* 2010; Ramírez-Reyes *et al.* 2017). The detailed delimitation of the populations that conform to species of the *P. lanei* clade helps to highlight the diversity that may be underestimated by traditional taxonomy methods (Figs. 2–4).

TABLE 9. Hotelling's paired test of bioclimatic variables to four species of *Phyllodactylus*, significant values are shown in bold ($P < 0.05$).

	<i>P. lanei</i>	<i>P. rupinus</i>	<i>P. benedettii</i> sp. nov.	<i>P. kropotkini</i> sp. nov.
<i>P. lanei</i>				
<i>P. rupinus</i>	4.52×10^{-185}			
<i>P. benedettii</i> sp. nov.	0	0		
<i>P. kropotkini</i> sp. nov.	1.31×10^{-107}	1.01×10^{-20}	0	

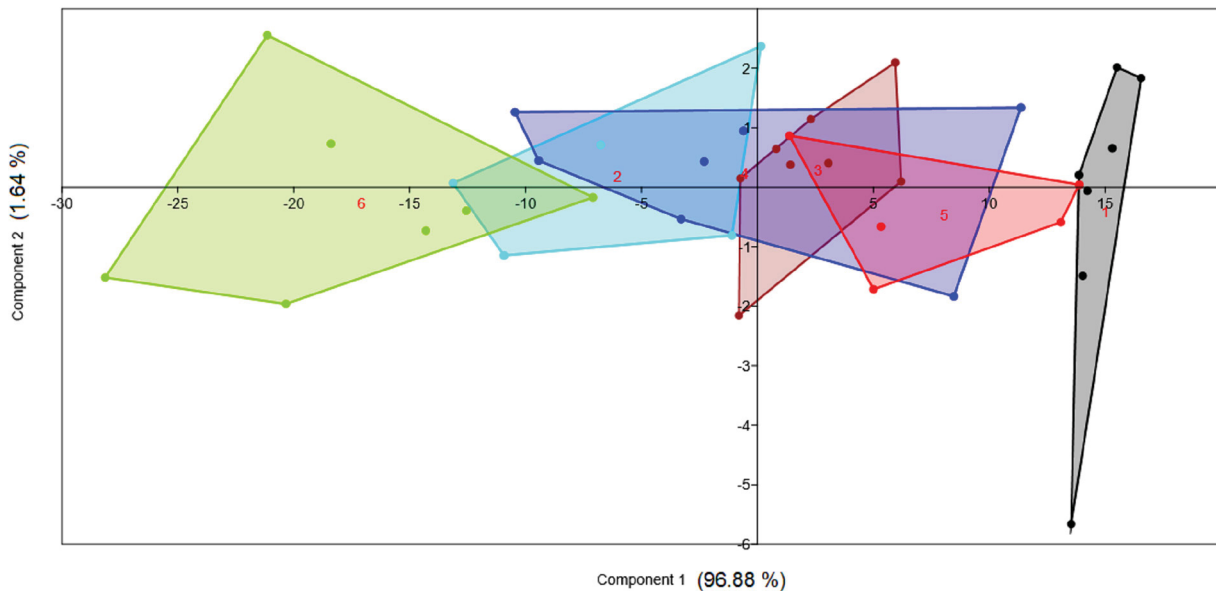


FIGURE 7. Scatter plot of 11 morphometric variables for six species of the *P. lanei* complex: *P. benedettii* (black, group 1), *P. kropotkini* (aqua blue, group 2), *P. rupinus* (brown, group 3), *P. lanei* (blue, group 4), *P. lupitae* (red, group 5), *P. isabelae* (green, group 6). The first two components are shown with the percentage of variance on the axes.

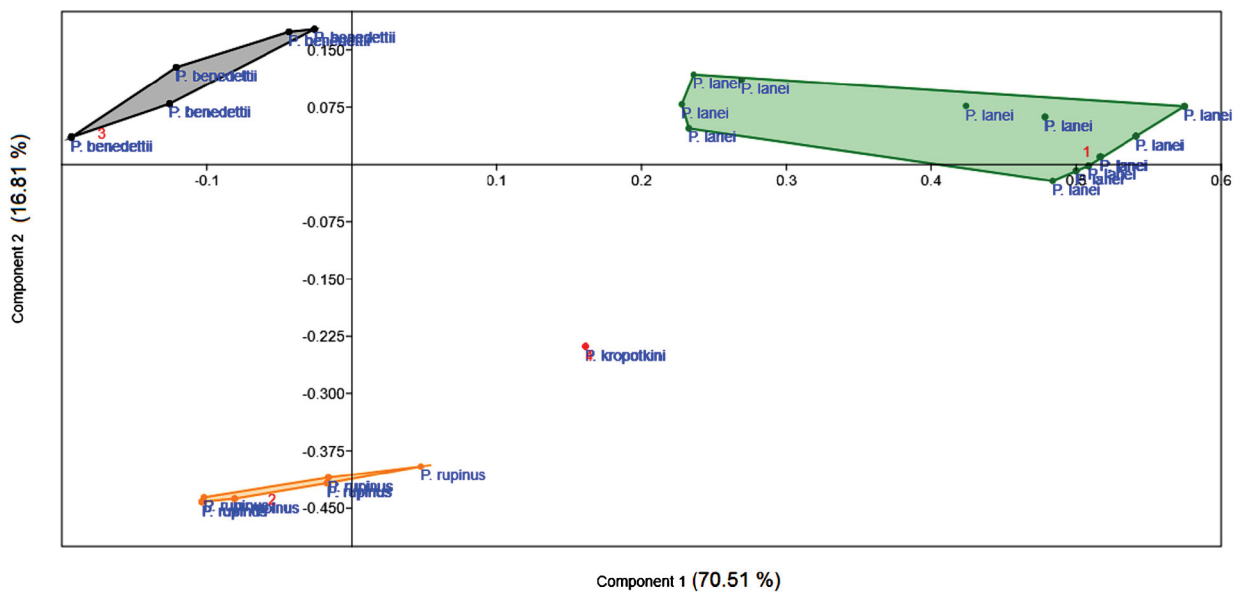


FIGURE 8. Scatter plot of 19 bioclimatic variables to four species: *P. lanei* (green, group 1), *P. rupinus* (orange, group 2), *P. benedettii* (Black, group 3) and *P. kropotkini* (Red dot, group 4). The first two components are shown with the percentage of variance on the axes.

Systematics

Phyllodactylus benedettii sp. nov.

Holotype. Adult male (MZFC 28774) collected at Chamela Biological Station, La Huerta, state of Jalisco (19.50 N, -105.44W WGS84) on September 15, 2014 by Tonatiuh Ramírez Reyes and Alfredo Villarruel.

Paratypes (14). An adult female (MZFC 28773) collected at Chamela Biology Station, La Huerta municipality (19.50 N, -105.44W) on September 15, 2014 by Tonatiuh Ramírez Reyes and Alfredo Villarruel; (MZFC 21817-male, MZFC 21818-male, MZFC 21877, MZFC 21878-male, MZFC 21879, MZFC 21880-female, MZFC 21885-male) collected at the Chamela Biology Station, La Huerta municipality (19.50 N, -105.44 W) by Oscar Flores Villela in 2007; an adult female (IBH 2133-2) and five adult males (IBH 2133-3, 2133-4, 2133-5, 2133-7, 2133-9) collected at 2 km. SE, of the Station of Biology, Chamela (19.51 N, -104.94 W) on October 27, 1971 by Cornelio Sánchez; an adult female (IBH 2138-4) collected at 5 km. S., de Chamela, Biology Station, UNAM, municipality La Huerta (19.49 N, -104.95 W) on May 25, 1974 by Gustavo Casas Andreu.

Etymology. The species is dedicated to the memory of the great Uruguayan writer Mario Benedetti in recognition of his prolific literary production and critical thinking of great importance in the political and social life of Latin America.

Diagnosis. *Phyllodactylus benedettii* sp. nov. is a species with the largest average size within the *P. lanei* complex, with a maximum SVL of 75.2 mm. Dixon (1964) established three fundamental characteristics to include species and subspecies within the *P. lanei* complex and differentiate them from *P. tuberculosis*: species of the *P. lanei* complex have a low number of interorbital scales (12–19), white venter and low number of scales across the snout between the third labials (does not specify range of values). *Phyllodactylus benedettii* shows white-yellow venter, 14.4 interorbital scales on average, and 22.3 scales across the snout between the third labials.

Within the *P. lanei* complex (including insular and continental species), the only species that exceed 70 mm of SVL are *P. lupitae* and *P. lanei*, two species that are very isolated geographically. It is clearly different from the nearest species *P. rupinus*, which has a maximum SVL of 69.4 mm, considered as a medium size species. According to the statistical analyzes previously carried out, the combination of diagnostic morphological characters are the following (in addition to the SVL): It differs clearly from all species of *Phyllodactylus* as it presents 62.6 (60–69) longitudinal scales, 27 (24–30) tubercles from head to tail, 14 (11–13) interorbital scales, 29 (25–32) scales across venter, 22 (22–23) third labial–snout scales, 13 (13–14) rows of tubercles across dorsum. Although *P. benedettii* is very similar to *P. lupitae* in some meristic characters, they present differences in the morphometric space (Fig. 7). Some measures allow us to differentiate these species are the head-length and axilla-groin length: *P. benedettii* (17.9 mm and 28.4 mm) and *P. lupitae* (16.86 mm and 27.93 mm). According to Castiglia et al. (2009; 2010), the karyotypes of *P. l. lanei* (Tierra Colorada, Guerrero) and *P. l. rupinus* from Chamela, Jalisco (here named *P. benedettii*) are different. According to their studies *P. lanei* has $2n = 33–34$ and $FN = 40–41$, while *P. benedettii* has $2n = 38$ and $FN = 38$.

Phyllodactylus benedettii has fewer than 30 tubercles from head to tail (24–30, 27.4 avg.) similar to *P. lupitae* (27–31, 28.8 avg.), *P. paucituberculatus* (28.7), *P. kropotkini* (25–31, 28.4 avg.) and *P. rupinus* (26–30, 28 avg.); other species have more than 30 tubercles from head to tail on average: *P. lanei* (32–34, 33.2 avg.), *P. isabelae* (30–35, 32.2 avg.), *P. t. magnus* (35–40, 37 avg.), *P. muralis* (30–40, 33 avg.) and *P. tuberculosis* (33–41, 36.4 avg.). *Phyllodactylus benedettii* showed 62 longitudinal ventral scales (LVS) on average (60–69), other values were *P. isabelae* (52–58, 56.2 avg.), *P. lupitae* (60–64, 61.8 avg.), *P. lanei* (60–74, 66 avg.), *P. rupinus* (56–67, 63 avg.), *P. kropotkini* (63–73, 67 avg.), *P. t. magnus* (52–58, 54 avg.), *P. muralis* (57–61, 59 avg.) and *P. tuberculosis* (51–64, 57 avg.). *Phyllodactylus benedettii* presents 14.4 interorbital scales similar to *P. kropotkini* (14–16, 14.6 avg.) and differs from *P. isabelae* (14–20, 15.1 avg.), *P. lupitae* (14–20, 16.8 avg.), *P. lanei* (15–17, 15.5 avg.), *P. rupinus* (14–17, 15.5 avg.), *P. t. magnus* (21–23, 23.3 avg.), *P. muralis* (21–27, 23.2 avg.), and *P. tuberculosis* (16–22, 19.2 avg.). *Phyllodactylus benedettii* presents 29 scales across venter and differs from *P. isabelae* (26–29, 27.8 avg.), *P. lupitae* (26–29, 24.6 avg.), *P. lanei* (29–32, 30 avg.), *P. rupinus* (24–28, 26.5 avg.), *P. kropotkini* (29–33, 30.6 avg.), *P. t. magnus* (26–29, 27.3 avg.), *P. muralis* (33) and *P. tuberculosis* (27–33, 30.2 avg.). *Phyllodactylus benedettii* presents 22 third labial–snout scales on average (22–23) and differs from *P. isabelae* (19–24, 21.4 avg.), *P. lupitae* (23–28, 25.5 avg.), *P. lanei* (20–23, 21.2 avg.), *P. rupinus* (18–22, 20.6 avg.), *P. kropotkini* (19–21, 20.2 avg.), *P. t. magnus* (24–26, 24.6 avg.), *P. muralis* (24–28, 25.2 avg.) and *P. tuberculosis* (21–26, 24.2 avg.). *Phyllodactylus*

benedettii presents 13.8 rows of tubercles across dorsum on average (13–14) and differs from *P. isabelae* (15–18, 16.7 avg.), *P. lupitae* (14–15, 14.8 avg.), *P. lanei* (14–16, 15.6 avg.), *P. rupinus* (13–15, 14 avg.), *P. krotokini* (12–14, 13.4 avg.), *P. t. magnus* (13–15, 14.3 avg.), *P. muralis* (12–13, 12.2 avg.) and *P. tuberculosus* (12–17, 14 avg.). Finally, *P. benedettii* presents the largest values in the following measures: 5.50 mm in length of the 4th toepad and 35.8 mm in axilla-groin length (LAG); compared to *P. isabelae* (4.1 mm, 22.2 mm), *P. lupitae* (4.9 mm, 31 mm), *P. lanei* (4.6 mm, 21.1 mm), *P. rupinus* (5 mm, 25.6 mm) and *P. krotokini* (5 mm, 23 mm).

Description of holotype (Fig. 9). (All bilateral counts are given as right/left). Adult male, robust body, head not flattened, neck slightly differentiated from the head. The head scales are granular, most are slightly globose, and are interspersed with circular-oblique flat scales that are mainly located between the eyes towards the tip of the snout. The rostral scale presents an intermediate striation near to middle of the scale (a groove that extends longitudinally to the middle part of the rostral scale); nostril bordered by a simple supranasal (one supranasal scale only), first labial, rostral and two postnasals; two supranasal scales contact each other, bordered by 7 postnasals; 22 interorbital scales beginning at the anterior ocular border; 15 scales across the snout from the second right labial, 24 scales across the snout at the level of the third labial scale on the right side; 8/9 loreal scales from the first ocular scale to the nostril; 11/10 supralabial scales; posterior border of the first supralabial in contact with the nostril (right and left); 8/8 infralabial scales; elongated auricular opening smaller than ocular diameter; occipital scales different in size and shape to the interorbital scales, while the interorbital scales are more or less uniform in size and shape (oval shape), they are smaller than the occipital ones. The occipital scales are larger than the interorbital scales, they have irregular shapes and presents some circular tubercles intermixed; mental scale is equally wide as long (3.6 mm), forms an irregular "V" towards the posterior section, two postmental scales closely in contact each other and with the first and second infralabials; postmental scales in contact with a row of 4 scales, the 2 intermediates larger than the extremes, 10 scales of uniform size border the row of scales.



FIGURE 9. Dorsal and ventral view of the holotype of *Phyllodactylus benedettii* sp. nov. (MZFC 28774). The black bars represent the scale (10 mm).

Body with granular scales; 13 rows of strongly keeled dorsal tubercles with variable size; 25 tubercles in a middle dorsal row from base of the head to base of the tail; 21/15 tubercles from axilla to groin; 34 rows of cycloid scales across the venter; 87 longitudinal ventral scales from the first differentiated scale on the gular region to the cloacal opening; ventral scales larger compared to the lateral scales of the body and the gular region; scales slightly imbricate on the anterior and posterior extremities, scales dorsally granular intercalated with strongly keeled tubercles of variable size. The tail of the specimen is original (not regenerated) and measures 55.5 mm with the tip

broken. Dorsal scales of the tail are imbricate with intercalated tubercles and juxtaposed ventral scales, keeled tubercles extend to more than half of the tail, as they extend to the tip of the tail the tubercles gradually flatten until they form keeled scales. Does not present femoral or precloacal pores.

Digital lamella formulae: right posterior (7-9-12-13-10), left posterior (6-8-11-13-9); right anterior (6-9-12-11-11), left anterior (6-10-13-11-12), fourth finger of the extremities longer than others; digital toepads longer than wide on all fingers.

Measurements in mm: snout-vent length 70.9; axilla-groin 35.8; head length 16.5; head width 13.2; snout length (to eye) 10.05; eye diameter 4.1; auricular opening (maximum) 1.6; length of fourth finger 5.5; length of fourth toe 5.7; width between eye supercilliaris 9; internarial 2.1.

Coloration of holotype in ethanol (Fig. 8). The holotype exhibits relatively little coloration, the dorsal background color varies from brown to creamy yellow, with dark brown faint irregular spots (less evident compared to live coloration), the ventral surface varies yellowish and cream; half of the ventral color on the tail to the tip is cream.

Pattern and color in life (Fig. 10). Dorsally presents a clear background, a mixture of cream-pink, on this background, patterns of irregular patches dark brown color and some completely black spots are present, some of these spots are slightly surrounded by yellowish scales; on the middle dorsal part a longitudinal line of the background color runs from head to tail; scales around the eyes and some supralabials are slightly colored light yellow; ventrally presents a white-cream coloration in combination with light yellow, more evident towards the ventral region; the pupils are black on a bronze iris. Dorsal coloration of the tail is white-cream with brown stripes and some black points.



FIGURE 10. *Phyllodactylus benedettii* sp. nov. from the type locality (Chamela-Cuixmala Biosphere Reserve, Jalisco) in life (Photo by Israel Solano Zavaleta).

Variation. All meristic and morphometric characters are presented with mean values, standard deviation and range of meristic (Table 2) and morphometric variables (Table 7).

Distribution and habitat. *Phyllodactylus benedettii* sp. nov. is an endemic species to the state of Jalisco, restricted to the Chamela-Cuixmala Biosphere Reserve. According to the INEGI digital map of elevation (resolution of 15 m), the type locality is located at 100 masl, located in the biogeographic province of the Western

Pacific surrounded by deciduous tropical forests (Fig. 11). The microhabitats reported for this species are diverse: soil, trees, shrubs and in habitats modified by man as houses or bridges or some other constructions (meteorological stations). They are particularly abundant in rocks and crevices and in people's houses or buildings where it feeds on insects and other invertebrates (García & Ceballos 1994; Ponce-Campos & García 2007; Vitt & Caldwell 2014; pers. obs.). Males of *P. benedettii* have an extended period of reproduction (August–March) with two peaks, one in rainy season (August–October) and another one in dry season (November–March). Reproductive behavior (courtship and mating) begins in August which coincides with the beginning of rainy season. The females produce clutches of two eggs, with up to three clutches during the breeding season, with a peak of egg production from December to March coinciding with the dry season (Ramírez-Sandoval *et al.* 2006). This species presents a distinct karyotype from *P. lanei* presumably due to Robertsonian fusions/fissions with 19 pairs of telocentric chromosomes ($2n = 38$, $FN = 38$) (Castiglia *et al.* 2009). They are lizards of nocturnal habits and feed on insects, although to date there have been no studies on the composition of their diet (García & Ceballos 1994; Vitt & Caldwell 2014). Representative species of tropical dry forest of Chamela-Cuixmala Biosphere Reserve are: *Sciadodendrom excelsum*, *Brosimum alicastrum*, *Orbignya cohune* and *Tabebuia donell-smithi* (Ceballos *et al.* 1999). The deciduous tropical forests is near the mouth of the Cuixmala River and is characterized by the abundance of water in the rainy season, the climate is tropical (warm-humid), has an annual average temperature of 25 °C and the annual rainfall varies from 748–1000 mm (García & Ceballos 1994; Ceballos *et al.* 1999). Other species of reptiles with nocturnal activity that inhabit the deciduous tropical forests are: *Hemidactylus frenatus*, *Boa constrictor*, *Lampropeltis triangulum*, *Leptodeira maculata*, *Pseudoficimia frontalis*, *Senticolis triaspis*, *Tropidodipsas philippii* (*Sibon philippii*), *Tantilla bocourti*, *Thamnophis valida*, *Trimorphodon biscutatus*, *Micrurus distans*, *Agkistrodon bilineatus*, and *Crotalus basiliscus* (García & Ceballos 1994).



FIGURE 11. Deciduous tropical forests from the type locality (Chamela-Cuixmala Biosphere Reserve, Jalisco) habitat of *Phyllodactylus benedettii* sp. nov. (Photos by Tonatiuh Ramírez Reyes).

Comments on conservation and threats. This species inhabits the Chamela-Cuixmala Biosphere Reserve decreed in 1993. There is a minor threat posed by the localities bordering the reserve, and according to the observations made by the first author, apparently there is a large population of *P. benedettii* geckos inside Chamela-Cuixmala Biology Station (UNAM). There are two main threats: the false beliefs of some people who consider this species as poisonous (local inhabitants), and the possible negative effects due to the presence of invasive gecko *Hemidactylus frenatus*, a species with a very large population that may exploit the same ecological niche. To date there is no specific study on niche overlap between *H. frenatus* and *Phyllodactylus* species in Mexico, however, its potential danger to local biodiversity has been documented, including interspecific negative interactions with native geckos from different areas of the world; one example of this is the displacement and reduction of six gecko species of the genus *Nactus* on the Mascarene Islands and *Lepidodactylus lugubris* throughout Pacific islands. In these cases *H. frenatus* has been observed stalking, lunging towards and biting at other geckos (Global Invasive Species Database 2015). Due to the above, and as a potential risk to local biodiversity in Mexico, it is classified as a high risk invasive species (CONABIO 2016).

***Phyllodactylus kropotkini* sp. nov.**

Holotype. Adult male (MZFC 28736) collected in Nueva Filadelfia (Huerta Vieja) in the municipality of Tlapehuala, Guerrero (18.29 N, -100.49 W WGS84), collected on March 15, 2014 by Tonatiuh Ramírez Reyes and Joel Rosas Avila.

Paratypes (4). Four male adults (MZFC 28735, MZFC 28737, MZFC 28738, MZFC 28739) collected at the type locality, Nueva Filadelfia (Huerta Vieja), Tlapehuala, Guerrero (18.29 N, -100.49 W WGS84) collected on March 16, 2014 by Tonatiuh Ramírez Reyes and Joel Rosas Ávila.

Etymology. The species is dedicated to the memory of the great Russian philosopher, geographer and naturalist Piotr Kropotkin, who made great scientific and theoretical contributions about mutual support and altruism in some animal populations (including human society).

Diagnosis. *Phyllodactylus kropotkini* **sp. nov.** is a medium-sized gecko within the *P. lanei* complex. Dixon (1964) established three fundamental characteristics to include species and subspecies within the *P. lanei* complex and differentiate them from *P. tuberculosus*, species of the *P. lanei* complex have a low number of interorbital scales (12–19), white venter and low number of scales across the snout between the third labials (does not specify range of values). *Phyllodactylus kropotkini* has 14.6 interorbital scales on average (14–15), white venter and 20.2 third labial–snout scales on average (19–21). *Phyllodactylus kropotkini* presents a maximum recorded SVL of 62.3 mm that clearly differs from the nearest species *P. lanei* (max. 71 mm) and it differs from other species: *P. isabelae* (max. 57.5), *P. lupitae* (max. 73.3 mm), *P. rupinus* (max. 69.4), *P. benedettii* (max. 74.2) and *P. bordai* (max. 58.9 mm). *Phyllodactylus kropotkini* **sp. nov.** shows the following combination of characters: 28 (25–31) tubercles from head to tail, 67 (63–73) longitudinal scales, 13 (12–14) rows of tubercles across dorsum, 30 (29–33) scales across venter, 14 (14–15) interorbital scales and 20 (19–21) third labial–snout scales. *Phyllodactylus kropotkini* has a partial overlap with *P. lanei* and *P. isabelae* on morphometric space (Fig. 7), however *P. kropotkini* is clearly differentiated from *P. lanei* by maximum length (SVL) (Fig. 6); it also presents the follow measures: axilla-groin length (22.54 mm), snout length (9.34 mm), auricular opening (1.78 mm), while *P. lanei* has 24.7 mm axilla-groin length, 10.61 mm snout length and auricular opening (1.95 mm) and *P. isabelae* has 18.7 mm axilla-groin length, 8.18 mm snout length and auricular opening 1.51 mm.

P. kropotkini has a low number of interorbital scales (14–15, 14.6 avg.) similar to *P. benedettii* (13–16, 14.4 avg.), all other species of *Phyllodactylus* exceed 15 interorbital scales on average, *P. isabelae* (14–16, 15.1 avg.), *P. lupitae* (14–20, 16.83 avg.), *P. lanei* (15–17, 15.5 avg.), *P. rupinus* (14–17, 15.5 avg.), *P. t. magnus* (21–23, 22.3 avg.), *P. muralis* (21–27, 23.2 avg.), *P. tuberculosus* (16–22, 19.2 avg.). There are an average of 30.6 scales across the venter (29–33), unlike *P. isabelae* (26–29, 27.8 avg.), *P. lupitae* (23–26, 24.6 avg.), *P. lanei* (29–32, 30 avg.), *P. rupinus* (24–28, 26.5 avg.) and *P. benedettii* (25–32, 29.1 avg.). *Phyllodactylus kropotkini* presents 67.6 longitudinal scales from the gular region to the anus on average (63–73), compared to *P. rupinus* (63–73, 63.6 avg.), *P. lanei* (60–74, 66 avg.), *P. benedettii* (60–69, 62.6 avg.), *P. t. magnus* (52–58, 54.6 avg.), *P. muralis* (57–61, 59 avg.) and *P. tuberculosus* (51–64, 57.7 avg.). This species also has 28.4 tubercles from head to tail on average (25–31), different from *P. rupinus* (26–30; 28 avg.), *P. lanei* (32–34, 33.2 avg.), *P. benedettii*, (24–30, 27.4 avg.), *P. isabelae* (30–35, 32.2 avg.), *P. lupitae* (27–31, 28.8 avg.), *P. t. magnus* (35–40, 38 avg.), *P. muralis* (30–40, 33.6 avg.) and *P. tuberculosus* (33–41, 36.4 avg.) tubercles. It also presents 13.4 rows of tubercles on average across the dorsum (12–14), different from *P. rupinus* (13–15, 14 avg.), *P. benedettii* (13–14, 14.4 avg.), *P. lupitae* (14–15, 14.8 avg.), *P. lanei* (14–16, 15.6 avg.), *P. isabelae* (15–18, 16.7 avg.), *P. t. magnus* (13–15, 14.33 avg.), *P. muralis* (12–13, 12.2 avg.) and *P. tuberculosus* (12–17, 14 avg.). Finally *P. kropotkini* presents 20.2 third labial–snout scales (19–21), similar to *P. rupinus* (18–22, 20.6 avg.) and it differs from the other species of *Phyllodactylus*: *P. isabelae* (19–24, 21.4 avg.), *P. lupitae* (23–28, 25.5 avg.), *P. lanei* (20–23, 21.2 avg.), *P. benedettii* (22–23, 22.3 avg.), *P. t. magnus* (24–26, 24.6 avg.), *P. muralis* (24–28, 25.2 avg.) and *P. tuberculosus* (21–26, 24.2 avg.).

Description of holotype (Fig. 12). Adult male, medium body proportions (non-robust), short neck, head differentiated from the body. The head scales are granular, mostly flattened and some slightly globose towards the anterior part of the eye openings. Rostral scales have an intermediate longitudinal groove that reaches the middle part of the scale; nasal orifice bordered by a simple supranasal, rostral and 2 postnasals; nasal orifice in contact with the first supralabial, this has a fold that resembles a 3rd postnasal scale; 2 supranasal scales in contact with each other, bordered by 6 postmental scales; 25 interorbital scales from the anterior ocular border; 18 scales across snout starting with the 2nd labial; 26 scales across snout starting with 3rd labial scales; 12/12 loreal scales from the nostril to eye; 12/12 supralabials; edge of 1st supralabial in contact with the nostril (right and left) forming a groove

near mental scale (right and left); 10/11 infralabial scales; auricular opening elongated and smaller than ocular diameter; occipital scales different in size and shape to interorbital with some interspersed circular tubercles; mental scale forms an irregular "V" towards the posterior region; two postmental scales in contact each other and with the 1st and 2nd infralabial scales (right and left); postmental scales in contact with a row of 5 scales, the central scale (pentagon shape) is larger than pair of adjacent scales (right and left). Body with granular scales, has 13 rows of strongly keeled dorsal tubercles of variable size; 30 tubercles in a dorsal row starting in the base of the head to base of the tail; 24/19 tubercles axilla-groin; 32 rows of cycloid scales across venter; 81 ventral longitudinal scales from the first differentiated scale in the gular region to the anus; ventral scales larger than the lateral scales of the body and the gular region; scales slightly imbricate on the four extremities. The tail of the specimen is original (not regenerated) and measures 39.6 mm with the tip broken, dorsal scales of the tail are subimbricate and mostly flattened. Therefore, the tubercles are clearly defined. Does not present femoral or precloacal pores. Lamellar formulae: anterior right leg (8-10-12-13-11), anterior left leg (9-10-13-13-11), posterior right leg (8-11-14-15-13), posterior left leg (8-12-14-14-13).



FIGURE 12. Dorsal and ventral view of the holotype of *Phyllodactylus kropotkini* sp. nov. (MZFC 28736). The black bars represent the scale (10 mm).

Measurements in mm. Snout-vent length 62.2; axilla-groin 23; head length 16.9; head width 12.3; snout length (to eye) 7.5; eye diameter 3.3; auricular opening (maximum) 1.7; length of fourth finger 5; length of fourth toe 6; width between eye supercilliaris 8.1; internarial 1.5.

Coloration of holotype in ethanol (Fig. 12). The holotype presents a coloration that mixes the cream and light gray coloration on dorsal background, with a few dorsal dark brown spots; the ventral coloration is white with a slight light yellowish on posterior legs. The ventral coloration of the tail tip is dark gray, as well as the tips of the toepads.

Variation. All characters are presented with mean values, standard deviation and range of meristic (Table 2) and morphometric variables (Table 7).

Distribution and habitat. *Phyllodactylus kropotkini* is endemic to the middle region of the Balsas Basin at locality Nueva Filadelfia (Huerta Vieja), municipality of Tlapehuala, Guerrero (Fig. 13). This species was observed mainly on rocks and between cracks in caves near the type locality. The specimens were collected in the house of a person who allowed collection inside his home. Due to its presumably small distribution area and its new taxonomic status, no further information on its reproduction or ecology is known. According to the digital elevation model of INEGI (resolution 15 m), the locality is at 579 m of elevation in relict lowland tropical dry

forest in a habitat clearly disturbed by agricultural and livestock activity. Annual temperature for the locality is of 27 °C, with maximum temperatures of 38.6 °C and annual precipitation of 1099 mm on average. The Balsas Basin contains a great diversity of species of the genus *Bursera*, in fact this biogeographic province is considered the likely center of diversification and endemism of *Bursera* (Toledo 2003; Pineda-García *et al.* 2007). Other species of reptiles that inhabit this province are: *Hemidactylus frenatus*, *Ctenosaura pectinata*, *Sceloporus horridus*, *Urosaurus bicarinatus*, *Drymarchon corais*, *Leptodeira maculata*, *Salvadora mexicana*, *Crotalus simus*, *Micrurus laticollaris* (Reyna-Álvarez *et al.* 2010).



FIGURE 13. Residuals of Tropical dry Forest at the type locality (Nueva Filadelfia, Tlapehuala, Guerrero) habitat of *Phyllodactylus kropotkini* sp. nov. (Photo by Tonatiuh Ramírez Reyes).

Comments about conservation and threats. This species inhabits the middle region of Balsas Basin, and the type locality is a remnant tropical dry forest; the species inhabits an area highly disturbed by agricultural and livestock activities, however, this species is able to adapt effectively to modified habitats, inhabiting houses or other types of buildings (bridges, fences, etc.). The main threat to this species (and in general to all species of the *P. lanei* complex) are the myths and false beliefs of the people, who consider this species as dangerous or poisonous (García & Ceballos 1994). This false belief has led some people to implement "eradication" campaigns of this species in houses or wherever geckos are seen.

Taxonomic changes. Although the purpose of the present study was not to re-describe the species of the *P. lanei* complex, we will mention some points that are important to consider for the previously described species *P. lanei*, *P. rupinus*, *P. isabelae* and *P. lupitae*. The original description of *P. lanei* can be consulted in Smith (1935), *P. rupinus* can be consulted in Dixon (1964) and *P. isabelae* and *P. lupitae* in Castro-Franco & Uribe-Peña (1992). The last publication includes an identification key for *P. lanei*, *P. rupinus*, *P. isabelae* and *P. lupitae* and agrees mostly with the results presented here.

The original descriptions are extensive enough and can be reviewed for a detailed taxonomic identification,

here we will only mention characters that can help us identify the taxa.

***Phyllodactylus lanei* Smith, 1935**

Holotype. Adult male, CNHM 100067, collected by Edward H. Taylor and Hobart M. Smith near Tierra Colorada Guerrero, June 30, 1932.

Diagnosis. A large gecko according to Dixon (1964) attaining a snout-vent length of 78 mm. This observation agrees with ours, as the largest species in the *P. lanei* complex are *P. lanei*, *P. benedettii* and *P. lupitae*. Has more than 30 tubercles from head to tail (33.2), similar to *P. isabelae* (32.2) and *P. muralis* (33.6). The other species of the *P. lanei* complex have fewer than 30, *P. lupitae* (28.8), *P. rupinus* (28), *P. benedettii* (27.4), *P. krotokini* (28.4). Other species of geckos with more tubercles are *P. t. magnus* (37) and *P. tuberculosus* (36.4). *Phyllodactylus lanei* presents 30 scales across the venter similar to *P. krotokini* (30.6) and *P. tuberculosus* (30.2), but differing from *P. isabelae* (27.8), *P. lupitae* (24.6), *P. rupinus* (26.5), *P. benedettii* (29.1) and *P. t. magnus* (27.3).

Distribution. This species is restricted to the localities of Tierra Colorada and Chilpancingo, Guerrero and adjacent locations of medium-low altitude localities.

***Phyllodactylus rupinus* Dixon, 1964**

Holotype. Adult male. KU 67501, collected by James R. Dixon. Mike Sabath, and Richard Worthington. from 7 miles south Lombardia, on the bank of the Rio Marquez. Michoacan. Elevation 461 meters, August 25, 1960.

Diagnosis. A medium-sized gecko although on average larger than *P. krotokini*; it presents 28 tubercles from head to tail, similar to *P. lupitae* (28.8) and *P. krotokini* (28.4). It differs from *P. isabelae* (32.2), *P. lanei* (33.2), *P. benedettii* (27.4), *P. t. magnus* (37), *P. muralis* (33.6) and *P. tuberculosus* (36.4) in tubercular counts. *Phyllodactylus rupinus* presents 14 rows of tubercles across its dorsum similar to *P. t. magnus* (14.3) and *P. tuberculosus* (14), and differs from *P. isabelae* (16.7), *P. lupitae* (14.8), *P. lanei* (15.6), *P. benedettii* (13.8), *P. krotokini* (13.4) and *P. muralis* (12.2). *Phyllodactylus rupinus* is clearly differentiated from other gecko species because it presents 26.5 scales across venter, while the others present: *P. isabelae* (27.8), *P. lupitae* (24.6), *P. lanei* (30), *P. benedettii* (29.1), *P. krotokini* (30.6), *P. t. magnus* (27.33), *P. muralis* (33) and *P. tuberculosus* (30.2).

Distribution. This species is restricted to the locality of Lombardia, Michoacan.

***Phyllodactylus isabelae* Castro-Franco & Uribe-Peña, 1992**

Holotype. An adult female, ZUP 1152 collected by Zeferino Uribe Peña on Marietas Islands, Nayarit, Mexico, February 23, 1978.

Diagnosis. This species clearly differs from the others because it is the smallest of the analyzed in the present study (Fig. 6). It presents 56.2 longitudinal scales on average, it differs clearly from the others: *P. lupitae* (61.8), *P. lanei* (66), *P. rupinus* (63.6), *P. benedettii* (62.6), *P. krotokini* (67.6), *P. t. magnus* (54.6), *P. muralis* (59) and *P. tuberculosus* (57.7). Also *P. isabelae* presents 27.8 scales across the venter similar to *P. t. magnus* (27.3) and differs from the others: *P. lupitae* (24.6), *P. lanei* (30), *P. rupinus* (26.5), *P. benedettii* (29.1), *P. krotokini* (30.6), *P. muralis* (33) and *P. tuberculosus* (30.2). *Phyllodactylus isabelae* differs clearly from the others analyzed since it has the highest number of rows of tubercles across dorsum (16.7 on average) compared to the others: *P. lupitae* (14.8), *P. lanei* (15.6), *P. rupinus* (14), *P. benedettii* (13.8), *P. krotokini* (13.4), *P. t. magnus* (14.3), *P. muralis* (12.2) and *P. tuberculosus* (14).

Distribution. *Phyllodactylus isabelae* is endemic of the Marietas islands, Nayarit, Mexico.

***Phyllodactylus lupitae* Castro-Franco & Uribe-Peña, 1992**

Holotype. Adult female, EBUM 1242 collected by R. Gonzalo Gaviño de la Torre on La Peña Island (or Coral island), Nayarit, Mexico, November 21, 1986.

Diagnosis. This is a larger gecko along with *P. lanei* and *P. benedettii* of the *P. lanei* complex. It presents 28.8 tubercles from head to tail, similar to *P. rupinus* (28) and *P. krotokini* (28.4). These counts differ from the other gecko species: *P. isabelae* (32.2), *P. lanei* (33.2), *P. benedettii* (27.4), *P. t. magnus* (37), *P. muralis* (33.6) and *P. tuberculosus* (36.4). *Phyllodactylus lupitae* differs clearly from the other species as it shows 25.5 third labial–snout scales, the others: *P. isabelae* (21.4), *P. lanei* (21.2), *P. rupinus* (20.6), *P. benedettii* (22.3), *P. krotokini* (20.2), *P. t. magnus* (24.6), *P. muralis* (25.2) and *P. tuberculosus* (24.2). It is a unique species because it shows 24.6 scales across venter, the others: *P. isabelae* (27.8), *P. lanei* (30), *P. rupinus* (26.5), *P. benedettii* (29.1), *P. krotokini* (30.6), *P. t. magnus* (27.3), *P. muralis* (33) and *P. tuberculosus* (30.2). Also presents 61.8 longitudinal scales, the others: *P. isabelae* (56.2), *P. lanei* (66), *P. rupinus* (63.6), *P. benedettii* (62.6), *P. krotokini* (67.6), *P. t. magnus* (54.6), *P. muralis* (59) and *P. tuberculosus* (57.7).

Distribution. This species is endemic to Coral Island (or La Peña island), Nayarit, Mexico.

Discussion

The combination of genetic, phylogenetic, species delimitation and validation, morphological differences and bioclimatic profiles (part of niche realized) strongly support the distinction of lineages that evolve independently and that should be considered at the species level within the *P. lanei* complex (Ramírez-Reyes *et al.* 2017). Elevation of taxa previously recognized as subspecies are needed to avoid existence of paraphyletic groups within the *P. lanei* clade (*sensu stricto* Dixon 1964) or polyphyletic taxa, since several herpetologists currently continue to classify populations of geckos in Nayarit and other states of Mexico as *P. lanei* (Bañuelos-Alamillo *et al.* 2017; Woolrich-Piña *et al.* 2016). The taxon previously recognized as *P. l. lanei* grouped all the populations of Guerrero, ignoring the phylogenetic relationships that exist between them; one example of this is the recovery of *P. krotokini* as a sister species of *P. lanei*, the first restricted to the Balsas Basin and the second to lower Pacific Coast on southern of Mexico in at least two localities, Tierra Colorada and Chilpancingo, both in Guerrero state. These species are divided by the Sierra Madre del Sur; this mountain chain represents the main geographical barrier to gene flow and migration of these populations and allowed the differentiation of these species (Ramírez-Reyes *et al.* 2017). On the other hand the taxon previously recognized as *P. l. rupinus* grouped a large number of populations and clades recovered with different ancestors in both gene trees and species tree (Figs. 2 and 3). From this contribution it is recognized that *P. rupinus* is restricted to the type locality (Lombardia, Michoacan) in the western portion of the Balsas Basin and relates the southern clade (*P. lanei* + *P. krotokini*) to the clade with the westernmost distribution of the entire complex (*P. benedettii* and *Phyllodactylus* sp.). In addition to the differences present in the resolved topology of the species tree (Fig. 3), the 7-species model within the *P. lanei* clade is the one with the highest posterior probability of validation according to the MSC model, for the set of genes concatenated with the priors of deep branches (ppv = 0.98) and shallow branches (ppv = 0.92). Models that collapse branches to test different species models (below 7) presented very low probabilities, as well as large population size models, a result highly congruent with that previously reported by Blair *et al.* (2014) which suggested that the geckos of the genus *Phyllodactylus* present small population sizes (historical and recent).

The trees estimated in the present contribution using concatenation and multispecies coalescent methods generated the same topologies, except *P. lanei* + *P. krotokini* were recovered as sister species in the coalescent tree; however, given the low phylogenetic signal obtained from nuclear loci and possibly high levels of incomplete lineage sorting (ILS) in nuclear genes we prefer the topology resolved in *BEAST to illustrate the phylogenetic relationships between lineages of the *P. lanei* complex (Fig. 3). Although we know that the ILS is not the only process responsible for the discordance between gene trees and species tree, to date, other sources of discordance have not been recognized in this group of geckos, such as hybridization or gene duplication and extinction (Maddison 1997; Tonini *et al.* 2015; Ramírez-Reyes *et al.* 2017). As the techniques of obtaining hundreds or thousands of loci and bioinformatic platforms to analyze genomic data advance, currently there are possibilities to study biodiversity at various scales (spatial and temporal) with great precision (McCormack *et al.* 2013; Potter *et al.* 2016), therefore, future genomic studies will solve the potentially hidden diversity that exists within the *Phyllodactylus* genus in Mexico (Blair *et al.* 2015; Ramírez-Reyes *et al.* 2017).

Proposals of taxonomic changes within the genus *Phyllodactylus* have been recurrent. Dixon (1964) mentioned the difficulty of assigning individuals and populations to defined taxa, due to the large variation particularly

noticeable within the *tuberculosis* group (*P. tuberculosis*, *P. xanti*, *P. homolepidurus*, *P. muralis*, *P. lanei*, *P. insularis*) and attempted to group “natural populations” into infraspecific categories for each species. With these changes he tried to increase the knowledge about the taxonomy and systematics within the *tuberculosis* group, although he admitted the great task pending for the taxonomists in the study of this particular group. Later, the studies of Castiglia *et al.* (2009; 2010) showed that there are important karyotypic differences between *P. l. lanei* and *P. l. rupinus* ($2n = 33-34$, $FN = 40-41$ for the first and $2n = 38$, $FN = 38$ for the second subspecies), as well as significant genetic distances in DNAm (8% within the 16S gene); the genetic differences within the mitochondrial genome were corroborated by Ramírez-Reyes *et al.* (2017), they found 25% genetic distance on average in the *Cytb* gene between the population of Chamela (*P. benedettii*) and *P. lanei* of Tierra Colorada.

Although the four continental species inhabit only two biogeographic provinces, the bioclimatic profiles for each one are well delimited and differentiated among them, (Fig. 8). The Pacific coast has one of the highest degrees of richness and endemism in Mexico (Flores-Villela 1993). The genus *Phyllodactylus* is an important component of the herpetofauna of this zone, since it is practically restricted at the region (Dixon 1964), however the diversity of this genus of geckos has been underestimated due to the poor sampling that has been done in several areas and the conservative morphology of this group. Recent efforts to study the group with molecular techniques have shown the hidden diversity that exists and new species have been discovered (Murphy *et al.* 2009; Blair *et al.* 2015; Ramírez-Reyes *et al.* 2017). In addition, in other groups recently studied, a greater diversity has been found, such as the *Trimorphodon* (LaDuc & Johnson, 2003; Devitt *et al.* 2008) and *Hypsiglena* (Mulcahy 2008) snakes. It is to be expected that other groups are in the same situation and waiting to be studied.

Morphologically the most differentiated species of the *P. lanei* complex is *P. isabelae*, easily diagnosed since it is the smallest species in the adult stage, has the largest number of tubercles between the axilla and groin, most rows of tubercles across the dorsum and has the fewest longitudinal scales. The medium-sized species are *P. rupinus* and *P. kropotkini*, easily differentiated because *P. rupinus* has a higher number of SBP, SBI and SAV on average, whereas *P. kropotkini* has a greater number of SBNE. The largest species (in descending order) are *P. lupitae*, *P. lanei* and *P. benedettii*, of which the third species has the highest SBP, and fewer number of SBNE, IS, TAD, LFT. In general all species of *Phyllodactylus* can be morphologically differentiated with the meristic and morphological characters, in combination with the geographical distribution; the clear delimitation of distribution of populations (or individuals) gives much information about the possible identity of a taxon, as well as opens the possibility of discovering and describing more species of geckos in Mexico (Blair *et al.* 2014; 2015; Ramírez-Reyes *et al.* 2017).

Since our objective is identify evolutionary species we consider that the taxonomic conclusions are fully justified by the congruence in the different lines of evidence (genetic, phylogenetic on gene and species trees, geographic, morphological and ecological). The seven species included within the *P. lanei* clade are clearly differentiated by several lines of evidence, showing that these species are not as cryptic as previously thought. However, we consider that by increasing the number of populations over large geographic areas and placing them under the same taxon, the main microevolutionary characteristics that have allowed the diversification of geckos in Mexico are being omitted (Blair *et al.* 2013; 2014; 2015), as a result, populations and lineages with distinct evolutionary trends are grouped under artificial taxa (species and subspecies), causing the great taxonomic confusion within the genus *Phyllodactylus* in Mexico (Dixon 1964; Ramírez-Reyes *et al.* 2017).

Finally, it is important to mention that leaf-toed gecko species are threatened by extermination campaigns by people which consider these species as poisonous or dangerous, from the coast of Guerrero to the coast of Nayarit. On the other hand *P. lupitae* may be in serious threat of extinction, due to the severe environmental degradation at the small Coral Island, mainly from the incorrect use of the natural resources of this island, campaigns of extermination and also to the recent arrival of the exotic species *Hemidactylus frenatus*, a species classified as “high risk” (CONABIO 2016; Ramírez-Reyes *et al.* 2015). The exotic gecko *H. frenatus* may be competing to occupy the same ecological niche with native gecko species (*Phyllodactylus*) and according to Blair *et al.* (2014) can have a direct impact by reducing effective population sizes (N_e) and may also affect the migration rate by forcing the displacement of native geckos in Mexico. These phenomena (natural and anthropogenic) have direct repercussions on some populations of native geckos which causes the loss of biodiversity, it is urgent to take mitigation measures and avoid threats of extinction of the insular species, we consider that is particularly serious in the population of *P. lupitae*, until now the only known endemic species of reptile that inhabits the small and damaged Coral Island.

Acknowledgments

TRR thanks Posgrado en Ciencias Biológicas (PCBIOL-UNAM) for allowing me to complete my research project, to Daniel Piñero for managing the support for fieldwork and genetic analysis at the Instituto de Ecología (IE-UNAM), Consejo Nacional de Ciencia y Tecnología (CONACYT) for scholarship support (CVU 586418), the Dirección General de Vida Silvestre SEMARNAT for granting the permit of scientific collection: SGPA/DGVS/10934/13. Thanks to J. Rosas-Avila, C. Melo-Leon, A. Villarruel, M. Q. Pureco-Rivera for their support in the field work, to V. H. Reynoso-Rosales for the review of specimens at the CNAR-IBUNAM, to E. Pérez-Ramos and I. Solano-Zavaleta for their support in the herpetological collection of the MZFC-UNAM, and to J. C. Lopez-Vidal, C. Elizalde-Arellano and G. Campillo for allowing access to specimens of the herpetological collection ENCB-IPN. Finally we thank to the anonymous reviewers and the associate editor for their comments that allowed a significant improvement in the manuscript.

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APPENDIX I. Samples used in molecular analyses, with proposed taxonomic identification, sample code and voucher and GenBank accession numbers.

Species	Sample Code	Voucher Code	Locality	Latitude	Longitude	Cyt b	16s rRNA	BDNF	C-mos
<i>P. isabelae</i>	IL1	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KY411648	KT008675	KT008788	KT008825
<i>P. isabelae</i>	IL2	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008731	KT008676	KT156571	KT008826
<i>P. isabelae</i>	IL3	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008732	KT008677	KT008787	KT008823
<i>P. isabelae</i>	IL4	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KY401166	KT008678	KY236062	KY236075
<i>P. isabelae</i>	IL5	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KY401165	KT008679	-	KT008819
<i>P. isabelae</i>	IL6	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KY411649	KT008680	KY236066	KY236077
<i>P. isabelae</i>	IL7	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	-	-	-	KT008822
<i>P. isabelae</i>	IL8	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	-	-	-	KT008820
<i>P. isabelae</i>	IL9	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008735	-	KT156588	KY236079
<i>P. isabelae</i>	IL10	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	-	-	KT008790	KT008821
<i>P. isabelae</i>	ILC1	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008729	KT008673	KT008786	KT008818
<i>P. isabelae</i>	ILC2	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008723	KT008674	KY236063	KT008824
<i>P. isabelae</i>	ILC3	-	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008730	KT008681	KY236064	KY236081
<i>P. isabelae</i>	IL11	MZFC28712	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008789	KT008682	KY236065	KY401173
<i>P. isabelae</i>	IL12	MZFC28711	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008733	KT008683	KT156570	KY236083
<i>P. isabelae</i>	IL13	MZFC28713	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	20.7	-105.58	KT008734	KT008684	KT008791	KY236085
<i>P. lupitae</i>	COR3	-	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008738	-	KY236067	KT008838
<i>P. lupitae</i>	COR4	MZFC28717	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008740	KT008685	KT156572	KT008836
<i>P. lupitae</i>	COR6	MZFC28718	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008727	-	-	KY236093
<i>P. lupitae</i>	COR7	MZFC28714	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008736	KT008686	KT008793	KY236089
<i>P. lupitae</i>	COR8	MZFC28719	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008737	-	KY236068	KY236087
<i>P. lupitae</i>	COR9	MZFC28716	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008728	KT008687	KT008794	KT008837
<i>P. lupitae</i>	COR10	MZFC28715	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	21.05	-105.27	KT008739	-	KT008792	KY236091
<i>P. lanei</i>	TC1	MZFC28725	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KY236056	-	KT156569	KY236097
<i>P. lanei</i>	TC2	MZFC28729	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	-	-	-	KT008831
<i>P. lanei</i>	TC3	MZFC28730	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008742	KY218785	KT156586	KY236099
<i>P. lanei</i>	TC4	MZFC28727	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008743	-	-	KY236101
<i>P. lanei</i>	TC7	-	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008741	KT008688	KT156568	KT008833
<i>P. lanei</i>	TC9	MZFC28726	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KY236057	KT008689	KT008782	KT008828
<i>P. lanei</i>	TC10	MZFC28728	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008748	-	KT008783	KY236095

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APPENDIX 1. (Continued)

Species	Sample Code	Voucher Code	Locality	Latitude	Longitude	Cyt b	16s rRNA	BDNF	C-mos
<i>P. lanei</i>	TC11	MZFC28732	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KY236058	-	KT008784	KT008829
<i>P. lanei</i>	TC12	MZFC28731	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KY236059	KT008690	KY236069	KT008834
<i>P. lanei</i>	TC14	-	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008745	KT008691	KT008785	KT008832
<i>P. lanei</i>	TC15	-	Tierra Colorada, Juan R. Escudero, Guerrero	17.16	-99.53	KT008744	KY218786	KY236070	KT008830
<i>P. lanei</i>	MZ4	-	Chilpancingo de los Bravo, Guerrero	17.55	-98.49	KT008746	KT008692	KY401169	KT008835
<i>P. lanei</i>	MZ5	-	Chilpancingo de los Bravo, Guerrero	17.55	-98.49	KT008747	KT008693	KT156587	KT008827
<i>P. leopotkini</i> sp. nov.	NF1	-	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008750	-	KY236071	KT008864
<i>P. leopotkini</i> sp. nov.	NF2	MZFC28738	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008749	KT008694	KY236072	KT008861
<i>P. leopotkini</i> sp. nov.	NF3	-	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008752	KT008695	KY401171	KY236105
<i>P. leopotkini</i> sp. nov.	NF4	MZFC28736	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008751	-	KY236074	KT008862
<i>P. leopotkini</i> sp. nov.	NF5	MZFC28735	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008753	KT008696	KT156562	KY236103
<i>P. leopotkini</i> sp. nov.	NF6	MZFC28739	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KY236060	-	KT008772	KY401175
<i>P. leopotkini</i> sp. nov.	NF7	MZFC28737	Nueva Filadelfia, Tlapehuala, Guerrero	18.29	-100.49	KT008754	-	KY236073	KT008863
<i>P. rupinus</i>	LM1	MZFC28767	Lombardía, Michoacán	19.18	-102.04	KT008762	KT008697	KT156567	KT008856
<i>P. rupinus</i>	LM2	MZFC28768	Lombardía, Michoacán	19.18	-102.04	KT008768	KT008698	KT156566	KT008860
<i>P. rupinus</i>	LM3	MZFC28769	Lombardía, Michoacán	19.18	-102.04	KT008766	KT008699	KT008781	KT008857
<i>P. rupinus</i>	LM4	MZFC28770	Lombardía, Michoacán	19.18	-102.04	KT008769	KT008700	KT008778	KY236107
<i>P. rupinus</i>	LM5	MZFC28771	Lombardía, Michoacán	19.18	-102.04	KT008770	KT008701	KT008779	KT008853
<i>P. rupinus</i>	LM6	-	Lombardía, Michoacán	19.18	-102.04	KT008771	KT008702	KT156584	KT008858
<i>P. rupinus</i>	LM7	-	Lombardía, Michoacán	19.18	-102.04	KT008763	KT008703	KT156585	KT008859
<i>P. rupinus</i>	LM8	-	Lombardía, Michoacán	19.18	-102.04	KT008767	KT008704	KT008780	KT008854
<i>P. rupinus</i>	LM9	-	Lombardía, Michoacán	19.18	-102.04	KT008764	KT008705	-	KT008852
<i>P. rupinus</i>	LM10	-	Lombardía, Michoacán	19.18	-102.04	KT008765	KT008706	-	KT008855
<i>P. benedettii</i> sp. nov.	CH1	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008716	KT008707	-	KT008846
<i>P. benedettii</i> sp. nov.	CH2	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008717	-	-	-
<i>P. benedettii</i> sp. nov.	CH3	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008714	KY218787	KT156564	KT008843
<i>P. benedettii</i> sp. nov.	CH4	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008758	KT008708	-	KT008847
<i>P. benedettii</i> sp. nov.	CH5	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008725	-	-	KY236111

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APPENDIX 1. (Continued)

Species	Sample Code	Voucher Code	Locality	Latitude	Longitude	Cyt b	16s rRNA	BDNF	C-mos
<i>P. benedettii</i> sp. nov.	CH6	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KY236061	KY218788	KT008774	KT008844
<i>P. benedettii</i> sp. nov.	CH7	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008756	KY218789	KT156565	KT008839
<i>P. benedettii</i> sp. nov.	CH8	MZFC28773	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008720	-	-	KY236109
<i>P. benedettii</i> sp. nov.	CH9	MZFC28774	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008760	KY218790	KT008773	KT008845
<i>P. benedettii</i> sp. nov.	CH10	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008719	KY218791	-	KY218791
<i>P. benedettii</i> sp. nov.	CH11	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008715	-	-	KT008851
<i>P. benedettii</i> sp. nov.	CH12	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008724	-	-	-
<i>P. benedettii</i> sp. nov.	CH13	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008759	-	-	-
<i>P. benedettii</i> sp. nov.	CH14	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008755	-	-	-
<i>P. benedettii</i> sp. nov.	CH15	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008757	-	-	KT008840
<i>P. benedettii</i> sp. nov.	CH16	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008726	-	-	-
<i>P. benedettii</i> sp. nov.	CH17	-	Estación de Biología Chamela UNAM, La Huerta, Jalisco	19.5	-105.04	KT008722	-	-	KT008850
<i>Phyllodactylus</i> sp.	AC1	-	Amatlan de Cañas, Nayarit	20.81	-104.4	KT008761	KT008709	KT008776	KT008842
<i>Phyllodactylus</i> sp.	AC2	-	Amatlan de Cañas, Nayarit	20.81	-104.4	KT008721	KT008710	KT156563	KT008849
<i>Phyllodactylus</i> sp.	MZ1	MZFC17325	Carretera Tepic-Puerto Vallarta, Nayarit	20.83	-105.41	KT008718	KT008711	KT008775	KT008848
<i>Phyllodactylus</i> sp.	MZ2	MZFC17326	Carretera Tepic-Puerto Vallarta, Nayarit	20.69	-105.25	KT008713	KT008712	KT008777	KT008841
<i>Phyllodactylus</i> sp.	MZ7	MZFC21620	Aprox km 192 de la carretera Puerto Escondido-Oaxaca	16.14	-96.90	KY401164	KT156602	KT156594	KT156606
<i>Phyllodactylus</i> sp.	MZ8	-	Tres Cruces carretera Mx 49 aprox 7km S de la desviación a Guichichu	-	-	-	KT156603	KT156595	KT156607
<i>P. bordai</i>	MZ10	-	Carretera Texcala-Zapotitlan Salinas	-	-	KY401166	KT156604	KT156598	KY271622
<i>P. bordai</i>	MZ11	-	Zapotitlan Salinas	-	-	KY401168	KT156605	KT156599	KY271624
<i>P. tuberculatus</i>	MZ12	-	Chihuahua	-	-	KY401177	KY238291	KY271620	KY271626

APPENDIX II. Morphologically examined specimens, new taxonomic combinations for all taxa analyzed (species level), voucher number, locality and measurements of meristic and morphometric characters. Holotypes of the new species are identified in bold and paratypes are underlined.

Species	Voucher code	Locality	SVL (mm)	LH (mm)	4ATR	4ATL	4PTR	4PTL	SAV	THT	TAG	RTD	IS	SBI	TLS	SNE	SBP	LS
<i>P. isabellae</i>	MZFC28709	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	55	13.5	11	12	11	11	29	30	22	17	15	6	22	13	6	74
<i>P. isabellae</i>	MZFC28710	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	50.5	13.5	12	12	12	13	27	32	22	15	15	6	19	12	6	66
<i>P. isabellae</i>	MZFC28711	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	48.3	13.2	13	13	13	14	29	34	23	16	15	5	20	12	6	67
<i>P. isabellae</i>	MZFC28712	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	42.6	12	12	13	12	13	28	35	20	18	15	6	21	11	6	68
<i>P. isabellae</i>	MZFC28713	Isla Larga, Islas Marietas, Bahía de Banderas, Nayarit	35.7	10.3	13	13	13	13	28	31	20	17	14	5	21	13	6	64
<i>P. isabellae</i>	MZFC13850	Isla Redonda, Bahía del Encuentro, Islas Marietas	45	13.4	11	11	11	12	29	31	25	16	16	5	21	11	6	68
<i>P. isabellae</i>	MZFC13851	Isla Redonda, Bahía del Encuentro, Islas Marietas	42.6	12.9	12	12	12	13	30	33	26	18	15	5	24	12	5	68
<i>P. lupitae</i>	MZFC28714	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	63.7	16.8	14	13	13	13	28	27	20	15	14	6	27	14	5	77
<i>P. lupitae</i>	MZFC28715	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	73.3	18.7	13	13	-	14	27	28	21	15	16	6	23	11	4	77
<i>P. lupitae</i>	MZFC28716	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	72.3	18.1	13	14	13	13	27	27	22	15	20	7	26	11	4	78
<i>P. lupitae</i>	MZFC28717	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	64.9	16.9	13	14	13	13	27	-	-	15	16	6	28	11	5	72
<i>P. lupitae</i>	MZFC28718	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	65	16.2	13	13	14	14	27	31	21	15	17	7	26	12	5	76
<i>P. lupitae</i>	MZFC28719	Isla El Coral (La Peña), Rincon de Guayabitos, Nayarit	51.5	13.7	13	13	13	12	27	31	20	14	18	6	23	10	5	75
<i>P. lanei</i>	MZFC28725	Bachillerato de Tierra Colorada, Guerrero	21.4	7.3	14	-	14	13	32	34	20	14	15	6	22	12	5	90
<i>P. lanei</i>	MZFC28726	Bachillerato de Tierra Colorada, Guerrero	26.8	8.7	10	13	13	13	34	32	20	16	15	5	20	13	5	92
<i>P. lanei</i>	MZFC28727	Bachillerato de Tierra Colorada, Guerrero	24.8	9	12	14	13	14	30	33	21	16	17	6	21	12	6	93
<i>P. lanei</i>	MZFC28728	Bachillerato de Tierra Colorada, Guerrero	29.1	9.4	13	13	-	14	34	32	19	16	16	6	21	12	5	89
<i>P. lanei</i>	MZFC28729	Bachillerato de Tierra Colorada, Guerrero	28.7	9.4	14	14	12	12	32	34	21	16	15	5	21	13	4	92
<i>P. lanei</i>	MZFC28730	Bachillerato de Tierra Colorada, Guerrero	52	15.5	12	12	14	14	31	34	18	15	15	5	20	10	4	83
<i>P. lanei</i>	MZFC28731	Bachillerato de Tierra Colorada, Guerrero	33.2	12	13	13	13	14	30	33	17	16	15	6	22	12	4	87

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APPENDIX II. (Continued)

Species	Voucher code	Locality	SVL (mm)	LH (mm)	4ATR	4ATL	4PTR	4PTL	SAV	THT	TAG	RTD	IS	SBI	TLS	SNE	SBP	LS
<i>P. lanei</i>	MZFC28732	Bachillerato de Tierra Colorada, Guerrero	50.9	14.1	12	13	13	14	32	34	18	16	16	6	23	12	5	90
<i>P. lanei</i>	MZFC20472	Agua de Obispo, Chilpancingo, Guerrero	27.3	9.7	12	13	14	14	32	33	20	15	18	7	25	13	6	-
<i>P. lanei</i>	MZFC25076	Tierra Colorada, La Laguna, Guerrero	25	8.6	12	12	15	12	32	31	20	14	15	7	20	11	4	84
<i>P. lanei</i>	IBH130	Tierra Colorada, Guerrero	54.5	17.7	10	12	11	11	36	31	22	15	18	5	23	12	4	-
<i>P. lanei</i>	IBH131	Tierra Colorada, Guerrero	39.7	11.7	11	11	13	11	32	30	18	15	18	5	20	10	6	-
<i>P. lanei</i>	IBH10114	Chilpancingo, Acahuizotla, Guerrero	-	18.2	11	13	13	12	-	-	-	-	15	6	23	10	4	-
<i>P. rupinus</i>	MZFC28767	Lombardia cerca de las Pintadas, Michoacan	60.1	16.4	11	12	11	11	35	28	22	14	16	7	20	13	8	92
<i>P. rupinus</i>	MZFC28768	Lombardia cerca de las Pintadas, Michoacan	65.5	17.5	12	12	11	11	34	28	18	13	16	5	18	12	5	86
<i>P. rupinus</i>	MZFC28769	Lombardia cerca de las Pintadas, Michoacan	60.5	15.9	13	13	12	11	31	30	17	15	15	7	22	10	8	93
<i>P. rupinus</i>	MZFC28770	Lombardia cerca de las Pintadas, Michoacan	65.5	16.5	12	12	13	13	36	28	21	14	15	7	22	11	7	91
<i>P. rupinus</i>	MZFC28771	Lombardia cerca de las Pintadas, Michoacan	59.6	15.7	11	11	13	13	32	28	21	14	16	7	22	9	4	91
<i>P. rupinus</i>	MZFC12717	Nuevo Urecho, Michoacan	62.2	-	12	13	13	13	31	30	20	14	14	6	19	9	6	74
<i>P. rupinus</i>	MZFC12731	Nuevo Urecho, Michoacan	62.5	16.6	12	12	13	13	30	26	19	14	17	6	22	11	6	88
<i>P. rupinus</i>	MZFC12788	Nuevo Urecho, Michoacan	63.4	16.3	12	12	12	13	28	26	19	14	15	5	20	9	7	77
<i>P. benedictii</i>	MZFC28773	Estacion de Biologia Chamela IBUNAM, Jalisco	69	19.1	13	13	13	12	34	25	18	14	14	7	23	10	4	79
<i>P. benedictii</i>	MZFC28774	Estacion de Biologia Chamela IBUNAM, Jalisco	70.3	18.3	13	13	11	13	34	24	19	13	13	6	22	11	4	87
<i>P. benedictii</i>	MZFC21885	Estacion de Biologia Chamela	74.2	20.4	11	-	-	12	-	28	17	14	13	7	22	10	6	78
<i>P. benedictii</i>	MZFC21817	Chamela	65.1	18	11	12	11	11	35	28	19	14	16	6	23	10	5	78
<i>P. benedictii</i>	MZFC21818	Chamela	44	11.9	12	12	13	12	32	29	20	13	14	6	23	12	5	70
<i>P. benedictii</i>	MZFC21877	Puente Juan Pérez I, Chamela	39.3	10.6	10	11	11	12	31	29	25	14	16	7	22	10	7	65
<i>P. benedictii</i>	MZFC21878	Puente Juan Pérez I, Chamela	61	16.6	11	10	12	13	30	27	18	14	14	6	22	11	5	76
<i>P. benedictii</i>	MZFC21879	Puente Juan Pérez I, Chamela	43.7	12	-	11	13	12	32	29	23	14	13	6	22	10	6	79
<i>P. benedictii</i>	MZFC21880	Puente Juan Pérez I, Chamela	65.3	16.9	11	11	11	12	36	30	24	14	16	5	23	10	5	73
<i>P. benedictii</i>	MZFC287	Melaque, La Huerta, Jalisco	53.1	14.5	12	12	11	12	30	29	23	14	14	7	22	10	6	78
<i>P. benedictii</i>	MZFC5940	La Huerta, Jalisco	40.2	11	13	12	13	13	-	24	20	-	16	7	22	13	6	-

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APPENDIX II. (Continued)

Species	Voucher code	Locality	SVL (mm)	LH (mm)	4ATR	4ATL	4PTR	4PTL	SAV	THT	TAG	RTD	IS	SBI	TLS	SNE	SBP	LS
<i>P. benedictii</i>	IBH2138	5 km. S., de Chamela, Estación de Biología, UNAM	63.1	18.1	-	14	12	13	34	32	20	15	17	5	22	12	7	-
<i>P. benedictii</i>	IBH2133	2 km. SE., de Chamela, Estación de Biología	63.7	18.6	12	13	12	12	31	32	21	14	16	5	20	10	5	-
<i>P. benedictii</i>	IBH2133-9	2 km. SE., de Chamela, Estación de Biología	68.6	18	13	13	12	12	31	27	21	13	15	6	21	11	4	87
<i>P. benedictii</i>	IBH2133-3	2 km. SE., de Chamela, Estación de Biología	65	17.8	-	12	12	12	30	29	21	14	14	5	21	11	6	85
<i>P. benedictii</i>	IBH2133-5	2 km. SE., de Chamela, Estación de Biología	59	12.6	11	11	13	13	30	31	21	14	15	6	20	11	6	80
<i>P. benedictii</i>	IBH2133-2	2 km. SE., de Chamela, Estación de Biología	57	15.6	-	-	12	12	30	29	22	15	16	6	22	10	4	80
<i>P. benedictii</i>	IBH2133-4	2 km. SE., de Chamela, Estación de Biología	69.6	19	13	13	12	11	31	27	22	13	16	7	20	10	4	86
<i>P. benedictii</i>	IBH2133-2	2 km. SE., de Chamela, Estación de Biología	72	19.6	12	12	13	12	30	30	22	15	15	5	23	9	5	80
<i>P. benedictii</i>	IBH2138-4	2 km. SE., de Chamela, Estación de Biología	70.7	19.3	13	13	12	11	35	31	20	14	18	7	22	12	5	88
<i>P. benedictii</i>	IBH2138-2	5 km. S., de Chamela, Estación de Biología, UNAM	67	17.2	12	12	13	13	29	31	20	16	17	6	25	11	7	80
<i>P. benedictii</i>	IBH2138-3	5 km. S., de Chamela, Estación de Biología, UNAM	71	19.1	12	11	11	10	27	31	21	14	15	7	24	10	5	-
<i>P. benedictii</i>	IBH2170	Rio San Nicolás, 20 km. NW. carretera Chamela	56.1	15.1	12	13	14	13	32	27	22	14	15	6	23	12	5	83
<i>P. benedictii</i>	IBH2133-7	2 km. SE., de Chamela, Estación de Biología	70.5	20.3	12	12	12	12	30	31	24	14	16	5	22	12	5	82
<i>P. benedictii</i>	IBH2135	6 km. SE., de Chamela, Estación de Biología	63.8	17.3	12	12	12	11	-	33	23	14	17	7	21	11	4	-
<i>P. benedictii</i>	IBH2136	6 km. SE., de Chamela, Estación de Biología	61.3	18.2	12	12	11	11	31	26	23	16	15	7	21	11	5	-
<i>P. kropotkini</i>	MZFC28735	Nueva Filadelfia, Tlapehuala, Guerrero	59.2	15.1	13	13	12	13	31	28	20	14	15	6	20	11	6	91
<i>P. kropotkini</i>	MZFC28736	Nueva Filadelfia, Tlapehuala, Guerrero	62.3	16.6	13	13	14	12	31	31	17	14	14	6	20	13	5	80
<i>P. kropotkini</i>	MZFC28737	Nueva Filadelfia, Tlapehuala, Guerrero	49.9	13.7	14	14	13	13	27	29	19	14	15	5	19	10	5	79
<i>P. kropotkini</i>	MZFC28738	Nueva Filadelfia, Tlapehuala, Guerrero	56	14.8	13	13	13	12	31	29	22	13	14	5	21	13	5	90
<i>P. kropotkini</i>	MZFC28739	Nueva Filadelfia, Tlapehuala, Guerrero	51.6	13.5	13	14	13	14	31	25	21	12	15	5	21	10	5	81

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APPENDIX II. (Continued)

Species	Voucher code	Sex	SVL	LAG	HL	HW	SL	ED	AO	LFF	LFT	WES	LI
<i>P. benedetti</i> sp. nov.	<u>MZFC28774</u>	M	70.9	35.8	16.5	13.2	10.05	4.1	1.6	5.5	5.7	9	2.1
<i>P. benedetti</i> sp. nov.	<u>MZFC28773</u>	F	68.4	28	18.6	13.3	12.4	4	2.7	5.8	6.7	9.4	2.1
<i>P. benedetti</i> sp. nov.	<u>MZFC21885</u>	M	73.4	31	21.3	14.6	13.9	4.3	3	5.7	7	9.5	2.2
<i>P. benedetti</i> sp. nov.	<u>MZFC21817</u>	M	65.1	26.1	17.8	13.2	11.7	4	1.9	5	5.9	7.7	2
<i>P. benedetti</i> sp. nov.	<u>MZFC21880</u>	F	66.9	26	17.5	13	12	3.8	2	4.7	5.4	7.3	2
<i>P. benedetti</i> sp. nov.	<u>MZFC21878</u>	M	60.8	24.5	16.4	11	10.7	3.4	1.9	4	5.3	6.9	1.9
<i>P. benedetti</i> sp. nov.	<u>MZFC21818</u>	M	44.1	18.9	12	8.7	8.7	2.7	1.4	3.7	4.4	6	1.6
<i>P. benedetti</i> sp. nov.	IBH2138	F	65.6	28	17.7	12	12	4.2	2.2	5	6.2	8.3	1.9
<i>P. benedetti</i> sp. nov.	IBH2138-3	F	72	31.5	19.7	13.7	13	4.4	2.4	5	6	9.9	2.2
<i>P. benedetti</i> sp. nov.	IBH2136	M	64.9	27	18	12	11.7	4.1	2.6	5	6.4	8	2
<i>P. benedetti</i> sp. nov.	IBH2133-3	M	65.4	29.6	17.7	12	12.5	4.1	2.5	5.3	6.6	8.4	1.7
<i>P. benedetti</i> sp. nov.	IBH2133-9	M	69	29.4	18.3	13.4	12.3	4	2.8	5.2	6.3	9	2
<i>P. benedetti</i> sp. nov.	IBH2133	F	65.2	28.3	18.6	13	12.3	4.1	2.8	5.7	6	9	2
<i>P. benedetti</i> sp. nov.	IBH2135	M	64.4	29.4	17.7	13	11.5	3.7	2.6	5.3	6.3	8.9	2
<i>P. benedetti</i> sp. nov.	IBH2133-7	M	73.2	31.7	19.6	15	13.5	4.6	3	6	6.6	9.5	2.2
<i>P. benedetti</i> sp. nov.	IBH2133-4	M	72	31.9	19.3	15	12.6	4.3	3	6	7.4	9.4	2.2
<i>P. benedetti</i> sp. nov.	IBH2137	M	75.2	31	20	14	13.4	4.3	3.2	6.2	6.5	9	2.3
<i>P. benedetti</i> sp. nov.	IBH2138-4	F	71.5	33	18.8	14.1	13	4.4	2.3	6.3	6.3	9.4	2.5
<i>P. benedetti</i> sp. nov.	IBH2138-2	F	67.3	30	17.7	12.8	12	4	2.3	5.5	6	9	2.3
<i>P. benedetti</i> sp. nov.	IBH2133-8	F	63.6	24	17.7	11.7	11.4	3.7	1.8	5	6.1	7.7	2.2
<i>P. benedetti</i> sp. nov.	IBH2133-10	F	59.3	21.4	15.3	11.2	10.3	3.1	1.4	4.4	5.6	8	2
<i>P. kroptukini</i> sp. nov.	MZFC28736	M	62.2	23	16.9	12.3	7.5	3.3	1.7	5	6	8.1	1.5
<i>P. kroptukini</i> sp. nov.	<u>MZFC28735</u>	M	59.4	25.7	15.4	11.6	10.6	3.3	2	4.6	5.8	7.6	1.7
<i>P. kroptukini</i> sp. nov.	<u>MZFC28737</u>	M	49.1	20	14	10	9.2	3.4	1.7	4.1	4.6	7	1.4
<i>P. kroptukini</i> sp. nov.	<u>MZFC28738</u>	M	55	22	14.9	10.7	10	3.3	1.7	4.3	6.1	7.3	1.6
<i>P. kroptukini</i> sp. nov.	<u>MZFC28739</u>	M	50.6	22	13.9	10.3	9.4	3	1.8	4.2	5	7	1.5
<i>P. rupinus</i>	MZFC28767	F	60.5	24.8	15.4	11.5	10.3	3.4	2	4	5.5	7	1.8
<i>P. rupinus</i>	MZFC28768	F	66.4	26.2	18	12.3	12	3.7	2	5.1	6.3	7.8	2
<i>P. rupinus</i>	MZFC28769	F	62.2	25.7	16.4	11	11.2	3.4	2	4.7	5.5	7.5	1.6
<i>P. rupinus</i>	MZFC28770	M	66.6	27.7	16.6	11.9	11.1	3.7	2.3	5	5.6	7.5	1.7
<i>P. rupinus</i>	MZFC28771	F	59.3	27.1	15.3	11	10.8	3.2	1.5	4.7	5.8	6.4	1.8
<i>P. rupinus</i>	MZFC12717	M	61	25.6	17.1	13.4	-	-	2.1	5	7	6	1.9

.....continued on the next page

APPENDIX II. (Continued)

Species	Voucher code	Sex	SVL	LAG	HL	HW	SL	ED	AO	LFF	LFT	WES	LI
<i>P. rupinus</i>	MZFC12731	F	63.7	26.4	17	11.5	11.1	3.5	1.7	4.2	5.4	6.8	1.9
<i>P. rupinus</i>	MZFC12788	F	63.1	25.3	16.7	11.7	11	3.5	1.6	4.8	5.8	8.7	2
<i>P. lanei</i>	MZFC28730	F	52.8	21.1	14.6	9.8	9.4	3.2	1.7	4.6	5.2	6.2	1.6
<i>P. lanei</i>	MZFC28732	M	52.2	19.9	14.5	9.6	9.4	3.2	2	4.2	5	7	1.7
<i>P. lanei</i>	EPR1558	F	57.6	24.5	14.7	11.5	11	3.4	2	4.9	5.5	7	1.7
<i>P. lanei</i>	ENCB18936	M	61	24	15.2	11.4	11	3.7	2	4.1	4.6	7.6	2
<i>P. lanei</i>	ENCB18937	F	71	29	18.4	13.4	12	3.7	2.1	5.4	7	8	2.4
<i>P. lanei</i>	ENCB18935	M	59	24	15.5	11	10.5	4	1.8	4.6	5.4	7	2.7
<i>P. lanei</i>	ENCB18966	M	67.8	30.4	16.5	11.9	11	3.8	2.1	5	6.5	8	2.5
<i>P. lupitae</i>	MZFC28714	F	62.3	25.2	16.3	11.3	11	3.4	2	5.1	6.4	7.4	2
<i>P. lupitae</i>	MZFC28715	M	72.1	31.5	19	13.5	13.2	4.3	2.1	6	7	9.4	2.3
<i>P. lupitae</i>	MZFC28716	F	71.2	31.7	18.6	13.8	13	4.4	2.2	5.9	6.4	9.2	2.3
<i>P. lupitae</i>	MZFC28717	F	64.1	29.3	17	11.7	11.3	3.9	2.3	5	6	8.4	2.3
<i>P. lupitae</i>	MZFC28718	M	64.8	28.3	16.6	12.4	11.6	4	2	5.1	6.6	9	2
<i>P. lupitae</i>	MZFC28719	M	51	21.6	13.7	9.8	9.7	3	1.4	4.5	5.3	6.4	1.6
<i>P. isabelae</i>	MZFC28709	F	55.2	22.2	13.7	10.2	9	3.3	2	4.1	5.1	6.8	1.6
<i>P. isabelae</i>	MZFC28710	F	49.8	20.5	13.7	10	8.7	2.7	1.7	3.8	4.7	6.3	1.7
<i>P. isabelae</i>	MZFC28711	M	48.3	20	13.2	9.4	8.5	2.8	1.4	3.7	4.3	6.4	1.4
<i>P. isabelae</i>	MZFC28712	M	43	18.4	11.3	8.2	7.3	2.6	1.4	3.2	4.1	5.4	1.4
<i>P. isabelae</i>	MZFC28713	M	36.6	14.6	9.6	7.3	6.6	2	1	3	3.5	4.4	1.4
<i>P. isabelae</i>	MZFC13850	F	45.2	17	12.8	8.6	8.6	3	1.6	3.6	4	6.4	1.7
<i>P. isabelae</i>	MZFC13851	F	43.3	14.3	12.9	8.7	8.6	3.2	1.5	3.5	4.4	5.9	1.7
<i>P. bordai</i>	MZFC9048	M	53.4	24.4	14.7	10.2	9.6	3.1	1.2	3.4	5	7	1.8
<i>P. bordai</i>	MZFC9049	F	55.8	22.8	14.6	11	9.8	3.4	1.7	3.3	4.6	7.3	2
<i>P. bordai</i>	MZFC9050	M	57.5	24	14.6	10.7	9	3.2	1.1	3.4	5.3	7.3	2
<i>P. bordai</i>	MZFC9051	M	52	23	14	10.4	8.3	3.1	1	3.2	5.5	7.3	1.8
<i>P. bordai</i>	MZFC9052	M	52.6	23	13.7	9.1	8.8	3.1	1.1	3.6	5.2	6.4	1.8
<i>P. bordai</i>	MZFC9054	M	51.2	20.4	12.5	9.4	8.6	3.2	2	3.2	4.6	6.3	1.7
<i>P. bordai</i>	MZFC9055	M	58.9	24.3	14.9	11.7	9.3	3.6	2	3.7	5.5	7.6	1.7
<i>P. bordai</i>	MZFC9056	M	58.4	23.6	15.3	11.1	9.6	3.4	1.7	3.9	5.6	7	1.7
<i>P. bordai</i>	MZFC9057	F	56.7	23.7	14	10	9.3	3.4	1.4	3.4	5	6.7	1.7
<i>P. bordai</i>	MZFC10475	M	52.4	22.2	13.5	9.7	8.4	2.8	1.4	3	4.4	6	1.6
<i>P. bordai</i>	MZFC16980	F	55.3	23.8	14	11	9	3	1.4	3.2	4.6	7.1	1.7
<i>P. bordai</i>	MZFC16979	M	49.3	18.8	13.4	10	8.3	3.2	1.2	3.4	4	6.7	1.6

APPENDIX III. Mean values of meristic characters for 17 species of *Phyllodactylus* in Mexico. Some of the data were published by Murphy *et al.* (2009), these data were used as framework and to determine differences among characters for *Phyllodactylus* species in Mexico.

Species	SBP	SBI	SBNE	IS	TLS	TAD	THT	TAG	SAV	LFT
<i>P. unctus</i>	7	6	11.4	19.3	21.7	0	0	0	29.4	12.8
<i>P. paucituberculatus</i>	7	5.3	10.2	17.5	19.5	10	28.7	14.7	25.2	13.5
<i>P. duellmani</i>	7	6.6	10.8	15.6	19.9	11.2	37.1	24	23.6	11.5
<i>P. delcampi</i>	6.3	5.7	13.8	20.2	21	14.6	63.4	37	30	15
<i>P. bordai</i>	5.6	5.1	10.9	15.2	19.4	14.9	32.9	18	28.8	12.6
<i>P. davisi</i>	7.1	6.6	11.6	19.2	23.7	15.7	41.6	22.9	30.8	12.2
<i>P. muralis</i>	8	7	13.1	21.4	26.1	13.6	33.1	17	29.6	12.3
<i>P. homolepidurus</i>	6.7	0.5	11.9	20.5	22.5	13.2	35.9	20.2	30.3	14.1
<i>P. xanti</i>	8.3	0.1	10.8	19.2	16.5	13.6	37	24.1	34.4	11.2
<i>P. lanei*</i>	4.7	5.7	11.6	16	21.6	15.1	32.4	18.6	32.1	12.9
<i>P. tuberculatus</i>	5.9	6.8	12.3	18.9	24.1	15.2	35.6	19.3	30.1	13.6
<i>P. papenfussi</i>	6.4	5.1	9.8	17.5	17.8	14.5	33.2	18.9	24.6	10.1
<i>P. isabelae*</i>	5.9	5.4	12	15	21.1	16.7	32.3	22.6	28.6	12.7
<i>P. lupitae*</i>	4.7	6.3	11.5	16.8	25.5	14.8	28.8	20.8	27.2	13.2
<i>P. rupinus*</i>	6.4	6.3	10.5	15.5	20.6	14	28	19.6	32.1	12.3
<i>P. benedettii sp. nov.*</i>	5.2	6.2	10.8	15.2	22	14.1	28.8	21.1	31.5	12
<i>P. kropotkini sp. nov.*</i>	5.2	5.4	11.4	14.6	20.2	13.4	28.4	19.8	30.2	12.8

* Data compiled by the first author, the data without the mark come from the study of Murphy *et al.* (2009).

APPENDIX IV. Bioclimatic variables used to characterize bioclimatic profiles, correlation with the principal components, and eigenvalues and explanative power of the PCs.

Variable	Variable meaning	PC 1	PC 2	PC 3	PC 4
BIO1	Annual Mean Temperature	0.030462	-0.02416	-0.02356	-0.080415
BIO2	Mean Diurnal Range	0.060922	-0.15931	0.058765	0.010235
BIO3 (BIO2/BIO7)	Isothermality (BIO2/BIO7)(*100)	0.033573	0.072958	-0.025464	-0.078863
BIO4	Temperature Seasonality (standard deviation *100)	-0.35673	-0.14253	0.025722	0.21649
BIO5	Maximum Temperature of Warmest Month	0.055602	-0.11271	0.014259	-0.020635
BIO6	Minimum Temperature of Coldest Month	0.085743	0.040315	-0.068961	-0.15455
BIO7 (BIO5-BIO6)	Temperature Annual Range (BIO5-BIO6)	0.027349	-0.23227	0.084229	0.089098
BIO8	Mean Temperature of Wettest Quarter	-0.0096698	0.013387	-0.032051	-0.10611
BIO9	Mean Temperature of Driest Quarter	0.080732	-0.07155	0.021712	-0.018173
BIO10	Mean Temperature of Warmest Quarter	0.016171	-0.04209	-0.021648	-0.056291
BIO11	Mean Temperature of Coldest Quarter	0.061521	-0.016389	-0.03033	-0.094807
BIO12	Annual Precipitation	0.35995	0.03377	0.22206	0.28083
BIO13	Precipitation of Wettest Month	0.297	0.12375	0.1696	0.32346
BIO14	Precipitation of Driest Month	-0.011216	-0.18314	0.86557	-0.35843
BIO15	Precipitation Seasonality (Coefficient of Variation)	0.0039904	-0.020129	0.045813	0.11143
BIO16	Precipitation of Wettest Quarter	0.29859	0.046016	0.25568	0.39253
BIO17	Precipitation of Driest Quarter	-0.56348	0.33574	0.23984	-0.12445
BIO18	Precipitation of Warmest Quarter	-0.10913	0.74359	0.14583	0.25781
BIO19	Precipitation of Coldest Quarter	0.45677	0.39322	-0.078653	-0.56915
Eigenvalue		0.083	0.02	0.01	0.001
Explained variance		70.15	16.80	9.9	1.64