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The sprightly little sphaerodactyl: Systematics and biogeography of the Puerto Rican dwarf geckos *Sphaerodactylus* (Gekkota, Sphaerodactylidae)

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Abstract

Studies of the Caribbean herpetofauna (amphibians and reptiles) have made significant contributions to our knowledge of evolutionary patterns and processes. A prerequisite for these studies are accurate taxonomies and robust phylogenetic hypotheses. One notable Caribbean radiation lacking such data are dwarf geckos of the genus *Sphaerodactylus*. Systematics of the Puerto Rican *Sphaerodactylus* have been turbulent since the initial species descriptions and no molecular phylogenies exist that include complete or near-complete taxon sampling. Here, we combine a multi-locus molecular phylogeny with extensive morphological information to investigate the current diversity of *Sphaerodactylus* geckos from the Puerto Rican Bank, with a large number of species from Hispaniola as an outgroup. In particular, we focus our efforts on resolving the taxonomy of the *Sphaerodactylus macrolepis* Günther species complex. We find *S. macrolepis sensu lato* (currently two nominal species with nine subspecies) is made up of at least four diagnosable species within two clades: (1) the sister species *Sphaerodactylus macrolepis sensu stricto* from the Virgin Islands (including St. Croix) and Culebra, and *S. parvus* King from islands in the northern Lesser Antilles; and (2) all other *Sphaerodactylus macrolepis* subspecies from Puerto Rico, Vieques, and Culebra. We resurrect *Sphaerodactylus grandisquamis* Stejneger from synonymy to refer to all subspecies from Puerto Rico and elevate the subspecies *Sphaerodactylus inigoi* Thomas & Schwartz for geckos from Vieques and western Culebra. The resulting phylogeny and revised taxonomy will be a useful tool for subsequent research into *Sphaerodactylus* conservation and evolution.

Key words: biogeography, Caribbean, Hispaniola, lizard, morphology, Puerto Rico, taxonomy, species delimitation, Squamata, Virgin Islands

Introduction

"I know of no genus that more amply repays finding, catching and classifying than the sprightly little sphaerodactyl."—*Major Chapman Grant (1931)*

The study of island flora and fauna has made significant contributions to our understanding of evolution (Darwin 1859; Losos 2009; MacArthur & Wilson 1967). In fact, the bulk of data regarding speciation and adaptive radiations comes from studying island taxa (Gillespie 2004; Grant & Grant 2011; Losos *et al.* 1998). A common 'textbook ex-

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ample' of an adaptive radiation, Caribbean *Anolis* lizards have repeatedly evolved convergent, habitat-specific phenotypes, or ecomorphs, across the islands of the Greater Antilles (Losos 2009; Losos *et al.* 1998; Williams 1983). Expanding the scope of evolutionary studies to incorporate additional Caribbean fauna will allow empiricists to determine whether the adaptive patterns observed in *Anolis* are generalizable across co-distributed taxa, particularly as they relate to biogeography and the evolution of distinct ecomorphs. However, testing broader evolutionary hypotheses requires accurate descriptions of relevant species, their phylogenetic relationships, and their biogeographic history.

While numerous studies have made significant headway addressing the biological diversity and systematics of the Caribbean herpetofauna (e.g. Hedges *et al.* 2014; Hedges & Conn 2012; Heinicke *et al.* 2007; Mahler *et al.* 2010), one group that remains conspicuously understudied is dwarf geckos of the genus *Sphaerodactylus*. The systematics and taxonomy of *Sphaerodactylus* within the Puerto Rican Bank and proximal islands have been turbulent. *Sphaerodactylus macrolepis*, originally described from St. Croix (Günther 1859), exemplifies this taxonomic instability. Stejneger (1904) differentiated the Virgin Island *S. macrolepis* from the Puerto Rican form, naming the Puerto Rican geckos *Sphaerodactylus grandisquamis*, with a type specimen from Luquillo, Puerto Rico. However, *S. grandisquamis* and *S. macrolepis*, along with *Sphaerodactylus monensis* Meerwarth from Mona Island (Meerwarth 1901), were later synonymized (Barbour 1921; Schmidt 1920). Soon after, Grant (1931) conducted a major revision of Puerto Rican *Sphaerodactylus*, describing five new species. Among these were a new form from Culebra, *Sphaerodactylus danforthi* Grant, and the resurrection of *S. monensis*. Grant (1932a) later revived *S. grandisquamis* and expanded the distribution of *S. danforthi* to include Vieques (Grant 1932b; Grant 1932c). Later, the subspecies *S. macrolepis parvus* was added from Anguilla, St. Barts, and surrounding islands (King 1962). This arrangement was significantly altered by a monographic revision of the Puerto Rican *Sphaerodactylus* by Thomas & Schwartz (1966), synonymizing *S. grandisquamis* and *S. danforthi* with *S. macrolepis* and erecting subspecies to describe morphological differences among *S. macrolepis* populations in Puerto Rico and surrounding islands. In all, Thomas & Schwartz (1966) divided *S. macrolepis* into ten subspecies, seven of which were newly described.

Thomas & Schwartz (1966) broadly recognized two sub-groups in the *S. macrolepis* species complex. Geckos from the Virgin Islands and Culebra, which they called *S. m. macrolepis*, were distinguishable by smooth dorsal scales with microscopic, hair-bearing organs with only one hair each, called A2 scales by King (1962; Fig. 1A–B). Geckos from Puerto Rico and Vieques, further divided into eight subspecies, had dorsal scales having one hair each and knoblike organs (scale type A3 of King 1962; Fig. 1C–J, Fig. 2). Like others before them (Stejneger 1904; Schmidt 1928; Grant 1932b), Thomas & Schwartz (1966) struggled to make sense of the Vieques animals, which resembled the Puerto Rican geckos in having type A3 scales but also resembled orange-headed geckos from Culebra that had previously been classified as *S. danforthi*. Grant (1931) noted significant polymorphism among male *S. danforthi* specimens on Culebra, some of which were patternless with orange heads whereas others had a 'blue-ish' speckled head, and he suggested they may represent distinct species. Thomas & Schwartz (1966) synonymized *S. danforthi* with *S. m. macrolepis*, and erected *S. m. inigoi* for the Vieques populations. Following the revisions of Thomas & Schwartz (1966), the only major taxonomic change in the *S. macrolepis* complex was the elevation of *S. macrolepis parvus* to species level using morphological data (Powell & Henderson 2001); *S. parvus* found on the Anguilla Bank and *S. macrolepis macrolepis* from St. Croix are the only subspecies occurring outside of the Puerto Rican Bank. Most recently, the morphological distinction of Culebra and Vieques geckos was again noted by Padilla (2006).

We extensively sampled Puerto Rican species of *Sphaerodactylus* and their close relatives from Hispaniola (Dominican Republic) to resolve the taxonomy of the *Sphaerodactylus macrolepis* species complex, currently defined as *S. macrolepis* subspecies plus *S. parvus*. We use a multi-locus molecular phylogeny to delimit species, using the general lineage species concept (de Queiroz 1998; de Queiroz 2007), and integrate phenotypic data, such as color and patterning, traditional scale characters, and other traits. Our analyses support the hypothesis of dispersal from Hispaniola to the Puerto Rican Bank, and subsequently to the Lesser Antilles, Jamaica, and back to Hispaniola. Finally, we provide an updated checklist of the *Sphaerodactylus* species from Puerto Rico and the Virgin Islands, accompanied by a dichotomous key to the *S. macrolepis* species complex.

Materials and methods

Taxon Sampling. We included individuals from all available described Puerto Rican *Sphaerodactylus* species and subspecies except the Monito Island gecko, *Sphaerodactylus micropithecus* Schwartz (missing both molecular and morphological data) and molecular data from *S. m. stibarus* Thomas & Schwartz from Isla Piñeros (Fig. 3). Multiple individuals of most species were sampled, including exemplars from most described subspecies (Appendices A and B). As all previously-published phylogenies (Hass 1991; Hass 1996; Díaz-Lameiro *et al.* 2013) indicated paraphyly of Puerto Rican *Sphaerodactylus*, we sampled ~25 additional species-level lineages of *Sphaerodactylus*, to serve as outgroups in the phylogenetic analyses, and to more accurately reconstruct the origins and biogeographic history of *Sphaerodactylus* on the Puerto Rican Bank.

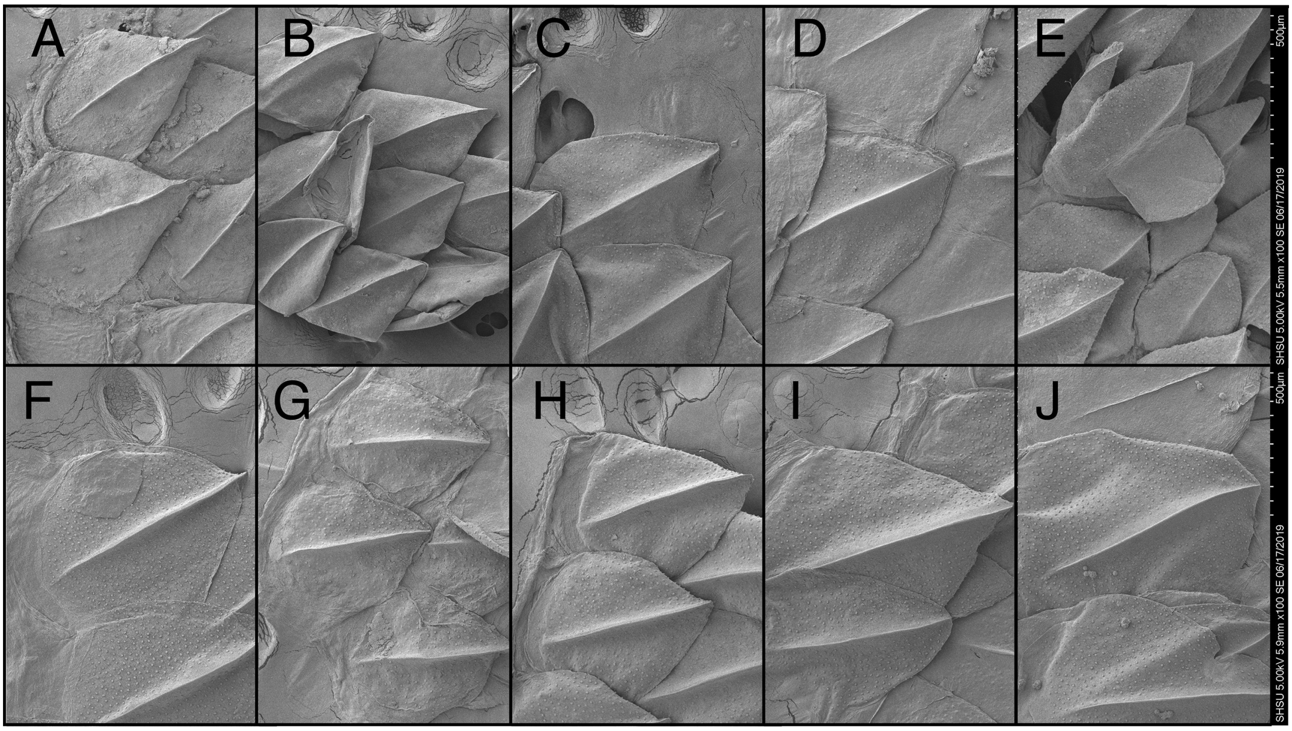

FIGURE 1. SEM of the dorsal scales of species from *S. macrolepis* complex, scales sampled on the dorsum, just behind the scapular patch. A) *S. macrolepis* from Great Thatch (UPRRP 4465); B) *S. macrolepis* from Southeast Culebra (TG 2741); C) *S. inigoi* from West Culebra (JDD 259); D) *S. inigoi* from Vieques (RT 10767); E) *S. g. stibarus* from Isla Piñeros (JDD 546); F) *S. g. grandisquamis* from Loiza Puerto Rico (RT 14665); G) *S. g. guarionex* from Toa Baja, Puerto Rico (RT 15625), H) *S. g. ateles* from CanÞo Boquilla, Puerto Rico (RT 14641); I) *S. g. mimetes* from Patillas, Puerto Rico (RT 14675); J) *S. g. spanius* from Toro Negro, Puerto Rico (RT 14789). All images to the same scale, note the smaller scale size of *S. macrolepis* (A–B) in comparison with *S. grandisquamis* and *S. inigoi* (C–J).

Molecular Data. We extracted genomic DNA from tail clips using the Qiagen® DNeasy Blood and Tissue kit. We used PCR to amplify fragments of two mitochondrial genes (mtDNA), 16S and ND2, and five nuclear genes: (nDNA), ACM4, CMOS, PTPN12, RAG1, and RBMX. Detailed descriptions of primers and PCR conditions have been discussed elsewhere (Gamble *et al.* 2008a; Gamble *et al.* 2008b; Gamble *et al.* 2011; Gamble *et al.* 2012). PCR clean-up and Sanger sequencing were performed at the University of Minnesota Genomics Center (St. Paul, MN) or Beckman Coulter Genomics (Danvers, MA, USA). Sequences have been deposited on GenBank (Appendix A). Sequences were assembled and checked for accuracy using Sequencher [v5.0.1] (Gene Codes©) or Geneious® [v10.2.2] (Kearse *et al.* 2012). We aligned each locus individually using MUSCLE (Edgar, 2004), implemented in Geneious Prime® [v2019.1.3] (Kearse *et al.* 2012). We subsequently concatenated 16S and ND2 sequences hereafter referred to as our mtDNA dataset. For *Sphaerodactylus* from the Puerto Rican Bank, we phased allelic variants for nuclear genes using PHASE software (Stephens *et al.* 2001), with default settings, implemented in DNAsp [v5.10.1] (Librado & Rozas 2009). We conducted model selection for each locus using MEGA7 [v0.26] (Kumar *et al.* 2016) and selected the best-fit model (available in downstream software) using BIC. For all nuclear loci, the best-fit model was HKY+G model, while the best-fit model for mtDNA was GTR+G+I. We calculated net between-group p-distances (Nei & Li 1979) from each of our mtDNA loci separately using MEGA7 [v0.26] (Kumar *et al.* 2016). Standard error was estimated using 1000 bootstrap replicates.

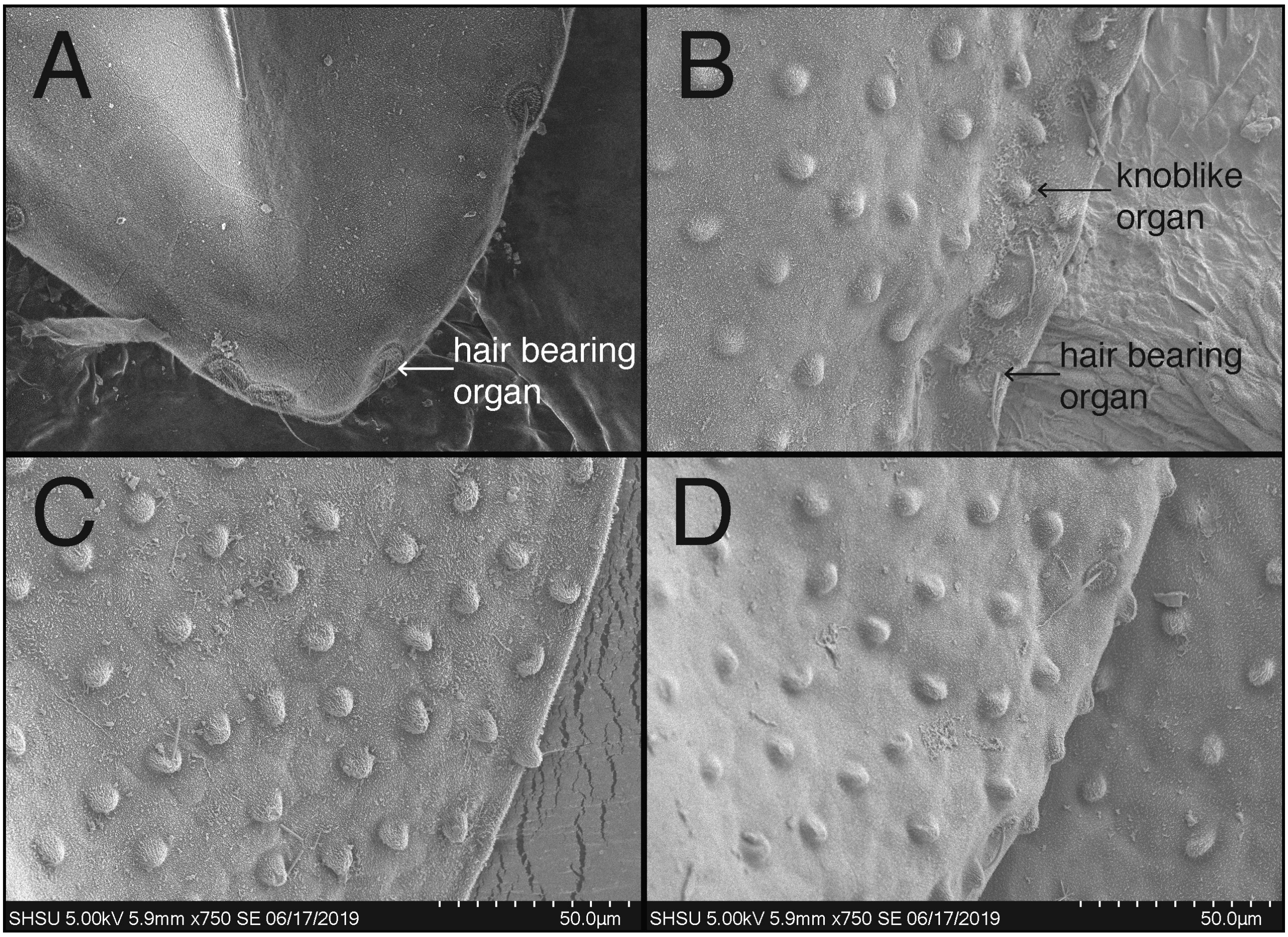

FIGURE 2. SEM of the dorsal scales of species from *S. macrolepis* species complex, showing details of the hair bearing organs, with one hair each, and knoblike organs on the dorsal scales. A) *S. macrolepis* from Great Thatch island (UPRRP 4465), which lack knoblike organs; B) *S. inigoi* from Vieques (RT 10767); C) *S. g. grandisquamis* from Loiza, Puerto Rico (RT 14665); D) *S. g. mimetes* from Patillas, Puerto Rico (RT 14675). All images to the same scale.

Phylogenetic Analyses. We built an initial maximum likelihood phylogeny for all sampled individuals using RAxML-HPC BlackBox [v8.2.12] (Stamatakis 2014) using only mtDNA. This tree was used to identify clades corresponding to putative species-level divergences and used for building the multi-locus species tree and subsequent species delimitation analyses. We conducted this analysis, along with all other phylogenetic reconstructions (StarBEAST2 and STACEY, below), on the CIPRES cluster (Miller *et al.* 2010).

We generated a multi-locus, time-calibrated species tree under a Yule model implemented in the StarBEAST2 [0.15.2] (Ogilvie *et al.* 2017) module of BEAST2 [v2.5.1] (Bouckaert *et al.* 2014). Each locus, consisting of the mtDNA data (one locus) and each nDNA gene (five loci), was provided an uncorrelated lognormal clock with all other priors estimated from a log-normal distribution. To time-calibrate this phylogeny we used the amber fossil of *Sphaerodactylus dommeli* Böhme from the Dominican Republic (Daza & Bauer 2012; Daza *et al.* 2013) as a minimum clade age for Caribbean *Sphaerodactylus*, using a log normal distribution offset by the minimum estimated age of the fossil (13.82 million years ago [mya]). We conducted three independent chains of $5x10^8$ mcmc replicates, storing every 10000 samples, with a 40% burn-in, and examined likelihood values for convergence using Tracer [v1.6] (Rambaut *et al.* 2018). One mcmc chain failed to converge with the other two and was discarded from subsequent analysis. Tree files were combined using LogCombiner and the tree generated in TreeAnnotator, both distributed with the BEAST2 [v2.5.1] package.

Species Delimitation. We initially assessed species limits among members of the *S. macrolepis* species complex with a trimmed version of the multi-locus StarBEAST2 dataset, with *S. roosevelti* Grant as the outgroup, using the STACEY [v1.2.5] (Jones 2017) module in BEAST2 [v2.5.1] (Bouckaert *et al.* 2014). In parallel, we assessed the ability of nDNA-only species delimitation by conducting the same analysis excluding mtDNA. All priors were estimated from (default) log-normal distributions, unless specifically stated below. In accordance with program documentation and additional specifications outlined by Barley *et al.* (2018), we provided an exponential distribution with a mean of 0.1 for the "popPriorScale" parameter, a lognormal distribution with a mean of 5 and a standard deviation of 2 to the "bdcGrowthRate" prior, and the "collapseWeight" was provided a uniform distribution with the lower and upper bounds set at 0 and 1, respectively. In addition, each partition was provided an independent strict molecular clock, with rate priors calculated from a log-normal distribution that were given a mean of 0 and standard deviation of 1. For each analysis, we conducted two independent chains of $10x10^7$ mcmc replicates, sampling every 10000, with a 10% burn-in, and examined likelihood values for convergence using Tracer (v1.6) (Rambaut *et al.* 2018). Tree files for both analyses were compiled using LogCombiner, and species delimitation was conducted using the SpeciesDelimitationAnalyzer [v1.8.0] under a "collapseheight" of 0.001 (SpeciesDA). We then visualized topology forests using DensiTree software [v2.2.6] (Bouckaert & Heled 2014).

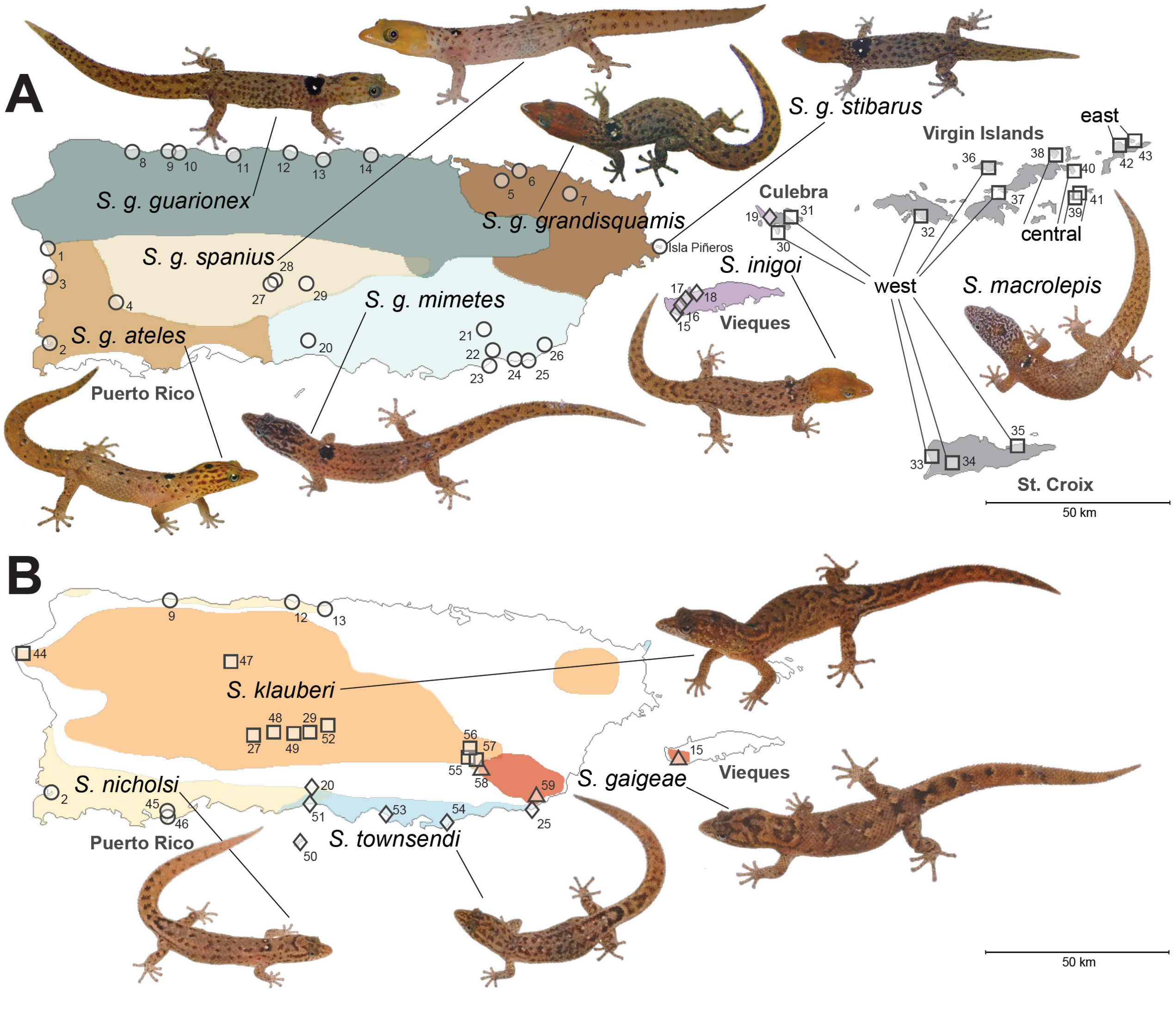

FIGURE 3. Sampling localities and approximate distributions for select species of *Sphaerodactylus* from Puerto Rico and islands on the Puerto Rican Bank. Different shaped symbols are used for each species. A. *Sphaerodactylus macrolepis* species complex (excluding *S. parvus*). *Sphaerodactylus macrolepis* (square); *S. grandisquamis* (circle); *S. inigoi* (diamond). B. *Sphaerodactylus klauberi* (square), *S. gaigeae* (triangle), *S. townsendi* (diamond), and *S. nicholsi* (circle). Numbered localities are listed in Appendix A.

Morphological Data. We scored 115 external features in all recognized taxa within the *S. macrolepis* species complex. The list included multiple, external morphological characters including meristic, morphometric, scalation, and coloration traits (Appendix B). The majority of the characters followed Thomas & Schwartz (1966) and coloration characters used by Padilla (2006), the most comprehensive study of color and pattern variation of the *S. macrolepis* species complex, which included data from 1141 specimens collected from 167 localities. We focused on the variable characters that diagnosed the different groups, but also used the general features common to the members of the *S. macrolepis* species complex. While some characters were considered for populations as a whole, in many cases we also examined sexually dimorphic characters, especially with regard to coloration, from the different nominal lineages. We used the presence of escutcheon scales to distinguish males from females (Grant 1931).

We used the following acronyms when referring to vouchered specimens. BMNH = The Natural History Museum, London (Formerly the British Museum [Natural History]); Glor = Rich Glor field series; MCZ = Museum of Comparative Zoology, Harvard University; MPM = Milwaukee Public Museum; RT = Richard Thomas field series; Scantle = Dan Scantlebury field series; SHSUHerp = Sam Houston State University Herpetology collection; TG = Tony Gamble field series; UF = Florida State Museum, University of Florida, Gainesville; USNM = U. S. National Museum, Smithsonian.

Imaging. Scanning Electron Microscopy. Samples were adhered to the SEM stub using carbon tape and sputter coated with gold for 60 sec (~200A) using a Cressington 108. The sputtered samples were imaged under high vacuum at 3–5 kV with a working distance of 5 mm on a Hitachi SU3500 scanning electron microscope using secondary electron detector. Further image analysis was performed using ImageJ software (Schneider *et al.* 2012).

Specimen photos. To describe the coloration of live specimens, pictures were taken in the field soon after they were captured using several models of digital cameras, including SONY DSC-F828, Leica V-Lux, Olympus Stylus TG4, Canon EOS Rebel XT, and Nikon D90. High resolution pictures of the preserved specimens were taken using the 3D stitching function on a Keyence Digital Microscope VHX-7000 series.

Biogeography. Previous inferences of paraphyly of Puerto Rican *Sphaerodactylus* with regards to Hispaniolan and Jamaican species prompted us to explore the biogeographic history of sampled species (Hass 1991 & 1996). In particular, we were interested in whether *Sphaerodactylus* on Puerto Rico and the rest of the Puerto Rican Bank were monophyletic. We used the species tree produced from the StarBEAST2 analyses to test whether or not the paraphyletic relationship of Hispaniolan *Sphaerodactylus* represented single or successive colonizations of the Puerto Rican Bank.

We categorized species as occurring in one of the following four biogeographic regions: Hispaniola; the Puerto Rican Bank; Jamaica; or the Lesser Antilles. *Sphaerodactylus argus* Gosse occurs on Jamaica, Cuba, and the Bahamas. Previous phylogenetic analyses have placed it in a clade with Jamaican species (Hass 1996) and we provisionally used Jamaica as its distribution here. We identified the transition rate matrix that best fit the data by comparing likelihood scores among alternate models using Akaike Information Criterion (AIC) in ape 5.2 (Paradis & Schilep 2018) implemented in R [v3.5.1]. We considered three transition rate models: a twelve-parameter model that had different rates for every transition type (the ARD model); a six-parameter model with equal forward and reverse rates between states (the symmetrical rates (SYM) model); and a single-parameter model with equal rates among all transitions (ER). We identified transitions in biogeographic region using stochastic mapping (Nielsen 2002; Huelsenbeck *et al.* 2003), implemented in phytools [v0.6-64] (Revell 2012) using the transition rate matrix that best fit the data. We ran 1,000 simulations using the *make.simmap* command and summarized results using the *describe.simmap* command.

Results

Taxon Sampling and Molecular Data. We collected molecular data from 48 putative taxa (species, subspecies, and mito-clades) from across the Dominican Republic, Puerto Rico, and the Virgin Islands. In addition to new sequence data generated here, we included data generated by a previous study of Puerto Rican *Sphaerodactylus* geckos (Pinto *et al.* 2019a). Preliminary phylogenetic analyses using mtDNA provided evidence of twelve well-supported mitochondrial lineages within the *S. macrolepis* species complex (Fig. 4). We coded these mitochondrial lineages as putative “species” in our StarBEAST2 and STACEY analyses (Fig. 5). Uncorrected genetic distances among sampled *Sphaerodactylus* taxa ranged from 0.2% to 15.7% for 16S and 0.9% to 25.3% for ND2 (Table 1; Supplementary Tables 1 & 2).

Phylogenetic Analyses. The mtDNA phylogeny (Fig. 4) grouped taxa into three broad clades. A clade comprising *S. thompsoni* Schwartz & Franz, *S. leucaster* Schwartz, and *S. rhabdotus* Schwartz was sister to the remaining sampled species, which were split into a Hispaniolan clade and a clade with Puerto Rican, Virgin Islands, Jamaican, and some additional Hispaniolan species. Bootstrap support was variable across the tree, with some clades being well-supported (bootstrap ≥70) while others were poorly supported. We found that several previously recognized taxa were not monophyletic, and we split these into multiple putative species for the subsequent species tree analyses. These included samples of *S. difficilis* Barbour*, S. ladae* Thomas & Hedges*,* and *S. darlingtoni* Shreve from Hispaniola, and *S. macrolepis guarionex* Thomas & Schwartz and *S. macrolepis spanius* Thomas & Schwartz from Puerto Rico. Additionally, some species and subspecies had considerable population structure that warranted splitting them into putative species for subsequent analyses. These included *S. gaigeae* Grant*, S. klauberi* Grant*,* and *S. macrolepis macrolepis*. Low sequence divergence (ND2 p-distances among individuals between 0.0–1.1%) coupled with the lack of diagnostic morphological traits (Padilla 2006) prompted us to collapse putative *S. m. phoberus* samples into *S. m. grandisquamis* for subsequent analyses.

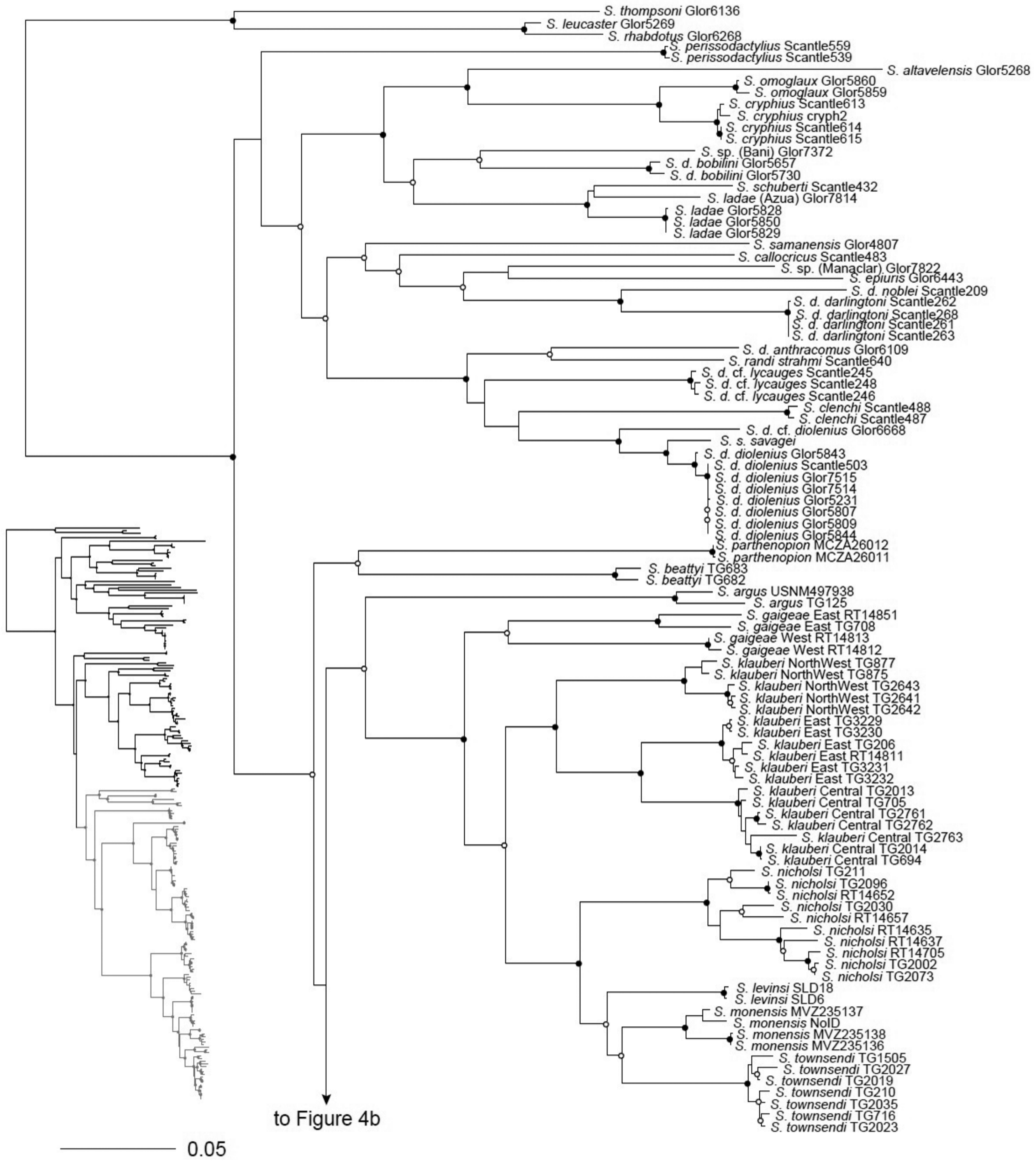

FIGURE 4A. Maximum likelihood mitochondrial DNA (mtDNA) phylogeny of sampled species of *Sphaerodactylus*. Species names are followed by specimen ID. Black circles: bootstrap = 100; white circles: bootstrap ≥70 and ≤99; no circle: bootstrap <70.

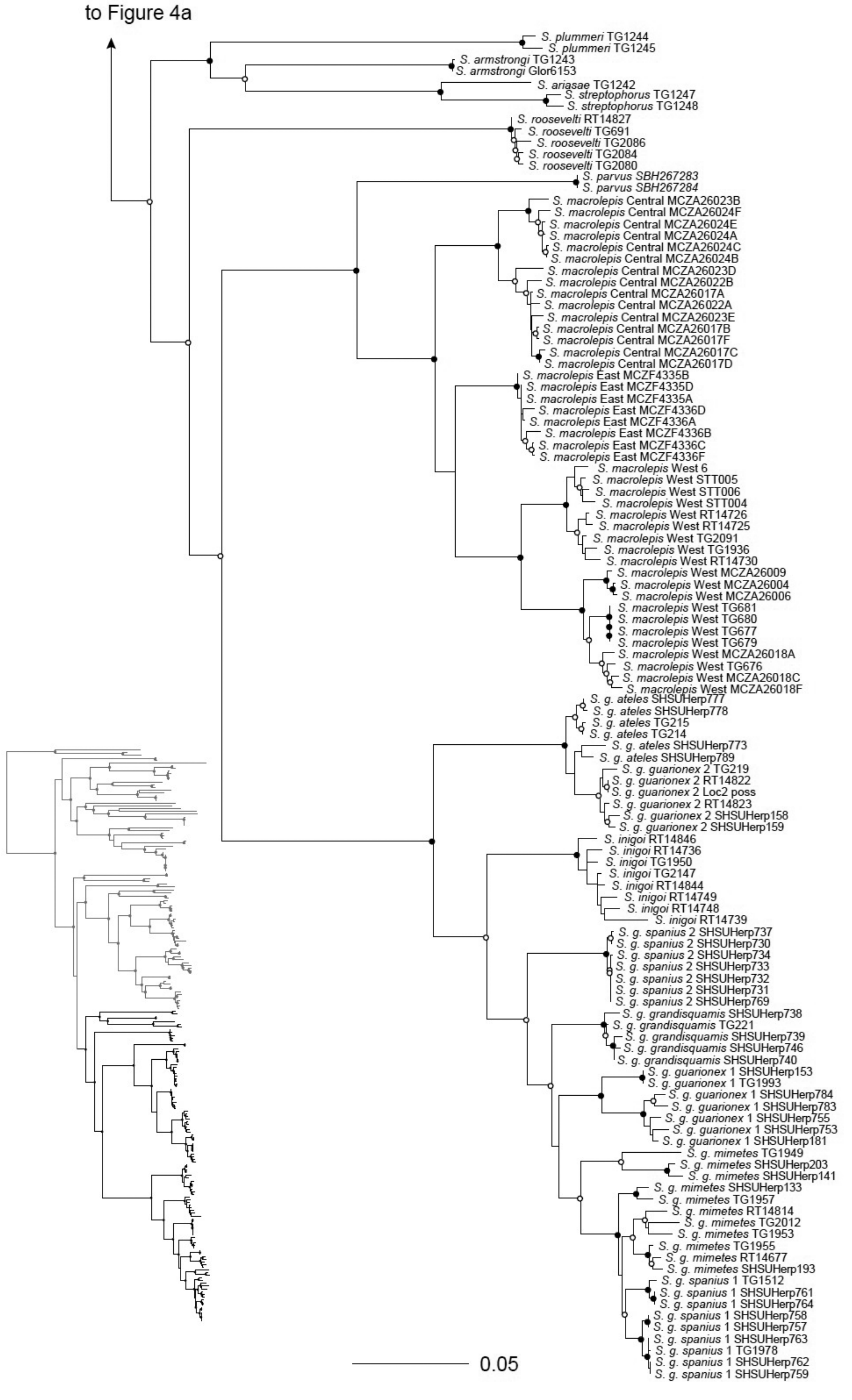

FIGURE 4B. Maximum likelihood mitochondrial DNA (mtDNA) phylogeny of sampled species of *Sphaerodactylus*. Species names are followed by specimen ID. Black circles: bootstrap = 100; white circles: bootstrap ≥70 and ≤99; no circle: bootstrap <70.

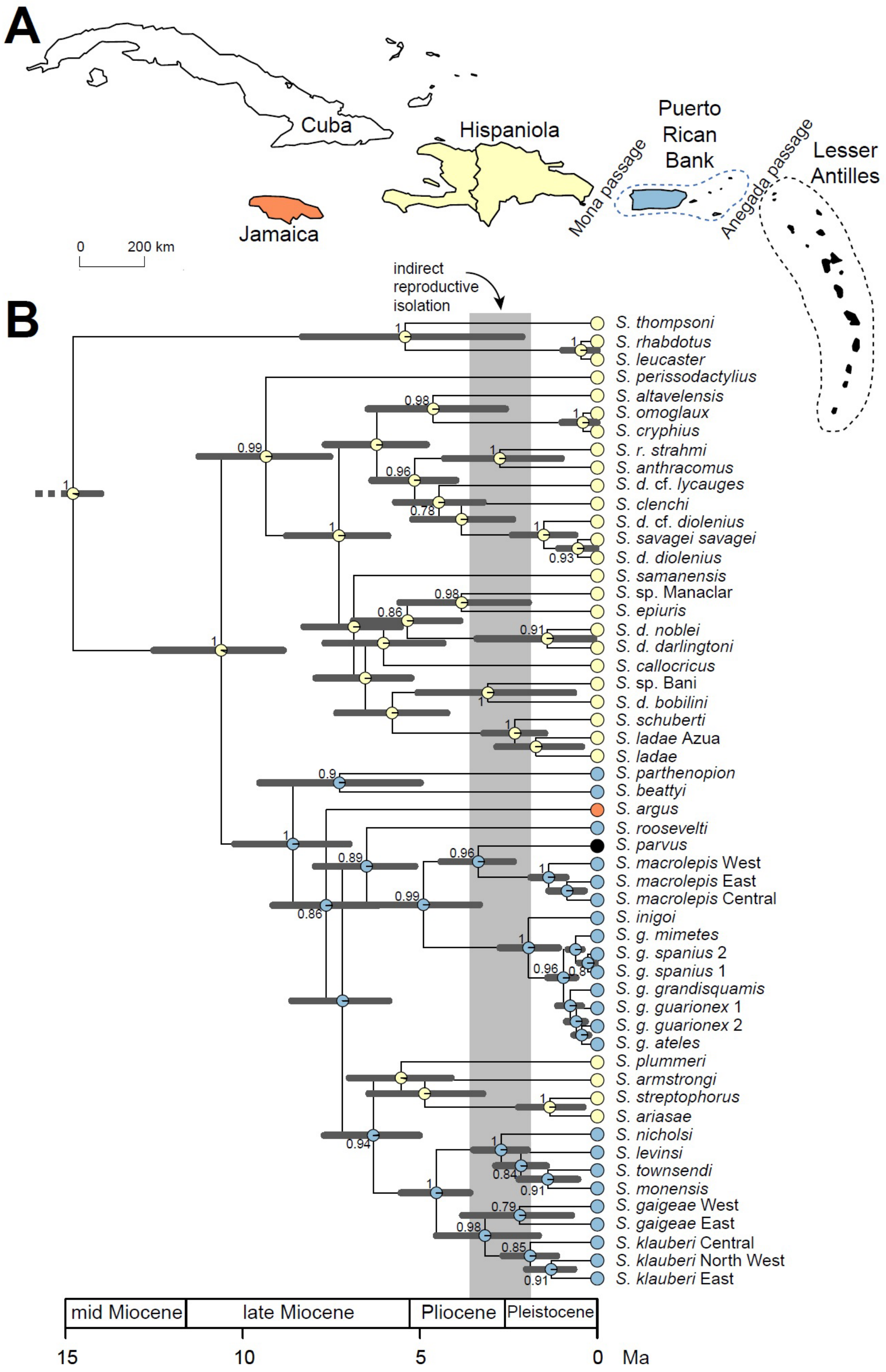

FIGURE 5. Phylogeny and biogeography of sampled *Sphaerodactylus* geckos. A. Map of the Greater and Lesser Antilles. Sampled regions are color coded: Hispaniola = yellow; Puerto Rico and the islands of the Puerto Rican bank = blue; Jamaica = orange; Lesser Antilles = black. B. Time-calibrated species tree of sampled *Sphaerodactylus* species estimated using Star-BEAST2. Numbers at nodes indicate Bayesian posterior probabilities (BPP), unlabeled nodes have BPP <0.75. Dark gray horizontal lines at nodes are Bayesian posterior distributions of divergence time, in millions of years. Colored circles at tips indicate geographical distribution and colored nodes correspond to ancestral area reconstruction using stochastic mapping. Time line at the bottom of the tree is in millions of years ago (Ma) with geological periods labelled. The light gray vertical box, labelled "indirect reproductive isolation", encompasses the posterior distribution of divergence times between *S. townsendi* and *S. nicholsi*, two species that exhibit post-zygotic reproductive isolation (Pinto *et al.* 2019). Assuming this is the time necessary to evolve reproductive isolation, this can be an indirect measure for species delimitation. Taxa with divergence time distributions that overlap or are older than the *S. townsendi* and *S. nicholsi* split are old enough to have evolved reproductive isolating barriers and are thus candidate species.

The multi-locus species tree recovered the same three well-supported clades as the mtDNA tree (Fig. 5). The first clade consisted of three Hispaniolan species (*S. thompsoni*, *S. leucaster*, and *S. rhabdotus*) and was used to root the rest of the phylogeny. The remaining *Sphaerodactylus* species were split into two larger clades, one made up entirely of Hispaniolan species and the other comprised mostly of Puerto Rican, Virgin Island, and Jamaican species with some additional Hispaniolan species. Consistent with a previously-published phylogenetic hypothesis (Hass 1996) and the mtDNA tree, we found a clade of Hispaniolan *Sphaerodactylus*, made up of *S. plummeri* Thomas & Hedges*,* *S. armstrongi* Noble*,* *S. ariasae* Hedges & Thomas*,* and *S. streptophorus* Thomas & Schwartz, nested within the focal clade of Puerto Rican and Virgin Islands geckos.

The mtDNA and species trees had some topological discordance, although in almost all instances these discordant nodes had low support in one or both trees. In particular, many of the deeper relationships among species and species groups in the Hispaniolan and Puerto Rican clades were discordant and/or poorly resolved. For example, in the species tree, *S. klauberi* and *S. gaigeae* formed a clade that was sister to a clade comprised of *S. nicholsi* Grant*,* *S. levinsi* Heatwole*, S. monensis,* and *S. townsendi* Grant (the *S. nicholsi* clade). However, the mtDNA topology had *S. gaigeae* as sister to the *S. klauberi* plus *S. nicholsi* clade.

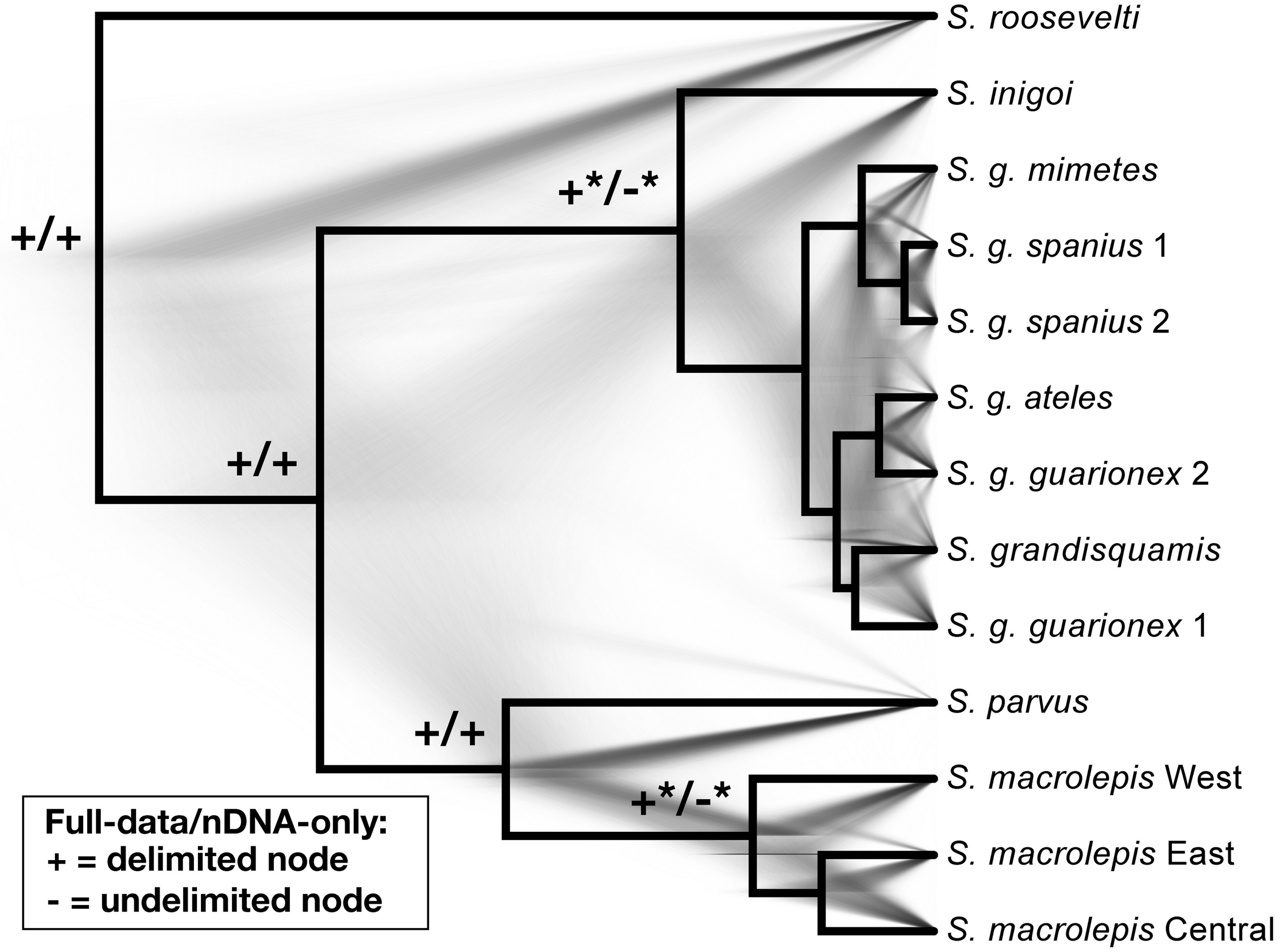

FIGURE 6. DensiTree representation of STACEY species-delimitation analysis using the subsampled StarBEAST2 dataset focusing on the *Sphaerodactylus macrolepis* species complex with *S. roosevelti* as an outgroup. Plotted onto well-supported nodes across the tree are + or - indicating whether the node is delimited in either one or both parallel STACEY analyses with SpeciesDA using either all genes (mtDNA and nDNA) or just the nDNA data. Astrices (*) indicate that all taxa subtending the labelled node share the same (+/-) delimitation status for that analysis.

The *S. macrolepis* species complex was split into two well-supported clades in both the mtDNA tree and multi-locus species tree (Fig. 4 & 5). One clade included *S. parvus* and *S. m. macrolepis* whereas the second clade included all other sampled *S. macrolepis* subspecies. *Sphaerodactylus m. macrolepis* was further split into three groups: an eastern clade including samples from Necker and Moskito Islands in the British Virgin Islands (BVI); a central clade including samples from Cooper, Salt, Beef, and Guana Islands (BVI); and a western clade that included samples from Jost Van Dyke and Little Thatch Islands (BVI), St. Thomas and St. Croix (US Virgin Islands), and eastern and southern Culebra. Relationships among the *S. m. macrolepis* clades differed between the mtDNA and species trees and were not well-supported in either phylogeny. Phylogenetic relationships among taxa in the clade with the remaining *S. macrolepis* subspecies from Puerto Rico, Vieques, and Culebra were discordant between the species and mtDNA trees. The species tree had a well-supported split between *S. m. inigoi*, including specimens from the islands of Vieques and (western) Culebra, and all other samples on Puerto Rico. *Sphaerodactylus m. inigoi* was nested within other *S. macrolepis* subspecies in the mtDNA tree but with low bootstrap support.

Species Delimitation. STACEY and SpeciesDA analysis of the *S. macrolepis* species complex using all of the molecular data (both mtDNA and nDNA) recovered strong support (posterior probability=0.993) for a species delimitation hypothesis in which all putative taxa within the *S. macrolepis* species complex were a distinct, species-level lineage (Fig. 6). The parallel analysis conducted using only nDNA data found the best delimitation model for *S. macrolepis*, *S. parvus*, and *S. grandisquamis* as distinct species, but collapsed the remaining taxa into *S. grandisquamis* (Fig. 6). However, even this best-scoring delimitation model with nDNA provided only moderate support (posterior probability=0.865). Further interpretation and considerations of species delimitation analyses are continued below (see *Discussion: Species Delimitation and Taxonomy*). However, herein, we recognize four species in the *S. macrolepis* species complex (*sensu* Thomas & Schwartz 1966): *S. parvus*, *S. macrolepis*, *S. inigoi,* and *S. grandisquamis*. The last species is restricted to the island of Puerto Rico and some satellite islands and retains almost all the subspecies described in Thomas & Schwartz (1966). Based on morphological features only, *S. m. stibarus* from Piñeros island is provisionally classified as S. *grandisquamis stibarus*.

Biogeography. AIC scores for the three transition rate models were: ARD = 55.96182; SYM = 48.14358; and ER = 43.09697. The ER model had the best AIC score and was used for subsequent analyses. Stochastic mapping of species distributions recovered Hispaniola as the ancestral area among sampled species with a single transition to Puerto Rico and the Puerto Rican Bank (Fig. 5). Within the mostly-Puerto Rican clade were subsequent transitions to Jamaica (*S. argus*), the Lesser Antilles (*S. parvus*), and back to Hispaniola (the ancestor of a clade composed of species occurring on and near the Península de Pedernales in southern Hispaniola: *S. plummeri, S. armstrongi, S. ariasae,* and *S. streptophorus*).

Morphological Variation. Considering the morphological variation within the *S. macrolepis* species complex, 41 morphological features were invariant among the specimens examined. These invariant features were used to describe the general characteristics of the *S. macrolepis* species complex. We highlight the diagnostic traits that facilitate recognition of the taxa within this group as well as characters that are congruent with the molecular data.

General traits among geckos within the *S. macrolepis* species complex

Members of the *S. macrolepis* species complex were described in detail in previous studies (King 1962; Thomas & Schwartz 1966; Padilla 2006) and our intention is not to redefine these. In this paper we focus on essential diagnostic features that facilitate the identification of species and subspecies, we refer the reader to the original descriptions for further details.

Geckos from the *S. macrolepis* species complex have acute, flattened, keeled, and imbricate dorsal scales (including the tail and limbs); keeled scales in the gular area; and, following an abrupt transition, smooth scales in the collar, chest, belly, and ventral side of the tail. The scales on the belly are rounded rather than acute. They also have three supralabials and infralabials to mid-eye, one or two internasals (sometimes none or three in *S. parvus*), and males with escutcheon scales that extend into the ventral surface of the thighs. All species except *S. parvus* exhibit marked sexual dichromatism. In the sexually dimorphic species, coloration is highly variable, and females and juveniles have more marked patterning than males. Males and females both possess scattered darker scales that vary in color from light brown to black. Males in the *S. macrolepis* species complex lack pigmented rings on the neck or bands around the body. Males can have a uniformly colored head that varies from blue to orange-brownish. Females never have a colored head, but instead exhibit bold markings. A dark ocular line is always present in both males and females. Females always have a canthal line that extends from the snout, crosses the eye, and extends onto the neck. In all females, the postorbital lines meet in the nuchal area and surround a dark parietal spot, and a scapular patch with ocelli is usually present. The scapular patch is not present in some males. In terms of size, males are generally larger than females (SVL $\bar{x}$ males = 27.51 mm, SVL $\bar{x}$ females = 24.86; Padilla 2006). Further, taxa within the *S. macrolepis* species complex (*S. macrolepis, S. parvus, S. inigoi,* and *S. grandisquamis*) vary in maximum and minimum sizes. The largest members are *S. grandisquamis* populations on Puerto Rico, while species and populations inhabiting other islands of the Puerto Rican Bank, and the St. Croix and Anguilla banks are smaller, e.g. *S. g. stibarus*, *S. inigoi*, *S. macrolepis*, *S. parvus* (Fig. 7).

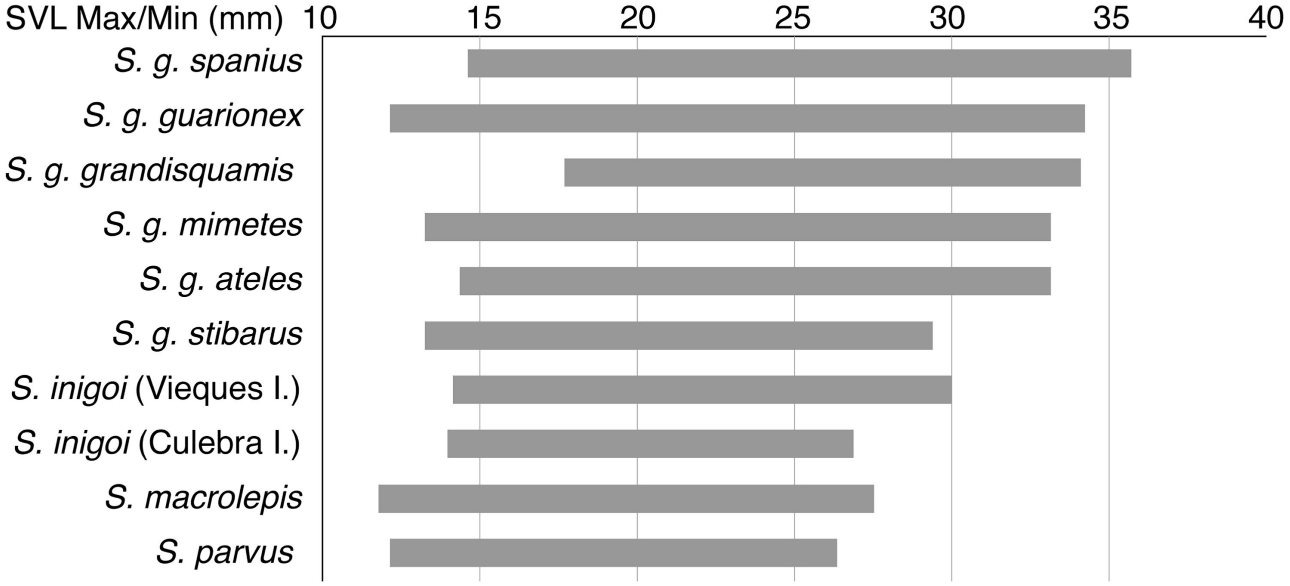

FIGURE 7. Maximum and minimum SVL measured for adult geckos from the *Sphaerodactylus macrolepis* species complex.

Taxonomy

Sphaerodactylus parvus King, 1962

Figure 8

Holotype—UF 10034.1

Type locality: "the island of St. Martin, 2-½ miles west, ¼ mile north of Philipsburg."

Diagnosis: This species was originally described as a subspecies of *S. macrolepis* by King (1962) and was elevated by Powell & Henderson (2001) who differentiated this species on the basis of 1) dorsal scales with hair bearing scale organs, with only one hair each along the dorso-distal edge; 2) maximum SVL size of 24 mm (18–24 mm, $\bar{x} = 21.7$); 3) having a higher mean number of midbody scale rows (48.4 ± 1.5); and 4) weak sexual dichromatism nor ontogenetic variation (King 1962; Thomas & Schwartz 1966). Nava *et al.* (2002) described six additional differences with other members of the *S. macrolepis* species complex: 5) less bulky habitus; 6) ventral scales keeled on the sides of abdomen of some specimens (King 1962); 7) less densely pigmented throat; 8) less conspicuous head patterns; 9) smaller scapular patch on females; and 10) ten toe lamellae on the fourth toe (9–11; King 1962). Our work shows that only characters 2, 3, 4, and 9 are actually diagnostic (Appendix 2). SVL Min/Max is 12.17/26.39 mm. Additional diagnostic traits for *S. parvus* include a scapular patch that can be brown and black (also present in *S. macrolepis*); males and females with no well-defined occipital spots and postorbital line; pale or yellowish ocelli from the scapular patch very close or united; males and females with no well-defined head patterns; males and females without dorsal lines, color pattern more 'salt and pepper'. Females seem to have a more defined gular pattern than males.

Color in life: Color of male and female varies from pale pink to brown, with scattered dark brown scales (Thomas & Schwartz 1966) producing a salt and pepper effect on dorsum. Head and tail color usually lighter than the body, scapular patch bicolored (brown anteriorly and black posteriorly) with light margin surrounding the patch. Males and females with a marked pattern on throat.

Distribution: The only member, aside from *S. macrolepis*, of the *S. macrolepis* species complex found outside of the Puerto Rican Bank. This species is found exclusively on the Anguilla Bank near the northern end of the Lesser Antilles, including the islands of Anguilla, St.-Barthélémy, St.-Martin, Tintamarre I., and Dog. I.

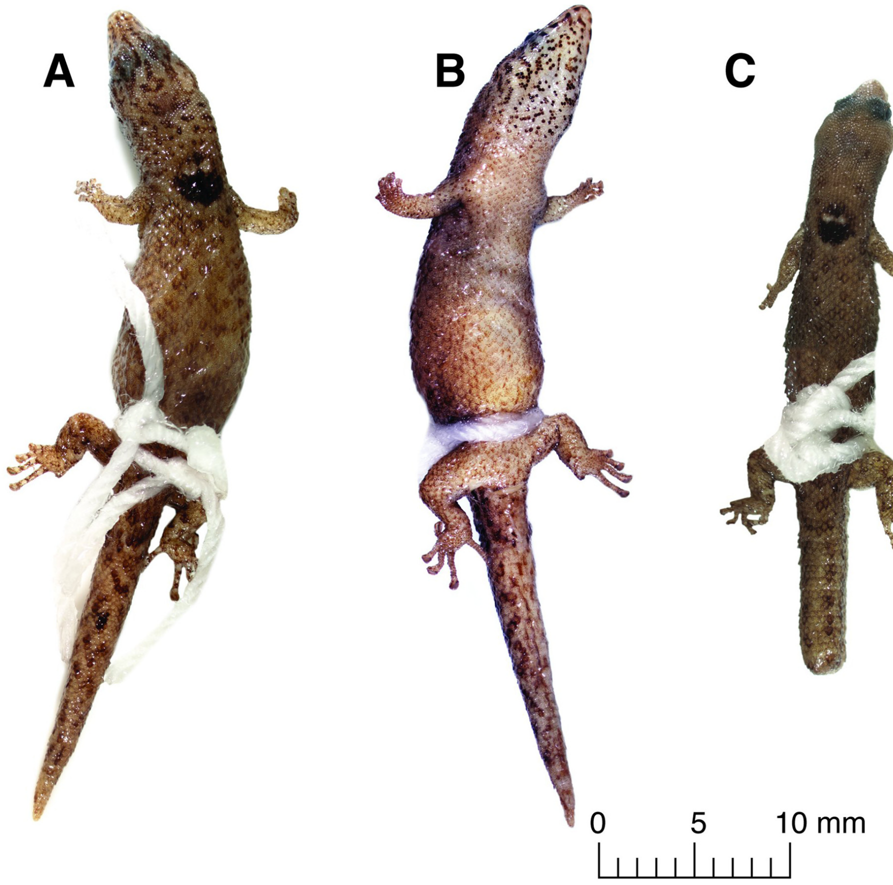

FIGURE 8. Adult specimens of *Sphaerodactylus parvus*. A–B, Female from Saint Maarten (MPM23023), C–D male from Saint Barthélemy (MPM23053).

***Sphaerodactylus macrolepis sensu stricto* Günther, 1859**
Figures 9–10

Syntypes—BMNH 1946.8.30.74 and BMNH 1946.8.30.75

Type locality: "St. Croix, West Indies."

Synonyms: *Sphaerodactylus danforthi* Grant, 1931

Diagnosis: SVL Min/Max is 11.81/27.54 mm, dorsal scales without knob-like organs, dorsal body scales are small, and can be rounded or acute. Tail also has dorsal scales with the free edge rounded, and fourth toe with six to eight lamellae. This species has several distinctive coloration features, including males with marked reticulated head (marbled); males without dorsal lines or salt and pepper (this shared with *S. inigoi* and *S. parvus*); males with a blue head (background color, similar to the head in *S. g. mimetes*); males with reticular pattern on the gular area (also in *S. g. mimetes* and *S. parvus*); males with indistinct cephalic figure (or pattern); males and females with head pattern either black or dark brown; females with a fragmented head pattern; females with fainter reticulation on the throat especially next to the jaw; females with dorsal medial lines fused to form a blotch or imperfect line (also present in *S. inigoi*); scapular patch of males (when present) and females could be bicolor (brown and black) with brown anterior part of the scapular patch (the area anterior to the ocelli); scapular patch well defined with two anterior lateral projections or could be formed by two united circles (but not rectangular), pale or yellowish ocelli inside the scapular patch; females with anterolateral lines that contact the scapular patch; central parietal dot with two lateral lines that extend from the snout and meet posterior to the parietal dot; shortened snout (also seen in *S. parvus*, *S. inigoi,* and *S. g. stibarus*).

Color in life (Fig. 9): Female: ground color fluctuates from dark brown to straw, head and tail fluctuates from gray to orange, head pattern well defined. Medial lines forming a blotch, ocelli color pale or yellowish. Male ground color fluctuates from reddish-brown to straw. Head blueish with strong marble pattern. Iris color reddish-brown to yellow.

Distribution: Culebra including Cayo Luis Peña, the Virgin Islands including St. Croix, and the Prickly Pear Cays of Anguilla.

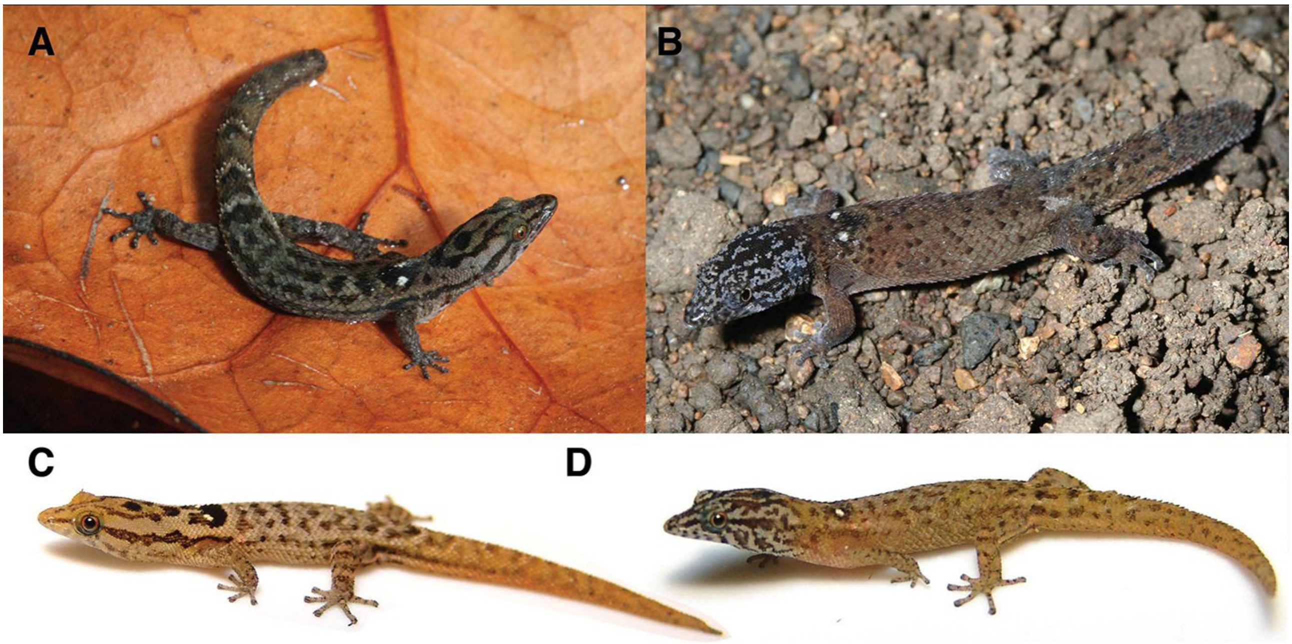

FIGURE 9. Live specimens of *Sphaerodactylus macrolepis* from St. Croix (A, female and B, male) and Culebra Island, Zoni Beach (C, female and D, male). A–B photographs courtesy of Toby Hibbits, Texas A&M Biodiversity Research and Teaching Collections.

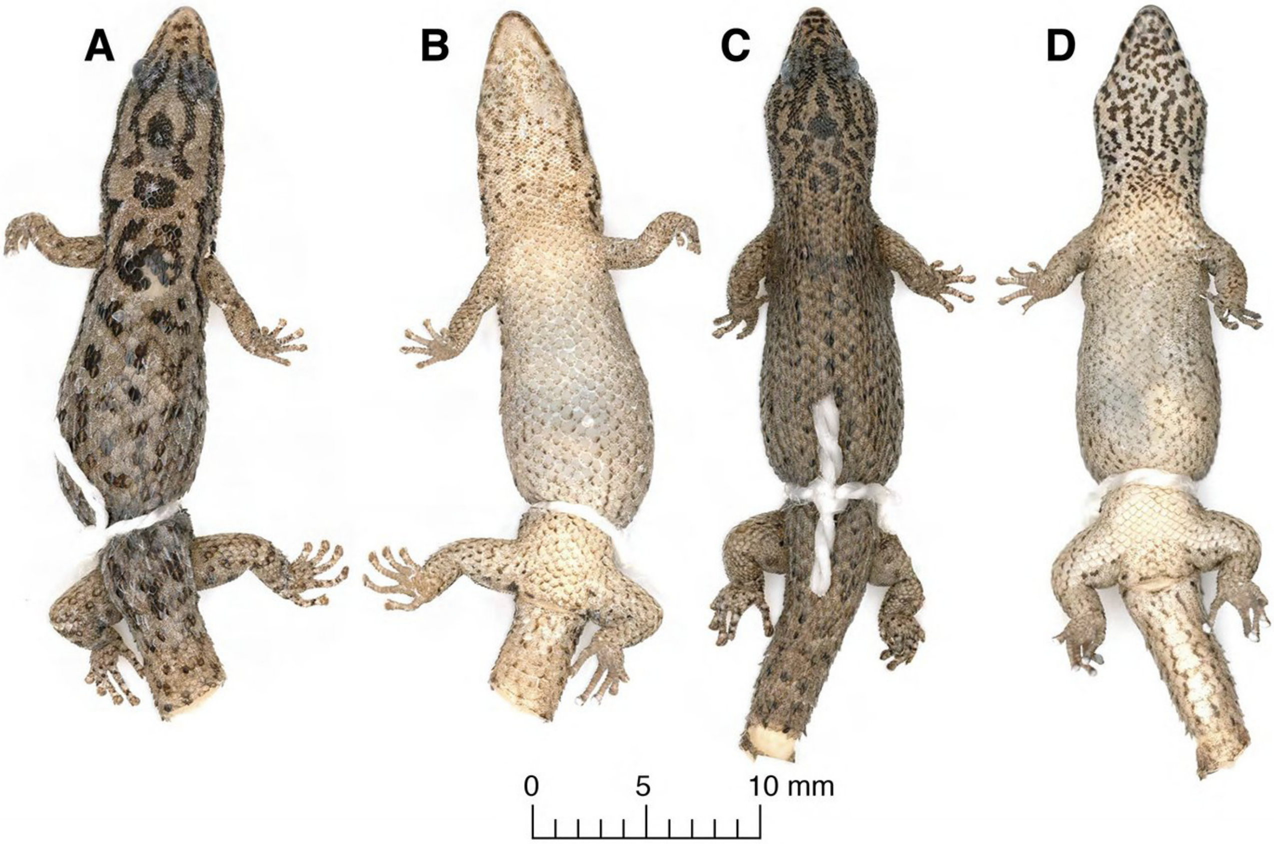

FIGURE 10. Adult specimens of *Sphaerodactylus macrolepis* from Culebra island. A–B, Female (SHSUHerp000845), C–D male (SHSUHerp000818).

Sphaerodactylus inigoi comb. nov. Thomas & Schwartz, 1966
Figures 11–13

Holotype—MCZ R-81055

Type locality: "Ensenada Sun Bay (= Ensenda Sombe), Isla Vieques, Puerto Rico."

Diagnosis: SVL Min/Max (14.18/30 mm), midbody scales 33–41 ($\bar{x}$ 36.8), four or five loreal scales (also in *S. parvus*, contrasting with five or six in *S. macrolepis* and *S. grandisquamis*), two or three postmental scales (two in *S. macrolepis*, *S. grandisquamis*, and *S. parvus*), a low number of dorsal body scales from axilla to groin (15 to 18, differing from *S. parvus* and *S. grandisquamis* except *S. g. stibarus* [14–16 scales]). Males dorsal head pattern absent or very faint except a dull parietal spot (Thomas & Schwartz 1966); males with no pigmentation on throat, females with throat pattern; males from Culebra might have some pigmentation on the throat; males with red to yellow head; males and females with reduced scapular patch; males and females with dorsal lines stippled; males dorsal pattern salt and pepper; females with medial lines fused to form a blotch or imperfect line; shortened snout. SVL is smaller in specimens from West Culebra (Min=14.04 mm, Max=26.88 mm) than in specimens from Vieques (Min=14.18 mm, Max=30 mm).

Color in life (Fig. 11): Female: ground color fluctuates from tan to gray, head and tail fluctuates from gray to light brown, head pattern well defined, medial lines forming a blotch, ocelli color pale or yellowish. Male ground color fluctuates from gray to light brown, head red-orange with absent head pattern or faint remains of it (e.g. parietal or nuchal spot). Iris color brown, copper, or orange.

The color of female *S. inigoi* is similar to the female coloration of *S. g. mimetes*, while the male coloration is more similar to the males of *S. g. ateles* (Padilla 2006), although the former has a marked head, unlike *S. inigoi* males, where the pattern is absent or very faint.

Distribution: Vieques Island and satellites, and western part of Culebra Island.

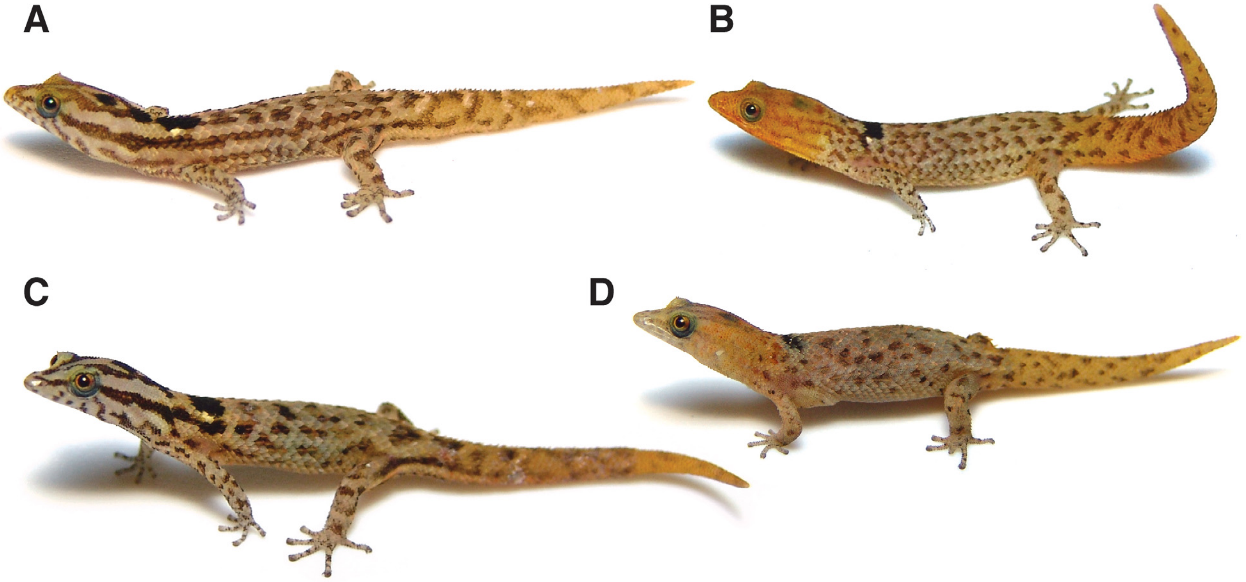

FIGURE 11. Live specimens of *Sphaerodactylus inigoi* from Vieques (A, female and B, male) and Culebra Island, Flamenco beach (C, female and D, male).

Sphaerodactylus grandisquamis Stejneger, 1904

All populations of the *S. macrolepis* complex occurring on Puerto Rico and its satellite islands (e.g. Piñeros) are restricted to this taxon. *S. grandisquamis* was originally described by Stegneger (1904) and was reaffirmed as a valid taxon by Grant (1932c) but referred to as a subspecies of *S. macrolepis s.l.* by Thomas & Schwartz (1966). This taxon may include several undescribed species and in this paper we keep most of the subspecific names from Thomas & Schwartz (1966). Additional study is needed to better resolve the relationships among these subspecies, but at the moment we highlight the monophyly of this taxon, which is comprised of the subspecies: *S. g. grandisquamis*, *S. g.*

guarionex, S. g. ateles, *S. g. mimetes*, *S. g. spanius*, and *S. g. stibarus* (*S. g. phoberus* was not supported by either molecular [this study] or morphological data [Padilla, 2006] and is thus synonomized with *S. g. grandisquamis*).

General traits of *Sphaerodactylus grandisquamis*. Compared to other members of the *S. macrolepis* complex, *S. grandisquamis* males have a higher number of escutcheon scales (67–95); males with dorsal stippled lines (except in *S. g. mimetes*); males exhibit a cephalic figure; males have a light line behind the eye; females with dorsal medial lines separated (except in *S. stibarus* where it forms a blotch or imperfect line); and a long and narrow snout (except in *S. stibarus*).

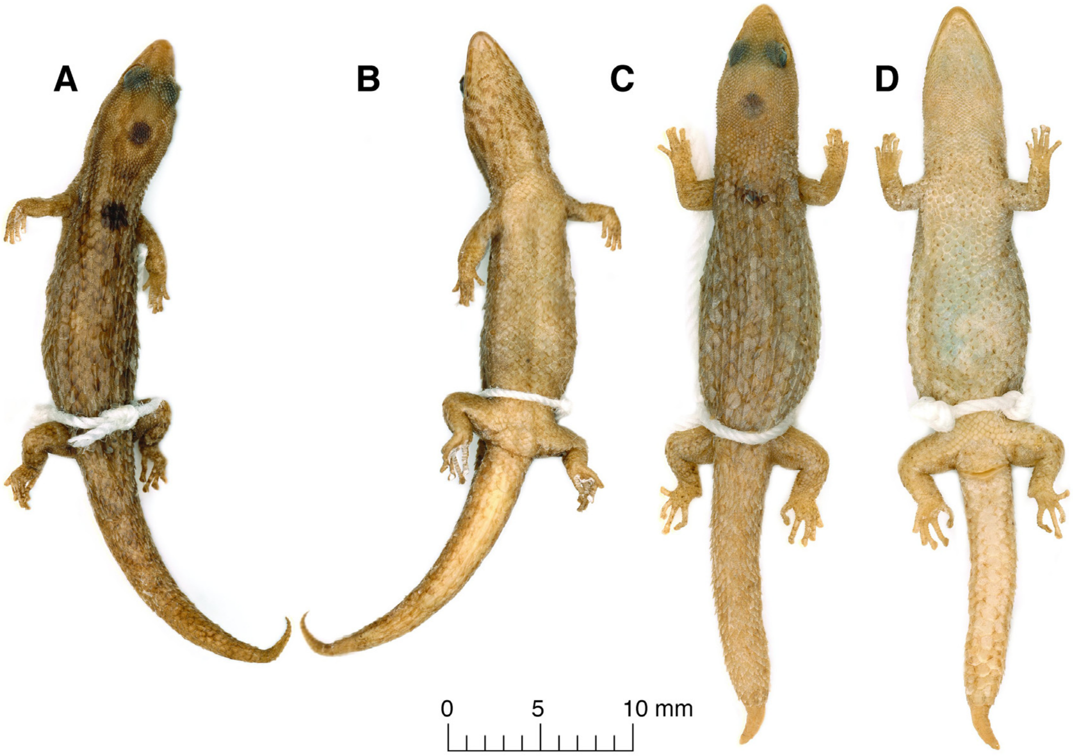

FIGURE 12. Adult specimens of *Sphaerodactylus inigoi* from Vieques island. A–B, Female (SHSUHerp000725), C–D male (SHSUHerp000916).

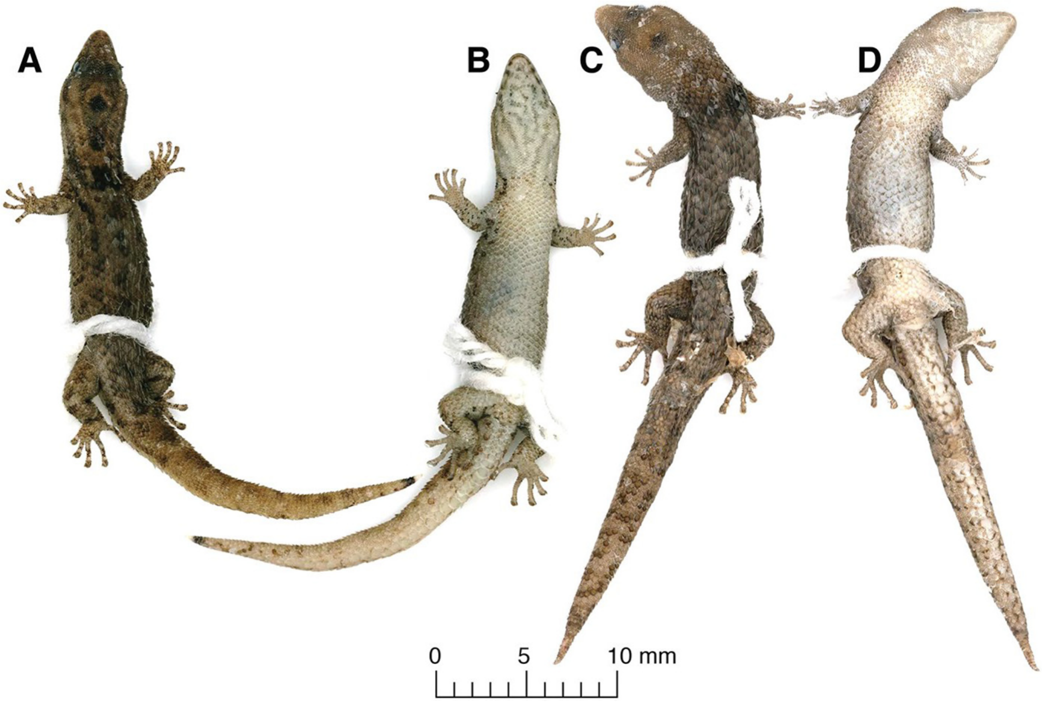

FIGURE 13. Adult specimens of *Sphaerodactylus inigoi* from Culebra island. A–B, Female (SHSUHerp000210), C–D male (SHSUHerp000210).

***Sphaerodactylus grandisquamis grandisquamis* Stejneger, 1904**
Figures 14–15

Holotype—USNM 27007

Type locality: "Luquillo, Porto Rico."

Synonyms: *Sphaerodactylus g. phoberus* Thomas & Schwartz, 1966

Diagnosis: SVL Min/Max (17.79/34.08 mm); midbody scales 36–46 ($\bar{x}$ 41.2); scales on the snout are rounded (also in *S. g. guarionex* and *S. g. stibarus*); head ventral scales with faint keels (contrary to the other species where the keels are more defined); seven toe lamellae on the fourth toe; males with faint head pattern (also in *S. g. guarionex* and *S. g. stibarus*); males with faint throat pattern; females without throat pattern; males and females with a large hexagonal black scapular patch; ocelli enclosed on the scapular patch, and patch usually surrounded by a white margin (also in *S. g. stibarus* and *S. g. ateles*).

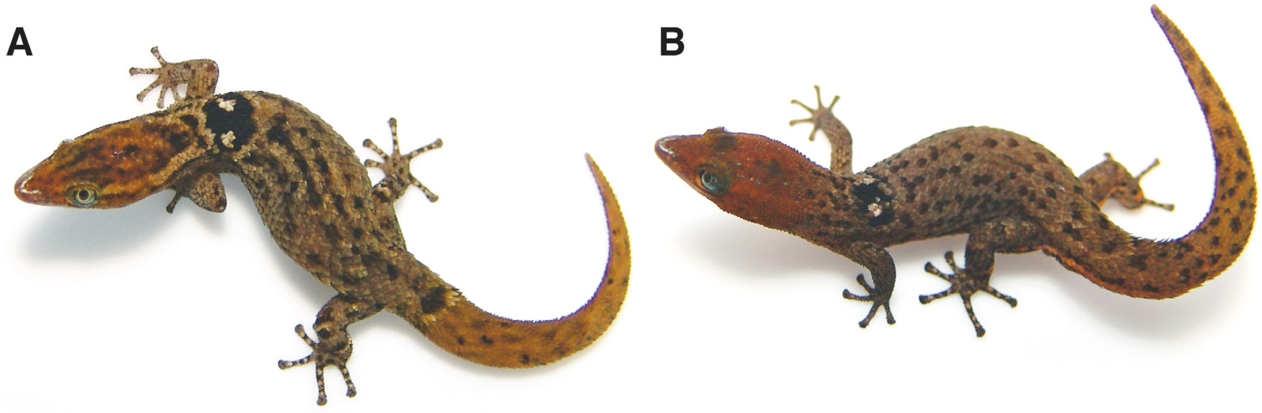

FIGURE 14. Live specimens of *Sphaerodactylus g. grandisquamis* from Piñones, Puerto Rico (A, female and B, male).

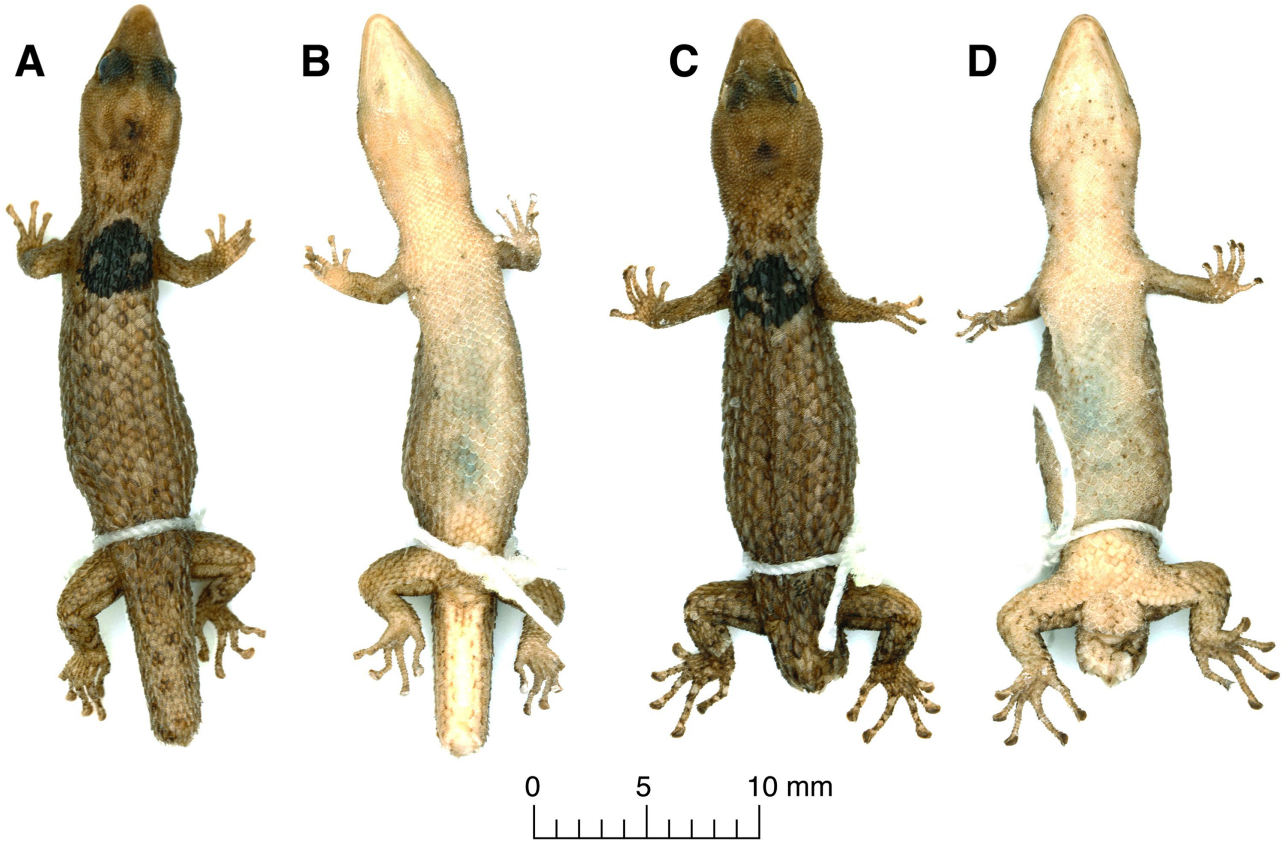

FIGURE 15. Adult specimens of *Sphaerodactylus g. grandisquamis* from Rio Grande, Puerto Rico. A–B, Female (SHSUHerp000743), C–D male (SHSUHerp000739).

Color in life (Fig. 14): Female: ground color brown to yellowish, head and tail fluctuates from orange to yellow, head pattern well defined, medial lines separated and parallel, ocelli color white. Males ground color brown to yellowish brown, head red-orange to yellowish. Iris color variable, greenish-yellow, black suffused with yellow, golden or grayish-yellow (Thomas & Schwartz 1966).

Distribution: Low elevation coastal areas of northeastern Puerto Rico, Cayo Santiago and Cayo Batata, a transition to *S. g. guarionex* around San Juan and to *S. g. mimetes* in the Maunabo area.

Sphaerodactylus grandisquamis guarionex comb. nov. Thomas & Schwartz, 1966

Figures 16–17

Holotype—MCZ R-81048

Type locality: "Officers' Club Beach, Ramey Air Force Base, Puerto Rico." [Currently called Punta Borinquen Golf and Country Club, Aguadilla, Puerto Rico.]

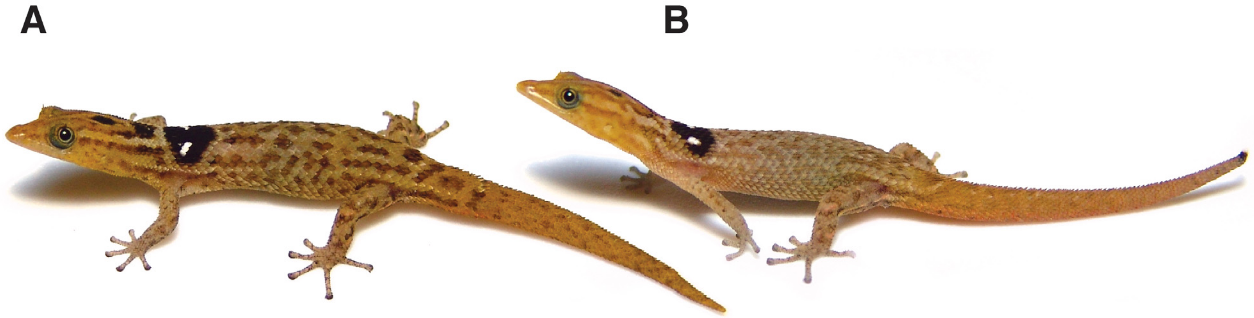

FIGURE 16. Live specimens of *Sphaerodactylus g. guarionex* from Barceloneta, Puerto Rico (A, female and B, male).

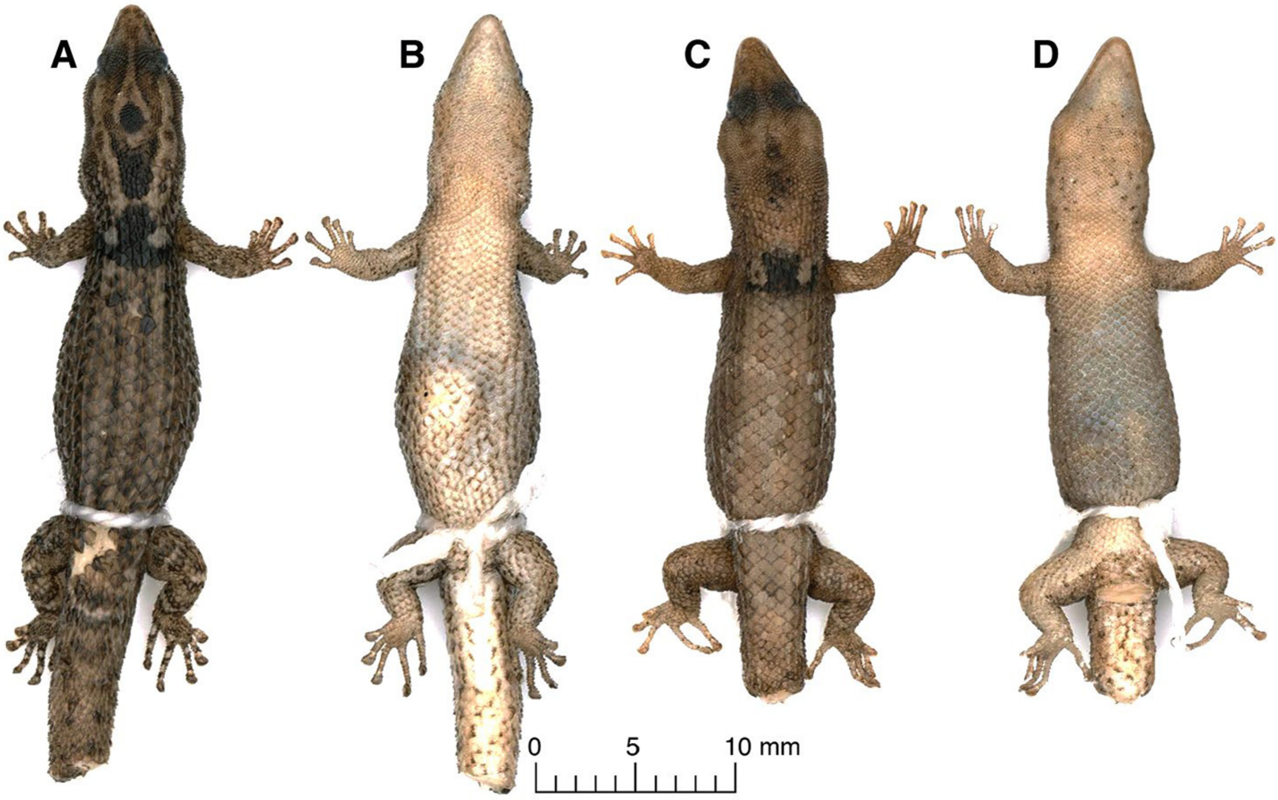

FIGURE 17. Adult specimens of *Sphaerodactylus g. guarionex* from Barceloneta, Puerto Rico. A–B, Female (SHSUHerp000187), C–D male (SHSUHerp000183).

Diagnosis: SVL Min/Max (12.17/34.2 mm); midbody scales 36–49 ($\bar{x}$ 41.3); number of dorsal body scales very reduced (around 14) compared to the other subspecies of *S. grandisquamis* (17–23); rounded snout scales;

one internasal scale; low number of escutcheon scales (around 67, other subspecies of *S. grandisquamis* [73–95]); nine toe lamellae on the fourth toe; males with orange head; males throat patterned (also in *S. g. mimetes* and *S. g. spanius*) and variable in females; the scapular patch is the largest among all members of the *S. macrolepis* complex, especially in females, and is usually hexagonal enclosing the ocelli.

Color in life (Fig. 16): Female: ground color light brown, head and tail fluctuates from orange to yellow, head pattern well defined, medial lines separated and parallel, ocelli color white. Male ground color light brown to gray, head yellow to light orange. Iris color yellow copper.

Distribution: Low elevation coastal areas of northern Puerto Rico from the lowlands of El Yunque National Forest to Rincón, a transition to *S. m. ateles* around Mayaguez and with *S. g. spanius* on high elevations of the Cordillera Central.

Sphaerodactylus grandisquamis ateles **comb. nov. Thomas & Schwartz, 1966**

Figures 18–19

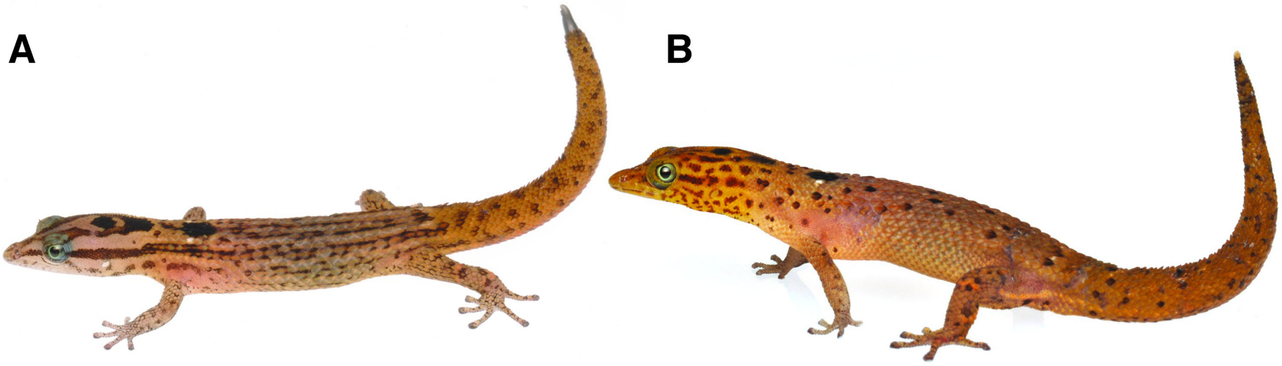

FIGURE 18. Live specimens of *Sphaerodactylus g. ateles* from Lajas, Puerto Rico (A, female and B, male). Photographs courtesy of Stuart V. Nielsen, University of Florida.

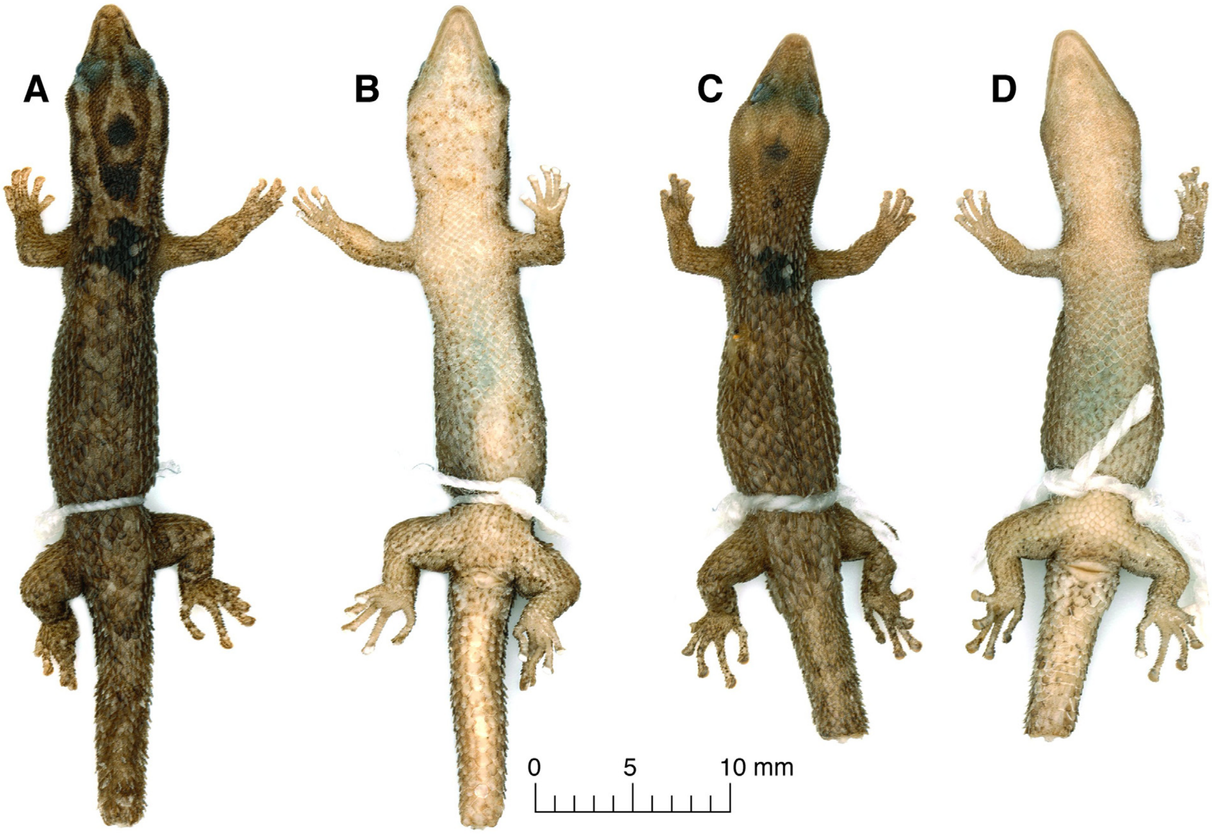

FIGURE 19. Adult specimens of *Sphaerodactylus g. ateles* from Caño Boquilla, Puerto Rico. A–B, Female (SHSUHerp000770), C–D male (SHSUHerp000771).

Holotype—MCZ R-81043

Type locality: "Balneario de Boquerón, Cabo Rojo, Puerto Rico."

Diagnosis: SVL Min/Max (14.38/33 mm); midbody scales 36–42 (x̄ 39.4); nine to ten toe lamellae on the fourth toe; males head pattern absent (also in *S. g. spanius*); males with no pigmentation on chest, variable pigmentation on throat; males with two light lines extending from the orbits to the scapular patch (also in some *S. g mimetes* and *S. g. stibarus*); males and females with a large black scapular patch, ocelli near the edge of the patch; some specimens have the patch surrounded by a white margin (also in *S. g. stibarus* and *S. g. ateles*) or absent patch; males with a red head.

Color in life (Fig. 18): Female: ground color light gray to pink, head and tail orange to gray, head pattern well defined, medial lines separated and parallel, ocelli color white. Male ground color light brown or gray to orange, head red to light orange. Iris color green, copper, or gray.

Distribution: Low elevation coastal areas of southwestern Puerto Rico from Mayagüez to Ponce, transition to *S. g. mimetes* occur near Ponce.

Sphaerodactylus grandisquamis mimetes comb. nov. Thomas & Schwartz, 1966

Figures 20–21

Holotype—MCZ R-81036

Type locality: "12.3 km SE Patillas, Puerto Rico." [Thomas & Schwartz (1966) incorrectly listed the type locality as 12.3 km SE Patillas, but the correct distance is 1.23 km SE Patillas Puerto Rico.]

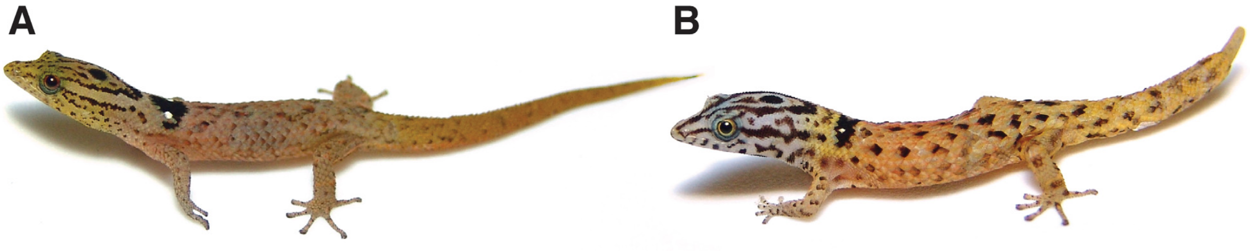

FIGURE 20. Live specimens of *Sphaerodactylus g. mimetes* from Patillas, Puerto Rico (A, female and B, male).

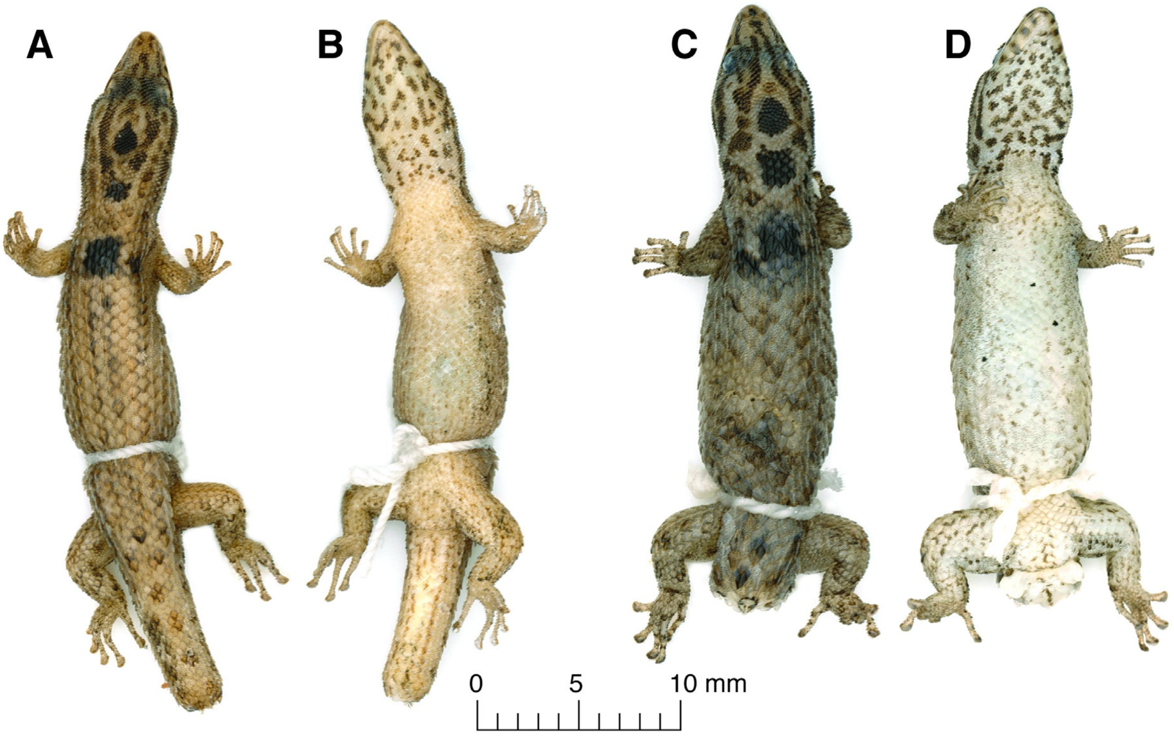

FIGURE 21. Adult specimens of *Sphaerodactylus g. mimetes* from Patillas, Puerto Rico. A–B, Female (SHSUHerp000193), C–D male (SHSUHerp000204).

Diagnosis: SVL Min/Max (13.3/33.19 mm); midbody scales 31–40 ($\bar{x}$ 36.1); nine toe lamellae on the fourth toe; males with salt and pepper dorsal pattern; males with very marked lineated or fragmented head pattern; males with blue head (background color); males with reticulate pattern on the gular area; males with or without scapular patch, ocelli on the periphery or enclosed on the patch. The males of this species are superficially similar to the males of *S. macrolepis* but lack the bicolored scapular patch and the head pattern is less fragmented than in *S. macrolepis*.

Color in life (Fig. 20): Female: ground color light brown to pink, head and tail yellow to gray, head pattern well defined, medial lines separated and parallel, ocelli color white. Male ground color light yellow to orange, head blue to gray, tail orange. Iris color red to yellow-brown.

Distribution: Low elevation coastal areas of southeastern Puerto Rico, from Ponce to Maunabo where it transitions to *S. g. grandisquamis*.

Sphaerodactylus grandisquamis spanius **comb. nov. Thomas & Schwartz, 1966**

Figures 22–23

Holotype—MCZ R-81047

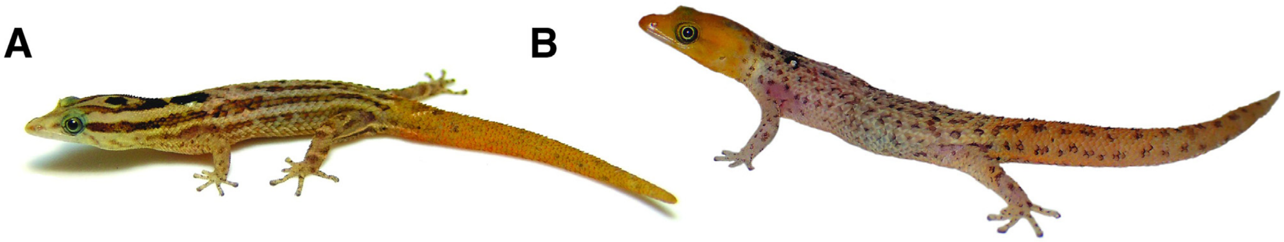

FIGURE 22. Live specimens of *Sphaerodactylus g. spanius*. A, female from Toro Negro, Puerto Rico. B, male from Divisoria, Puerto Rico.

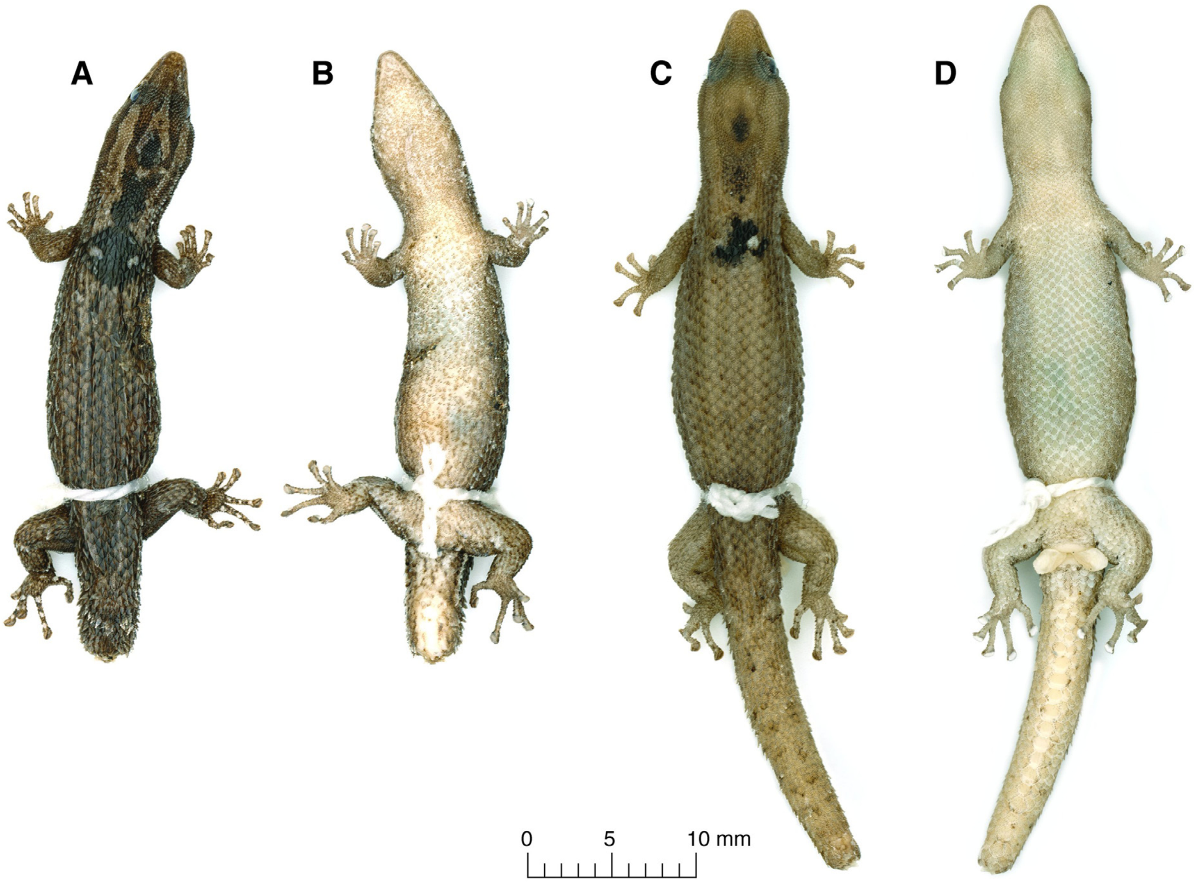

FIGURE 23. Adult specimens of *Sphaerodactylus g. spanius* from Maricao, Puerto Rico. A–B, Female (SHSUHerp000790), C–D male (SHSUHerp000791).

Type locality: "17.7 km NE Utuado (~ about 8 km airline), 1100 feet, Puerto Rico."

Diagnosis: SVL Min/Max (14.68/35.68 mm); midbody scales 41–47 ($\bar{x}$ 43.6); males with elevated number of escutcheon scales (~95); ten toe lamellae on the fourth toe; males with marked lineated head pattern; males with marked reticular pattern; scapular patch reduced to a midcentral rectangle, and ocelli located on the periphery of the patch; scapular patch in contact with nuchal spots (Padilla 2006).

Color in life (Fig. 22): Female: ground color light brown to straw, head and tail orange to light gray, head pattern well defined, medial lines separated and parallel, ocelli color white, or sometimes gray (Thomas & Schwartz 1966). Male ground color light brown, head and tail orange. Iris color yellow, green, brown, copper, or golden.

Distribution: Uplands of the Cordillera Central and the Sierra of Cayey from 335 m to 850 m. Thomas & Schwartz (1966) report some intergrades with *S. g. mimetes* near Aibonito.

***Sphaerodactylus grandisquamis stibarus* comb. nov. Thomas & Schwartz, 1966**

Figures 24–25

Holotype—MCZ R-81022

Type locality: "Isla Piñeros, Puerto Rico."

Diagnosis: SVL Min/Max (13.34/29.44 mm); midbody scales 36–41 ($\bar{x}$ = 38.6); snout scales rounded; five loreal scales; eight toe lamellae on the fourth toe; males with faint lineated head pattern; males with two light lines extending from the orbits to the scapular patch, scapular patch surrounded by white margin, and patch can also have brown color; the ocelli are large in proportion to the scapular patch and are more separated than in any other member of the *S. macrolepis* species complex (Padilla 2016); males with anterior dorsolateral lines not contacting the scapular patch; males with marked throat pattern.

Color in life (Fig. 24): Female: ground gray with dark brown or black scales, head and tail orange to light brown, head pattern well defined, medial lines poorly defined and forming a blotch, ocelli color white. Male ground color is light brown, scattered brown scales, salt and pepper, head and tail orange. Iris color dark gray, or golden.

Distribution: Known only from the type locality.

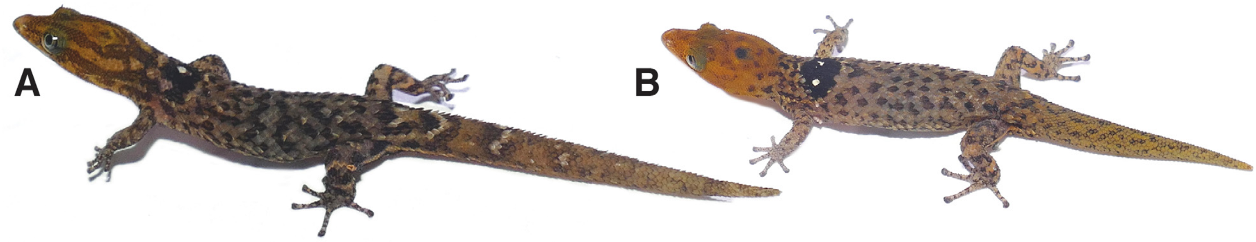

FIGURE 24. Live specimens of *Sphaerodactylus g. stibarus* from Isla Piñeros, Puerto Rico (A, female and B, male).

Discussion

Phylogeny and Undescribed Diversity**.** Only a handful of previous phylogenetic reconstructions have approached this level of taxon sampling in *Sphaerodactylus*. We recovered a robust, multi-locus phylogeny for 48 *Sphaerodactylus* taxa, including species, subspecies, and multiple undescribed lineages. The earliest *Sphaerodactylus* molecular phylogeny, using protein electrophoresis of 15 loci, examined 46 species (Hass 1991) but suffered from poor resolution and low nodal support (Page & Lydeard, 1994). However, relationships among some taxa were recovered in both studies. These include a clade comprised of coastal, large-bodied species: *S. savagei* Shreve, *S. clenchi* Shreve, and *S. randi* Shreve as the sister clade of small-bodied, inland species: *S. omoglaux* Thomas and *S. cryphius* Thomas & Schwartz clade; an *S. townsendi* plus *S. nicholsi* clade, and an *S. klauberi* plus *S. gaigeae* clade. Both studies also recovered an *S. thompsoni*, *S. rhabdotus*, and *S. leucaster* clade as sister to the "*argus*" series, *sensu* Hass (1991), which included all of our other sampled taxa. The biggest inconsistency between studies involved broader relationships among Puerto Rican *Sphaerodactylus*: Hass (1991) found Puerto Rican *Sphaerodactylus* to be polyphyletic, but these relationships were poorly supported by the allozyme data.

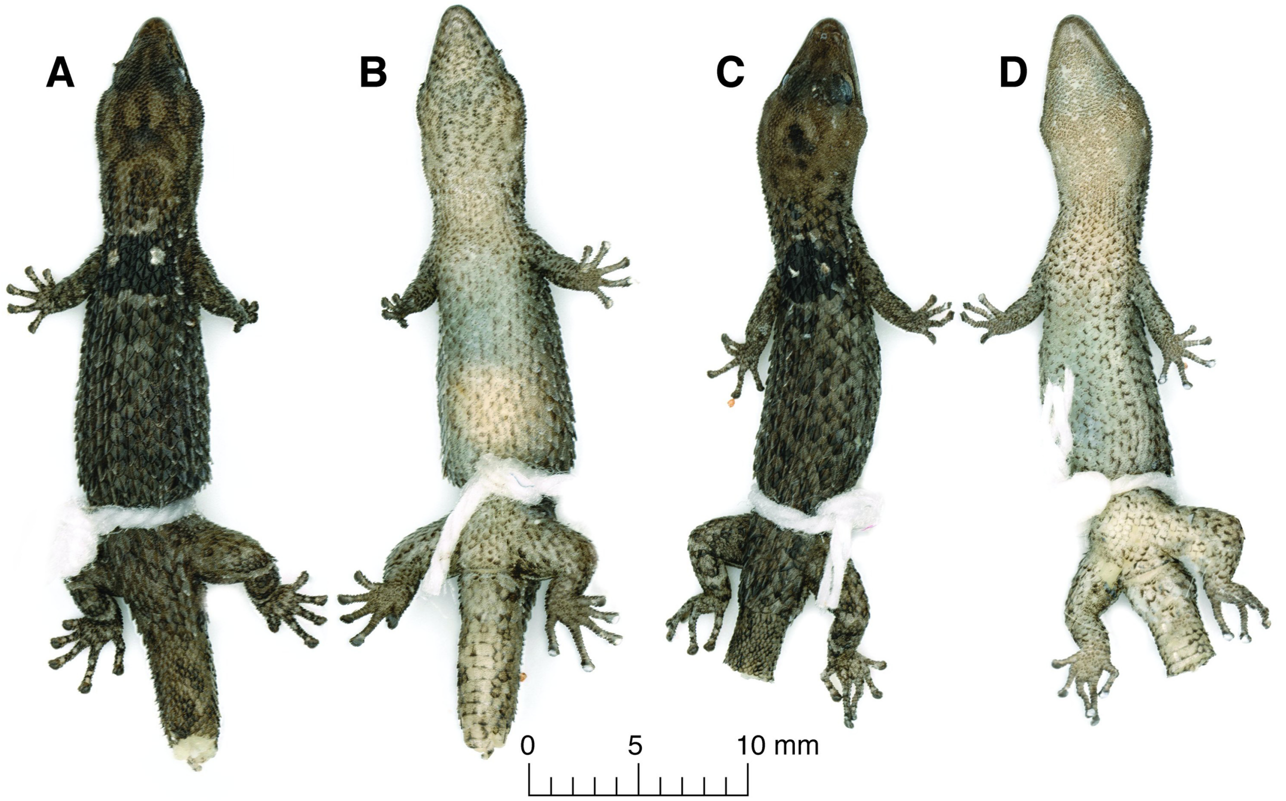

FIGURE 25. Adult specimens of *Sphaerodactylus g. stibarus* from Isla Piñeros, Puerto Rico. A–B, Female (SHSUHerp000917), C–D male (SHSUHerp000918).

Our results were also largely concordant at well-supported nodes with previously published mtDNA phylogenies (Hass 1996; Diaz-Lameiro *et al.* 2013). Specifically, all studies recovered a clade of several southern Hispaniolan taxa which were previously hypothesized to be closely related on morphological grounds (Hedges and Thomas 2001). Similarly, we recovered a monophyletic "*argus*" series consisting of Hispaniolan and Puerto Rican species.

Genetic distances among many of the sampled *Sphaerodactylus* mito-clades were comparable to mtDNA genetic distances among recognized gecko sister species, for which ND2 distances typically range from 4.1% to 35.5% (Botov *et al.* 2015; Grismer *et al.* 2014; Oliver *et al*. 2007; Pepper *et al.* 2006; Portik *et al*. 2013), and 4% to 10% for 16S (Bauer & Lamb 2002; Gamble *et al.* 2012; Rocha *et al.* 2009; Ziegler *et al.* 2008). For example, genetic distances among the four species in the *S. macrolepis* species group ranged from 4.7–15.4% (ND2) and 1.9 to 9.1% (16S) (Table 1). Genetic distances among the eastern, central and western *S. macrolepis* clades ranged from 5.3 to 5.4% (ND2) and 1.8 to 2.7% (16S), and among *S. grandisquamis* subspecies 0.9 to 10.4% (ND2) and 0.2 to 3.8% (16S). Consistent with previous observations of Hispaniolan species (Scantlebury 2014), genetic distances among sampled populations and subspecies of *S. darlingtoni*: *S. d. darlingtoni* Shreve*, S. d. noblei* Shreve*, S. d. bobilini* Thomas & Schwartz*,* and *S. d.* cf. *noblei* (from near Manaclar, Dominican Republic) had large genetic distances, ranging from 10.8 to 18.2% with ND2. ND2 genetic distances between eastern and western populations of *S. gaigeae* were 9.2%, and 6 to 9.3% among three *S. klauberi* clades. Thus, even with the taxonomic changes undertaken here (elevating *S. inigoi* and *S. grandisquamis* to full species), there remain a substantial number of undescribed species-level lineages within *Sphaerodactylus*. Some of this undescribed diversity has been noted previously. For example, a divergent mitochondrial clade of *S. klauberi*, corresponding to our north-west *S. klauberi* clade, was recovered by Díaz-Lameiro *et al.* (2013). Our multi-locus data confirm this lineage is distinct from at least two other divergent *S. klauberi* clades. Similarly, *S. gaigeae* and *S. macrolepis* both include several distinct lineages and the Hispaniolan species *S. difficilis, S. ladae,* and *S. darlingtoni* are all polyphyletic. Taken together, additional taxonomic work is needed for *Sphaerodactylus* on the Puerto Rican Bank and Hispaniola. Additional research that includes broad geographic sampling and integrates both molecular and morphological data will be necessary to identify and diagnose these currently undescribed species and ensure taxonomy is isomorphic with phylogeny.

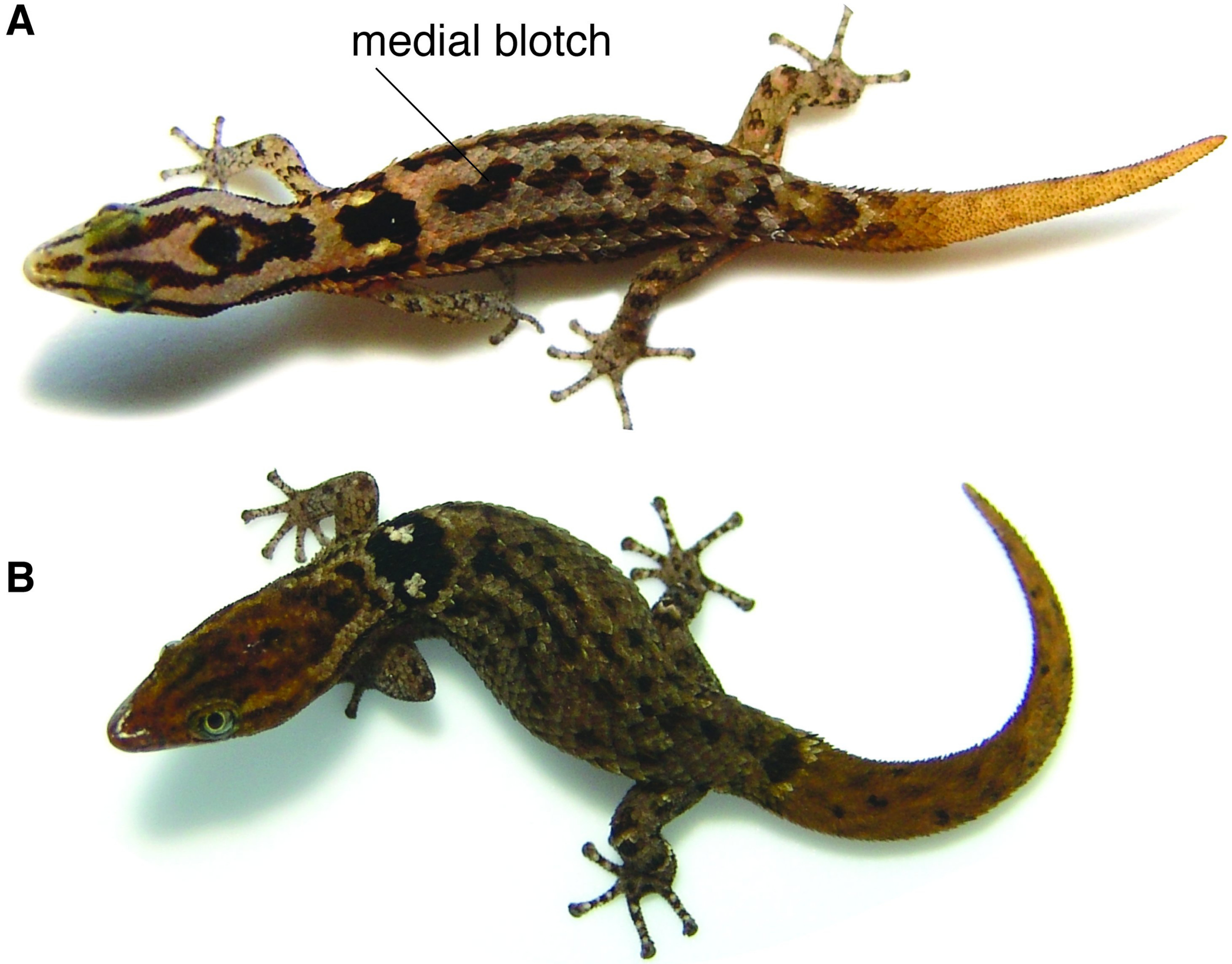

FIGURE 26. Dorsal lines forming a blotch (A, *Sphaerodactylus inigoi* from Culebra, Flamenco) or with separated lines, not forming a blotch (B, S*phaerodactylus g. grandisquamis*, Piñones, Puerto Rico).

TABLE 1. Net between group genetic distances among species in the *S. macrolepis* species complex. ND2 p-distances on bottom and 16S p-distances on top.

	S. grandisquamis	*S. inigoi*	*S. parvus*	*S. macrolepis*
S. grandisquamis		0.019	0.078	0.062
S. inigoi	0.047		0.091	0.079
S. parvus	0.132	0.154		0.045
S. macrolepis	0.097	0.124	0.090	

Species Delimitation and Taxonomy. Clades with empirical data regarding reproductive isolation can be used to calibrate species delimitation efforts by providing biologically-relevant criteria, such as the degree of post-zygotic reproductive isolation due to genetic drift as a function of time (Singhal *et al*. 2018). Within Puerto Rican *Sphaerodactylus*, a hybrid zone between *S. nicholsi* and *S. townsendi* shows strong signatures of genome-wide post-zygotic reproductive isolation (Pinto *et al.* 2019a). Using the time-calibrations in the present study, the divergence between *S. nicholsi* and *S. townsendi* occurred 2.72 (±0.76) mya. This provides a reasonable timeframe for *Sphaerodactylus* geckos to become reproductively-isolated and delimit them as nominal species. Thus, most currently-described species of Puerto Rican *Sphaerodactylus* as well as several, as yet undescribed lineages have diverged at or before this conservative reproductive isolation 'cutoff'. This includes the divergence of *S. grandisquamis* with *S. inigoi* and *S. parvus* with *S. macrolepis* (Fig. 5).

STACEY and SpeciesDA analyses using the combined mtDNA dataset provide strong support for a species delimitation hypothesis where all putative taxa in the *S. macrolepis* species complex represent distinct lineages, perhaps even distinct species. However, coalescent methods may be prone to over-splitting taxa due to assumptions of the model, e.g., no genetic structure within nominal taxa and speciation modeled as an instantaneous process (Sukumaran & Knowles 2017; Pinto *et al.* 2019b). Furthermore, STACEY and SpeciesDA using just the nDNA found little support for most of these species and was not able to distinguish *S. inigoi* and *S. grandisquamis* as distinct (Fig. 6). This difference was most likely due to added resolution of the mtDNA data, which have, on average, a shorter coalescent time than nDNA (Palumbi *et al*. 2001; Zink & Barrowclough 2008). This discordance between datasets led us to be cautious with our taxonomic conclusions. Both molecular and morphological data leave little doubt that *S. macrolepis* and *S. parvus* are distinct lineages from each other and from other taxa in the *S. macrolepis* species complex. However, our justification for delimiting *S. inigoi* from *S. grandisquamis* and recognizing both as species under the general lineage species concept (de Queiroz 1998; de Queiroz 2007) includes: (1) pre-zygotic reproductive isolation due to allopatry, (2) reciprocal monophyly in our species tree analysis, (3) morphological diagnosability, and (4) a divergence time estimation preceding the clade-specific estimate of reproductive isolation (detailed above). Further work is needed to determine whether the *S. grandisquamis* subspecies on Puerto Rico warrant species status. We have declined to elevate these taxa to species largely because of lack of phylogenetic resolution due to incomplete lineage sorting, ongoing gene flow, or some combination of both (Figs. 5 and 6). Large effective population sizes, recent divergence times, and possible ongoing gene flow will make delimiting *S. grandisquamis* subspecies a particularly challenging task. Genome-scale datasets using RADseq or targeted enrichment are likely necessary to tease apart the historical and demographic processes that have generated current diversity. However, until additional work is completed, we believe that current subspecific names are the best way to describe the phenotypic and genetic diversity occurring on Puerto Rico.

Although the use of subspecies as a taxonomic rank is increasingly unpopular (Burbrink *et al*. 2000; Torstrom *et al*. 2014; Wilson & Brown 1953; Zink 2004), we favored a conservative approach to retain subspecies of *S. grandisquamis*. A frequently-used definition of subspecies is, "a collection of populations within a biological species that are diagnosably distinct from other such collections of populations" (Patten & Unitt 2002), which fits with Thomas & Schwartz's (1966) rationale for describing populations within the *S. macrolepis* species complex as subspecies rather than species. The intermediate forms on Culebra and elsewhere suggested the ability to interbreed and, given the prevalence of the Biological Species Concept (Mayr 1942) at the time, a taxonomic rank below the species level provided the best solution (Thomas & Schwartz 1966). However unpopular subspecific designations have become over the past 50+ years, our re-evaluation of the subspecific diagnostic traits of *S. grandisquamis* showed that these characters effectively delimit geographical color and pattern variation. Here, we resolved some of the taxonomic confusion within the *S. macrolepis* species complex and believe that the retention of the *S. grandisquamis* subspecies may prove useful for future systematic work and population-level research involving geographical differences in color, pattern, and size in Puerto Rican *Sphaerodactylus*.

Further effort should be put forth to sample the Monito Island dwarf gecko, *S. micropithecus*, which was hypothesized to be closely-related to the Mona Island dwarf gecko, *S. monensis* (Thomas & Schwartz 1966). Given that previous species delimitation hypotheses found limited support for species-level divergence between *S. monensis* and *S. townsendi* (Pinto *et al.* 2019a) the species status of *S. micropithecus* should be explicitly tested. Including *S. micropithecus* in both phylogenetic and species delimitation analyses may show that it is most-closely related to *S. monensis* or may point to a more complex biogeographic scenario, if located outside of the clade containing *S. monensis* and *S. townsendi*.

Two Distinct Species of* Sphaerodactylus *on Culebra. We found Culebra inhabited by two species of *Sphaerodactylus*, *S. inigoi* on the northwestern side of the island and *S. macrolepis* on the eastern and southern parts of the island. Their co-occurrence on Culebra seems to have caused much of the previous taxonomic confusion in the *S. macrolepis* species complex. Grant (1931) and Thomas & Schwartz (1966) both found sufficient differences between *S. macrolepis* and *S. grandisquamis* (including *S. inigoi*) to classify them as separate species. Further, Grant's (1931) description of *S. danforthi* from Culebra describes two male color/pattern phases, a phenotype with patternless, red/orange heads, which corresponds to *S. inigoi*, and a phenotype with a patterned/speckled head, which is *S. macrolepis*. The *S. danforthi* holotype, MCZ R-34403, is a male with patterned head and reticulated throat consistent with *S. macrolepis*. Therefore, Thomas & Schwartz (1966) were correct in synonomizing *S. danforthi* with *S. macrolepis*.

Sphaerodactylus inigoi and *S. macrolepis* are easy to distinguish from each other (Figs. 9 & 11) and further work, using museum collections and additional field sampling, is needed to determine each species' distribution on Culebra. Their co-occurrence on Culebra also provides opportunities for future research. For example, do these sexually dichromatic species show evidence of reinforcement on Culebra, compared to other parts of their distribution where they are not sympatric? Is there evidence of competitive exclusion in areas of non-sympatry?

Biogeography. The current distributions of *Sphaerodactylus* geckos from Hispaniola, the Puerto Rican Bank, St. Croix, Jamaica, and Anguilla are puzzling, but divergences among clades coincide with some relevant geological processes. We estimated the split between the extant *Sphaerodactylus* of Hispaniola and the Puerto Rican Bank (*argus* series *sensu* Hass 1991) during the mid-to-late Miocene, ~10 mya (8.8–12.5 mya; Fig. 5), which likely post-dates the formation of the Anegada Trough (11.2–16.4 mya) separating the Greater Antilles from St. Croix (Iturralde-Vinent & MacPhee 1999). We can place *Sphaerodactylus* across the Puerto Rican Bank ≥8.8 mya. Since *S. parthenophion* Thomas occurs near the western extent of the Virgin Islands (Virgin Gorda), we can hypothesize that *S. beattyi* Grant arrived in St. Croix via north-to-south dispersal from the other Virgin Islands ~7.27 mya (4.99–9.52 mya). Around this time, east-to-west dispersal from the Puerto Rican Bank to Jamaica ~7.65 mya (6.18–9.19 mya), and subsequent dispersals to Cuba and the Bahamas, explain the current distribution of *S. argus*. Given proper sampling across the range of *S. argus*, this could be explicitly tested. Similarly, we estimate the divergence of the clade from southern Hispaniola (*S. plummeri, S. armstrongi, S. ariasae* and *S. streptophorus*), nested within our focal clade of Puerto Rican Bank species, at ~5.5 mya (4.12–6.99). Since southern Hispaniola collided with northern Hispaniola during early Miocene (16–23 mya; Mann *et al.* 1991) and has never been in contact with Puerto Rico, the occurrence of this group in Hispaniola is best-explained by a single east-to-west dispersal from the Puerto Rican Bank and subsequent speciation. The southern Hispaniolan species (with the exception of *S. armstrongi*) and their close relatives on Puerto Rico (*S. nicholsi* and *S. townsendi)* and nearby islands (*S. monensis* and *S. levinsi*) are xerophilic, dwarf species. Small size and xerophilic adaptations may help species with these traits better survive overwater dispersal or they may occur in areas that are more prone to being washed out to sea on flotsam (Heatwole & Levins 1972). Most dispersal events likely occurred from east-to-west following oceanic currents, from the Puerto Rican Bank to Hispaniola, Mona, Desecheo, and Jamaica (Fig. 5).

We only found one exception to this theme, *S. parvus*, whose occurrence in the northern Lesser Antilles is anomalous as the Anguilla Bank has never been in contact with the Puerto Rican Bank. *Sphaerodactylus parvus* diverged from a common ancestor with *S. macrolepis* in the mid-Pliocene, ~3.36 mya (2.36–4.41 mya). *Sphaerodactylus macrolepis* occurs throughout the Virgin Islands, thus, dispersal from the Virgin Islands to the Anguilla Bank seems likely. However, since this west-to-east dispersal cannot be readily explained by oceanic currents, it is possible that another type of dispersal mechanism is responsible for this distribution, such as storm-driven dispersal, e.g. hurricanes (Carlton *et al.* 2017; Heatwole & MacKenzie 1967).

Across the Puerto Rican Bank, the Pliocene (2.58–5.33 mya) was an epoch of lowland inundations, when Puerto Rico, Culebra, and Vieques became isolated from the Virgin Islands by the formation of the Virgin Passage (Iturralde-Vinent 2006). Indeed, the formation of the Virgin Passage loosely coincides with the divergence between *S. macrolepis* and the clade of *S. grandisquamis* plus *S. inigoi*, ~4.9 mya (3.32–6.51 mya), suggesting vicariance as the initial isolating mechanism for these groups. Populations of *S. macrolepis* occur outside of the Virgin Islands portion of the Puerto Rican Bank on Culebra, St. Croix, and Prickly Pear Cays, Anguilla. As mitochondrial haplotypes from Culebra form a well-supported clade with those from St. Thomas (Fig. 4b), the population on Culebra is likely a result of east-to-west dispersal from the Virgin Islands, Pleistocene vicariance, or perhaps human-mediated introduction. The origins of *S. macrolepis* on St. Croix are also unclear. While they do not share mtDNA haplotypes with any other sampled populations, there is almost no genetic variation among our sampled St. Croix specimens, which suggests either a population bottleneck or a selective sweep. This is consistent with a recent north-to-south dispersal event out of the other Virgin Islands, analogous to the cladogenesis between *S. parthenopion* and *S. beattyi* millions of years prior, or consistent with a human-mediated introduction, which has been suggested by others (Grant & Beatty 1944; MacLean & Holt 1979), similar to a recent introduction of *Eleutherodactylus antillensis* Stejneger (Barker *et al.* 2012). The *S. macrolepis* population on Prickly Pear Cays, Anguilla, is almost certainly a recent human-mediated introduction (Questel 2018).

More recently, glacial and interglacial periods caused sea level fluctuations during the Pleistocene (Ehlers & Gibbard 2007; Hearty *et al.* 2007). Approximately 80 glaciation cycles occurred during the inferred time interval of the split between *S. inigoi* and *S. grandisquamis* (1.09–2.74 mya). Indeed, Quaternary climatic fluctuations, including those resulting in glaciation and interglaciation events, have been hypothesized as historical events promoting diversification both in temperate and tropical regions (Bennett 2004; Hewitt 2004; Lovette 2005; Rull 2006; Lin *et al.* 2010). It is possible that isolation during glaciations between populations from Puerto Rico and Vieques were a causal factor in the divergence between the *S. grandisquamis* and *S. inigoi*. However, since the population of *S. inigoi* sampled from Culebra was nested within the populations from Vieques, we find it likely that this dispersal was very recent and perhaps also human-mediated. Given its ubiquitous distribution across the Virgin Islands, *S. macrolepis* is an excellent model to test hypotheses related to fluctuating sea levels and dispersal across the region. Comparisons with co-distributed species (Barker *et al.* 2012; Papadopoulou & Knowles 2015; Reynolds *et al.* 2017) would be particularly useful in elucidating the complex biogeography of the region.

Evolution of Color and Pattern. Consistent with conclusions drawn by Regalado (2015), sexual dichromatism appears to have been lost independently in *S. parvus* and in the clade containing *S. klauberi* and *S. nicholsi*. Similarly, other lineages in the Puerto Rican Bank have converged on similar schemes of color and patterning. One example is the convergence in male head coloration in shades of gray/blue in both *S. g. mimetes* and *S. macrolepis*. These two taxa also share similar head patterning although the pattern is more diffuse in *S. macrolepis* males and more defined in *S. g. mimetes*. This convergent coloration is not seen in the rest of the male body and is not seen in females of these two taxa. *Sphaerodactylus macrolepis* males frequently have a poorly defined scapular patch that is bicolored when present, whereas *S. g. mimetes* males typically have a well-defined scapular patch.

There is also a contrasting pattern between the males of the two subspecies that inhabit southern Puerto Rico. *Sphaerodactylus g. mimetes* (southeast) has a gray to blue head and a predominantly orange-yellowish body, while in *S. g. ateles* (southwest) the head is red to light orange and the body is light gray (Fig. 3). Male head patterning is quite divergent between these two subspecies, being heavily patterned in *S. g. mimetes* and faint in *S. g. ateles*, which resembles the near patternless male head pattern of *S. inigoi*. Orange heads are also seen in *S. g. spanius* males, which inhabit high elevations of the Cordillera Central and the Sierra de Cayey. *Sphaerodactylus g. spanius* also develop the largest body size, similar to other high-elevation species (e.g. *S. klauberi*). In the lowlands of the Puerto Rican Bank, *Sphaerodactylus* are generally smaller, with the exception of the (nocturnal) *S. roosevelti*. *Sphaerodactylus grandisquamis* populations from Puerto Rico are larger than *S. g. stibarus* on Isla Piñeros. Extreme miniaturization has evolved in the Puerto Rican Bank in three species from three different localities, *S. nicholsi* from Punta Verraco (southwest Puerto Rico), *S. townsendi* from Caja de Muertos (Thomas, Gamble, & Daza pers. obs.), and *S. parthenopion* from Virgin Gorda (Thomas 1965; MacLean 1985); these extreme miniaturized populations are comparable in size to *S. ariasae*, the smallest gekkotan species, and *S. schwartzi* Thomas, Hedges, & Garrido, the smallest known Cuban species (Thomas *et al.* 1992; Hedges & Thomas 2001).

Convergent Evolution in Habitat-specific Morphology. Thomas *et al.* (1992) described xeric and mesic forest ecomorphs for *Sphaerodactylus*. In the northern areas of Puerto Rico, the subtropical wet forests (Erickson *et al.* 2014) offers more mesic habitats where the leaf litter decomposition develops a dark compost underneath (e.g. under sea grapes leaves and in the forest of the Karst region), which might favor selection of darker colored geckos with a well-defined scapular patch surrounded by a white margin, as seen in *S. grandisquamis* inhabiting the north of Puerto Rico and Isla Piñeros (*S. g. grandisquamis*, *S. g. guarionex*, and *S. g. stibarus*). In these mesic habitats, geckos are generally hard to detect in the dense leaf litter layer. In the southern subtropical dry forests of Puerto Rico (Erickson *et al.* 2014), the xeric areas are covered by accumulation of small leaves in open, semi-deciduous forests (Rivero 1998; López-Ortiz & Lewis 2002), which covers a mostly-sandy or drier forest subfloor. This microhabitat favors lighter coloration as in *S. g. ateles*, *S. townsendi, S. nicholsi,* and, to some extent *S. roosevelti,* which are frequently found in higher solar radiance habitats (e.g. *S. ariasae* or *S. plummeri* in Hispaniola; Hedges and Thomas 2001; Scantlebury 2014). In high elevations (such as the Cordillera Central, Sierra de Cayey and El Yunque forest), the habitats are subtropical wet/rain forests (Erickson *et al.* 2014), where *S. klauberi* and *S. g. spanius* occur. *S. klauberi* is consistent in coloration with the mesic forest ecomorph, while *S. g. spanius* are lighter in coloration and appear inconsistent with the predictions for this habitat type. Scantlebury (2014) showed that head shape broadly correlates with xeric-mesic environmental gradient, and also pointed out that current definitions of xeric and mesic forest ecomorphs are limited, and perhaps inaccurate, being incongruent in many cases, as with *S. g. spanius*. Although this may be the case, it is also important to take other factors into account, namely phylogeny and population genetic structure and sexual selection. For instance, *S. g. spanius* is nested within the *S. grandisquamis* group, an ancestrally sexually dichromatic group, with strong evidence of historical and ongoing gene flow with conspecifics. Further, there is reasonable suspicion that *S. grandisquamis* ssp. possess massive effective population sizes, or N_e (*S. macrolepis* occurs at higher population densities than most all other terrestrial vertebrates; Rodda *et al.* 2001), may heavily constrain local adaptation to a montane ecomorph in *S. g. spanius*. Indeed, here, we largely ignore specific microhabitat preferences of the Puerto Rican *Sphaerodactylus* geckos and the natural history of specific taxa.

The adaptive radiation of Caribbean *Anolis* lizards has long been touted as exceptional in both its species richness and ecomorphological diversity (Losos 2009). However, *Sphaerodactylus* and *Eleutherodactylus* frogs have also been considered potential replicate radiations as both genera are species rich and appear to exhibit habitat-specific adaptations on different Caribbean islands (Hedges 1989; Thomas *et al.* 1992; Hedges *et al.* 2008; Thorpe *et al*. 2008). Recently, Dugo-Cota *et al*. (2019) showed *Eleutherodactylus* have independently evolved similar ecomorphs across the Greater Antilles. This leaves *Sphaerodactylus* as the last unstudied putative adaptive radiation among the species rich Caribbean herpetofaunal clades. There are sufficient preliminary data on body size, coloration, physiology, and diurnal/nocturnal behavior to indicate potential ecomorphological variation among *Sphaerodactylus* species (Dunson & Bramham 1981; MacLean 1985; Thomas *et al.* 1992; Hedges & Thomas 2001; Nava 2006; Steinberg *et al.* 2007; Scantlebury *et al*. 2011; Gamble *et al.* 2015). Thus, more work is needed to elucidate the mode and tempo of the *Sphaerodactylus* radiation by examining associations between ecology, physiology, and morphology across the entire Caribbean, similar to work done in *Anolis* lizards.

Conclusions. As seen in many other Neotropical lizards (Geurgas & Rodrigues, 2010; Werneck *et al.* 2012; Guarnizo *et al.* 2016; Pinto *et al.* 2019b), the diversity of *Sphaerodactylus* has been underestimated. Examining species on the Puerto Rican Bank, we used an integrative approach, combining morphological and molecular data, to elevate previously recognized subspecies of *S. macrolepis* to full species status and identified other Puerto Rican lineages (e.g., *S. klauberi* and *S. gaigeae*) that warrant a closer taxonomic evaluation. Although not the focus of this study, we also identified multiple paraphyletic lineages on Hispaniola (especially within nominal *S. difficilis* and *S. darlingtoni* groups). In light of the previous phylogenetic studies (Hass 1991; Hass 1996; Diaz-Lameiro *et al*. 2013; Pinto *et al*. 2019a), our findings provide further support for an emerging consensus on *Sphaerodactylus* relationships that shows Hispaniolan and Jamaican species nested within an otherwise Puerto Rican clade, which permits a clearer interpretation of the complex historical processes driving diversification in this group. For example, we observed a single expansion eastward from Hispaniola to Puerto Rico with most subsequent dispersals either southward towards St. Croix or westward back towards Hispaniola (and Jamaica). However, our study has limited taxonomic and geographic sampling and further work is needed—requiring the inclusion of Cuban and additional Jamaican taxa—to conclusively describe the overall biogeographic patterns observed in the genus across the Caribbean. We also uncovered interesting patterns involving the evolution of sexual dichromatism within the *S. macrolepis* and *S. grandisquamis* clades. Specifically, convergence upon similar coloration (e.g. gray/blue heads in both *S. macrolepis* and *S. g. mimetes*) and stark differences in male coloration that is geographically-structured (e.g. corresponding to recognized *S. grandisquamis* subspecies). Finally, we propose future research should leverage ecological, physiological, and genome-scale data to elucidate the biological context that drives the observed patterns and test whether Caribbean *Sphaerodactylus* are an adaptive radiation.

A Checklist to the *Sphaerodactylus* of Puerto Rico and Nearby Islands

Sphaerodactylus beattyi Grant, 1937
    Sphaerodactylus beattyi beattyi Grant, 1937
    Sphaerodactylus beattyi seamani Thomas & Schwartz, 1966
Sphaerodactylus gaigeae Grant, 1932
Sphaerodactylus grandisquamis Stejneger, 1904
    Sphaerodactylus grandisquamis grandisquamis Stejneger, 1904
    Sphaerodactylus grandisquamis guarionex Thomas & Schwartz, 1966
    Sphaerodactylus grandisquamis ateles Thomas & Schwartz, 1966
    Sphaerodactylus grandisquamis mimetes Thomas & Schwartz, 1966
    Sphaerodactylus grandisquamis spanius Thomas & Schwartz, 1966
    Sphaerodactylus grandisquamis stibarus Thomas & Schwartz, 1966
Sphaerodactylus inigoi Thomas & Schwartz, 1966
Sphaerodactylus klauberi Grant, 1931
Sphaerodactylus levinsi Heatwole, 1968
Sphaerodactylus macrolepis Günther, 1859
Sphaerodactylus micropithecus Schwartz, 1977

Sphaerodactylus monensis Meerwarth, 1901
Sphaerodactylus nicholsi Grant, 1931
Sphaerodactylus parthenopion Thomas, 1965
Sphaerodactylus roosevelti Grant, 1931
Sphaerodactylus townsendi Grant, 1931

Key to the *Sphaerodactylus macrolepis* species complex

1A. Sexual dichromatism present, distribution within the Puerto Rico Bank, scapular patch with discrete ocelli, body dorsal scales larger than ventral scales (Figs.13, 14). 2
1B. Sexual dichromatism absent, distribution on the Anguilla Bank, scapular patch ocelli very close or fused, body dorsal scales and ventral scales subequal. . . . . **_Sphaerodactylus parvus_** (Fig. 8).
2A. Dorsal body scales large and imbricate, dorsal scales with knob-like and hair-bearing organs in the free edge (Fig. 2), scapular patch mainly black, variable in size and shape, but never with two anteriorly projecting points or formed by two dark circles surrounding the ocelli, males with or without pattern on the head. 3
2B. Dorsal body scales small and almost juxtaposed, dorsal scales without knob-like organs (Fig. 1), scapular patch oftentimes bicolor (brown and black), scapular patch with anteriorly projecting points (Fig. 10) or made by two dark circles surrounding the ocelli, males with marbled pattern on the head. Distributed on the U.S. and British Virgin Islands, also in the eastern and southern parts of Culebra Island. . . . . **_Sphaerodactylus macrolepis_** (Figs. 9, 10).
3A. Males marked with head pattern, distributed in Puerto Rico and satellite islands (e.g. Piñeros), females with two medial lines separated, not forming a medial blotch. 4
3B. Males without marked head pattern, distributed in Vieques and Western part of Culebra Island, females with two medial lines forming a medial blotch (Fig. 26). . . . . **_Sphaerodactylus inigoi_** (Figs 11,12).
4A. Males dorsal pattern formed by continuous or stippled lines, male head color variable from red to yellow. 5
4B. Males dorsal pattern salt and pepper, male head color blue or gray. . . . . . . **_Sphaerodactylus g. mimetes_** (Figs. 20, 21).
5A. Maximum SVL more than 32 mm (Fig. 7). 6
5B. Maximum SVL equal or less than 30 mm.. . . . .**_Sphaerodactylus g. stibarus_** (Figs. 24, 25).
6A. Scapular patch reduced and not enclosing the ocelli, scapular patch not surrounded by white margin, snout scales hexagonal. 7
6B. Scapular patch large and enclosing the ocelli, scapular patch surrounded by white margin. snout scales rounded. 8
7A. Nuchal spot well separated from with scapular patch.. . . . . **_Sphaerodactylus g. ateles_** (Figs. 18, 19)
7B. Nuchal spot approaching or in contact with scapular patch. . . . .**_Sphaerodactylus g. spanius_** (Figs. 22, 23).
8A. Males head color brownish red, females with pigmentation on the belly and ventral side of the tail, seven lamellae on fourth toe. . . . . **_Sphaerodactylus g. grandisquamis_** (Figs. 14, 15).
8B. Males head color orange, females without pigmentation on the belly and ventral side of the tail, nine lamellae on fourth toe. . . . .**_Sphaerodactylus g. guarionex_** (Figs. 16, 17).

Author Contributions

J.D.D. participated in field work, conducted morphological analyses, diagnosed new species, and helped write the paper; B.J.P. participated in field work, assisted in generating sequence data, generated molecular phylogenies, conducted species delimitation, and helped write the paper; R.T. participated in field work, conducted morphological analyses, diagnosed new species, and conceived the initial project; A.H-M. participated in field work, biogeographical interpretations, and helped write the paper; G.P. participated in field work; L.F.P.G. participated in field work, conducted morphological analyses, and diagnosed new species; R.P.B. conducted SEM imaging; D.P.S. participated in field work, generated sequence data, and conducted preliminary analyses; T.G. participated in field work, generated and aligned sequence data, conducted preliminary analyses, and drafted the manuscript. All authors read and approved the final manuscript.

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APPENDIX A. Sample information and collection metadata. *Map #*: corresponding numbers from Fig. 3; *Species Tree ID*: described and putative taxa used to produce species tree, see Figures 5 and 6; *Specimen ID*: field tag, tissue ID, or museum catalog number specific to each sample, see Fig. 4 [RT = Richard Thomas field series; TG = Tony Gamble field series; Scantle = Dan Scantlebury field series; Glor = Rich Glor field series; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; MCZ = Museum of Comparative Zoology, Harvard University; SBH = S. Blair Hedges; USNM = U. S. National Museum, Smithsonian]; *Locality*: Description of the collection locality; *Lat/Long*: collection locality coordinates (if available); *Morphology*: specimens with DNA sequence data that were also examined morphologically (*S. macrolepis* species complex only); *SHSUHerp#*: if these specimens were accessioned in the Sam Houston State University Herp collection; and GenBank accession numbers for genes used for each individual, in alphabetical order (16S, ACM4, CMOS, ND2, PTPN12, RAG1, and RBMX).

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
1	*S. grandisquamis ateles*	RT14642	Caño Boquilla, Mayaquez, Puerto Rico	18.25102	-67.17663	Yes	SHSUHerp773	MN414636	MN415016	MN415223	MN415608	MN415418	MN415800	MN414813
2	*S. grandisquamis ateles*	RT14646	Balneario Boqueron, Cabo Rojo, Puerto Rico	18.01783	-67.17178	Yes	SHSUHerp777	MN414637	MN415017	MN415224	MN415609	MN415419	MN415801	MN414814
2	*S. grandisquamis ateles*	RT14647	Balneario Boqueron, Cabo Rojo, Puerto Rico	18.01783	-67.17178	Yes	SHSUHerp778	MN414638	MN415018	N/A.	MN415610	MN415420	MN415802	MN414815
2	*S. nicholsi*	RT14652	Balneario Boqueron, Cabo Rojo, Puerto Rico	18.01783	-67.17178	N/A.	N/A.	MN414716	MN415121	MN415320	MN415703	MN415513	MN415899	MN414877
2	*S. nicholsi*	RT14657	Balneario Boqueron, Cabo Rojo, Puerto Rico	18.01783	-67.17178	N/A.	N/A.	MN414717	MN415122	MN415321	MN415704	MN415514	MN415900	MN414878
2	*S. nicholsi*	TG2096	Balneario Boqueron, Cabo Rojo, Puerto Rico	18.01783	-67.17178	N/A.	N/A.	MK336993	MN415127	MK337592	MK337508	MK337313	MK337404	MN414883
3	*S. grandisquamis ateles*	TG214	3 km S. Mayaguez, Puerto Rico	18.18055	-67.16988	Yes	N/A.	MN414745	MN415159	MN415374	MN415734	MN415564	MN415956	MN414925
3	*S. grandisquamis ateles*	TG215	4 km S. Mayaguez, Puerto Rico	18.18055	-67.16988	Yes	N/A.	MN414746	MN415160	MN415376	MN415735	MN415566	MN415958	MN414926
4	*S. grandisquamis ateles*	TG2045	Maricao, Puerto Rico	18.11820	-67.00043	N/A.	SHSUHerp789	MN414767	MN415179	MN415364	MN415755	MN415554	MN415946	MN414915
5	*S. grandisquamis grandisquamis*	TG221	near canal, San Juan Park, Puerto Rico	18.41801	-66.00438	Yes	N/A.	MN414748	MN415162	MN415378	MN415737	MN415568	MN415960	MN414928
6	*S. grandisquamis grandisquamis*	RT14660	Piñones, Puerto Rico	18.44216	-65.95861	Yes	SHSUHerp738	MN414639	MN415019	MN415225	MN415611	MN415421	MN415803	MN414816
7	*S. grandisquamis grandisquamis*	RT14665	Rio Grande, Puerto Rico	18.38566	-65.82801	Yes	SHSUHerp739	MN414640	MN415020	MN415226	MN415612	MN415422	MN415804	MN414817

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
7	*S. grandisquamis grandisquamis*	RT14666	Rio Grande, Puerto Rico	18.38566	-65.82801	Yes	SHSUHerp740	MN414641	MN415021	MN415227	MN415613	MN415423	MN415805	MN414818
7	*S. grandisquamis grandisquamis*	RT14673	Rio Grande, Puerto Rico	18.38566	-65.82801	Yes	SHSUHerp746	MN414642	MN415022	MN415228	MN415614	MN415424	MN415806	MN414819
8	*S. grandisquamis guarionex* (2)	Loc2_poss	Loc2, Guajataca, Puerto Rico	18.48879	-66.95881	Yes	N/A.	MN414604	MN414983	MN415190	MN415574	MN415384	MN415766	MN414779
8	*S. grandisquamis guarionex* (2)	RT14822	Loc2, Guajataca, Puerto Rico	18.48879	-66.95881	Yes	N/A.	MN414665	MN415048	MN415254	MN415637	MN415450	MN415832	MN414845
8	*S. grandisquamis guarionex* (2)	TG219	Rio Guajataca river mouth, Puerto Rico	18.48879	-66.95881	Yes	N/A.	MN414747	MN415161	MN415377	MN415736	MN415567	MN415959	MN414927
9	*S. grandisquamis guarionex* (2)	RT14631	Playa Los Pinos, Camuy, Puerto Rico	18.49080	-66.86539	Yes	SHSUHerp158	MN414634	MN415014	MN415221	MN415606	MN415416	MN415798	MN414811
9	*S. grandisquamis guarionex* (2)	RT14632	Playa Los Pinos, Camuy, Puerto Rico	18.49080	-66.86539	Yes	SHSUHerp159	MN414635	MN415015	MN415222	MN415607	MN415417	MN415799	MN414812
9	*S. nicholsi*	RT14635	Playa Los Pinos, Camuy, Puerto Rico	18.49080	-66.86539	N/A.	N/A.	MN414714	MN415120	MN415318	MN415701	MN415511	MN415897	MN414875
9	*S. nicholsi*	RT14637	Playa Los Pinos, Camuy, Puerto Rico	18.49080	-66.86539	N/A.	N/A.	MN414715	N/A.	MN415319	MN415702	MN415512	MN415898	MN414876
10	*S. grandisquamis guarionex* (2)	RT14823	Camuy, Puerto Rico	18.48681	-66.83721	Yes	N/A.	MN414666	MN415049	MN415255	MN415638	MN415451	MN415833	MN414846
11	*S. grandisquamis guarionex* (1)	TG1993	Aricebo, Puerto Rico	18.48080	-66.69689	Yes	N/A.	MN414762	MN415176	MN415361	MN415751	MN415551	MN415943	MN414912
11	*S. grandisquamis guarionex* (1)	TG2095	near Aricebo, Puerto Rico	18.48080	-66.69689	Yes	SHSUHerp153	MN414776	MN415188	MN415373	MN415764	MN415563	MN415955	MN414924
12	*S. grandisquamis guarionex* (1)	TG2001	Barceloneta, Puerto Rico	18.48674	-66.55009	Yes	SHSUHerp181	MN414763	MN415177	MN415362	MN415752	MN415552	MN415944	MN414913
12	*S. nicholsi*	TG2002	Barceloneta, Puerto Rico	18.48674	-66.55009	N/A.	N/A.	MN414764	MN415124	MK337589	N/A.	MK337310	MN415902	MN414880
12	*S. nicholsi*	TG2073	Barceloneta, Puerto Rico	18.48674	-66.55009	N/A.	N/A.	MK336992	MN415126	MK337591	MK337507	MK337312	MN415904	MN414882
13	*S. grandisquamis guarionex* (1)	RT14700	4.4km N/NE Manati, Puerto Rico	18.46916	-66.46505	Yes	SHSUHerp753	MN414646	MN415026	MN415232	MN415618	MN415428	MN415810	MN414823
13	*S. grandisquamis guarionex* (1)	RT14702	4.4km N/NE Manati, Puerto Rico	18.46916	-66.46505	Yes	SHSUHerp755	MN414647	MN415027	MN415233	MN415619	MN415429	MN415811	MN414824
13	*S. nicholsi*	RT14705	4.4km N/NE Manati, Puerto Rico	18.46916	-66.46505	N/A.	N/A.	MN414718	MN415123	MN415322	MN415705	MN415515	MN415901	MN414879
14	*S. grandisquamis guarionex* (1)	RT14626	Balneario Cerro Gordo, Toa Baja, Puerto Rico	18.48076	-66.34189	Yes	SHSUHerp783	MN414632	MN415012	MN415219	MN415604	MN415414	MN415796	MN414809

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
14	*S. grandisquamis guarionex* (1)	RT14627	Balneario Cerro Gordo, Toa Baja, Puerto Rico	18.48076	-66.34189	Yes	SHSUHerp784	MN414633	MN415013	MN415220	MN415605	MN415415	MN415797	MN414810
15	*S. gaigeae* (East)	RT14851	Mt Pirata, Vieques, Puerto Rico	18.09335	-65.55131	N/A.	N/A.	MN414694	MN415089	MN415296	MN415680	MN415487	MN415874	MN414857
15	*S. inigoi*	RT14844	Mt Pirata, Vieques, Puerto Rico	18.09335	-65.55131	N/A.	N/A.	MN414667	MN415050	MN415256	MN415639	MN415452	MN415834	MN414847
16	*S. inigoi*	RT14846	Cerro Buey, Vieques, Puerto Rico	18.10627	-65.54166	Yes	N/A.	MN414668	MN415051	N/A.	MN415640	MN415453	MN415835	MN414848
17	*S. inigoi*	RT14748	West of Mosquito Pier, Vieques, Puerto Rico	18.12373	-65.53173	Yes	N/A.	MN414653	MN415033	MN415239	MN415625	MN415435	MN415817	MN414830
17	*S. inigoi*	RT14749	West of Mosquito Pier, Vieques, Puerto Rico	18.12373	-65.53173	Yes	N/A.	MN414654	MN415034	MN415240	MN415626	MN415436	MN415818	MN414831
18	*S. inigoi*	TG2147	Curva de Sixto, Vieques, Puerto Rico	18.13387	-65.50585	Yes	N/A.	MN414778	MN415189	MN415375	MN415765	MN415565	MN415957	N/A.
19	*S. inigoi*	RT14736	Flamenco Beach, Culebra, Puerto Rico	18.32897	-65.31406	Yes	N/A.	MN414651	MN415031	MN415237	MN415623	MN415433	MN415815	MN414828
19	*S. inigoi*	RT14739	Flamenco Beach, Culebra, Puerto Rico	18.32897	-65.31406	N/A.	N/A.	MN414652	MN415032	MN415238	MN415624	MN415434	MN415816	MN414829
19	*S. inigoi*	TG1950	Flamenco Beach, Culebra, Puerto Rico	18.32897	-65.31406	Yes	N/A.	MN414757	MN415171	MN415356	MN415746	MN415546	MN415938	MN414908
20	*S. grandisquamis spanius* (1)	TG1512	near Juana Diaz, Puerto Rico	18.02418	-66.50414	Yes	N/A.	MN414754	MN415168	MN415353	MN415743	MN415543	MN415935	MN414906
20	*S. townsendi*	TG1505	near Juana Diaz, Puerto Rico	18.02418	-66.50414	N/A.	N/A.	MN414737	MN415151	MN415347	MN415729	N/A.	MN415928	MN414897
21	*S. grandisquamis mimetes*	RT14677	Patillas, Puerto Rico	18.05188	-66.05007	Yes	N/A.	MN414643	MN415023	MN415229	MN415615	MN415425	MN415807	MN414820
21	*S. grandisquamis mimetes*	RT14678	Patillas, Puerto Rico	18.05188	-66.05007	Yes	SHSUHerp193	MN414644	MN415024	MN415230	MN415616	MN415426	MN415808	MN414821
21	*S. grandisquamis mimetes*	TG1953	Lago Patillas, Puerto Rico	18.05188	-66.05007	Yes	N/A.	MN414758	MN415172	MN415357	MN415747	MN415547	MN415939	MN414909
21	*S. grandisquamis mimetes*	TG1957	Lago Patillas, Puerto Rico	18.05188	-66.05007	Yes	N/A.	MN414760	MN415174	MN415359	MN415749	MN415549	MN415941	MN414911
21	*S. grandisquamis mimetes*	TG2012	Lago Patillas, Puerto Rico	18.05188	-66.05007	Yes	N/A.	MN414765	MN415178	MN415363	MN415754	MN415553	MN415945	MN414914

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
22	*S. grandisquamis mimetes*	RT14685	Arroyo Punta Guilarte, Puerto Rico	17.96193	-66.03602	Yes	SHSUHerp133	MN414645	MN415025	MN415231	MN415617	MN415427	MN415809	MN414822
23	*S. grandisquamis mimetes*	RT14814	PR184, Patillas, Puerto Rico	18.00022	-66.02733	Yes	N/A.	MN414664	MN415047	MN415253	MN415636	MN415449	MN415831	MN414844
24	*S. grandisquamis mimetes*	TG1955	Arroyo, Puerto Rico	17.97785	-65.97079	Yes	N/A.	MN414759	MN415173	MN415358	MN415748	MN415548	MN415940	MN414910
24	*S. grandisquamis mimetes*	TG2093	East of Arroyo, Puerto Rico	17.97785	-65.97079	Yes	SHSUHerp141	MN414775	MN415187	MN415372	MN415763	MN415562	MN415954	MN414923
25	*S. grandisquamis mimetes*	TG2075	Caribe Playa, Puerto Rico	17.97486	-65.93507	Yes	SHSUHerp203	MN414771	MN415183	MN415368	MN415759	MN415558	MN415950	MN414919
25	*S. townsendi*	TG716	Caribe Playa, East of Arroyo, Puerto Rico	17.97486	-65.93507	N/A.	N/A.	MK336985	MN415150	MK337594	MK337500	MK337315	MN415931	MN414902
26	*S. grandisquamis mimetes*	TG1949	Maunabo, Puerto Rico	18.01400	-65.89320	Yes	N/A.	MN414756	MN415170	MN415355	MN415745	MN415545	MN415937	N/A.
27	*S. grandisquamis spanius* (1)	TG1978	Toro Negro, Puerto Rico	18.16309	-66.60139	Yes	N/A.	MN414761	MN415175	MN415360	MN415750	MN415550	MN415942	N/A.
27	*S. grandisquamis spanius* (1)	TG2053	Toro Negro, Puerto Rico	18.16309	-66.60139	Yes	SHSUHerp762	MN414768	MN415180	MN415365	MN415756	MN415555	MN415947	MN414916
27	*S. grandisquamis spanius* (1)	TG2054	Toro Negro, Puerto Rico	18.16309	-66.60139	Yes	SHSUHerp763	MN414769	MN415181	MN415366	MN415757	MN415556	MN415948	MN414917
27	*S. klauberi* (Central)	TG2014	Toro Negro, Puerto Rico	18.16309	-66.60139	N/A.	N/A.	MK337004	MN415111	MK337607	MK337513	MK337327	MK337415	MN414861
28	*S. grandisquamis spanius* (1)	RT14788	near Cerro Punta, Puerto Rico	18.17246	-66.58965	Yes	SHSUHerp758	MN414661	MN415044	MN415250	MN415633	MN415446	MN415828	MN414841
28	*S. grandisquamis spanius* (1)	RT14789	near Cerro Punta, Puerto Rico	18.17246	-66.58965	Yes	SHSUHerp759	MN414662	MN415045	MN415251	MN415634	MN415447	MN415829	MN414842
28	*S. grandisquamis spanius* (1)	RT14790	near Cerro Punta, Puerto Rico	18.17246	-66.58965	Yes	SHSUHerp757	MN414663	MN415046	MN415252	MN415635	MN415448	MN415830	MN414843
29	*S. grandisquamis spanius* (1)	TG2076	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp761	MN414772	MN415184	MN415369	MN415760	MN415559	MN415951	MN414920
29	*S. grandisquamis spanius* (1)	TG2077	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp764	MN414773	MN415185	MN415370	MN415761	MN415560	MN415952	MN414921
29	*S. grandisquamis spanius* (2)	RT14778	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp730	MN414655	MN415038	MN415244	MN415627	MN415440	MN415822	MN414835
29	*S. grandisquamis spanius* (2)	RT14779	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp731	MN414656	MN415039	MN415245	MN415628	MN415441	MN415823	MN414836
29	*S. grandisquamis spanius* (2)	RT14780	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp732	MN414657	MN415040	MN415246	MN415629	MN415442	MN415824	MN414837

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
29	*S. grandisquamis spanius* (2)	RT14781	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp733	MN414658	MN415041	MN415247	MN415630	MN415443	MN415825	MN414838
29	*S. grandisquamis spanius* (2)	RT14782	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp734	MN414659	MN415042	MN415248	MN415631	MN415444	MN415826	MN414839
29	*S. grandisquamis spanius* (2)	RT14785	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp769	MN414660	MN415043	MN415249	MN415632	MN415445	MN415827	MN414840
29	*S. grandisquamis spanius* (2)	TG2065	Divisoria, Puerto Rico	18.16446	-66.50890	Yes	SHSUHerp737	MN414770	MN415182	MN415367	MN415758	MN415557	MN415949	MN414918
29	*S. klauberi* (Central)	TG2013	Divisoria, Puerto Rico	18.16446	-66.50890	N/A.	N/A.	MN414696	MN415110	MN415298	MN415682	MN415489	MN415876	MN414860
30	S. macrolepis (West)	TG2091	Punta Soldado, Culebra, Puerto Rico	18.28184	-65.28660	N/A.	N/A.	MN414774	MN415186	MN415371	MN415762	MN415561	MN415953	MN414922
31	S. macrolepis (West)	RT14725	Zoni Beach, Culebra, Puerto Rico	18.32002	-65.25611	N/A.	N/A.	MN414648	MN415028	MN415234	MN415620	MN415430	MN415812	MN414825
31	S. macrolepis (West)	RT14726	Zoni Beach, Culebra, Puerto Rico	18.32002	-65.25611	N/A.	N/A.	MN414649	MN415029	MN415235	MN415621	MN415431	MN415813	MN414826
31	S. macrolepis (West)	RT14730	Zoni Beach, Culebra, Puerto Rico	18.32002	-65.25611	N/A.	N/A.	MN414650	MN415030	MN415236	MN415622	MN415432	MN415814	MN414827
31	*S. macrolepis* (West)	TG1936	Zoni Beach, Culebra, Puerto Rico	18.32002	-65.25611	N/A.	N/A.	MN414755	MN415169	MN415354	MN415744	MN415544	MN415936	MN414907
32	*S. macrolepis* (West)	S_mac_6	St. Thomas, U.S. Virgin Islands	18.32815	-64.92071	N/A.	N/A.	MN414713	MN415118	MN415317	MN415700	MN415510	MN415896	MN414873
32	*S. macrolepis* (West)	STT004	St. Thomas, U.S. Virgin Islands	18.32815	-64.92071	N/A.	N/A.	MN414742	MN415156	MN415350	MN415731	MN415540	MN415932	MN414903
32	*S. macrolepis* (West)	STT005	St. Thomas, U.S. Virgin Islands	18.32815	-64.92071	N/A.	N/A.	MN414743	MN415157	MN415351	MN415732	MN415541	MN415933	MN414904
32	*S. macrolepis* (West)	STT006	St. Thomas, U.S. Virgin Islands	18.32815	-64.92071	N/A.	N/A.	MN414744	MN415158	MN415352	MN415733	MN415542	MN415934	MN414905
33	*S. macrolepis* (West)	TG680	Rainbow Beach, St. Croix, U.S. Virgin Islands	17.72766	-64.88625	N/A.	N/A.	MN414752	MN415166	MN415382	MN415741	MN415572	MN415964	MN414932
34	*S. macrolepis* (West)	TG676	Good Hope, St. Croix, U.S. Virgin Islands	17.69556	-64.84889	N/A.	N/A.	MN414749	MN415163	MN415379	MN415738	MN415569	MN415961	MN414929
34	*S. macrolepis* (West)	TG677	Good Hope, St. Croix, U.S. Virgin Islands	17.69556	-64.84889	N/A.	N/A.	MN414750	MN415164	MN415380	MN415739	MN415570	MN415962	MN414930
34	*S. macrolepis* (West)	TG681	Good Hope, St. Croix, U.S. Virgin Islands	17.69556	-64.84889	N/A.	N/A.	MN414753	MN415167	MN415383	MN415742	MN415573	MN415965	MN414933

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
35	*S. macrolepis* (West)	TG679	Shay's Beach, St. Croix, U.S. Virgin Islands	17.75927	-64.67422	N/A.	N/A.	MN414751	MN415165	MN415381	MN415740	MN415571	MN415963	MN414931
36	*S. macrolepis* (West)	MCZA26004	Jost Van Dyke, British Virgin Islands	18.44532	-64.74373	N/A.	N/A.	MN414605	MN414984	MN415191	MN415575	MN415385	MN415767	MN414780
36	*S. macrolepis* (West)	MCZA26006	Jost Van Dyke, British Virgin Islands	18.44532	-64.74373	N/A.	N/A.	MN414606	MN414985	MN415192	MN415576	MN415386	MN415768	MN414781
36	*S. macrolepis* (West)	MCZA26009	Jost Van Dyke, British Virgin Islands	18.44532	-64.74373	N/A.	N/A.	MN414607	MN414986	MN415193	MN415577	MN415387	MN415769	MN414782
37	*S. macrolepis* (West)	MCZA26018A	Little Thatch Island, British Virgin Islands	18.38178	-64.71474	N/A.	N/A.	MN414613	MN414992	MN415199	MN415583	MN415393	MN415775	MN414788
37	*S. macrolepis* (West)	MCZA26018C	Little Thatch Island, British Virgin Islands	18.38178	-64.71474	N/A.	N/A.	MN414614	MN414993	MN415200	MN415584	MN415394	MN415776	MN414789
37	*S. macrolepis* (West)	MCZA26018F	Little Thatch Island, British Virgin Islands	18.38178	-64.71474	N/A.	N/A.	MN414615	MN414994	MN415201	MN415585	MN415395	MN415777	MN414790
38	*S. macrolepis* (Central)	MCZA26024A	Guana Island, British Virgin Islands	18.47394	-64.56842	N/A.	N/A.	MN414621	MN415000	MN415207	MN415591	MN415401	MN415783	MN414796
38	*S. macrolepis* (Central)	MCZA26024B	Guana Island, British Virgin Islands	18.47394	-64.56842	N/A.	N/A.	MN414622	MN415001	MN415208	MN415592	MN415402	MN415784	MN414797
38	*S. macrolepis* (Central)	MCZA26024C	Guana Island, British Virgin Islands	18.47394	-64.56842	N/A.	N/A.	MN414623	MN415002	MN415209	MN415593	MN415403	MN415785	MN414798
38	*S. macrolepis* (Central)	MCZA26024E	Guana Island, British Virgin Islands	18.47394	-64.56842	N/A.	N/A.	MN414624	MN415003	MN415210	MN415594	MN415404	MN415786	MN414799
38	*S. macrolepis* (Central)	MCZA26024F	Guana Island, British Virgin Islands	18.47394	-64.56842	N/A.	N/A.	MN414625	MN415004	MN415211	MN415595	MN415405	MN415787	MN414800
39	S. *macrolepis* (Central)	MCZA26022A	Salt Island, British Virgin Islands	18.37284	-64.52694	N/A.	N/A.	MN414616	MN414995	MN415202	MN415586	MN415396	MN415778	MN414791
39	*S. macrolepis* (Central)	MCZA26022B	Salt Island, British Virgin Islands	18.37284	-64.52694	N/A.	N/A.	MN414617	MN414996	MN415203	MN415587	MN415397	MN415779	MN414792
40	*S. macrolepis* (Central)	MCZA26023B	Beef Island, British Virgin Islands	18.44136	-64.52399	N/A.	N/A.	MN414618	MN414997	MN415204	MN415588	MN415398	MN415780	MN414793
40	*S. macrolepis* (Central)	MCZA26023D	Beef Island, British Virgin Islands	18.44136	-64.52399	N/A.	N/A.	MN414619	MN414998	MN415205	MN415589	MN415399	MN415781	MN414794
40	*S. macrolepis* (Central)	MCZA26023E	Beef Island, British Virgin Islands	18.44136	-64.52399	N/A.	N/A.	MN414620	MN414999	MN415206	MN415590	MN415400	MN415782	MN414795
41	*S. macrolepis* (Central)	MCZA26017A	Cooper Island, British Virgin Islands	18.38168	-64.51076	N/A.	N/A.	MN414608	MN414987	MN415194	MN415578	MN415388	MN415770	MN414783

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
41	*S. macrolepis* (Central)	MCZA26017B	Cooper Island, British Virgin Islands	18.38168	-64.51076	N/A.	N/A.	MN414609	MN414988	MN415195	MN415579	MN415389	MN415771	MN414784
41	*S. macrolepis* (Central)	MCZA26017C	Cooper Island, British Virgin Islands	18.38168	-64.51076	N/A.	N/A.	MN414610	MN414989	MN415196	MN415580	MN415390	MN415772	MN414785
41	*S. macrolepis* (Central)	MCZA26017D	Cooper Island, British Virgin Islands	18.38168	-64.51076	N/A.	N/A.	MN414611	MN414990	MN415197	MN415581	MN415391	MN415773	MN414786
41	*S. macrolepis* (Central)	MCZA26017F	Cooper Island, British Virgin Islands	18.38168	-64.51076	N/A.	N/A.	MN414612	MN414991	MN415198	MN415582	MN415392	MN415774	MN414787
42	*S. macrolepis* (East)	MCZF4336A	Moskito Island, British Virgin Islands	18.51028	-64.39530	N/A.	N/A.	MN414627	MN415007	MN415214	MN415599	MN415409	MN415791	MN414804
42	*S. macrolepis* (East)	MCZF4336B	Moskito Island, British Virgin Islands	18.51028	-64.39530	N/A.	N/A.	MN414628	MN415008	MN415215	MN415600	MN415410	MN415792	MN414805
42	*S. macrolepis* (East)	MCZF4336C	Moskito Island, British Virgin Islands	18.51028	-64.39530	N/A.	N/A.	MN414629	MN415009	MN415216	MN415601	MN415411	MN415793	MN414806
42	*S. macrolepis* (East)	MCZF4336D	Moskito Island, British Virgin Islands	18.51028	-64.39530	N/A.	N/A.	MN414630	MN415010	MN415217	MN415602	MN415412	MN415794	MN414807
42	*S. macrolepis* (East)	MCZF4336F	Moskito Island, British Virgin Islands	18.51028	-64.39530	N/A.	N/A.	MN414631	MN415011	MN415218	MN415603	MN415413	MN415795	MN414808
43	*S. macrolepis* (East)	MCZF4335A	Necker Island, British Virgin Islands	18.52676	-64.35855	N/A.	N/A.	MN414626	N/A.	N/A.	MN415596	MN415406	MN415788	MN414801
43	*S. macrolepis* (East)	MCZF4335B	Necker Island, British Virgin Islands	18.52676	-64.35855	N/A.	N/A.	N/A.	MN415005	MN415212	MN415597	MN415407	MN415789	MN414802
43	*S. macrolepis* (East)	MCZF4335D	Necker Island, British Virgin Islands	18.52676	-64.35855	N/A.	N/A.	N/A.	MN415006	MN415213	MN415598	MN415408	MN415790	MN414803
44	*S. klauberi* (Northwest)	TG2641	Rincón - Playa Domes, Puerto Rico	18.36221	-67.26575	N/A.	N/A.	MN414704	MN415098	MN415307	MN415690	MN415499	MN415886	MN414982
44	*S. klauberi* (Northwest)	TG2642	Rincón - Playa Domes, Puerto Rico	18.36221	-67.26575	N/A.	N/A.	MN414705	MN415099	MN415308	MN415691	MN415500	MN415887	MN414981
44	*S. klauberi* (Northwest)	TG2643	Rincón - Playa Domes, Puerto Rico	18.36221	-67.26575	N/A.	N/A.	MN414706	MN415100	MN415309	MN415692	MN415501	MN415888	MN414980
45	*S. nicholsi*	TG2030	Park Office, Guanica State Forest, Puerto Rico	17.96920	-66.86880	N/A.	N/A.	MN414766	MN415125	MK337590	MK337506	MK337311	MN415903	MN414881
46	*S. nicholsi*	TG211	Bahia De La Ballena, Guanica, Puerto Rico	17.95072	-66.86501	N/A.	N/A.	MK336989	HQ426411	MK337588	MK337504	MK337309	HQ426328	N/A.

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
47	*S. klauberi* (Northwest)	TG875	Rio Abajo, Puerto Rico	18.3331	-66.71695	N/A.	N/A.	MK337002	MN415108	MK337605	MK337511	MK337325	MK337413	MN414868
47	*S. klauberi* (Northwest)	TG877	Rio Abajo, Puerto Rico	18.3331	-66.71695	N/A.	N/A.	MK337003	MN415109	MK337606	MK337512	MK337326	MK337414	MN414869
48	*S. klauberi* (Central)	TG694	143/139 junction, Toro Negro, Puerto Rico	18.1571	-66.6231	N/A.	N/A.	MN414708	MN415105	MN415302	MN415694	MN415493	MN415880	MN414865
49	*S. klauberi* (Central)	TG705	Powerhouse, Toro Negro, Puerto Rico	18.1583	-66.54213	N/A.	N/A.	MK337001	MN415107	MK337604	MK337510	MK337324	MK337412	MN414867
50	*S. townsendi*	TG2019	Caja de Muertos, Puerto Rico	17.88684	-66.52592	N/A.	N/A.	MN414738	MN415152	MK337595	MK337501	MK337316	MN415929	MN414898
50	*S. townsendi*	TG2027	Caja de Muertos, Puerto Rico	17.89233	-66.52359	N/A.	N/A.	MN414740	MN415154	MK337597	MK337502	MK337318	MK337406	MN414900
51	*S. townsendi*	TG2035	Hwy 149 & Hwy1, Puerto Rico	17.99721	-66.49655	N/A.	N/A.	MN414741	MN415155	MN415348	MN415730	MN415539	MN415930	MN414901
52	*S. klauberi* (Central)	TG2761	Ovocovis, Puerto Rico	18.17748	-66.46884	N/A.	N/A.	MN414697	MN415091	MN415299	MN415683	MN415490	MN415877	MN414977
52	*S. klauberi* (Central)	TG2762	Ovocovis, Puerto Rico	18.17748	-66.46884	N/A.	N/A.	MN414698	MN415092	MN415300	MN415684	MN415491	MN415878	MN414978
52	*S. klauberi* (Central)	TG2763	Ovocovis, Puerto Rico	18.17748	-66.46884	N/A.	N/A.	MN414699	MN415093	MN415301	MN415685	MN415492	MN415879	MN414979
53	*S. townsendi*	TG210	Salinas, Puerto Rico	17.97421	-66.30901	N/A.	N/A.	MK336984	HQ426412	MK337593	MK337499	MK337314	HQ426331	MN414896
54	*S. townsendi*	TG2023	Bosque Aguirre, Puerto Rico	17.93815	-66.14429	N/A.	N/A.	MN414739	MN415153	MK337596	N/A.	MK337317	MK337405	MN414899
55	*S. klauberi* (East)	RT14811	near Carite, Puerto Rico	18.1083	-66.0735	N/A.	N/A.	MN414707	MN415101	MN415303	MN415693	MN415494	MN415881	MN414859
56	*S. klauberi* (East)	TG3229	Bosque Estatal De Carite, Puerto Rico	18.12681	-66.0712	N/A.	N/A.	MN414700	MN415094	MN415304	MN415686	MN415495	MN415882	MN414976
56	*S. klauberi* (East)	TG3230	Bosque Estatal De Carite, Puerto Rico	18.12681	-66.0712	N/A.	N/A.	MN414701	MN415095	MK337608	MN415687	MN415496	MN415883	MN414975
56	*S. klauberi* (East)	TG3231	Bosque Estatal De Carite, Puerto Rico	18.12681	-66.0712	N/A.	N/A.	MN414702	MN415096	MN415305	MN415688	MN415497	MN415884	MN414974
56	*S. klauberi* (East)	TG3232	Bosque Estatal De Carite, Puerto Rico	18.12681	-66.0712	N/A.	N/A.	MN414703	MN415097	MN415306	MN415689	MN415498	MN415885	MN414973
57	*S. klauberi* (East)	TG206	near Carite, Puerto Rico	18.0994	-66.0616	N/A.	N/A.	MK337000	MN415102	MK337603	MK337509	MK337323	MK337411	MN414862
58	*S. gaigeae* (West)	RT14812	Patillas, Puerto Rico	18.0762	-66.0561	N/A.	N/A.	MN414692	MN415087	MN415294	MN415678	MN415485	MN415872	MN414855
58	*S. gaigeae* (West)	RT14813	Patillas, Puerto Rico	18.0762	-66.0561	N/A.	N/A.	MN414693	MN415088	MN415295	MN415679	MN415486	MN415873	MN414856

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
59	*S. gaigeae* (East)	TG708	North of Maunabo, Puerto Rico	18.0035	-65.9054	N/A.	N/A.	MN414695	MN415090	MN415297	MN415681	MN415488	MN415875	MN414858
N/A.	*S. altavelensis*	Glor5268	Barahona Province, Dominican Republic	18.34775	-71.14616	N/A.	N/A.	MN414669	MN415053	MN415258	MN415642	N/A.	MN415837	N/A.
N/A.	*S. argus*	TG125	Key West, Florida	24.55700	-81.77994	N/A.	N/A.	N/A.	HQ426407	HQ426578	JX041436	MN415456	HQ426324	MN414849
N/A.	*S. argus*	USNM497938	Playa Giron, Matanzas, Cuba	22.06504	-81.03106	N/A.	N/A.	MN414671	MN415055	MN415260	MN415644	MN415457	MN415839	MN414850
N/A.	*S. ariasae*	TG1242	Isla Beatta, Dominican Republic	17.60893	-71.51868	N/A.	N/A.	MN414672	MN415056	MN415261	MN415645	MN415458	MN415840	MN414851
N/A.	*S. armstrongi*	TG1243	near Las Mercedes, Pedernales, Dominican Republic	18.11335	-71.62098	N/A.	N/A.	MN414673	MN415057	MN415262	MN415646	MN415459	MN415841	MN414852
N/A.	*S. beattyi*	TG682	East end Firestation, St. Croix, U.S. Virgin Islands	17.75789	-64.62226	N/A.	N/A.	MN414674	MN415058	MN415263	MN415647	MN415460	MN415842	MN414853
N/A.	*S. beattyi*	TG683	Mt. Fancy Pond Beach, St. Croix, U.S. Virgin Islands	17.72337	-64.63620	N/A.	N/A.	MN414675	MN415059	MN415264	MN415648	MN415461	MN415843	MN414854
N/A.	*S. callocricus*	Scantle483	near La Boca Del Diablo, Dominican Republic	19.27070	-69.16080	N/A.	N/A.	N/A.	MN415060	MN415265	MN415649	MN415462	MN415844	MN414943
N/A.	*S. d.* cf. *lycauges*	Scantle246	Dajabón Province, Dominican Republic	19.62331	-71.54761	N/A.	N/A.	MN414688	MN415082	MN415289	MN415673	N/A.	MN415867	MN414965
N/A.	*S. d.* cf. *lycauges*	Scantle248	Dajabón Province, Dominican Republic	19.56017	-71.27767	N/A.	N/A.	MN414689	MN415083	MN415290	MN415674	N/A.	MN415868	MN414966
N/A.	*S. clenchi*	Scantle487	near La Boca Del Diablo, Dominican Republic	19.27071	-69.16080	N/A.	N/A.	N/A.	N/A.	MN415266	MN415650	MN415463	N/A.	MN414952
N/A.	*S. clenchi*	Scantle488	near La Boca Del Diablo, Dominican Republic	19.27070	-69.16080	N/A.	N/A.	N/A.	N/A.	MN415267	MN415651	MN415464	MN415845	MN414953
N/A.	*S. cryphius*	cryph2	N/A.	N/A.	N/A.	N/A.	N/A.	MN414676	MN415061	MN415268	MN415652	MN415465	MN415846	MN414963
N/A.	*S. cryphius*	Scantle613	Duvergé Province, Dominican Republic	18.36453	-71.63940	N/A.	N/A.	N/A.	MN415062	MN415269	MN415653	MN415466	MN415847	MN414947

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
N/A.	*S. cryphius*	Scantle614	Duvergé Province, Dominican Republic	18.36453	-71.63940	N/A.	N/A.	N/A.	MN415063	MN415270	MN415654	MN415467	MN415848	MN414948
N/A.	*S. cryphius*	Scantle615	Duvergé Province, Dominican Republic	18.36453	-71.63940	N/A.	N/A.	N/A.	MN415064	MN415271	MN415655	MN415468	MN415849	MN414949
N/A.	*S. darlingtoni darlingtoni*	Scantle261	Valverde Province, Dominican Republic	19.67266	-70.94437	N/A.	N/A.	MN414679	MN415067	MN415274	MN415658	MN415470	MN415852	MN414944
N/A.	*S. darlingtoni darlingtoni*	Scantle262	Valverde Province, Dominican Republic	19.67266	-70.94437	N/A.	N/A.	MN414680	MN415068	MN415275	MN415659	MN415471	MN415853	MN414945
N/A.	*S. darlingtoni darlingtoni*	Scantle263	Valverde Province, Dominican Republic	19.67266	-70.94437	N/A.	N/A.	MN414681	MN415069	MN415276	MN415660	MN415472	MN415854	MN414946
N/A.	*S. darlingtoni darlingtoni*	Scantle268	Valverde Province, Dominican Republic	19.67266	-70.94437	N/A.	N/A.	MN414690	MN415084	MN415291	MN415675	MN415482	MN415869	N/A.
N/A.	*S. darlingtoni bobilini*	Glor5657	Barahona Province, Dominican Republic	18.35758	-70.94547	N/A.	N/A.	MN414677	MN415065	MN415272	MN415656	MN415469	MN415850	MN414967
N/A.	*S. darlingtoni bobilini*	Glor5730	Barahona Province, Dominican Republic	18.35758	-70.94547	N/A.	N/A.	MN414678	MN415066	MN415273	MN415657	N/A.	MN415851	MN414955
N/A.	*S. darlingtoni noblei*	Scantle209	near La Vega and Jarabacoa, Domincan Republic	19.15895	-70.55139	N/A.	N/A.	N/A.	MN415072	MN415279	MN415663	MN415475	MN415857	MN414969
N/A.	*S. d.* cf. *lycauges*	Scantle245	Dajabón Province, Dominican Republic	19.62331	-71.54761	N/A.	N/A.	MN414687	MN415081	MN415288	MN415672	N/A.	MN415866	MN414964
N/A.	*S. difficilis anthracomus*	Glor6109	Pedernales Province, Dominican Republic	17.87014	-71.26475	N/A.	N/A.	MN414670	MN415054	MN415259	MN415643	MN415455	MN415838	MN414935
N/A.	*S. difficilis* cf. *diolenius*	Glor6668	near Las Lagunas de Nisibon, Dominican Republic	18.83542	-68.60960	N/A.	N/A.	N/A.	MN415078	MN415285	MN415669	MN415479	MN415863	N/A.
N/A.	*S. difficilis diolenius*	Glor5231	S of Monte Plata, Dominican Republic	18.78045	-69.77097	N/A.	N/A.	MN414682	MN415073	MN415280	MN415664	N/A.	MN415858	N/A.

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
N/A.	*S. difficilis diolenius*	Glor5807	Azua Province, Dominican Republic	18.36580	-70.92033	N/A.	N/A.	MN414683	MN415074	MN415281	MN415665	N/A.	MN415859	MN414960
N/A.	*S. difficilis diolenius*	Glor5809	Azua Province, Dominican Republic	18.37021	-70.90380	N/A.	N/A.	MN414684	MN415075	MN415282	MN415666	MN415476	MN415860	MN414956
N/A.	*S. difficilis diolenius*	Glor5843	near Las Calderas, Dominican Republic	18.21189	-70.47230	N/A.	N/A.	MN414685	MN415076	MN415283	MN415667	MN415477	MN415861	MN414957
N/A.	*S. difficilis diolenius*	Glor5844	near Las Calderas, Dominican Republic	18.21189	-70.47230	N/A.	N/A.	MN414686	MN415077	MN415284	MN415668	MN415478	MN415862	MN414958
N/A.	*S. difficilis diolenius*	Glor7514	Azua Province, Dominican Republic	18.39349	-70.83845	N/A.	N/A.	N/A.	MN415079	MN415286	MN415670	MN415480	MN415864	MN414961
N/A.	*S. difficilis diolenius*	Glor7515	Azua Province, Dominican Republic	18.39349	-70.83845	N/A.	N/A.	N/A.	MN415080	MN415287	MN415671	MN415481	MN415865	MN414962
N/A.	*S. difficilis diolenius*	Scantle503	near Las Calderas, Dominican Republic	18.21091	-70.46788	N/A.	N/A.	N/A.	MN415085	MN415292	MN415676	MN415483	MN415870	MN414959
N/A.	*S. elegans*	No_ID	N/A.	N/A.	N/A.	N/A.	N/A.	X86048	EF534869	EF534912	JN393942	JF416868	EF534787	JF416901
N/A.	*S. epiuris*	Glor6443	La Altagracia, Dominican Republic	18.71526	-68.90655	N/A.	N/A.	MN414691	MN415086	MN415293	MN415677	MN415484	MN415871	MN414938
N/A.	*S. ladae*	Glor5828	Azua Province, Dominican Republic	18.37021	-70.90380	N/A.	N/A.	MN414709	MN415112	MN415313	MN415695	MN415505	MN415892	MN414939
N/A.	*S. ladae*	Glor5829	Azua Province, Dominican Republic	18.37021	-70.90380	N/A.	N/A.	MN414710	MN415113	MN415314	MN415696	MN415506	MN415893	MN414940
N/A.	*S. ladae*	Glor5850	Azua Province, Dominican Republic	18.37021	-70.90380	N/A.	N/A.	MN414711	MN415114	MN415315	MN415697	MN415507	MN415894	N/A.
N/A.	*S. ladae* (Azua)	Glor7814	Azua Province, Dominican Republic	18.43682	-70.57996	N/A.	N/A.	N/A.	MN415115	MN415316	MN415698	MN415508	MN415895	MN414941
N/A.	*S. leucaster*	Glor5269	Barahona Province, Dominican Republic	18.34775	-71.14616	N/A.	N/A.	MN414712	KP640628	KP640624	MN415699	MN415509	KP640632	MN414870
N/A.	*S. levinsi*	SLD18	Desecheo Island, Puerto Rico	18.38979	-67.47722	N/A.	N/A.	MK336995	MN415117	MK337599	MK337494	MK337319	MK337409	MN414871
N/A.	*S. levinsi*	SLD6	Desecheo Island, Puerto Rico	18.38979	-67.47722	N/A.	N/A.	MK336994	MN415116	MK337598	MK337493	MK337320	MK337408	MN414872
N/A.	*S. monensis*	MVZ235136	Mona Island, Puerto Rico	18.08598	-67.89236	N/A.	N/A.	MK336998	N/A.	MK337601	MK337497	MK337322	N/A.	N/A.
N/A.	*S. monensis*	MVZ235137	Mona Island, Puerto Rico	18.08598	-67.89236	N/A.	N/A.	MK336999	N/A.	MK337602	MK337496	N/A.	N/A.	N/A.

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
N/A.	*S. monensis*	MVZ235138	Mona Island, Puerto Rico	18.08598	-67.89236	N/A.	N/A.	MK336997	N/A.	N/A.	MK337498	N/A.	N/A.	N/A.
N/A.	*S. monensis*	No_ID	Mona Island, Puerto Rico	18.08598	-67.89236	N/A.	N/A.	MK336996	MN415119	MK337600	MK337495	MK337321	MK337410	MN414874
N/A.	*S. omoglaux*	Glor5859	Independencia Province, Dominican Republic	18.39754	-71.72551	N/A.	N/A.	MN414719	MN415128	MN415323	MN415706	MN415516	MN415905	MN414951
N/A.	*S. omoglaux*	Glor5860	Independencia Province, Dominican Republic	18.39754	-71.72551	N/A.	N/A.	MN414720	MN415129	MN415324	MN415707	MN415517	MN415906	MN414950
N/A.	*S. parthenopion*	MCZA26011	Moskito Island, British Virgin Islands	N/A.	N/A.	N/A.	N/A.	MN414721	MN415130	MN415325	MN415708	MN415518	MN415907	MN414884
N/A.	*S. parthenopion*	MCZA26012	Moskito Island, British Virgin Islands	N/A.	N/A.	N/A.	N/A.	MN414722	MN415131	MN415326	MN415709	MN415519	MN415908	MN414885
N/A.	*S. parvus*	SBH267283	Anguilla, a "British Overseas Territory"	18.23453	-63.05938	N/A.	N/A.	MN414723	MN415132	MN415327	MN415710	MN415520	MN415909	MN414886
N/A.	*S. parvus*	SBH267284	Anguilla, a "British Overseas Territory"	18.23453	-63.05938	N/A.	N/A.	MN414724	MN415133	MN415328	MN415711	MN415521	MN415910	N/A.
N/A.	*S. perissodactylius*	Scantle539	Barahona Province, Dominican Republic	18.34480	-71.03295	N/A.	N/A.	N/A.	MN415134	MN415329	MN415712	MN415522	MN415911	MN414936
N/A.	*S. perissodactylius*	Scantle559	Barahona Province, Dominican Republic	18.34522	-71.03208	N/A.	N/A.	N/A.	MN415135	MN415330	MN415713	N/A.	N/A.	MN414937
N/A.	*S. plummeri*	TG1244	N of Cabo Rojo, Domincan Republic	18.00153	-71.64627	N/A.	N/A.	MN414725	N/A.	MN415331	MN415714	MN415523	MN415912	MN414887
N/A.	*S. plummeri*	TG1245	Dominican Republic, Hispaniola	18.00153	-71.64627	N/A.	N/A.	MN414726	MN415136	MN415332	MN415715	MN415524	MN415913	MN414888
N/A.	*S. rhabdotus*	Glor6268	near Iglesia Católica Church, Dominican Republic	18.40069	-71.58076	N/A.	N/A.	N/A.	N/A.	MN415334	MN415717	MN415526	MN415915	MN414970
N/A.	*S. roosevelti*	RT14827	Guanica, Puerto Rico	17.95327	-66.86513	N/A.	N/A.	MN414728	MN415138	MN415335	MN415718	MN415527	MN415916	MN414889
N/A.	*S. roosevelti*	TG2080	Guanica, Puerto Rico	17.95327	-66.86513	N/A.	N/A.	MN414730	MN415140	MN415336	MN415720	MN415528	MN415917	MN414890
N/A.	*S. roosevelti*	TG2084	Guanica, Puerto Rico	17.95327	-66.86513	N/A.	N/A.	MN414731	MN415141	MN415337	MN415721	MN415529	MN415918	MN414891

Map #	Species Tree ID	ID	Locality	Latitude	Longitude	Morphology	SHSUHerp #	16S	ACM4	CMOS	ND2	PTPN12	RAG1	RBMX
N/A.	*S. roosevelti*	TG2086	Caja de Muertos, Puerto Rico	17.88684	-66.52592	N/A.	N/A.	MN414732	MN415142	MN415338	MN415722	MN415530	MN415919	MN414892
N/A.	*S. roosevelti*	TG691	Guanica, Puerto Rico	17.95327	-66.86513	N/A.	N/A.	MN414729	MN415139	MN415339	MN415719	MN415531	MN415920	MN414893
N/A.	*S. samanensis*	Glor4807	near Cueva de Willy, Dominican Republic	19.08047	-69.46439	N/A.	N/A.	MN414733	MN415144	MN415341	MN415724	MN415533	MN415922	MN414971
N/A.	*S. savagei*	No_ID	N/A.	N/A.	N/A.	N/A.	N/A.	N/A.	MN415143	MN415340	MN415723	MN415532	MN415921	MN414954
N/A.	*S. schuberti*	Scantle432	near La Descubierta, Dominican Republic	18.57062	-71.75228	N/A.	N/A.	MN414734	MN415145	MN415342	MN415725	MN415534	MN415923	MN414942
N/A.	*S. schuberti*	Scantle433	near La Descubierta, Dominican Republic	18.57062	-71.75228	N/A.	N/A.	N/A.	MN415146	MN415343	N/A.	MN415535	MN415924	N/A.
N/A.	*S. sp.* (Bani)	Glor7372	Peravia Province, Dominican Republic	18.36133	-70.33228	N/A.	N/A.	N/A.	MN415070	MN415277	MN415661	MN415473	MN415855	MN414968
N/A.	*S. sp.* (Manaclar)	Glor7822	Coffee Plantation S of Manaclar, Dominican Republic	18.40697	-70.37127	N/A.	N/A.	N/A.	MN415071	MN415278	MN415662	MN415474	MN415856	N/A.
N/A.	*S. randi strahmi*	Scantle640	Cayo Pisaje, Dpmincan Republic	17.84228	-71.27914	N/A.	N/A.	N/A.	MN414727	MN415137	MN415333	MN415716	MN415525	MN415914
N/A.	*S. streptophorus*	TG1247	near Pedernales, Dominican Republic	18.02092	-71.73059	N/A.	N/A.	MN414735	MN415147	MN415344	MN415726	MN415536	MN415925	MN414894
N/A.	*S. streptophorus*	TG1248	near Pedernales, Dominican Republic	18.02092	-71.73059	N/A.	N/A.	MN414736	MN415148	MN415345	MN415727	MN415537	MN415926	MN414895
N/A.	*S. thompsoni*	Glor6136	North of Jaragua National Park, Domican Republic	18.00153	-71.64627	N/A.	N/A.	N/A.	MN415149	MN415346	MN415728	MN415538	MN415927	MN414934

APPENDIX B. Morphological characters and scores for species of the *Sphaerodactylus macrolepis* species complex.

1) Maximum SVL.
2) Minimum SVL.
3) Dorsal body scales axilla to groin.
4) Ventral body scales axilla to groin.
5) Midbody scales number.
6) Escutcheon number.
7) Internasal number.
8) Postmental number.
9) Loreal number.
10) Upper labials to mid eye number.
11) Lower labials to mid eye number.
12) Sex dichromatism, (0) absent, (1) present.
13) Dorsal body scales large, (0) small, (1) large.
14) Dorsal body scales, (0) rounded, (1) acute.
15) Dorsal body scales, (0) weakly keeled, (1) strongly keeled.
16) Dorsal body scales, swollen (0), flattened (1).
17) Dorsal body scales, (0) juxtaposed, (1) imbricate.
18) Dorsal scales with knob-like and hair-bearing organs, the latter, each with one hair on the free posterior edge of each scale, (0) absent, (1) present.
19) Dorsal scales with only hair bearing organs on the free posterior edge of each scale, (0) absent, (1) present.
20) Dorsal tail scales, (0) not keeled, (1) keeled.
21) Dorsal tail scales, (0) rounded, (1) acute.
22) Dorsal tail scales, (0) juxtaposed, (1) imbricate.
23) Dorsal tail scales, swollen (0), flattened (1).
24) Snout scales shape, (0) rounded, (1) hexagonal.
25) Snout scales, (0) smooth, (1) keeled.
26) Head dorsal scales, (0) smooth, (1) keeled.
27) Head ventral scales, (0) smooth, (1) keeled.
28) Anterior limb scales, (0) smooth, (1) keeled.
29) Posterior limbs scales, (0) smooth, (1) keeled.
30) Body dorsal scales, (0) smooth, (1) keeled.
31) Body ventral scales, (0) smooth, (1) keeled.
32) Scales on collar, (0) smooth, (1) keeled.
33) Scales on chest, (0) smooth, (1) keeled.
34) Scales on belly, (0) smooth, (1) keeled.
35) Tail dorsal scales, (0) smooth, (1) keeled.
36) Tail ventral scales, (0) smooth, (1) keeled.
37) Wide midventral caudals, (0) absent, (1) present.
38) Ventral tail scales, (0) acute, (1) rounded.
39) Ventral body scales, (0) acute, (1) rounded.
40) Ventral body scales, (0) juxtaposed, (1) imbricate.
41) Scales comparison, (0) dorsal scales smaller than ventral scales, (1) dorsal scales and ventral subequal, (2) dorsal scales larger than ventral scales.
42) Postnasal size, (0) smaller than nasal, (1) subequal or larger than nasal.
43) Scutcheon extended into thighs, (0) absent (1) present.
44) Four toe lamellae number.
45) Male dorsal ground color, (0) tan to brown, (1) yellowish, (2) grayish.
46) Male ventral ground color, (0) white, (1) yellowish to gray, (2) dark.
47) Male pigmentation on chest, (0) absent, (1) present.
48) Male pigmentation on belly, (0) absent, (1) present.

49) Male pigmentation on tail, (0) absent, (1) present.
50) Male scattered scales color, (0) brown, (1) black.
51) Male dorsal pattern, (0) lines continuous or stipple, (1) salt and pepper (2) absent uniform.
52) Male dorsal lines, (0) continuous, (1) stippled.
53) Male head pattern, (0) marked, (1) faint or (2) absent.
54) Male head pattern color, (0) brown, (1) black.
55) Male head pattern, (1) lineate, (2) fragmented, (3) reticulated, (4) no pattern).
56) Male color of head, (0) blue, (1) red to brownish, (2) orange, (3) yellow.
57) Male color of chin and throat, (0) tan, yellowish, (1) white (2) brown.
58) Male reticular pattern on the throat, (0) absent, (1) present.
59) Male color of underside of tail, (0) tan, (1) white.
60) Male head pattern, (0) marked, (1) faint or absent.
61) Male cephalic figure, (0) absent, (1) present.
62) Male with dark parietal spot, (0) absent, (1) present.
63) Male with two light lines extending from the orbits to the scapular patch, (0) absent, (1) present.
64) Male neck rings, (0) absent, (1) present.
65) Male body bands expression, (0) absent, (1) present.
66) Male dark eye line, (0) absent, (1) present.
67) Male light eye line, (0) absent, (1) present.
68) Male scapular patch color, (0) mostly black, (1) black and brown.
69) Male and female scapular patch in contact with nuchal spots, (0) absent, (1) present.
70) Male scapular patch, (0) absent, (1) present.
71) Male scapular patch surrounded by white margin, (0) absent, (1) present.
72) Male scapular patch with a pair of ocelli, (0) absent, (1) present.
73) Male ocelli, (0) enclosed on the patch, (1) near the periphery.
74) Male ocelli color, (0) pale or yellowish, (1) white.
75) Male and female distance between ocelli, (0) well-spaced and discrete, (1) joint or fused.
76) Male anterior dorsolateral lines contacting the scapular patch, (0) present, (1) absent.
77) Male throat pattern, (0) immaculate, (1) marked.
78) Male sacral pattern, (0) absent, (1) present.
79) Male venter pale, (0) absent, (1) present.
80) Female color of head, (0) brown and tan, (1) yellow.
81) Female dorsal color, (0) yellow, (1) tan to brown.
82) Female ground color of chin and throat, (0) tan, (1) white.
83) Female throat pattern, (0) immaculate, (1) marked.
84) Female ventral ground color, (0) tan, (1) white, (2) yellow.
85) Female pigmentation on chest, (0) absent, (1) present.
86) Female pigmentation on belly, (0) absent, (1) present.
87) Female pigmentation on tail, (0) absent, (1) present.
88) Female scattered scales color, (0) brown, (1) black.
89) Female head pattern color, (0) brown, (1) black.
90) Female head pattern, (0) lineate, (1) fragmented, (2) reticulate or (3) no pattern).
91) Female with uniform colored head, (0) absent, (1) present.
92) Female color of head and tail, (0) yellowish to light brown, (1) dark brown.
93) Female color of chin and throat, (0) white, (1) yellowish to gray, (2) dark.
94) Female pattern on the throat, (0) absent, (1) present.
95) Female color of underside of tail, (0) tan, (1) white.
96) Female with boldly marked head, (0) absent, (1) present.
97) Female with dark parietal spot, (0) absent, (1) present.
98) Female parietal spot color, (0) black, (1) brown.
99) Female with two white lines extending from the orbits to the scapular patch (0) absent, (1) present.
100) Female dark eye line in the ventral ocular scales, (0) absent, (1) present.

101) Female light eye line, (0) absent, (1) present.
102) Female dorsal lines, (0) absent, (1) present.
103) Female dorsal lines, (0) continuous, (1) stippled.
104) Female with medial lines, (0) fused to form a blotch, (1) separated lines.
105) Female canthal line from snout, passing the eye and onto the side of the neck, (0) absent, (1) present.
106) Female canthal line from snout, and a pair of postorbital lines that meet at the nuchal spot and surround a dark parietal spot, (0) absent, (1) present.
107) Female scapular patch, (0) absent, (1) present.
108) Female scapular patch, (0) mostly black, (1) black and brown.
109) Female scapular patch with a pair of ocelli, (0) absent, (1) present.
110) Female ocelli, (0) enclosed on the patch or (1) near the periphery.
111) Female ocelli color, (0) pale or yellowish (1) white.
112) Female anterior dorsolateral lines contacting the scapular patch, (0) absent, (1) present.
113) Female venter pale, (0) absent, (1) present.
114) Female underside of tail, (0) white, (1) tan to yellow or straw.
115) Head shape, (0) short and blunt (1) long and narrow.

Sphaerodactylus parvus [26.39][18.42][23-29]?[44-54]42[0-3][4,5]330111111111111111111[0,1]??[0,1]10?1111008[0,1]111101-[1,2]02,430[0,1]0111100111011110111011[0,1]010111003001101110111--00111000110

Sphaerodactylus macrolepis [27.54][19.59][23][25][38]58[1][2][5, 6]33101111001111[0,1]111111010010111120161111102-0[0,1]3001000[0,1][0,1]001010[0,1]0[0,1]100010101[0,1]111110[0,1]100111111011010111111000100

Sphaerodactylus inigoi (Vieques) [30][17.41][15-18][16][33-41] 55[1,2][2][4,5]3311111111111[0,1]1111110100101111201910[0,1][0,1]101-2-410011010001000101[0,1]000001011111110000011111111101011101101100

Sphaerodactylus inigoi (West Culebra) [26.88][17.03][16-18][20-24][37]57[1,2][2,3][4,5]3311111111111[0,1]111111010010111120191111101-2-4[2,3][1,2]00101000100010110000010111111100000011111[0,1]11101011101101100

Sphaerodactylus g. grandisquamis [34.08][17.06][17-23][24-32][36-46] 80[1,2][2][5,6]3311111111111011011101001011112017[0,1]1[0,1][0,1][0,1]00110110101110001100111010010101102[0,1]11000001011101110[0,1]111101111101

Sphaerodactylus g. guarionex [34.2][17.24][14][20][36-49] 67[1][2][6]3311111111111011111101001011112019011110011[0,1]1201011100011001010100101010[0,1]0000000001[0,1]011011100111101011101

Sphaerodactylus g. ateles [33][17.05][18-22]24-29[36-42]78[1,2][2][5,6]3311111111111111111101001011112019-12210[0,1]100120410[0,1]01111001100[0,1] [0,1]11100001010101110000011011011101111101011121

Sphaerodactylus g. mimetes [33.19][17.15][17][17][31-40]76[1,2][2][5]3311111111111111111101001011112019[0,1][0,1][0,1][0,1]101-00[1,2]0010011[0,1]001100[0,1]01[0,1]1001010[0,1]1120110000001111[0,1][0,1]110[0,1]111101[0,1]11121

Sphaerodactylus g. spanius [35.68][14.6][19][20][41-47] 95[1,2][2][5]331111111111111111110100101111201101[0,1]1110010012010011000110010110/100101[0,1]101011100000[0,1]10110111001111011[0,1]1101

Sphaerodactylus g. stibarus [29.44][25.07][20][21][36-41] 65[1,2][2][5]331111111111101111110100101111201821111[0,1]01101100011110011001110101100010101110000011011[0,1]11101011111011100