



Article

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Two new species of geckos from Honduras and resurrection of *Sphaerodactylus continentalis* Werner from the synonymy of *Sphaerodactylus millepunctatus* Hallowell (Reptilia, Squamata, Gekkonoidea, Sphaerodactylidae)

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Abstract

We performed a morphological and molecular study on various Honduran populations of the *Sphaerodactylus millepunctatus* complex. As a result, we resurrect *S. continentalis* from the synonymy of *S. millepunctatus* and describe two new species from the Islas de la Bahía. Our results also suggest the possibility that other cryptic species might occur in our concept of *S. continentalis*.

Key words: *Sphaerodactylus millepunctatus* complex, Honduras, *Sphaerodactylus leonardovaldesi* sp. nov., *Sphaerodactylus guanajae* sp. nov., morphology, mtDNA, 12S, cytochrome b

Introduction

Harris & Kluge (1984) provided an excellent review of the geckos of the genus *Sphaerodactylus* of Middle America. In that review, those authors considered *S. millepunctatus* Hallowell to range from Oaxaca, Mexico, to northern Costa Rica, with populations also occurring on Cozumel Island, Quintana Roo, Mexico, the Honduran Bay Islands (Islas de la Bahía), and Great Corn Island, Nicaragua. Harris & Kluge (1984: 23) noted “Mexican specimens of *S. millepunctatus* were found to have substantially higher dorsal scale counts than those from Costa Rica.” Harris & Kluge (1984) attributed those dorsal scale size differences to a clinal increase in dorsal scale sizes from north (in Mexico) to south (in Costa Rica). However, Harris & Kluge (1984) lacked specimens of *S. millepunctatus* from between Barranco, Colón, Honduras, and Musawas, Atlántico Norte, Nicaragua. Although a distance of only ca. 200 km separates those two localities, that hiatus represents the Mosquitia lowlands of northeastern Honduras and adjacent northeastern Nicaragua. The Mosquitia region of northeastern Honduras contains 17 species of snakes (McCranie 2011a, 2011b; Cadle 2012) not known elsewhere in Honduras, with all but three of those species ranging southward to at least northern Costa Rica. Also, six species of lizards and turtles are also known only in Honduras from the Mosquitia lowlands (McCranie unpub. data), all of which also range southward to at least northern Costa Rica. While examining specimens of *S. millepunctatus* from throughout Honduras, JRM independently noted that specimens of that nominal form from the Mosquitia lowlands had larger dorsal scales similar to the counts for those specimens from Costa Rica provided by Harris & Kluge (1984).

Harris & Kluge (1984) also noted that specimens they assigned to *Sphaerodactylus millepunctatus* from Roatán Island in the Honduran Bay Islands differed from all other *S. millepunctatus* they examined in having indefinite dark speckling and short pale dorsolateral lines that pass above the pelvic area and then curve slightly inward on the base of the tail. All subsequently collected Roatán specimens of the *S. millepunctatus* complex that were seen in life had a muted dorsal pattern of dark flecks and usually indistinct dark lines on the head and a short pale pelvic line. That pattern is also visible in the majority of the Roatán preserved specimens examined for this

study. Recently collected specimens of the *S. millepunctatus* complex from Isla de Guanaja, Islas de la Bahía, Honduras, also have a similar dorsal pattern to those from Roatán, with the exception that the pelvic lines are more distinct and connect with each other dorsally across the base of the tail. The short pale line above the pelvis is not present in preservation in any other Honduran specimens examined, nor is it seen in photographs in life of any specimens from the Honduran mainland and Utila Island in the Honduran Bay Islands, nor the few published photographs of Guatemalan and Mexican specimens (Campbell 1998; Savage 2002; Taylor 1956, as *S. lineolatus*). Close examination of the Roatán specimens of this complex also found that they average fewer scales around the midbody or have fewer dorsal scales than those from the remaining populations in Honduras. Also, close examination of the Guanaja specimens revealed that they have fewer subdigital lamellae on the fourth toes than do all other Honduran populations. In addition, the Guanaja specimens have fewer subdigital lamellae on the fourth fingers than do those from Roatán.

Methods

The description of the holotype of the two new species generally follows the format for the description of the neotype of *Sphaerodactylus millepunctatus* in Harris & Kluge (1984). After it was discovered that there were apparent differences in subdigital lamellae numbers on the fourth toes between the Roatán and Guanaja specimens, those counts were repeated in those two populations. Number of subdigital lamellae on the fourth digit of the forelimbs was then also counted in the Roatán and Guanaja specimens. Color codes and names used herein follow those of Smithe (1975–1981). Museum acronyms follow those of Leviton *et al.* (1985). For coordinates we use decimal degrees under the WGS84 system.

Recently, JRM collected *Sphaerodactylus millepunctatus* (sensu lato) tissues representing Honduran populations from the Mosquitia lowlands, those from west of the Mosquitia, and from Islas de Roatán and Guanaja. DNA sequence analyses of those samples, by SBH, support the morphological evidence in showing substantial genetic divergence (Fig. 1) and together indicate that these four populations are best treated as distinct evolutionary species.

The molecular data set comprised 12 individuals (see accounts for the two new species and Appendix 1) and 1400 total aligned nucleotide sites from two mitochondrial genes: 12S ribosomal RNA (rRNA) and cytochrome b (cyt b). Methods used for the collection of the new DNA sequences are detailed elsewhere (Heinicke *et al.* 2007; Hedges *et al.* 2008; Hedges & Conn 2012). Localities, Genbank accession numbers, and museum numbers for all sequences used are in the accounts for the two new species and Appendix 1. For outgroup we choose a morphologically distinct species, *S. durni*, also occurring in Honduras and which is a member of the same species group as *S. millepunctatus* in a molecular phylogeny (SBH, unpublished). Alignments were performed with MUSCLE in MEGA 5.0 (Tamura *et al.* 2011). A maximum likelihood (ML) analysis was performed using MEGA 5.0 (Tamura *et al.* 2011), unpartitioned, using the best-fitting evolutionary model under the Bayesian Information Criterion, the GTR + I + Γ option (general time reversible + invariant sites + gamma distribution of changes). Gaps were treated as missing data. All parameters for the ML analyses were estimated by the program during the run. Branch support in the trees was provided by bootstrap analysis (2,000 replicates). A Bayesian phylogenetic analysis using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) also was performed, using the GTR + I + Γ model. The Bayesian analysis was set to two parallel runs for five million generations, sampled every 100 generations, each run employed three heated and one cold chain, with a temperature parameter of 0.20. The first 10% of samples were discarded as burn-in. Convergence was assessed by the standard deviation of split frequencies (< 0.01 in all cases).

Systematics

Sphaerodactylus leonardovaldesi sp. nov.

(Fig. 2)

Sphaerodactylus continentalis—Meyer & Wilson, 1973:12 (part).

Sphaerodactylus continentalis—Wilson & Hahn, 1973:105 (part).

Sphaerodactylus millepunctatus—Harris & Kluge, 1984:17 (part).
Sphaerodactylus millepunctatus—Grismer *et al.*, 2001:135.
Sphaerodactylus millepunctatus—McCranie *et al.*, 2005:80 (part).
Sphaerodactylus millepunctatus—McCranie *et al.*, 2006:110 (part).

Holotype. FMNH 282785, an adult male from Palmetto Bay, 16.359033°, -86.486717°, Isla de Roatán, Islas de la Bahía, Honduras, near sea level, collected 22 May 2011 by James R. McCranie and Leonardo Valdés Orellana.

Paratypes (13). FMNH 282786–88, USNM 579988–89, same locality as holotype; FMNH 282791 (genetic sample 3, JX073109, JX073120), USNM 579990–93, from Camp Bay, 16.429467°, -86.286300°; FMNH 282789 (genetic sample 1, JX073110, JX073121), 282790 (genetic sample 2, JX073111, JX073122), from 1 km E of Pollytilly Bight, 16.406300°, -86.388083°; all adults from Isla de Roatán and collected 21–22 May 2011 by James R. McCranie and Leonardo Valdés Orellana or 18–19 November 2011 by McCranie. USNM 579987, juvenile from Palmetto Bay, Isla de Roatán, collected 18 November 2011 by McCranie. Appendices II and III list other specimens for this new species.

Geographic distribution. *Sphaerodactylus leonardovaldesi* is known to occur at low elevations on Isla de Roatán and several satellite islands in the Islas de la Bahía, Honduras (Fig. 3).

Diagnosis. *Sphaerodactylus leonardovaldesi* can be distinguished from *S. millepunctatus* (*sensu stricto*), the species it was previously identified as, and from *S. continentalis*, herein removed from the synonymy of *S. millepunctatus*, in usually having a short pale longitudinal line located above each pelvic area that frequently curves slightly inward posteriorly, in having scattered dark dorsal spots that occupy single scales, and in having indistinct lines on the head and body (versus short pelvic lines absent, dark dorsal spots on body occupying more than one scale, and dark lines distinct on posterior end of head and anterior part of body in *S. millepunctatus* and *S. continentalis*). *Sphaerodactylus leonardovaldesi* also differs from *S. millepunctatus* in having smaller and more numerous dorsal scales (58–66, $x = 61.7 \pm 2.7$ dorsal scales between levels of axilla and groin in 13 *S. leonardovaldesi* versus 42–57, $x = 51.7 \pm 5.0$ in 15 *S. millepunctatus*) and also differs from *S. continentalis* in having fewer scales around the midbody (48–67, $x = 59.8 \pm 6.0$ in 13 *S. leonardovaldesi* versus 64–80, $x = 71.9 \pm 4.8$ in 20 *S. continentalis*). *Sphaerodactylus leonardovaldesi* occurs sympatrically with one other species of *Sphaerodactylus*, *S. rosaurae* Parker of the *S. copei* species group (Schwartz and Garrido 1981), but is most easily distinguished from that species in having all dorsal body scales of a similar size (versus middorsal row of granular scales that are sharply and distinctly differentiated from the much larger surrounding dorsal scales in *S. rosaurae*). *Sphaerodactylus leonardovaldesi* differs from the second new species described herein in having more subdigital lamellae under the fourth toes and fourth fingers (9–12, $x = 10.2 \pm 0.8$ and 8–10, $x = 9.0 \pm 0.4$ on 26 sides, respectively, and 36–42, $x = 38.5 \pm 1.6$ fourth digits combined versus 8–9, $x = 8.6 \pm 0.5$ and 7–8, $x = 7.6 \pm 0.5$ on 12 sides, respectively, and 31–34, $x = 32.3 \pm 1.5$ fourth digits combined in the second new species) and in not having the pelvic stripes connected with its counterpart on the other side (versus pelvic lines usually connected [narrowly divided in one of seven] in the second new species). *Sphaerodactylus leonardovaldesi* also differs from *S. millepunctatus*, *S. continentalis*, and the second new species described herein, in an amount of cytochrome b DNA sequence divergence (7.7–10.1 %; Fig. 1) comparable to that seen among other species of lizards (Johns & Avise 1998; Hedges & Conn 2012).

Description of holotype. A moderate-sized *Sphaerodactylus* with a snout-vent length (SVL) of 24.5 mm; snout-ear length (head length) 5.5 mm; head width 4.2 mm; head depth 2.0 mm; snout length 2.3 mm, snout length/eye-ear length 1.21; tail length 22.4 mm, tail length/SVL 0.91.

Rostral with long median cleft and short posterior notch occupied by a single small scale; supranasals two, anterior one largest, rounded, dorsally confined, in contact with nasal opening, separated from first supralabial by posterior supranasal and two small postnasals, anterior supranasal contacting rostral above nasal opening; internasals three, occupying space wider than greatest width of anterior supranasal; snout scales swollen, keeled, juxtaposed, 14 along midline from orbits to rostral, five per interorbital width (IOW); scales between eyes narrower than snout scales; parietal surfaces and nape covered with swollen keeled granules, about 6–7 per IOW; superciliary spine short, located at level anterior to mideye; fourth supralabial lies below anterior half of eye, shorter fifth supralabial lies below center and posterior portion of eye; third infralabial lies below anterior half of eye, fourth infralabial lies below posterior half of eye, first infralabial largest, its length equals nearly 2.0 times IOW; mental large, about as long as wide, with oblique sutures between infralabials; postmentals two, polygonal, not elongated; gular scales smooth, granular, juxtaposed, five per IOW.

Dorsal scales of trunk oval, flattened, keeled, imbricate, about four per IOW, 60 along midline between levels of axilla and groin; lateral scales similar to dorsals; ventrals smooth, flat, about two per IOW, 33 along midline between levels of axilla and groin; scales around midbody 64; escutcheon somewhat bell-shaped, with lateral extension 14 scales wide on subfemoral surface, escutcheon also extending slightly onto groin region; supracaudal scales rhomboid, flat, imbricate, keeled at base of tail to about point reached by extended hind limb, smooth distal to that point, about two per IOW; subcaudal scales smooth, larger than supracaudals, scales of median series largest, slightly widened, enlarged median series extending about two-thirds length of tail; pair of distinctly swollen granules at each corner of vent; subdigital lamellae smooth, 10 present on each fourth toe, 9 present on each fourth finger, 38 total subdigital lamellae on combined fourth digits.

Color in life: dorsal ground color of body Mikado Brown (121C) with Vandyke Brown (121) small spots and scattered flecking; dorsal surface of head Ground Cinnamon (239) with Vandyke Brown stripes and reticulations; dorsal surfaces of limbs Mikado Brown with golden brown spot on knee and band on shank; dorsal surface of tail brownish yellow with Vandyke Brown mottling, Vandyke Brown band presently distally on tail followed by pinkish brown tail tip; venter of head and body cream with scattered brown flecking; subcaudal surface pink; iris yellow above and below pupil, golden brown anterior and posterior to pupil.

Color in alcohol: dorsal surfaces brown with scattered darker brown scales on body, giving impression of scattered dark flecks; snout medium brown with brown postnasal stripe extending nearly to orbit; supraocular scales dark brown, top of head posterior to that point medium brown with indistinct reticulated pattern of brown lines; medium brown postocular stripe bordered above and below by brown line extending posteriorly and upward on nape region to connect with stripe on other side to form inverted V-shape; dorsal surfaces of limbs and tail similar to that of dorsal surface of body, but with pale brown dorsal spot on knee and pale brown dorsal band on shank; supralabials pale brown with dark brown flecking; mental and infralabials pale brown with dark brown, interrupted, longitudinal lines on mental and infralabials 1–2 and incomplete vertical lines on infralabials 3–4; gular region cream with brown flecking; belly cream with brown flecking on scale edges; subcaudal surface cream with brown flecking on scale edges, forming incomplete lineate pattern; distinct ventrolateral cream stripe extending from base of tail onto posterior surface of thighs; pale pelvic line not evident.

Variation. The type series of the 13 adults have a SVL of 22.8–26.8 (25.3 ± 1.1) mm, 58–66 (61.7 ± 2.7) dorsal scales, 29–34 (31.8 ± 1.6 , $n = 12$) ventral scales, 48–67 (59.8 ± 6.0) scales around midbody, 10–14 (11.5 ± 1.3) snout scales, 9–12 (10.2 ± 0.8) subdigital lamellae on the fourth toe, 8–10 (9.0 ± 0.4) subdigital lamellae on the fourth finger, 36–42 (38.5 ± 1.6) combined subdigital lamellae on the fourth digits, and 11 of the 13 have the pale lines above the pelvic region visible in preservative. None of the paratypes have the V-shaped pattern on the nape region as seen in the holotype, however all have the dorsal dark spots confined to one scale and the dark lines on the dorsal and lateral surfaces of the head are indistinct or absent.

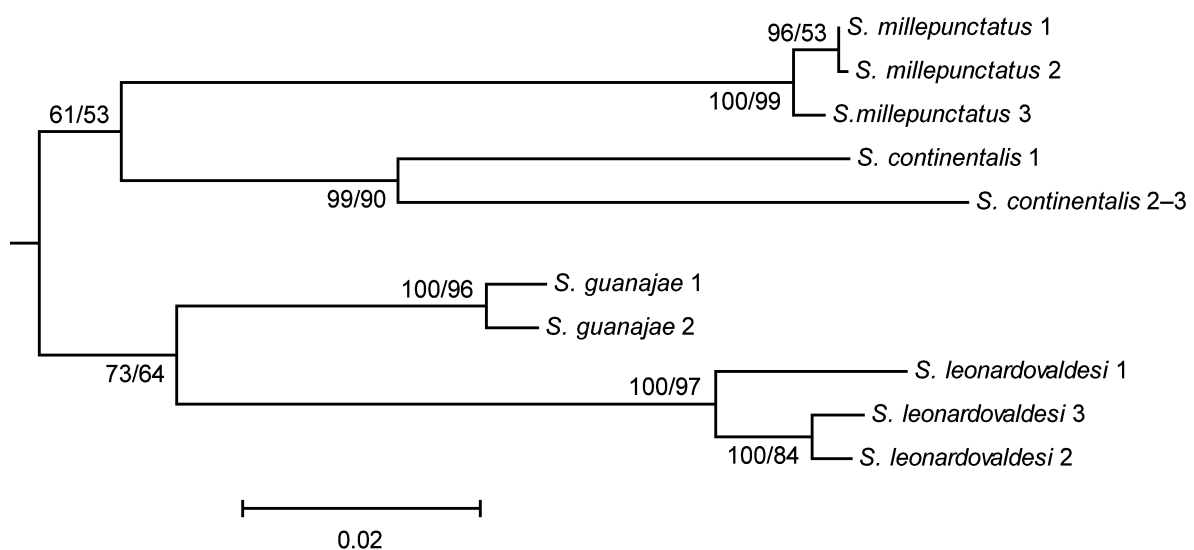


FIGURE 1. Phylogenetic tree of four species of Middle American *Sphaerodactylus* from a maximum-likelihood analysis of DNA sequences of two mitochondrial genes (12S rRNA and cytochrome b). A scale bar is indicated below. The numbers at nodes are bootstrap (left) and Bayesian (right) support values. The tree is rooted with the Middle American species *S. dunni* (not shown, for better visualization of ingroup).



FIGURE 2. Adult male (USNM 570186) of *Sphaerodactylus leonardovaldesi* sp. nov. from West End Point, Isla de Roatán (SVL 29.1 mm). Photograph by J.R. McCranie.

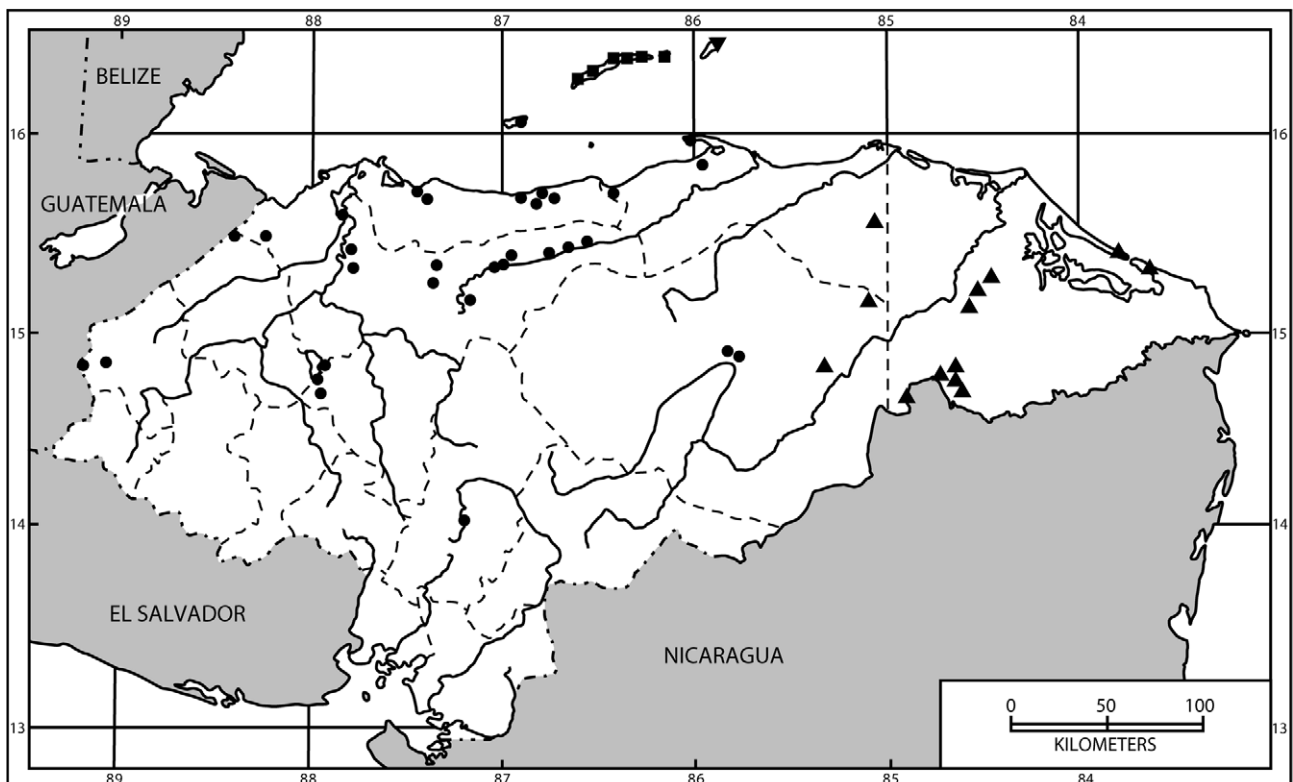


FIGURE 3. Map of Honduras showing localities for specimens examined of *Sphaerodactylus continentalis* (circles), *S. guanajae* (inverted triangles), *S. leonardovaldesi* (squares), and *S. millepunctatus* (triangles).

Color in life of an adult female paratype (FMNH 282791): dorsal ground color Flesh Color (5) with indistinct, scattered brown flecking; top of head same as that for dorsum, except with one poorly indicated, interrupted pale brown dorsolateral stripe; posterior nape region cream; short cream pelvic line, line curving slightly inward distally, line bordered above by brown posteriorly and above inward curved portion; dorsal brown mark present between inward curved portions of pale lines; dorsal surfaces of limbs Flesh Color with poorly-indicated pinkish brown spot on knee and band on shank; dorsal surface of tail pinkish brown with small pink spots; subcaudal surface pink; iris yellowish pink above and below pupil, pinkish brown anterior and posterior to pupil. Color in life of a juvenile paratype (USNM 579987): dorsal surface of tail Sepia (119) with scattered pale brown dorsal flecks, Salmon Color (106) ring also present near tip; subcaudal surface otherwise reddish brown.

Habitat. Active individuals were in leaf litter during the morning and afternoon and the species was also found under leaf litter, palm fronds, rocks, brush piles, and other debris on the ground. One was also seen at night on the wall of a building feeding on insects attracted to an electric light.

Etymology. The specific name *leonardovaldesi* is a patronym honoring Leonardo Valdés Orellana, an enthusiastic Honduran biologist who was instrumental in collecting part of the type series of this new species as well as other populations of the *Sphaerodactylus millepunctatus* complex over the last three years.

***Sphaerodactylus guanajae* sp. nov.**

(Fig. 4)

Sphaerodactylus continentalis—Meyer & Wilson, 1973:12 (part).

Sphaerodactylus continentalis—Wilson & Hahn, 1973:105 (part).

Sphaerodactylus millepunctatus—Harris & Kluge, 1984:17 (part).

Sphaerodactylus millepunctatus—McCranie *et al.*, 2005:80 (part).

Sphaerodactylus millepunctatus—McCranie *et al.*, 2006:110 (part).

Holotype. USNM 580000, an adult male from East End, 16.486°, -85.832°, Isla de Guanaja, Islas de la Bahía, Honduras, near sea level, collected 16 November 2011 by James R. McCranie.

Paratypes (6). USNM 579994–95, 579996 (genetic sample 1, JX073112, JX073123), 579997 (genetic sample 2, JX073113, JX073124), 579998–99, same data as holotype, except 16–17 November 2011; all adult females except USNM 579997 is a juvenile. Appendix II lists additional specimens of this new species.

Geographic distribution. *Sphaerodactylus guanajae* is known to occur at low elevations on Isla de Guanaja in the Islas de la Bahía, Honduras. The species is known only from three nearby localities on the northeastern end of the island (Fig. 3).

Diagnosis. *Sphaerodactylus guanajae* can be distinguished from *S. millepunctatus* (*sensu stricto*), the species it was previously identified as, and from *S. continentalis*, herein removed from the synonymy of *S. millepunctatus*, in having a short pale longitudinal line located above each pelvic area that curves inward posteriorly to almost always connect with its counterpart on the other side, dark dorsal spots on the body occupying single scales, and dark lines on the head and body indistinct (versus short pale pelvic line absent, dark dorsal spots on body occupying more than one scale, and dark lines usually distinct on posterior portion of head and anterior portion of body in *S. millepunctatus* and *S. continentalis*). *Sphaerodactylus guanajae* also differs from *S. continentalis* and *S. millepunctatus* in having fewer subdigital lamellae on the fourth digit of the hind limb (8–9, $x = 8.6 \pm 0.5$ on 12 sides in *S. guanajae* versus 9–12, $x = 10.0 \pm 0.8$ on 40 sides in *S. continentalis* and 9–12, $x = 9.7 \pm 0.8$ on 30 sides in *S. millepunctatus*). *Sphaerodactylus guanajae* differs from *S. leonardovaldesi* in having fewer subdigital lamellae under the fourth toes and fourth fingers (8–9, $x = 8.6 \pm 0.5$ and 7–8, $x = 7.6 \pm 0.5$ on 12 sides, respectively, and 31–34, $x = 32.3 \pm 1.5$ combined subdigital lamellae on fourth digits in *S. guanajae* versus 9–12, $x = 10.2 \pm 0.8$ and 8–10, $x = 9.0 \pm 0.4$ on 26 sides, respectively, and 36–42, $x = 38.5 \pm 1.6$ combined subdigital lamellae on fourth digits in *S. leonardovaldesi*) and in usually having the pelvic lines dorsally crossing the base of the tail to connect (in 5 of the 6 adults [narrowly separated in one adult] and in the juvenile) with their counterparts on the other side (versus pelvic stripes widely separated from their counterparts on other side in *S. leonardovaldesi*). *Sphaerodactylus guanajae* occurs sympatrically with one other species of *Sphaerodactylus*, *S. rosaurae* Parker, but is most easily distinguished from that species in having all dorsal body scales of a similar size (versus middorsal row of granular scales that are sharply and distinctly differentiated from the much larger surrounding dorsal scales in *S. rosaurae*). *Sphaerodactylus guanajae* also differs from *S. continentalis*, *S. leonardovaldesi*, and *S. millepunctatus* in an amount of cytochrome b DNA sequence divergence (6.8–10.1 %; Fig. 1) comparable to that seen among other species of lizards (Johns & Avise 1998; Hedges & Conn 2012).

Description of holotype. A moderate-sized *Sphaerodactylus* with a snout-vent length (SVL) of 26.2 mm; snout-ear length (head length) 5.9 mm; head width 2.5 mm; head depth 2.2 mm; snout length 3.0 mm, snout length/eye-ear length 1.30; tail length 23.2 mm (partially regenerated), tail length/SVL 0.89.

Rostral with long median cleft and short posterior notch occupied by a single small scale; supranasals two, anterior one largest, rounded, dorsally confined, in contact with nasal opening, separated from first supralabial by posterior supranasal and two small postnasals, anterior supranasal contacting rostral above nasal opening; internasals three, occupying space wider than greatest width of anterior supranasal; snout scales swollen, keeled, juxtaposed, 9 along midline from orbits to rostral, four per interorbital width (IOW); scales between eyes narrower than snout scales; parietal surfaces and nape covered with swollen keeled granules, about 5–6 per IOW;

superciliary spine short, located at level anterior to mideye; fourth supralabial lies below anterior half of eye, shorter fifth supralabial lies below center and posterior portion of eye; third infralabial lies below anterior half of eye, fourth infralabial lies below posterior half of eye, first infralabial largest, its length equals nearly 2.0 times IOW; mental large, about as long as wide, with oblique sutures between infralabials; postmentals two, polygonal, not elongated; gular scales smooth, granular, juxtaposed, five per IOW.



FIGURE 4. Adult male holotype of *Sphaerodactylus guanajae* sp. nov. (SVL 26.2 mm). Photograph by J.R. McCranie.

Dorsal scales of trunk oval, flattened, keeled, imbricate, about four per IOW, 57 along midline between levels of axilla and groin; lateral scales similar to dorsals; ventrals smooth, flat, about two per IOW, 33 along midline between levels of axilla and groin; scales around midbody 63; escutcheon somewhat bell-shaped, with lateral extension ca. 10 scales wide on subfemoral surface, escutcheon also extending slightly onto groin region; supracaudal scales rhomboid, flat, imbricate, keeled at base of tail to about point reached by extended hind limb, smooth distal to that point, about two per IOW; subcaudal scales smooth, larger than supracaudals, scales of median series largest, slightly widened, enlarged median series extending about two-thirds length of tail; pair of distinctly swollen granules at each corner of vent; subdigital lamellae smooth, 8–9 present on fourth toe, 7–7 present on fourth finger, 31 combined subdigital lamellae on fourth digits.

Color in life: dorsal surface of body Brussels Brown (121B) with pale brown mottling and scattered Sepia (119) scales; dirty white pelvic stripe extending posteriorly from level above groin to base of tail where it crosses dorsal surface of tail to connect with similarly colored stripe on other side of tail and body; dorsal and lateral surfaces of head Sayal Brown (223C) with scattered Sepia scales forming indication of lines; dorsal surfaces of limbs Brussels Brown with pale brown bands on lower parts of limbs and on all digits; dorsal surface of unregenerated portion of tail Sayal Brown with scattered Sepia scales and pale brown indications of cross lines; dorsal surface of regenerated portion of tail Cinnamon (39); chin pale brown; throat cream; belly pale brown with dark brown flecking; subcaudal surface of original portion of tail Flesh Ocher (132D).

Color in alcohol: dorsal surface of body brown without distinctive markings; dorsal surface of head pale brown with faint dark brown line on snout and posterior to eye, latter line extending to about shoulder region; supraocular scales dark brown; dorsal surfaces of limbs and tail similar to that of dorsal surface of body, but with pale brown dorsal spot on knee and pale brown dorsal band on shank; supralabials pale brown with dark brown flecking; ventral surface of head cream with brown flecking; belly pale brown with brown flecking on scale edges; subcaudal surface cream with brown flecking on scale edges, forming incomplete lineate pattern; distinct ventrolateral cream stripe extending from base of tail onto posterior surface of thighs; pelvic line distinct, pale brown, crossing dorsally on base of tail to connect with counterpart on other side.

Variation. The six adults in the type series have a SVL of 24.4–26.2 (25.6 ± 0.7) mm, 57–66 (61.3 ± 3.3) dorsal scales, 32–35 (33.5 ± 1.2) ventral scales, 60–70 (64.4 ± 3.8 , $n = 5$) scales around midbody, 9–13 (11.0 ± 1.4) snout scales, 8–9 (8.6 ± 0.5) subdigital lamellae on the fourth toe, 7–8 (7.6 ± 0.5) subdigital lamellae on the fourth finger, 31–34 (32.3 ± 1.5) combined subdigital lamellae on fourth digits, and all have the short pale lines above the pelvic region visible in preservative, with 5 of the 6 having those lines connected with their counterparts on the other side (the single exception [USNM 579996] has those two pale lines only narrowly interrupted medially by brown). Otherwise, all six adults are similar to the holotype in coloration. The juvenile has a brown lined pattern on the head and much of the body. One adult paratype (USNM 579994) was similar in color in life to that of the holotype, except that the subcaudal surface was yellowish brown.

Habitat. The type series was found only in association with Sea Grape (*Cocoloba uvifera*) leaf litter. Two were active during the morning on top of the leaves and the others were found by raking through the leaf litter. Efforts to find specimens under other types of ground debris on Guanaja at that time were unsuccessful.

Etymology. The specific name *guanajae* is formed from Guanaja and the Latin suffix *-ae* (used herein as a derivation), and alludes to this species occurring on Isla de Guanaja. The name is a feminine genitive singular noun.

Sphaerodactylus continentalis Werner

(Fig. 5)

Sphaerodactylus argus var. *continentalis* Werner 1896: 345. Holotype ZIN 8880 (see Harris & Kluge 1984: 25). Type locality “Honduras” (see Discussion).

Geographic distribution. Low and moderate elevations from the Isthmus of Tehuantepec in northern Oaxaca, Mexico, to about the Catacamas, Olancho, region of east-central Honduras. *Sphaerodactylus continentalis* also occurs on Utila Island in the Honduran Bay Islands and possibly on Cozumel Island, Quintana Roo, Mexico (see Discussion; see Fig. 3 for Honduran localities).

Diagnosis. *Sphaerodactylus continentalis* can be distinguished from *S. millepunctatus* (sensu stricto) in having smaller and more numerous dorsal scales (59–70, $x = 63.5 \pm 3.4$ in 20 *S. continentalis* versus 42–57, $x = 51.7 \pm 5.0$ in 15 *S. millepunctatus* examined for this study; but see Discussion and Appendix I). *Sphaerodactylus continentalis* differs from both *S. guanajae* and *S. leonardovaldesi* in lacking a short thin pale yellow line above each pelvis, in usually having distinct dorsal spots that are larger than one scale, and in usually having distinct dark stripes on the posterior end of the head and anterior portion of the body (versus short pale pelvic lines almost always present, only scattered dark spots on body that are confined to one scale, and indistinct dark stripes on head and body in those two species). *Sphaerodactylus continentalis* also differs from *S. guanajae* in having more subdigital lamellae on the fourth toe (9–12, $x = 10.0 \pm 0.8$ on 40 sides versus 8–9, $x = 8.6 \pm 0.5$ on 12 sides in *S. guanajae*) and also differs from *S. leonardovaldesi* in having more scales around the midbody (64–80, $x = 71.9 \pm 4.8$ in 20 *S. continentalis* versus 48–67, $x = 59.8 \pm 6.0$ in 13 *S. leonardovaldesi*). *Sphaerodactylus continentalis* also differs from *S. guanajae*, *S. millepunctatus*, and *S. leonardovaldesi* in molecular data (Fig. 1). *Sphaerodactylus glaucus* Cope and *S. dunnii* Schmidt can occur sympatrically with *S. continentalis*. The former has smooth dorsal scales (versus keeled in *S. continentalis*) and *S. dunnii* has the superciliary spine located posterior to the level of the mideye, the third supralabial lying below the anterior half of the eye, and the medium subcaudal scales alternating (versus superciliary spine at mideye or anterior to that point, fourth supralabial below anterior half of eye, and median subcaudal scales aligned in a single row in *S. continentalis*). *Sphaerodactylus rosaurae* occurs sympatrically with *S. continentalis* on Isla de Utila, but *S. continentalis* is most easily distinguished from that

species in having all dorsal body scales of a similar size (versus middorsal row of granular scales sharply and distinctly differentiated from much larger surrounding dorsal scales in *S. rosaurae*).



FIGURE 5. Adult male (USNM 570166) of *Sphaerodactylus continentalis* (SVL 28.2 mm) from Estación Forestal CURLA, Atlántida, Honduras. Photograph by J.R. McCranie.

Sphaerodactylus millepunctatus Hallowell

(Fig. 6)

Sphaerodactylus millepunctatus Hallowell 1861: 480. Neotype UMMZ 173053 (designated by Harris & Kluge 1984: 18). Restricted type locality “NICARAGUA: Río San Juan; Isla Mancarrón of the Solentiname Archipiélago, 11°10'N, 85°02'W” (Harris & Kluge 1984: 18).

Geographic distribution. Low and moderate elevations from the Mosquitia region of northeastern Honduras to northern Costa Rica. The species also occurs on Isla de Maíz Grande, Nicaragua (see Fig. 3 for Honduran localities).



FIGURE 6. Adult male (FMNH 282793) of *Sphaerodactylus millepunctatus* (SVL 27.3 mm) from Dos Bocas, Gracias a Dios, Honduras. Photograph by J.R. McCranie.

Diagnosis. *Sphaerodactylus millepunctatus* can be distinguished from *S. continentalis* in having slightly larger and fewer dorsal scales (42–57, $x = 51.7 \pm 5.0$ in 15 *S. millepunctatus* versus 59–70, $x = 63.5 \pm 3.4$ in 20 *S. continentalis* examined for this study; see Discussion and Appendix I). *Sphaerodactylus millepunctatus* differs from both *S. guanajae* and *S. leonardovaldesi* in lacking a short thin pale yellow line above each pelvis, in usually having distinct dorsal spots that are larger than one scale, and in usually having distinct dark stripes on the posterior end of the head and anterior portion of the body (versus short pale pelvic lines almost always present, only scattered dark spots on body that are confined to one scale, and indistinct dark stripes on head and body in those two species). *Sphaerodactylus millepunctatus* also differs from *S. guanajae* in having more subdigital lamellae on the fourth toe (9–12, $x = 9.7 \pm 0.8$ on 30 sides versus 8–9, $x = 8.6 \pm 0.5$ on 12 sides in *S. guanajae*) and also differs from *S. leonardovaldesi* in having larger dorsal scales (42–57, $x = 51.7 \pm 5.0$ in 15 *S. millepunctatus* versus 58–66, $x = 61.7 \pm 2.7$ in 13 *S. leonardovaldesi*). *Sphaerodactylus millepunctatus* also differs from *S. continentalis*, *S. guanajae*, and *S. leonardovaldesi* in molecular data (Fig. 1). *Sphaerodactylus homolepis* Cope also narrowly occurs sympatrically with *S. millepunctatus* in southeastern Nicaragua and adjacent northeastern Costa Rica, but *S. homolepis* has a single supranasal scale and has alternating median subcaudal scales (versus two supranasals and subcaudals aligned in a single series in *S. millepunctatus*).

Discussion

Harris & Kluge (1984) gave thorough descriptions of the neotype of *Sphaerodactylus millepunctatus* and the holotype of *S. continentalis*. Their diagnostic data for those two specimens conform to those two species as recognized herein. The neotype of *S. millepunctatus* has 51 dorsal scales between the axilla and groin, whereas the holotype of *S. continentalis* has 62 dorsals. From Fig. 9 in Harris & Kluge (1984), specimens they examined from Nicaragua and Costa Rica have 43–58 dorsals in agreement with the 42–57 counts obtained for this study for 20 specimens from the Mosquitia of Honduras assigned herein to *S. millepunctatus*. Also, from Fig. 9 in Harris & Kluge (1984), their dorsal scale counts of specimens of *Sphaerodactylus continentalis* (sensu stricto) range from 58 to 80 in agreement with our concept of *S. continentalis* (but see below).

The holotype (ZIN 8880) of *Sphaerodactylus continentalis* carries only the locality data “Honduras.” That specimen was collected by “W. Schlüter” a professional collector who sold his collection from “Honduras” to museums (see Dunn & Saxe 1950). Of the 28 species of reptiles listed by Werner from the Schlüter collection, 26 (including the holotype of *S. continentalis*) are believed by JRM to have come from northwestern Honduras (two of Werner’s species names are not assignable to any named species). At any rate, the dorsal scale count of 62 obtained by Harris & Kluge (1984) for the *S. continentalis* holotype is in agreement with our concept of *S. continentalis*.

Harris & Kluge (1984) counted 47–74 (58.8 ± 5.0) dorsals for a series of 57 *Sphaerodactylus* from Coyoles, Yoro, Honduras, herein assigned to *S. continentalis*. Although those counts show more of an overlap in dorsal counts between *S. millepunctatus* and *S. continentalis* than obtained for this study, their mean count is nearer to the mean obtained herein for *S. continentalis* (63.5) than it is to our mean for *S. millepunctatus* (51.7). Our dorsal counts for 12 specimens from the Aguán Valley near Coyoles are 59–70 (63.7 ± 3.7). Thus, some of the differences between the Harris & Kluge (1984) counts and our counts for the Coyoles specimens might be due to individual differences in counting those scales on these tiny lizards. However, the two specimens sampled molecularly from the Aguán Valley near Coyoles, Honduras, differ by 7.6 % sequence divergence at the cytochrome b gene from specimens of *S. millepunctatus* from the Mosquitia of northeastern Honduras.

Harris & Kluge (1984) also mentioned that the specimens from Cozumel Island, Quintana Roo, Mexico, differed in dorsal pattern from all other populations of the *Sphaerodactylus millepunctatus* complex they studied. Molecular data from the Cozumel population might demonstrate that they also represent a distinct evolutionary species.

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APPENDIX I. Comparative specimens examined. Specimens from which morphological data were included herein are in bold. Genbank accession numbers are listed, in parentheses, for the genetic samples (12S rRNA, cytochrome b).

Sphaerodactylus continentalis: Honduras: ATLÁNTIDA-Estación Forestal CURLA, USNM 570164, **570165–68**; 7.4 km SE of La Ceiba, **USNM 570163**; La Ceiba, USNM 55245; 11.3 km W of La Ceiba, TCWC 21966; Lancetilla, ANSP 25869, 33108–10, FMNH 21832, MCZ R-32200, 39711; Tela, FMNH 13183, LSUMZ 24599, USNM 64173 (on bananas in Baltimore, USA), 69863, 70460–61 (all three on bananas in New Orleans, USA). COLÓN-Balfate, AMNH 58621; Puerto Castilla, USNM 64932 (collected on bananas); 0.5 km S of Trujillo, LACM 47809. COMAYAGUA-about 8 km S of La Misión, MCZ R-49975; 1.6 km S of Pito Solo, LSUMZ 28528–29; Pito Solo, CM 64526. COPÁN-Copán, USNM 570169; Rancho El Jaral, LACM 45391. CORTÉS-Laguna Ticamaya, FMNH 5032–35, 5226; Los Pinos, UF 166397–400, USNM 573096 (genetic sample 1, JX073108, JX073119), USNM 573097–98; Río Santa Ana, FMNH 5029. FRANCISCO MORAZÁN-Tegucigalpa, **USNM 570170** (specimen found on floor of a gymnasium and likely transported there from a more northerly location). ISLAS DE LA BAHÍA-Isla de Utila, Don Quickset Pond, SMF 77998; Isla de Utila, trail to Rock Harbor, SMF 77997; Isla de Utila, 3 km N of Utila, SMF 77118–19. OLANCHO-4.5 km SE of Catacamas, LACM 47777; Catacamas, LACM 45137–39; Piedra Blanca, **USNM 579972**, 579973. SANTA BÁRBARA-tributary of Río Listón, USNM 573884. YORO-0.5 km N of Coyoles, LACM 47779–80, LSUMZ 21441; Coyoles, LACM 47783, 47784 (C&S), 47785–808, LSUMZ 21442–74; El Progreso, UMMZ 58380; Los Indios, MCZ R-38796; 21 km WSW of Olanchito, UF 90207–08; 41 km WSW of Olanchito, UF 90209–10; Rancho San Lorenzo, LACM 47781–82; San Francisco, MVZ 52401, **USNM 579974**; near San Lorenzo Abajo, USNM 570193, **579975**, **575976** (genetic sample 2, JX073106, JX073118), **579977** (genetic sample 3, JX073107, sequence not obtained), **579978**; 5.5 km SSE of San Lorenzo Arriba, **USNM 579979–82**; 4.7 km ESE of San Lorenzo Arriba, USNM 565402–06, **570194–95**; vicinity of San Lorenzo Arriba, **USNM 579983–84**; Subirana Valley, MCZ R-38795; Yoro, KU 203087. “HONDURAS”-USNM 71733, 79951, 82573–74, 86862, 95866–67, 98909.

Sphaerodactylus dunni: Honduras: YORO-Vicinity of San Patricio, USNM 579605 (JX073114, JX073125).

Sphaerodactylus millepunctatus: Honduras: COLÓN-near Barranco, UMMZ 58408. GRACIAS A DIOS-Awasbila, USNM 570171; Bachi Kiamp, **FMNH 282792**, **USNM 579985**, 579986; Bodega de Río Tapalwás, **USNM 570172–73**; Caño Awalwás, UF 140810, **150310–11**; Cauquira, **UF 150304**; Dos Bocas, **FMNH 282793** (genetic sample 1, JX073104, JX073115), **282794** (genetic sample 2, JX073105, JX073116), **282795** (genetic sample 3, sequence not obtained, JX073117), **282796**; Leimus (Río Warunta), USNM 573094; Rus Rus, **UF 150302**, **USNM 570174**, 570175, **570176**; San San Hil Kiamp, USNM 570177–78; Tapalwás, USNM 570179; Yahurabila, USNM 573095. OLANCHO: Matamoros, SMF 79852–53, **USNM 570191**; confluence of Ríos Sausa and Wampú, USNM 570192.

APPENDIX II. Other specimens examined of the two new species described herein, but measurements and scale counts not taken.

Sphaerodactylus leonardovaldesi: All from Isla de Roatán, Honduras: near Coxen Hole, FMNH 34541; near Diamond Rock, USNM 570180; about 3.2 km W of French Harbor, LSUMZ 22390, 22392, UMMZ 152733 (C&S; formerly LSUMZ 22391); near French Harbor, CM 64525; Gibson Bight, LSUMZ 33796–97; near Oak Ridge, UTA R-10723–32; near Port Royal Harbor, LSUMZ 33801, 33806–08, MCZ R-150935, TCWC 52427–28; 3.2 km W of Roatán, CM 64527; Roatán, LSUMZ 22338–40, UF 28489; Rocky Point, USNM 570181–82; near Sandy Bay, KU 203127, 203132–33; West End Point, USNM 570183–88; West End Town, USNM 570189; no other data, USNM 570190.

Sphaerodactylus guanajae: All from Isla de Guanaja, Honduras: 2 km W of Savannah Bight, LACM 47778; Savannah Bight, USNM 520269.

APPENDIX III. Associated specimens (not examined) of *Sphaerodactylus leonardovaldesi*.

Islas de Barbareta and Morat, Islas de la Bahía, Honduras (Grismer *et al.*, 2001).