

<http://dx.doi.org/10.11646/zootaxa.3694.1.3>

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A new species of *Phyllodactylus* (Reptilia, Squamata, Gekkonoidea, Phyllodactylidae) from Isla de Guanaja in the Honduran Bay Islands

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Abstract

Morphological and molecular analyses of the *Phyllodactylus* populations on the Honduran Bay Islands of Guanaja, Roatán, and Utila demonstrate that the Guanaja population is best treated as a species distinct from the two other island populations. Thus, *P. palmeus* is restricted in distribution to Roatán and Utila islands and the Cayos Cochinos and a new species name is provided for the Guanaja Island population of the *P. palmeus* species group.

Key words: Guanaja Island, Honduras, *Phyllodactylus palmeus*, *Phyllodactylus paralepis* sp. nov., morphology, mtDNA, 16S rRNA

Introduction

Dixon (1968) described the gecko species *Phyllodactylus palmeus* from a group of 14 specimens collected on Roatán Island and eight others collected on Guanaja Island in the Honduran Bay Islands. Dixon (1968) chose a Roatán specimen as the name bearing holotype of the new species. During 2011, JRM started collecting tissues from various reptile species occurring on the Honduran Bay Islands. Roatán and Guanaja islands are uplifted islands separated from each other and from the Honduran mainland by deep seawater trenches. Thus, Roatán and Guanaja have apparently been separated from each other and from the mainland since at least the late Pliocene and early Pleistocene (discussed in Villa & McCranie 1995). We recently (2011) began work on a series of projects combining morphological and molecular data to understand the relationships between various species groups of lizards occurring on the Honduran Bay Islands. Three studies have already been completed (McCranie & Hedges, 2012, 2013a, 2013b), and herein we report the results of a fourth study, the third involving geckos.

Methods

The description of the holotype of the new species generally follows the format for the description of *Phyllodactylus palmeus* in Dixon (1968). We use longitude for the long axis of the body and transverse for across the short axis. Color codes and names used herein follow those of Smithe (1975–1981) and museum acronyms follow those of Leviton *et al.* (1985). We use the WGS84 geodetic datum system herein.

The new molecular data set comprised six sequences of the 16S rRNA mitochondrial gene from six individuals of *Phyllodactylus* collected on Islas de Guanaja, Roatán, and Utila and two individuals of *P. tuberculosus* Wiegmann from southern Honduras (see new species description and Appendix I). These new sequences were aligned (816 base pairs after excluding positions of ambiguous alignment) with sequences from Genbank of three species of *Phyllodactylus* from the West Indies (AY763275–83, AY763285–86; Weiss & Hedges 2007) and rooted with the phyllodactylid species *Gymnodactylus amarali* Barbour (JN935544; Gamble *et al.* 2012). Methods used

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for the collection of the new DNA sequences are detailed elsewhere (Heinicke *et al.* 2007; Hedges *et al.* 2008; Hedges & Conn 2012). The primers used (Hedges 1994) were 16L2 (GGCCTAAAAGCAGCCACCTGTAAAGA CAGCGT) and 16H1 (CTCCGGTCTGAACTCAGATCACGTAGG). Alignments (MUSCLE) and best-fit model selection were performed in MEGA 5.0 (Tamura *et al.* 2011). A maximum likelihood (ML) analysis was performed using RAxML 7.3.0 (Stamatakis 2006), unpartitioned, using the evolutionary model GTRGAMMA, the maximized available option (the best-fitting evolutionary model under the Bayesian Information Criterion, HKY + Γ is not recommended in RAxML). Gaps were treated as missing data. All parameters for the ML analyses were estimated by the program during the run. Ten ML searches were performed to find the best tree. Branch support in the trees was provided by standard bootstrap analysis (2,000 replicates). A Bayesian phylogenetic analysis using MrBayes 3.2.1 (Ronquist *et al.* 2012) also was performed, also using the GTR + 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 0.10. 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). A separate analysis was performed with additional sequences (16S rRNA) of *Phyllodactylus* species in Genbank, but because of the short length and number of ambiguous sites in those other sequences, they were not useful for building a robust genealogy.

Systematics

Study of the Bay Island populations of *Phyllodactylus palmeus* indicates that two species are involved that can be diagnosed at both the molecular (Fig. 1) and morphological levels. The populations on Roatán and Utila are similar to each other (as well as to those of the Cayos Cochinos) in morphology, whereas the populations on Guanaja are distinct. The holotype of *P. palmeus* (LSUMZ 16986) is from Isla de Roatán, thus we herein propose a new name for the *Phyllodactylus* population on Isla de Guanaja.

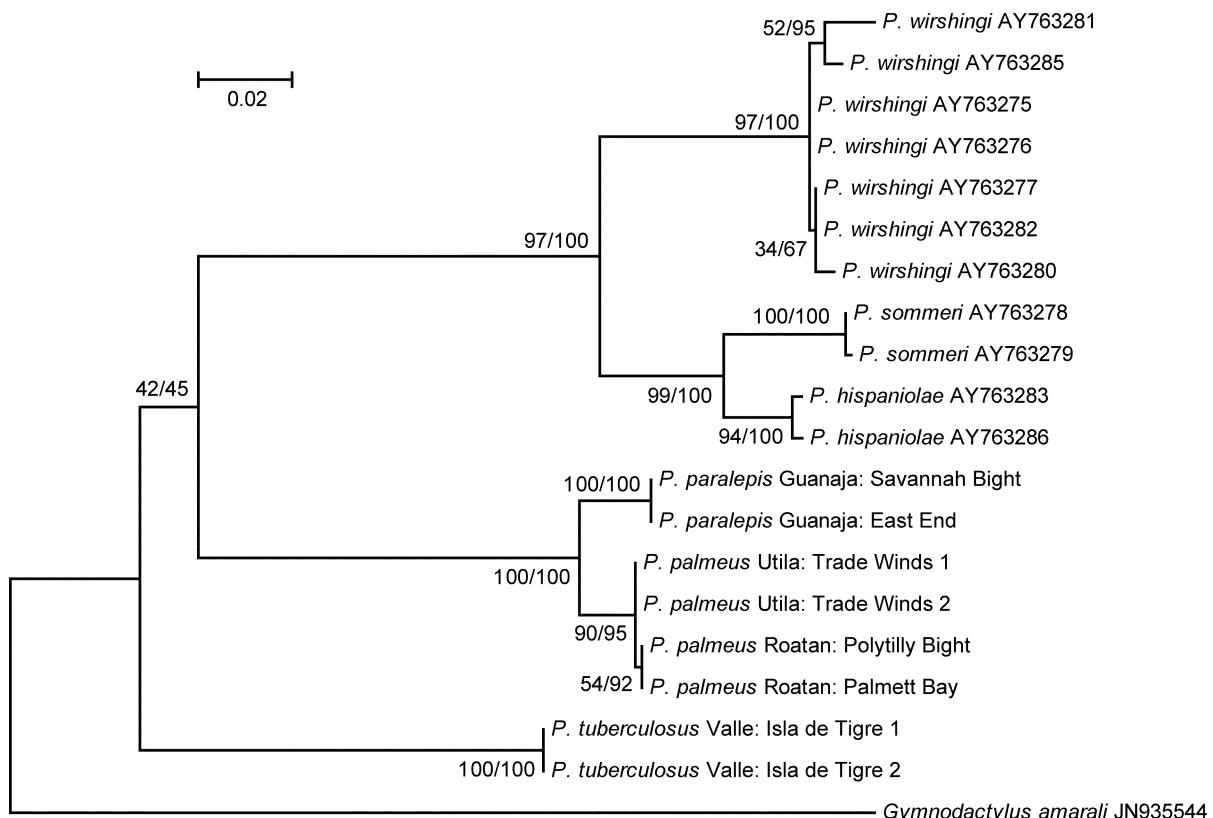


FIGURE 1. Phylogenetic tree of six species of *Phyllodactylus* from a maximum-likelihood analysis of DNA sequences of 16S rRNA. A scale bar is indicated. The numbers at nodes are bootstrap (left) and Bayesian (right) support values. The tree is rooted with the phyllodactylid species *Gymnodactylus amarali*.

***Phyllodactylus paralepis* sp. nov.**

(Fig. 2, 3)

Phyllodactylus palmeus Dixon, 1968:419 (part).*Phyllodactylus insularis* Echternacht, 1968:151.*Phyllodactylus palmeus* Wilson & Hahn, 1973:104 (part).*Phyllodactylus palmeus* McCranie et al., 2005:78 (part).

Holotype. FMNH 283552 (genetic sample 1, Genbank accession KF245415), an adult male from Savannah Bight, 16.29078°, -85.50300°, Isla de Guanaja, Islas de la Bahía, Honduras, 15 m elevation, collected 20 September 2012 by James R. McCranie & Leonardo Valdés Orellana.

Paratypes (7). FMNH 283553, adult female from East End, 16.486°, -85.832°, Isla de Guanaja, near sea level, collected 19 September 2012 by James R. McCranie & Leonardo Valdés Orellana; USNM 580288 (genetic sample 2, Genbank accession KF245416), 580289, adult males, 580290, an adult female, East End, Isla de Guanaja, collected 16 November 2011 by James R. McCranie; FMNH 283554, an adult female from Hotel Posada del Sol ruins, Isla de Guanaja, 16.462117°, -85.853867°, near sea level, collected 21 September 2012 by James R. McCranie and Leonardo Valdés Orellana; USNM 565401, an adult female from East Bight, Isla de Guanaja, collected 9 May 2007 by Alexander Gutsche & James R. McCranie; KU 101377, an adult male, Isla de Guanaja, no other data, 30 m, collected on 10 July 1996 by A. C. Echternacht.

Referred specimens. See Appendix I.

Geographic distribution. *Phyllodactylus paralepis* is known to occur only at low elevations on Isla de Guanaja in the Islas de la Bahía, Honduras (Fig. 4).

Diagnosis. *Phyllodactylus paralepis* has more closely spaced (0–1 granules separating) tubercles (Fig. 3) on the dorsal surfaces than does *P. palmeus* (1–3 granules separating dorsal tubercles). In addition, *P. paralepis* has 41–53 tubercles in the paravertebral row from the rear of the head to the tail and 16–17 dorsal tubercle rows across the midbody (versus 35–43 tubercles from head to tail and 11–15 tubercle rows across midbody in *P. palmeus*). Those two species also differ from each other in amount of sequence divergence (2.9 %; Fig. 1). *Phyllodactylus paralepis* also differs significantly in sequence divergence (9.8 %) from the remaining species of *Phyllodactylus* occurring in Honduras (*P. tuberculosus*). Morphologically, *P. paralepis* differs from *P. tuberculosus*, which occurs in southern Honduras, in having 41–53 tubercles in the paravertebral row from the rear of the head to the tail and 29–36 tubercles in the paravertebral row between the levels of the axilla and groin (versus 26–32 tubercles from head to tail and 20–24 tubercles between axilla and groin in *P. tuberculosus*). Dixon (1960) described *P. insularis* from Half Moon Cay in Belize about 230 km W of Isla de Guanaja. According to Dixon (1960), *P. insularis* has a distinct white subocular spot and dark brown dorsal surfaces, and lacks enlarged tubercles on the dorsal surfaces of the thighs (versus white subocular spot absent, pale brown dorsal surfaces, and enlarged tubercles present on thighs in *P. paralepis*).

Description of holotype. Rostral ca. two-thirds as high as wide, its dorsal edge with slight posterior inward curve, and with a median groove about half length of rostral; internasals paired, somewhat rectangular, in broad contact medially, bordered posteriorly by six granules and postnasal of each side; nostril surrounded by rostral, first supralabial, internasal, and two postnasals; shallow internasal and frontal depressions present; 16 scales present between nostril and eye (ioreals); scales in medial loreal region ca. three times larger than interorbital scales; 22 scales across snout between third supralabials; 16 scales between anterior edges of orbits and 24 midorbital scales; eye large, its diameter contained in snout length slightly less than two times; pupil vertically elliptical, with reticulated edges; eyelid with one row of granules and one larger outer row of scales, ultimate 4–5 pointed; diameter of ear contained in eye diameter ca. five times; ear opening vertically subtriangular, not denticulate, scales on anterior and posterior edges rounded, subequal in size; rear of head with many large tubercles intermixed with granular scales; six supralabials and infralabials to point below center of eye; mental bell-shaped, slightly longer than wide, bordered posteriorly by two postmentals; postmentals much longer than wide, their median edges in broad contact with one another; postmentals bordered posteriorly by eight smaller scales; postmentals contacting only first infralabial on each side.

Dorsum with 16 transverse (across body) rows of enlarged, keeled tubercles at midbody, paravertebral row with 49 tubercles from rear of head to base of tail, 30 between levels of axilla to groin; paravertebral rows separated from each other by 0–1 rows of granules; four rows of tubercles reach to rear of head on right side, three

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on left side; six rows of tubercles across base of tail; 3–3 enlarged preanal scales present; venter with 60 longitudinal and 27 transverse scale rows.

Dorsal surface of upper arm with flattened scales, forearm with scattered tubercles dispersed among smaller flattened scales; dorsal surface of thigh with 4–5 larger tubercles among smaller scales; lower hind limb with 12–14 tubercles dispersed among smaller scales; fourth finger lamellae 9–10, that of fourth toe 12–12; claw hidden when viewed from below; terminal pad large, paired pad scales longer than wide, truncated.

Measurements in mm: snout-vent length 60.1; axilla-groin length 27.9; forelimb length 15.5; hind limb length 24.1; tail length 69; head length 15.6; head depth 6.8; head width (midorbital) 9.2; eye diameter 3.9; ear longitudinal diameter 0.8; snout length 6.3; eye-ear length 5.4.



FIGURE 2. Adult male holotype (FMNH 283552; SVL 60.1 mm) of *Phyllodactylus paralepis* sp. nov. in life. Photograph by J.R. McCranie.

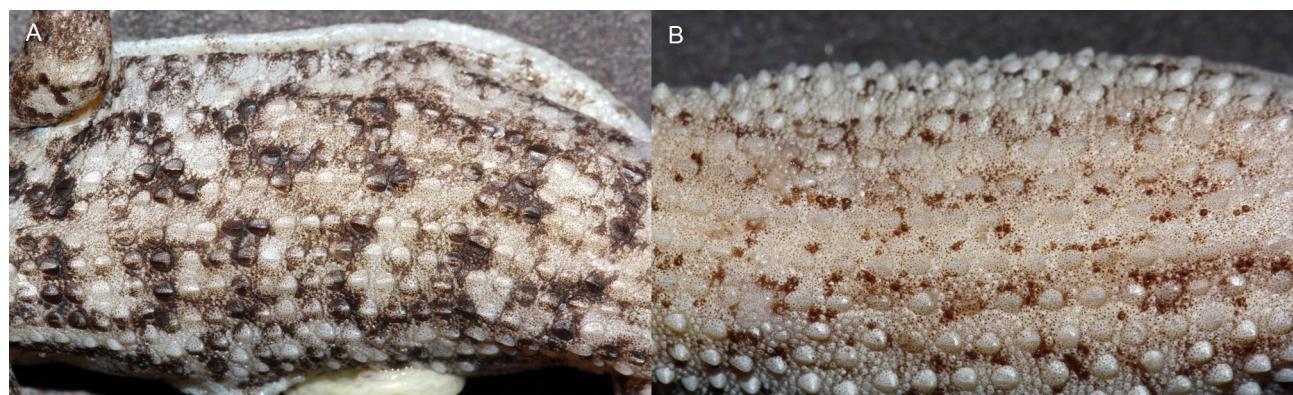


FIGURE 3. Comparison of spacing of enlarged dorsal tubercles between A) *Phyllodactylus paralepis* sp. nov. (FMNH 283552) and B) *P. palmeus* (KU 203123). Photographs by J.R. McCranie.

Color in life (Fig. 2): dorsum pale greenish brown with Sepia (219) mottling and Mikado Brown (121C) tubercles; top and lateral surfaces of head similar to that of body, except Sepia pigment forming longitudinal lines on snout and supralabials; dorsal surface of tail brown with Sepia crossbands; dorsal surfaces of limbs pale brown with Sepia and Raw Umber (123) mottling and crossbands; chin, throat, and belly pale brown with Raw Umber mottling on anterior half of belly and Sepia mottling and blotches on posterior half of belly; ventral surfaces of limbs pale brown, except soles and palms pinkish brown; digital pads dirty white to white; iris golden brown.

Color in alcohol: dorsal ground color pale tan with narrow dark brown, incomplete medially, reticulated crossbands; dorsal surfaces of limbs pale tan with dark brown reticulated crossbands; top of head pale brown with reticulated dark brown lines; side of head with dark brown postnasal and postorbital lines; tail tannish brown with narrow reticulated dark brown crosslines; supralabials cream with small dark brown spots on those anterior to eye;

ventral surfaces of head and body nearly immaculate cream; venter of limbs nearly immaculate cream, except that posterior ventrolateral edges mottled with dark brown; palms, soles, and digits tan; subcaudal surface cream with dark brown mottling on anterior third, becoming crossbanded with dark brown on tan ground color on distal half.

Variation. Snout-vent length of the type series ranges from 55.6–70.4 (60.8 ± 6.7) in males, 60.1–63.3 (61.8 ± 1.5) in females; postmentals number two in all, with postmentals contacting only first infralabial on each side in all; midorbital scales 20–25 (22.9 ± 1.6); scales across snout between third supralabials 20–29 (25.1 ± 3.1); longitudinal and transverse ventral scales 53–61 (57.6 ± 3.4) and 25–28 (26.9 ± 1.0), respectively; scales bordering postmentals 4–8 (6.3 ± 1.4); scales bordering posterior edge of internasals 5–8 (6.5 ± 0.9); scales between nostril and eye (loreals) 12–16 (14.3 ± 1.6); fourth toe lamellae 12–14 (12.6 ± 0.7); fourth finger lamellae 9–12 (10.6 ± 1.0); tubercles in paravertebral row from rear of head to base of tail and between axilla–groin 41–53 (47.3 ± 3.7) and 29–36 (31.4 ± 2.3), respectively; tuberculate rows across base of tail 6–8 (7.0 ± 1.1); supralabials and infralabials six in all but one with eight.

The paratypes have a somewhat more muted dorsal pattern in alcohol than does the holotype that consists of scattered dark brown spotting and mottling, otherwise they are similar in color to that described above for the holotype. A juvenile referred specimen (FMNH 283555; SVL 27.1 mm) is very similar in color in alcohol to that of the holotype, except that the dark dorsal crossbands on the anterior third of the body are solid, thus more distinct than in the holotype. The photographs of *Phyllodactylus paralepis* in Köhler (2000, 2003, 2008; all as *P. palmeus*) show a dorsal pattern similar to that seen in the holotype (Fig. 2).

Habitat. *Phyllodactylus paralepis* is a nocturnal gecko that before the invasion of *Hemidactylus* species was common on the walls of buildings in Savannah Bight. Those *Hemidactylus* species appear to have replaced *P. paralepis* in edificarian situations in recent years. However, *P. paralepis* remains common in non-edificarian situations on Guanaja. Other places of nocturnal activity include in walls of caves and on coconut and thorn palms. Its diurnal hiding places include termite nests, beneath tree bark, and especially within the bases of palm fronds and associated coverings. It can also be seen inside coconut palm debris lying on the ground and occasionally in Sea Grape (*Coccoloba uvifera*) leaf litter. Echternacht (1968: 151) reported finding one under “loose palm bark about 1.5 m above ground.” *Phyllodactylus paralepis* occurs sympatrically with two other native gekkotan species, *Sphaerodactylus alpinus* McCranie & Hedges and *S. guanajae* McCranie & Hedges. See Conservation status for comments on co-occurrence with recently introduced gecko species.

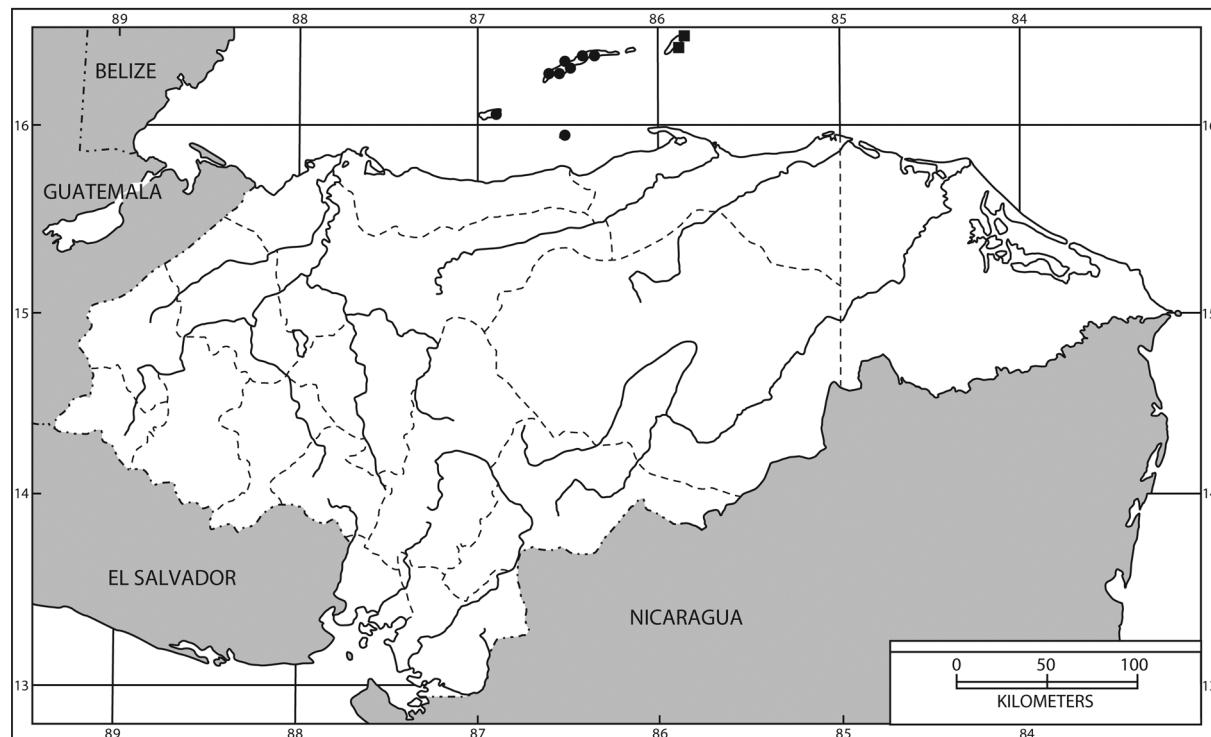


FIGURE 4. Map of Honduras showing localities for specimens examined of *Phyllodactylus paralepis* sp. nov. (squares) and *P. palmeus* (circles).

Conservation status. Two species of *Hemidactylus*, *H. frenatus* Schlegel and *H. mabouia* (Moreau de Jonnès) have been introduced to Isla de Guanaja in recent years. *Hemidactylus mabouia* was abundant on the walls of a hotel in Savannah Bight during 2007 (Gutsche & McCranie 2009), but that species has now apparently been displaced by the more aggressive *H. frenatus* (JRM personal observations). *Hemidactylus frenatus* was first introduced on the Honduran Bay Islands on the island of Utila (Köhler 2001). *Phyllodactylus palmeus* was formally a common species on Isla de Utila, but has now been completely eradicated in edificarian situations on Utila by *H. frenatus*. To make matters worse, *H. frenatus* has successfully invaded non-edificarian situations on Utila, where during September 2012 it was a more commonly found species in forested areas along the east coast than was *P. palmeus*. As *H. frenatus* populations on Utila apparently have at least a seven year head start on that island compared to the populations of *Hemidactylus* on Guanaja, it can be expected that *H. frenatus* will likewise invade the similar non-edificarian situations on Guanaja and begin the process of displacing *P. paralepis* there as well.

The introduced *Hemidactylus mabouia* population on the island of Curaçao has been noted to have displaced the native *Phyllodactylus martini* van Lith de Jeude in houses on that island (van Buurt 2005). Apparently, island populations of *Phyllodactylus* are generally more vulnerable to displacement by invasive species of *Hemidactylus*.

Etymology. The specific epithet *paralepis* is formed from the Greek *para* (near) and *lepis* (scale) and refers to the closely spaced tuberculate dorsal scales in this Guanaja Island endemic.

Discussion

Phyllodactylus paralepis is the fifth gecko species discovered as a result of combined morphological and molecular studies by the authors (McCranie & Hedges 2012, 2013a, this study). We have now studied molecular data on all native gecko species on the main Bay Islands of Guanaja, Roatán, and Utila, with the exceptions of the relatively widespread *Thecadactylus* and *Coleonyx* on Utila. We have not had the opportunity to sample gecko tissues from the Cayos Cochinos, which like Utila, are located on the continental shelf. Morphologically, the Cayos Cochinos gekkotan lizards appear to most closely resemble their Roatán counterparts, but molecular studies of Cayos Cochinos geckos are desired to test that scenario. We have, however, studied the molecular systematics of the resident *Cnemidophorus* (Squamata: Teiidae) species on Cayo Cochino Pequeño (McCranie & Hedges 2013b). That study allied the Cayo Cochino population most closely with those of the other Bay Island populations (Roatán and Utila), rather than those with the Honduran mainland.

The phylogeny and species groups of *Phyllodactylus* are not yet well established. In the two recent studies that have included diverse species (Gamble *et al.* 2011; Pyron *et al.* 2013), there has been little correspondence with species groups based on morphology (Dixon 1964). When *Phyllodactylus wirshingi* Kerster & Smith was included in one study, it was the closest relative of all other species of *Phyllodactylus* (Pyron *et al.* 2013). When we performed an analysis with available Genbank data (16S rRNA) for *Phyllodactylus*, mostly short sequences, we obtained similar results (not shown) to our tree using higher quality data (Fig. 1), which shows a large separation between the Bay Islands clade (*P. palmeus* and *P. paralepis*) and others. Based on these results, the two Bay Island species are best placed in their own species group (*P. palmeus* species group), which is well separated from the Greater Antillean species (*P. wirshingi* species group) and the remaining species in Honduras (*P. tuberculosus* of the *P. tuberculosus* species group).

Acknowledgments

Collecting (Dictamen DVS-ICF-016-2009, Resolución DE-MP-102–2012) and export (Resolución DE-MP-023-2009, Constancia's 011-2011-DVS-ICF, 042-2011-DVS-ICF, and 038-2012-ICF-DVS) permits were issued to JRM by Iris Acosta, Carla Cárcamo, and Saíd Laínez of the Instituto Nacional de Conservación y Desarrollo Forestal, Áreas Protegidas y Vida Silvestre, Tegucigalpa. Copies of those permits are on file at the FMNH and USNM. Leonardo Valdés Orellana provided field assistance during September 2012 and Alexander Gutsche assisted during May 2007. Jennifer Stella, Jessica Preston, and Angela Marion assisted with the DNA sequence collection and analysis. Hedges was supported by grants from the U.S. National Science Foundation. McCranie's

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fieldwork for this study that resulted in the specimens and tissues studied herein was supported by the Marshall Field Fund at the FMNH, Chicago, which made this project possible. A special thanks goes to Alan Resetar for his help with that assistance.

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APPENDIX I. Comparative specimens examined. Genbank accession numbers are listed (in parentheses) for the genetic samples (16S rRNA).

Phyllodactylus paralepis sp. nov. (referred specimens): HONDURAS: ISLAS DE LA BAHÍA: Isla de Guanaja, southeast shore opposite Guanaja, LACM 38514–15, LSUMZ 22402–03; Isla de Guanaja, La Playa Hotel, LACM 38516–20, MVZ 52402; Isla de Guanaja, Posada del Sol Hotel ruins, FMNH 283555; Isla de Guanaja, Savannah Bight, CM 64513.

Phyllodactylus palmeus: HONDURAS: ISLAS DE LA BAHÍA: Cayo Cochino Grande, near La Ensenada, KU 220098–99; Cayo Cochino Grande, UTA R-53953; Isla de Roatán, Fiddlers Bight, UMMZ 142650; Isla de Roatán, Flowers Bay, USNM 570146–47; Isla de Roatán, Fort Key, UMMZ 142649 (2); Isla de Roatán, near French Harbor, UF 28560–61; Isla de Roatán, Gibson Bight, LSUMZ 33782–83; Isla de Roatán, W of Oak Ridge, UTA R-10707 (formerly MCZ 89385), 10722 (formerly MCZ 89384); Isla de Roatán, near Oak Ridge, TCWC 52410, UTA R-10708, 55240–43; Isla de Roatán, Palmetto Bay, FMNH 283556, 283558 (genetic sample, Genbank accession KF245418), MVZ 267203; Isla de Roatán, 1 km E of Pollytilly Bight, FMNH 282617–20, UNAH 253815 (genetic sample, Genbank accession KF245417); Isla de Roatán, near Port Royal Harbor, LSUMZ 33787–91, TCWC 52411–13; Isla de Roatán, near Port Royal, USNM 578824–27; Isla de Roatán, 0.5–1.0 km N of Roatán, TCWC 24016; Isla de Roatán, about 3 km N of Roatán, LSUMZ 16986–94; Isla de Roatán, about 3.2 km W of Roatán, CM 64514; Isla de Roatán, about 1.6 km W of Roatán, LSUMZ 33792; Isla de Roatán, about 4.8 km W of Roatán, LSUMZ 22350–51; Isla de Roatán, near Roatán, CM 57185, 64515, UF 28458, 28541–42; Isla de Roatán, Roatán, LSUMZ 22335–37; Isla de Roatán, Rocky Point, USNM 570148–50; Isla de Roatán, 1.2 km E, 0.4 km S of Sandy Bay, KU 203121–22; Isla de Roatán, near Sandy Bay, USNM 570151–53; Isla de Roatán, Sandy Bay, KU 203123–26, LSUMZ 33784–86; Isla de Roatán, 6.6 km E of West End, MVZ 263856–58; Isla de Roatán, West End, USNM 578822–23; Isla de Roatán, West End Point, USNM 570154–55; Isla de Roatán, West End Town, USNM 570156–57; “Isla de Roatán,” UF 149596; Isla de Utila, east coast near Trade Winds, FMNH 283557 (genetic sample 2, Genbank accession KF245420), 283559 (genetic sample 1, Genbank accession KF245419); Isla de Utila, 2 km S of Rock Harbour, SMF 77108; Isla de Utila, Utila, UF 28398; “Isla de Utila,” SMF 77109–10.

Phyllodactylus tuberculosus: HONDURAS: CHOLUTECA: 1.0 km N of Cedeño, LSUMZ 33667, 33687; 1.6 km N of Cedeño, KU 209312–13; 31.0 km NE of Cedeño, LSUMZ 33669–72; 1.9 km E of Choluteca, UMMZ 117500 (7); Choluteca, LACM 64254, LSUMZ 33668, MSUM 4640; El Madreal, USNM 570158–61; El Ojochal (Botija), SDSNH 72758–59; Finca Monterrey, USNM 579599–600; La Fortuna, SDSNH 72742; Finca La Libertad, SDSNH 72761; Quebrada del Horno, SDSNH 72760. EL PARAÍSO: El Rodeo, USNM 580932–33. FRANCISCO MORAZÁN: near El Zamorano, AMNH 70365–66; El Zamorano, AMNH 70367, MCZ R-49756; 3.2 km SE of Sabanagrande, TCWC 19185; San Antonio de Oriente, AMNH 70364; Tegucigalpa, CAS 152992, LSUMZ 24130, 38813–14, UF 124698–99, USNM 60498, 133029. VALLE: Isla Conejo, USNM 580267–69; Isla de La Vaca, USNM 580285; Isla de Las Almejas, USNM 580286; Isla El Coyote, USNM 580279–82; Isla El Pacar, USNM 580935–36; Isla El Tigre, near Amapala, USNM 580270 (genetic sample 1, Genbank accession KF245421), 580271 (genetic sample 2, Genbank accession KF245422), 580272; Isla El Tigre, Amapala, MCZ R-49748–50; Isla Inglesera, USNM 580273–77; Isla Tigrito, USNM 580938; Isla Violín, USNM 580934; Isla Zacate Grande, KU 194256–57, LSUMZ 36580–81; La Laguna, SDSNH 72762–64, USNM 580278; Nacaome, LACM 47301; Playona Exposición, USNM 579601–02; Puerto Salamar, LSUMZ 16049; Punta El Molino, USNM 580937; San Carlos, USNM 580283–84; 11.9 km SSW of San Lorenzo, TCWC 61763.