

A Distinctive New Species of *Gonatodes* (Squamata: Sphaerodactylidae) from Isla La Blanquilla, Venezuela, with Remarks on the Distribution of Some Other Caribbean Sphaerodactylid Lizards

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Abstract. A new sphaerodactylid gecko of the genus *Gonatodes* is described from La Blanquilla Island, located 170 km north of the Venezuelan mainland. This new species exhibits the following suite of characters that immediately separate it from other taxa in the genus: vertically elliptical pupil, small size, uniformly reddish brown, non-sexually dimorphic coloration, and a subcaudal scale pattern type C (1'1"). The new species is the fourth *Gonatodes* endemic to Caribbean islands, the other three being *G. antillensis* (Bonaire, Curaçao, the archipelagos of Las Aves and Los Roques), *G. daudini* (Union Island, The Grenadines), and *G. ocellatus* (Tobago). Finally, we discuss the close phylogenetic relationship (based on nuclear genes *c-mos* and *NT3*) between the new species and *Gonatodes daudini*, as well as its zoogeographical implications, showing interesting parallels with that of other Caribbean lizards.

Keywords. Gekkota; South America; Systematics; Taxonomy.

Resumen. Se describe un nuevo lagarto sphaerodactílido del género *Gonatodes* proveniente de la Isla de La Blanquilla, localizada 170 km al norte de la tierra firme de Venezuela. La nueva especie se diferencia fácilmente de otros congéneres por la siguiente combinación de caracteres morfológicos: pupila verticalmente elíptica, diminuto tamaño, coloración uniforme, pardo rojiza en ambos sexos y un patrón subcaudal tipo C (1'1"). El nuevo taxón es el cuarto miembro del género *Gonatodes* endémico de una isla del mar caribe, las otras son *G. antillensis* (Bonaire, Curaçao, y los archipiélagos de Las Aves y Los Roques), *G. daudini* (Isla Unión, Las Granadinas) y *G. ocellatus* (Tobago). Finalmente, se discute la cercana relación evolutiva entre la nueva especie y *G. daudini*, así como sus implicaciones zoogeográficas, mostrando interesantes paralelismos con otras especies de lagartos del Caribe.

INTRODUCTION

The taxonomy of reptiles from continental and oceanic islands of the Venezuelan Caribbean coast has, until recently, remained unchanged and overlooked for many years. Herpetological collecting efforts and research on these islands began towards the end of the 1800s and early 1900s by researchers and travelers who sporadically explored the area. The most important of these early works are those by Peters (1873), Meek (1910), and Hummelinck (1940), in which several species (e.g., *Anolis blanquillanus* Hummelinck 1940, *Cnemidophorus nigricolor* Peters 1873, and *Phyllodactylus rutteni* Hummelinck 1940) were described. However, in recent years, new research has brought to light the fact that the real diversity of herpetofauna from these islands has been greatly underestimated (Ugueto *et al.*, 2009; Ugueto and Harvey, 2010; Ugueto and Rivas, 2010; unpublished data for the authors).

The Venezuelan Antilles (La Blanquilla, La Orchila, and the archipelagos of Las Aves, Los Hermanos, and

Los Roques) are separated from one another and from the mainland by deep-sea trenches probably since their emergence. It is very likely that these have never been connected to the continent, for sure not during the last glacial maxima (Neill *et al.*, 2011), resulting in each possessing a unique but depauperate herpetofauna. In this study, we describe a new diminutive and distinctive sphaerodactylid lizard of the genus *Gonatodes* from one of these islands. The new taxon was collected during recent fieldwork on Isla La Blanquilla (also known as Isla Blanca), Venezuela. This species was apparently first collected at the end of the 1930s by Hummelinck (1940) on the nearby Los Hermanos Archipelago but was never formally described. Hummelinck (1940) reported the specimens he collected as "*Gonatodes* spec. (? *Gymnodactylus* aff.)" and deposited them in the Nationaal Natuurhistorisch Museum (Leiden) and in the Zoölogische Museum (Amsterdam). The collection of the Zoölogisch Museum has been incorporated into the collection of the National Natuurhistorisch Museum. Currently, they are now all housed in the former, and will be integrated into a new center for

biodiversity. For this reason we were unable to obtain a loan of these specimens (Ronald de Ruiter “in litt”). Here we describe this enigmatic species based on eight newly collected specimens possessing a suite of unique features. Additionally, we examine the phylogenetic position of this new species based on molecular data.

MATERIALS AND METHODS

Descriptive methods

Specimens examined are deposited in the following collections (Appendix I): at Museo de Biología, Universidad del Zulia, Maracaibo, Zulia, Venezuela (MBLUZ); Museo de la Estación Biológica de Rancho Grande, Aragua, Venezuela (EBRG); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS); Milwaukee Public Museum, Milwaukee, Milwaukee, USA (MPM); and the Amphibian and Reptile Diversity Research Center, The University of Texas at Arlington, Arlington, Texas, USA (UTA).

Measurements of specimens were recorded with a digital caliper (to the nearest 0.1 mm) and include snout-vent length (SVL, from tip of snout to cloacal opening), tail length (TL, from cloacal opening to tip of tail), head length (HL, from the tip of the snout to the anterior margin of the ear opening), head width at widest section (HW, at widest section of head), axilla-groin distance (AXG, from posterior margins of arm insertion to anterior margin of hind limb insertion). Loreal scales were counted in straight line between postnasals and anterior border of orbit. Scale counts include ventral scales (VS, along a mid-ventral line from anterior level of arm insertion to vent, excluding the small granules at its edge) and scales around midbody (SAMB). Terminology and scale counts follow Avila-Pires (1995) and Rivero-Blanco and Schargel (2012).

Phylogenetic analysis

In order to examine the phylogenetic position of the new species we conducted an analysis based on DNA sequences from two nuclear genes (C-mos and NT3) that have been previously used to investigate the systematics of the genus (Gamble *et al.*, 2008; Schargel *et al.*, 2010). The protocols for DNA isolation and PCR follow Schargel *et al.* (2010). We included sequences of two individuals of the new species (MBLUZ 1011 and 1013), as well as several Genbank (Benson *et al.*, 2005) sequences from other species in the genus and other sphaerodactylid genera to be used as outgroups. The sequences used are listed in the Appendix II with the corresponding Genbank accession numbers. Sequences were imported into MEGA 5 (Tamura *et al.*, 2011) and aligned using the ClustalW algorithm

(Thompson *et al.*, 1994). MEGA 5 was also used for calculating genetic distances. The sequences from both genes were concatenated in TREEFINDER Version of March 2011 (Jobb, 2011), and two partition filters (gene and codon position) were added manually. We used the “propose model” option with default settings in TREEFINDER to select, under the Corrected Akaike Information Criterion (AICc), the best-fit model of nucleotide substitution for each partition. A maximum likelihood (ML) bootstrap analysis (1000 replications) was also conducted in TREEFINDER loading the best-fit models for the different partitions and the partition rates set to optimum. Results of the bootstrap analysis were summarized in a consensus tree collapsing all clades that received a support value level less than 50.

Species description and results

Gonatodes naufragus sp. nov.

(Figs. 1–10, Table 1)

Gonatodes spec. (? *Gymnodactylus* aff.): Hummelinck 1940: 74 [four specimens collected in Morro Pando, Archipelago Los Hermanos, Dependencias Federales, Venezuela; also observed in Morro Fondeadero].

Holotype. EBRG 5224 (Figs. 1, 4E), an adult female, collected on Playa Juan Gerardo (11°52'34.92"N–64°37'36.68"W), 3 m above sea level (asl), La Blanquilla, Dependencias Federales, Venezuela, 20 October 2010, by Gilson A. Rivas, José J. Rodríguez and Ronnis Guevara.

Paratypes. MBLUZ 1010, an adult male, with same data as holotype. MBLUZ 1011, female, between Playa Juan Gerardo and Playa El Barco, La Blanquilla (11°53'22.84"N–64°37'10.62"W) by Gilson A. Rivas, José J. Rodríguez and Ronnis Guevara. MBLUZ 1012, female, and MBLUZ 1013, hatchling, from Playa Piedra Ahogada, La Blanquilla (11°49'23.87"N–64°38'09.15"W), 10 m asl, obtained on 21 October 2010 by Gilson A. Rivas, José J. Rodríguez and Ronnis Guevara. MBLUZ 1147, male, on 1 February 2012 by Gilson A. Rivas, Angel Fernández, Jose J. Rodríguez and Jackeline Reid. MBLUZ 1146, juvenile, lomas de granito, La Blanquilla (11°51'53.42"N–64°37'25.41"W), 15 m asl on 25 January 2012, 5 m asl. by Gilson A. Rivas, Angel Fernandez, Jose J. Rodriguez and Jackeline Reid. MBLUZ 1148, female, La Blanquilla (11°51'32.24"N–64°37'27.17"W), 20 m asl. on 2 February 2012, by Gilson A. Rivas, Angel Fernandez, Jose J. Rodriguez and Jackeline Reid.

Diagnosis. The new species can be distinguished from all congeners by the following unique combination of characters: (1) small body size, with adults ranging

Table 1. Selected morphometric measurements (in mm) and scale counts of the type series of *Gonatodes naufragus* sp. nov. M = male, F = female, J = juvenile, H = hatchling, EYN = eye-nostril distance. Other abbreviations are defined in the text. TL = corresponds to the complete tail of MBLUZ 1010 only; all other tails are incomplete or regenerated.

Specimen number	Sex	SVL	TL	HL	HW	EYN	AXG	VS	SAMB
EBRG 5224	F	27.0	25.2	6.8	4.9	1.7	12.2	36	63
MBLUZ 1010	M	23.3	26.2	5.6	3.9	1.5	10.3	35	60
MBLUZ 1011	F	27.2	11.5	6.7	4.5	1.7	11.1	38	67
MBLUZ 1012	F	24.7	–	5.7	4.3	1.6	10.5	37	–
MBLUZ 1013	H	14.8	13	4	2.7	0.9	5.6	–	–
MBLUZ 1146	J	21.6	7	5.5	4	1.4	8.3	33	65
MBLUZ 1147	M	24.8	23.4	6.1	4.6	1.6	9.8	35	66
MBLUZ 1148	F	27.2	12	6.1	4.2	1.7	12.3	38	60

from 23.3–27.2 mm SVL, (2) rostral distinctly acuminate and elongated, (3) pupil vertically elliptical, (4) absence of a clearly differentiated elongate supraciliary spine, (5) dorsal scales bulky and relatively small but not granular, (6) absence of clusters of distinctly enlarged conical scales on sides, (7) 52–53 scales around midbody, (8) 35–38 ventral scales counted in a longitudinal row, (9) escutcheon scales on posterior belly and ventral

surfaces of thighs in males evident, (10) one to two lateral rows of scales on distal part of finger and toes (Fig. 2), (11) midventral scales distinctly wider than long, forming a repetitive sequence (only in the original tail) of a single midventral scale in contact laterodistally with one scale per side followed by a single midventral scale in contact with two scales per side (1'1" *sensu* Avila-Pires, 1995; subcaudal pattern type C *sensu* Rivero-Blanco and Schargel, 2012, Fig. 3), (12) adults (both sexes) with uniform reddish brown dorsal coloration and hatchlings with striped pattern, conspicuously different from that of adults.

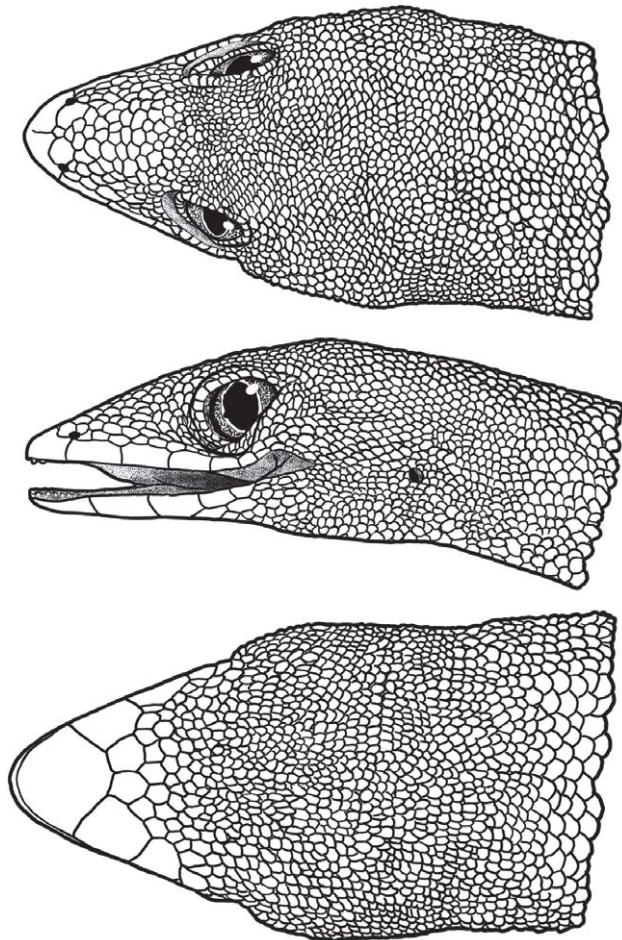


Figure 1. Dorsal (upper), lateral (middle) and ventral (below) views of head in *Gonatodes naufragus* sp. nov. (holotype EBRG 5224, adult female, SVL 27.2 mm).

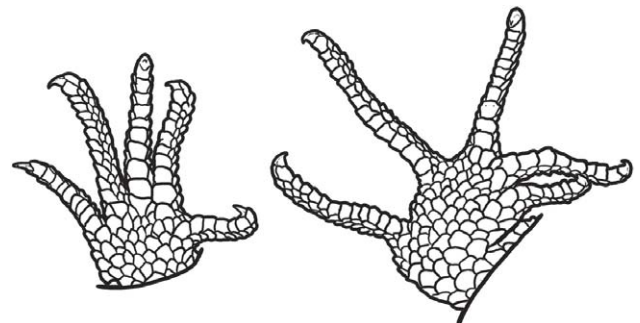


Figure 2. Ventral aspect of right hand (left) and foot (right) of *Gonatodes naufragus* sp. nov. (paratype MBLUZ 1012, adult female).

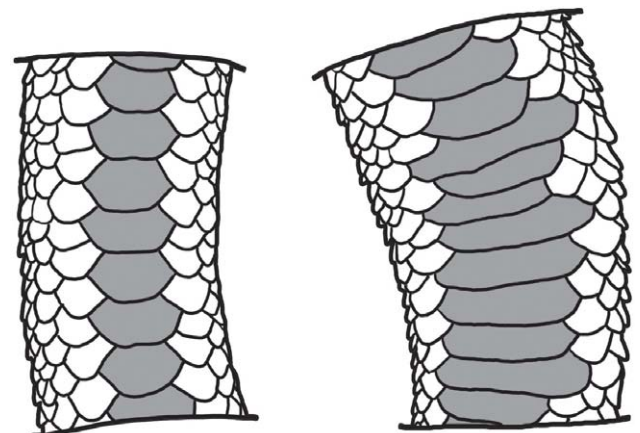


Figure 3. Ventral aspect of tail in *Gonatodes naufragus* sp. nov.: left, paratype MBLUZ 1010, adult male with original tail; right, holotype EBRG 5224, adult female with regenerated tail.

Description of holotype. An adult female, with SVL 27.0 mm. Head approximately 1.3 times longer than wide (HL: 6.8 mm; HW: 4.9 mm), 0.25 times SVL. Snout 4.1 mm long (0.60 times HL), acuminate in dorsal view, 45° sloping toward top of head. Neck barely narrower than head and body; more elongated and thick than that of other *Gonatodes* species, which gives the lizard an appearance similar to that of *Sphaerodactylus*. Body nearly cylindrical but wider than high; AXG 11.5 mm. Limbs short, well developed with short digits, fourth toe length 2.3 mm, 2.7 times shank length (6.3 mm). Tail thick, round in cross section, tapering toward tip. TL 25.2 mm in length. Tongue elongate, immaculate, with the tip rounded, without medial cleft. Teeth small, conical and subequal in length.

Rostral large, V-shaped, visible from above and pointed, very sharp, contrary to that observed in other *Gonatodes* in which it is less acuminate (e.g., *G. antillensis* and *G. daudini*) or rounded (most species); posterior margin slightly indented by median postrostral and semidivided by a moderately long medial cleft. Three postrostral scales; lateral ones (supranasals) distinctly larger than median, which is slightly smaller than adjacent posterior scale. Nasal bordered by rostral, lateral postrostral (supranasal), two postnasals, and first supralabial; nostril located relatively far from tip of the snout (more distantly than in any other species of *Gonatodes*). Postnasals roughly subequal in size to each other and lower one both sides of the head; postnasals subequal in size to scales on loreal region. Scales on top of snout quadrangular, flat and juxtaposed, gradually becoming slightly imbricate towards loreal region. Loreal scales number about eight (right side) and nine (left side) on a line between postnasals and anterior margin of orbit. Scales decrease noticeably in size from the postrostrals to the interocular area, posteriorly increasing slightly in size toward the occipital region. Supraciliary flap well developed, with a few conical supraciliaries slightly enlarged, but none forming a distinctly elongate spine. Pupil vertically oval. Supralabials 4 (both sides) to center of eye, first two the largest (first slightly longest than second), third slightly smaller and fourth much smaller, followed by 3 (both sides) much smaller scales along lip to rictus of mouth, all similar in size to scales on temporal region. Scales on temporal region similar in size and shape to those on top of head. Ear opening roughly rounded, about 1/5 the size of the orbit; a deep auditory meatus.

Mental large, with angular posterior margin. Postmentals two, polygonal distinctly larger than adjacent posterior scales and polygonal. Scales on chin directly behind postmentals similar in shape to them, posteriorly rounded and much smaller; a few larger, polygonal, juxtaposed scales adjacent to infralabials. Infralabials four (both sides) to center of eye, decreasing in size

posteriorly, the anterior two very large (first much longer than second); anterior three infralabials projecting onto the ventral plane, although the third barely visible from below.

Scales on nape and sides of neck continuous with those on posterior part of head (small, rounded, slightly bulky and subimbricate) but slightly larger. Scales on the gular region smooth and imbricate, with round posterior margin, and with an anterior segment with much smaller scales, and a posterior segment with larger scales. Dorsal scales not granular, but round, bulky and subimbricate, distinctly larger than those on top of head and neck; dorsolaterally and on flanks slightly larger than those mid-dorsally. Limit between subimbricate scales on flanks and imbricate ventrals not clearly demarcated. Ventral region with scales distinctly larger than dorsals, similar on chest and on belly, smooth, with round margin; ventrals in oblique rows, with 36 scales. SAMB about 63, of which about 12 are ventrals. There are diminutive scales around the vent arranged irregularly.

Scales on dorsal part of tail larger than on body, slightly bulky, imbricate, with round posterior margin; limit between body and caudal scales not clearly demarcated. Subcaudal scales larger than those dorsally, smooth, flat, imbricate, with round posterior margin; midventralscale single, conspicuously enlarged transversally, laterally in contact with either two or three smaller adjacent caudal scales. The tail has been regenerated twice; midventral scales of regenerated portions much shorter and wider than those on original portion (see Fig. 3).

Scales on limbs rounded and juxtaposed, except ventrally and on anterior surface of forearms and thighs where they are smooth, flat and imbricate. Scales under thighs and anterior part of belly, close to the vent, less pigmented. Lamellae under first (I) through fifth (V) finger (right/left side): I: 5/6, II: 9/9, III: 10/10, IV: 11/12, V: 8/7 (the fifth finger on right side is partially broken on third lamellae). Lamellae under first (I) through fifth (V) toe (right/left side): I: 5/5, II: 9/7, III: 10/11, IV: 14/14 (the fourth finger on left side is partially broken on seventh lamellae), V: 12/12. Fingers and toes with a single or two lateral rows of scales distally. Claws exposed, non-retractile, between two basal scales (one dorsal and one ventral).

Color of holotype in life. Dorsum uniformly dark reddish brown with the tips of some scales on trunk pale yellow (Fig. 4E). Head and neck scales are uniform without yellow color on the tips of the scales. Venter light brown, with the abdominal region slightly darker. The non-regenerated portion of the tail is similar in coloration to that of dorsum; the remainder of the tail has been regenerated twice, the middle portion has light brown longitudinal stripes. Iris reddish brown with an ochraceous-golden ring around the pupil.

Variation in paratypes. Paratypes consist of three adult females (SVL 24.7–27.2 mm), two adult males (SVL 23.3–24.8 mm), a juvenile (SVL 21.6 mm) and a hatchling

(SVL 14.8 mm). Table 1 provides scale counts and measurements of the type series. Supralabials 4–6, followed by 2–3 much smaller scales along the lip to rictus of



Figure 4. Top: adult male (A) and adult female (B) *Gonatodes antillensis* in life. Gran Roque, archipelago Los Roques, Venezuela (both specimens uncollected). Center: dorsal view of the adult female paratype of *G. naufragus* sp. nov. in life (MBLUZ 1148) (C), and ventral view of the same specimen (D). Bottom: Illustration of juvenile (above) and adult (below) *Gonatodes naufragus* sp. nov. in life. Drawings based on MBLUZ 1013 and EBRG 5224, respectively (E). Photographs: Luis Alejandro Rodríguez J.; Illustration: Gabriel N. Ugueto.

mouth, infralabials four, followed by 2–3 much smaller scales along the lip to rictus of mouth. Loreal scales range from seven to eight. Scales around midbody range from 57 to 67, of which 12–14 are ventrals. There are 33–38 scales on an imaginary line between the anterior part of the insertion of the arm to the vent. Both males have an evident escutcheon (Fig. 5) formed by a cluster of approximately 37 scales on the posterior portion of the abdomen, distinctly different from other ventrals, unpigmented except slightly on their outer margins. The same unpigmented scales are present under the thighs where they are arranged in 3 (left leg)–4 (right) transverse rows of about 29 (right)–26 (left) scales each. Variation in the number of lamellae under first (I) through fifth (V) finger is as follow: I: 5–6, II: 8–9, III: 9–10, IV: 10–11, V: 7–9. Variation in the number of lamellae under first (I) through fifth (V) toe is as follow: I: 4–6, II: 8–9, III: 9–11, IV: 12–14, V: 10–12.

The coloration of the adult (Fig. 4C–D) is essentially the same as in the holotype, except for MBLUZ 1147, a presumably young male which has pale yellow reticulations overlaid on the head. The coloration of the single

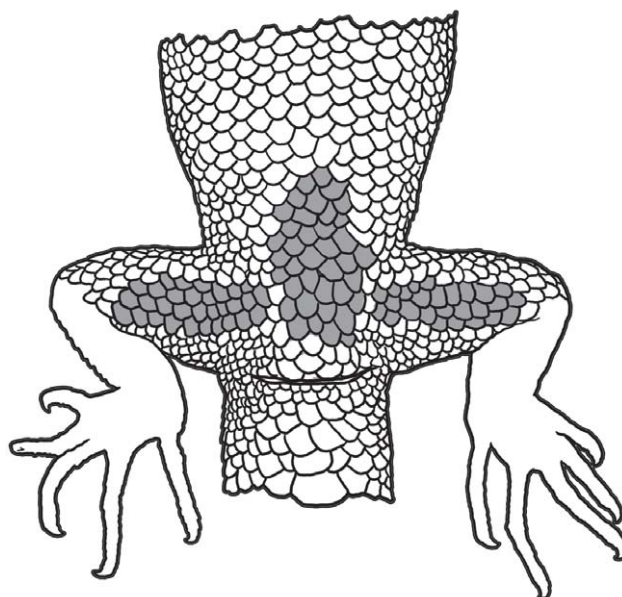


Figure 5. Ventral view showing escutcheon areas (shaded in gray) on posterior abdomen and ventral aspect of thighs in *Gonatodes naufragus* sp. nov. (paratype MBLUZ 1010, adult male).

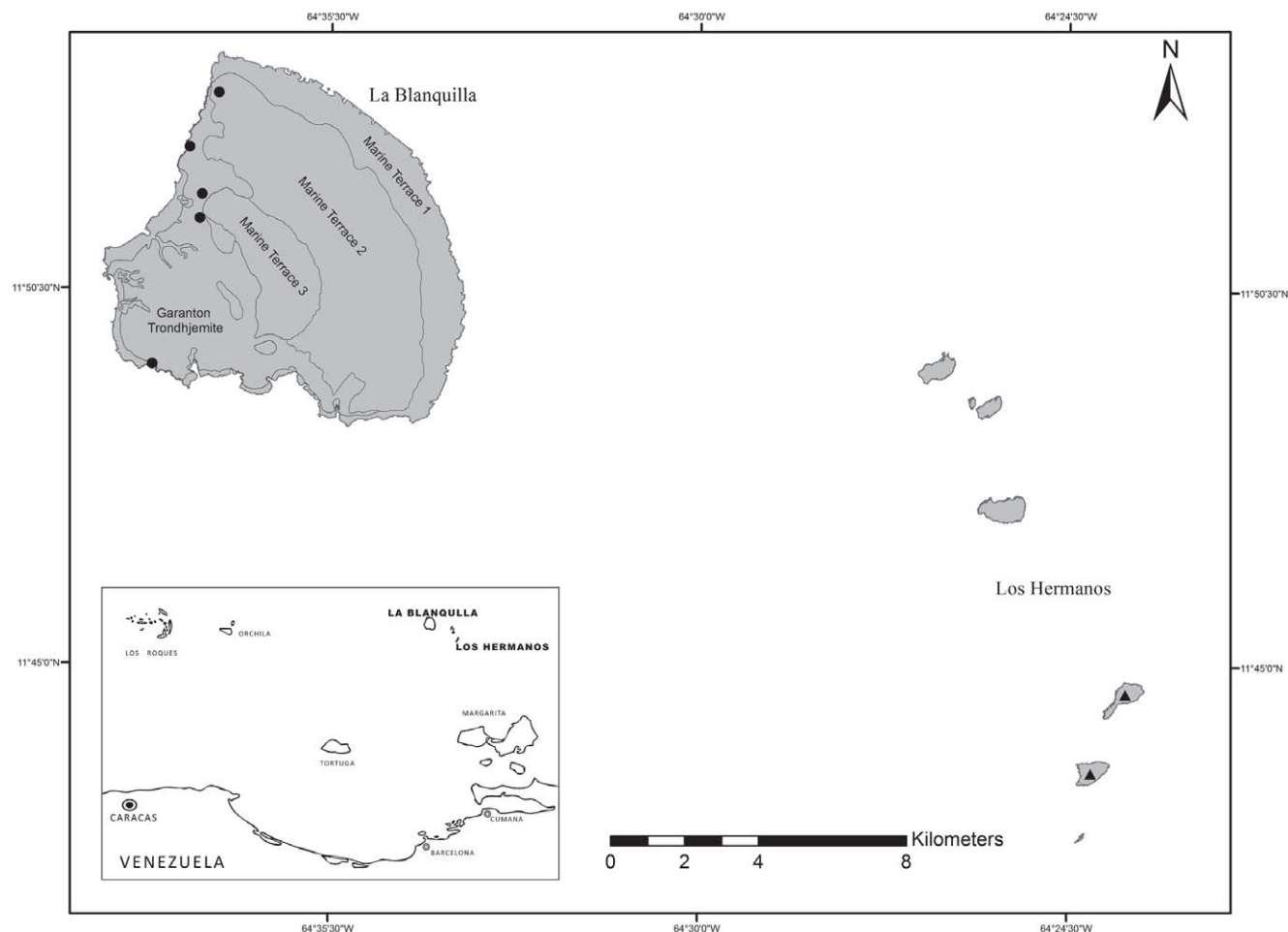


Figure 6. Map showing localities where *Gonatodes naufragus* sp. nov. was collected on La Blanquilla Island (black dots). Records of “*Gonatodes spec.*” by Hummelinck (1940) on the neighboring archipelago of Los Hermanos (black triangles) that likely represent other populations of the new species.

hatchling (MBLUZ 1013) is the following: anterior flanks and scapular region reddish with small yellow spots; dorsum reddish with a dark brown dorsolateral stripe with narrow yellow borders at each side of the body, extending from the nostril to the sides of anterior third of tail, with interrupted on scapular region. Dorsum and tail brown peppered with yellow, but less distinctly than on flanks (see Fig. 4E). The subadult specimen (MBLUZ 1146) has a color pattern intermediate between the hatchling and the adults. It is reddish grey with tiny white dots on the side of the body; the head is grey overlaid with red reticulations; the venter is grey.

Hummelinck (1940) briefly described the coloration of adults and juveniles from the specimens he collected on Los Hermanos Archipelago as follows:

Upperparts greyish (in life reddish), without any well marked design, underparts much lighter. Juveniles with a well marked laterodorsal, dark-brown stripe, abruptly beginning in occipital region, narrowing and becoming more vague on tail; each stripe with an irregular series of several spots in groundcolor medially, with a little yellow dot in each centre anteriorly; two narrow yellow stripes below and above the eye, disappearing in occipital region.

He also provided a brief morphological description (e.g., snout acutely pointed, 12 lamellae beneath fourth finger, 14 beneath fourth toe, 40–45 scales between anterior border of arm and vent). It is clear by the color and morphological descriptions provide by Hummelinck (1940) that Los Hermanos specimens are conspecific with the species described here from Isla La Blanquilla. This is not surprising since La Blanquilla is located with Los Hermanos Archipelago on a shallow marine platform (Maloney 1971).

Distribution and natural history. *Gonatodes naufragus* is known only from La Blanquilla, Dependencias Federales and from at least two islets or “morros” from Los Hermanos Archipelago, Venezuela (Fig. 6). The holotype EBRG 5224 and MBLUZ 1010 were found under the bark of a large dead tree a few meters from the beach. On the same tree, but about 1.5–2 m aboveground, two *Phyllodactylus rutteni* were collected. MBLUZ 1011 was collected on a rainy morning while removing some fallen tree trunks on a coral substrate with scarce vegetation matter. The juvenile (MBLUZ 1013) and an adult female (MBLUZ 1012) were found around noon, under two decaying logs that maintained a higher level of moisture than in the areas around it. We found shells of at least five eggs and an unhatched egg inside a crevice of one of these logs. MBLUZ 1146 was found under a rock just in the base of a small tree in storm scrub. MBLUZ 1147 was found

in a vertical terrace a few meters from the shore line in a shaded, very humid, area. MBLUZ 1148 was found on the ground inside the roots of a big tree. This area was covered with abundant leaf litter (Fig. 7B). All localities where this species has been observed come from the granitic area, except the specimen from the patch from Playa Juan Gerardo and Playa El Barco, which come from an area where the marine terraces are in contact with the granitic basement. It is particularly important, because the granite basement is older than the terraces and offers more suitable and humid conditions with shaded areas than those found on the terraces. We did not observe *G. naufragus* at night; however, the vertically oval pupil suggests possible crepuscular or nocturnal habits. The condition of the iris is similar to that of *G. antillensis*, the only known species of the genus with nocturnal habits.

On October 2010 we had the opportunity to observe a feral cat around the camp. On the trip of 2012, several cats were observed, including on the most distant parts of the island. Several rats and mice were also observed. All



Figure 7. Typical landscape of hills in La Blanquilla Island (A). The hills are formed from exposed granitic lithology sparsely covered with grasses. Sediments from erosion and detritus accumulate at the bottom of the hills, which creates a matrix that retains moisture and allows for shrubs and small trees to grow. Microhabitat of *Gonatodes naufragus* under a *Ficus* tree (B) on La Blanquilla Island. Photographs by Lenin Parra (A) and Gilson A. Rivas (B).

these three invasive species might affect the survival of the native reptile fauna of the island.

La Blanquilla, is located approximately 100 km northwest of Isla de Margarita. The island has an area of 52.5 km² and the highest altitude over 30 m above sea level (Fig. 7A). On the isla La Blanquilla, a sequence of reef limestone, called Blanquilla formation, crops out on the island. This formation consists of three marine terraces. The Blanquilla formation lies unconformably above the basement of the island, which consists of the Garantón Trodhjemite, of Paleocene age, while the age of the Blanquilla formation is Pleistocene (Schubert, 1976). Other species endemic to both Isla La Blanquilla and Los Hermanos Archipelago are *Anolis blanquillanus* Hummelinck, 1940, *Phyllodactylus rutteni* Hummelinck, 1940, and *Cnemidophorus leucopsammus* Ugueto and Harvey, 2010. Except for the Green Iguana, all lizards described from these islands are endemic. Populations of *P. rutteni* reported from other islands of the Venezuelan Antilles represent undescribed species to be described by the authors elsewhere.

Etymology. The specific epithet *naufragus* is a Latin masculine adjective, meaning “shipwrecked” or “cast-away”, alluding to how a putative ancestor of this species could have colonized Isla La Blanquilla, remaining stranded on this small island and evolving in isolation from its congeners.

Comparisons. With a maximum SVL 31.1 mm (Rivera Rodríguez *et al.*, 2011), *Gonatodes daudini* Powell and Henderson 2005, from the tiny Union island, Grenadines, was until now considered the smallest species of its genus (Powell and Henderson, 2005). However, that title can now be assigned to *G. naufragus*, with adult females (the largest sex) reaching a maximum SVL of just 27.2 mm. The diminutive size of both taxa readily separates them from all the other 28 known species of *Gonatodes* (Rivero-Blanco and Schargel, 2012), all of which reach or exceed SVL 35 mm. Not only do *G. naufragus* and *G. daudini* share a small size, but they exhibit a suite of other characters unique to these two species. Both taxa have a conspicuously elongated and sharply pointed snout, with a larger

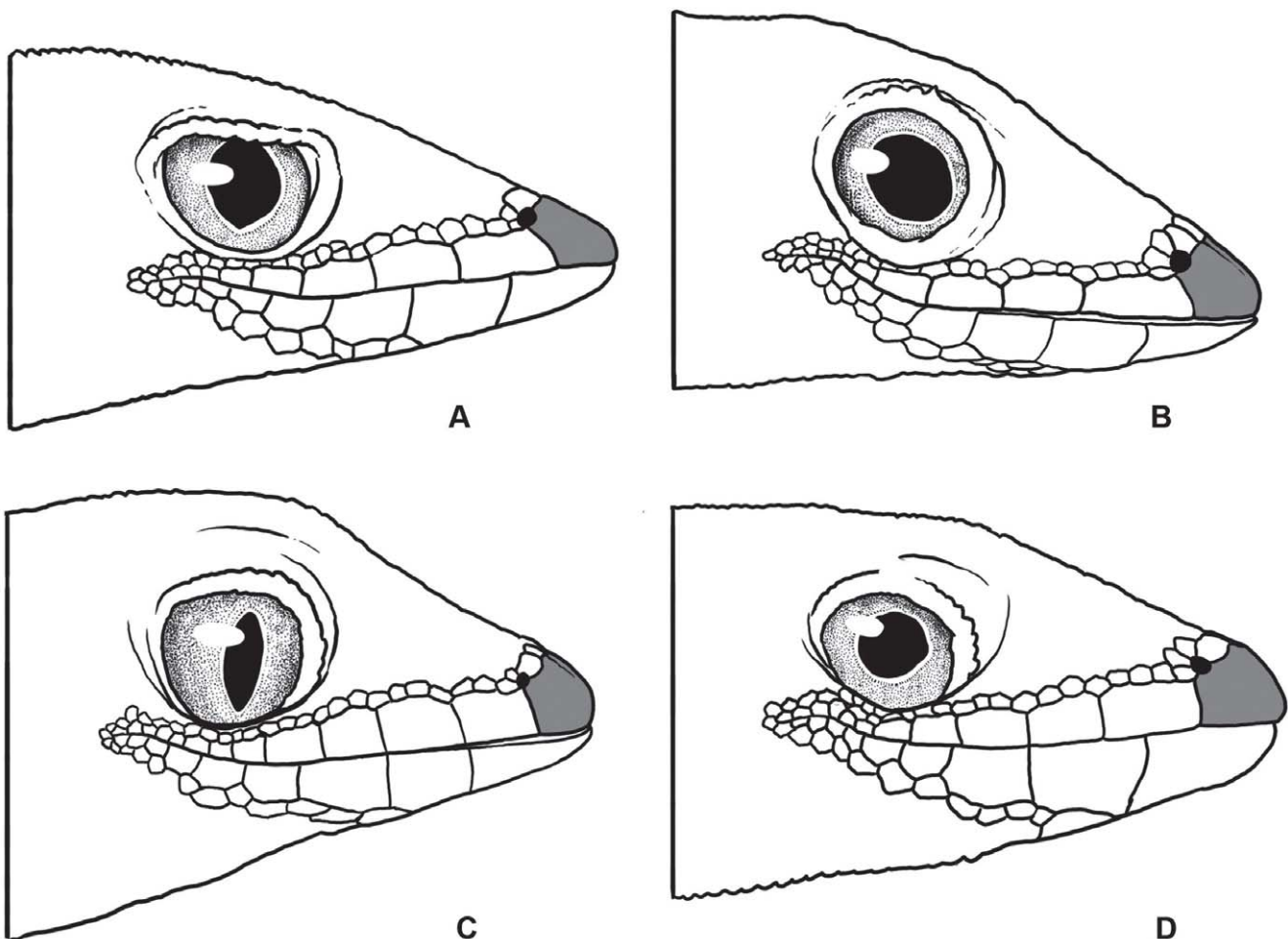


Figure 8. Schematic drawing of the shape of the pupil and the snout in three species of *Gonatodes*. (A) *Gonatodes naufragus* sp. nov. (paratype MBLUZ 1012, adult female). (B) *Gonatodes daudini* (MPM 33975, adult male). (C) *Gonatodes antillensis* (MBLUZ 1001, adult female). (D) *Gonatodes* aff. *albugularis* (MBLUZ 1036, adult male).

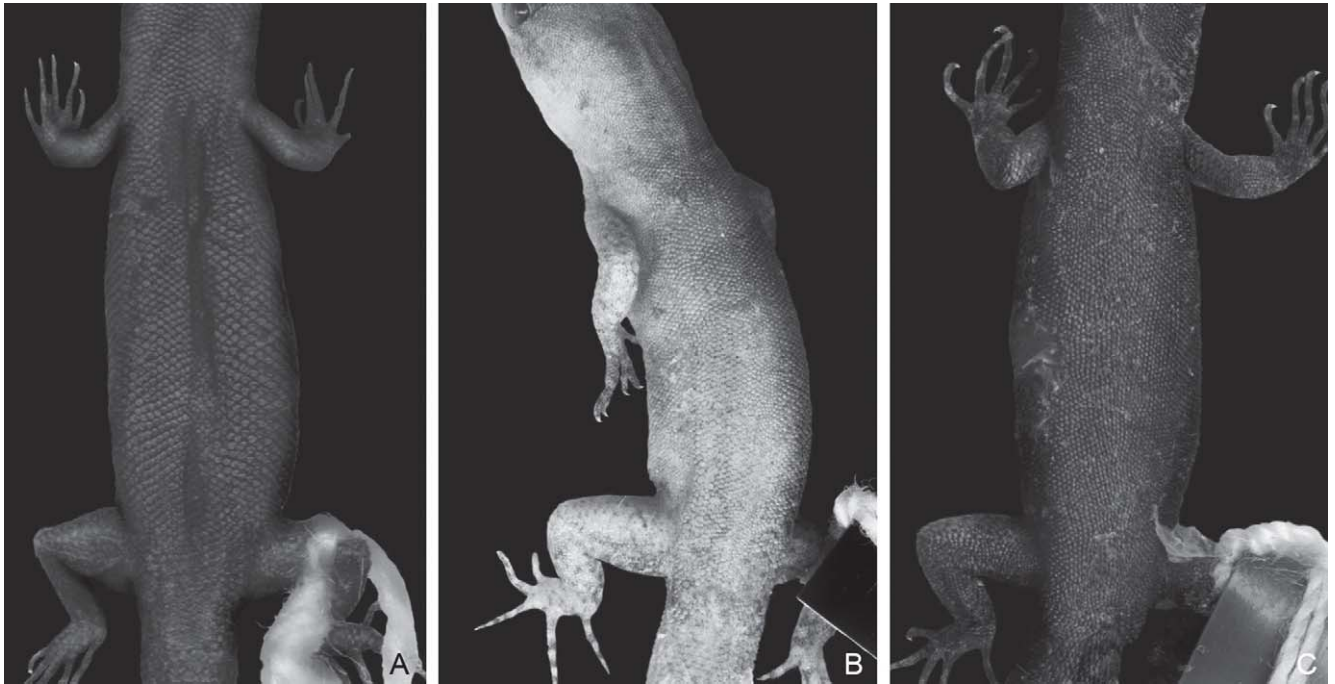


Figure 9. Dorsal squamation in three species of *Gonatodes* from Venezuela. **(A)** *Gonatodes naufragus* sp. nov. (holotype EBRG 5224, adult female). **(B)** *Gonatodes antillensis* (MBLUZ 1002, adult male). **(C)** *Gonatodes* aff. *albobularis* (MBLUZ 1037, adult male).

distance between the nostril and the tip of the rostral scale compared to that in all other species of *Gonatodes* (Fig. 8). The pointed snout in *G. naufragus* and *G. daudini* is reminiscent of that in *Sphaerodactylus*.

Both *Gonatodes naufragus* and *G. daudini* are unique in having relatively (*G. naufragus*) to conspicuously (*G. daudini*) enlarged and bulky dorsals instead of the typical granules that are only slightly larger than the scales on the top of the head found in all other *Gonatodes* (Fig. 9). The diagnostic low counts of scales around the midbody exhibited by both species (60–67 in *G. naufragus* and 33–44 in *G. daudini*) reflect that. However, this character is much more pronounced in *G. daudini* than in the new species (compare Fig. 9A–C with Powell and Henderson, 2005: fig. 3), with much larger, bulkier and juxtaposed dorsals in the former, noticeably smaller and subimbricate in *G. naufragus*. In some aspects, the condition exhibited by *G. naufragus* would appear to represent an intermediate stage between the small granules typical of most *Gonatodes* and the large scales of *G. daudini*. Additionally, both taxa are atypical in that neither taxon is sexually dichromatic (see Rivera Rodriguez *et al.*, 2011 for data on *G. daudini*). In most of *Gonatodes* sexual dichromatism is evident, with males often being brightly ornamented whereas females are cryptically colored. The only other *Gonatodes* reported to lack sexual dichromatism is the recently described *G. lichenosus* from Sierra de Perijá in northwestern Venezuela (Rojas-Runjaic *et al.*, 2010), which can be easily distinguished by numerous other characters (*i.e.*, larger SVL, granular dorsal scales, rounded snout, clusters of enlarged spine-like scales along flanks).

The new species differs from *Gonatodes daudini* in other characteristics (data of the latter taxon in parentheses): dorsal coloration uniformly reddish brown (yellowish to grayish-brown with one or more pairs of conspicuous lateral ocelli), reddish brown iris (bright red iris), and a vertically elliptical pupil (round). In this latter characteristic, *G. naufragus* differs from all other species of the genus except *G. antillensis*, which is currently believed to be the only consistently nocturnal *Gonatodes* (Schargel *et al.*, 2010). Currently, it is not known whether *G. naufragus* is also nocturnal in habits but the presence of a vertically elliptical pupil appears to indicate this possibility. The new species can be easily separated from *G. antillensis* (data of the latter taxon in parentheses) in having much larger dorsals, with approximately 60 scales around midbody (granular dorsals, with approximately 80 scales around midbody), males with distinct escutcheon on abdomen (escutcheon absent), and no sexual dimorphism in coloration (sexual dimorphism conspicuous; see Fig. 4A–B).

Sequence characteristics and phylogenetic relationships

The selected model for all six partitions (all nucleotide sites separated by gene and codon position) under AICc was HKY with or without gamma parameter depending on the partition. Because the nucleotide substitution model was the same (HKY+G) for the first and second codon positions for both genes, and because of the low number of substitution for these codon positions, we

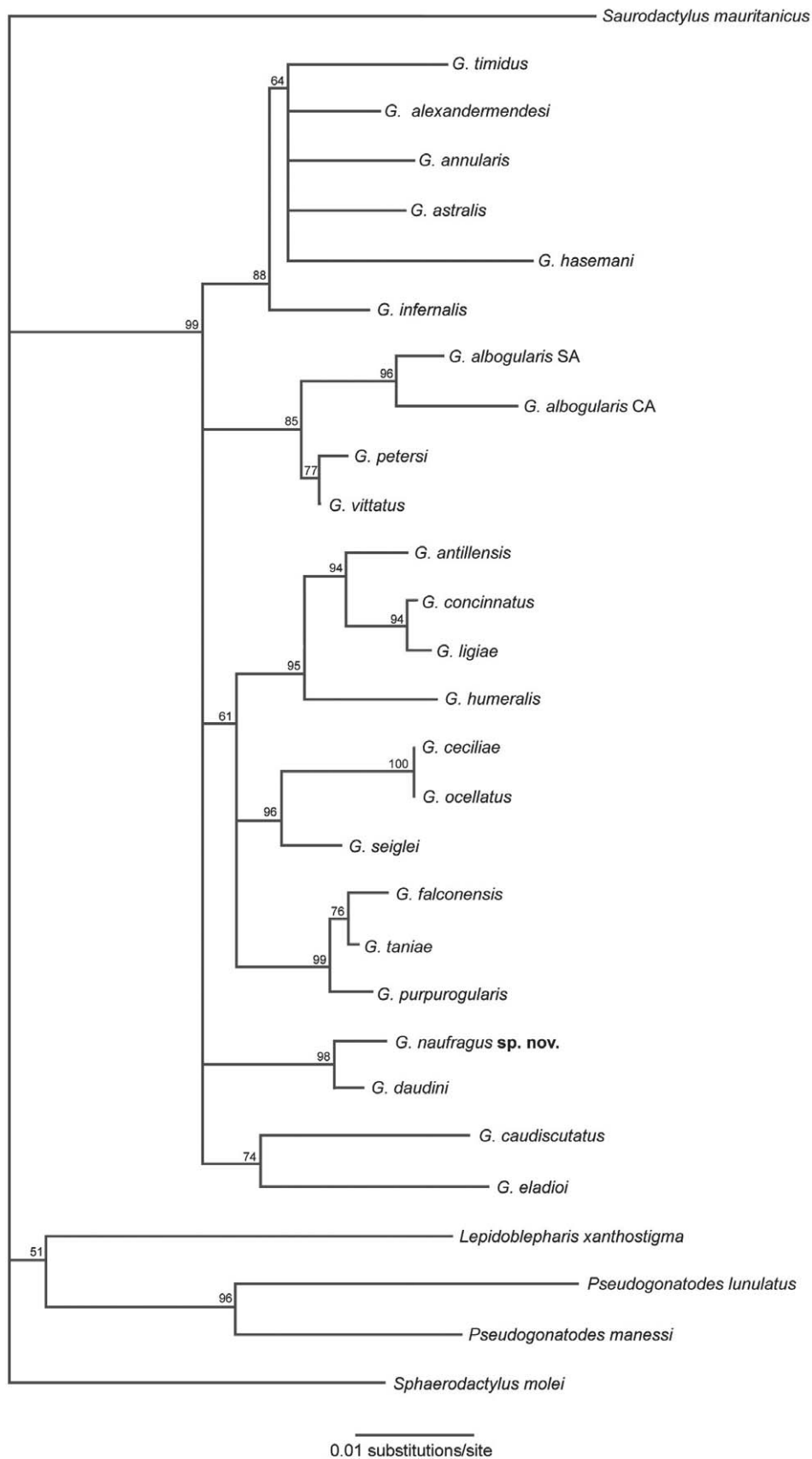


Figure 10. Consensus phylogenetic tree (consensus level: 50) of a maximum likelihood bootstrap analysis (bootstrap values shown on nodes) of two nuclear genes (C-mos and NT3) for the genus *Gonatodes*.

decided to combine them into a single partition while keeping them separated by gene. The “propose model” option in TREEFINDER as described above was conducted once again with the new partition scheme yielding the HKY+G model for all partitions except for the third codon position of C-mos, which was simply HKY. The ML bootstrap consensus tree obtained is shown in Fig. 10. The phylogenetic analysis suggests a strongly supported (bootstrap value: 98) sister species relationship between *Gonatodes daudini* and *G. naufragus*, corroborating with our observations on the morphological similarities between both taxa. The relationship of this clade to other *Gonatodes* remains uncertain, as the basal relationships within the genus are poorly resolved.

DISCUSSION

The fact that *Gonatodes naufragus* and *G. daudini* share unique morphological features within the genus, along with the strongly supported sister relationship inferred, and low genetic divergence (uncorrected p is 0.007 and 0.008 for C-mos and NT3, respectively) leaves little doubt of a close relationship and, perhaps, even relatively recent divergence between both taxa. The relationship of this clade to other *Gonatodes* remains uncertain, which is consistent with the unresolved placement of *G. daudini* in both the maximum parsimony and Bayesian analyses conducted by Schargel *et al.* (2010). However, we note that in the Bayesian analysis conducted by Gamble *et al.* (2008), *G. daudini* was recovered as the sister species to a clade containing *G. albogularis* and *G. vittatus*. It is possible that the higher resolution obtained by Gamble *et al.* (2008), as far as basal relationships of *Gonatodes*, results from the larger character dataset used by these authors.

The close phylogenetic relationship between *Gonatodes naufragus* (from La Blanquilla Island) and *Gonatodes daudini* (from Union Island, The Grenadines) shows interesting parallels with that of other Caribbean lizards. For example, species in the *Anolis roquet* series are restricted to the southern Lesser Antilles and the islands of La Blanquilla and Bonaire. Gorman and Stamm (1975) examined the evolutionary relationships within the *Anolis roquet* series and concluded that *A. blanquillanus* from La Blanquilla and *A. bonairensis* from Bonaire are closely related to *A. luciae* from St. Lucia, north of the Grenada bank. Yang *et al.* (1974) postulated two possible events for how these anoles could have colonized the Lesser Antilles and the islands of the southern Caribbean. A primary event of stepwise colonization of the Lesser Antillean island banks closest to the South American mainland followed by a secondary event where lizards from St. Lucia colonized La Blanquilla and then dispersed from the latter westward towards Bonaire. An ancestor of South American origin can also be inferred for whiptail lizards

of *Cnemidophorus* present on these islands. At least six species of *Cnemidophorus* are distributed throughout non-continental landmasses in the southern Caribbean (Dutch and Venezuelan Antilles), whereas one closely related taxon (*C. vanzoi*) is present on the tiny Maria Major and Minor islands, off the southeastern coast of St. Lucia (Ugueto and Harvey, 2010). The latter species share numerous morphological characteristics with the southern Caribbean *Cnemidophorus* (Harvey *et al.*, 2012), once again strengthening a probable zoogeographical link between these islands. Considering the similarities, the common ancestor of *Gonatodes naufragus* and *G. daudini* could also have a South American origin. The putative ancestor must have been able to colonize these islands and establish populations that gave rise to the two presently known taxa.

Notes on the distribution of some other Caribbean *Gonatodes*

The islands of Curaçao, Bonaire and La Orchila, as well as the archipelagoes of Los Roques and Las Aves, are all inhabited by at least one native species of *Gonatodes*. The most widespread taxon is *G. antillensis*, found in Bonaire, Curaçao, Las Aves and Los Roques (although the conspecificity of these populations has not been rigorously tested). Los Roques is also inhabited by *G. aff. vittatus*, whereas the small neighboring island of La Orchila is populated by a taxon associated with *G. albogularis*, currently being described by the authors.

The situation in Aruba is less clear. Three species of *Gonatodes* have been reported to occur on the island: *G. albogularis*, *G. antillensis* and *G. vittatus* (van Buurt, 2001). Lidth de Jeude (1887) recorded *G. antillensis* from Aruba and stated: “Many specimens were captured in Curaçao and Aruba”. Hummelinck (1940) did not find this species on the latter island, in spite of extensively collecting there, and considered that Aruba could be safely excluded as part of the distribution of *G. antillensis*. However, van Buurt (2005) once again included *G. antillensis* as part of the Aruban herpetofauna and considered that the species was probably introduced from Curaçao. Cope (1885) reported *G. albogularis* from Aruba. Neither Ruthven (1923) nor Hummelinck (1940) recorded new specimens from this island but van Buurt (2005) still considered it part of the Aruban herpetofauna. According to van Buurt (*pers. com.*), he has never observed either *G. antillensis* or *G. albogularis* on the island but reported them as present based on a checklist of the herpetofauna of Aruba by Odum (1992). Odum himself had never observed *G. albogularis* or *G. antillensis* on Aruba but preferred not to exclude them from his checklist since his fieldwork on the island had been fairly short, thus not being able to confidently demonstrate that the

lizards were not present on Aruba (van Buurt, *pers. com.*). Whether *G. albogularis* and *G. antillensis* were or are still present on Aruba cannot be assured at the present moment, but it is very likely that if they were ever found on the island, this was due to human introductions. In the past, building material (where these small lizards or their eggs could have been inadvertently transported) would ship from places such as Coro and Punto Fijo on nearby mainland Venezuela (van Buurt, *pers. com.*), where *G. albogularis* is common. This could probably explain the possible historic occurrence of the latter species on Aruba. The origins of *G. antillensis* on the island are more difficult to ascertain but they could also be attributed to a mislabeled specimen.

Contrary to the situation of *Gonatodes albogularis* and *G. antillensis* on Aruba, *G. vittatus* is quite common and has been repeatedly recorded on the island (e.g., Ruthven, 1923; Hummelinck, 1940; van Buurt, 2005). However, *G. vittatus* also appears to have been introduced on Aruba. Ruthven (1923) found it only in and about the town of Oranjestad, although searches for this lizard were carefully carried out in other localities of the island. Photographs of specimens from Aruba (e.g., photo 26 and 27, p. 53 in van Buurt, 2005) show animals identical to those found on the Venezuelan mainland. Purported absence of native *Gonatodes* on Aruba is surprising because of its proximity to the Venezuelan mainland and because the island was probably connected to the mainland through a land bridge at some point during the Pleistocene (van Buurt, 2005). It would be the only southern Caribbean island lacking a native *Gonatodes* species. In contrast, Aruba is home to other endemic lizards (*Cnemidophorus arubensis* and *Phyllodactylus julieni*), which belong to genera that also have endemic taxa on other islands of the Dutch and Venezuelan Antilles.

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inventario nacional de Fauna), Maracaibo, and Fundación La Salle de Ciencias Naturales (use of tissue samples, Oficio No. 0053, project sistemática, filogenia y taxonomía de las lagartijas del género *Gonatodes* (Reptilia: Gekkonidae), Caracas. For help with molecular lab work we are indebted to C.L. Cox. Finally we would like to thank T.C.S. Avila-Pires, R.C. Jadin P.J.R. Kok and an anonymous reviewer for their comments and suggestions to improve a preliminary version of this manuscript.

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APPENDIX I

List of comparative material examined

Gonatodes aff. *albogularis* (7). VENEZUELA: Dependencias Federales: La Orchila, MBLUZ 1035–1041.

Gonatodes antillensis (7). VENEZUELA: Dependencias Federales: Archipiélago de Las Aves (Barlovento), MBLUZ 999–1004. Los Roques: Gran Roque, MHNLS 1031 [holotype of *Gonatodes vitattus roquensis*].

Gonatodes astralis (1). VENEZUELA: Bolívar: Serranía de los Pijiguaos, Distrito Cedeño, 600 m, MBLUZ 931 [paratype].

Gonatodes daudini (1). ST. VINCENT AND THE GRENADINES: Union Island, Water Rock Reserve on the northern slope of Mt. Taboi above Chatham Bay (12°35'N, 61°25'W), MPM 33975 [paratype]

Gonatodes infernalis (2). VENEZUELA: Amazonas: sector El Infierno, on road Puerto Ayacucho-Gavilán, ca. 100 m, UTA R-55378-79 [paratypes].

Gonatodes aff. *vittatus* (3). Los Roques: Gran Roque, MHNLS 1033, 1037, 1039 [paratypes of *Gonatodes vitattus roquensis*].

APPENDIX II

Genbank accession numbers for sequences (c-mos, nt3) used in the phylogenetic analysis

Gonatodes albogularis (GU139825, GU139877), *Gonatodes albogularis* (GU139826, GU139878), *Gonatodes alexandermendesi* (GU139803, GU139856), *Gonatodes antillensis* (GU139827, GU139879), *Gonatodes annularis* (GU139807, GU139860), *Gonatodes astralis* (GU139820, GU139873), *Gonatodes caudiscutatus* (EF534920, no sequence), *Gonatodes concinnatus* (EF564070, no sequence), *Gonatodes daudini* (GU139832, GU139885), *Gonatodes eladioi* (EF564081, no sequence), *Gonatodes falconensis* (GU139829, GU139882), *Gonatodes humeralis* (GU139836, GU139889), *Gonatodes infernalis* (GU139816, GU139869), *Gonatodes ligiae* (GU139831, GU139884), *Gonatodes naufragus* (JQ039940, JQ039941), *Gonatodes ocellatus* (GU139839, GU139892), *Gonatodes petersi* (GU139841, GU139894), *Gonatodes purpurogularis* (GU139830, GU139883), *Gonatodes seiglei* (GU139837, GU139890), *Gonatodes taniae* (GU139838, GU139891), *Gonatodes timidus* (GU139824, no sequence), *Gonatodes vittatus* (GU139840, GU139893), *Lepidoblepharis xanthostigma* (GU139842, GU139895), *Pseudogonatodes lunulatus* (GU139844, GU139897), *Pseudogonatodes manessi* (GU139845, GU139898), *Saurodactylus mauritanicus* (GU139846, GU139899), *Sphaerodactylus molei* (GU139843, GU139896).