A new genus and species of Caribbean forest lizard (Diploglossidae; Celestinae) from southern Hispaniola

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Abstract

A new genus and species of Caribbean forest lizard of the subfamily Celestinae Schools & Hedges are described. This new taxon is known only from two small adjacent keys in the Laguna de Oviedo of the Parque Nacional Jaragua in the Barahona Peninsula, Dominican Republic, at the southernmost region of the Caribbean island of Hispaniola. The genus Guarocuyus gen. nov. is genetically more closely related to the clade containing Celestus Gray, Comptus Schools & Hedges, and Panolopus Cope; nevertheless, we compare it to all celestine genera. Morphologically, it differs from other celestines by having an interdigital web on three toes and by having the widest ear opening. Additionally, the species Guarocuyus jaraguanus sp. nov. has some ecological attributes that when combined, appear to be unique, including nocturnal habits, a semiprehensile tail, and a facultatively arboreal lifestyle. We note sexual dimorphism in the new species and in two other celestines, Caribicus darlingtoni (Cochran) and the poorly known Celestus macrotus Thomas & Hedges, and report a range extension of the latter species into the Dominican Republic. We also discuss several scale topography conditions considered of taxonomic value for the group.

Key words: Neoanguimorpha, Anguidae, Celestus, Hispaniola, Barahona Peninsula

Introduction

The Neotropical forest lizards of the family Diploglossidae Cope are distributed throughout Middle America, South America, and islands of the Caribbean. Twenty-eight species are found on Caribbean islands (Schools & Hedges 2021),
and most of these are distributed among the large islands of the Greater Antilles, with single species on Cayman Brac and Little Cayman, Navassa, and Montserrat islands. After Schwartz (1964, 1965) made comprehensive revisions of the Hispaniolan species of this group of lizards, only six species were recognized. Subsequently, descriptions (Schwartz 1970; Thomas 1971; Schwartz & Incháustegui 1976; Schwartz et al. 1979; Thomas & Hedges 1989) and checklists increased the number (with the synonymy of one; Powell et al. 1996) to the current twelve species found on the island (Powell 1999; Hedges 2022; Schools & Hedges 2021). The family Diploglossidae was recognized based on its deep divergence from other anguioids (Hedges & Vidal 2009), and a recent revision (Schools & Hedges 2021) recognized three subfamilies: Celestinae Schools & Hedges, Diploglossinae Cope, and Siderolamprinae Schools & Hedges. Six of the seven celestine genera are Caribbean, all of which occur on the island of Hispaniola and its satellites, with Celestus also occurring on Jamaica. Molecular analyses have shown that Celestinae contains many cryptic species (Schools & Hedges, 2021). In addition, newly collected material from a poorly-known area in southern Hispaniola differs both genetically and morphologically from all currently known lineages, warranting the creation of an additional genus, which we herein describe.

Little is known about diploglossid ecology and natural history given the cryptic habits of most species. Schools & Hedges (2021) recently discussed natural history of some species and reviewed ecomorphology (Schools et al. 2022). Having the opportunity to study this new species in the field, we obtained preliminary information on activity patterns and diet. Ontogenetic variation in scale topography (strigae shape and keeling) has been noted by some authors, such characters being considered of taxonomic value (Schwartz 1964; Thomas & Hedges 1989). Also, sexual dimorphism has been said to be minimal in this group; however, we found differences between the sexes in three characters, supporting observations of one of the characters from previously published information (Inchaustegui et al. 1985).

Material and Methods

Molecular analyses

The molecular data set comprised 66 taxa (Appendix 1) and 6,949 total aligned sites from mitochondrial genes (CytB, ND2, 12S rRNA, and 16S rRNA) and nuclear genes (AMEL, BDNF, PRLR, RAG1, and ZFP36). In total, the phylogeny represents 31 diploglossid species. DNA was extracted, amplified, and aligned according to the methods outlined in previous work (Schools & Hedges 2021). Localities, Genbank accession numbers, and museum numbers (if applicable) for all previously published sequences are reported elsewhere (Schools & Hedges 2021, Appendix 1). This information for all new sequences and specimens is in Appendix 1.

We used Maximum Likelihood (ML) and Bayesian methods to conduct phylogenetic analyses, with the anguid species Pseudopus apodus, as the outgroup. We generated our phylogeny using IQ tree v2.1.2 (Minh et al. 2020) and assessed branch support with 2000 ultrafast bootstrap replicates. We used a GTR + Γ + I model in Bayesian analyses performed with MrBayes 3.2.7 (Ronquist et al. 2012). We ran four chains for one million generations each, with a 25% burn-in and sampling every 100 generations. We quantified nodal support for Bayesian trees with posterior probabilities (PP) and assessed convergence by monitoring the standard deviation of split frequencies (<0.01 in all cases).

Morphological analyses

Lizards were captured by hand and were fixed with 95% ETOH and then preserved in 70% ETOH. Measurements were taken using digital calipers, and an ocular micrometer through Motic K-400 stereoscopes for some characters. In the morphological description below, we follow the methods of Hedges & Conn (2012) and Schools & Hedges (2021), adding three characters: the presence/absence of an interdigital web on feet (foot webbing = FW; Fig. 1), the relative size (%) of the ear width (EW/snout-vent length –SVL), and the relative axilla-to-cloaca distance (% ACD/SVL, see below; Table 1). Abbreviations: head width (HW) and head length (HL); rostral height (RH) and rostral width (RW); interparietal distance (IPD); and frontonasal (FN) distance. For morphometric characters, we excluded specimens having less than 75% the SVL of the largest specimen (i.e. juveniles); however, we did include all except the smallest specimens of the new species to analyze sexual dimorphism. Furthermore, some measurements of the smallest specimens are provided for allometric reference. We scored meristic data and other morphological
characters from all size categories, except for the dorsal keel in small Panolopus costatus Cope (an ontogenetic trait, see Discussion). We used all specimens that were available for comparisons of morphological traits such as FW as well as for a fourth character, the dorsal tail scale condition (DTC; Fig. 2): scored as enlarged & swollen (ES) or flat and similar (to dorsals) in size and shape (FSSS). One morphometric character has been corrected from previous analyses (Schools & Hedges 2021): the relative axilla-to-groin distance (% AGD/SVL). This measure was previously presented in error, where for some genera the relative axilla-cloaca distance was reported, while for other genera the relative axilla-groin distance was reported. Herein we present both measurements, correctly separated.

For comparisons at the species level (Table 2), we used other structural (i.e. snout and body shape, meristic) characters (number of ventral and midbody scales, number of strigae) as well as chromatic characters (coloration and pattern), similar to Schwartz (1964), who found coloration and pattern to be the most diagnostic for the Comptus of Hispaniola and Panolopus. Dorsal scale strigae was scored as in Thomas & Hedges (1989) for up to ten scales per specimen. For scoring dorsal pattern (number of chevrons/crossbands), we counted those markings on the trunk (interlimb region) only. We scored venter condition (semi-translucent or completely pigmented) from photographs of living individuals (Fig. 3) and from primary literature records. Sexually dimorphic patterns were noted for some species in which sexes were confirmed (eversion of hemipenes in males, or the lack of them, and presence of ova in females), and observations of allometry were noted for the new species.

Museum abbreviations for specimens listed in Appendix 2 are as follows: ANSP (Academy of Natural Sciences, Philadelphia, Pennsylvania, USA), BMNH (Natural History Museum, London, England, UK), “C-00” (“Celestus”, individual coding from the monitoring program of Caribicus warreni Schwartz by the Ministerio de Medio Ambiente & Recursos Naturales, Santo Domingo, Dominican Republic), CAS (California Academy of Sciences, San Francisco, California, USA), CHFURG (Coleção Herpetológica da Fundação Universidade do Rio Grande, Brazil), CHUNB (Coleção Herpetológica da Universidade do Rio Grande, Brazil), CURC (Centro Universitario de Riviera, Uruguay), IIBZ-HER (Colecção Herpetológica del Instituto de Investigaciones Botánicas y Zoológicas, Universidad Autónoma de Santo Domingo), MALT (field tag series, Miguel A. Landestoy T., Dominican Republic), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA), MHCH (Museo Herpetológico de Chiriquí, David, Chiriquí, Panama), MNHNCU (Museo Nacional de Historia Natural de Cuba, La Habana, Cuba), MNHNSD (Museo Nacional de Historia Natural “Prof. Eugenio de Jesús Marcano”, Santo Domingo, Dominican Republic), MVZ (University of California, Museum of Vertebrate Zoology, Berkeley), SBH (Frozen tissue and voucher collection, S. Blair Hedges, Temple University, Philadelphia, Pennsylvania, USA), SMF (Senckenberg Forschungsinstitut und Naturmuseum [alternatively Senckenberg Research Institute and Natural History Museum], Frankfurt am Main, Germany), USNM (National Museum of Natural History, Washington, D.C., USA), UTA (University of Texas at Arlington, Department of Biology, Texas, USA).

Results

Molecular analyses

The molecular phylogeny of 31 diploglossid species represents all but one of the 11 genera of diploglossid lizards (Fig. 4). In our ML analyses, all nodes that defined genera and subfamilies were significant (≥ 95%). In our Bayesian analyses, all nodes defining genera were significant. In those analyses, the nodes defining Celestinae and Diploglossinae were significant, whereas the node defining Siderolamprinae had a value of 94. The placement of the newly collected material from southern Hispaniola (seven specimens; Fig. 4) is supported by an 87% bootstrap value in ML analyses, and a value of 100 in Bayesian analyses. We thus describe below these specimens as representatives of a new genus.

Morphological analyses

Systematic accounts
Diploglossidae Cope
Celestinae Schools & Hedges
TABLE 1. Diagnostic characters used to distinguish genera of the subfamily Celestinae in Schools and Hedges (2021), with additional characters (see Methods): (1) claw sheath: absent (a), present (p), (2) scales in contact with the nasal scale, (3) postnasal scales, (4) medial keel on dorsal body scales, (5) digits per limb, (6) foot webbing: absent (a), present (p), vestigial (v), (7) longest toe lamellae, (8) dorsal scale rows, (9) DTC, (10) EW/SVL, (11) HW/SVL, (12) RH/RW, (13) FN/SVL, (14) IPD/SVL, (15) AGD/SVL, and (16) ACD/SVL. A dash indicates that no value was obtained for that trait. An asterisk (*) represents very rare values (1–2 cases). Parentheses for each character represent sample size.

| Species          | Sample Size | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|------------------|-------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| Advenus montisilvestris | 1           | p | 4 | 1 | a | 5 | - | 17 | 96 | -  | 0.99 | 12 | 50.2 | 2.46 | 0.632 | 60 | 67.5 |
| Caribicus anelpistus       | 3           | a | 4–5* | 1 | p (2) | 5 | a (2) | 16–19 | 92–95 (2) | ES (1) | 1.12–1.69 (2) | 17.0–17.2 (2) | 52.9 (1) | 4.11 (1) | 0.571 (1) | 55.6 (1) | 66.1 (1) |
| Caribicus darlingtoni     | 21          | a | 4 | 1 | a (15) | 5 | a (14) | 13–16 | 80–87 (15) | ES (13) | 1.17–1.99 (10) | 13.0–16.8 (8) | 50.3–64.5 (7) | 2.98–4.37 (7) | 0.340–0.586 (7) | 51.7–60.4 (7) | 62.8–67.4 (9) |
| Caribicus warreni         | 10          | a | 4–5* | 1 | p | 5 | a | 15–20 (9) | 82–102 | ES (7) | 1.20–1.88 (8) | 13.3–18.4 (8) | 50.3–64.5 (7) | 2.98–4.37 (7) | 0.340–0.586 (7) | 51.7–60.4 (7) | 62.8–67.4 (9) |
| Celestus barbouri         | 12          | a | 4 | 1 | p | 5 | v (1) | 12–16 (13) | 138–140 (2) | - | 1.19–1.93 (8) | 11.8–14.1 (2) | 59.1–63.1 (2) | 2.13–2.61 (2) | 0.473–0.714 (2) | 57.6–57.6 (2) | 63.2–66.2 (8) |
| Celestus crusculus        | 34          | a | 4 | 1 | a | 5 | a (1) | 10–18 (35) | 99–103 (2) | FSSS | 1.16–2.18 (28) | 12.5–12.8 (2) | 49.5–59.5 (2) | 2.83–3.14 (2) | 0.451–0.758 (2) | 52.5–58.6 (2) | 62.0–63.7 (29) |
| Celestus duquesneyi       | 2           | a | 4 | 1 | p | 5 | - | 19–23 (3) | - | - | 1.58 (1) | 16.67 (1) | 66.5 (1) | 3.58 (1) | 0 (1) | 56.0 (1) | 60.9–61.8 |
| Celestus fowleri         | 1           | a | 4 | 1 | p | 5 | - | 21 | 105 | - | 1.16 | 14.1 | 47.7 | 2.95 | 0.571 | 55.3 (1) | 66.4 |
| Celestus hewardii        | 7           | a | 4 | 1 | p | 5 | v (1) | 15–20 (8) | - | - | 1.54–2.21 (11) | - | - | - | - | 62.7–65.0 |
| Celestus macrolepis      | 1           | a | 4 | 1 | p | 5 | - | 24 | 109 | - | 1.62 | 13.71 | 2.82 | 0.161 | 0.161 | 53.2 | 64.9 |
| Celestus macrotus       | 11          | a | 4 | 1 | a | 5 | a (10) | 14–17 | 82–89 (10) | FSSS (8) | 1.61–1.99 (8) | 13.8–16.4 (8) | 51.3–62.1 (8) | 2.87–3.41 (8) | 0.557–0.977 (8) | 50.3–55.4 (8) | 60.5–65.8 (8) |
| Celestus microblepharis  | 1           | a | 4 | 1 | p | 5 | - | 11–12 (2) | 105 | - | 0.66 | 12.6 | 50 | 2.43 | 0.565 | 61.2 | 66.3 |

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<table>
<thead>
<tr>
<th>Species</th>
<th>Sample Size</th>
<th>Table 1 (Continued)</th>
</tr>
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<tbody>
<tr>
<td>Celestus molesworthi</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Celestus occidentis</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Celestus aratus</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Comptus hastus</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Comptus maculatus</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Comptus sternatus</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Guarocuyus jaraguanus sp.</td>
<td>19</td>
<td>4</td>
</tr>
<tr>
<td>Panolopus costatus</td>
<td>107</td>
<td>4</td>
</tr>
<tr>
<td>Panolopus curtissi</td>
<td>43</td>
<td>4</td>
</tr>
<tr>
<td>Panolopus marcanoi</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Sauresia sepsoides</td>
<td>62</td>
<td>4</td>
</tr>
<tr>
<td>Wetmorena agasepsoides</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>Wetmorena haetiana</td>
<td>60</td>
<td>4</td>
</tr>
</tbody>
</table>

**Table 1** (Continued)
TABLE 2. Diagnostic characters as in Schwartz (1964) and Thomas & Hedges (1989). Sample sizes for SVL (including those in this study) are limited to those above 75% of the SVL of the largest examined specimen (see Methods). *Meristics from the literature besides this paper. **Four specimens, 1–3 scales.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample Size</th>
<th>SVL (mm)</th>
<th>Body Shape</th>
<th>Snout Shape</th>
<th>Ventral Scales</th>
<th>Strigae</th>
<th>Dorsal Coloration</th>
<th>Ventral Coloration</th>
<th>Dorsal Pattern</th>
<th>Lateral Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caribicus warreni</td>
<td>8</td>
<td>233–300</td>
<td>Subcylindrical</td>
<td>Rounded</td>
<td>84–102**</td>
<td>46-69**</td>
<td>pale tan/yellow-tan/deep or medium brown</td>
<td>cream to very pale orange</td>
<td>12–15 crossbands</td>
<td>12–15 stripes</td>
</tr>
<tr>
<td>Celestus macrotus</td>
<td>8</td>
<td>68.6–86.1</td>
<td>Subcylindrical</td>
<td>Rounded</td>
<td>85–93*</td>
<td>5-17*</td>
<td>bronzy brown</td>
<td>cream to light beige/light salmon/burnt orange/bronzy greenish</td>
<td>15–21 herringbone to crossbands</td>
<td>usually a dark zone with 14–19 stripes + vertically arranged dots</td>
</tr>
<tr>
<td>Comptus stenurus</td>
<td>14</td>
<td>108.2–142.2</td>
<td>Depressed</td>
<td>Rounded</td>
<td>81–105*</td>
<td>19-27*</td>
<td>brown to tan/dull grayish-brown/metallic bronzy + greenish sheen</td>
<td>beige (1); dull yellowish/dull pale orange</td>
<td>usually 2 paramedian nuchal stripes + dark herringbone or crossbars</td>
<td>usually a dark zone</td>
</tr>
<tr>
<td>Guarocuyus jaraguanus sp. nov.</td>
<td>19</td>
<td>84.6–110.1</td>
<td>Subcylindrical to squarish</td>
<td>Rounded</td>
<td>100–114</td>
<td>19–34</td>
<td>orange-tan to tan</td>
<td>semi-translucent cream or pale beige</td>
<td>7–9 crossbands</td>
<td>7–10 stripes</td>
</tr>
<tr>
<td>Panolopus costatus</td>
<td>19</td>
<td>89.1–117.6</td>
<td>Depressed</td>
<td>Sharp</td>
<td>77–106*</td>
<td>18-28</td>
<td>bronzy/dark bronzy/dull bronzy/dull tan/brown/dark brown/reddish brown/bronzy brown/metallic brown/dark metallic brown</td>
<td>grayish-yellow/cream to pale yellow/dull yellow/pale orange/pale orange to yellow/dull yellow-orange/dull orange/purplish-gray/dull bronze greenish/pale or metallic bronzy</td>
<td>2 paramedian nuchal stripes, at times with herringbone or a vague suggestion of it (scattered dim brownish spots) + creamy dorsolateral lines</td>
<td>usually a dark zone</td>
</tr>
<tr>
<td>P. curtissi</td>
<td>1</td>
<td>76.3–100.4</td>
<td>Depressed</td>
<td>Sharp</td>
<td>83–101*</td>
<td>-</td>
<td>pale or dark metallic/pale metallic tan/dark bronze brownish</td>
<td>white/pale bufy/dull pinkish</td>
<td>usually patternless</td>
<td>a dark zone</td>
</tr>
</tbody>
</table>


FIGURE 1. Ventral view of the left foot of *Guarocuyus jaraguanus* sp. nov. (IIBZ-HER00001), showing foot webbing (indicated by the blue arrows). Note that the webbing is formed by lamellar extension and lacks scales.

FIGURE 2. Dorsal tail scale condition (DTC): enlarged and swollen in *Caribicus warreni* (MNHNSD 23.884).

*Guarocuyus* gen. nov.

urn:lsid:zoobank.org:act:1BA79AB3-AAB2-4F7C-BDC8-D449A622F228

Type species. *Guarocuyus jaraguanus* sp. nov., herein described (Figs. 6–9).
**Distribution.** Cayo de las Iguanas and adjacent Cayo Pei, Laguna de Oviedo, in the Barahona Peninsula, Dominican Republic, the southernmost part of Hispaniola (Fig. 5).

**Etymology.** The generic name is a latinized masculine patronym honoring the taíno Guarocuya (a.k.a Enriquillo), the last cacique of the Jaragua region and a hero of the last standing free community of this native Antillean people, who died around the first half of the 16th century (Altman 2007; Ozuna 2018).

**Diagnosis.** The new genus can be distinguished by the following combination of characters (see Schools & Hedges 2021): (1) claw sheath, absent or present, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four or five (mode 5), (4) postnasal scales, one or two (mode 1), (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, present, (7) digits per limb, five, (8) longest toe lamellae, 21–25, (9) dorsal scale rows, 88–98, (10) relative head width, 12.0–13.9, (11) relative rostral height, 54.1–64.5, (12) relative frontonasal length, 3.07–4.48, (13) relative interparietal distance, 0.179–0.755, (14) relative axilla-groin distance, 53.2–58.7, (15) relative axilla-cloaca distance, 62.5–67.7.

Within Celestinae, *Guarocuyus gen. nov.* is distinguished from *Advenus* Schools & Hedges by the presence of keels on the dorsal scales (vs. absent in *Advenus*), longest toe lamellae count (21–25 vs. 17 in *Advenus*), relative width of the ear opening (EW/SVL 2.33–2.90 vs. 0.99 in *Advenus*), RH/RW (54.1–64.5 vs. 50.1 in *Advenus*), relative frontonasal length (FN/SVL 3.07–4.48 vs. 2.46 in *Advenus*), and by the AGD/SVL (53.2–58.7 vs. 60.0 in *Advenus*). From *Caribicus* Schools & Hedges, *Guarocuyus gen. nov.* can be distinguished by the presence of an interdigital scaleless web between toes II–IV (vs. absent in *Caribicus*), longest toe lamellae count (21–25 vs. 13–20 in *Caribicus*), EW/SVL (2.33–2.90 vs. 1.17–1.88 in *Caribicus*), and by the DTC, FSSS (vs. ES in *Caribicus*). From *Celestus* Gray, *Guarocuyus gen. nov.* differs by the presence of an interdigital scaleless web between toes II–IV (vs. absent or vestigial scaly web only between toes III–IV in *Celestus barbouri* Grant; Table 1), and by the EW/SVL (2.33–2.90 vs. 0.99–2.21 in *Celestus*). From *Comptus* Schools & Hedges, *Guarocuyus gen. nov.* differs by the presence of an interdigital scaleless web between toes II–IV (vs. absent in *Comptus*, except for vestigial scaly web only between toes III–IV in some *Comptus stenurus* Cope), and by the EW/SVL (2.33–2.90 vs. 0.76–2.07 in *Comptus*). From *Panolopus* Cope, *Guarocuyus gen. nov.* differs by the presence of keels on the dorsal scales (vs. absent in adult *Panolopus*), presence of an interdigital scaleless web between toes II–IV (vs. absent in *Panolopus*), EW/SVL (2.33–2.90 vs. 0.57–2.24 in *Panolopus*), and by the RH/RW (54.1–64.5 vs. 37.6–52.8 in *Panolopus*). From *Sauresia* Gray, *Guarocuyus gen. nov.* differs by the presence of keels on the dorsal scales (vs. absent in *Sauresia*), number of digits per limb (5 vs. 4 in *Sauresia*), presence of an interdigital scaleless web between toes II–IV (vs. absent in *Sauresia*), longest toe lamellae count (21–25 vs. 8–12 in *Sauresia*), number of dorsal scales (88–98 vs. 101–127 in *Sauresia*), EW/SVL (2.33–2.90 vs. 0.43–1.17 in *Sauresia*), FN/SVL (3.07–4.48 vs. 1.70–2.56 in *Sauresia*), and by both AGD/SVL and ACD/SVL (53.2–58.7 vs. 63.9–69.9 in *Sauresia*, and 62.5–67.7 vs. 69.2–76.3, respectively). From *Wetmorena* Cochran, *Guarocuyus gen. nov.* differs by the presence of keels on the dorsal scales (vs. absent in *Wetmorena*), number of digits per limb (5 vs. 4 in *Wetmorena*), presence of an interdigital scaleless web between toes II–IV (vs. absent in *Wetmorena*), longest toe lamellae count (21–25 vs. 8–12 in *Wetmorena*), EW/SVL (2.33–2.90 vs. 0–0.63 in *Wetmorena*), FN/SVL (3.07–4.48 vs. 1.47–2.69 in *Wetmorena*), and by the AGD/SVL (53.2–58.7 vs. 59.9–65.7).

**Content.** The new genus currently bears a single species, *Guarocuyus jaraguanus sp. nov.* (described below).

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**FIGURE 3.** Ventral views of living females of *Guarocuyus jaraguanus sp. nov.* showing the semi-translucent condition. A) MNHNSD 23.3913 and B) IIBZ-HER00004.
FIGURE 4. Maximum likelihood phylogenetic tree of diploglossid lizards based on the concatenated dataset of nine genes (66 individuals, 6,949 sites): four mitochondrial genes (CytB, ND2, 12S rRNA, and 16S rRNA) and five nuclear genes (AMEL, BDNF, PLPR, RAG1, and ZFP36). A scale bar indicates 6% sequence divergence. The numbers at nodes are ML bootstrap values, followed by Bayesian posterior probabilities; asterisks indicate significant (≥ 95%) support, and a dash or zero value indicates weak (< 50%) support. The tree is rooted with *Pseudopus apodus* (Anguidae).
FIGURE 5. Map showing known locality for Guarocuyus jaraguanus sp. nov. marked with a red circle. Inset shows all of Hispaniola, with a red box indicating the mapped area.

Guarocuyus jaraguanus sp. nov.
Jaragua Forest Lizard
(Figs. 6–9)
urn:lsid:zoobank.org:pub:B98E34A9-E3CA-4B50-BD05-41CC093E6A0D

Holotype. MNHNSD 23.3937 (MALT1004; Fig. 8) collected by Miguel A. Landestoy on 22 September 2021 on Cayo de las Iguanas, Laguna de Oviedo, Parque Nacional Jaragua, Pedernales Province, Dominican Republic (17.73205, -71.37126, datum WGS84; elev. near sea level).


Diagnosis. See generic account above, description of the holotype and variation below.

The new species requires close comparison with Panolopus costatus and P. curtissi Grant, two species found in the neighboring mainland. Besides the traits listed above diagnosing the genus, Guarocuyus jaraguanus sp. nov. further differs from those two species by body shape (subcylindrical to squarish vs. depressed in P. costatus and P. curtissi) and a rounded snout (vs. a sharp snout in P. costatus and P. curtissi), which is reflected by a higher rostral scale (RH/RW 54.1–64.5 vs. 37.6–52.8 in Panolopus). It is also distinguished by long limbs (vs. short limbs in P. curtissi). In coloration and pattern, the new species differs by having a dorsum with 7–9 broad dark brown to blackish transverse chevronate crossbands on a tan or orange-tan ground color (vs. an usually unpatterned to narrow herringbone patterned bronze-tan dorsum in P. costatus and P. curtissi), sides with invading bars from
dorsal chevrons but ground color much paler (vs. sides highly pigmented, creating a two-zone area—dorsum light and a lateral dark band along the sides in *P. costatus* and *P. curtissi*), and by the presence of 8–10 longitudinal (transversed) blackish lines (vs. sometimes two broad paramedian nuchal lines in *P. costatus*, which more often occur in *Comptus stenurus*; Schwartz 1964).

The new species similarly differs from *Comptus stenurus* in body shape, being slender, subcylindrical to squarish in habitus (vs. a fusiform, somewhat depressed habitus in *Comptus stenurus*), and dorsal coloration and pattern consisting of 7–9 broad dark brown transverse crossbands or chevrons on an orange-tan ground color (vs. unpatterned to a pattern of herringbone on a bronze-tan dorsum in *Comptus stenurus*); a lateral pattern of 7–10 dark brown to blackish vertical stripes (vs. a dark continuous band along the sides in *C. stenurus*). Additionally, both species are allopatric. Also differing from *Panolopus costatus*, *P. curtissi*, and *Comptus stenurus*, is the lack of complete coalescence in the dorsal scale strigae (tuberculate and not continuous ridges; Thomas & Hedges 1989) in all specimens. This condition had been noted previously by Thomas (1966) in juvenile *Comptus badius* (Cope).

The new species also merits comparison with another South Paleo-island endemic that has a relatively large ear opening (mean EW/SVL 1.82) and a dark dorsal pattern, *Celestus macrotus* (the only member of the genus on Hispaniola), but differing in the presence of keels on the dorsal scales (vs. absent in *C. macrotus*), the high number of strigae of the dorsal scales (19–34 vs. 5–17 in *C. macrotus*), the high number of longest toe lamellae (21–25 vs. 14–17 in *C. macrotus*), and a narrower head (HW/SVL 12.0–13.9 vs. 13.8–16.4 in *C. macrotus*) with a complete separation in males (13.2–13.9 vs. 15.0–16.4 in *C. macrotus*); in coloration, it differs in dorsal ground color (orange-tan to tan vs. bronzy brown in *C. macrotus*) with a dorsal pattern of 7–9 dorsal chevronate crossbands (vs. 15–21 herringbone bars in *C. macrotus*), and a lateral ground color orange-tan to pale cream with 7–10 dark brown to blackish stripes (vs. predominantly dark brown to blackish by the 14–19 dark stripes in *C. macrotus*) usually without vertically arranged whitish dotting on the lateral zone (one specimen only vs. white dotting present in all specimens of *C. macrotus*); in the ventral coloration, the new species is semi-translucent cream to beige (vs. cream to light beige, light salmon, or burnt orange).
The dorsal coloration and pattern is somewhat similar to the large species in the genus *Caribicus* (*C. anelpistus* Schwartz and *C. warreni*), but the chevronate crossbands are wider in the new species, reflected in the lower count of these (7–9 vs. 12–15; Incháustegui *et al.* 1985; Table 2).

**Etymology.** The specific epithet *jaraguanus* is a masculine nominative singular adjective meaning “pertaining to Jaragua,” the name of the national park that encompasses the type locality. The common name Jaragua Forest Lizard follows proposed guidelines (Hedges *et al.* 2019; Schools & Hedges 2021).

**Description of the holotype.** A male (MNHNSD 23.3937 - MALT1004; Fig. 8) of moderate size (SVL 96.0 mm; Table 1); limbs long; body habitus relatively slender and somewhat elongate (AGD/SVL and ACD/SVL, 54.0 and 63.3, respectively) and not depressed, subcylindrical to squarish; tail cylindrical, partially regenerated; head proportions HW/SVL 13.9 and HW/SVL 18.6 (HW/HL 74.5); ear opening squarish, very large, EW/SVL 2.71; snout rounded; and pupil nearly elliptical.

Supralabials 10, with 7th and 8th supralabials contacting the angled subocular scale, the latter narrow and widely obtuse; postnasal one, scales contacting nasal four, loreals two, infralabials contacting postmental six; RH/RW 58.3, FN/SVL 4.15, and relative frontal length (FL/SVL) 5.95.

Dorsal scales 91, midbody scales 40, and ventral scales 106; dorsal scale strigae 23–27 (mode 27); lamellae on the longest toe (IV) 24. Interdigital scaleless webbing between toes IV and II, well developed between toes IV and III, covering up to the second lamella of the former, but running along the latter laterally as a fringe to the 5th lamella.
FIGURE 8. Holotype MNHNSD 23.3937 (MALT1004) *Guarocuyus jaraguanus* sp. nov. in dorsal (A), lateral (B), and ventral (C) views. Scale bar = 10 mm.
FIGURE 9. Lateral view of the head of *Guarocuyus jaraguanus* sp. nov. (MNHNSD 23.3912) showing two (red shading) postnasal scales.

FIGURE 10. Claw sheath variation in *Guarocuyus jaraguanus* sp. nov. Lines and arrows indicate the limits of the ungual scale. Toes of MNHNSD 23.3915 (A) and MNHNSD 23.3948 (B) showing the presence of a claw sheath, which is absent in IIBZ-HER00001 (C).

*Coloration and pattern in life.* Dorsal ground color orange-tan, with a dorsal pattern of nine dark brown to blackish inverted chevrons/crossbands, and two on the nuchal region traversed by 10 longitudinal blackish lines that depart from the parietal area, the six central lines intermittently joining and becoming irregular and diffuse, some of the parallel lines merging into one thicker than those that are isolated; each of all these lines usually narrower than a scale, placed along their half or center, altogether extending posteriorly to form the basis of the crossbands that compose the dorsal pattern to the postsacral area; the dorsal, sacral and postsacral crossbands more clearly defined because of interruptions that increase posteriorly showing the lighter dorsal ground color. Dorsal and lateral surfaces of the tail with eight broad blackish bands similarly formed as those on the dorsum. Nine lateral vertical stripes as continuations of the dorsal crossbands but most are centrally hollow by invasion of the paler latero-ventral coloration (grading from orange-tan into pale cream). Limbs dorsally burnt orange, their outer surfaces, elbows, and knees with blackish markings and lines, and articulations of fingers and toes blackish.

Two to three blackish temporal longitudinal lines depart from the postorbital area on both sides, the lower fading and blending into the other(s) above the ear opening. Four lateral, nearly vertical facial dark brown stripes, the first originating between the postnasal and loreal areas, traversing the third and fourth labial scales into the posterior edge of the first chin shield; the second facial stripe descends from the sixth supralabial down to the third chin shield; the third facial stripe (nearly diagonal) departs from the subocular angular scale through the eighth supralabial down into the edge of the throat; the fourth facial stripe is the longest (nearly diagonal and about a dozen scales long), departing from between the last supralabial and the ear opening and bent toward the posterior region of the throat; a less prominent diagonal stripe below the ear opening extends posteriorly; the first two labials, rostral, and mental scales dark brown.

The lateral region of the head a bone color, with dark brown smudges especially at the lower margin of
supralabials, and from below the eye through the upper half of preocular and loreal scales. Dorsal surface of the head predominantly dark brown to blackish, with contrasting pale yellowish-cream irregular streaks and a vague suggestion of a W at the posterior margins of parietal scales. Venter somewhat translucent with faded invading lateral stripes beige, and the intervening areas pale cream. Cloacal flap unpigmented. Iris dark bronze-red.

Coloration and pattern in preservative. Dorsal ground color tan, dorsal surface of hindlimbs of same color, that of forelimbs light beige; the pale markings on the head whitish cream. The patterning as described in life but of dark chocolate brown instead of blackish. Venter pale cream.

Variation. See also Tables 1 and 2. Scalation. Eight of the 19 specimens have two postnasal scales on at least one side (Fig. 9). Ten specimens have five scales contacting the nasal scale. In two specimens (MNHNSD 23.3913 and IIBZ-HER00005) in which only 1 postnasal is present, 5 scales contact the nasal, thus, the scoring for this trait does not depend on the number of postnasals. One specimen has 3 loreal scales on the left side (IIBZ-HER00004). Considerable frontonasal length variation exists both intra- and interspecifically (Table 1). The claw sheath trait is also variable (Fig. 10): three specimens have full claw sheaths. Three other specimens have half sheaths; they were scored as absent.

General morphology. Dorsal scale keeling is prominent and constant in the series, except in the largest males, MNHNSD 23.3934 and IIBZ-HER00005 (SVL 110.1 and 103.9 mm, respectively), in which fewer keels were less conspicuous. The third largest, MNHNSD 23.3936 (SVL 101.0 mm) has prominent keels both on the dorsum and sides. The number of strigae on the dorsal scales is high, varying from 19–34 (mean 24.1, mode 24). The strigae are knobbed, not continuous well-defined ridges as in adults of other species.

Coloration and pattern in life. The dorsal ground color varies from orange-tan to tan. The lateral area grades from the dorsal color to a pale beige or pale cream toward the venter. MNHNSD 23.3934–3935 (males) have the broadest and darkest crossbands (Fig. 7 A and E), with intercalating streaks of one half-to-one scale wide, and the longitudinal lines of the head still evident, covering the center of scales. The dorsal crossbands in some specimens are more solid, with almost no evidence of the longitudinal lines (IIBZ-HER00008; Fig. 7 H). The crossbands are chevronate (inverted) in most specimens, and there are some crossbands that split into an X, which at times

FIGURE 11. Predominant habitat on Cayo de las Iguanas. Note the large bromeliads on the rocky limestone floor and mangroves.
is incomplete (missing an extension on one side). IIBZ-HER00004 has the crossbands in the shape of anteriorly oriented chevrons. MNHNSD 23.3948 has very short and diffuse lateral stripes, with most of the sides very pale as a result. The second smallest specimen (MNHNSD 23.3916) has solid broad dark bands and thinner, lighter lateral stripes. An uncollected smaller juvenile showed a similarly contrasted pattern, which suggests ontogenetic pattern change. MNHNSD 23.3936 (Fig. 7 B) has diffuse whitish-cream spotting at the edge of the lateral stripes. Iris color varies from dark golden-bronze to scarlet red.

The venter is semi-translucent-cream to beige, especially in juveniles and in gravid females. The specimen MNHNSD 23.3935 has lateral stripes extending far onto the venter, though not converging at midventer, reaching the closest posteriorly toward the vent. The number of lines originating from the parietal-nuchal area is 14–16 in the series. Facial stripes four, with an accessory infra-auricular stripe and 2–3 on the lateral area of the neck. Sexual dichromatism is not evident other than males’ dorsal pattern turning darker with increasing SVL, and females having more translucent venters with beige suffusions from the sides.

Sexual dimorphism. In adult Guarocuyus jaraguanus sp. nov. (n=17), SVL in males (n=10) reaches 110.1 mm, in females (n= 7) 95.4 mm (Table 1). Values of male head measurements were higher and at least one proportion is completely separated from that of females: HW/SVL 13.3–13.9 (mean 13.7) vs. 12.0–13.1 (12.6) in females, and nearly so in males with HL/SVL 18.0–19.1 (18.6) vs. 16.6–18.0 (17.5) in females. These proportions have the highest values in the smallest females (18.0 for both IIBZ-HER00003–00004, with SVL of 75.9 and 77.5 mm, respectively), as well as for the HW/SVL (12.9 and 13.1 vs. 12.0–12.8 in all other females). This may reflect ontogenetic changes (see below). Females have a tendency toward slightly more elongate bodies, with AGD/SVL of 54.0–58.7 (55.9), whereas males have 53.2–54.7 (54.0), as well as for the relative ACD/SVL with 63.2–67.7 (64.9) vs. 62.5–64.4 (63.4) in males. One of the smallest specimens (sex undetermined), MNHNSD 23.3916, with an SVL of 65.7 mm, had the greatest values of head proportions, with HW/SVL of 14.3 and HL/SVL 19.2. Also, this specimen has the shortest relative AGD/SVL (52.0) followed by the second smallest confirmed male, MNHNSD 23.3912, and the second shortest ACD/SVL (62.3) after MNHNSD 23.3912.

FIGURE 12. Juvenile Guarocuyus jaraguanus sp. nov. (MNHNSD 23.3916) using its semiprehensile tail.
Natural History. Habitat. The habitat on Cayo de las Iguanas is dry forest on limestone bedrock (Fig. 11), in which the arboreal vegetation is dominated by Bursera simaruba, Metopium toxiferum, and Conocarpus erectus. Other dominant plants are Plumeria sp. (reaching unusually tall heights > 4 m), Comocladia dodonaeae, Myrtaceae spp., Tillandsia spp., and Agave sp. Cacti and thorn scrub occurs near the shore, but the interior of the key is largely shaded. The smaller Cayo Pei is similar, with less dense, shorter vegetation and fewer bromeliads.

Lizards were found exposed on the ground (rocks, leaf litter, and black mangrove roots) and under large bromeliads and agaves at and after dusk. In spite of most individuals (52 seen in total) being observed on rocks on the ground, several were foraging on dry mud within the root system of black mangroves (Avicennia germinans) 2–3 m from the lagoon shore. One was seen (not collected) 1.5 m high within epiphytic bromeliads (Tillandsia utriculata) on a tree 5 m in height.

Activity. On the first night of collecting (April 2021), the first individual was seen moving at about 1900 h, and during a subsequent visit (late September) at 1930 h. Individuals were observed active to at least 2130 h. Glue traps were set up at dusk and checked every 30 minutes. Male IIBZ-HER00001 was trapped in a glue trap at 2130 h. The specimen captured in the glue trap and the individual found in the bromeliad at night are suggestive of nocturnal activity and arboreal foraging. Environmental data for 22 September at 1925 h was temperature 28.7 °C and relative humidity 78.6% under a clear sky. A short diurnal survey between 1645–1745 h on 17 May 2022 yielded eight individuals, with at least one apparently active in the leaf litter. The other seven were under bromeliads. During the hour spent in the key, the sky was overcast, with a drizzle by the end of the survey. A fourth visit on 4 and 5 June 2022 included a diurnal survey on Cayo de las Iguanas on the first day and a nocturnal survey on Cayo Pei on the second day, during which several individuals were active at night (1940 h).

The semiprehensile ability of the tail (Fig. 12, see below) was observed only in individuals with a complete natural tail (IIBZ-HER00001, IIBZ-HER00004, and MNHNSD 23.3916, relative length of tail 133.3, 139.0, 141.3, respectively). Other individuals had regenerated tails and displayed no prehensility. Tail prehensility is a convergent trait found in multiple lizard lineages associated with climbing in arboreal habitats (Higham 2019). Some Anolis (Hardy 1958), and other anguidioid lizards (Etheridge 1967; Ariano-Sánchez & Melendez 2009; Lamar et al. 2015) are New World species that exhibit this trait.

Reproduction. All females gravid, of which only the second smallest (IIBZ-HER00004, SVL 77.5 mm) was dissected and contained a single, well-developed fetus (IIBZ-HER00012, SVL 27.8 mm).

Defensive behavior. Guaroctopus jaraguanus sp. nov. escapes into limestone crevices, and when handled, employs body rotation, caudal movement as an apparent distraction, gaping, and biting.

Injuries and tail autotomy. MNHNSD 23.3934–3937, IIBZ-HER00005–00007 were missing either portions of or entire fingers and toes (two per appendage per specimen at the most, four total), some of which involved missing toe phalanges. Only three individuals had complete natural tails, the rest (16) had some degree of regeneration.

Parasites. Most specimens collected were infested with mites and ticks. One dissected specimen (MNHNSD 23.3915) had unidentified chestnut-brown colored elongate nematodes in its liver and bile duct. A female regurgitated food that contained shorter, whitish nematodes associated with prey (caterpillars; see below).

Diet. Five fecal pellets were collected and examined (IIBZ-HER00002, MNHNSD 23.3915, MNHNSD 23.3936, IIBZ-HER00006, and MNHNSD 23.3948); these contained identifiable parts of Mollusca (land gastropod shells of at least two species included both crushed shells and an entire tiny shell), Myriapoda (Diplopoda: Spirobolida), Insecta (both larvae and adult Coleoptera, lepidopteran wing scales and larvae, legs of Orthoptera, and wings of cockroaches), and plant material (a piece of a small seedpod, tree bark, and small flowers). The female (MNHNSD 23.3949) regurgitated (during preservation) two caterpillars (lepidopteran larvae) and one winged termite (Blattodea: Isoptera).

Herpetological community. Other reptiles on the key include Cyclura cornuta, Anolis longitibialis, Aristelliger expectatus, Sphaerodactylus aff. randi, S. streptophorus, S. thompsoni, and Chilabothrus striatus. A Typhlops sp. was collected on the neighboring key (Cayo Pei; 17.73101, -71.37564) in the axis of a large bromeliad (Tillandsia utriculata) that was attached to a tree about 2 m high. No anurans have been recorded on these keys.

Ecomorphology. With little data on this species, we tentatively place it in the Tree ecomorph (Schools et al. 2022), as it has a semiprehensile tail and has been observed in epiphytic bromeliads to heights of 1.5 m in trees. Similarly, it shares a trait, a high number of lamellae on the longest toe, with a Jamaican species (Celestus fowleri Schwartz) known to live in bromeliads.
**Discussion**

The scaleless web between toes II to IV in *Guarocuyus jaraguanus* appears to be a lateral extension of the basal lamellae of those toes (Fig. 1). In many examined specimens (29) of *Comptus stenurus* and at least one *Celestus barbouri* this trait is vestigial, as it is barely evident basally to the interdigital space only between toes III and IV, is covered in scales, and never extends to the first lamellae of the toes. The function of this trait in the new species remains unknown. Higham (2019) reviewed this trait in other lizards, noting that it has several functions, some of which may involve burrowing or movements in compliant surfaces (loose sand or mud, the latter a substrate in which an individual was found). Although the species is assumed to be facultatively arboreal, it is so far the second-largest known lizard from the small keys (after the massive, largely herbivorous *Cyclura cornuta*), and the species may in fact be a generalist exploiting a variety of available spatial niches.

Within Celestinae, *G. jaraguanus* is the only species that commonly presents variation in the number of postnasal scales as well as in those contacting the nasal scale. Nevertheless, the intraspecific variation (absence and presence) of a claw sheath is unique. That three specimens have fairly developed ungual scales that can be interpreted as intermediate (scored as absent) is noteworthy.

The genus *Caribicus* is the outgroup to other members of Celestinae (Fig. 4), and the three species in this genus were found to share swollen dorsal tail scales. Adults of the two giant species of *Caribicus* (*C. anelpistus* and *C. warreni*) have short tails that are somewhat laterally compressed and broad at their bases but which tend to taper sharply posteriorly, and have conspicuously enlarged (relative to those in the rest of the dorsum) swollen scales. Also, *Caribicus darlingtoni*, although not mentioned in the original description (Cochran 1939), has been reported to have keeled dorsal scales (Schwartz & Henderson 1991; Schools & Hedges 2021); however, the examination of a freshly collected series (MNHNSD 23.3922–3933) that includes a wide range of sizes (SVL 41–74.9 mm) did not reveal any keeled dorsal scales. Instead, and similar to the giant species, that species possesses shallow grooves between scales that deepen in the dorsal tail region, accentuated by the swollen scales that bear bumps that taper toward the scale’s edges. This scale topography was possibly misinterpreted as keels by previous authors.

As far as scale topography is concerned, ontogeny seems to play an important role. Thomas (1966) reported that the strigae in juveniles of several species are knob-like, not forming continuous ridges, and instead are disrupted. However, we observed this condition in all sizes of *Guarocuyus jaraguanus*. Dorsal keels are present in juveniles and small individuals of at least *Panolopus costatus* and *P. curtissi* (Schwartz 1964), a condition that is lost with increased age/size (Schwartz 1964; Thomas 1966). Considerations of size/age groups should be taken into account when relying on these morphological characters as diagnostic at the generic or specific level.

The dorsal scales are mucronate in two juvenile *Caribicus*, *C. anelpistus* (MNHNSD 23.206-C, SVL 108 mm) and *C. warreni* (live individual C-4, SVL 80 mm), a condition that becomes more noticeable posteriorly, toward and onto the tail itself. A medium-sized living female *C. warreni* (C-11, SVL 240 mm) likewise showed slightly mucronate scales. The larger specimens did not have mucronate scales. Also, the more “cobbed” aspect of the tail becomes more evident only in larger individuals.

Sexual dimorphism has been previously reported in diploglossids (Fitch 1981; Incháustegui *et al.* 1985), with males of *Caribicus warreni* having wider heads (Incháustegui *et al.* 1985). This is true, also, of our samples of that species, as well as of *Guarocuyus jaraguanus*, *Celestus macrotus*, and *Caribicus darlingtoni*. Thus, sexual dimorphism should be considered when comparing relative head width (HW/SVL).

The relatively dry Barahona Peninsula is the southernmost land projection of Hispaniola and contains a diverse herpetofauna that is not completely known. Schwartz (1980) acknowledged the endemism in the herpetofauna of the region, with xeric species restricted to the lowlands south of the Bahoruco-La Selle mountain range, in a pattern he called the “Barahona Entrapment.” Recent and ongoing work reaffirms Schwartz’s statement (Landestoy *et al.* 2018; Landestoy *et al.* 2021; this paper; Landestoy, accepted manuscript). Even within the peninsula itself, habitat differentiation might erect ecological barriers as inferred from the known distribution of species of *Sphaerodactylus* (Hedges & Thomas 2001). Of the other celestine genera occurring on the “South Paleo-island,” *Wetmorena* is also found on the neighboring North Paleo-island (*W. agasepsoides* also occurs in the dry areas of the Sierra Martín Garcia). Interestingly, the genus *Celestus* in Hispaniola is found only on the South Paleo-island with one species (*C. macrotus*) inhabiting the highest elevations of the Sierra de Bahoruco-
Massif de la Selle range. Also noteworthy is that Comptus is absent from the Barahona Peninsula. Guarocuyus gen. nov. is both morphologically and genetically closer to the genera Celestus, Comptus, and Panolopus, and in spite of its unique traits, could represent an ecological equivalent of Comptus stenurus and Panolopus costatus in the area.

However, Guarocuyus gen. nov. might also represent a relic of a formerly widespread lineage. The fact that the new species has been found on only two small well-vegetated keys in the middle of the lagoon, free of non-volant mammals (both herbivores and predators), makes us consider such hypotheses. The Small Indian Mongoose has been attributed with the disappearance of several species in the West Indies, especially mabuyine skinks (Hedges & Conn 2012), which are lizards with habits similar to those of celestines. Free-roaming cattle and both wild and provoked fires along the coast of Laguna de Oviedo have altered the natural vegetation. Bromeliads may be an important component of this species’ habitat. Unfortunately, we noticed fewer bromeliads and almost none on the ground on the surrounding mainland, a fact that could explain such apparent confinement. The few bromeliads observed on the ground were chewed by cattle, an observation corroborated by locals, as cows obtain water stored at the plant’s axils.

Despite stable management of the keys and its endorheic lagoon providing natural protection, the apparent geographical restriction of Guarocuyus jaraguanus sp. nov., warrants additional in-depth research aiming to reveal its actual distribution and conservation status. The largest key is a popular destination of tourists, and it may be subject to some levels of disturbance; in addition, potential invasions from harmful species should be considered. Based on IUCN Redlist criteria (IUCN 2022), we assess the conservation status of Guarocuyus jaraguanus as Critically Endangered (CR B2a), based on its very small distribution and threats from habitat alteration and introduced predators.

Finally, we report two new localities of Celestus macrotus, a poorly known and endangered species previously known only from the Haitian side of the Massif de la Selle-Sierra de Bahoruco mountain range. These are the first records from the Dominican Republic, where the Sierra de Bahoruco reaches as high as 2,400 m asl. Each locality lies above 2,000 m elevation: 1) The helipad aside the border road from Puerto Escondido to Pedernales at the foot of the peak of Loma del Toro, elevation 2,315 m asl (7 km NE Los Arroyos, 18.287270, -71.712442); 2) Caseta Dos (El Codo; 18.206339, -71.563394), 2,103 m asl. Locality 1 represents a range extension ESE into the Dominican Republic of ca. 17 airline km, and locality 2 is 18 km ESE from 1. Locality 1 also represents a new elevational record (from the previous 2,020 m reported in Henderson & Powell 2009 for this species).

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APPENDIX 1: specimens and sequences used in the molecular analyses

Genbank numbers are listed for each of the nine genes. We collected 34 new sequences (OP413907–40) and include them with 300 existing sequences. Locality data are summarized below. In addition, the Genbank database (Genbank 2020) should be consulted for other information on sequences, including authors, citations, localities, and sources of material; other information can be found in the original articles (see Materials and Methods). NA = not applicable (sequence not obtained).

Specimen vouchers (if known), laboratory numbers (“SBH”), and localities of samples used in molecular analyses.

Celestinae. Caribicus darlingtoni (USNM 328806; Dom. Rep., Independencia, 9.0 km N of Cacique Enriquillo; 18.673758, -71.91447), Caribicus warreni (Voucher not available, SBH 194521; Dom. Rep., Puerto Plata, presumably the region of Puerto Plata), Celestus crusculus crusculus 1 (USNM 328158; Jamaica, Westmoreland, 7.0 km WSW of Old Hope), Celestus crusculus crusculus 2 (USNM 328169; Jamaica, St. Elizabeth, Knoxwood), Celestus crusculus crusculus 3 (USNM 328174; Jamaica, St. Mary, 6.2 km W of Oracabessa), Celestus crusculus crusculus 4 (USNM 328154; Jamaica, Hanover, 3.2 km SE of Content), Celestus crusculus crusculus 5 (USNM 328160; Jamaica, Trelawny, 0.3 km W of Duncans, jct. with Silver Sands road), Celestus crusculus crusculus 6 (USNM 328144; Jamaica, Portland, 1.3 km WSW of Section, on road to Hardwar Gap), Celestus crusculus crusculus 7 (Voucher not available, SBH 274632; Jamaica, St. Thomas, 5.9 km W of Trinity Ville by road), Celestus barbouri (USNM 328153; Jamaica, Trelawny, vicinity of Quick Step), Celestus duquesneyi (Voucher not available, SBH 267952; Jamaica, St. Catherine, Hellshire Hills), Celestus hewardii (Voucher not available, SBH 267097; Jamaica, Manchester, Mandeville), Celestus macrotus (ANSP 38506; Haiti, Ouest, southeast of Pic La Selle; 18.323253, -71.91447), Comptus badius (Voucher not available, SBH 194964; United States Caribbean, Navassa Island), Comptus maculatus (ANSP 38507; Cayman Islands, Cayman Brac, 0.7 km E Hawkesbill Bay on A7, ~10km E West End, 1.7 km E Ashton Reid Drive; 19.7142, -79.7864), Comptus stenurus stenurus 1 (ANSP 38540; Haiti, Grand’Anse, Belandier, 5.0 km N of Dame Marie [turn back locality]; 18.585683, -74.076717), Comptus stenurus stenurus 2 (USNM 328836; Haiti, de la Grand’Anse, between Rampe des Lions and Bois Sec, 6.5–1.5 km S and 0.1–4.5 km E Marche Leon; 18.504301, -74.09717), Comptus stenurus rugosus (USNM 328830; Dom. Rep., Maria Trinidad Sanchez, 4.0 km SE of Nagua), Comptus stenurus weilandi (USNM 328808; Dom. Rep., Barahona, 16.0 km ESE of Canoa), Guarocuyus jaraguanus 1 (MNHNSD 23.3914: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Guarocuyus jaraguanus 2 (IIBZ-HER00001: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Guarocuyus jaraguanus 3 (MNHNSD 23.3915: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Guarocuyus jaraguanus 4 (IIBZ-HER00003: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Guarocuyus jaraguanus 5 (IIBZ-HER00004: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Guarocuyus jaraguanus 6 (MNHNSD 23.3913: Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las
Guanocuys jaraguanus 7 (MNHNSD 23.3912; Dom. Rep., Perdernales, Parque Nacional Jaragua, Laguna de Oviedo, Cayo de las Iguanas; 17.73205, -71.37126), Panolopus costatus costatus (ANSP 38558; Haiti, Grand’Anse, Abricots [outskirts]; 18.64783, -74.307212), Panolopus costatus leionotus 1 (ANSP 38566; Dom. Rep., San Juan, 1.6 mi NNE El Azul; 18.717, -71.413), Panolopus costatus leionotus 2 (ANSP 38570; Haiti, Artibonite, Morne Boeuf; 19.072394, -72.250208), Panolopus costatus neibea (ANSP 38578; Haiti, Artibonite, 11.8 km W of Ça Soleil; 19.469546, -72.777129), Panolopus costatus newobus (ANSP 38583; Haiti, Sud, Ile a Vache; 18.105163, -73.69288), Panolopus costatus oreistes (USNM 328792; Haiti, Sud-Est, 9.5 km E of Jacmel; 18.227064, -72.44959), Panolopus curtissi aporus (USNM 328800; Dom. Rep., Pedernales, Juancho, 6.4 km SW, 0.7 km SE by road SW of Enriquillo), Panolopus curtissi curtissi (ANSP 38632; Dom. Rep., Independencia, 5.1 km NW of La Descubierta; 18.5711, -71.7549), Panolopus curtissi diastatus (ANSP 38646; Haiti, Nord’Ouest, Mole St. Nicolas; 19.805831, -73.735556), Panolopus curtissi hylonomus (ANSP 38647; Dom. Rep., Peravia, 14.8 N, 7.8 km SE of Cruce de Ocoa on dirt road, at Martinez near La Palma; 18.46, -70.45), Panolopus marcanoi (ANSP 38657; Dom. Rep., Santiago, Valle de Bao; 19.054054, -79.085646), Sauresia seposides 1 (ANSP 38667; Haiti, Ouest, Berry; 18.307945, -72.253894), Sauresia seposides 2 (USNM 328846; Dom. Rep., Hato Mayor, 9.5 km W of Sabana de la Mar [airline] in Los Haitises; 19.05293, -69.47899), Sauresia seposides 3 (ANSP 38684; Haiti, Nippes, Morn Bois Pangol; 18.418689, -73.775122), Sauresia seposides 4 (ANSP 38675; Haiti, Grand’Anse, Grande Cayemite; 18.635615, -73.751749), Wtemorena agaspeposides (ANSP 38712; Dom. Rep., Barahona, 0.3 km S, 13.5 km E [airline] of Canoa; 18.3448, -71.032), Wtemorena haetiana haetiana (ANSP 38745; Haiti, Ouest, Waterfall in Parc La Visite; 18.34014, -72.269826), Wtemorena haetiana mylica (USNM 328858; Dom. Rep., Barahona, 15.3 km S, 6.7 km E of Cabral by road; 18.103139, -71.216981), Wtemorena haetiana surda (USNM 328899; Dom. Rep., Pedernales, 10.3 km S of El Aguaucate, on Haitian border road; 18.26879, -71.72703), Diploglossinae. Diploglossus lessonae (CHUNB 62432; Brazil), Diploglossus monotypus (SMF 100420; Costa Rica), Diploglossus pleii (ANSP 38556; United States, Puerto Rico, Reserva Forestal, Rio Abajo (8 km airline SSE Arciibo); 18.4000, -66.6913), Diploglossus garridoi (MNHNCS 4420; Cuba, Granma, El Manguito), Diploglossus nigropunctatus (USNM 512238; Cuba, Pinar del Rio, 4.0 km NW of San Vicente, north base of Sierra de San Vicente), Ophiodes striatus (MVZ 191047; Brazil, Edo. Sao Paulo), Ophiodes sp. (CURCR 94). Siderolamprinae. Mesoamerican bilobatus 1 (SMF 94584; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), Mesoamerican bilobatus 2 (SMF 94583; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), Mesoamerican bilobatus 3 (MVZ 207334; Costa Rica, Moravia), Mesoamerican bilobatus 4 (SMF 101026; Costa Rica, Limon, Finca Curré, northern limit, close to creek; 9.61823, -82.71195), Mesoamerican bilobatus 5 (SMF 89549; Panama, Veraguas, PNSF, Cerro Mariposa: water supply hut near Alto de Piedra; 8.51607, -81.11849), Mesoamerican bilobatus 6 (SMF 89546; Panama, Veraguas, PNSF, Cerro Mariposa: water supply hut near Alto de Piedra; 8.51607, -81.11849), Siderolamprus bivittatus (UTA R-46542; Guatemala, Jalapa, Cerro Tablon de las Minas), Siderolamprus cyanochloris (MVZ 204069; Costa Rica, Refugio National Tapaniti), Siderolamprus enneagrammus 1 (UTA R-30338; Mexico, Oaxaca, Sierra Mixes, 0.8 km S Totontpec; 17.26, -96.04), Siderolamprus enneagrammus 2 (MVZ 191044; Mexico, La Joya), Siderolamprus laf (SMF 90177; Panama, Chiriqui, Lost and Found Echolost; 8.67462, -82.21958), Siderolamprus rozellae (UTA R-46107; Guatemala, Izabal, Morales, Finca Karen), Pseudopus apodus (CAS 182911; Russia).

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APPENDIX 2: Specimens examined

Caribicus anelpistus: MNHNSD 23.206-C (Dom. Rep., born in captivity at local zoo presumably from individuals of the type series), MNHNSD 23.3893 (Dom. Rep., San Cristobal, Villa Altagracia, La Lomita; 18.665944, -70.222361), USNM 197336 (Dom. Rep., San Cristobal, Villa Altagracia, Ingenio Catarye, 'Come Hombre'; 18.6864, -70.1778). Caribicus darlingtoni: IIBZ-HER00011 (Dom. Rep., La Vega, 16.9 km SSE of Constanza; 18.78396, -70.64690), MCZ R-44374 (Dom. Rep., Valle Nuevo; 18.8, -70.6833), MNHNSD 23.3922–3933 (Dom. Rep., La Vega, 16.9 km SSE of Constanza; 18.78396, -70.64690), USNM 107563–107564 (Dom. Rep., Valle Nuevo, SE of Constanza, Cordillera Central; 18.8, -70.6833), USNM 328801–328804 (Dom. Rep., La Vega, 36.7 km SE Constanza via old road to San Jose de Ocoa; 8.7175, -70.6011), USNM 328805–328807 (Dom. Rep., La Vega ca. 37 km SE of Constanza via new road to San Jose de Ocoa; 18.7056, -70.5981). Caribicus warreni: ANSP 38501 (Haiti, locality not available), ANSP 38502 (Dom. Rep., locality not available [pet trade]), MNHNSD 23.879 (Dom. Rep., Puerto Plata, Fundación, Los Cacaos), MNHNSD 23.880, (Dom. Rep., Duarte, San Francisco de Macoris, MNHNSD 23.881 (Dom. Rep., Valverde, Juibon, Pozo Prieto), MNHNSD 23.882 (Dom. Rep., locality not available), MNHNSD 23.883 (Haiti, Nord, Saint-Raphael, 4.5 km SE of Dondon, Boisneuf), MNHNSD 23.884 (Dom. Rep., Hermanas Mirabal, Tenares, between Salcedo and Tenares), MNHNSD 23.885–886 (Dom. Rep., Duarte, San Francisco de Macoris), USNM 59435 (Haiti, Nord-Ouest, Riviere des Barres), USNM 197369 (Dom. Rep., Puerto Plata, Comedero, La Isabela; 19.8183, -71.0617). Celestus barbouri: ANSP 38503 (Jamaica, Trelawny, 0.5 km N of Windsor; 18.3579, -77.6482), MCZ R-45169 (Jamaica, Mandeville; 18.041682, -77.507141), USNM 38949–38950 (Jamaica, Manchester Parish, Mandeville), USNM 328145–328147 (Jamaica, Trelawny Parish, ca. 0.8 km N of Quick Step), USNM 328148–328149, USNM 328151–328153 (Jamaica, Trelawny Parish, vicinity of Quick Step). Celestus crusculus crusculus: ANSP 38504 (Jamaica, Trelawny, 0.3 km W Duncans (jet with Silver Sands access road); 18.47105, -77.53887), USNM 251897–251898 (Jamaica, St. Elizabeth, 5.6 mi N of Malvern by road), USNM 326601 (Jamaica, Trelawny, ca. 1 mi S, 1 mi W of [airline]) Rio Bueno, USNM 328154–328155 (Jamaica, Hanover, 3.2 km SE of Content), USNM 328157 (Jamaica, Westmoreland, 4.5 km W of Old Hope, at Little Bay), USNM 328158 (Jamaica, Westmoreland, 7.0 km WSW of Old Hope), USNM 328159–328167 (Jamaica, Trelawny, 0.3 km W of Duncans), USNM 328168–328169 (Jamaica, St. Elizabeth, Knoxwood), USNM 328170 (Jamaica, Clarence, Jackson's Bay, on beach at hunting club), USNM 328171 (Jamaica, Clarence, ca. 1.6 km ESE of Jackson's Bay, at entrance to Jackson’s Bay Caves), USNM 328172 (Jamaica, St. Mary, vicinity of Jacks River (town of)), USNM 328173 (Jamaica, St. Mary, ca. 1.6 km S of Orcabessa, on road to Jacks River), USNM 328174–5 (Jamaica, St. Mary, 6.2 km W of Orcabessa), USNM 328176 (Jamaica, St. Mary, Salt Gut, vicinity of Boscobel Airport (E side)), USNM 328177–9 (Jamaica, St. Mary, 2.9 km N of Port Maria), USNM 328180, 328182–4 (Jamaica, St. Mary, ca. 6.4 km S of Port Maria), USNM 328186 (Jamaica, St. Catherine, 5.6 km SW of Breeton, at Hellshire Beach in Hellshire Hills). Celestus crusculus candulli: MCZ R-45163 (Jamaica, Mandeville), USNM 108220–108222 (Jamaica, Manchester Parish, Mandeville), USNM 328170 (Jamaica, Clarence, Jackson’s Bay, on beach at the hunting club), USNM 328171 (Jamaica, Clarence, ca. 1.6 km ESE of Jackson’s Bay, at entrance to Jackson’s Bay caves), USNM 328172 (Jamaica, St. Mary, vicinity of town of Jack’s River), USNM 328173 (Jamaica, St. Mary, ca. 1.6 km S of Orcabessa, on road to Jacks River), USNM 328174–5 (Jamaica, St. Mary, 6.2 km W of Orcabessa), USNM 328176 (Jamaica, St. Mary, Salt Gut, vicinity of Boscobel Airport [E side]), USNM 328177–28179 (Jamaica, St. Mary, 2.9 km N of Port Maria), USNM 328180, USNM 328182–328184 (Jamaica, St. Mary, ca. 6.4 km S of Port Maria), USNM 328185 (Jamaica, St. Catherine, 9.0 km W of Ewarton). Celestus duquesneyi: MCZ R-45194 (Jamaica, Portland Point; 17.755728, -77.164708), USNM 108310 (Jamaica, Clarence). Celestus fowleri: MCZ R-125601 (Jamaica, Trelawny Forest; 18.35195, -77.64782). Celestus hewardii: USNM 102651 (Jamaica, Kensworth), USNM 108231, 108234, 108238 (Jamaica, Manchester, Mandeville), USNM 108329–108335 (Jamaica, St. James, 5 mi W of Montego Bay), USNM 251918 (Jamaica, Trelawny, 1.1 mi NW of Windsor; 18.3722, -77.6583), USNM 251919 (Jamaica, St. Ann, 1.5 mi NE of Orange Valley). Celestus macrolepis: BMNH 1946.8.3.82 (no locality; restricted here to Jamaica). Celestus macrurus: ANSP 38505 (Haiti, Sud-Est, Pic La Selle, Sud-Ouest; 18.32887, -72.021842), ANSP 38506 (Haiti, Ouest, Southeast of Pic La Selle; 18.332253, -71.91447), MNHNSD 23.3989–3901 (Dom. Rep., Pedernales, 7 km NNE of Los Arroyos, helipad at Loma del Toro; 18.28727, -71.71244), IIBZ-HER00009–00010, MNHNSD 23.3943–44 (Dom. Rep., Independencia, Caseta Dos “El Codo”, Parque Nacional Sierra de Bahoruco; 18.20634, -71.56339), USNM 86917 (Haiti, Ouest, ca. 15 km W of Gros Cheval (by logging roads), northeastern slope of Morne La Selle in the Massif de la Selle; 18.337421, -71.868056), USNM 286917 (Haiti, Ouest, ca. 15 km W of Gros Cheval (by logging roads), northeastern slope of Morne La Selle in the Massif de la Selle; 18.3367, -71.8686). Celestus microblepharis: MCZ R-55764 (Jamaica, St. Mary, Boscobel; 18.404055, -76.968794). Celestus molesworthi: USNM
NEW GENUS AND SPECIES OF DIPLOGLOSSIDAE