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Phylogenetics, classification, and biogeography of the Neotropical forest lizards (Squamata, Diploglossidae)

MOLLY SCHOOLS[1] & S. BLAIR HEDGES[2]
Department of Biology, Center for Biodiversity, 1925 N 12th St Suite 502, Philadelphia, PA 19122, USA
[1]*Corresponding author. molly.schools@temple.edu; https://orcid.org/0000-0002-2687-7885*
[2] *sbh@temple.edu; https://orcid.org/0000-0002-0652-2411*

Abstract

Lizards of the family Diploglossidae occur in moist, tropical forests of Middle America, South America, and Caribbean islands. Our analyses based on new molecular and morphological data indicate that the widely distributed genera *Celestus* Gray, 1839 and *Diploglossus* Wiegmann, 1834 are paraphyletic. We restrict the former to Caribbean islands and the latter to South America and Caribbean islands. We assign species in Middle America, formerly placed in *Celestus* and *Diploglossus*, to *Advenus* **gen. nov.**, *Mesoamericus* **gen. nov.**, and *Siderolamprus* Cope, 1861. We assign species on Caribbean islands, formerly placed in *Celestus*, to *Caribicus* **gen. nov.**, *Comptus* **gen. nov.**, *Celestus*, *Panolopus* Cope, 1862, *Sauresia* Gray, 1852, and *Wetmorena* Cochran, 1927. Our phylogenetic tree supports three major clades in the family: Celestinae **subfam. nov.** (*Advenus* **gen. nov.**, *Caribicus* **gen. nov.**, *Comptus* **gen. nov.**, *Celestus, Panolopus*, *Sauresia*, and *Wetmorena*), Diploglossinae (*Diploglossus* and *Ophiodes* Wagler, 1828), and Siderolamprinae **subfam. nov.** (*Mesoamericus* **gen. nov.** and *Siderolamprus*). Our timetree indicates that the diploglossid lineage originated in the early Cenozoic and established three major centers of diversification in the Americas: Middle America (siderolamprines and one celestine), South America (diploglossines), and Caribbean islands (celestines and diploglossines). The majority of threatened species are on Caribbean islands, with the major threats being deforestation and predation by the introduced mongoose. Molecular and morphological data indicate that there are many undescribed species in this family of lizards.

Key words: evolution, systematics, biogeography, taxonomy, lizard, Reptilia, Central America, South America, Caribbean, West Indies, deforestation, mongoose

Introduction

Diploglossidae is a family of smooth-scaled, forest-dwelling lizards distributed throughout the neotropics, including the Caribbean islands, Middle America, and South America. It is grouped together with Anguidae and Anniellidae in the superfamily Anguioidea. Currently, there are 53 diploglossid species placed in three genera: *Celestus* Gray, 1839*, Diploglossus* Wiegmann, 1834*,* and *Ophiodes* Wagler, 1828. The number of recognized genera has varied because of conflicting diagnostic characters and a lack of genetic data. No authors have questioned the monophyly of *Ophiodes* and its relationship to the remaining genera. However, the recognition of *Celestus*, *Sauresia*, and *Wetmorena*, in addition to the relationship between *Celestus* and *Diploglossus*, remains a subject of controversy.

Diploglossids go by various colloquial names depending on the country, with "galliwasp" (originally, "galley wasp") being the most commonly used name in English. The name is from the British West Indies, especially Jamaica, and refers to the false belief that these lizards have venom like a wasp, such as those that infested wooden ships in past centuries (Encyclopaedia Britannica 1810). Initially, unrelated lizards, including those in Australia, also were called "galley wasps" (e.g., Griffiths 1831). Because most colloquial names (e.g., coqui's for Puerto Rican frogs) are not used globally for species in the same taxon, and because the word "galliwasp" lacks descriptive utility, we suggest that diploglossids are more aptly called "Neotropical forest lizards," given their typical habitat.

Authors have used several key morphological characteristics to describe species relationships within Diploglossidae. Boulenger (1885) recognized two groups of *Diploglossus* (including species currently in *Celestus*) based on the presence or absence of a claw sheath. Subsequent authors have used the claw sheath trait, concluding that *Diploglossus* and *Celestus* are widely distributed, occurring on Caribbean islands and the mainland (e.g. Barbour 1910; Peters & Donoso-Barros 1970; Savage & Lips 1993; Savage *et al.* 2008).

In contrast, other authors have not found the claw sheath trait to be useful in diagnosing the two genera and have considered *Celestus* to be a synonym of *Diploglossus* (Dunn 1939; Underwood 1959; Campbell & Camarillo 1994; Werler & Campbell 2004). Separately, the presence or absence of contact between the nasal and rostral scale was used to argue that two different groups of diploglossid lizards should be recognized, both placed in the genus *Diploglossus* (Underwood 1959). Hass *et al.* (2001) found that their DNA sequence data and immunological data agreed more with the nasal-rostral contact trait than with the claw sheath trait.

Further questions exist regarding the taxonomy and relationships of the tetradactyl groups, previously referred to as the genera *Sauresia* and *Wetmorena* but now placed in *Celestus*. Savage & Lips (1993) claimed that *Sauresia* and *Wetmorena* are more closely related to *Diploglossus* than *Celestus* because of the presence of a claw sheath, however this was not supported by other authors using genetic data (Macey *et al.* 1999; Hedges *et al.* 1992; Hass *et al.* 2001). Based on immunological distance data, *Sauresia* and *Wetmorena* aligned more closely with *Celestus* than *Diploglossus*, leading Hass *et al.* (2001) to place them in the synonymy of *Celestus*.

Few molecular studies have included diploglossid lizards. Support for the monophyly of Diploglossidae was inconclusive based on the mitochondrial DNA study previously noted of six diploglossid species (Macey *et al.* 1999), a small subset of the total known species diversity in the family. High level squamate phylogenies used these same sequence data to recreate the same topology (Wiens & Slingluff 2001; Wiens *et al.* 2006). Based on this and new information from nuclear gene sequences, Hedges & Vidal (2009) elevated Diploglossidae from subfamily status to its own family based on similar levels of divergence from the recognized family Anniellidae. These high-level relationships were corroborated in later molecular studies (Vidal *et al.* 2012; Wiens *et al*. 2012; Pyron *et al.* 2013). However, until now, only a small number of diploglossid species have been sampled in molecular studies, leaving in question their evolutionary relationships, taxonomy, biogeography, and morphological evolution.

The purpose of this study is to revise the supraspecific taxonomy of diploglossid lizards with new, expanded, molecular and morphological data sets, and use these new data to resolve their evolutionary and biogeographic history. Our genetic and morphological results warrant the definition of four new genera and the resurrection of four genera that have been synonyms of *Celestus*. In addition, we introduce subfamilies to better accommodate the species diversity in the family and deep levels of divergence, consistent with the use of subfamilies in other families of squamate reptiles.

Materials and Methods

Distribution maps

We constructed distribution maps of higher taxa of diploglossids (genera and family) using species range maps from two databases, CaribHerp (www.caribherp.org) and the Redlist (www.iucnredlist.org), which are largely synchronized (for Caribbean species) because of the second author's (SBH) association with both efforts. We supplemented these with primary literature records (Lotzkat *et al.* 2016; Entiauspe-Neto *et al.* 2017). The resulting distribution maps corresponded closely with other sources of information, such as locality records for vouchered museum specimens (GBIF 2020) and modeled distributions (Meiri *et al.* 2017). We constructed a map of the family from a synthesis of subfamily range polygons using mapping software (QGIS 2020). The subfamily range polygons are displayed on high quality basemaps (Hijmans 2015).

Phylogenetic analyses

The molecular data set comprised 59 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). Nearly all (98%) of the sequences are new. In total, the phylogeny represents 30 diploglossid species. We performed DNA extractions with the DNeasy Blood and Tissue kit (Qiagen, Massachusetts, USA), and we used phenol chloroform extractions for degraded samples and those with a low yield. We performed PCR amplification under standard reaction conditions as outlined elsewhere (Hedges *et al.* 2008). Localities, Genbank accession numbers, and museum numbers (if applicable) for all sequences used are in Appendix 1. Using MEGA X, we performed alignments (MUSCLE) and best-fit model selection (Kumar *et al.* 2018).

We used Maximum Likelihood (ML) and Bayesian methods to conduct phylogenetic analyses, with *Pseudopus apodus* as the outgroup. We used a GTR + Γ model, as recommended in Stamatakis (2006), in Maximum Likelihood (ML) analyses performed with RAxML 8.2.12 (Stamatakis 2014) for 2000 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).

We generated a timetree of divergence times in BEAST 2.4.7 (Suchard *et al.* 2018) and BEAUTi 2.4.7, with the following parameters: unlinked GTR + Γ + I substitution model; relaxed lognormal clock; a yule process to model speciation events; 20 million generations with sampling every 1000 steps, and a 10% burn-in. We assessed convergence with an infinite sites plot comparing replicate runs, in addition to confirming high ESS values in Tracer 1.6 (Rambaut *et al.* 2018). No fossil or geological calibrations were available and therefore we used six calibration points corresponding to shared nodes between our timetree and those of other studies, displayed in Table 1.

TABLE 1. Studies and their dates used to calibrate nodes in the timetree.

Citation	Diploglossidae/*P. apodus*	Celestinae+Diploglossinae/ Siderolamprinae	*Mesoamericus /Siderolamprus*	Celestinae / Diploglossinae	*Diploglossus/ Ophiodes*	*Wetmorena agasepsoides/ W. haetiana*
Wiens *et al.* 2006	70	60	51	51	26.1	10.8
Hedges & Kumar 2009	69	-	-	-	-	-
Hedges & Vidal 2009	65	-	-	-	-	-
Pyron & Burbrink 2014	68	51	42	42	22.4	8.6
Hedges *et al.* 2015	63	46	38	38	20.6	7.4
Wright *et al.* 2015	72	53	42	44	24.2	8.7
Tonini *et al.* 2016	53	50	45	42	21.5	6.6
Zheng & Wiens 2016	68	55	46	47	24.7	9.6
Mean	66	52.5	44	44	23.3	8.6
Confidence interval	61.9–70.1	48.7–56.3	40.5–47.5	40.4–47.6	21.6–24.9	7.4–9.8

Morphological analyses

We identified non-overlapping, diagnostic, morphological characters that distinguish all genera after examining representatives of 37 different species (Appendix 2). We scored a primary suite of 14 morphological traits used in the diagnoses including eight of scalation, five of body proportions, and one of anatomy. Those characters included some used in past studies of diploglossid lizards (e.g., presence of claw sheath, contact between the nasal and rostral scale, etc.) as well as non-conventional characters not used previously or commonly. Scale terminology follows the descriptions and definitions from Savage *et al.* (2008).

Although we could diagnose some new taxa by conventional characters alone, the non-conventional characters also proved to be useful in diagnoses. These non-conventional measurements included the scales in contact with the nasal scale, the postnasal scales, the position of the nostril in the nasal scale, keels on dorsal body scales, relative rostral height, relative frontonasal length, and relative interparietal distance.

To avoid bias from allometric growth differences in quantitative traits, we used sexually mature individuals. Because many specimens were inaccessible for gonadal examination, including types and those in museums with restrictions on dissection, direct observation of sexual maturity was not possible. Therefore, we inferred sexual maturity for each species with body size, using only individuals that were within 25% of the largest individual of that species for body proportion measurements (Wiens *et al.* 2006). Diploglossids exhibit little or no sexual dimorphism in body size or shape (Fitch 1981; Schwartz & Henderson 1991; Wiens & Slingluff 2001). For that reason, and because of the limited data on specimen sex, males and females are not differentiated in the following list of measurements. From a taxonomic standpoint, this means that our diagnoses are more inclusive because they separate all individuals and not just one sex.

Body proportions. We used the standard definitions of length and width (along, or transverse to, the body axis, respectively) and measured widths at the widest straight-line distance and length at longest straight-line distance. We measured the following characters: snout-vent length (SVL; tip of snout to vent opening), head width (HW), rostral height (RH; measured from the base to the top of the rostral), rostral width (RW), frontonasal length (FN), distance between the parietal scales (DP; the shortest distance between the parietal scales), and axilla-groin distance (AG). We divided character measurements by SVL to produce relative sizes that would allow comparison among adult individuals of different body size. In the case of rostral measurements, we divided rostral height by rostral width.

Anatomy. We report the digits per limb for each species.

Scalation. Our standard suite of characters included four counts, three presence/absence traits, and the position of the nostril in the nasal scale (Fig. 1). Scale terminology follows the descriptions and definitions from Savage *et al.* (2008).

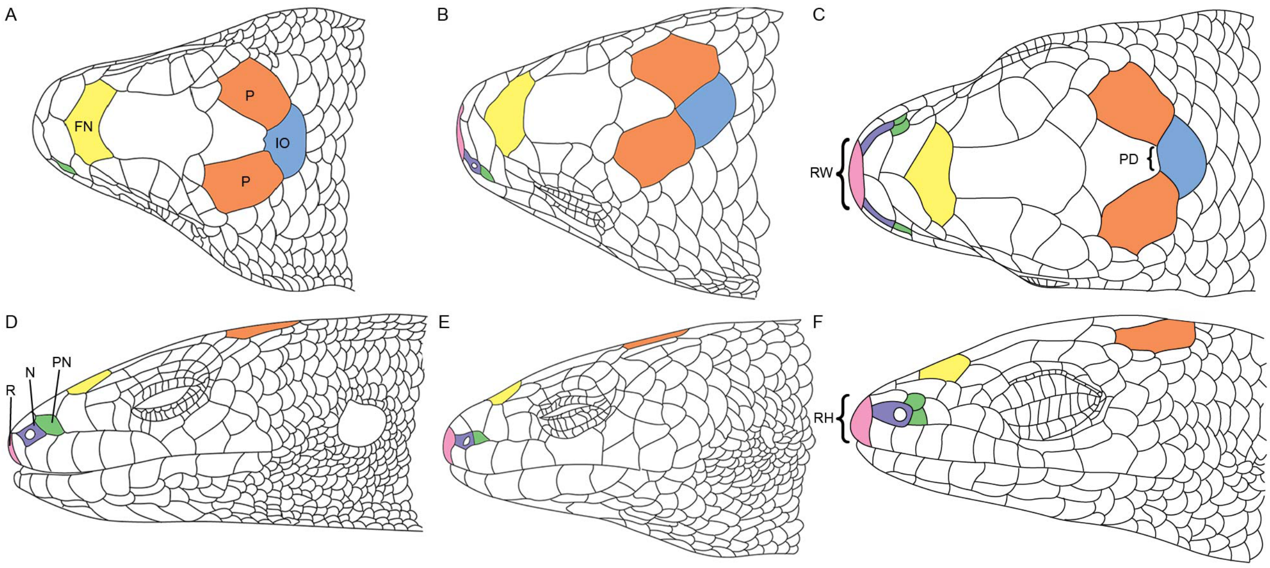

FIGURE 1. Head scalation of diploglossid lizards. Locations and names of scales on top (A–C) and side (D–F) of head are indicated along with selected measurements (brackets). Abbreviations are FN (frontonasal), IO (interoccipital), N (nasal), P (parietal), PD (distance between parietals), PN (postnasal), R (rostral), RH (rostral height), and RW (rostral width). Differences between the three subfamilies are seen with *Celestus barbouri* (MCZ R-45169) (A, D), *Diploglossus nigropunctuatus* (MCZ R-42563) (B, E), and *Siderolamprus laf* (SMF-90177) (C, F).

We scored the claw sheath on presence or absence. Previously, studies reported several taxa as having "half-sheathed" claws or claws that are partially sheathed (Underwood 1959; Myers 1973; Strahm & Schwartz 1977). We follow Savage *et al.* 2008 in categorizing all species reported to have intermediate sheaths as having either exposed or sheathed claws based on the number of scales comprising the claw sheath.

Studies have suggested using contact between the nasal and rostral scales as a diagnostic feature to differentiate the genera *Celestus* and *Diploglossus* (Underwood 1959; Hass *et al.* 2001). A head scale diagram of *Celestus badius* (Cochran 1941) depicted this species as having contact between the nasal and rostral scale, setting it apart from all other Caribbean *Celestus* species. Examination of photos of the specimen (USNM 25818) used for this illustration clearly show that it is lacking contact between the nasal and rostral scales. In addition, members of the genus

Ophiodes were reported to lack contact between the nasal and rostral scale (Savage *et al.* 2008). However, we did not observe any individual *Ophiodes* lacking nasal-rostral contact.

Counts of the scales in contact with the nasal scale and the postnasal scales, as well as the position of the nostril in the nasal scale, showed diagnostic value at the subfamily level. The presence or absence of a median keel on the dorsal scales and the digits per limb (zero, four, or five) had diagnostic value at the generic level.

Ophiodes lacks limbs and digits, but for all others we counted digital lamellae, the plate-like scales below each digit, from the base (junction with adjacent digit) to the tip (claw), on the longest toe (usually IV). The genera *Sauresia* and *Wetmorena* have only four toes and thus we counted this trait on toe III (the longest toe).

We counted dorsal scales in a longitudinal series from the interoccipital to the base of the tail. Some previous authors have referred to the interoccipital as the postparietal or the occipital (Myers 1973; Campbell & Camarillo 1994; Werler & Campbell 2004).

Museum abbreviations are as follows: ANSP (Academy of Natural Sciences, Philadelphia, Pennsylvania, USA), BMNH (Natural History Museum, London, England, UK), CAS (California Academy of Sciences, San Francisco, California, USA), CHFURG (Coleção Herpetológica da Fundação Universidade do Rio Grande, Brazil), CHUNB (Coleção Herpetológica da Universidade de Brasília, Brazil), CURC (Centro Universitario de Riviera, Uruguay), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA), MHCH (Museo Herpetológico de Chiriquí, Davíd, Chiriquí, Panama), MNHNCU (Museo Nacional de Historia Natural de Cuba, La Habana, Cuba), 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).

Systematic accounts

For genera, we identified 14 key (diagnostic) characters (Table 2) as follows: (1) claw sheath (p, present) (a, absent), (2) contact between the nasal and rostral scales (p, present) (a, absent), (3) scales in contact with the nasal scale, (4) postnasal scales, (5) position of the nostril in the nasal scale (c, central) (po, posterior), (6) medial keel on dorsal body scales (p, present) (a, absent), (7) digits per limb, (8) longest toe lamellae, (9) dorsal scale rows, (10) relative head width (% head width/SVL), (11) relative rostral height (% rostral height/rostral width), (12) relative frontonasal length (% frontonasal length/SVL), (13) relative interparietal distance (% interparietal distance/SVL), and (14) relative axilla-groin distance (% axilla-groin distance/SVL).

TABLE 2. Taxonomic summary of diagnostic morphological variation for lizards of the family Diploglossidae. We show sample sizes along with diagnostic characteristics used to distinguish the genera and subfamilies. The traits are: (1) claw sheath, (2) contact between the nasal and rostral scales, (3) scales in contact with the nasal scale, (4) postnasal scales, (5) position of the nostril in the nasal scale, (6) medial keel on dorsal body scales, (7) digits per limb, (8) longest toe lamellae, (9) dorsal scale rows, (10) relative head width, (11) relative rostral height, (12) relative frontonasal length, (13) relative interparietal distance, and (14) relative axilla-groin distance. Abbreviations: a (absent), c (central), n/a (not applicable), p (present), and po (posterior). Traits only from literature sources have an asterisk (*) in the sample size column. A dash indicates that no value was obtained for that trait.

	Sample Size	1	2	3	4	5	6	7	8	9
Celestinae										
Advenus montisilvestris	*	p	a	4	1	c	a	5	16–17	96
Caribicus darlingtoni	8	a	a	4	1	c	p	5	12–16	80–86 (1)
Caribicus anelpistus	1	a (*)	a	4	1	c	-	5 (*)	16–19 (*)	-
Caribicus warreni	2	a	a	4	1	c	p	5	13–18	211–233

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TABLE 2. (Continued)

	Sample Size	1	2	3	4	5	6	7	8	9
Celestus barbouri	12	a	a	4	1	c	p	5	12–16	138–140 (2)
Celestus crusculus	34	a	a	4	1	c	a	5	10–18	99–103 (2)
Celestus duquesneyi	2	a	a	4	1	c	p	5	19–23	-
Celestus fowleri	1	a	a	4	1	c	p	5	18–21	105
Celestus hewardii	7	a	a	4	1	c	p	5	15–20	-
Celestus macrolepis	1	a	a	4	1	c	p	5	24	109
Celestus macrotus	3	a	a	4	1	c	a	5	14–15	82–89 (2)
Celestus microblepharis	1	a	a	4	1	c	p	5	11–12	105
Celestus molesworthi	2	a	a	4	1	c	-	5	14–15	112 (1)
Celestus occiduus	2	a	a	4	1	c	p	5	16–23	128 (1)
Celestus striatus	1	a	a	4	1	c	a	5	24–26	112
Comptus badius	3	a	a	4	1	c	p	5	17–21	103–105 (2)
Comptus maculatus	6	a	a	4	1	c	p	5	13–15	91–107
Comptus stenurus	65	a	a	4	1	c	p	5	13–23	88–103 (49)
Panolopus costatus	90	a	a	4	1	c	a	5	12–22	83–100 (64)
Panolopus curtissi	43	a	a	4	1	c	a	5	12–19	84–100 (25)
Panolopus marcanoi	15	a	a	4	1	c	a	5	13–19	91–98
Sauresia sepsoides	61	p	a	4	1	c	a	4	8–12	101–127 (47)
Wetmorena agasepsoides	9	p	a	4	1	c	a	4	9–11	98–108 (7)
Wetmorena haetiana	51	p	a	4	1	c	a	4	8–12	102–117 (40)
Diploglossinae										
Diploglossus delasagra	16	p	p	6	1	po	a	5	8–10	92–99 (*)
Diploglossus fasciatus	4	p	a/p	5–6	1–2	po	a	5	12–15	93–98
Diploglossus garridoi	*	p	p	6	1	po	a	5	8	90
Diploglossus lessonae	3	p	p	5–6	1	po	a	5	10–11	90 (*)
Diploglossus microlepis	*	a	p	-	1	-	p	5	-	-
Diploglossus millepunctatus	1	p	p	6	2	po	a	5	18	91
Diploglossus monotropis	14	p	p	6	2	po	p	5	11–13	-
Diploglossus montisserrati	*	p	p	6	2	po	p	5	11	91
Diploglossus nigropunctuatus	5	p	p	6	1	po	a	5	9–12	88–95 (*)
Diploglossus pleii	14	p	p	5	2	po	a	5	10–13	89–91 (3)
Ophiodes enso	1	n/a	p	5	1	po	-	0	0	140–151

...*Continued on the next page*

TABLE 2. (Continued)

	Sample Size	1	2	3	4	5	6	7	8	9
Ophiodes fragilis	*	n/a	p	5	1	po	a	0	0	130–147
Ophiodes intermedius	*	n/a	p	5	1	po	a	0	0	139–158
Ophiodes luciae	*	n/a	p	-	1	po	-	0	0	171
Ophiodes striatus	5	n/a	p	5	1	po	a	0	0	147–164 (*)
Ophiodes vertebralis	*	n/a	-	5	1	po	a	0	0	136-150
Siderolamprinae										
Mesoamericus bilobatus	4	p	p	6	2	po	a	5	11–18	-
Siderolamprus adercus	*	a	p	6	2	po	a	5	24	79
Siderolamprus atitlanensis	*	a	p	6	2	po	a	5	17–18	72–76
Siderolamprus bivittatus	5	a	a/p	6	2	po	a	5	14–17	72–77 (*)
Siderolamprus cyanochloris	*	a	p	-	2	po	a	5	20–25	65–73
Siderolamprus enneagrammus	4	a	p	6	2	po	a	5	14–17	77–85 (*)
Siderolamprus hylaius	*	a	p	-	2	po	-	5	22–27	76–81
Siderolamprus ingridae	*	a	p	6	2	po	a	5	14–17	79–84
Siderolamprus laf	*	a	p	6	2	po	a	5	24–25	72
Siderolamprus legnotus	*	a	p	6	2	po	a	5	15–17	75–79
Siderolamprus montanus	*	a	p	6	2	po	a	5	23–35	72
Siderolamprus orobius	*	a	p	6	2	po	-	5	21–22	66
Siderolamprus owenii	*	a	-	-	-	-	p	5	-	-
Siderolamprus rozellae	2	a	p	6	2	po	p	5	20–24	71–76
Siderolamprus scansorius	1	a	p	6	2	po	p	5	21–22	74

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TABLE 2. (Continued)

	10	11	12	13	14
Celestinae					
Advenus montisilvestris	12	50.1	2.46	0.632	60
Caribicus darlingtoni	14.4–16.0 (1)	39.7–56.4 (1)	2.98–3.17 (1)	1.36–1.42 (1)	67.1–67.6 (4)
Caribicus anelpistus	17.2 (*)	-	-	-	-
Caribicus warreni	13.6–15.0	57.9–58.3	2.98–3.32	0.468–0.517	67.8–69.1
Celestus barbouri	11.8–14.1 (2)	59.1–63.1 (2)	2.12–2.61 (2)	0.473–0.714 (2)	63.2–66.2 (8)
Celestus crusculus	12.5–12.8 (2)	49.5–59.5 (2)	2.84–3.15 (2)	0.451–0.761 (2)	62.0–63.7 (29)
Celestus duquesneyi	16.7 (1)	66.5 (1)	3.58 (1)	0 (1)	60.9–61.8
Celestus fowleri	14.1	47.7	2.95	0.571	66.4
Celestus hewardii	16.0 (*)	-	-	-	62.7–65.0

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TABLE 2. (Continued)

	10	11	12	13	14
Celestus macrolepis	13.7	-	2.82	0.161	64.9
Celestus macrotus	14.5–14.6 (2)	51.3–58.8 (2)	2.87–3.00 (2)	0.054–0.953 (2)	65.8–66.2 (2)
Celestus microblepharis	12.6	50	2.43	0.566	66.3
Celestus molesworthi	15.9 (1)	52.4 (1)	2.22 (1)	0 (1)	63.8–65.5
Celestus occiduus	15.0–20.0 (1)	-	3.20 (1)	0.160 (1)	65.8
Celestus striatus	15	47.6	3.94	0.415	61.6
Comptus badius	12.0–12.8 (2)	53.2 (1)	3.11 (1)	0.332 (1)	57.8–59.0
Comptus maculatus	12.7–13.9 (4)	55.1–59.8 (4)	2.97–3.06 (4)	0.131–0.435 (4)	58.2–58.3 (4)
Comptus stenurus	11.9–15.0 (22)	53.6–65.5 (22)	2.95–3.65 (22)	0–0.423 (22)	51.9–60.0 (28)
Panolopus costatus	10.9–15.2 (9)	43.0–51.9 (9)	2.36–2.94 (9)	0.0691–0.615 (9)	49.7–58.6 (21)
Panolopus curtissi	10.6–15.5 (10)	37.6–51.6 (10)	1.93–2.83 (10)	0.157–0.652 (10)	51.7–59.6 (17)
Panolopus marcanoi	11.9–14.8	41.0–48.7	2.22–2.94	0.0699–0.911	51.9–58.4
Sauresia sepsoides	9.36–12.2 (37)	41.3–66.2 (37)	1.70–2.56 (37)	0–0.431 (37)	63.9–69.9 (47)
Wetmorena agasepsoides	8.52–9.75 (6)	38.7–58.0 (7)	1.47–1.99 (7)	0.659–1.03 (7)	69.2–71.4 (8)
Wetmorena haetiana	11.1–14.5 (12)	40.3–61.8 (12)	2.04–2.69 (12)	0.447–0.627 (12)	59.9–63.6 (19)
Diploglossinae					
Diploglossus delasagra	9.20 (*)	-	-	-	62.5–72.0 (5)
Diploglossus fasciatus	15.5–16.3	50.0–60.6	2.73–2.79	0–0.658	65.4–66.7
Diploglossus garridoi	9.32	53.8	2.92	0.311	68.9
Diploglossus lessonae	-	-	-	-	62.1–63.9 (2)
Diploglossus microlepis	14.9	-	-	-	-
Diploglossus millepunctatus	12.4	49.6	3.73	0	66.2
Diploglossus monotropis	15 (*)	-	-	-	56.2–57.8 (2)
Diploglossus montisserrati	19	49.8	4.44	0	52.8
Diploglossus nigropunctuatus	12.9 (1)	62.1 (1)	2.11 (1)	0 (1)	64.1–76.6
Diploglossus pleii	10.7–12.1 (2)	50.0–60.2 (2)	2.29–2.54 (2)	0.335–0.472 (2)	66.1–66.6 (6)
Ophiodes enso	-	-	-	-	-
Ophiodes fragilis	-	-	-	-	-
Ophiodes intermedius	-	-	-	-	-
Ophiodes luciae	-	-	-	-	-
Ophiodes striatus	-	-	-	-	-
Ophiodes vertebralis	-	-	-	-	-
Mesoamericus bilobatus	12.0–14.0 (*)	65.0–67.0 (*)	-	-	57.1 (1)
Siderolamprus adercus	12.1	51.4	2.79	0.744	60.7
Siderolamprus atitlanensis	11.9	55.6	-	0.778	-
Siderolamprus bivittatus	15.6 (*)	63.2 (*)	-	-	58.9–61.8
Siderolamprus cyanochloris	12.5–14.2	-	-	-	53.5–65.3
Siderolamprus enneagrammus	13.0 (*)	50.0 (*)	-	-	58.7–63.0

...Continued on the next page

TABLE 2. (Continued)

	10	11	12	13	14
Siderolamprus hylaius	9.88–12.1	-	-	-	58.6–63.6
Siderolamprus ingridae	12.3	51.7	-	-	-
Siderolamprus laf	14	63.9	2.57	1.14	54.6
Siderolamprus legnotus	12.3	44.7	2.88	0.794	-
Siderolamprus montanus	15.4	54.1	-	-	-
Siderolamprus orobius	12.2	-	-	0.651	60.7
Siderolamprus owenii	-	-	-	-	-
Siderolamprus rozellae	15.3 (1)	51 (1)	2.46 (1)	1.01 (1)	55.7–63.2
Siderolamprus scansorius	13.1–13.3	56.7	2.56	0.561	58.1–59.5

In some cases, specimen damage precluded scoring of a character or specific characters that were not mentioned in species descriptions, and therefore the total number scored for that character was fewer than the total number of specimens listed as examined. In addition, we recorded characters through a combination of measurements, pictures, and primary literature, resulting in varying sample sizes for each trait.

Results

Molecular analyses

The molecular phylogeny of 30 diploglossid species represents all but one of the 11 genera of diploglossid lizards diagnosed in this study (Fig. 2). Of the three subfamilies, all had Bayesian support values ≥ 95% and all had ML support values ≥ 93%. Of the ten genera, all had Bayesian support values of 100% and eight had ML support values of 100%. *Diploglossus* and *Ophiodes* had ML support values of 81% and 77%, respectively.

The molecular timetree (Fig. 3) uses the same nine-gene dataset and topology of Fig. 2. The split between Siderolamprinae and Diploglossinae+Celestinae was estimated to be 48.5 Mya. The split between Diploglossinae and Celestinae was estimated to be 43.5 Mya, while the split between the Caribbean diploglossines and closest mainland diploglossines was estimated to be 20.4 Mya. Divergences (stem times) among genera were 41.3–10.6 Mya, while divergences of species (stem times) within genera were 24.7–1.75 Mya.

For the purpose of biogeography, and assuming a directionality of dispersal, the dispersal times can be constrained by two nodes in the tree, the stem and crown nodes leading to the originating group (confidence limits on those nodes also should be considered). The initial dispersal from Middle America (siderolamprines) to South America (celestine/diploglossine clade) was 48.5–43.5 Mya. The origin of the Caribbean celestines from South America was 43.5–13.9 Mya. The origin of the Caribbean diploglossines from South American diploglossines was 20.4–12.4 Mya.

Morphological analyses

We assembled data for 14 morphological traits in Table 2. For each taxon in the systematic accounts, we present a summary of the data and identify diagnostic differences that completely separate each taxon from every other taxon. We also present drawings of head scalation and images of types or representative specimens. We drew head scale illustrations in vector format, with illustration software, directly on a digital image of the head, thus avoiding the distortions of scale and perspective that sometimes accompany camera lucida drawings.

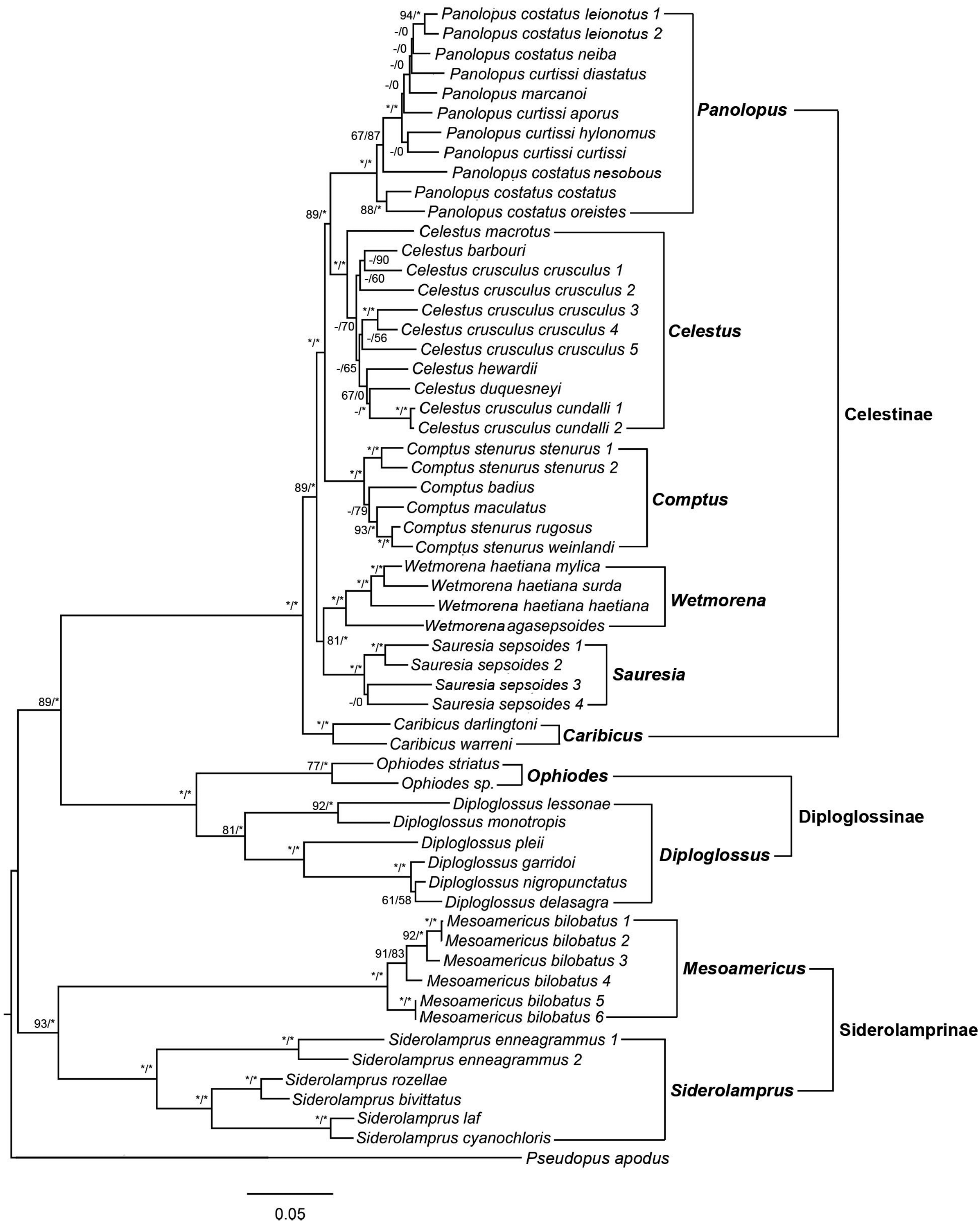

FIGURE 2. Phylogenetic tree of diploglossid lizards based on sequences of nine genes: four mitochondrial genes (CytB, ND2, 12S rRNA, and 16S rRNA) and five nuclear genes (AMEL, BDNF, PLPR, RAG1, and ZFP36). Maximum likelihood tree obtained from the nine-gene dataset (59 individuals; 6,949 sites). A scale bar indicates 5% 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).

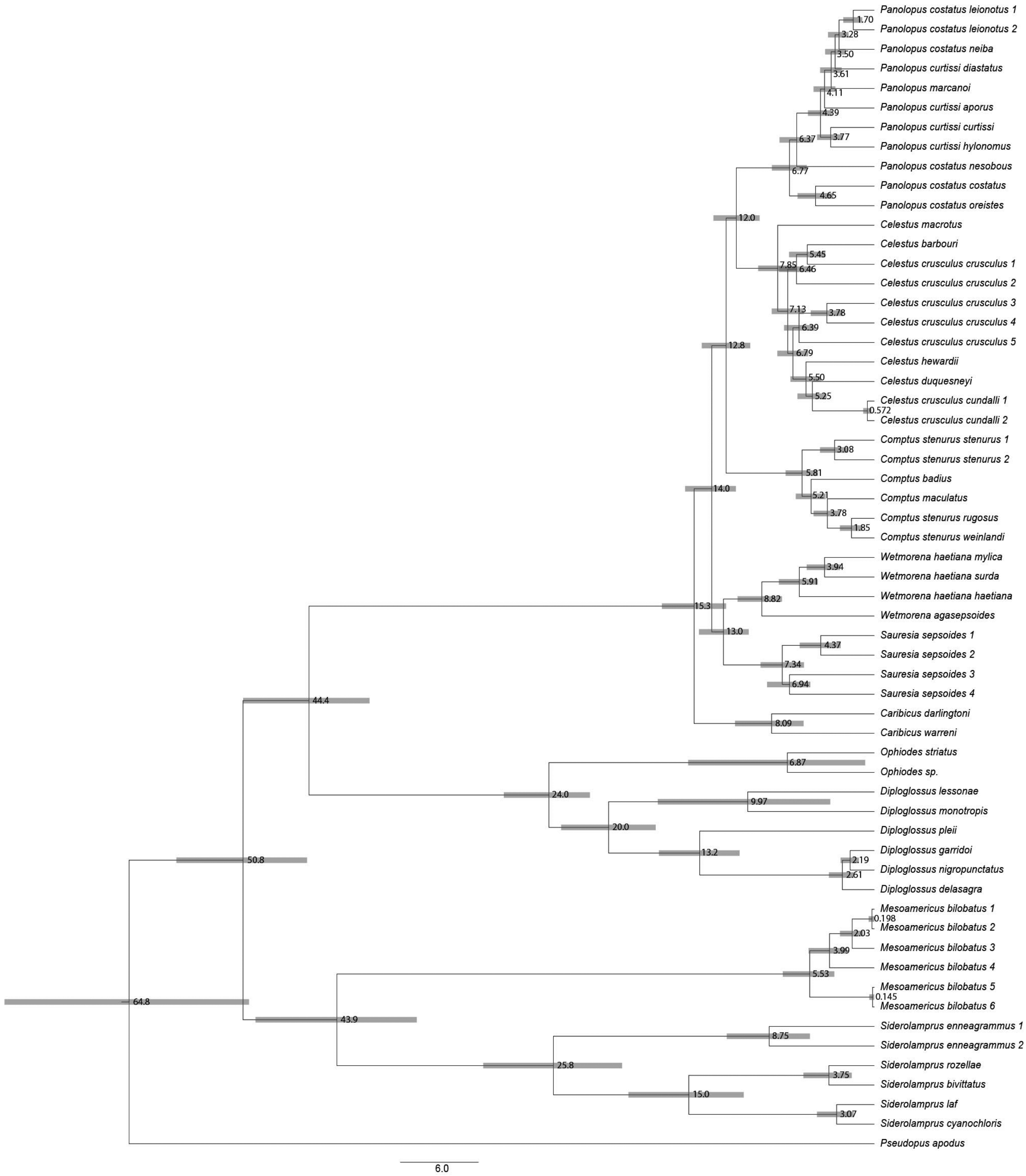

FIGURE 3. Timetree of Diploglossidae based on sequences of nine genes: four mitochondrial genes (CytB, ND2, 12S rRNA, and 16S rRNA) and five nuclear genes (AMEL, BDNF, PLPR, RAG1, and ZFP36). Nodes show divergence times in millions of years. A scale bar indicates time (6 million years ago, Mya). We show Bayesian credibility ranges as gray bars at nodes.

Systematic Accounts

Order Squamata Oppel, 1811

Toxicofera Vidal & Hedges, 2005

Anguimorpha Fürbringer, 1900

Neoanguimorpha Vidal & Hedges, 2009

Superfamily Anguioidea Gray, 1825

Family Diploglossidae Cope, 1865
Neotropical Forest Lizards
Fig. 4

Diagnosis. Members of this family have (1) claw sheath, present or absent, (2) contact between the nasal and rostral scales, present or absent, (3) scales in contact with the nasal scale, 4–6, (4) postnasal scales, 1–2, (5) position of the nostril in the nasal scale, central or posterior, (6) keels on dorsal body scales, present or absent, (7) digits per limb, zero, four, or five, (8) longest toe lamellae, 8–35 except for limbless species, (9) dorsal scale rows, 65–171, (10) relative head width, 8.52–20.0, (11) relative rostral height, 37.6–67.0, (12) relative frontonasal length, 1.47–4.44, (13) relative interparietal distance, 0–1.42 (14) relative axilla-groin distance, 49.7–76.6.

Content. Fifty-five currently recognized species in three subfamilies (Table 3): *Celestinae* **subfam. nov.**, *Diploglossinae*, and *Siderolamprinae* **subfam. nov**.

Distribution. Diploglossidae occurs in Middle America, South America, and on islands in the Caribbean (Fig. 4).

Etymology. As for the type genus.

Subfamily Celestinae subfam. nov.
Caribbean Forest Lizards
Figs. 5–6

Type genus. *Celestus* Gray, 1839.

Diagnosis. Members of this subfamily have (1) claw sheath, present or absent, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, present or absent, (7) digits per limb, four or five, (8) longest toe lamellae, 8–26, (9) dorsal scale rows, 80–233, (10) relative head width, 8.52–20.0, (11) relative rostral height, 37.6–66.5, (12) relative frontonasal length, 1.47–3.65, (13) relative interparietal distance, 0–1.42, (14) relative axilla-groin distance, 49.7–71.4.

The subfamily Celestinae **subfam. nov.** is distinguished from the other two subfamilies by scales in contact with the nasal scale (four versus 5–6 in Diploglossinae and Siderolamprinae), the postnasal scales (one versus two in Siderolamprinae), and the position of the nostril in the nasal scale (central versus posterior in Diploglossinae and Siderolamprinae).

Content. Twenty-four currently recognized species in seven genera (Table 3): *Advenus* **gen. nov.**, *Caribicus* **gen. nov.**, *Comptus* **gen. nov.**, *Celestus* Gray, 1839, *Panolopus* Cope, 1862, *Sauresia* Gray, 1852, and *Wetmorena* Cochran, 1927.

Distribution. One species in this subfamily occurs in eastern Panama, near the border with Colombia. All others occur on Caribbean islands, including Cayman Brac, Little Cayman, Jamaica, Navassa, and Hispaniola.

Etymology. As for the type genus.

Remarks. The subfamily Celestinae **subfam. nov.** is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). We have defined seven genera that fall into this subfamily based on molecular and morphological evidence (*Advenus* **gen. nov.**, *Caribicus* **gen. nov.**, *Comptus* **gen. nov.**, *Celestus, Panolopus, Sauresia,* and *Wetmorena*). Our phylogeny includes six of the seven genera, with *Advenus* **gen. nov.** not being present. Here, we resurrect one of the seven genera, *Panolopus* (Cope, 1862). Previous authors have accepted or disregarded *Sauresia* and *Wetmorena* based on usage of the presence or absence of a claw sheath as a diagnostic characteristic trait (see above). For most of the time since being named, *Sauresia* and *Wetmorena* have been recognized as a valid genera, distinct from *Celestus*. The genera were synonomized with *Celestus* by Hass *et al.* (2001) because their study using immunological data found relationships that differed from previous studies (Savage & Lips 1993).

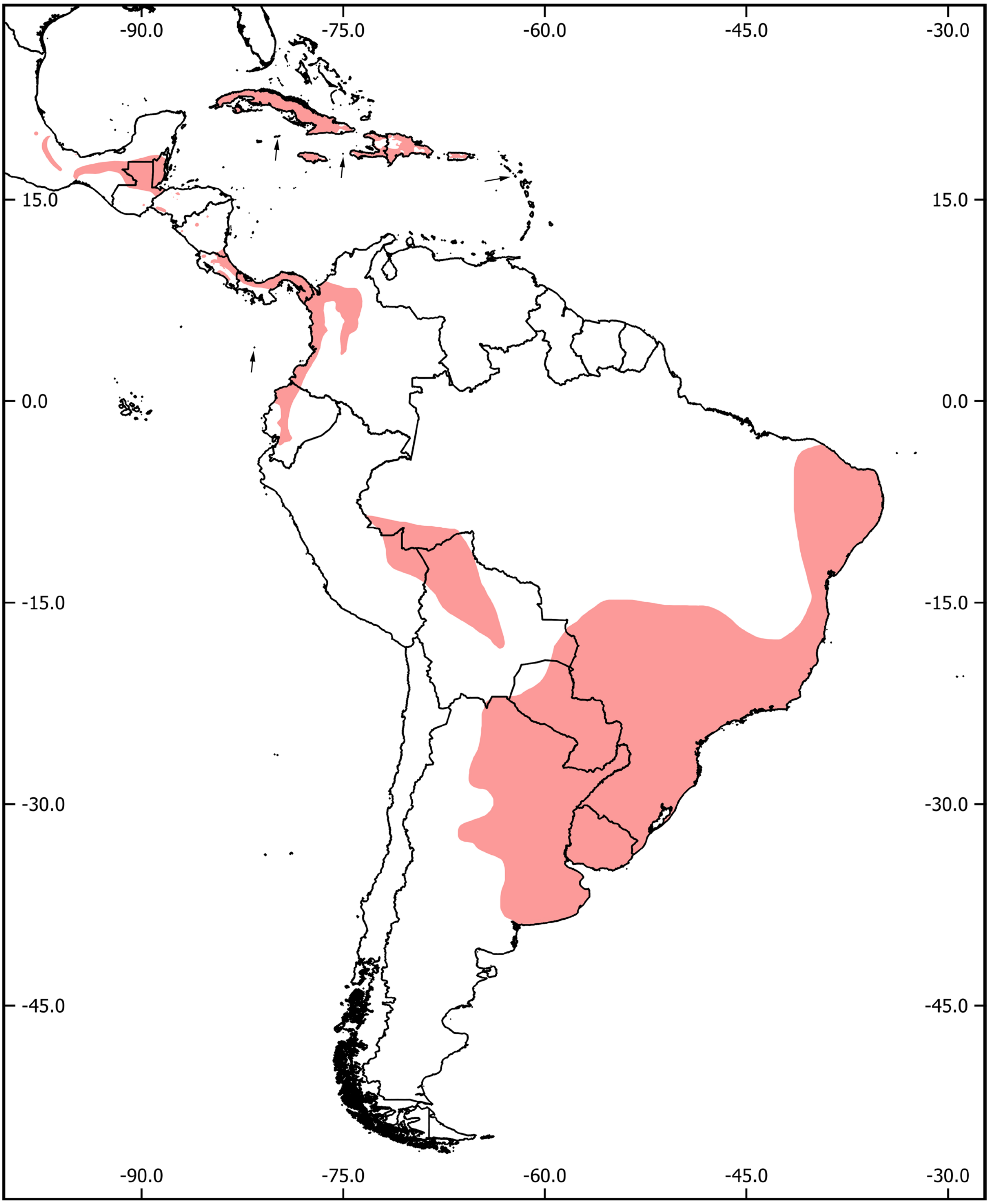

FIGURE 4. Map showing the distribution of Diploglossidae. Arrows indicate distribution (from left to right) on Malepo Island, Little Cayman and Cayman Brac, Navassa Island, and Montserrat.

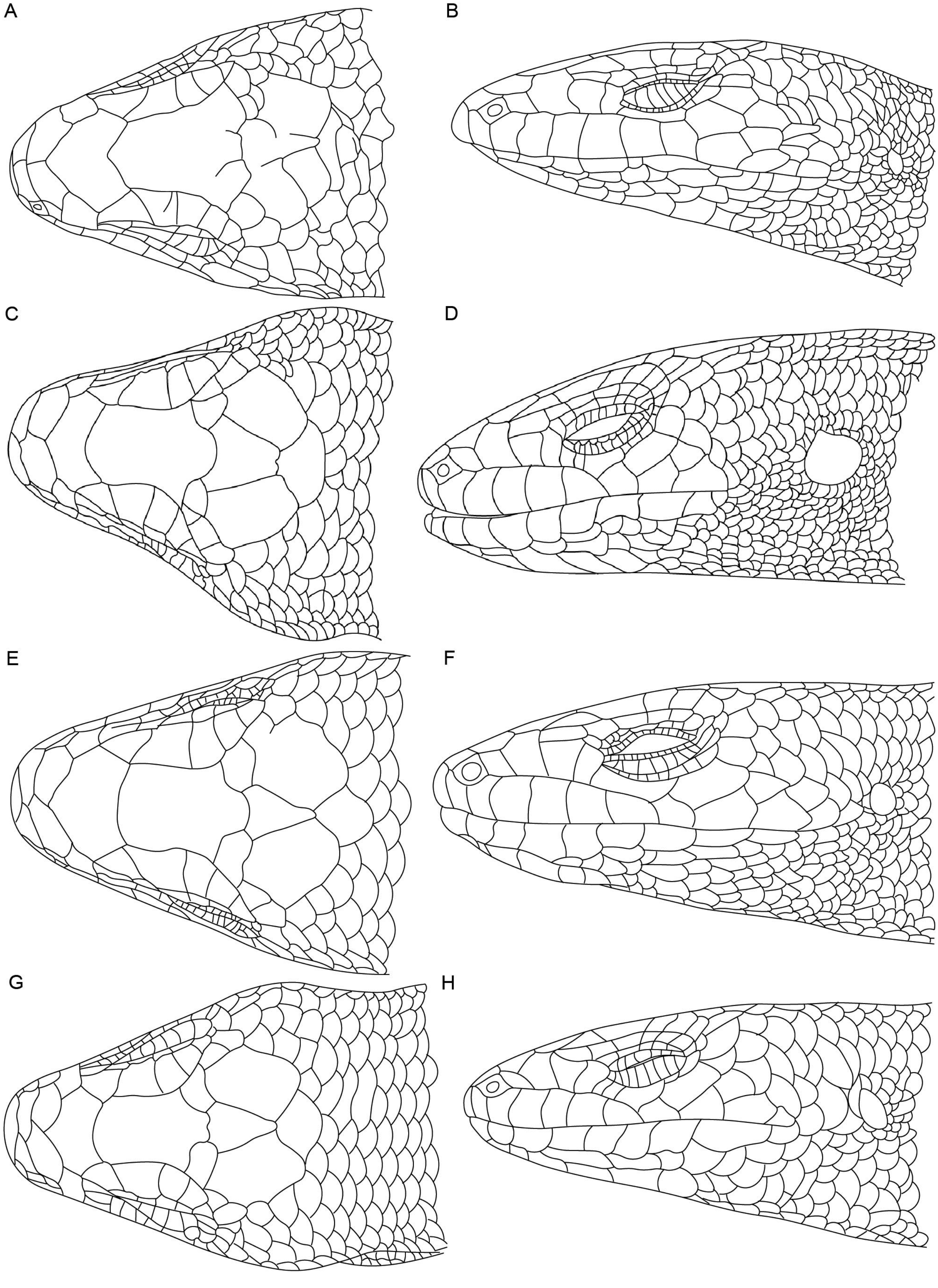

FIGURE 5. Head scalation of celestine genera from top (left) and side (right) views. (A–B) *Caribicus warreni* (ANSP 38502), HW 31.8 mm, HL 44.2 mm. (C–D) *Celestus barbouri* (MCZ R-45169). (E–F) *Comptus stenurus alloeides* (MCZ R-77152), HW 14.1 mm, HL 19.3 mm. (G–H) *Panolopus curtissi hylonomus* (MCZ R-77160), HW 10.1 mm, HL 13.2 mm.

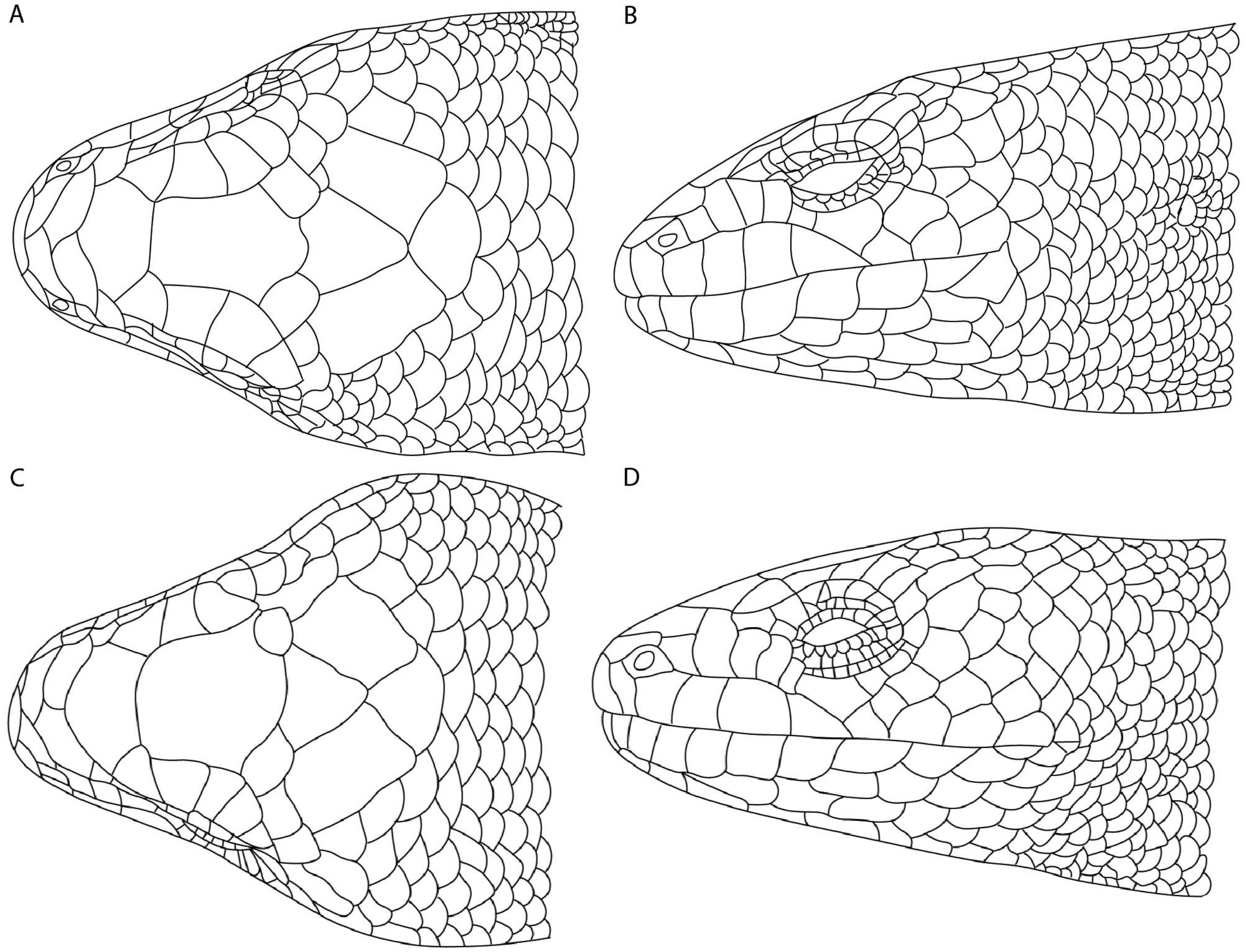

FIGURE 6. Head scalation of celestine genera from top (left) and side (right) views. (A–B) *Sauresia sepsoides* (ANSP 38667), HW 8.15 mm, HL 9.37 mm. (C–D) *Wetmorena haetiana mylica* (MCZ R-77049), HW 12.0 mm.

TABLE 3. Classification and distribution of lizards of the family Diploglossidae (55 species). For common names we use modifying words from literature sources, in some cases modified for consistency following guidelines (Hedges *et al.* 2019). The IUCN Redlist threat status is indicated in parentheses (NA = not assessed).

Species	Distribution
Celestinae (24 sp.)	
Advenus montisilvestris (Myers 1973); Pirre Mountain Forest Lizard (DD)	Panama
Caribicus anelpistus (Schwartz *et al.* 1979); Altagracia Giant Forest Lizard (CR)	Hispaniola
Caribicus darlingtoni (Cochran 1939); Hispaniolan Striped Forest Lizard (EN)	Hispaniola
Caribicus warreni (Schwartz 1970); Hispaniolan Giant Forest Lizard (VU)	Hispaniola, Ile de la Tortue
Celestus barbouri (Grant 1940a); Limestone Forest Lizard (EN)	Jamaica
Celestus crusculus (Garman 1887); Jamaican Forest Lizard (LC)	Jamaica
Celestus duquesneyi (Grant 1940b); Blue-tailed Forest Lizard (CR)	Jamaica
Celestus fowleri (Schwartz 1971); Bromeliad Forest Lizard (VU)	Jamaica
Celestus hewardii (Gray 1845); Red-spotted Forest Lizard (EN)	Jamaica
Celestus macrolepis (Gray 1845); Large-scaled Forest Lizard (NA)	Jamaica
Celestus macrotus (Thomas & Hedges 1989); La Selle Forest Lizard (EN)	Hispaniola
Celestus microblepharis (Underwood 1959); Small-eyed Forest Lizard (CR)	Jamaica

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TABLE 3. (continued)

Species	Distribution
Celestus molesworthi (Grant 1940b); Portland Coast Forest Lizard (EN)	Jamaica
Celestus occiduus (Shaw 1802); Jamaican Giant Forest Lizard (CR)	Jamaica
Celestus striatus (Gray 1839); Golden Forest Lizard (NA)	Jamaica
Comptus badius (Cope 1868); Navassa Forest Lizard (LC)	Navassa Island
Comptus maculatus (Garman 1887); Lesser Cayman Forest Lizard (EN)	Cayman Islands
Comptus stenurus (Cope 1862); Hispaniolan Keeled Forest Lizard (LC)	Hispaniola, Ile-a-Vache, Ile a Cabrit, and Ile Grande Cayemite
Panolopus costatus (Cope 1862); Hispaniolan Smooth Forest Lizard (LC)	Hispaniola
Panolopus curtissi (Grant 1951); Hispaniolan Khaki Forest Lizard (LC)	Hispaniola
Panolopus marcanoi (Schwartz & Incháustegui 1976); Pico Duarte Forest Lizard (LC)	Hispaniola
Sauresia sepsoides (Gray 1852); Common Four-toed Forest Lizard (LC)	Hispaniola
Wetmorena agasepsoides (Thomas 1971); Serpentine Four-toed Forest Lizard (EN)	Hispaniola
Wetmorena haetiana (Cochran 1927); Earless Four-toed Forest Lizard (EN)	Hispaniola
Diploglossinae (16 sp.)	
Diploglossus delasagra (Cocteau & Bibron 1838); Cuban Pale-necked Forest Lizard (LC)	Cuba
Diploglossus fasciatus (Gray 1831); Banded Forest Lizard (LC)	Brazil
Diploglossus garridoi (Thomas & Hedges 1998); Cuban Small-eared Forest Lizard (NT)	Cuba
Diploglossus lessonae (Peracca 1890); Brazilian Forest Lizard (LC)	Brazil
Diploglossus microlepis (Gray 1831); Small-scaled Forest Lizard (NA)	Unknown
Diploglossus millepunctatus (O'Shaughnessy 1874); Malpelo Island Forest Lizard (LC)	Malpelo Island
Diploglossus monotropis (Kuhl 1820); Yellow-headed Forest Lizard (LC)	Colombia, Costa Rica, Ecuador, Nicaragua, Panama
Diploglossus montisserrati (Underwood 1964); Montserrat Forest Lizard (CR)	Montserrat
Diploglossus nigropunctuatus (Barbour & Shreve 1937); Cuban Spotted Forest Lizard (LC)	Cuba
Diploglossus pleii (Duméril & Bibron 1839); Puerto Rican Forest Lizard (LC)	Puerto Rico
Ophiodes enso (Entiauspe-Neto *et al*. 2017); Pelotas Glass Lizard (NA)	Brazil
Ophiodes fragilis (Raddi 1826); Yacupoi Glass Lizard (NA)	Argentina, Bolivia, Brazil, Paraguay
Ophiodes intermedius (Boulenger 1894); Asuncion Glass Lizard (LC)	Argentina, Bolivia, Paraguay, Uruguay
Ophiodes luciae (Cacciali & Scott 2015); Pale-striped Glass Lizard (NA)	Paraguay
Ophiodes striatus (Spix 1824); Dark-striped Glass Lizard (LC)	Brazil, Paraguay, Uruguay
Ophiodes vertebralis (Bocourt 1881); Uruguayan Glass Lizard (NA)	Argentina, Brazil, Uruguay
Siderolamprinae (15 sp.)	
Mesoamericus bilobatus (O'Shaughnessy 1874); Talamancan Forest Lizard (LC)	Costa Rica, Nicaragua, Panama
Siderolamprus adercus (Savage *et al.* 2008); Panamanian Forest Lizard (DD)	Panama
Siderolamprus atitlanensis (Smith 1950); Atitlan Forest Lizard (DD)	El Salvador, Guatemala, Mexico
Siderolamprus bivittatus (Boulenger 1895); Two-striped Lesser Forest Lizard (EN)	El Salvador, Guatemala, Honduras, Nicaragua
Siderolamprus cyanochloris (Cope 1894); Irazu Forest Lizard (LC)	Costa Rica

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TABLE 3. (continued)

Species	Distribution
Siderolamprus enneagrammus (Cope 1861); Huasteca Lesser Forest Lizard (LC)	Mexico
Siderolamprus hylaius (Savage & Lips 1993); Costa Rican Forest Lizard (NT)	Costa Rica
Siderolamprus ingridae (Werler & Campbell 2004); Veracruz Forest Lizard (DD)	Mexico
Siderolamprus laf (Lotzkat *et al*. 2016); Chiriqui Forest Lizard (NA)	Panama
Siderolamprus legnotus (Campbell & Camarillo 1994); Campbell's Forest Lizard (LC)	Mexico
Siderolamprus montanus (Schmidt 1933); Montane Lesser Forest Lizard (EN)	Honduras
Siderolamprus orobius (Savage & Lips 1993); Hortensia Forest Lizard (DD)	Costa Rica
Siderolamprus owenii (Duméril *et al.*1839); Owen's Forest Lizard (NA)	Guatemala, Mexico
Siderolamprus rozellae (Smith 1942); Mayan Forest Lizard (LC)	Belize, Guatemala, Mexico
Siderolamprus scansorius (Mccranie & Wilson 1996); Yoro Forest Lizard (EN)	Honduras

Myers (1973) used a single specimen of *Advenus montisilvestris* to define this species that he collected on the southeastern slope of Cerro Pirre, Serranía de Pirre, Province of Darién, Republic of Panama. Morphologically, it groups with Celestinae **subfam. nov.** because of contact between the nasal and rostral scale, the scales in contact with the nasal scale, the number of postnasal scales, and the position of the nostril in the nasal scale.

We have chosen to use generic names to classify species in this subfamily for several reasons. First, we do so for a more manageable classification. While the current number of species (24) is not excessive, we know that the actual number is more than twice that amount. Four species in this subfamily are not monophyletic and there are deep divergences among populations within most species (Fig. 3). Our greater sampling of populations has confirmed this, indicating that more than 30 additional species of celestines are undescribed (Schools & Hedges, unpubl.). Secondly, the times of divergence of the celestine genera (10–15 Mya) are typical of squamate reptile genera (mode of 485 genera, 13.3 Mya; Hedges *et al.* 2015). Thirdly, the use of genera for clades in this subfamily has been the status quo. Four of the six clades (*Celestus, Panolopus, Sauresia*, and *Wetmorena*) already had generic names, and three of them (*Celestus*, *Sauresia,* and *Wetmo*rena) have been in use, on and off, for much of the last two centuries.

Genus *Advenus* gen. nov.

Pirre Mountain Forest Lizards

Fig. 7

Type species. *Diploglossus montisilvestris* Myers, 1973:3.

Diagnosis. Species of *Advenus* **gen. nov.** have (1) claw sheath, present, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, absent, (7) digits per limb, five, (8) longest toe lamellae, 16–17, (9) dorsal scale rows, 96, (10) relative head width, 12.0, (11) relative rostral height, 50.1, (12) relative frontonasal length, 2.46, (13) relative interparietal distance, 0.632, (14) relative axilla-groin distance, 60.0.

From *Caribicus* **gen. nov.**, we distinguish *Advenus* **gen. nov.** by the claw sheath (present versus its absence in *Caribicus* **gen. nov.**), keels on the dorsal scales (absent versus their presence in *Caribicus* **gen. nov.**), relative head width (12.0 versus 13.6–17.2), relative frontonasal length (2.46 versus 2.98–3.32), and the relative axilla-groin distance (60.0 versus 67.1–69.1). From *Celestus,* we distinguish *Advenus* **gen. nov.** by the claw sheath (present versus its absence in *Celestus*) and the relative axilla-groin distance (60.0 versus 60.9–66.3). From *Comptus* **gen. nov.**, we distinguish *Advenus* **gen. nov.** by the claw sheath (present versus its absence in *Comptus* **gen. nov.**), keels on dorsal scales (absent versus their presence in *Comptus* **gen. nov.**), relative rostral height (50.1 versus 53.2–65.5), relative frontonasal length (2.46 versus 2.95–3.65), and the relative interparietal distance (0.632 versus 0–0.435). From *Panolopus,* we distinguish *Advenus* **gen. nov.** by the claw sheath (present versus its absence in *Panolopus*) and the relative axilla-groin distance (60.0 versus 49.7–59.6). From *Sauresia,* we distinguish *Advenus* **gen. nov.** by the digits per limb (five versus four), the longest toe lamellae (16–17 versus 8–12), the dorsal scale rows (96 versus

101–127), the relative interparietal distance (0.632 versus 0–0.431), and the relative axilla-groin distance (60.0 versus 63.9–69.9). From *Wetmorena,* we distinguish *Advenus* **gen. nov.** by the digits per limb (five versus four), the number of longest toe lamellae (16–17 versus 8–12), and the dorsal scale rows (96 versus 98–117).

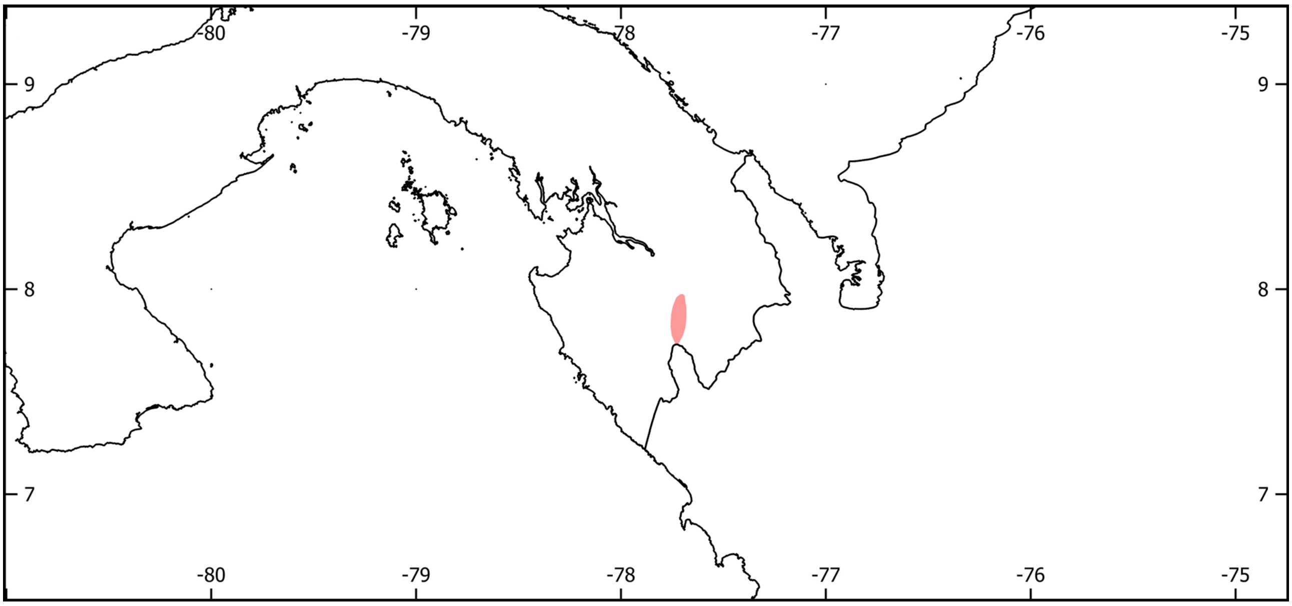

FIGURE 7. The distribution of *Advenus* **gen. nov**. in southeastern Panama, near the border with Colombia.

Content. One species (Table 3): *Advenus montisilvestris.*

Distribution. Known from only one specimen collected on the southeastern slope of Cerro Pirre (1440 m), Serranía de Pirre, Province of Darién, Republic of Panama (Fig. 7). By our calculation, the location is 7.9242, -77.7000.

Etymology. The generic name *Advenus* is a masculine noun derived from the Latin *advena* ("stranger"), referring to the distribution of this species in Middle America when all of its close relatives are on Caribbean islands.

Remarks. *Advenus montisilvestris* is the only member of the subfamily Celestinae **subfam. nov.** that is found outside of the Caribbean. The name *montisilvestris* refers to the mountain forest at the type locality. Morphological traits align this species with the other members of Celestinae **subfam. nov.** that are distributed in the western Caribbean, on the islands of Jamaica and Hispaniola, but not with any one genus. Genetic data are necessary to further clarify the relationship of *Advenus montisilvestris* within the Diploglossidae.

Genus *Caribicus* gen. nov.

Northern Hispaniola Forest Lizards

Figs. 8–9

Type species. *Celestus darlingtoni* Cochran, 1939:2.

Diagnosis. Species of *Caribicus* have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (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, 12–19, (9) dorsal scale rows, 80–233, (10) relative head width, 13.6–17.2, (11) relative rostral height, 39.7–58.3, (12) relative frontonasal length, 2.98–3.32, (13) relative interparietal distance, 0.468–1.42, (14) relative axilla-groin distance, 67.1–69.1.

From *Advenus* **gen. nov.***,* we distinguish *Caribicus* **gen. nov.** by the claw sheath (absent versus its presence in *Advenus* **gen. nov.**), keels on the dorsal scales (present versus their absence in *Advenus* **gen. nov.**)), relative head width (13.6–17.2 versus 12.0), relative frontonasal length (2.98–3.32 versus 2.46), and the relative axilla-groin distance (67.1–69.1 versus 60.0). From *Celestus,* we distinguish *Caribicus* **gen. nov.** by the relative axilla-groin distance (67.1–69.1 versus 60.9–66.4). From *Comptus* **gen. nov.***,* we distinguish *Caribicus* **gen. nov.** by the relative interparietal distance (0.468–1.42 versus 0–0.435), and the relative axilla-groin distance (67.1–69.1 versus 51.9–60.0).

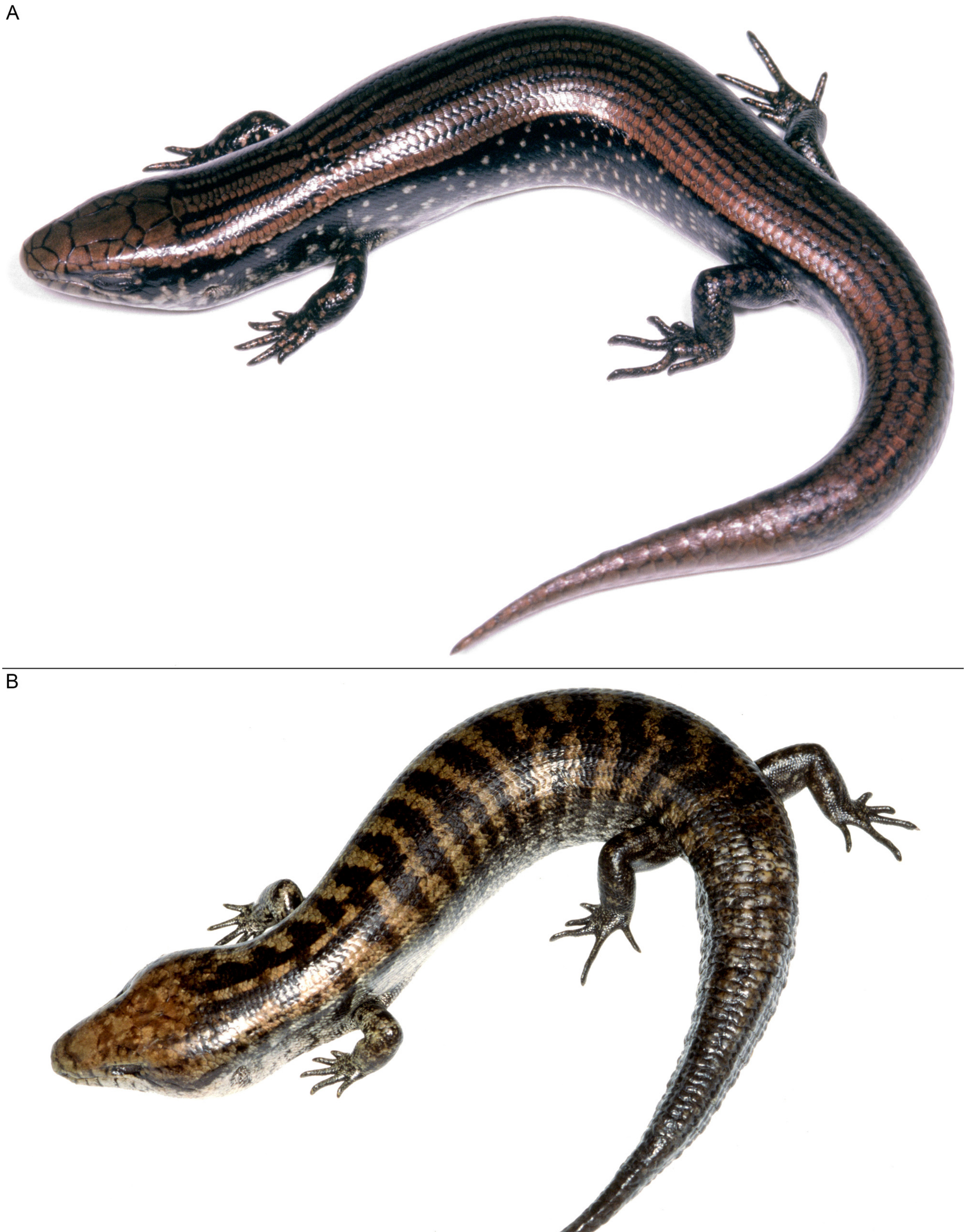

FIGURE 8. In life images of (A) *Caribicus darlingtoni* (USNM 328807, SVL 45.5 mm) and (B) *Caribicus warreni* (Voucher not available, SBH 194521, SVL 263 mm). Photographs by S. B. Hedges.

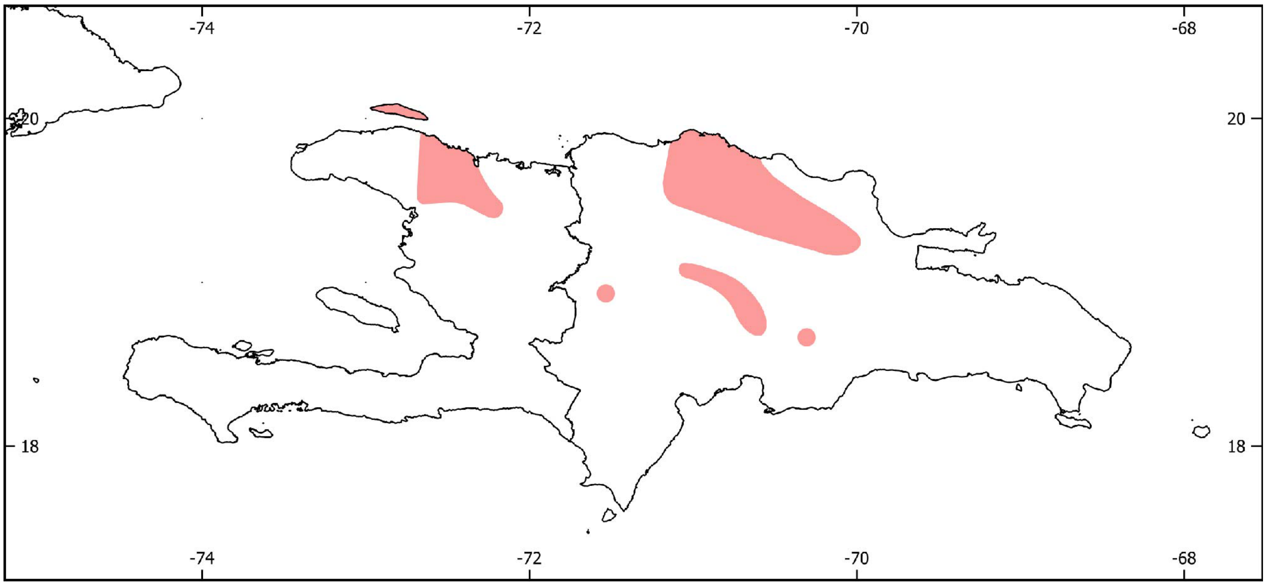

FIGURE 9. The distribution of *Caribicus* **gen. nov.** on Hispaniola**.**

From *Panolopus,* we distinguish *Caribicus* **gen. nov.** by keels on the dorsal body scales (present versus their absence in *Panolopus*), relative frontonasal length (2.98–3.32 versus 1.93–2.94), and the relative axilla-groin distance (67.1–69.1 versus 49.7–59.6). From *Sauresia*, we distinguish *Caribicus* **gen. nov.** by the claw sheath (absent versus its presence in *Sauresia*), keels on the dorsal body scales (present versus their absence in *Sauresia*), digits per limb (five versus four), relative head width (13.6–17.2 versus 9.36–12.2), relative frontonasal length (2.98–3.32 versus 1.70–2.56), and the distance between the parietal scales (0.468–1.42 versus 0–0.431). From *Wetmorena,* we distinguish *Caribicus* **gen. nov.** by the claw sheath (absent versus its presence in *Wetmorena*), keels on the dorsal scales (present versus their absence in *Wetmorena*), digits per limb (five versus four), and the relative frontonasal length (2.98–3.32 versus 1.47–2.69).

Content. Three species (Table 3): *Caribicus anelpistus, C. darlingtoni,* and *C. warreni.*

Distribution. *Caribicus* **gen. nov.** occurs on the geological North Island of Hispaniola and adjacent Ile de Tortue (Fig. 9).

Etymology. The generic name (*Caribicus* **gen. nov.**) is a masculine noun derived from the name for the region (Caribbean) in which it occurs and the suffix *-icus* ("belonging to").

Remarks. *Caribicus* **gen. nov.** is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). Our phylogenies do not include *C. anelpistus*. That species and *C. warreni* are both giant (up to 279 mm SVL) whereas *C. darlingtoni* is much smaller (up to 85 mm SVL) and was never thought to be closely related to the giant species. For many years, the giant species were placed in *Diploglossus* and the small species was placed in *Celestus* (Schwartz & Henderson, 1991).

Genus *Celestus* Gray, 1839
Jamaican Forest Lizards
Figs. 10–14

Celestus Gray, 1839:288. Type species: *Celestus striatus* Gray, 1839:288, by original designation.
Macrogongylus Werner, 1901:299. Type species *Macrogongylus brauni* Werner, 1901:299, by original designation.

Diagnosis. Species of *Celestus* have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, present or absent, (7) digits per limb, five, (8) longest toe lamellae, 10–23, (9) dorsal scale rows, 82–140, (10) relative head width, 11.8–20.0, (11) relative rostral height, 47.6–66.5, (12) relative frontonasal length, 2.12–3.94, (13) relative interparietal distance, 0–0.953, (14) relative axilla-groin distance, 60.9–66.3.

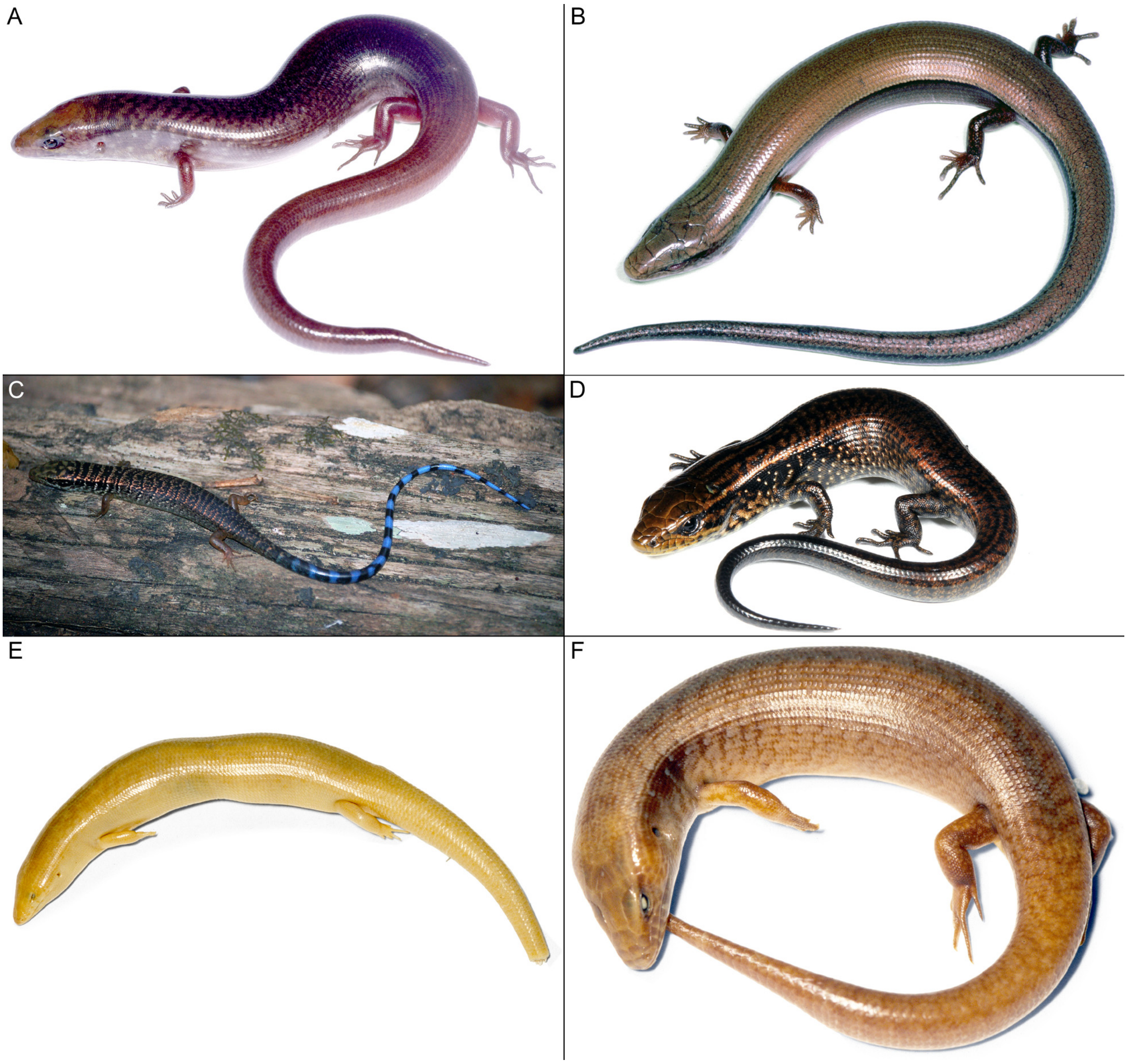

FIGURE 10. Images of (A) live adult *Celestus barbouri* (USNM 328151, SVL 78.4 mm), (B) live adult *Celestus crusculus* (USNM 328170, SVL 45.3 mm), (C) live adult *Celestus duquesneyi*, (D) live juvenile *Celestus macrotus* (ANSP 38506, SVL 42.1 mm), (E) *Celestus microblepharis* (MCZ R-55764, SVL 87.0 mm), and (F) *Celestus molesworthi* (MCZ R-45184, SVL 85.0 mm). Photographs by Byron S. Wilson (C) and S. B. Hedges (all others).

From *Advenus* **gen. nov.**, we distinguish *Celestus* by the claw sheath (absent versus its presence in *Advenus* **gen. nov.**) and the relative axilla-groin distance (60.9–66.3 versus 60.0). From *Caribicus* **gen. nov.**, we distinguish *Celestus* by the relative axilla-groin distance (60.9–66.3 versus 67.1–69.1). From *Comptus* **gen. nov.**, we distinguish *Celestus* by the relative axilla-groin distance (60.9–66.3 versus 51.9–60.0). From *Panolopus,* we distinguish *Celestus* by the relative axilla-groin distance (60.9–66.3 versus 49.7–59.6). From *Sauresia,* we distinguish *Celestus* by the claw sheath (absent versus its presence in *Sauresia*) and the digits per limb (five versus four). From *Wetmorena,* we distinguish *Celestus* by the absences of the claw sheath (versus its presence in *Wetmorena*) and the digits per limb (five versus four).

Content. Eleven species (Table 3): *Celestus barbouri, C. crusculus, C. duquesneyi, C. fowleri, C. hewardii, C. macrolepis, C. macrotus, C. microblepharis, C. molesworthi, C. occiduus,* and *C. striatus.*

Distribution. *Celestus* occurs almost entirely on Jamaica, with a single species (*C. macrotus*) on Hispaniola (Fig. 14). The map does not include the distributions of *Celestus macrolepis* and *C. striatus*, which are unknown other than being restricted to Jamaica.

FIGURE 11. (A–H) *Celestus striatus* (BMNH 1946.8.8.3, holotype), SVL 145 mm. White lines in (D) depict outline of a single large frontonasal scale missing, and dashed lines depict pseudosutures in the underlying integument. Photographs by S. B. Hedges.

Etymology. Not defined in the original description, but a masculine noun probably from the Latin *caelestis* (heavenly), in reference to the "silvery" color of the type species noted by Gray (1839).

Remarks. *Celestus* is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig.

2). Our phylogenies include five of the eleven species of *Celestus* (*Celestus barbouri, C. crusculus, C. duquesneyi, C. hewardii,* and *C. macrotus*). Our trees show that the two subspecies of *Celestus crusculus* (*C. c. crusculus* and *C. c. cundalli*) are not related, indicating that *cundalli* warrants species recognition (Schools & Hedges, unpubl.). In addition, *Celestus crusculus crusculus* is not monophyletic and includes populations with deep divergences (3.7–6.7 Mya; Fig. 3). These results, together with other molecular and morphological data, indicate that the genus *Celestus* includes at least six additional species (Schools & Hedges, unpubl.).

The origin and classification of *Celestus striatus*, the type species of the genus, are unresolved, even though the original describer indicated a general locality "West Indies" (Gray 1845; Boulenger 1885). Schwartz (1964) examined photographs of the type of *Celestus striatus* and concluded that it was not from the Caribbean based on its large size (145 mm SVL), low midbody scale count (41) and, that it had three prefrontal scales—this latter condition being virtually unknown among West Indian taxa. Strahm and Schwartz (1977) "provisionally" considered *C. striatus* to be Central American based on its unusual scalation. Savage *et al.* (2008) did not examine the holotype of *Celestus striatus* but followed Schwartz's (1964) characterization of its head scalation (one frontonasal and two prefrontals in the terminology of Savage *et al*.). However they did not readily accept a Central American origin for *C. striatus*, leaving its provenance a mystery.

One of us (S.B.H.) examined the type specimen of *Celestus striatus* in the Natural History Museum (London) and found that it is missing the frontonasal scale (Fig. 11). Instead, the underlying integument shows pseudosutures, which apparently led Schwartz to conclude, based on only a photograph, that there were three scales present instead of one, an easy error to make. We have available the photograph used by Schwartz and it shows the same pseudosutures, confirming that the specimen is missing the frontonasal scale. Boulenger (1885: pl. 16, fig. 1a) illustrated that specimen showing a single large frontonasal scale, apparently before it fell off. Now, with this correction, the head scalation is consistent with the notation by Gray (1845) that the specimen is from the "West Indies," where a single large frontonasal scale is common.

Celestus striatus has all three diagnostic characters of the subfamily Celestinae (Table 2). Within the Celestinae it differs from *Advenus* in lacking a claw sheath. Also, its combination of large size (144.5 mm SVL), high relative axilla-groin distance (89.0 mm = 61.6%), low midbody scale count, and high number of toe lamellae distinguish it from all genera in the family except *Celestus*, which is restricted to Jamaica and Hispaniola. The single species of *Celestus* in Hispaniola, *C. macrotus*, differs in many ways from *C. striatus* (Table 2) and therefore *Celestus striatus* is most likely a Jamaican species, which also makes sense from historical considerations, in that Jamaica was the major British colony in the West Indies and source of BMNH herpetological specimens in the early 19th century.

Barbour (1910) is one of the few researchers, besides us, to have considered that *Celestus striatus* is from Jamaica. He placed that species and *C. hewardii* in the synonymy of the Jamaican species *C. occiduus*. Both are diagnosable from *C. occiduus*, and most authors since have treated *C. hewardii* as a distinct species. However, after the status of *C. striatus* was placed in limbo following confusion over the frontonasal scale (Schwartz 1964), the species became forgotten and was not listed in any major checklist or synthesis of West Indian herpetology, even as a synonym (Schwartz & Thomas 1975; Schwartz & Henderson 1988; 1991; Henderson & Powell, 2009; Hedges *et al*. 2019). The Reptile Database (Uetz *et al*. 2020) lists it as a synonym of the Hispaniolan species *Comptus stenurus*, from which it differs in many ways, as noted above. Also, *Celestus striatus* is an older name so it should not be a synonym of that species.

Celestus striatus differs from all other species in the genus by a combination of its large size, lack of a claw sheath, absence of a median keel on the dorsal scales, a high number of toe lamellae (24–26), a rounded tail (not laterally flattened as in *C. occiduus*) and a pale (golden) coloration noted when it was described. The head shape is unusually flattened and the snout acuminate from above, resembling the head of the arboreal Jamaican species *C. fowleri*. That species differs from *C. striatus* by having a claw sheath but both are similar in their low midbody scale count and high number of toe lamellae, suggesting that they might be related and that *C. striatus* might be another arboreal species. Presumably, the introduction of the mongoose to Jamaica in 1872 (Hedges & Conn 2012) either severely decimated *C. striatus* or caused it to go extinct. This is not unexpected considering that another Jamaican species, *C. occiduus*, has not been seen since the 19th century, and several other Jamaican species are exceedingly rare, all attributed to the mongoose introduction (Barbour 1910; Hedges & Conn 2012).

We also recognize *Celestus macrolepis* as a valid species. It was given that name because of the presence of a large, seven-sided frontonasal scale purportedly representing the unusual fusion of the internasals and frontonasal (Gray 1845). One of us (S.B.H.) examined the holotype and it has the normal seven-sided frontonasal, not fused to

FIGURE 12. (A–G) *Celestus macrolepis* (BMNH 1946.8.3.82, holotype), SVL 248 mm. Photographs by S. B. Hedges.

FIGURE 13. (A–F) *Celestus occiduus* (BMNH XV.118A, holotype) from Jamaica. Photographs by S. B. Hedges.

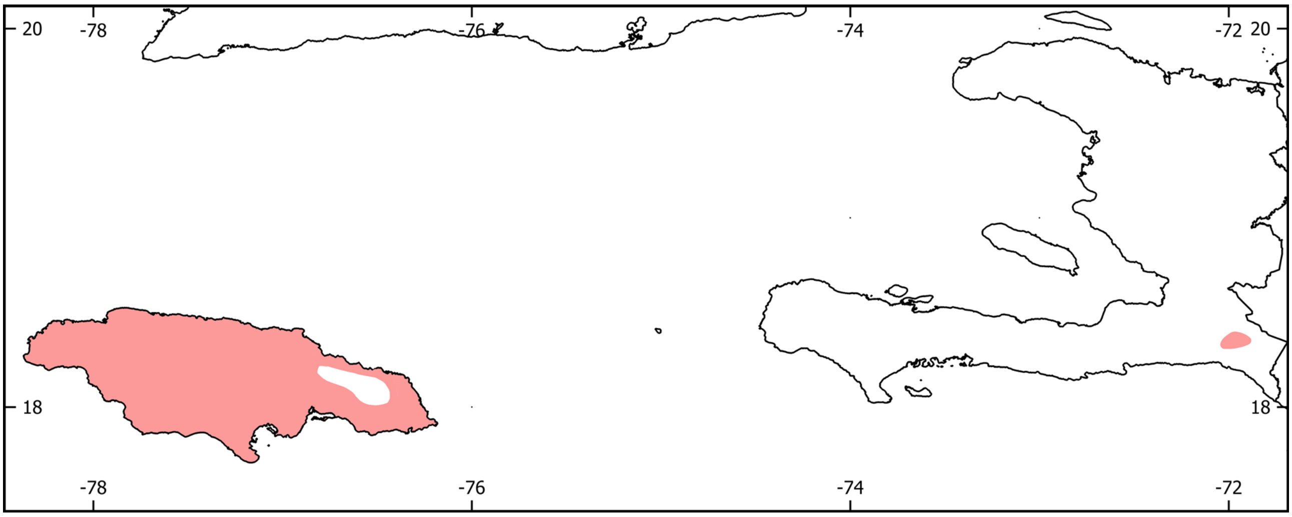

FIGURE 14. The distribution of *Celestus* in Jamaica and Haiti.

the internasals (Fig. 12). The two (normal) pairs of internasals are present. The specimen agrees in other important details with the description by Gray, including its unique bi-colored pattern (see below), so there is no doubt that it is the same specimen that he described. Because the enlarged, seven-sided frontonasal of *Celestus* is unusual among lizards, it was an easy error to make. Boulenger (1885) placed *Celestus macrolepis* in the synonymy of *C. occiduus* and it has been largely forgotten for 136 years. Neither Barbour (1910, 1914) nor Grant (1940a) mentioned the species, but its position as a synonym of *Celestus occiduus* was noted more recently (Schwartz & Thomas 1975; Schwartz & Henderson 1988).

The holotype of *Celestus macrolepis* (Fig. 12), 248 mm SVL, is surprisingly distinct from the similarly sized *C. occiduus*. It has a shorter, almost beak-like, snout and is mostly dark brown anteriorly (above and below) and paler posteriorly. The transition between the two colors is patch-like rather than gradual. A distinctive feature of scalation, noted by Gray (1845), is that the subocular scale is much smaller than in *Celestus occiduus* (and other species), barely pointed at the bottom, and does not protrude into the supralabial row. *Celestus occiduus* has a longer, more normal and slightly depressed (not beak-like) snout and a considerably larger subocular that protrudes into the supralabial scales. Other aspects of the head scalation also differ between the two species, as one would expect with such different head shapes. For these reasons, we consider *Celestus macrolepis* to be a valid species of Caribbean diploglossid lizard.

The holotype of *Celestus macrolepis* does not have a specific locality, only "West Indies," but the body proportions (large, long legs) agree more with Jamaican species than other diploglossids in the West Indies. For example, the giant *Caribicus* of Hispaniola have distinctly smaller and shorter legs, and longer tails. Also, only two Jamaican species, *Celestus occiduus* and *C. striatus*, approach the high number (24) of 4th toe lamellae of *Celestus macrolepis*. Based on these morphological characteristics, we consider *Celestus macrolepis* to be endemic to Jamaica, and a species that may have occupied an ecological niche different from others. As with *Celestus striatus*, the introduction of the mongoose in 1872 may have driven *C. macrolepis* to great rarity or extinction.

With the addition of *Celestus macrolepis, C. macrotus*, and *C. striatus*, the newly restricted genus *Celestus*, which is almost exclusively a Jamaican radiation, now contains 11 species. However, the additional six species that warrant recognition (see above), mostly confused with what is now *Celestus crusculus*, will bring the total in *Celestus* to 17 species.

Genus *Comptus* gen. nov.

Caribbean Rough-scaled Forest Lizards
Figs. 15–16

Type species. *Diploglossus stenurus,* Cope, 1862:188.

Diagnosis. Species of *Comptus* **gen. nov.** have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (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, 13–23, (9) dorsal scale rows, 88–107, (10) relative head width, 11.9–15.0, (11) relative rostral height, 53.2–65.5, (12) relative frontonasal length, 2.95–3.65, (13) relative interparietal distance, 0–0.435, (14) relative axilla-groin distance, 51.9–60.0.

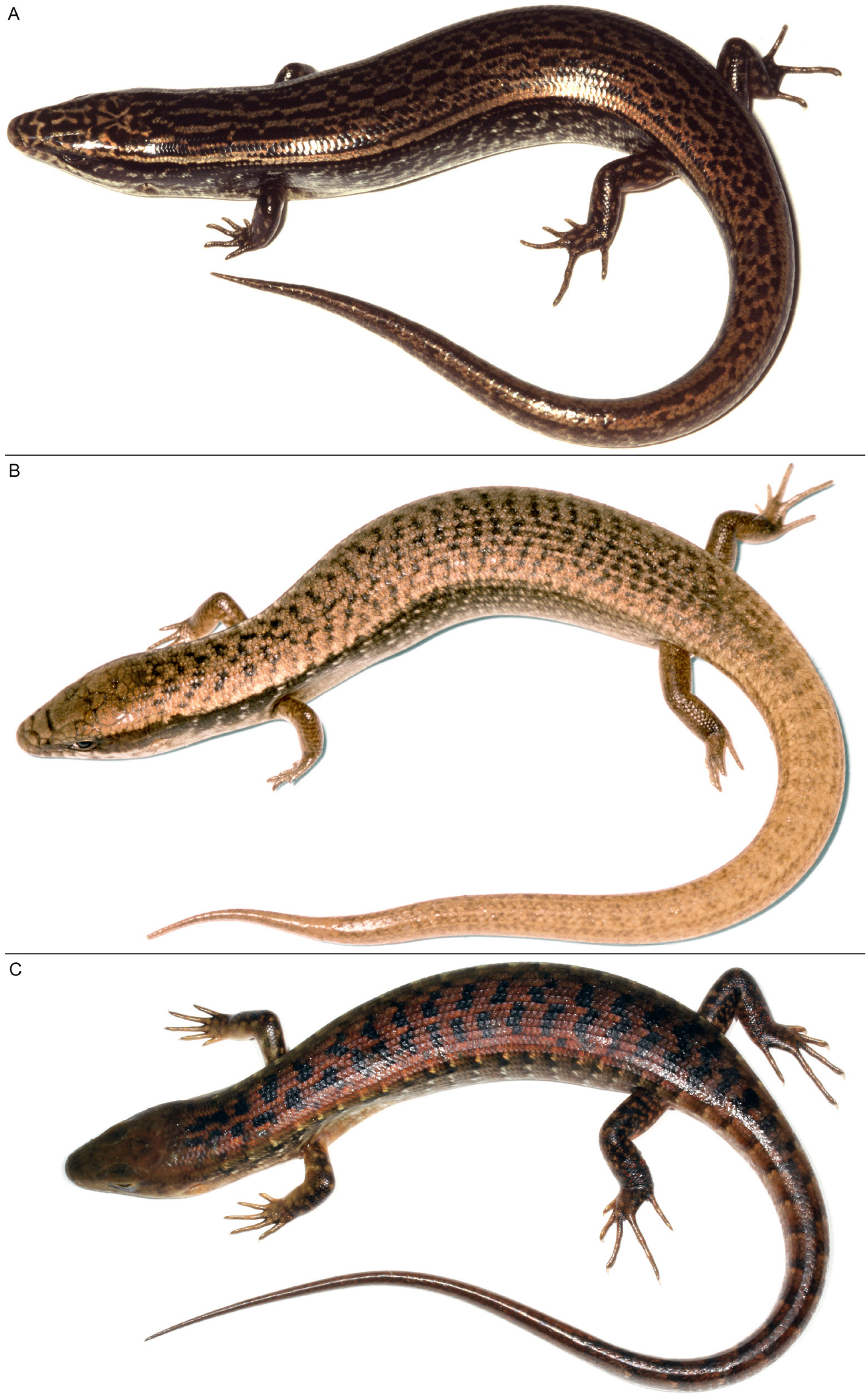

FIGURE 15. In life images of (A) *Comptus badius* (Voucher not available, SBH 194991, United States) (B) *Comptus maculatus* (ANSP 38511, SVL 49.7 mm) and (C) *Comptus stenurus* (ANSP 38538, SVL 123 mm). Photographs by S. B. Hedges.

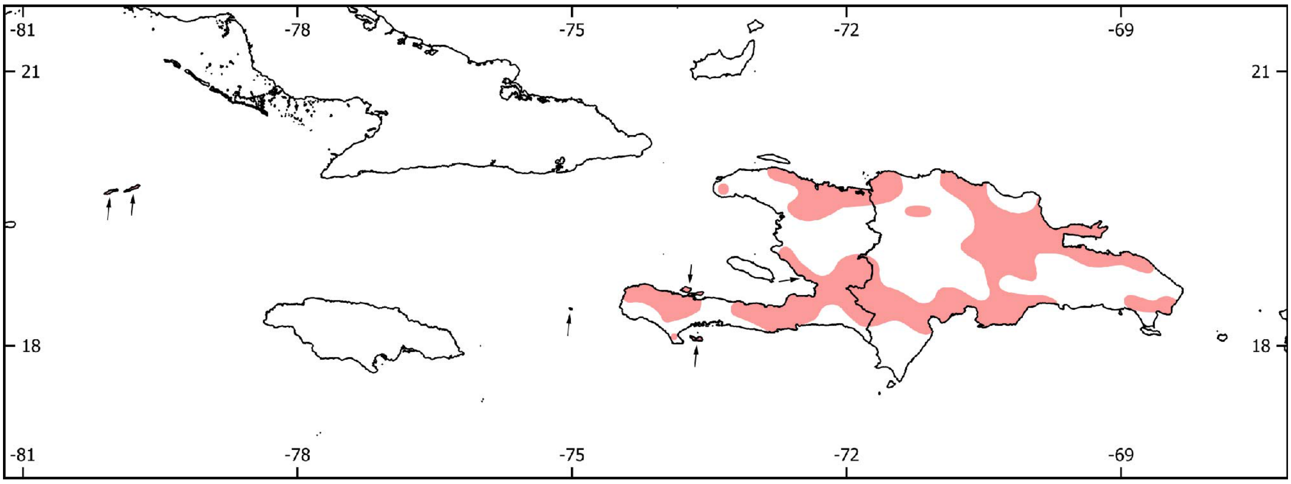

FIGURE 16. The distribution of *Comptus* **gen. nov.** Arrows indicate distributions on Little Cayman, Cayman Brac, Navassa Island, Grande Cayemite, Île-à-Vache, and Île à Cabrit.

From *Advenus* **gen. nov.**, *Comptus* **gen. nov.** is distinguished by the claw sheath (absent versus its presence in *Advenus* **gen. nov.**), keels on dorsal scales (present versus their absence in *Advenus* **gen. nov.**), relative rostral height (53.2–65.5 versus 50.1), relative frontonasal length (2.95–3.65 versus 2.46), and the distance between the parietal scales (0–0.435 versus 0.632). From *Caribicus* **gen. nov.**, we distinguish *Comptus* **gen. nov.** by the relative interparietal distance, (0–0.435 versus 0.468–1.42) and the relative axilla-groin distance (51.9–60.0 versus 67.1–69.1). From *Celestus,* we distinguish *Comptus* **gen. nov.** by the relative axilla-groin distance (51.9–60.0 versus 60.9–66.4). From *Panolopus,* we distinguish *Comptus* **gen. nov.** by keels on the dorsal scales (present versus their absence in *Panolopus*), relative rostral height (53.2–65.5 versus 37.6–51.9), and the relative frontonasal length (2.95–3.65 versus 1.93–2.94). From *Sauresia,* we distinguish *Comptus* **gen. nov.** by the claw sheath (absent versus its presence in *Sauresia*), keels on the dorsal body scales (present versus their absence in *Sauresia*), digits per limb (five versus four), the longest toe lamellae (13–23 versus 8–12), the relative frontonasal length (2.95–3.65 versus 1.70–2.56), and the relative axilla-groin distance (51.9–60.0 versus 63.9–69.9). From *Wetmorena,* we distinguish *Comptus* **gen. nov.** by the claw sheath (absent versus its presence in *Wetmorena*), keels on the dorsal body scales (present versus their absence in *Wetmorena*), digits per limb (five versus four), longest toe lamellae (13–23 versus 8–12), the relative frontonasal length (2.95–3.65 versus 1.47–2.69), and the distance between the parietal scales (0–0.435 versus 0.447–1.03).

Content. Three species (Table 3): *Comptus badius, C. maculatus,* and *C. stenurus.*

Distribution. *Comptus* **gen. nov.** occurs in the Cayman Islands, Navassa Island, and throughout most of Hispaniola, including the associated islets of Ile-a-Vache, Île à Cabrit, and Ile Grande Cayemite (Fig. 16).

Etymology. The generic name (*Comptus*) is a Latin masculine noun meaning adornment, referring to the keeling of the dorsal scales in this genus.

Remarks. *Comptus* **gen. nov.** is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). Our phylogenetic tree includes all three species of *Comptus* **gen. nov.** and three of the four subspecies of *Comptus stenurus* (*C. stenurus rugosus*, *C. stenurus stenurus*, and *C. stenurus weinlandi*), missing only *Comptus stenurus alloeides.*

Surprisingly, *Comptus maculatus* from the Cayman Islands, previously considered a subspecies of *Celestus crusculus* (Schwartz & Henderson 1991), a Jamaican species in a different genus, is nested within *Comptus stenurus* in the molecular phylogeny (Fig. 2). The character completely separating *Celestus* from *Comptus* **gen. nov.**, relative axilla-groin distance, supports that finding. The Navassa species, *Comptus badius*, also is nested within *Comptus stenurus*. *Comptus stenurus* is not monophyletic and includes populations with deep divergences (3.1 Mya; Fig. 3). These results, together with other molecular and morphological data, indicate that the genus *Comptus* includes at least three additional species (Schools & Hedges, unpubl.).

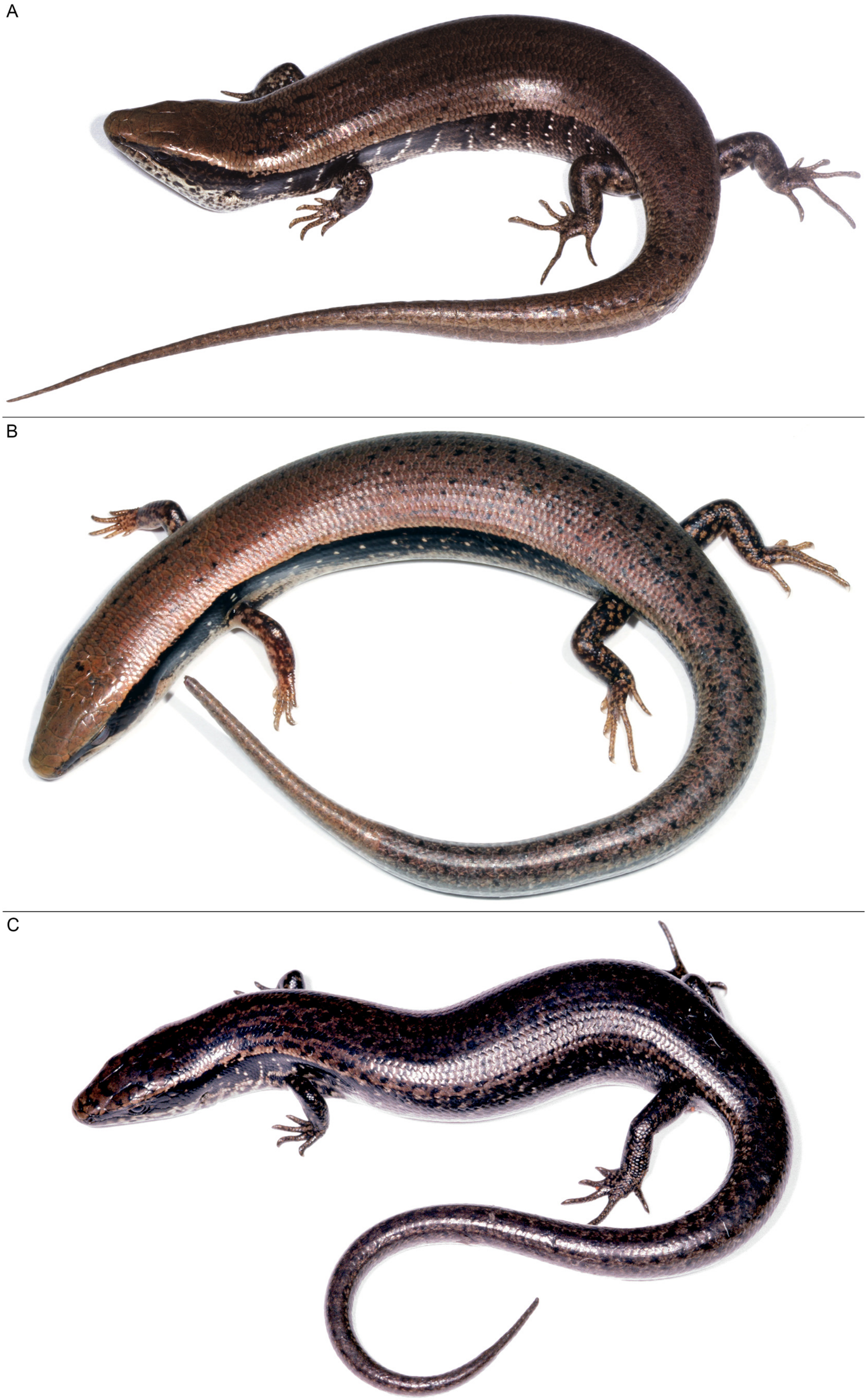

FIGURE 17. In life images of (A) *Panolopus costatus* (USNM 328744, SVL 97.81 mm) (B) *Panolopus curtissi* (ANSP 38634, SVL 77.5 mm), and (C) *Panolopus marcanoi* (ANSP 38662, SVL 73.5 mm). Photographs by S. B. Hedges.

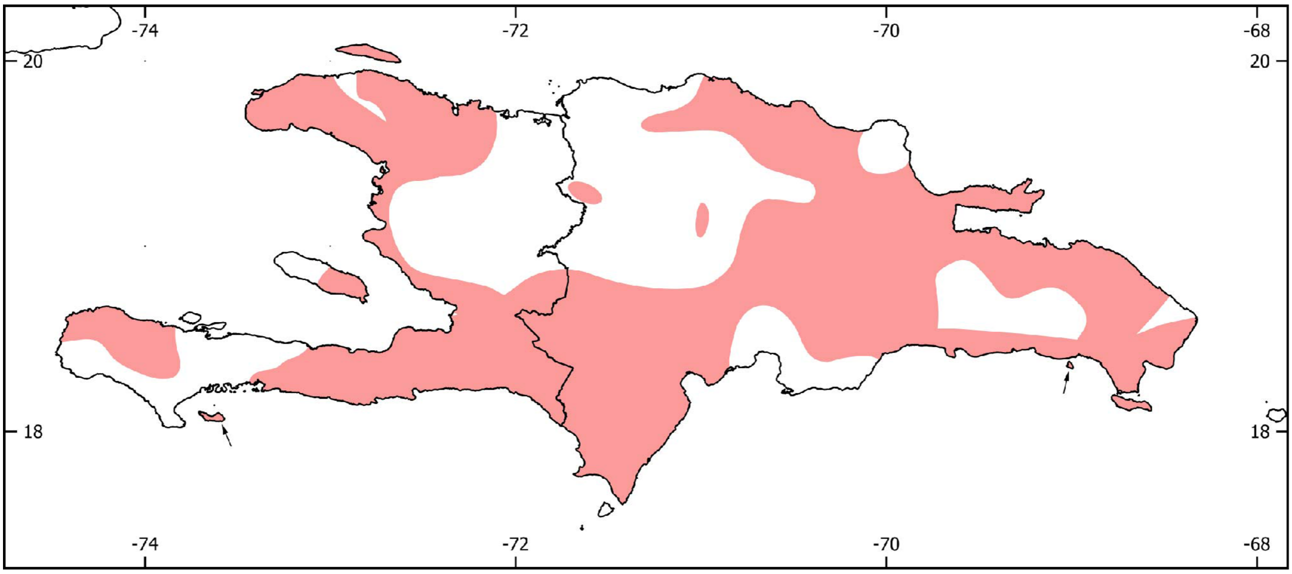

FIGURE 18. The distribution of *Panolopus.* Arrows indicate distributions on Île-à-Vache and Isla Catalina.

Genus *Panolopus* Cope, 1862
Caribbean Smooth-scaled Forest Lizards
Figs. 17–18

Panolopus Cope, 1862:494. Type species: *Panolopus costatus* Cope, 1862:494, by original designation.

Diagnosis. Species of *Panolopus* have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, absent, (7) digits per limb, five, (8) longest toe lamellae, 12–22, (9) dorsal scale rows, 83–100, (10) relative head width, 10.6–15.5, (11) relative rostral height, 37.6–51.9, (12) relative frontonasal length, 1.93–2.94, (13) relative interparietal distance, 0.0691–0.911, (14) relative axilla-groin distance, 49.7–59.6.

From *Advenus* **gen. nov.***,* we distinguish *Panolopus* by the absence of a claw sheath (present in *Advenus* **gen. nov.**) and the relative axilla-groin distance (49.7–59.6 versus 60.0). From *Caribicus* **gen. nov.***,* we distinguish *Panolopus* by the absence of keels on the dorsal body scales (present in *Caribicus* **gen. nov.**), the relative frontonasal length (1.93–2.94 versus 2.98–3.32), and the relative axilla-groin distance (49.7–59.6 versus 67.1–69.1). From *Celestus,* we distinguish *Panolopus* by the relative axilla-groin distance (49.7–59.6 versus 60.9–66.4). From *Comptus* **gen. nov.***,* we distinguish *Panolopus* by the absence of keels on the dorsal scales (present in *Comptus* **gen. nov.**), relative rostral height (37.6–51.9 versus 53.2–65.5), and relative frontonasal length (1.93–2.94 versus 2.95–3.65). From *Sauresia,* we distinguish *Panolopus* by the absence of a claw sheath (present in *Sauresia*), digits per limb (five versus four), dorsal scale rows (83–100 versus 101–127), and the relative axilla-groin distance (49.7–59.6 versus 63.9–69.9). From *Wetmorena,* we distinguish *Panolopus* by the absence of a claw sheath (present in *Wetmorena*), the digits per limb (five versus four), and the relative axilla-groin distance (49.7–59.6 versus 59.9–71.4).

Content. Three species (Table 3): *Panolopus costatus, P. curtissi,* and *P. marcanoi*.

Distribution. *Panolopus* occurs on Hispaniola and some surrounding islets (Fig. 18).

Etymology. Cope (1862) did not give the etymology of the generic name (*Panolopus*) but the name presumably refers to the fusion of numerous head scales mentioned in his diagnosis (*pan,* all; *lopus*, scale). Some of those traits are not diagnostic of the group and may represent healed injuries or deformities in a specimen he examined.

Remarks. *Panolopus* is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). Our phylogenies include all three species of *Panolopus* as well as five of the 11 subspecies of *Panolopus costatus* (*P. costatus costatus, P. costatus leionotus, P. costatus neiba, P. costatus nesobous, P. costatus oreistes*) and all four subspecies of *P. curtissi*. However, *P. costatus* and *P. curtissi* are not monophyletic and there are deep divergences (2–6 Mya) among populations of species and subspecies (Fig. 3). Our trees do not include *Panolopus costatus aenetergum, P. costatus emys, P. costatus saonae, P. costatus chalcorhabdus, P. costatus psychonothes,* and *P. costatus melanchrous*. These results, together with other molecular and morphological data, indicate that the genus *Panolopus* includes at least nine additional species (Schools & Hedges, unpubl.).

Genus *Sauresia* Gray, 1852

Long-headed Four-toed Forest Lizards

Fig. 19

Sauresia Gray, 1852:282. Type species: *Sauresia sepsoides* Gray, 1852:282, by original designation.
Embryopus Weinland, 1863:135. Type species: *Embryopus habichii* Weinland, 1863:135, by original designation.

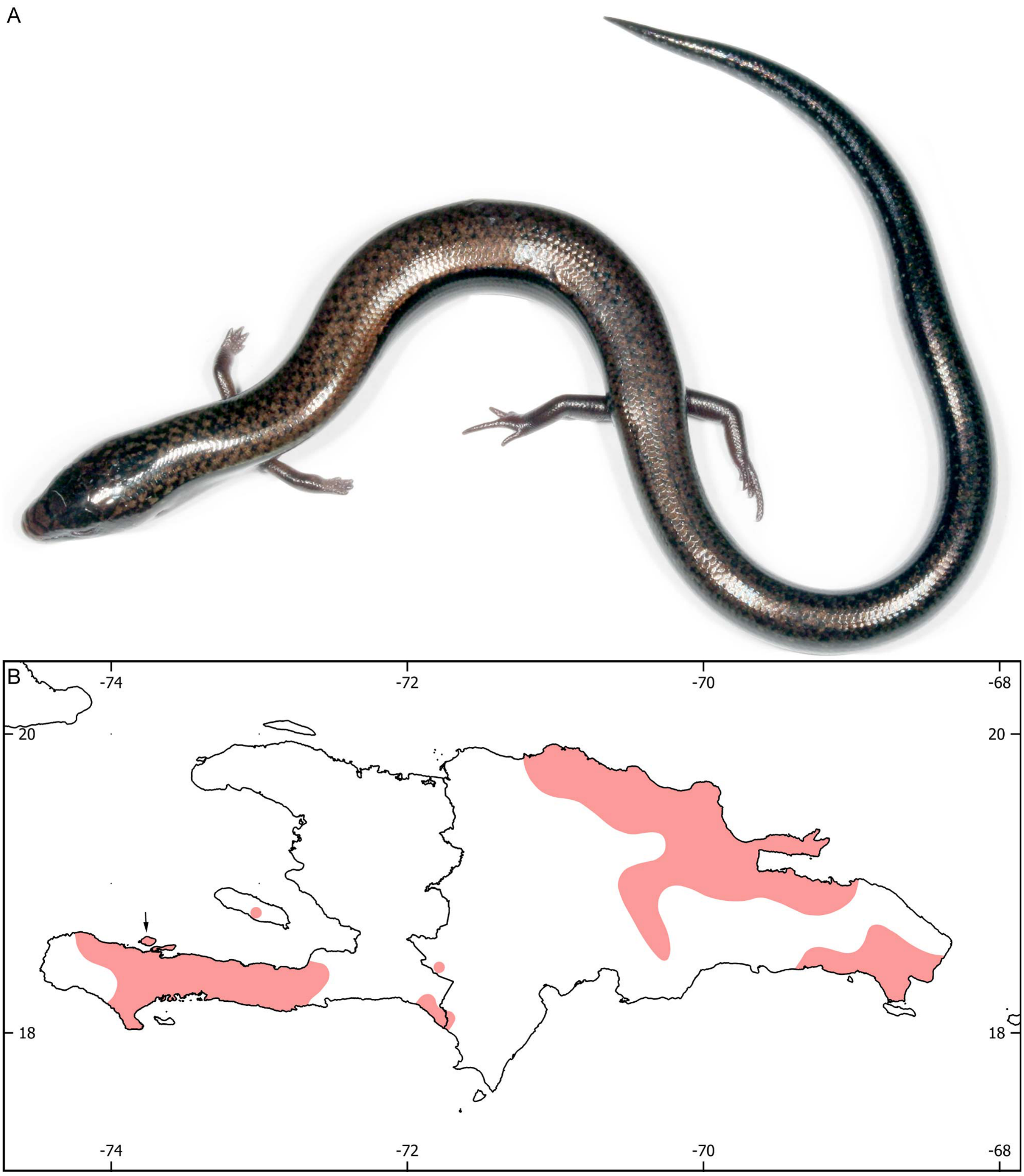

FIGURE 19. (A) In life image of *Sauresia sepsoides* (Voucher not available, SBH 267756). Photograph by S. B. Hedges. (B) The distribution of *Sauresia* on Hispaniola and islets. Arrow indicates distribution on Grande Cayemite.

Diagnosis. Species of *Sauresia* have (1) claw sheath, present, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, absent, (7) digits per limb, four, (8) longest toe lamellae, 8–12, (9) dorsal scale rows, 101–127, (10) relative head width, 9.36–12.2, (11) relative rostral height, 41.3–66.2, (12) relative frontonasal length, 1.70–2.56, (13) relative interparietal distance, 0–0.431, (14) relative axilla-groin distance 63.9–69.9.

From *Advenus* **gen. nov.**, we distinguish *Sauresia* by the digits per limb (four versus five in *Advenus* **gen. nov.**), the longest toe lamellae (8–12 versus 16–17), the dorsal scale rows (101–127 versus 96), the distance between the parietal scales (0–0.431 versus 0.632), and the relative axilla-groin distance (63.9–69.9 versus 60.0). From *Caribicus* **gen. nov.**, we distinguish *Sauresia* by the claw sheath (present versus absent in *Caribicus* **gen. nov.**), keels on the dorsal body scales (absent versus their presence in *Caribicus* **gen. nov.**), digits per limb (four versus five), relative frontonasal length (1.70–2.56 versus 2.98–3.32), and the distance between the parietal scales (0–0.431 versus 0.468–1.42). From *Celestus,* we distinguish *Sauresia* by the claw sheath (present versus its absence in *Celestus*) and the digits per limb (four versus five). From *Comptus* **gen. nov.**, we distinguish *Sauresia* by the claw sheath (present versus its absence in *Comptus* **gen. nov.**), keels on the dorsal body scales (absent versus their presence in *Comptus* **gen. nov.**), digits per limb (four versus five), the longest toe lamellae (8–12 versus 13–23), the relative frontonasal length (1.70–2.56 versus 2.95–3.65), and the relative axilla-groin distance (63.9–69.9 versus 51.9–60.0). From *Panolopus,* we distinguish *Sauresia* by the claw sheath (present versus its absence in *Panolopus*), digits per limb (four versus five), dorsal scale rows (101–127 versus 83–100), and the relative axilla-groin distance (63.9–69.9 versus 49.7–59.6). From *Wetmorena,* we distinguish *Sauresia* by the distance between the parietal scales (0–0.431 versus 0.447–1.03).

Content. One species (Table 3): *Sauresia sepsoides.*

Distribution. *Sauresia* is only known from Hispaniola but is notably absent from the driest parts of the island, including northwestern Haiti and some areas in the southern Dominican Republic (Fig. 19).

Etymology. The generic name (*Sauresia*) is a feminine noun derived from the Greek word *sauros* (lizard) and the suffix -*esia* (originating within), alluding to the fact that members of this genus resemble snakes but are actually lizards.

Remarks. *Sauresia* is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). For most of the time since it was named in 1852, *Sauresia* has been recognized as a valid genus, distinct from *Celestus*. The genus was synonomized with *Celestus* by Hass *et al.* (2001) because their study using immunological data found relationships that differed from previous studies (Savage & Lips 1993). Our study shows that the stem divergence time of *Sauresia* is comparable to the stem times of other genera of celestines (Fig. 3). Our phylogenies also show high levels of divergence (4–7 Mya) among populations of this species (Fig. 3). These results, together with other molecular and morphological data, and greater sampling of populations, indicate that the genus *Sauresia* includes at least 11 additional species (Schools & Hedges, unpubl.).

Genus *Wetmorena* Cochran, 1927

Short-headed Four-toed Forest Lizards
Fig. 20

Wetmorena Cochran, 1927:91. Type species. *Wetmorena haetiana* Cochran, 1927:91, by original designation.

Diagnosis. Species of *Wetmorena* have (1) claw sheath, present, (2) contact between the nasal and rostral scales, absent, (3) scales in contact with the nasal scale, four, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, central, (6) keels on dorsal body scales, absent, (7) digits per limb, four, (8) longest toe lamellae, 8–12, (9) dorsal scale rows, 98–117, (10) relative head width, 8.52–14.5, (11) relative rostral height, 38.7–61.8, (12) relative frontonasal length, 1.47–2.69, (13) relative interparietal distance, 0.447–1.03, (14) relative axilla-groin distance (59.9–71.4).

From *Advenus* **gen. nov.**, we distinguish *Wetmorena* by the digits per limb (four versus five in *Advenus* **gen. nov.**), longest toe lamellae (8–12 versus 16–17), and dorsal scale rows (98–117 versus 96). From *Caribicus* **gen. nov.**, we distinguish *Wetmorena* by the claw sheath (present versus its absence in *Caribicus* **gen. nov.**), keels on the dorsal scales (absent versus their presence in *Caribicus* **gen. nov.**), digits per limb (four versus five), and

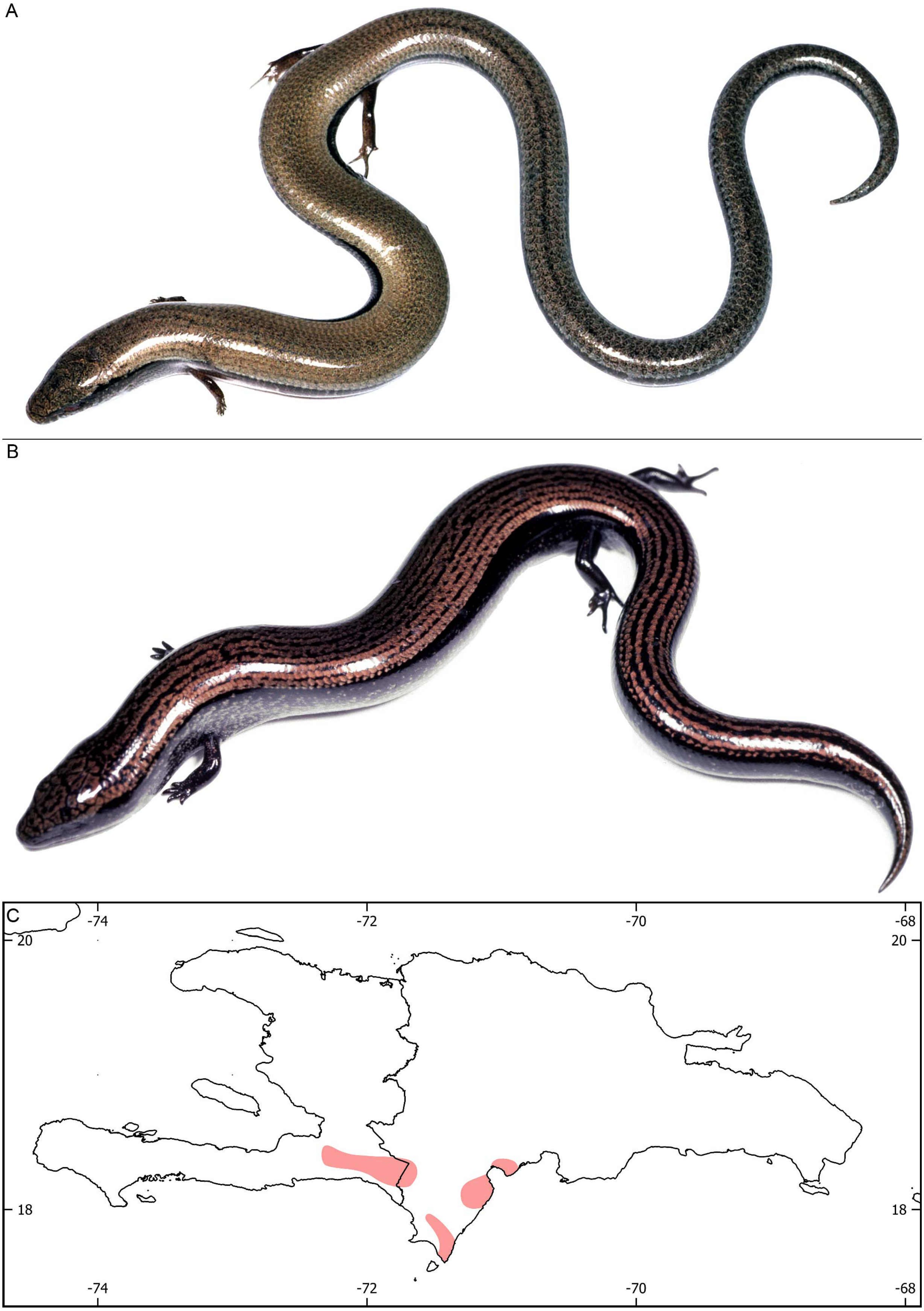

FIGURE 20. In life images of (A) *Wetmorena agasepsoides* (ANSP 38713, SVL 57.6 mm) and (B) *Wetmorena haetiana surda* (USNM 328897). Photographs by S. B. Hedges. (C) The distribution of *Wetmorena* on Hispaniola.

the relative frontonasal length (1.47–2.69 versus 2.98–3.32). From *Celestus,* we distinguish *Wetmorena* by the claw sheath (present versus its absence in *Celestus*) and the digits per limb (four versus five). From *Comptus* **gen. nov.***,* we distinguish *Wetmorena* by the claw sheath (present versus its absence in *Comptus* **gen. nov.**), keels on the dorsal body scales (absent versus their presence in *Comptus* **gen. nov.**), digits per limb (four versus five), longest toe lamellae (8–12 versus 13–23), the relative frontonasal length (1.47–2.69 versus 2.95–3.65), and the distance between the parietal scales (0.447–1.03 versus 0–0.435). From *Panolopus,* we distinguish *Wetmorena* by the claw sheath (present versus its absence in *Panolopus*), the digits per limb (four versus five), and the relative axilla-groin distance (59.9–71.4 versus 49.7–59.6). From *Sauresia,* we distinguish *Wetmorena* by the distance between the parietal scales (0.447–1.03 versus 0–0.431 in *Sauresia*).

Content. Two species (Table 3): *Wetmorena agasepsoides* (comb. nov.) and *W. haetiana.*

Distribution. *Wetmorena* occurs only on Hispaniola, in the Massif de la Selle (Haiti) and Sierra de Bahoruco (Dominican Republic) (Fig. 20).

Etymology. The generic name references Dr. Alexander Wetmore, who was Assistant Secretary of the Smithsonian Institution (Washington D.C.) at the time of description.

Remarks. *Wetmorena* is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). Our phylogenies include all three subspecies of *Wetmorena haetiana*. Previously, authors considered *Wetmorena agasepsoides* to be a species of *Sauresia* because of similarities in their appearance, including the presence of an ear opening. However, molecular data support the clustering of *Wetmorena agasepsiodes* with *W. haetiana* with a support value of 100% in Bayesian and ML analyses, which indicates that the loss of the auricular opening occurred within the clade recognized here as the genus *Wetmorena*.

For most of the time since it was named in 1927, *Wetmorena* has been recognized as a valid genus, distinct from *Celestus*. The genus was synonomized with *Celestus* by Hass *et al.* (2001) because their study using immunological data found relationships that differed from previous studies (Savage & Lips 1993). Our study shows that the stem divergence time of *Wetmorena* is comparable to the stem times of other genera of celestines (Fig. 3). The high levels of divergence (4–6 Mya) among subspecies of *Wetmorena haetiana* (Fig. 3), together with additional molecular and morphological data (Schools & Hedges, unpubl.), and greater sampling of populations, suggest that *Wetmorena* is a complex that includes four additional species.

Subfamily Diploglossinae Cope, 1865
Neotropical Forest Lizards
Fig. 21

Diploglossidae Cope, 1865:228. Type genus. *Diploglossus* Wiegmann, 1834.

Diagnosis. Members of this subfamily have (1) claw sheath, present or absent, (2) contact between the nasal and rostral scales, present or absent, (3) scales in contact with the nasal scale, 5–6, (4) postnasal scales, 1–2, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, present or absent, (7) digits per limb, 0 or 5, (8) longest toe lamellae, 8–18 except for limbless species, (9) dorsal scale rows, 88–171, (10) relative head width, 9.20–19.0, (11) relative rostral height, 49.6–62.1, (12) relative frontonasal length, 2.11–4.44, (13) relative interparietal distance, 0–0.658, (14) relative axilla-groin distance, 52.8–76.6.

The subfamily Diploglossinae is distinguished from the other two subfamilies by scales in contact with the nasal scale (5–6 instead of four in Celestinae **subfam. nov.**), the position of the nostril in the nasal scale (posterior instead of central in Celestinae **subfam. nov.**), and the number of dorsal scales (88–171 instead of 65–85 in Siderolamprinae **subfam. nov.**).

Content. Sixteen currently recognized species in two genera (Table 3): *Diploglossus* Wiegmann, 1834 and *Ophiodes* Wagler, 1828.

Distribution. Diploglossinae occurs on Caribbean islands (Cuba, Puerto Rico, and Montserrat) and in South America (including Malpelo Island).

Etymology. As for the type genus.

Remarks. The subfamily Diploglossinae is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). We place *Ophiodes* in this subfamily based on molecular and morphological evidence.

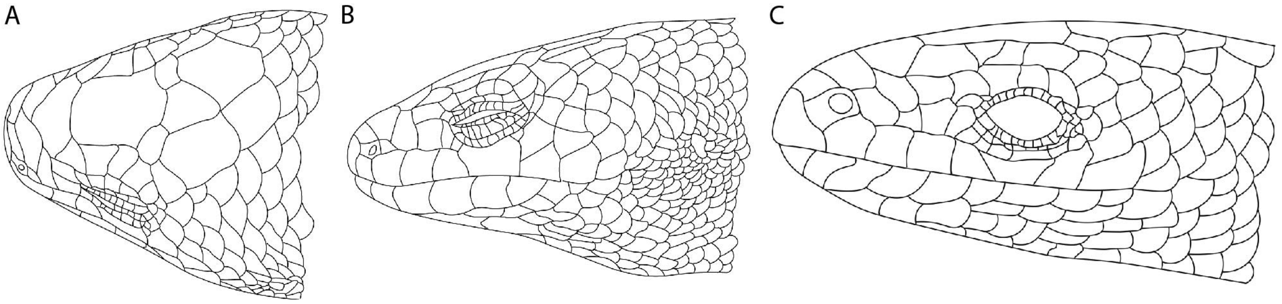

FIGURE 21. Head scalation of diploglossine genera. (A–B) *Diploglossus nigropunctatus* (MCZ R-42563) from top and side views. (C) *Ophiodes enso* (CHFURG 3589) from side view.

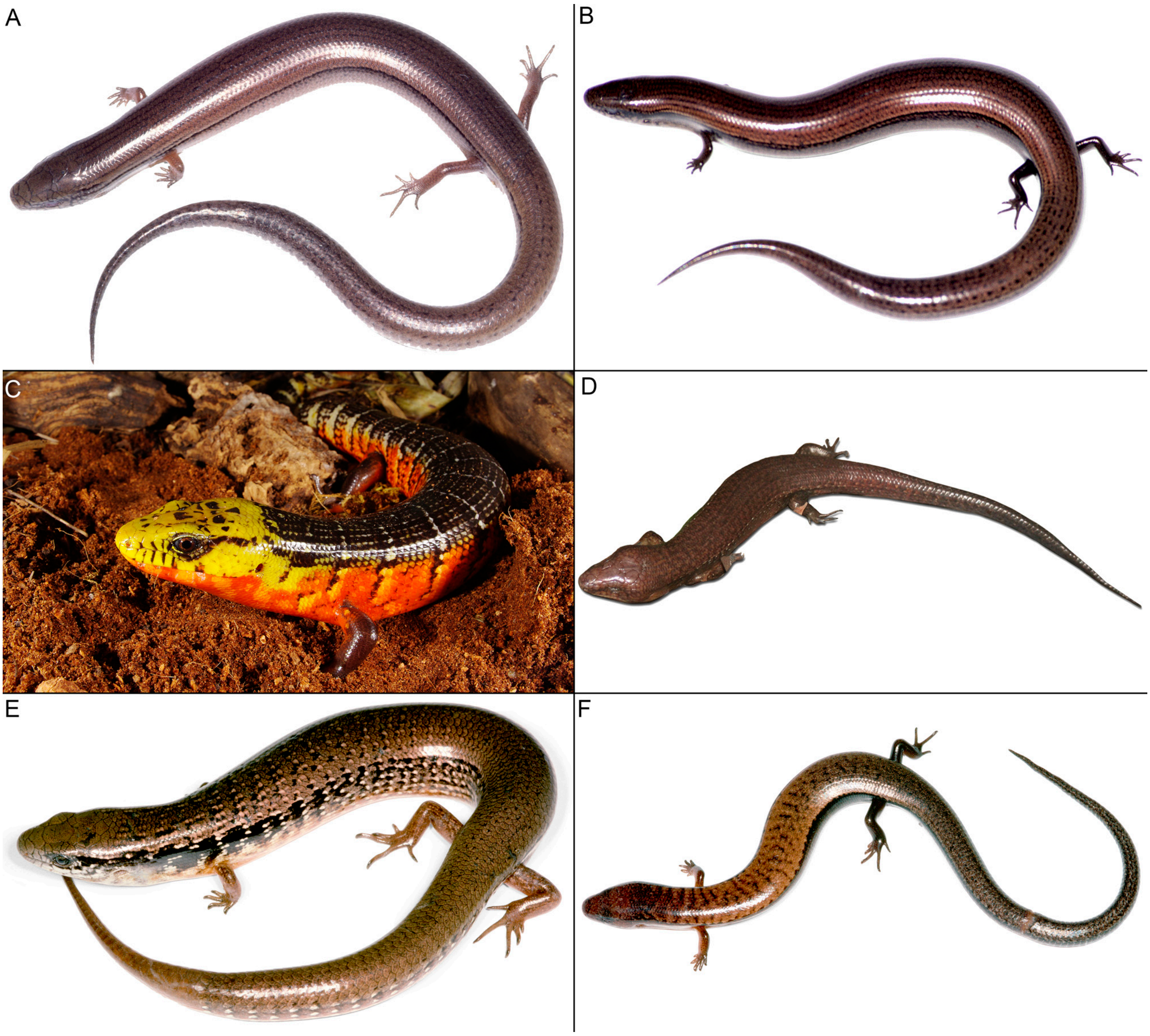

FIGURE 22. Images of (A) *Diploglossus delasagra* (USNM 512237, SVL 81.3 mm; photograph by S. B. Hedges), (B) *Diploglossus garridoi* (MNHNCU 4420, SVL 103 mm; photograph by S. B. Hedges), (C) *Diploglossus monotropis* (photograph by Sebastian Lotzkat), (D) *Diploglossus montisserrati* (photograph by Agnieszka Ogrodowczyk), (E) *Diploglossus nigropunctatus* (USNM 512241, SVL 111 mm; photograph by S. B. Hedges), and (F) *Diploglossus pleii* (USNM 326931; photograph by S. B. Hedges).

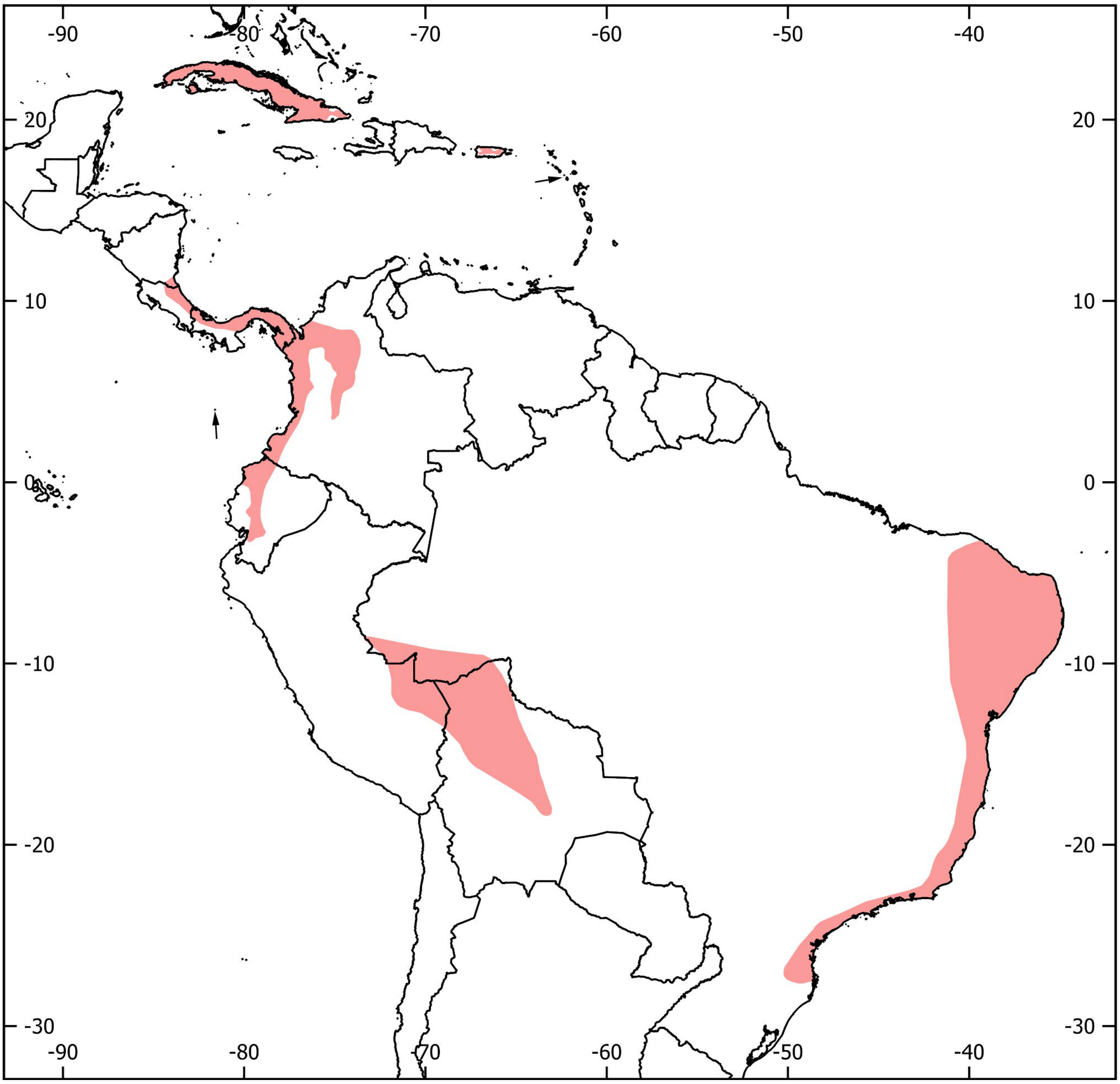

FIGURE 23. The distribution of *Diploglossus*. Arrows indicate distribution on Malpelo Island and Montserrat.

Genus *Diploglossus* Wiegmann, 1834

Neotropical Forest Lizards

Figs. 22–23

Diploglossus Wiegmann, 1834:36. Type species: *Tiliqua fasciatus* Gray, 1831:71, by subsequent designation (Fitzinger 1843:23).

Microlepis Gray, 1839:334. Type species: *Microlepis undulata* Gray, 1839:334, by original designation.

Camilia Gray, 1845:118. Type species: *Tiliqua jamaicensis* Gray, 1839:293, by original designation.

Diagnosis. Species of *Diploglossus* have (1) claw sheath, present or absent, (2) contact between the nasal and rostral scales, present or absent, (3) scales in contact with the nasal scale, 5–6, (4) postnasal scales, 1–2, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, present or absent, (7) digits per limb, five, (8) longest toe lamellae, 8–18, (9) dorsal scale rows, 88–99, (10) relative head width, 9.20–19.0, (11) relative rostral height, 49.6–62.1, (12) relative frontonasal length, 2.11–4.44, (13) relative interparietal distance, 0–0.658, (14) relative axilla-groin distance, 52.8–76.6.

From *Ophiodes,* we distinguish *Diploglossus* by the digits per limb (five versus none, because of lack of limbs in *Ophiodes*), number of lamella on longest toe (8–18 versus none, because of lack of limbs in *Ophiodes*), and the number of dorsal scales (88–99 versus 130–171).

Content. Ten species (Table 3): *Diploglossus delasagra, D. fasciatus, D. garridoi, D. lessonae, D. microlepis, D. millepunctatus, D. monotropis, D. montisserrati, D. nigropunctuatus,* and *D. pleii.*

Distribution. *Diploglossus* occurs throughout Cuba, Puerto Rico, and Montserrat, as well as in Lower Central America and South America including Malepo Island (Fig. 23). The map does not include the distribution of *Diploglossus microlepis*, which is unknown.

Etymology. The generic name is a masculine noun formed from the Latin words *diplo* (two) and *glossus* (tongue), meaning two tongues, referencing the two forms of papillae found on the anterior and posterior regions of the tongue.

Remarks. *Diploglossus* is a monophyletic clade with a Bayesian support value of 100% and a ML bootstrap value of 81% (Fig. 2). Our molecular phylogeny includes six of the ten species of *Diploglossus* (*D. delasagra, D. garridoi, D. lessonae, D. monotropis, D. nigropunctuatus,* and *D. pleii*).

Genus *Ophiodes* Wagler, 1828

South American Glass Lizards
Figs. 24–25

Ophiodes Wagler, 1828:740. Type species. *Pygopus striatus,* Spix, 1824:25.

Diagnosis. Species of *Ophiodes* have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, present, (3) scales in contact with the nasal scale, five, (4) postnasal scales, one, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, absent, (7) digits per limb, none, (8) longest toe lamellae, none, (9) dorsal scale rows, 130–171, (10) relative head width, n/a, (11) relative rostral height, n/a,(12) relative frontonasal length, n/a, (13) relative interparietal distance, n/a, (14) relative axilla-groin distance, n/a.

From *Diploglossus,* we distinguish *Ophiodes* by the lack of limbs (versus limbs present in *Diploglossus*), and the number of dorsal scales (130–171 versus 88–99).

Content. Six species (Table 3): *Ophiodes enso, O. fragilis, O. intermedius, O. luciae, O. striatus,* and *O. vertebralis.*

Distribution. *Ophiodes* occurs in southern South America (Argentina, Bolivia, Brazil, Paraguay, and Uruguay) (Fig. 25).

Etymology. The Greek stem (*ophio*-) means "snake" and Latin suffix (*-odes*) means "likeness," hence "like a snake."

Remarks. *Ophiodes* is a monophyletic clade with a Bayesian support value of 100% and a ML bootstrap value of 77% (Fig. 2). Cacciali & Scott (2015) provided a key to most of the species of *Ophiodes* and indicated the presence of several undescribed species.

Subfamily Siderolamprinae subfam. nov.

Mesoamerican Forest Lizards
Fig. 26

Type genus. *Siderolamprus* Cope, 1861.

Diagnosis. Members of this subfamily have (1) claw sheath, present or absent, (2) contact between the nasal and rostral scales, present or absent, (3) scales in contact with the nasal scale, six, (4) postnasal scales, two, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, present or absent, (7) digits per limb, five, (8) longest toe lamellae, 11–35, (9) dorsal scale rows, 65–85, (10) relative head width, 9.88–15.6, (11) relative rostral height, 44.7–67.0, (12) relative frontonasal length, 2.46–2.88, (13) relative interparietal distance, 0.561–1.14, (14) relative axilla-groin distance, 53.5–65.3.

The subfamily Siderolamprinae is distinguished from the other two subfamilies by scales in contact with the nasal scale (six instead of four in Celestinae **subfam. nov.**), the position of the nostril in the nasal scale (posterior instead of central in Celestinae **subfam. nov.**), and the number of dorsal scales (65–85 instead of 88–171 in Diploglossinae).

FIGURE 24. In life images of (A) *Ophiodes intermedius* (photograph by Paul Freed), (B) *Ophiodes striatus* (photograph by Santiago Carreira), and (C) *Ophiodes vertebralis* (photograph by Santiago Carreira).

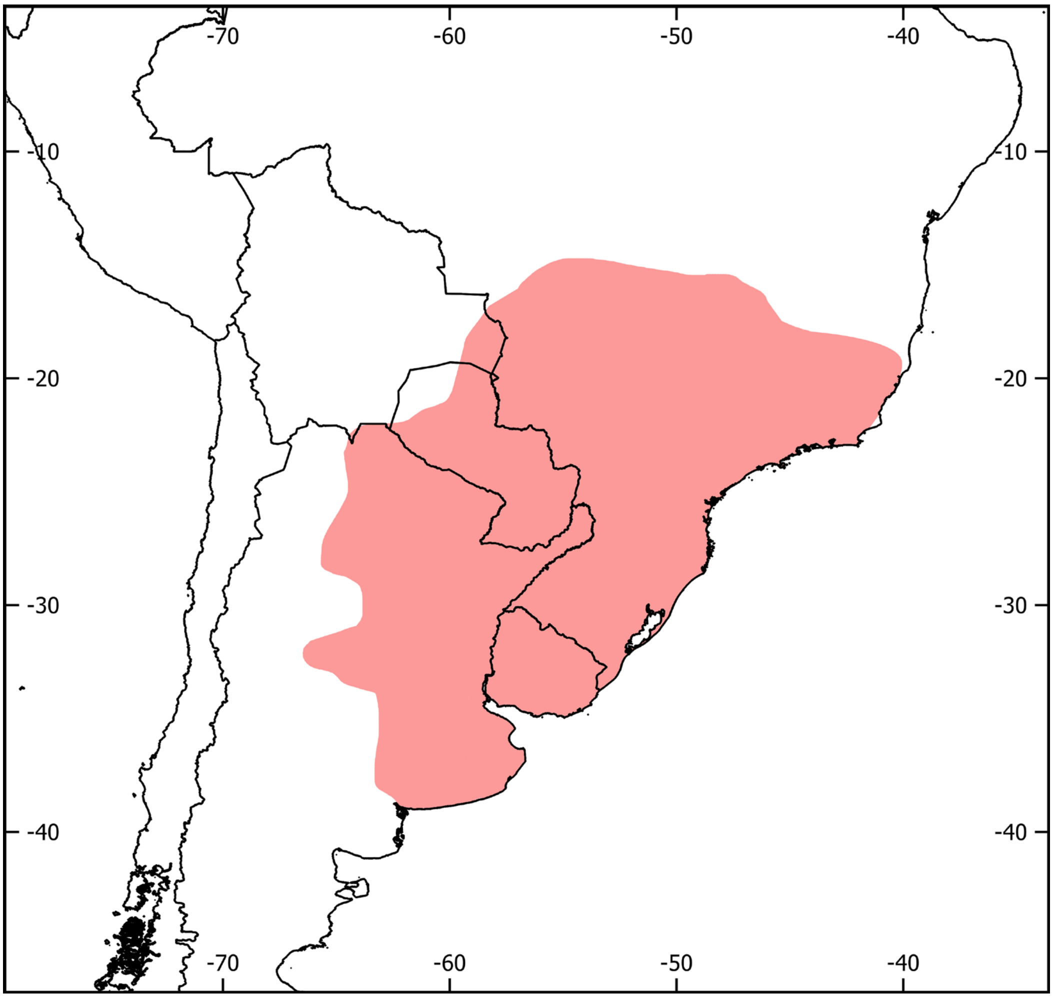

FIGURE 25. The distribution of *Ophiodes* in South America.

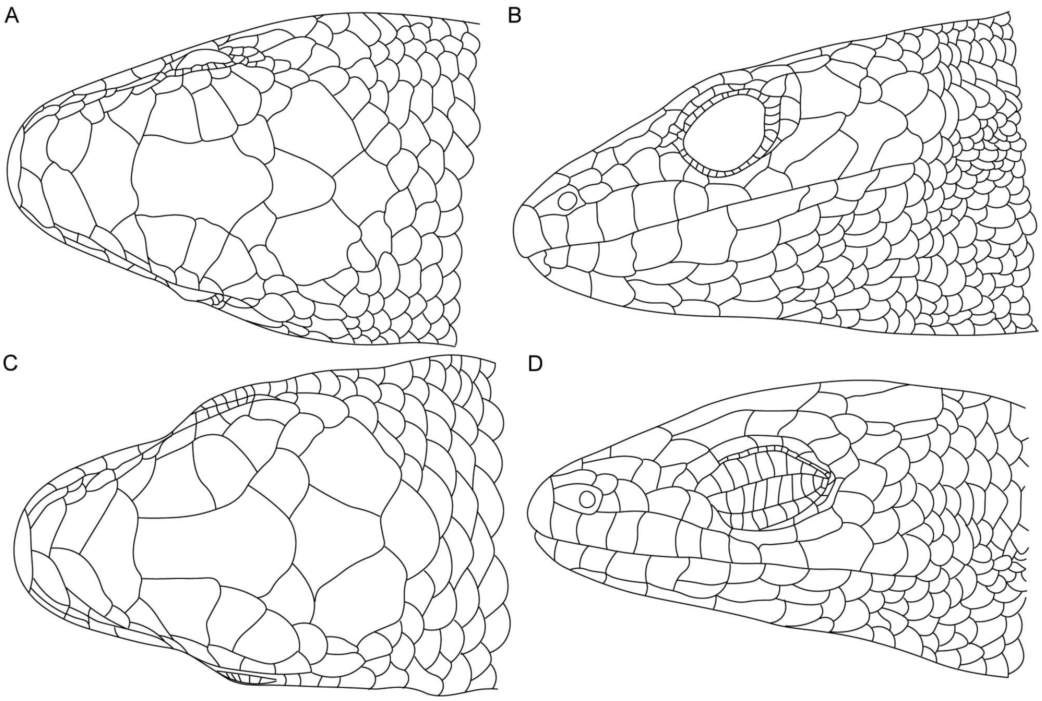

FIGURE 26. Head scalation of siderolamprine genera, top (left) and side (right) views. (A–B) *Mesoamericus bilobatus* (SMF 89549). (C–D) *Siderolamprus laf* (SMF 90177), HW 4.9 mm, HL 7.5 mm.

Content. Fifteen currently recognized species in two genera: *Siderolamprus* Cope, 1861 and *Mesoamericus* **gen. nov.** (15 sp.).

Distribution. This subfamily occurs in Middle America, from southern Mexico to Panama.

Etymology. As for the type genus.

Remarks. The subfamily Siderolamprinae is monophyletic with a Bayesian support value of 96% and a ML support value of 93% (Fig. 2). We have identified two genera that fall into this subfamily based on molecular and morphological evidence, *Mesoamericus* **gen. nov.** and *Siderolamprus*, both represented in our molecular phylogeny. Cope (1861) used *Siderolamprus* to define *Siderolamprus enneagrammus* before it became a synonym of *Celestus*.

Genus *Mesoamericus* gen. nov.

Central American Forest Lizards
Fig. 27

Type species. *Celestus bilobatus* O'Shaughnessy, 1874:257.

Diagnosis. Species of *Mesoamericus* **gen. nov.** have (1) claw sheath, present, (2) contact between the nasal and rostral scales, present, (3) scales in contact with the nasal scale, six, (4) postnasal scales, two, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, absent, (7) digits per limb, five, (8) longest toe lamellae, 11–18, (9) dorsal scale rows, n/a (10) relative head width, 12.0–14.0, (11) relative rostral height, 65.0–67.0, (12) relative frontonasal length, n/a, (13) relative interparietal distance, n/a, (14) relative axilla-groin distance, n/a.

From *Siderolamprus,* we distinguish *Mesoamericus* **gen. nov.** by the claw sheath (present versus absent in *Siderolamprus*) and relative rostral height (65.0–67.0 versus 44.7–63.9).

Content. One species (Table 3): *Mesoamericus bilobatus.*

Distribution. *Mesoamericus* **gen. nov.** occurs in Central America (Nicaragua, Costa Rica, and Panama) (Fig. 27).

Etymology. The generic name is a masculine noun derived from the name for the region (Mesoamerica) where it occurs.

Remarks. *Mesoamericus* **gen. nov.** is a monophyletic clade that has a support value of 100% in Bayesian and ML analyses (Fig. 2). The large molecular divergence among populations of *M. bilobatus*, with some splits as old as 5 Mya (Fig. 3), suggests the presence of three undefined species.

Genus *Siderolamprus* Cope, 1861

Middle American Forest Lizards
Fig. 28

Siderolamprus Cope, 1861:368. Type species. *Siderolamprus enneagrammus* Cope, 1861:368, by original designation.
Oneyda Gray, 1845:118. Type species: *Diploglossus owenii* Duméril & Bibron, 1839:594, by original designation.

Diagnosis. Species of *Siderolamprus* have (1) claw sheath, absent, (2) contact between the nasal and rostral scales, present or absent, (3) scales in contact with the nasal scale, six, (4) postnasal scales, two, (5) position of the nostril in the nasal scale, posterior, (6) keels on dorsal body scales, present or absent, (7) digits per limb, five, (8) longest toe lamellae, 14–35, (9) dorsal scale rows, 65–85, (10) relative head width, 9.88–15.6, (11) relative rostral height, 44.7–63.9, (12) relative frontonasal length, 2.46–2.88, (13) relative interparietal distance, 0.561–1.14, (14) relative axilla-groin distance, 53.5–65.3. From *Mesoamericus* **gen. nov.**, we distinguish *Siderolamprus* by the claw sheath (absent versus present in *Mesoamericus*) and relative rostral height (44.7–63.9 versus 65.0–67.0).

Content. Fourteen species (Table 3): *Siderolamprus adercus, S. atitlanensis, S. bivittatus, S. cyanochloris, S. enneagrammus, S. hylaius, S. ingridae, S. laf, S. legnotus, S. montanus, S. orobius, S. owenii, S. rozellae, S. scansorius.*

Distribution. *Siderolamprus* occurs in Middle America, from southern Mexico to Panama (Fig. 28). The map does not include the distribution of *Siderolamprus owenii* because its distribution is unknown.

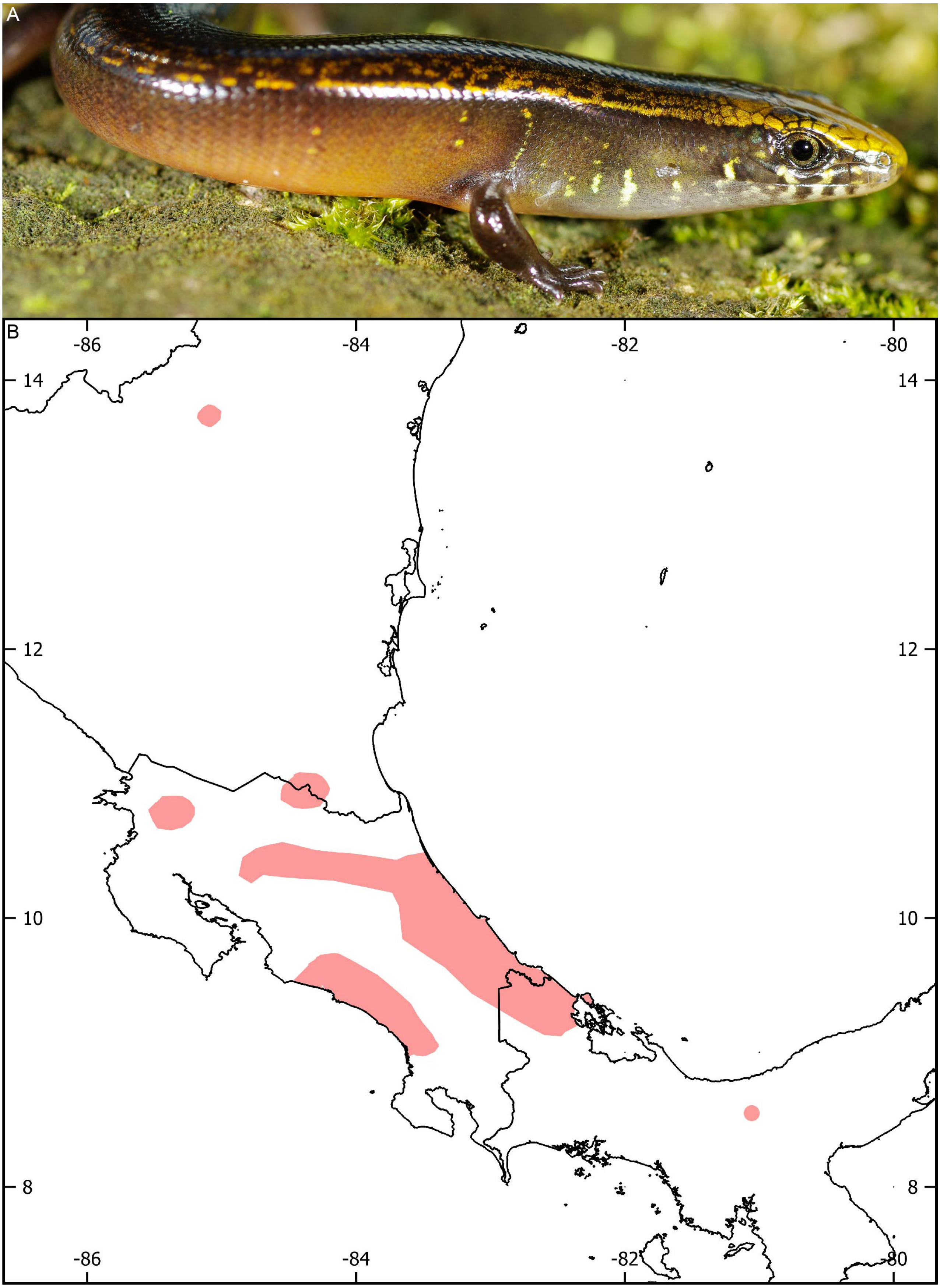

FIGURE 27. (A) In life image of *Mesoamericus bilobatus* (MHCH 2310, Cerro Mariposa, near Alto de Piedra, Veraguas, Panama). Photograph by Sebastian Lotzkat. (B) The distribution of *Mesoamericus* **gen. nov.** in Middle America.

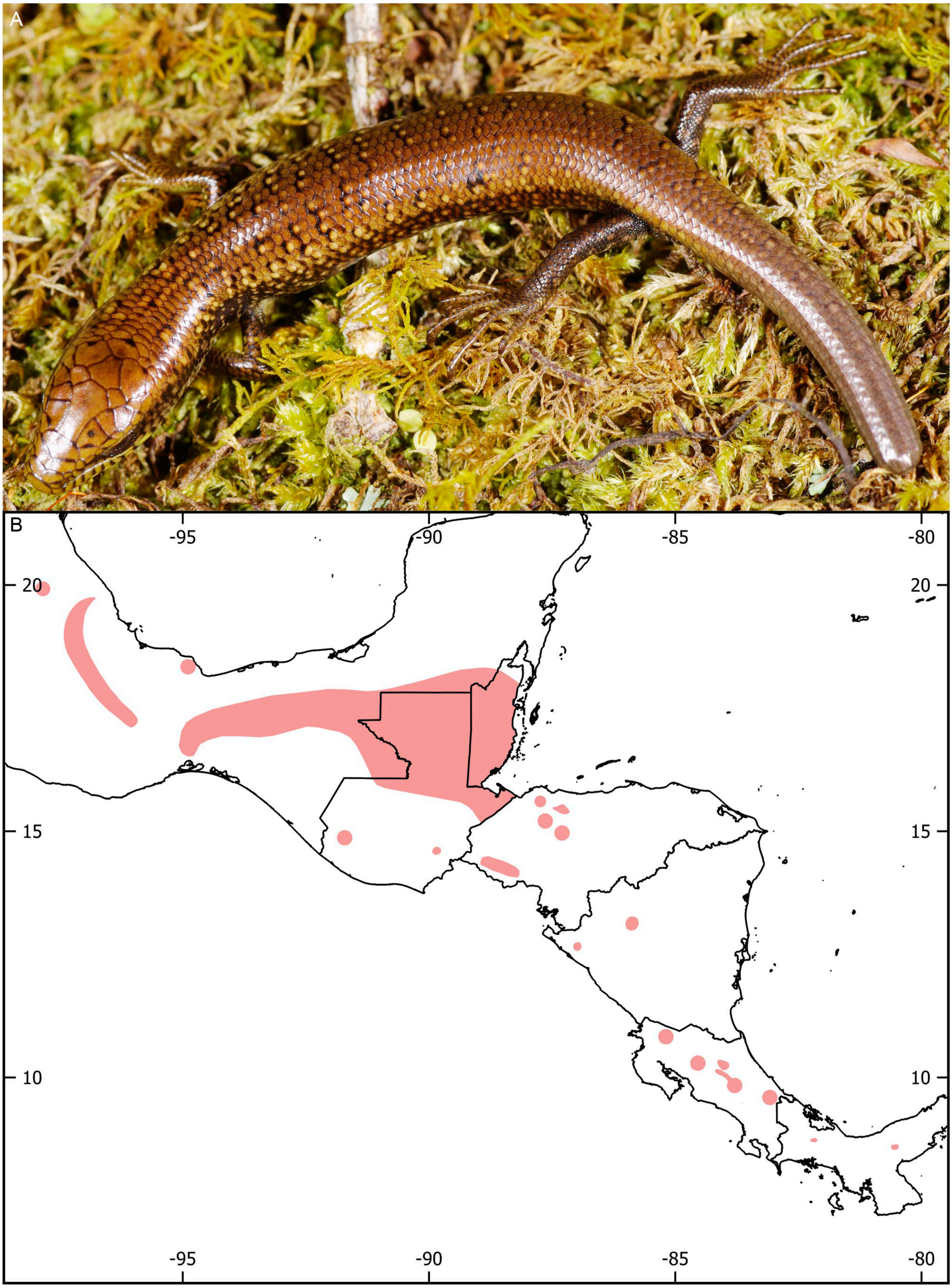

FIGURE 28. (A) In life image of *Siderolamprus laf* (SMF 90177, SVL 35 mm). Photograph by Sebastian Lotzkat. (B) The distribution of *Siderolamprus* in Middle America.

Etymology. The generic name is from the Greek *sideros* (iron) and *lampros* (bright, radiant), apparently in allusion to “glossy black” color of the type species, noted in the original description (Cope 1861).

Remarks. *Siderolamprus* is a monophyletic clade with a support value of 100% in Bayesian and ML analyses (Fig. 2). Our phylogenetic tree includes five of the 14 species of *Siderolamprus* (*S. bivittatus, S. cyanochloris, S. enneagrammus, S. laf,* and *S. rozellae*). The high levels of divergence (with some splits as old as 8 Mya) within the species *Siderolamprus enneagrammus* (Fig. 3) suggest that it is a complex that includes at least one undefined species.

Discussion

We have revised the supraspecific taxonomy of diploglossid lizards based on a re-evaluation of morphological characters in concert with a new molecular phylogeny. Our taxonomy better reflects the morphological and genetic diversity of the group, and provides insight into the evolutionary history and biogeography of diploglossids, a major radiation of lizards in the Western Hemisphere that began in the early Eocene, ~50 Mya (Fig. 3).

With the four newly defined genera and the four resurrected genera, Diploglossidae comprises eleven genera that we place in three subfamilies. The molecular phylogeny strongly supports all genera and subfamilies, each of which are morphologically diagnosable with non-overlapping traits. However, additional gene and morphological data will be needed to achieve full resolution of phylogeny of all diploglossid species.

The three subfamilies represent three evolutionary and biogeographic groups: the Middle American Clade (Siderolamprinae **subfam. nov.**), the South American Clade (Diploglossinae), and the Caribbean Clade (Celestinae **subfam. nov.**). The Middle American Clade is completely restricted to that region, and the deep divergence (41.3 Mya) of the two genera (*Mesoamericus* **gen. nov.**, *Siderolamprus*) indicates a long presence in Middle America. The South American Clade (Diploglossinae) contains the greatest morphological diversity in the family, and the deep split (25.0 Mya) between *Ophiodes* and *Diploglossus* suggests an origin for the clade in South America despite the existence of several species of *Diploglossus* on Caribbean islands. The Caribbean Clade (Celestinae **subfam. nov.**) is restricted to that region, except for the lone outlier (*Advenus montisilvestris*) in Panama. This clade of seven genera (*Advenus* **gen. nov.**, *Caribicus* **gen. nov.**, *Comptus* **gen. nov.**, *Celestus*, *Panolopus*, *Sauresia*, and *Wetmorena*) has the largest species diversity of the three clades.

The neoanguimorph lizards (North America) split from the paleoanguimorphs (Asia) in the early Cretaceous followed by a mid-Cretaceous divergence of three neoanguimorph lineages: Xenosauridae, Helodermatidae, and the anguioids (Anguidae, Anniellidae, and Diploglossidae) (Hedges *et al.* 2009). The anguioids then split up in the latest Cretaceous or Paleocene, forming the diploglossid lineage (Hedges *et al*. 2009), presumably in southern North America and/or Middle America. They were present in Middle America before 41 Mya (Eocene) based on the split of the two genera in that clade. The South American and Caribbean clades became emplaced in their respective regions during the first half of the Cenozoic (Fig. 3) by dispersal. A more recent dispersal, in the Miocene (Fig. 3), led to the radiation of Caribbean *Diploglossus.* The timing of those dispersals can be constrained by the timetree, using the stem and crown times, along with the direction of dispersal. The initial dispersal from Middle America to South America occurred 49–44 Mya, followed by the first dispersal from South America to the Caribbean islands (celestines) 44–14 Mya and the second dispersal (Caribbean diploglossines) 20–12 Mya. Molecular data are not available for the Montserrat species (*D. montisserrati*), which might represent an additional dispersal to the islands, almost certainly from South America.

The new molecular phylogeny and timetree (Fig. 3) for diploglossids does not support proto-Antillean vicariance, proposed by Savage & Lips (1993), as a mechanism for the biogeographic history of these lizards because the divergence times are too recent and the proto-Antilles were not continuously above water prior to the middle Eocene (Iturralde-Vinent & MacPhee 1999; Hedges 2006). A short-lived landbridge (35–33 Mya) between South America and the Greater Antilles has been proposed to explain dispersal of animals into the Caribbean islands (Iturralde-Vinent & MacPhee 1999). However, geologic support for the landbridge is conjectural (Ali 2011) and biological evidence does not support it (Hedges 2006). Moreover, the the geologic evidence is more compatible with a chain of islands like the current Lesser Antilles, which would have facilitated overwater dispersal (Hedges 2006). Therefore, claims that molecular divergence times at, or close to, 35–33 Mya reject overwater dispersal in favor of the landbridge hypothesis (Delsuc *et al*. 2019) are incorrect. Molecular divergence times at 35–33 Mya, and at other times, would be consistent with overwater dispersal.

The long (44–14 Mya) stem of the celestine lineage is intriguing. Biogeographically, it is not possible to conclude that the Caribbean Clade arrived to the Caribbean islands at either the beginning or the end of that time period, or any point in between, because there are no fossils. However, the presence of a single Celestine genus and species (*Advenus montisilvestris*) occurring outside of the Caribbean provides an opportunity to clarify the origin of the clade, phylogenetically and temporally. That species is known from only a single specimen, but it occurs in a remote area and there is no reason to believe that it is extinct. Genetic sampling in the future may answer these questions, and also provide a test of our tentative assignment of *Advenus* to the Caribbean Clade based only on morphology.

Of the three subfamilies of Diploglossidae, the Caribbean Clade (Celestinae **subfam. nov.**) is the most threatened (Table 3) for two primary reasons. First, the introduction of the Small Indian Mongoose (*Urva auropunctata*) in 1872 resulted in the decline and extinction of Caribbean reptile species (Hedges & Conn 2012). Most previous authors also have considered the mongoose to be a major, if not the major, cause of extirpations and extinctions of Caribbean island reptiles (Barbour 1910, 1930; Breuil 2002; Daltry 2009; Hedges & Conn 2012; Henderson 1992; Lewis et al. 2011; Lorvelec et al. 2007; Powell & Henderson 2005). The ground dwelling and diurnal habits of Caribbean diploglossids have made them especially susceptible to mongoose predation. Secondly, the decline of primary forest in the Caribbean by human activities (Hedges *et al.* 2018) continues to destroy habitat of Caribbean diploglossids. Remaining primary forest in Haiti accounts for <1% of the total land area, while remaining primary forest in the Dominican Republic is estimated to be ~5% (Hedges & Conn 2012; Hedges *et al.* 2018). While national parks and other protected areas exist in these countries, deforestation still takes place within their boundaries, meaning that they offer little to no protection.

Future studies incorporating additional molecular and morphological data will further clarify the diversity and phylogeny of diploglossid lizards. Four species are not monophyletic, and others have large times of divergence among populations, suggesting the presence of many additional species. In addition, further resolution of the diploglossid phylogeny, especially to the species and population level, will provide a basis for additional studies on the ecology, evolution, and biogeography of this family.

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References

Ali, J.R. (2011) Colonizing the Caribbean: is the GAARlandia land-bridge hypothesis gaining a foothold? *Journal of Biogeography*, 39, 431–433.
https://doi.org/10.1111/j.1365-2699.2011.02674.x

Barbour, T. (1910) Notes on the herpetology of Jamaica. *Bulletin of the Museum of Comparative Zoology*, 52, 273–301.

Barbour, T. (1914) A contribution to the zoögeography of the West Indies, with special reference to amphibians and reptiles. *Memoirs of the Museum of Comparative Zoölogy*, 44, 209–359, 201 pls. [includes 207 foldout tables]
https://doi.org/10.5962/bhl.title.49187

Barbour, T. (1930) A list of Antillean reptiles and amphibians. *Zoologica*, *New York*, 11, 61–116.

Barbour, T. & Shreve, B. (1937) Novitates Cubanae. *Bulletin of the Museum of Comparative Zoology*, 80, 377–387.

Bocourt, M.F. (1881) s.n. *In*: Duméril, A., Bocourt, M.F. & Moquard, F. (Eds.), Études sur les reptiles. *In: Recherches Zoologiques pour sevir a l'Histoire de la Faune de l'Amérique Centrale et du Mexique. Mission Scientifique au Mexique et dans l'Amerique Centrale. Troisiéme partie, Primière Section. Livrason 7*. Imprimerie Nationale, Paris, pp. 1–459.

Boulenger, G.A. (1885) *Catalogue of the Lizards in the British Museum. Vol. 2*. Taylor & Francis, London, 497 pp.

Boulenger, G.A. (1894) List of reptiles and batrachians collected by Dr. J. Bohls near Asuncion, Paraguay. *Journal of Natural History*, 13, 342–348.
https://doi.org/10.1080/00222939408677709

Boulenger, G.A. (1895) Second report on additions to the lizard collection in the Natural History Museum. *Proceedings of the Zoological Society of London*, 1894, 722–736.

Breuil, M. (2002) Histoire naturelle des Amphibiens et Reptiles terrestres de l'Archipel Guadeloupéen: Guadeloupe et dépendances, Saint-Martin, Saint-Barthélemy. *Patrimoines naturels IEGB, SPN MNHN*, 54, 1–339

Cacciali, P. & Scott, N.J. (2015) Key to the *Ophiodes* (Squamata: Sauria: Diploglossidae) of Paraguay with the description of a new species. *Zootaxa*, 3980 (1), 42–50.
https://doi.org/10.11646/zootaxa.3980.1.2

Campbell, J.A. & Camarillo, J.L. (1994) A new lizard of the genus *Diploglossus* (Anguidae: Diploglossinae) from Mexico, with a review of the Mexican and northern Central American species. *Herpetologica*, 50, 193–209.

Cochran, D.M. (1927) A new genus of anguid lizards from Haiti. *Proceedings of the Biological Society of Washington*, 40, 91–92.

Cochran, D.M. (1939) Diagnoses of three new lizards and a frog from the Dominican Republic. *Proceedings of the New England Zoölogical Club*, 18, 1–3.

Cochran, D.M. (1941) The herpetology of Hispaniola. *Bulletin of the United States National Museum*, 177, 1–398.
https://doi.org/10.5962/bhl.part.14437

Cocteau, J.T. (1838) Reptiles. *In*: Cocteau, J.T. & Bibron, G. (1838–1843), de la Sagra, R. (Ed.), *Historia Física, Política y Natural de la Isla de Cuba, Segundo Parte—Historia Natural, Tomo IV—Reptiles y Peces*. Arthus Bertrand, Paris, pp. 1–142.

Cope, E.D. (1861) Descriptions of reptiles from tropical America and Asia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 368–374.

Cope, E.D. (1862a) On the genera *Panolopus, Centropyx, Aristelliger* and *Sphaerodactylus*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 13, 494–500.

Cope, E.D. (1862b) Contributions to Neotropical saurology. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14, 176–188.

Cope, E.D. (1865) Third contribution to the herpetology of tropical America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 17, 185–198.

Cope, E.D. (1868) An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and the Upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20, 96–140.

Cope, E.D. (1894) Third addition to a knowledge of the batrachia and reptilia of Costa Rica. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 46, 194–206.

Daltry, J.C. (2009) *The Status and Management of Saint Lucia's Forest Reptiles and Amphibians. Technical Report No. 2 to the National Forest Demarcation and Bio-Physical Resource Inventory Project*. FCG International Ltd, Helsinki, 129 pp.

Delsuc, F., Kuch, M., Gibb, G.C., Karpinski, E., Hackenberger, D., Szpak, P., Martínez, J.G., Mead, J.I., McDonald, H.G., MacPhee, R.D.E., Billet, G., Hautier, L. & Poinar, H.N. (2019) Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Current Biology*, 29, 2031–2042.
https://doi.org/10.1016/j.cub.2019.05.043

Duméril, A.M.C. & Bibron, G. (1839) *Erpétologie Générale on Histoire Naturelle Complète des Reptiles. Vol.5*. Roret/Fain et Thunot, Paris, 871 pp.

Dunn, E.R. (1939) Zoological results of the George Vanderbilt South Pacific Expedition of 1937. Part III. The lizards of Malpelo Island, Colombia. *Notulae Naturae, Academy of Natural Sciences of Philadelphia*, 4, 1–3.

Entiauspe-Neto, O.M., Quintela, F.M., Regnet, R.A., Teixeira, V.H., Silveira, F. & Loebmann, D. (2017) A new and microendemic species of *Ophiodes* Wagler, 1828 (Sauria: Diploglossinae) from the Lagoa dos Patos Estuary, Southern Brazil. *Journal of Herpetology*, 51, 515–522.

https://doi.org/10.1670/17-007
Fitch, H.S. (1981) Sexual size differences in reptiles. Miscellaneous publication. *University of Kansas Museum of Natural History*, 70, 1–72.
https://doi.org/10.5962/bhl.title.16228
Fitzinger L.J. (1843) *Systema reptilium. Fasciculus primus, Amblyglossae*. Braumüller et Seidel, Vindobonae, 106 pp. [in Latin]
Fürbringer, M. (1900) Zur Vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Janaische Zeitschrift für Naturwissenschaf*, 34, 215–718.
https://doi.org/10.5962/bhl.title.52377
Garman, S. (1887) On West Indian Geckonidae and Anguide. *Bulletin of the Essex Institute*, 19, 17–24.
GBIF (2020) *Global Biodiversity Information Facility (GBIF) database.* Copenhagen, Denmark: GBIF Secretariat. Available from: https://www.gbif.org/ (accessed 3 October 2020)
Genbank (2020) *GenBank*. National Institutes of Health, Bethesda, Maryland. Available from: http://www.ncbi.nlm.nih.gov/genbank/ (accessed 16 December 2020)
Grant, C. (1940a) II. The reptiles. *In*: Lynn, W.G. & Grant, C. (Eds.), *The Herpetology of Jamaica*. The Institute of Jamaica, Kingston, pp. 61–148.
Grant, C. (1940b). Notes on the reptiles and amphibians of Jamaica, with diagnoses of new species and subspecies. *In*: *Jamaica Today*. Hazell, Watson, and Viney, London and Aylesbury, pp. 151–157.
Grant, C. (1951) The specific characters of the Celesti, with description of a new species of *Celestus* (Sauria: Anguidae). *Copeia*, 1, 67–69.
https://doi.org/10.2307/1438056
Gray, J.E. (1825) A synopsis of the genera of reptiles and Amphibia, with a description of some new species. *Annals of Philosophy*, 10, 193–217.
Gray, J.E. (1831) A synopsis of the species of Class Reptilia. *In*: Griffith, E. & Pidgeon, E. (Eds.), *The animal kingdom arranged in conformity with its organisation by the Baron Cuvier with additional descriptions of all the species hither named, and of many before noticed*, V Whittaker, Treacher and Co., London, pp. 1–481 + 1–110.
Gray, J.E. (1839) Catalogue of the slender-tongued saurians, with descriptions of many new genera and species. *Annals & Magazine of Natural History*, Series 1, 2 (11), 331–337.
https://doi.org/10.1080/00222933909512395
Gray, J.E. (1845) *Catalogue of the specimens of lizards in the collections of the British Museum.* British Museum, London, xxvii + 289 pp.
Gray, J.E. (1852) Description of *Sauresia*, a new genus of Scincidae from St. Domingo. *Annals and Magazine of Natural History*, 10, 281–282.
https://doi.org/10.1080/03745485609495697
Hass, C.A., Maxson, L.R. & Hedges, S.B. (2001) Relationships and divergence times of West Indian amphibians and reptiles: Insights from albumin immunology. *In*: Woods, C.A. & Sergile, F.E. (Eds.), *Biogeography of the West Indies: Patterns and Perspectives*. *2nd Edition*. CRC Press, Boca Raton, Florida, pp. 15–33.
https://doi.org/10.1201/9781420039481-11
Hedges, S.B. (2006) Paleogeography of the Antilles and the origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, 93, 231–244.
https://doi.org/10.3417/0026-6493(2006)93[231:POTAAO]2.0.CO;2
Hedges, S.B., Cohen, W.B., Timyan, J. & Yang, Z. (2018) Haiti's biodiversity threatened by nearly complete loss of primary forest. *Proceedings of the National Academy of Sciences*, 115, 11850–11855.
https://doi.org/10.1073/pnas.1809753115
Hedges, S.B. & Conn, C.E. (2012) A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa*, 3288 (1), 1–244.
https://doi.org/10.11646/zootaxa.3288.1.1
Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008) New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737 (1), 1–182.
https://doi.org/10.11646/zootaxa.1737.1.1
Hedges, S.B., Hass, C.A. & Maxson, L.R. (1992) Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proceedings of the National Academy of Sciences*, 89, 1909–1913.
https://doi.org/10.1073/pnas.89.5.1909
Hedges, S.B. & Kumar, S. (2009) Discovering the timetree of life. *In*: Hedges, S.B. & Kumar, S. (Eds.), *The Timetree of Life*. Oxford University Press, New York, pp. 3–18.
Hedges, S.B., Marin, J., Suleski, M., Paymer, M. & Kumar, S. (2015) Tree of life reveals clock-like speciation and diversification. *Molecular Biology and Evolution*, 32, 835–845.
https://doi.org/10.1093/molbev/msv037
Hedges, S.B., Powell, R., Henderson, R.W., Hanson, S. & Murphy, J.C. (2019) Definition of the Caribbean Islands biogeographic region, with checklist and recommendations for standardized common names of amphibians and reptiles. *Caribbean Herpetology*, 67, 1–53.

https://doi.org/10.31611/ch.67
Hedges, S.B. & Vidal, N. (2009) Lizards, snakes, and amphisbaenians (Squamata). *In*: Hedges, S.B. & Kumar, S. (Eds.), *The timetree of life.* Oxford University Press, New York, pp. 383–389.
Henderson, R.W. (1992) Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post Columbus West Indies. *Caribbean Journal of Science*, 28, 1–10.
Henderson, R.W. & Powell, R. (2009) *Natural history of West Indian amphibians and reptiles.* University Press of Florida, Gainesville, Florida, 495 pp.
Hijmans, R. & University of California, Berkeley, Museum of Vertebrate Zoology (2015) UC Berkeley, Museum of Vertebrate Zoology. Available from: http://earthworks.stanford.edu/ (accessed 5 September 2020)
Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.
IUCN (2020) *IUCN Redlist of Threatened Species*. Available from: http://www.iucnredlist.org/ Gland, Switzerland: International Union for the Conservation of Nature (accessed 20 August 2020).
Kuhl, H. (1820) *Beiträge zur Zoologie und vergleichenden Anatomie*. Hermannsche Buchhandlung, Frankfurt, 152 pp.
Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35, 1547–1549.
https://doi.org/10.1093/molbev/msy096
Lewis, D.S., Veen, R.V. & Wilson, B.S. (2011) Conservation implications of Small Indian Mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica. *Biological Invasions*, 13, 25–33.
https://doi.org/10.1007/s10530-010-9781-0
Lorvelec, O., Pascal, M., Pavis, C. & Feldmann, P. (2007) Amphibians and reptiles of the French West Indies: Inventory, threats and conservation. *Applied Herpetology*, 4, 131–161.
Lotzkat, S., Hertz, A. & Köhler, G. (2016) A new species of *Celestus* (Squamata: Anguidae) from western Panama. *Mesoamerican Herpetology*, 3, 962–975.
https://doi.org/10.1163/157075407780681356
Macey, J.R., Schulte II, J.A., Larson, A., Tuniyev, B.S., Orlov, N. & Papenfuss, T.J. (1999) Molecular phylogenetics, tRNA evolution, and historical biogeography in anguid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution*, 12, 250–272.
https://doi.org/10.1006/mpev.1999.0615
McCranie, J.R. & Wilson L.D. (1996) A new arboreal lizard of the genus *Celestus* (Squamata: Anguidae) from northern Honduras. *Revista de Biologia Tropical*, 44, 259–264.
Meiri, S., Roll, U., Grenyer, R., Feldman, A., Novosolov M. & Bauer, A. (2017) Data from: The global distribution of tetrapods reveals a need for targeted reptile conservation, Dryad, Dataset.
https://doi.org/10.5061/dryad.83s7k
Myers, C.W. (1973) Anguid lizards of the genus *Diploglossus* in Panamá, with the description of a new species. *American Museum Novitates*, 2523, 1–20.
Oppel, M. (1811) *Die Ordnungen, Familien und Gattungen der reptilien, als Prodrom einer Naturgeschichte derselben*. Joseph Lindauer, Munich, 86 pp.
https://doi.org/10.5962/bhl.title.4911
O'Shaughnessy, A.W.E. (1874) A description of a new species of Scincidae in the collection of the British Museum. *Annals & Magazine of Natural History*, Series 4, 13 (76), 298–301.
https://doi.org/10.1080/00222937408680864
Peracca, M.G. (1890) Descrizione di una nuova specie del gen. *Diploglossus* Wiegm. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino*, 5, 1–5.
Peters, J.A. & Donoso-Barros, R. (1970) Catalogue of the Neotropical Squamata: Part II. Lizards and amphisbaenians. *Bulletin of the United States National Museum*, 297, 1–347.
https://doi.org/10.5479/si.03629236.297.1
Powell, R. & Henderson, R.W. (2005) Conservation status of Lesser Antillean reptiles. *Iguana*, 12, 3–17.
Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 93.
https://doi.org/10.1186/1471-2148-13-93
Pyron, R.A. & Burbrink, F.T. (2014) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, 17, 13–21.
https://doi.org/10.1111/ele.12168
QGIS (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from: http://qgis.org (accessed 20 August 2020)
Raddi, G. (1826) Di alcune specie nuovi di rettili e piante brasiliana. *Atti ella Società Italiana di Scienze Moderna*, 18, 1–39.
Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67, 901–904.
https://doi.org/10.1093/sysbio/syy032
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. &

Huelsenbeck, J.P. (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029

Savage, J.M. & Lips, K.R. (1993) A review of the status and biogeography of the lizard genera *Celestus* and *Diploglossus* (Squamata: Anguidae), with description of two new species from Costa Rica. *Revista de Biología Tropical*, 41, 817–842.

Savage, J.M., Lips, K.R. & Ibáñez, D. (2008) A new species of *Celestus* from west-central Panama, with consideration of the status of the genera of the Anguidae: Diploglossinae (Squamata). *Revista de Biología Tropical*, 56, 845–859.

Schmidt, K.P. (1933) New reptiles and amphibians from Honduras. *Field Museum of Natural History*, 20, 15–22.

Schwartz, A. (1964) *Diploglossus costatus* Cope (Sauria, Anguidae) and its relatives in Hispaniola. *Reading Public Museum and Art Gallery*, 13, 1–57.

Schwartz, A. (1970) A new species of large *Diploglossus* (Sauria: Anguidae) from Hispaniola. *Proceedings of the Biological Society of Washington*, 82, 777–788.

Schwartz, A. (1971) A new species of bromeliad-inhabiting galliwasp (Sauria: Anguidae) from Jamaica. *Breviora*, 371, 1–10.

Schwartz, A., Graham, E.D. Jr. & Duval, J.J. (1979) A new species of *Diploglossus* (Sauria: Anguidae) from Hispaniola. *Proceedings of the Biological Society of Washington*, 92, 1–9.

Schwartz, A. & Henderson, R.W. (1988) West Indian amphibians and reptiles: a check-list. *Milwaukee Public Museum Contributions to Biology and Geology*, 74, 1–264.

Schwartz, A. & Henderson, R.W. (1991) *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. University of Florida Press, Gainesville, Florida, 720 pp.

Schwartz, A. & Inchaustegui, S.I. (1976) A new species of *Diploglossus* (Reptilia, Lacertilia, Anguidae) from Hispaniola. *Journal of Herpetology*, 10, 241–246.
https://doi.org/10.2307/1562985

Schwartz, A. & Thomas, R. (1975) A check-list of West Indian amphibians and reptiles *Carnegie Museum of Natural History Special Publication*, 1, 1–216.
https://doi.org/10.5479/si.03629236.199

Shaw, G. (1802) *General zoology or systematic natural history. Vol. 3*. Thomas Davison, London, viii + 312 pp.

Smith, H. (1942) Mexican herpetological miscellany. *Proceedings of the United States National Museum*, 92, 349–395.
https://doi.org/10.5479/si.00963801.92-3153.349

Smith, H.M. & Taylor, E.H. (1950) An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. *Bulletin of the United States National Museum*, 199, 1–253.
https://doi.org/10.5479/si.03629236.199

Spix, J.B. (1824) *Animalia nova sive species nova lacertarum quas in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis, suscepto, collegit et descripsit Dr. J. B. de Spix*. Typis Francis Seraphici Hübschmanni, Munich, 75 pp.
https://doi.org/10.5962/bhl.title.5117

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
https://doi.org/10.1093/bioinformatics/btl446

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Strahm, M.H. & Schwartz, A. (1977) Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. *Biotropica*, 9, 58–72.
https://doi.org/10.2307/2387862

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J. & Rambaut, A. (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution*, 4, vey016.
https://doi.org/10.1093/ve/vey016

Thomas, R. (1971) A new species of *Diploglossus* (Sauria: Anguidae) from Hispaniola. *Occasional papers of the Museum of Zoology Louisiana State University*, 40, 1–9.

Thomas, R. & Hedges, S.B. (1989) A new *Celestus* (Sauria: Anguidae) from the Chaine de Ia Selle of Haiti. *Copeia*, 4, 886–891.
https://doi.org/10.2307/1445973

Thomas, R. & Hedges, S.B. (1998) A new anguid lizard (*Diploglossus*) from Cuba. *Copeia*, 1, 97–103.
https://doi.org/10.2307/1447704

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W. & Pyron, R.A. (2016) Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, 204, 23–31.
https://doi.org/10.1016/j.biocon.2016.03.039

Uetz, P., Freed, P. & Hošek, J. (2020) *The Reptile Database*. Available from: http://www.reptile-database.org (accessed 21 October 2020)

Underwood, G. (1959) A new Jamaican galliwasp (Sauria, Anguidae). *Brevoria*, 102, 1–13.

Underwood, G. (1964) An anguid lizard from the Leeward Islands. *Breviora*, 200, 1–10.

Vidal, N. & Hedges, S.B. (2004) Molecular evidence for a terrestrial origin of snakes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, S226–S229.
https://doi.org/10.1098/rsbl.2003.0151

Vidal, N. & Hedges, S.B. (2005) The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes rendus biologies*, 328, 1000–1008.
https://doi.org/10.1016/j.crvi.2005.10.001

Vidal, N. & Hedges, S.B. (2009) The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *CR Biologies*, 332, 129–139.
https://doi.org/10.1016/j.crvi.2008.07.010

Vidal, N., Marin, J., Sassi, J., Battistuzzi, F.U., Donnellan, S., Fitch, A.J., Fry, B.G., Vonk, F.J., Rodriguez de la Vega, R.C., Couloux, A. & Hedges, S.B. (2012) Molecular evidence for an Asian origin of monitor lizards followed by Tertiary dispersals to Africa and Australasia. *Biology Letters*, 8, 853–855.
https://doi.org/10.1098/rsbl.2012.0460

Wagler, J. (1828) Auszüge aus seinem systema amphibiorum. *Isis von Oken*, 21, 740–742.

Werler, J.E. & Campbell, J.A. (2004) New lizard of the genus *Diploglossus* (Anguidae: Diploglossinae) from the Tuxtlan faunal region, Veracruz, Mexico. *The Southwestern Naturalist*, 49, 327–333.
https://doi.org/10.1894/0038-4909(2004)049%3C0327:NLOTGD%3E2.0.CO;2

Wiegmann, A.F.A. (1834) Herpetologia Mexicana seu descriptio amphibiorum novae Hispaniae. Pars prima saurorum species. Lüderitz, Berlin, 54 pp.

Wiens, J.J., Brandley, M.C. & Reeder, T.W. (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snakeline body form in squamate reptiles. *Evolution*, 60, 123–141.
https://doi.org/10.1111/j.0014-3820.2006.tb01088.x

Wiens, J.J., Hutter, C.R., Mulcahy, D.G., Noonan, B.P., Townsend, T.M., Sites Jr., J.W. & Reeder, T.W. (2012) Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biology Letters*, 8, 1043–1046.
https://doi.org/10.1098/rsbl.2012.0703

Wiens, J.J. & Slingluff, J.L. (2001) How lizards turn into snakes: a phylogenetic analysis of body ‐ form evolution in anguid lizards. *Evolution*, 55, 2303–2318.
https://doi.org/10.1111/j.0014-3820.2001.tb00744.x

Wright, A.M., Lyons, K.M., Brandley, M.C. & Hillis, D.M. (2015) Which came first: the lizard or the egg? Robustness in phylogenetic reconstruction of ancestral states. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324, 504–516.
https://doi.org/10.1002/jez.b.22642

Zheng, Y. & Wiens, J.J. (2016) Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution*, 94, 537–547.
https://doi.org/10.1016/j.ympev.2015.10.009

APPENDIX 1: specimens and sequences used in the molecular analyses

Genbank numbers are listed for each of the nine genes. We collected 261 new sequences (MW824662–MW824922) and include them with five 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 subfam. nov.** *Caribicus darlingtoni* (USNM 328806, SBH 161687; Dom. Rep., Independencia, Cacique Enriquillo, 9.0 km N of; 18.673758, -71.76908), *Caribicus warreni* (Voucher not available, SBH 194521; Dom. Rep., Puerto Plata, presumably the region of Puerto Plata), *Celestus crusculus crusculus 1* (USNM 328158, SBH 172441; Jamaica, Westmoreland, Old Hope, 7.0 km WSW of), *Celestus crusculus crusculus 2* (USNM 328169, SBH 103449; Jamaica, St. Elizabeth, Knoxwood), *Celestus crusculus crusculus 3* (USNM 328174, SBH 172438; Jamaica, St. Mary, Oracabessa, 6.2 km W of), *Celestus crusculus crusculus 4* (USNM 328154, SBH 101572; Jamaica, Hanover, Content, 3.2 km SE of), *Celestus crusculus crusculus 5* (USNM 328160, SBH 161123; Jamaica, Trelawny, Duncans, 0.3 km W of, jct. with Silver Sands road), *Celestus crusculus cundalli 1* (USNM 328144, SBH 172465; Jamaica, Portland, Section, 1.3 km WSW of, on road to Hardwar Gap), *Celestus crusculus cundalli 2* (Voucher not available, SBH 274632; Jamaica, St. Thomas, Trinity Ville, 5.9 km W of by road), *Celestus barbouri* (USNM 328153, SBH 161122; Jamaica, Trelawny, Quick Step, vicinity of), *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; 18.332253, -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, Dame Marie [turn back locality], 5.0 km N of; 18.585683, -74.407617), *Comptus stenurus stenurus 2* (USNM 328836, SBH 103900; Haiti, de laGrand'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, SBH 103083; Dom. Rep., Maria Trinidad Sanchez, Nagua, 4.0 km SE of), *Comptus stenurus weinlandi* (USNM 328808, SBH 102712; Dom. Rep., Barahona, Canoa, 16.0 km ESE of), *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 neiba* (ANSP 38578; Haiti, Artibonite, Ça Soleil, 11.8 km W of; 19.469546, -72.777129), *Panolopus costatus nesobous* (ANSP 38583; Haiti, Sud, Ile a Vache; 18.105163, -73.69288), *Panolopus costatus oreistes* (USNM 328792, SBH 104408; Haiti, Sud-Est, Jacmel, 9.5 km E of; 18.227064, -72.44959), *Panolopus curtissi aporus* (USNM 328800, SBH 102610; 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, La Descubierta, 5.1 km NW of; 18.5711, -71.7549), *Panolopus curtissi diastatus* (ANSP 38646; Haiti, Nord'Ouest, Mole St. Nicolas; 19.805831, -73.375556), *Panolopus curtissi hylonomus* (ANSP 38647; Dom. Rep., Peravia, Cruce de Ocoa, 14.8 N, 7.8 km SE on dirt road, at Martinez near La Palma; 18.46, -70.45), *Panolopus marcanoi* (ANSP 38657; Dom. Rep., Santiago, Valle de Bao; 19.054054, -70.985646), *Sauresia sepsoides 1* (ANSP 38667; Haiti, Ouest, Berry; 18.307945, -72.253894), *Sauresia sepsoides 2* (USNM 328846, SBH 102369; Dom. Rep., Hato Mayor, Sabana de la Mar, 9.5 km W [airline] in Los Haitises; 19.05293, -69.47899), *Sauresia sepsoides 3* (ANSP 38684; Haiti, Nippes, Morne Bois Pangnol; 18.418689, -73.775122), *Sauresia sepsoides 4* (ANSP 38675; Haiti, Grand'Anse, Grande Cayemite; 18.635615, -73.751749), *Wetmorena agasepsoides* (ANSP 38712; Dom. Rep., Barahona, Canoa, 0.3 km S, 13.5 km E airline; 18.3448, -71.032), *Wetmorena haetiana haetiana* (ANSP 38745; Haiti, Ouest, Waterfall in Parc La Visite; 18.34014, -72.269826), *Wetmorena haetiana mylica* (USNM 328858, SBH 102546; Dom. Rep., Barahona, Cabral, 15.3 km S, 6.7 km E by road; 18.103139, -71.216981), *Wetmorena haetiana surda* (USNM 328899, SBH 101406; Dom. Rep., Pedernales, El Aguacate, 10.3 km S, on Haitian border road; 18.26879, -71.72703). **Diploglossinae.** *Diploglossus lessonae* (CHUNB 62432; Brazil), *Diploglossus monotropis* (SMF 100420; Costa Rica), *Diploglossus pleii* (ANSP 38556; United States, Puerto Rico, Reserva Forestal, Rio Abajo (8 km airline SSE Arecibo); 18.4000, -66.6913), *Diploglossus garridoi* (MNHNCU 4420, SBH 193507; Cuba, Granma, El Manguito), *Diploglossus nigropunctatus* (USNM 512240, SBH 191015; Cuba, Guantanamo, San Luis de Potosi, 1 km SW of), *Diploglossus delasagra* (USNM 512238, SBH 191542; Cuba, Pinar del Rio, San Vicente, 4.0 km NW, north base of Sierra de San Vicente), *Ophiodes striatus* (MVZ 191047; Brazil, Edo. Sao Paulo), *Ophiodes sp.* (CURCR 94). **Siderolamprinae.** *Mesoamericus bilobatus 1* (SMF 94584; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), *Mesoamericus bilobatus 2* (SMF 94583; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), *Mesoamericus bilobatus 3* (MVZ 207334; Costa Rica, Moravia), *Mesoamericus bilobatus 4* (SMF 101026; Costa Rica, Limón, Finca Curré, northern limit, close to creek; 9.61823, -82.71195), *Mesoamericus bilobatus 5* (SMF 89549; Panama, Veraguas, PNSF, Cerro Mariposa: water supply hut near Alto de Piedra; 8.51607, -81.11849), *Mesoamericus 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 Tapanti), *Siderolampurs enneagrammus 1* (UTA R-30338; Mexico, Oaxaca, Sierra Mixes, 0.8 km S Totontepec; 17.26, -96.04), *Siderolamprus enneagrammus 2* (MVZ 191044; Mexico, La Joya), *Siderolamprus laf* (SMF 90177; Panama, Chiriquí, Lost and Found Ecohostel; 8.67462, -82.21958), *Siderolamprus rozellae* (UTA R-46107; Guatemala, Izabal, Morales, Finca Karen), *Pseudopus apodus* (CAS 182911, SBH 194938; Russia).

Species	RAG1	PLPR	AMEL	BDNF
Celestinae subfam. nov.				
Caribicus darlingtoni	MW824840	MW824819	NA	NA
Caribicus warreni	MW824841	MW824820	MW824760	MW824779
Celestus barbouri	MW824842	NA	NA	MW824780
Celestus crusculus crusculus 1	MW824844	NA	NA	MW824781
Celestus crusculus crusculus 2	NA	NA	NA	MW824783
Celestus crusculus crusculus 3	NA	NA	NA	MW824784

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APPENDIX 1: (Continued)

Species	RAG1	PLPR	AMEL	BDNF
Celestus crusculus crusculus 4	MW824843	NA	MW824761	NA
Celestus crusculus crusculus 5	NA	NA	NA	MW824782
Celestus crusculus cundalli 1	MW824845	NA	NA	NA
Celestus crusculus cundalli 2	NA	NA	NA	NA
Celestus duquesneyi	MW824846	NA	MW824762	MW824785
Celestus hewardii	MW824847	NA	MW824763	MW824786
Celestus macrotus	NA	NA	NA	NA
Comptus badius	MW824848	MW824821	NA	MW824787
Comptus maculatus	MW824849	NA	NA	NA
Comptus stenurus stenurus 1	MW824851	MW824823	NA	MW824789
Comptus stenurus stenurus 2	MW824852	MW824824	NA	MW824790
Comptus stenurus rugosus	MW824850	MW824822	MW824764	MW824788
Comptus stenurus weinlandi	NA	MW824825	NA	NA
Panolopus costatus costatus	MW824857	NA	MW824769	MW824802
Panolopus costatus neiba	MW824860	NA	MW824770	MW824805
Panolopus costatus nesobous	MW824861	NA	NA	MW824806
Panolopus costatus oreistes	MW824862	NA	MW824771	NA
Panolopus costatus leionotus 1	MW824858	NA	NA	MW824803
Panolopus costatus leionotus 2	MW824859	NA	NA	MW824804
Panolopus curtissi aporus	MW824863	NA	MW824772	MW824807
Panolopus curtissi curtissi	MW824864	NA	NA	MW824808
Panolopus curtissi diastatus	MW824865	NA	NA	MW824809
Panolopus curtissi hylonomus	MW824866	NA	NA	MW824810
Panolopus marcanoi	MW824867	NA	MW824773	NA
Sauresia sepsoides 1	NA	NA	NA	NA
Sauresia sepsoides 2	MW824869	MW824833	MW824775	MW824811
Sauresia sepsoides 3	NA	NA	NA	NA
Sauresia sepsoides 4	NA	NA	NA	NA
Wetmorena agasepsoides	MW824874	NA	MW824777	NA
Wetmorena haetiana haetiana	MW824875	MW824837	NA	MW824816
Wetmorena haetiana mylica	MW824876	MW824838	MW824778	MW824817
Wetmorena haetiana surda	MW824877	MW824839	NA	MW824818
Diploglossinae				
Diploglossus delasagra	NA	MW824826	NA	JQ845038
Diploglossus garridoi	MW824853	NA	MW824765	MW824791
Diploglossus lessonae	NA	NA	NA	MW824792
Diploglossus monotropis	NA	MW824827	NA	MW824793
Diploglossus nigropunctatus	MW824854	MW824828	MW824766	MW824794
Diploglossus pleii	MW824855	MW824829	MW824767	MW824795
Ophiodes sp.	NA	NA	NA	NA
Ophiodes striatus	NA	NA	NA	NA

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APPENDIX 1: (Continued)

Species	RAG1	PLPR	AMEL	BDNF
Siderolamprinae				
Mesoamericus bilobatus 1	NA	MW824832	NA	MW824800
Mesoamericus bilobatus 2	NA	MW824831	NA	MW824799
Mesoamericus bilobatus 3	MW824856	MW824830	MW824768	MW824796
Mesoamericus bilobatus 4	NA	NA	NA	MW824801
Mesoamericus bilobatus 5	NA	NA	NA	MW824798
Mesoamericus bilobatus 6	NA	NA	NA	MW824797
Siderolamprus bivittatus	MW824870	MW824834	NA	MW824812
Siderolamprus cyanochloris	MW824871	MW824835	MW824776	MW824813
Siderolampurs enneagrammus 1	NA	NA	NA	NA
Siderolamprus enneagrammus 2	MW824872	JN880817	NA	MW824814
Siderolamprus laf	NA	NA	NA	NA
Siderolamprus rozellae	MW824873	MW824836	NA	MW824815
Anguidae				
Pseudopus apodus	MW824868	NA	MW824774	NA

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APPENDIX 1: (Continued)

Species	ZFP36	ND2	CytB	12S & 16S
Celestinae subfam. nov.				
Caribicus darlingtoni	NA	MW824717	MW824662	MW824918
Caribicus warreni	MW824878	MW824718	MW824663	MW824910
Celestus barbouri	MW824879	MW824719	MW824664	MW824914
Celestus crusculus crusculus 1	NA	MW824721	MW824666	NA
Celestus crusculus crusculus 2	NA	MW824723	MW824668	NA
Celestus crusculus crusculus 3	NA	MW824724	MW824669	NA
Celestus crusculus crusculus 4	MW824880	MW824720	MW824665	MW824915
Celestus crusculus crusculus 5	NA	MW824722	MW824667	NA
Celestus crusculus cundalli 1	NA	MW824726	MW824671	NA
Celestus crusculus cundalli 2	NA	MW824725	MW824670	NA
Celestus duquesneyi	MW824881	MW824727	MW824672	MW824913
Celestus hewardii	MW824882	MW824728	MW824673	MW824912
Celestus macrotus	NA	MW824729	MW824674	NA
Comptus badius	MW824883	MW824730	MW824675	MW824911
Comptus maculatus	MW824884	NA	MW824676	MW824899
Comptus stenurus stenurus 1	NA	MW824732	MW824678	NA
Comptus stenurus stenurus 2	NA	MW824733	MW824679	NA
Comptus stenurus rugosus	MW824885	MW824731	MW824677	MW824919
Comptus stenurus weinlandi	NA	MW824734	MW824680	NA

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APPENDIX 1: (Continued)

Species	ZFP36	ND2	CytB	12S & 16S
Panolopus costatus costatus	MW824891	MW824740	MW824693	MW824901
Panolopus costatus neiba	MW824892	MW824743	MW824696	MW824902
Panolopus costatus nesobous	NA	MW824744	MW824697	NA
Panolopus costatus oreistes	MW824893	MW824745	MW824698	MW824916
Panolopus costatus leionotus 1	NA	MW824741	MW824694	NA
Panolopus costatus leionotus 2	NA	MW824742	MW824695	NA
Panolopus curtissi aporus	MW824894	MW824746	MW824699	MW824917
Panolopus curtissi curtissi	NA	MW824747	MW824700	NA
Panolopus curtissi diastatus	NA	MW824748	MW824701	NA
Panolopus curtissi hylonomus	NA	NA	MW824702	NA
Panolopus marcanoi	MW824895	MW824749	MW824703	MW824903
Sauresia sepsoides 1	NA	MW824751	MW824704	NA
Sauresia sepsoides 2	NA	MW824754	MW824707	MW824920
Sauresia sepsoides 3	NA	MW824753	MW824706	NA
Sauresia sepsoides 4	NA	MW824752	MW824705	NA
Wetmorena agasepsoides	NA	MW824756	MW824713	MW824904
Wetmorena haetiana haetiana	NA	MW824757	MW824714	NA
Wetmorena haetiana mylica	MW824897	MW824758	MW824715	MW824921
Wetmorena haetiana surda	NA	MW824759	MW824716	NA
Diploglossinae				
Diploglossus delasagra	MW824886	MW824735	MW824681	NA
Diploglossus garridoi	MW824887	MW824736	MW824682	MW824907
Diploglossus lessonae	NA	MW824737	NA	MW824906
Diploglossus monotropis	NA	NA	MW824683	NA
Diploglossus nigropunctatus	MW824888	MW824738	MW824684	MW824922
Diploglossus pleii	MW824889	MW824739	MW824685	MW824900
Ophiodes sp.	NA	NA	NA	NA
Ophiodes striatus	NA	AF085610	MW824692	NA
Siderolamprinae				
Mesoamericus bilobatus 1	NA	NA	MW824690	NA
Mesoamericus bilobatus 2	NA	NA	MW824689	NA
Mesoamericus bilobatus 3	MW824890	AF085608	MW824686	NA
Mesoamericus bilobatus 4	NA	NA	MW824691	NA
Mesoamericus bilobatus 5	NA	NA	MW824688	NA
Mesoamericus bilobatus 6	NA	NA	MW824687	NA
Siderolamprus bivittatus	NA	NA	MW824708	NA
Siderolamprus cyanochloris	NA	MW824755	MW824709	MW824909
Siderolampurs enneagrammus 1	NA	NA	MW824711	NA
Siderolamprus enneagrammus 2	NA	AF085607	MW824710	MW824908

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APPENDIX 1: (Continued)

Species	ZFP36	ND2	CytB	12S & 16S
Siderolamprus laf	NA	NA	MW824712	NA
Siderolamprus rozellae	NA	NA	AY525101	NA
Anguidae				
Pseudopus apodus	MW824896	MW824750	NA	MW824905

APPENDIX 2: specimens examined

Celestinae subfam. nov. *Caribicus darlingtoni*: MCZ R-44374 (Dom. Rep., Valle Nuevo; 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 anelpistus*: USNM 197336 (Dom. Rep., San Cristobal, Villa Altagracia, Ingenio Catarey, 'Come Hombre'; 18.6864, -70.1778). *Caribicus warreni*: ANSP 38501 (Haiti, locality not available), ANSP 38502 (Dom. Rep., locality not available [pet trade]). *Celestus barbouri*: ANSP 38503 (Jamaica, Trelawny, Windsor, 0.5 km N of; 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, Quick Step, ca. 0.8 km N of), USNM 328148–328149, USNM 328151–328153 (Jamaica, Trelawny Parish, Quick Step, vicinity of). *Celestus crusculus crusculus*: ANSP 38504 (Jamaica, Trelawny, Duncans, 0.3 km W (jct with Silver Sands access road); 18.47105, -77.53887), USNM 251897–251898 (Jamaica, St. Elizabeth, Malvern, 5.6 mi N of by road), USNM 326601 (Jamaica, Trelawny, Rio Bueno, ca. 1 mi S, 1 mi W of [airline]), USNM 328159–328167 (Jamaica, Trelawny, Duncans, 0.3 km W of), USNM 328168–328169 (Jamaica, St. Elizabeth, Knoxwood), USNM 328154–328155 (Jamaica, Hanover, Content, 3.2 km SE of), USNM 328186 (Jamaica, St. Catherine, Braeton, 5.6 km SW of, at Hellshire Beach in Hellshire Hills). *Celestus crusculus cundalli*: MCZ R-45163 (Jamaica, Mandeville), USNM 328170 (Jamaica, Clarendon, Jackson's Bay, on beach at the hunting club), USNM 328171 (Jamaica, Clarendon, Jackson's Bay, ca. 1.6 km ESE of, at entrance to Jackson's Bay caves), USNM 328172 (Jamaica, St. Mary, vicinity of town of Jack's River), USNM 328173 (Jamaica, St. Mary, Orcabessa, ca. 1.6 km S of, on road to Jacks River), USNM 328174–5 (Jamaica, St. Mary, Oracabessa, 6.2 km W of), USNM 328176 (Jamaica, St. Mary, Salt Gut, vicinity of Boscobel Airport [E side]), USNM 328177–328179 (Jamaica, St. Mary, Port Maria, 2.9 km N of), USNM 328180, USNM 328182–328184 (Jamaica, St. Mary, Port Maria, ca. 6.4 km S of), USNM 328185 (Jamaica, St. Catherine, Ewarton, 9.0 km W of). *Celestus duquesneyi*: MCZ R-45194 (Jamaica, Portland Point; 17.755728, -77.164708), USNM 108310 (Jamaica, Clarendon). *Celestus fowleri*: MCZ R-125601 (Jamaica, Trelawny Forest; 18.35195, -77.64782). *Celestus hewardii*: USNM 108329–108335 (Jamaica, St. James, Montego Bay, 5 mi W of). *Celestus macrolepis*: BMNH 1946.8.3.82 (no locality; restricted here to Jamaica). *Celestus macrotus*: 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), USNM 86917 (Haiti, Ouest, Gros Cheval, ca. 15 km W of, (by logging roads) northeastern slope of Morne La Selle in the Massif de la Selle). *Celestus microblepharis*: MCZ R-55764 (Jamaica, St. Mary, Boscobel; 18.404055, -76.968794). *Celestus molesworthi*: USNM 326600 (Jamaica, St. Thomas, Hordley, 4.8 mi N of). *Celestus occiduus*: BMNH XV.118a (Jamaica), USNM 102652 (Jamaica, Manchester, Kensworth, near Newport). *Celestus striatus*: BMNH 1946.8.8.3 (no locality; restricted here to Jamaica). *Comptus badius*: USNM 25817–25818, USNM 157378 (Navassa Island; 18.4028, -75.0125). *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), ANSP 38512 (Cayman Islands, Cayman Brac, West End, 1.2 km E of; 19.698, -79.8696)), ANSP 38508–38511 (Cayman Islands, Cayman Brac, West End, Tiara Beach Hotel and surrounding area; 19.7192, -79.8263). *Comptus stenurus alloiedes*: USNM 259971 (Dom. Rep., Samana, Las Galeras, 8.5 km SW of; 19.23, -69.2214), USNM 259972–259973 (Dom. Rep., Samana, Sanchez, 2.0 km NE of). *Comptus stenurus rugosus*: ANSP 38523 (Dom. Rep., El Seibo, Nisibon, 4.2 km N, 8.4 km W of [airline], at Playa Cucharera [= beach W Punta Limon]; 18.9936, -68.87), ANSP 38529–38531 (Dom. Rep., Duarte, San Francisco de Macoris, 10.1 km NE of; 19.34473, -70.18077), ANSP 38534–38537 (Dom. Rep., Los Tabucos, Tenares, 8.8 km N thence 0.5 km W of; 19.4324, -70.3525), ANSP 38532–533 (Dom. Rep., Salcedo, Tenares, 23.2 km N thence 4.5 km W of [= 0.2 km E Jaiba]; 19.5445, -70.3362), ANSP 38524–38525 (Dom. Rep., Hato Mayor, Sabana de la Mar, 7.8 km S of; 18.9883, -69.38955), ANSP 38515–38522 (Dom. Rep., Hato Mayor, Loma del Fresca, Sabana de la Mar 5.7 km airline SW of; 18.27942, -71.40496), ANSP 38513–38514 (Dom. Rep., Hato Mayor, El Valle, 5.6 km airline

W of; 18.97525, -69.43195), ANSP 38526–38527 (Dom. Rep., Hato Mayor, Hato Mayor, 7.8 km S of; 18.9883, -69.38955), ANSP 38528 (Dom. Rep., El Siebo, Sabana de Nisibon, 5 km airline W of; 18.953, -68.8605), USNM 328812–328813, USNM 328816, USNM 328820 (Dom. Rep., Hato Mayor, Sabana de la Mar, 1.7 km W of; 19.0531, -69.4028), USNM 328825 (Dom. Rep., Hato Mayor, El Valle, 22 km WNW of), USNM 328830–328831 (Dom. Rep., Maria Trinidad Sanchez, Nagua, 4 km SE of; 19.3481, -69.8244). *Comptus stenurus stenurus*: ANSP 38544–38545 (Haiti, Sud, Carretour Joute, 8.6 km SW of, near Riviere la Source on the Presquille de Port Salut; 18.071088, -73.899507), ANSP 38550 (Haiti, Sud, Port Salut Gumbwa near Ça Vilason; 18.049233, -73.7887), ANSP 38538–38540 (Haiti, Grand'Anse, Belandier, Dame Marie, 5.0 km N of; 18.585683, -74.407617), ANSP 38543 (Haiti, Grand'Anse, Carcasse, 1.5 km N of; 18.3852, -74.44755), ANSP 38546 (Haiti, Sud, Caye Madeline; 18.324191, -74.009491), USNM 328835, USNM 328839 (Haiti, Grand'Anse, Marché Léon, 6.5–1.5 km S and 0.1–4.5 km E (airline) of, between Rampe des Lions and Bois Sec; 18.4805, -74.0782). *Comptus stenurus weinlandi*: ANSP 38551–4, 191620, 191622–4, 191649–50, 191669 (Haiti, Ouest, Thomaseau, 18.7 km E of; 18.674761, -72.002853), ANSP 38542 (Haiti, Artibonite, Ça Soleil, 11.8 km W of; 19.469546, -72.777129), ANSP 38549 (Haiti, Ouest, Petionville, 10.1 km ENE of, 18.518933, -72.208555), ANSP 38547, ANSP 38548 (Dom. Rep., Independencia, La Descubierta, 5.1 km NW of; 18.5711, -71.7549), ANSP 38541 (Haiti, Nord'Ouest, Bombardopolis; 19.691346, -73.342091), USNM 117264 (Haiti, Trou Caiman; 18.6564, -72.1442), USNM 259969 (Dom. Rep., Barahona, Barahona; 18.2061, -71.0994), USNM 328781 (Haiti, Ouest, Soliette; 18.43, -71.92), USNM 328808 (Dom. Rep., Barahona, Canoa, 16 km ESE of; 18.3125, -71.0417), USNM 328828 (Dom. Rep., Independencia, Tierra Nueva, 1 km E of; 18.5847, -71.9042). *Panolopus costatus costatus*: ANSP 38558 (Haiti, Grand'Anse, Abricots [outskirts]; 18.64783, -74.307212), ANSP 38559 (Haiti, Grand'Anse, Beaumont, 17.0 km S of; 18.384724, -73.875691), ANSP 38561 (Haiti, Sud, Tiburon, ca. 1 km NE of; 18.329133, -74.387967), ANSP 38560 (Haiti, Sud, Les Anglais, 11.6 km NW of, on Morne Grand Bois; 18.374165, -74.299277), USNM 328773 (Haiti, Grand'Anse, vicinity of Castillion; 18.52, -74.1), USNM 328775–328779 (Haiti, Grand'Anse, Castillion; 18.52, -74.1), USNM 328780 (Haiti, Grand'Anse, Castillion, 3 km SW of; 18.4975, -74.1201). *Panolopus costatus leionotus*: ANSP 38562–38564, ANSP 38567–38568 (Dom. Rep., Baoruco, Loma Monte Bonito; 18.60139, -71.39056), ANSP 38565 (Dom. Rep., Baoruco, Apolinar Pelodroma, ca. 5 km N of; 18.593, -71.3979), ANSP 38573–38577 (Dom. Rep., Elias Pina, Rosa de la Piedra, 0.6 km NE of; 18.77689, -71.7157), ANSP 38569–38572 (Haiti, Artibonite, Morne Boeuf; 19.072394, -72.250208), USNM 328752–328758 (Dom. Rep., Elias Pina, Cacique Enriquillo, 17 km N of; 18.7069, -71.7703), USNM 328759 (Dom. Rep., Elias Pina, Cacique Enriquillo, 13 km N of; 18.6936, -71.7747), USNM 328763 (Dom. Rep., Independencia, Cacique Enriquillo 9 km N of.; 18.6783, -71.7883), USNM 328764 (Dom. Rep., Independencia, Cacique Enriquillo, 7 km N of; 18.6742, -71.7731). *Panolopus costatus neiba*: ANSP 38578 (Haiti, Artibonite, Ça Soleil, 11.8 km W of; 19.469546, -72.777129), ANSP 38579 (Dom. Rep., Independencia, Los Pinos, ca. 7 km W of by road; 18.600326, -71.808592), USNM 328745–328751 (Dom. Rep., Elias Pina, Los Pinos, ca. 24 km N of; 18.6919, -71.78), USNM 328765 (Dom. Rep., Independencia, Descubierta, 6.2 km N, 4.0 km W [airline] of; 18.6241, -71.774). *Panolopus costatus nesobous*: ANSP 38580–38582 (Haiti, Sud, Les Platons Citadel, 10.7 km WNW of, Caye Michel previously called Caye Paul; 18.331598, -74.022442), ANSP 38583 (Haiti, Sud, Ile a Vache; 18.105163, -73.69288). *Panolopus costatus oreistes*: ANSP 38609–38613, ANSP 38615–38621 (Dom. Rep., Independencia, Puerto Escondido, 23.9 km SE of; 18.21, -71.53), ANSP 38614 (Dom. Rep., Independencia, Puerto Escondido, 23.1 km SE of; 18.2204, -71.5102), ANSP 38584 (Dom. Rep., Pedernales, Aceitillar, 8.6 km NW of [44.6 km N of Cabo Rojo]; 18.17, -71.57), ANSP 38622 (Dom. Rep., Salcedo, Tenares, 23.2 km N of thence 4.5 km W [= 0.2 km E Jaiba]; 19.5445, -70.3362), ANSP 38598–38606 (Dom. Rep., Pedernales, Casetta Dos, Aceitillar, ca. 22 km N of, by road on ridge of Sierra de Bahoruco; 18.2125, -71.53417), ANSP 38597 (Haiti, Ouest, Berry, 1.0 km SW of; 18.308539, -72.720785), ANSP 38585–38596 (Haiti, Ouest, Berry; 18.307945, -72.253894), ANSP 38607–38608 (Haiti, Sud-Est, Morne D'Enfer, southwestern edge of plateau; 18.330052, -72.37095), USNM 328792 (Haiti, Sud-Est, Jacmel, 9.5 km E of; 18.227064, -72.44959). *Panolopus curtissi aporus*: ANSP 38623–38627 (Dom. Rep., Pedernales, Bucan Detwi; 17.73462, -71.50335), ANSP 38628–38629 (Dom. Rep., Pedernales, Pedernales town, in palm grove; 18.029, -71.7471), ANSP 38630–38631 (Haiti, Sud-Est, Pic La Selle, Sud-Ouest; 18.32388, -72.0264), USNM 328742 (Dom. Rep., Barahona, Barahona, ca. 4–5 km S, 2.7 km W of, via coast road and road to Filipinas; 18.1619, -71.0967), USNM 328743 (Dom. Rep., Barahona, Barahona, ca. 4.5 km S, 4.0 km W of, via coast road and road to Filipinas; 18.1531, -71.1025), USNM 328744 (Dom. Rep., Barahona, La Guazara, 15 km SSW of; 18.1333, -71.1667), USNM 328766–8 (Dom. Rep., Pedernales, Juancho; 17.8564, -71.295), USNM 328769–328772, (Dom. Rep., Pedernales, Los Arroyos; 18.2308, -71.7564), USNM 328793 (Dom. Rep., Barahona, Barahona 11.3 km S of; 18.1267, -71.0731), USNM 328794–328800 (Dom. Rep., Pedernales, Juancho 6.4 km SW, 0.7 km SE [road] of; 17.8358, -71.3439). *Panolopus curtissi curtissi*: ANSP 38632 (Dom. Rep., Independencia, La Descubierta, 5.1 km NW of; 18.5711, -71.7549), ANSP 38633–38635 (Haiti, Artibonite, Gonave; 18.912198, -73.052222). *Panolopus curtissi diastatus*: ANSP 38643–38646 (Haiti, Nord'Ouest, Mole St. Nicolas; 19.805831, -73.375556), ANSP 38636–38637 (Haiti, Nord'Ouest, Bombardopolis; 19.691346, -73.342091), ANSP 38641–38642 (Haiti, Nord'Ouest, Bombardopolis, about 3.5 mi SW of, on S facing slope of Morne Tony; 19.658058, -73.366717), ANSP 38638–38640 (Haiti, Nord'Ouest, Bombardopolis; 19.691346, -73.342091). *Panolopus curtissi hylonomus*: ANSP 38647 (Dom. Rep., Peravia, Cruce de Ocoa, 14.8 N, 7.8 km SE on dirt road, at Martinez near La Palma; 18.46, -70.45). *Panolopus marcanoi*: ANSP 38650–62 (Dom. Rep., Santiago, Valle de Bao; 19.0685, -71.0361), ANSP 38648 (Dom. Rep., Santiago, La Lagunas; 19.1512, -71.0102), ANSP 38649 (Dom. Rep., Santiago, Loma los Banaderos, east slope; 19.1177, -71.0362). *Sauresia sepsoides*: ANSP 38689 (Dom. Rep., Pedernales, at the Rio Mulito, 22 km N; 18.1544, -71.7581), ANSP 38690 –1 (Haiti, Grand'Anse, Pestel, 5.0 km S of; 18.513286, -73.784632), ANSP 38681–3 (Haiti, Grand'Anse, Marche Leon, 8.0 km S of Grand'Anse; 18.516777, -74.083109), ANSP 38663–38664 (Haiti, Grand'Anse, Baraderes, 8.0 km SSW of; 18.44032, -73.667556), ANSP 38678 (Dom. Rep., La Altagracia, La Zanga, 7.5 km W of, at Rio Maimon; 18.8807, -68.7749), ANSP 38670–38672 (Dom. Rep., Sanchez Ramirez, Cotui, 8.6 km NE thence 8.1 km E of; 19.1037, -70.0531), ANSP 38665–38666 (Dom. Rep., Duarte, Batez Piedra on west side of Rio Pazabo; 19.06997, -69.90815), ANSP 38679–38680 (Dom. Rep., Monte Plata, Majagual, 4.3 km N of; 19.07539, -69.82842), ANSP 38706–38709 (Dom. Rep., Los Tabucos, Tenares, 8.8 km N thence 0.5 km W of; 19.4324, -70.3525), ANSP 38703–38705 (Dom. Rep., Salcedo, Tenares, 23.2 km N, thence 4.5 km W of [= 0.2 km E Jaiba]; 19.5445, -70.3362), ANSP 38697–38702 (Dom. Rep., Hato Mayor, Sabana de la Mar, 7.8 km S of; 18.9883, -69.38955), ANSP 38692–38696 (Dom. Rep., Hato Mayor, Sabana de la Mar, 5.0 km [airline] SW of; 19.039683, -69.427367), ANSP 38667–38669 (Haiti, Ouest, Berry; 18.307945, -72.253894), ANSP 38685 (Haiti, Sud-Est, Morne D'Enfer; 18.330052, -72.37095), ANSP 38686–38688 (Haiti, Sud-Est, Morne D'Enfer, southwestern edge of plateau; 18.330052, -72.37095), ANSP 38673 (Haiti, Grand'Anse, Grande Cayemite (helipad-camp); 18.63316, -73.755241), ANSP 38674–38677 (Haiti, Grand'Anse, Grande Cayemite; 18.635615, -73.751749), ANSP 38684 (Haiti, Nippes, Morne Bois Pangnol; 18.418689, -73.775122), USNM 259989–259991 (Dom. Rep., Samana, Las Galeras, 1.8 km SW of; 19.2736, -69.2008), USNM 259992 (Dom. Rep., Samana, Las Galeras, 2.9 km S of; 19.2656, -69.1969), USNM 259993 (Dom. Rep., Samana, Las Galeras, 6.5 km S of; 19.2378, -69.2081), USNM 259995–259997 (Dom. Rep., Samana, Las Terrenas, 5.8 km SW of; 19.2778, -69.5531), USNM 328846 (Dom. Rep., Hato Mayor, Sabana de la Mar, 9.5 km W [airline] in Los Haitises; 19.05293, -69.47899), USNM 328848–328851 (Dom. Rep., Hato Mayor, El Valle, ca. 15 km W of, on road to Trepada Alta.; 18.9758, -69.5205), USNM 328852 (Haiti, Port Salut, 10.3 km NW of; 18.1419, -73.971). *Wetmorena agasepsoides*: ANSP 38713–38714 (Dom. Rep., Barahona, Canoa, 13.7 km due E [airline] of; 18.3477, -71.0314), ANSP 38715 (Dom. Rep., Pedernales, Los Arroyos, 14.5 km S of; 18.1541, -71.7585.), ANSP 38712 (Dom. Rep., Barahona, Canoa, 0.3 km S, 13.5 km E airline; 18.3448, -71.032), ANSP 38716 (Dom. Rep., Pedernales, Troudiye; 17.7548, -71.5284), ANSP 38710–38711 (Dom. Rep., Pedernales, Bucan Detwi; 17.73462, -71.50335), USNM 259974–259975 (Dom. Rep., Pedernales, Oviedo (Nuevo), 3.5 km WNW of; 17.8067, -71.4211). *Wetmorena haetiana haetiana*: ANSP 38719–38722 (Haiti, Ouest, Morne Cardineau; 18.346154, -72.182564), ANSP 38726 (Haiti, Ouest, Morne La Viste; 18.347367, 72.2835), ANSP 38744–5 (Haiti, Ouest, waterfall in Parc La Visite; 18.34014, -72.269826), ANSP 38717–38718 (Haiti, Ouest, Berry; 18.307945, -72.253894), ANSP 38723–38725 (Haiti, Sud-Est, Morne D'Enfer, southwestern edge of plateau; 18.330052, -72.37095), ANSP 38727–38742 (Haiti, Sud-Est, Pic La Selle; 18.32887, -72.021842), ANSP 38743 (Haiti, Ouest, Southeast of Pic La Selle; 18.332253, -71.91447). *Wetmorena haetiana mylica*: USNM 328854–328855, USNM 328857, USNM 328863, USNM 328865, USNM 328871–328872, USNM 328875–328876, USNM 328878, USNM 328881 (Dom. Rep., Barahona, Cabral, 15.3 km S and 6.7 km E [road] of; 18.1094, -71.2292). *Wetmorena haetiana surda*: ANSP 38748–38752 (Dom. Rep., Independencia, Puerto Escondido, 23.9 km SE of; 18.21, -71.53), ANSP 38753–38754 (Dom. Rep., Independencia, Puerto Escondido, 29.7 km SE of; 18.2051, -71.5503), ANSP 38746–38747 (Dom. Rep., Independencia, Puerto Escondido; 18.2204, -71.5102). **Diploglossinae.** *Diploglossus delasagra*: USNM 3141, USNM 4157, USNM 12356, USNM 11809, USNM 36807–36810 (Cuba), USNM 26365 (Cuba, Matanzas, Matanzas; 23.05, -81.58), USNM 27647 (Cuba, Pinar del Rio, Cabanas, Ing. Varila; 22.6167, -83.35), USNM 54405 (Cuba, Rio Honda), USNM 58170 (Cuba, Pinar del Rio; 22.4175, -83.6981), USNM 75840 (Cuba; Senado; 21.55, -77.6), USNM 512237–512238 (Cuba, Pinar del Rio, San Vicente, 4.0 km NW of, at north base of Sierra de San Vicente; 22.7088, -83.7442). *Diploglossus fasciatus*: MCZ R-154206 (Brazil, Juquia, São Paulo; -24.31667, -47.63333), MCZ R-17222 (Brazil, Leopodima, Espiritu Santo; -20.1, -40.53333), MCZ R-17223 (Brazil, Santos Praia do Juaruja), MCZ R-20685 (Brazil, São Paulo, Santos; -23.95, -46.33333). *Diploglossus lessonae*: USNM 115959 (Brazil, Ceara), USNM 209641 (Brazil, Pernambuco, EXU; -7.52, -39.72), USNM 209642 (Brazil, Pernambuco, Fazenda Cantarino, 10 km NE of, EXU; -7.45273, -39.6526). *Diploglossus millepunctatus*: MCZ R-27119 (Colombia, Malepo Island; 4.002226, -81.607201). *Diploglossus monotropis*: USNM 20609 (Ecuador, Esmeraldas, Plaza de Oro, Santiago River), USNM 22451 (Ecuador), USNM 24497 (Panama, Darién, Atlantic (east) side of Isthmus of Darien), USNM 30593 (Costa Rica), USNM 32173 (unknown), USNM 73302 (Colombia, Chocó, San Juan River), USNM 150091 (Panama, San Blas, Armila, Quebrada Venado), USNM 151507 (Colombia, Chocó, El Valle; 6.1, -77.43), USNM 153969 (Colombia, Antioquia, Chigorodó, near Turbo; 7.67, -76.68), USNM 196935 (Ecuador, Guayas, Hacienda Coffea Robusta, bank of Río Macu; -1.60417, -79.8678), USNM 196936 (Ecuador, Esmeraldas, San Lorenzo; 1.2883, -78.8369), USNM 285425 (Ecuador, Los Rios Province, Santo Domingo de los Colorados, 47 km S of, Centro Cientifico Río Palenque; -0.5917, -79.3611), USNM 524935–6 (Ecuador, Esmeraldas, San Lorenzo; 1.2883, -78.8369). *Diploglossus montisserrati*: MCZ R-76924 (Montserrat, Woodlands Spring; 16.74, -62.216667). *Diploglossus nigropunctatus*: MCZ R-42563 (Cuba, Oriente, Cuchillo de Guajimero; 20.6167, -75.0667), USNM 512239 (Cuba, Guantánamo, La Tagua, 5.4 km WSW of; 20.348, -75.2311), USNM 512240 (Cuba, Guantanamo, San Luis de Potosi, 1 km SW of), USNM 512241–512242 (Cuba, Guantánamo, Los Calderos, 4.7 km N of; 20.1592, -74.5833). *Diploglossus pleii*: ANSP 38555 (United States, Puerto Rico, Florida; 18.3628, -66.5578), ANSP 38556–38557 (United States, Puerto Rico, Reserva Forestal, Rio Abajo [8 km airline SSE Arecibo]; 18.4000, -66.6913), USNM 221102–221103 (United States, Puerto Rico, Trujillo Alto, ca. 5.5 km [airline] SSW of, west side of Lago Carraizo, km 6.3–6.4 on PR Route 175), USNM 25498, USNM 25634 (United States, Puerto Rico, Lares; 18.2967, -66.8775), USNM 25528 (United States, Puerto Rico, Adjuntas; 18.1647, -66.7225), USNM 27066 (United States, Puerto Rico, Catalina Plantation), USNM 326927–326929 (United States, Puerto Rico, Rio, 5.5 km N of [at junction of Routes 31 and 948]), USNM 326930 (United States, Puerto Rico, Maricao, ca. 5 km SE of [airline]; 18.173, -66.9443), USNM 326931 (United States, Puerto Rico, Sabana Grande, 6 km NW of [airline]; 18.1181, -67.0009). *Ophiodes enso:* CHFURG 3589 (Brazil, state of Rio Grande do Sul, municipality of Pelotas, Patos Lagoon estuary, Laranjal Beach; -31.7666, -52.2166). *Ophiodes striatus*: USNM 98609–98612 (Brazil, Rio de Janeiro, Nova Friburgo; -22.2667, -42.5333), USNM 207677 (Brazil, Rio de Janeiro, Petropolis, on road from Petropolis to Teresopolis, near km 7; -22.5167, -43.1667). **Siderolamprinae.** *Mesoamericus bilobatus*: USNM 37757 (Costa Rica, Cartago Province, Cachi; 9.83, -83.8), USNM 297881 (Panama, Bocas del Toro Province, Isla Popa, Deer Island channel, 1 km SE of), USNM 347178 (Panama, Bocas del Toro Province, Isla Popa, south end of Isla Popa, 1 km E Sumwood Channel), USNM 348149 (Panama, Bocas del Toro Province, Isla Cristobal [= Isla San Cristobal], Bocatorito camp). *Siderolamprus bivittatus*: USNM 335050–2, 335054–5 (Honduras, Intibucá, La Esperanza, 18.1 km NW of; 14.4157, -88.302). *Siderolamprus enneagrammus*: USNM 113524–113525 (Mexico, Veracruz, Tequeyutepec), USNM 6342 (Mexico, Veracruz, Orizaba), USNM 6603 (Mexico, Veracruz, mountains of Orizaba). *Siderolamprus rozellae*: USNM 496640 (Belize, Stann Creek, at confluence of Cockscomb Branch and Mexican Branch, Pearce Camp, Cockscomb Basin Wildlife Sanctuary; 16.7736, -88.5325), USNM 113526 (Mexico, Chiapas, Palenque; 17.5083, 91.9917). *Siderolamprus scansorius*: USNM 335049 (Honduras, Yoro, La Fortuna, 2.5 km [airline] NNE of, Cordillera Nombre de Dios; 15.43, -87.3).