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Phylogenomic data resolve the historical biogeography and ecomorphs of Neotropical forest lizards (Squamata, Diploglossidae)

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ABSTRACT

Few studies have been conducted on the biogeography and phylogenetic relationships of Neotropical forest lizards (Diploglossidae) because of incomplete taxon sampling, conflicting datasets, and low statistical support at phylogenetic nodes. Here, we enhance a recent nine-gene dataset with a genomic dataset of 3,232 loci and 642,775 aligned base pairs. The resulting phylogeny includes 30 diploglossid species, 10 of the 11 genera, and the three subfamilies. It shows significant support for all supra-specific taxa in either maximum likelihood or Bayesian analyses or both. With this well-supported phylogeny, we further investigate the historical biogeography of the group and how diploglossids reached the Caribbean islands. Our analyses indicate that Antillean diploglossid lizards originated from at least two overwater dispersals from South America. Our tests for the strength of convergent evolution between morphologically similar taxa support the recognition of a soil and a tree ecomorph. In addition, we propose grass, ground, rock, and swamp ecomorphs for species in this family based on ecological and morphological data and analyses.

1. Introduction

The islands of the Caribbean provide an ideal location to study evolutionary hypotheses because of their proximity to the mainland, allowing for colonization events to take place, while sufficiently isolated to preserve an endemic biota (Ricklefs and Bermingham, 2008; Shapiro et al., 2022). Reptiles and amphibians demonstrate high levels of endemism, with more than 1,000 species occurring in this region (Hedges et al., 2019). However, anthropogenic pressures resulting in habitat loss and degradation threaten species in this region leading to the loss of undescribed and unstudied species (Hedges et al., 2018).

The proximity of the Caribbean islands to the mainland raises questions pertaining to the origins of Caribbean taxa. Three theories have been proposed to explain the arrival of species to Caribbean islands: vicariance of a proto-Antillean land mass 70–100 Mya, dispersal over water, and dispersal over a dry land bridge from South America ~34 Mya. According to the vicariance theory, North and South America had a dry-land connection and shared biota 70–100 Mya, which broke apart and remained above water as the Caribbean plate drifted eastward, forming the present-day Antillean islands (Rosen, 1975). However, neither geological nor biological evidence supports this theory (Williams, 1989; Hedges et al., 1992; Hedges, 1996a, 2001, 2006; Iturralde-Vinent, 2006; Ali, 2012). The theory invoking a land bridge, "GAARlandia" (Iturralde-Vinent and MacPhee, 1999), has grown in support over the years despite a lack of geological evidence (Hedges, 2001, 2006; Ali, 2012). New geological evidence indicates that it did not exist (Ali and Hedges, 2021; Garrocq et al., 2021) and, moreover, an analysis of the timing of terrestrial vertebrate colonization does not support an unusual influx of clade arrivals at ~34 Ma (Ali and Hedges, 2021). Most lines of evidence including ocean current patterns, divergence time estimates, paleogeography, phylogenies, and taxonomy indicate that overwater dispersal was the major mechanism for the origin and spread of terrestrial vertebrates in the Caribbean (Hedges, 2006; Ali and Hedges, 2021). These lines of evidence also have indicated a South American point of origin for most groups, consistent with the direction of ocean currents (Hedges, 1996a, 1996b, 2001, 2006; Reynolds et al., 2013; Tucker et al., 2017). Studies that establish the historical biogeography of Caribbean taxa are important as they provide a framework to further investigate the geological and evolutionary processes that have promoted diversification and adaptive radiation in the region.

A highly supported genetic phylogeny is critical to understanding the historical biogeography of different groups on Caribbean islands. Diploglossidae is a lizard family of 55 species distributed throughout the

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Neotropics where it has radiated extensively on Caribbean islands. Until recently it was one of the most poorly known families of reptiles in the Western Hemisphere, but a nine-gene molecular phylogeny of 30 species (Schools and Hedges, 2021) laid the groundwork for a revised taxonomy at the species, genus, and subfamily levels. Because Diploglossidae was, until recently, an understudied family, little work has been attempted to investigate the biogeographic history and evolutionary processes that have influenced diversification and adaptive radiation in this group.

Here, we enhance the Schools and Hedges (2021) data set with genomic data for 27 species of Neotropical forest lizards. We targeted ultra-conserved elements (UCEs) to build our phylogenomic dataset as UCEs have the benefit of capturing orthologous loci from highly divergent taxa at varying time scales (Faircloth et al., 2012). The phylogenies we produced in our maximum likelihood (ML) and Bayesian analyses have nodes that are well supported at varying time scales within Diploglossidae. With these highly supported phylogenies, we reconstruct biogeographic history and evaluate the adaptive radiation and existence of distinct ecomorphs in this family. Adaptive radiations have occurred on Caribbean islands resulting in species adapted to various ecological niches (Carlquist, 1972). An ecomorph represents both a niche and the corresponding adaptations to that niche within a taxonomic group (Williams, 1972). Past studies have proposed ecomorphs for species of Caribbean anoles (Williams, 1972), landfrogs (Hedges, 1989a,b), geckolets (Thomas et al., 1992), and toads (Landestoy et al., 2018), and many subsequent studies have tested those proposals (e.g., see Losos, 2011 for a review). However, because of a lack of genetic and morphological data relevant to Diploglossidae, similar work was infeasible. The investigation of biogeographic history and adaptive radiations and their resulting ecomorphs in understudied groups, such as Diploglossidae, furthers our understanding of adaptation and biodiversity.

2. Materials and methods

2.1. Sampling and laboratory procedures

We included 30 of the 55 recognized species of Diploglossidae in our genetic dataset representing 10 of the 11 genera (Appendix A). We used *Pseudopus apodus* (Anguidae) as an outgroup because of its close relationship to Diploglossidae, as confirmed by other molecular studies (Vidal et al., 2012; Wiens et al., 2012; Pyron et al., 2013). We derived samples from frozen or ethanol-preserved tissues using standard protocols for extracting genomic DNA (Qiagen, Massachusetts, USA). For degraded samples, we used phenol chloroform extractions following the Pacific Biosciences protocol (from https://www.pacb.com). Localities, Genbank accession numbers, and museum numbers (if applicable) for all sequences are in Appendix A.

We built libraries for genomic (UCE) sequencing with the Lotus™ DNA Library Prep Kit using the xGen™ Stubby Adapter and UDI Primers Pairs (from https://www.idtdna.com). The UDI Primers Pairs assign unique primer combinations to each sample, allowing us to pool samples for sequencing. We followed the Lotus™ DNA Library Prep Kit protocol with several modifications. The first modification was that our Enzymatic Prep program was as follows: 4° (hold), 32° (10 min), 65° (40 min), 4° (hold). For our final PCR, our program was as follows: 98° (30 s), 7 cycles of [98° (10 s), 60° (30 s), 68° (one minute)], 4° (hold). In place of AMPure XP beads for cleaning steps, we used our own homebrew beads, prepared according to the Jolivet and Foley (2015) protocol (from https://ludmercentre.ca/). Prior to use, we tested our homebrew bead mix at different ratios to ensure that we were selecting for DNA fragments that were 300–500 basepairs in length. We verified fragment length using gel electrophoresis. Upon library completion, we ran each sample through an Agilent 2100 Bioanalyzer to verify size range and quantity of each library. After building the libraries, we used the Arbor Biosciences myBaits tetrapod 5Kv1 probe kit (from https://www.ultraconserved.org). This probe kit uses 5,472 unique probes to target 5,060 UCEs (with several probes targeting the same locus). During this stage, we used 65° as the hybridization temperature and the wash temperature. We performed two rounds of sequencing on an Illumina® NovaSeq SP200 cycle v1.5 flow cell machine at the Center for Applied Genomics at the Children's Hospital of Philadelphia (CHOP) (Philadelphia, Pennsylvania, USA; https://www.chop.edu/). To build a comprehensive phylogeny we incorporated the nine-gene dataset of Schools and Hedges (2021) (Appendix A).

2.2. Phylogenetic analyses

Raw sequences were demultiplexed and converted to FASTQ format through Base Space (https://basespace.illumina.com/). FASTQ files were submitted to GenBank (BioProject PRJNA769422). We checked the quality of our reads, including the number of single-end reads, average length, and raw coverage with BaseSpace FASTQC (https://basespace.illumina.com/apps/). We used PHYLUCE v1.7.0 (Faircloth, 2016) to process and assemble UCE data, generate contigs, and align loci. First, we trimmed the reads for adapter contamination with ILLUMIPROCESSOR v2.0.7 (Faircloth, 2013). Then, we assembled the trimmed reads *de novo* into contigs using VELVET v1.2.10 (Zerbino and Birney, 2008). Following assembly, we identified and extracted UCEs with LASTZ v1.02.00 (Harris, 2007). We aligned UCE contigs with MAFFT v7.130 (Katoh and Standley, 2013) and conducted both internal and external trimming using GBLOCKS v0.91b (Talavera and Castresana, 2007). The resulting aligned data matrix contained data from 3,232 loci and had 642,775 aligned base pairs. From this alignment, we generated data matrices requiring loci to have completeness from at least 0, 50, 75, 85, and 95% of taxa. For each of these matrices, we performed a phylogenetic analysis using IQ-tree v2.1.2 (Minh et al., 2020) and assessed branch support with 2000 ultrafast bootstrap replicates. We went forward in our analyses using the 85% matrix because increasing the data matrix from 85% to 95% completeness resulted in a large decrease in UCEs from 192 to 47 (57,720 bp to 22,857 bp) and produced phylogenies with considerably lower bootstrap values, likely because of the decrease in data. Phylogenies that we produced using data matrices below 85% contained topologies that are not supported by any other genetic or morphological data, i.e. *Caribicus* as the sister group of *Sauresia* and *Wetmorena*. We concatenated the 85% matrix with an additional nine-gene dataset that included both nuclear and mitochondrial genes. The final alignment was 64,669 base pairs in length.

We used the Bayesian Information Criterion (BIC) as implemented in ModelFinder (Kalyaanamoorthy et al., 2017) to determine an appropriate partitioning scheme and models of evolution for further analyses. We generated our phylogeny using IQ-tree v2.1.2 (Minh et al., 2020) and assessed branch support with 2000 ultrafast bootstrap replicates. ModelFinder identified the GTR + F + I + G4 model for the partition that included the nine-gene dataset, and a TVM + F + I + G4 model for the partition including our UCE data. We re-ran ModelFinder on our partitioned dataset to identify a model of sequence evolution that could be implemented in MrBayes. Based on those results, 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).

With our partitioned ML tree, we generated a timetree using RelTime (Tamura et al. 2012), as this program outperforms many other dating methods while using less computational power (Barba-Montoya et al., 2021; Kumar, 2022). As calibrations, we used a bounded uniform distribution with the 95% confidence intervals from internal nodes as maximum and minimums from the secondary calibrations (calibrations derived from other molecular dating studies) used in Schools and Hedges (2021). For this analysis we used a local clock type along with a GTR + Γ + I model.

2.3. Ancestral area estimation

We reconstructed historical biogeography with BioGeoBEARS (Matzke, 2013) using our timetree. For this analysis we pruned the outgroup of our phylogeny using the drop.tip function from R package ape (Paradis and Schliep, 2019). We then assigned species to one of the following eight regions (see Fig. 2): Cayman Brac, Cuba, Hispaniola, Jamaica, Middle America, Navassa Island, Puerto Rico, and South America based on their ranges (Schools and Hedges, 2021). We limited the maximum number of ancestral areas at each node to two. We tested six different models that have previously been used with BioGeoBEARS to investigate the biogeography of other Caribbean lizard groups (Tucker et al., 2017). These models included: (1) a Relaxed model, using only our phylogeny and the geographic distributions of the species, (2) a Relaxed + Distance model, including the distance between areas in our Relaxed model, (3) a Relaxed + Areas Adjacent model, including which areas are adjacent to one another in our Relaxed model, (4) a Relaxed + Distance + Areas Adjacent model, including the distance between areas and which areas are adjacent in our Relaxed model, (5) a Constrained model allowing dispersal in the direction of the ocean currents (North and West), and (6) a Half-constrained model allowing dispersal against the current patterns at half the probability of with the current patterns. Distances between regions were measured using Free Map Tools (https://www.freemaptools.com/). In our distance matrix, we divided all values by the shortest distance at the recommendation of the program.

Previously, BioGeoBEARS has received criticism as a model selection tool, particularly for the comparison of the DEC and the DEC + J models (Ree and Sanmartín, 2018). More recent evidence disproves this claim and shows that BioGeoBEARS is valid in comparing these two models (Klaus and Matzke, 2020; Matzke, 2021). In light of this, we ran the three standard biogeographical models in BioGeoBears (DEC, DIVALIKE, BAYAREALIKE) both with and without the + J parameter under the six different dispersal constraints (see above).

2.4. Ecomorph definition

Not surprisingly, all diploglossid species have body plans that intuitively correspond to the ecological niche that they occupy (Table 1). Based on this, we tested to see if there was a significant association between habitat use and morphology for groups of diploglossid lizards that occupy various niches. For our trait data, we used two morphological trait axes. We calculated these using the means of six traits (longest toe lamella count, ear width, upper arm length, forearm length, hand length, and eye length). We transformed these traits using log-shaped ratios before conducting a phylogenetic principal components analysis (pPCA) and retained the residuals of the first two axes. Species used in convergence analyses, the number of specimens per species, and the principal component scores (PC1 − PC2) are in Table S2. These values were then plotted in a phylomorphospace using the phylomorphospace function in the R package phytools (Revell, 2012) (Fig. S1–S2). The number of individuals differs between traits scored via counts (longest toe lamella count) versus measurements (ear height, ear width, upper arm length, forearm length, hand length, and eye length) as we only used individuals that were within 25% of the largest individual of that species for body proportion measurements to avoid bias from allometric growth differences (Wiens et al., 2006).

For all four ecomorphs represented in our phylogeny, we conducted a phylogenetic MANOVA to test for significant variation in habitat use along our two PCs. We did this using our RelTime tree and the aov.phylo function from the R package geiger (Pennell et al., 2014) which we ran for 1000 simulations and analyzed using Wilks' λ. We regarded results with *p*-values of ≤0.05 as significant. Following the MANOVA, we analyzed differences for the two different PCs using phylogenetic ANOVAs. This was also done using the aov.phylo function, run for 1000 simulations with *p*-values of ≤0.05 considered significant.

We then conducted additional tests on the strength and magnitude of convergent evolution for the soil and tree ecomorphs using the trait data from our earlier analyses, as these are the only two putative ecomorphs that have evolved more than once. For convergent ecomorphs, we defined two groups of convergent species represented in our tree based on the ecological traits and morphology discussed earlier (tree and soil groups) (Table 1). *Panolopus costatus* is not a monophyletic species. Because of this, we only designated *Panolopus c. costatus, Panolopus c. nesobous,* and *Panolopus c. oreistes* (as they are monophyletic with *Panolopus c. costatus* (Fig. 1)) as members of our tree ecomorph. After defining these convergent groups, we then estimated the degree of convergence between the convergent taxa using four distance-based C-metrics and our PC axes, in the R package CONVEVOL (Stayton, 2015). For all four metrics, higher C values indicate stronger convergence. These values represent: the proportion of phenotypic distance between two lineages shortened by subsequent evolution (C1), the proportion of convergent evolution to total evolution (C2), and standardized versions of the C2 proportion (C3 and C4). C3 measures the proportion of convergent evolution to total evolution in the clade of convergent taxa while C4 measures the proportion between C2 and the total evolution in the phylogeny. We calculated the four C metrics with 1,000 simulations of evolution using our RelTime tree. We treated results of these tests with a *p*-value of ≤0.05 as significant. Significant results imply that the observed C values were greater than what we would expect by chance. We also tested C5, a frequency-based measure of convergence, using 1,000 simulations of evolution. C5 counts the number of times that a suspected convergent lineage has invaded the convergent area of

Table 1
List of ecomorphs, species in each ecomorph, and the morphological traits that are characteristic of each ecomorph.

Ecomorph	Species	Traits
Grass	*Ophiodes enso, Ophiodes fragilis, Ophiodes intermedius, Ophiodes luciae, Ophiodes striatus, Ophiodes vertebralis*	No forelimbs, no ears, vestigial hindlimbs
Ground	*Caribicus anelpistus, Caribicus darlingtoni, Caribicus warreni, Celestus barbouri, Celestus crusculus, Celestus hewardii, Celestus macrotus, Celestus microblepharis, Celestus molesworthi, Comptus badius, Comptus maculatus, Diploglossus fasciatus, Diploglossus lessonae, Diploglossus microlepis, Diploglossus monotropis, Diploglossus montisserrati, Mesoamericus bilobatus, Panolopus curtissi, Panolopus marcanoi, Siderolamprus bivittatus, Siderolamprus enneagrammus, Siderolamprus legnotus, Siderolamprus orobius, Siderolamprus owenii*	Medium length limbs, medium length digits, medium lamellae counts
Rock	*Diploglossus millepunctatus*	Spotted pattern
Soil	*Diploglossus delasagra, Diploglossus garridoi, Diploglossus nigropunctuatus, Diploglossus pleii, Sauresia sepsoides, Wetmorena agasepsoides, Wetmorena haetiana*	Reduced limbs, reduced digits, reduced number of digits (sometimes), reduced ears, lack of ears (sometimes), low lamellae counts
Swamp	*Celestus macrolepis, Celestus occiduus*	Laterally compressed tail
Tree	*Advenus montisilvestris, Celestus duquesneyi, Celestus fowleri, Celestus striatus, Comptus stenurus, Panolopus costatus, Siderolamprus adercus, Siderolamprus atitlanensis, Siderolamprus cyanochloris, Siderolamprus hylaius, Siderolamprus ingridae, Siderolamprus laf, Siderolamprus montanus, Siderolamprus rozellae, Siderolamprus scansorius*	Long limbs, long digits, high lamellae counts

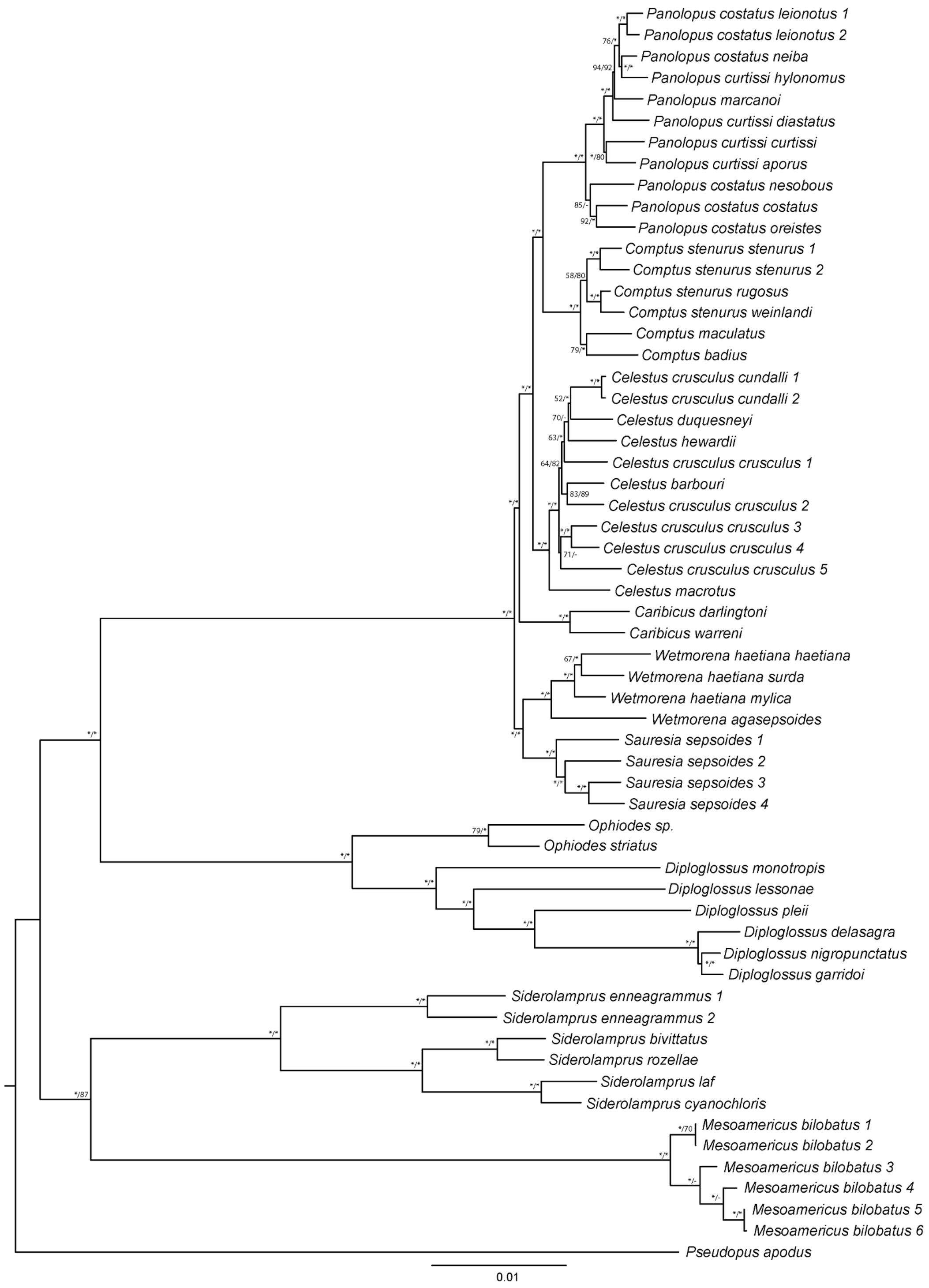

Fig. 1. A maximum likelihood tree of diploglossid lizards (59 individuals) based on 192 ultraconserved elements, concatenated with a previously-published nine-gene dataset of four mitochondrial genes (CytB, ND2,12S rRNA, and 16S rRNA) and five nuclear genes (AMEL, BDNF, PLPR, RAG1, and ZFP36) from Schools and Hedges (2021). A scale bar indicates 1% 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 the anguid lizard *Pseudopus apodus.*

morphospace. Because the tree ecomorph evolved more than twice, we calculated and averaged the C1–C4 metrics for all the pairs of the independent lineages (Table 2) (Stayton, 2015).

To estimate the strength of convergence, we employed the Wheatsheaf Index, implemented through the R package WINDEX (Arbuckle et al., 2014; Arbuckle and Minter, 2015). This index assesses the degree of similarity of focal (convergent) species to each other, and to non-convergent species, while also correcting for phylogenetic relatedness. Higher values of this index indicate stronger levels of convergence. As this analysis requires an ultrametric tree, we used our RelTime tree along with our two PC axes and 2,000 bootstrap replications to calculate the Wheatsheaf Index and 95% confidence intervals. We regarded results with p-values of ≤0.05 as significant.

3. Results

3.1. Phylogenomic analyses for Diploglossidae

Our molecular phylogeny of 30 diploglossid species includes representatives of all but one of the 11 diploglossid genera and all three subfamilies in the family (Fig. 1). All three subfamilies had maximum likelihood support values ≥95%. In Bayesian analyses, two had Bayesian

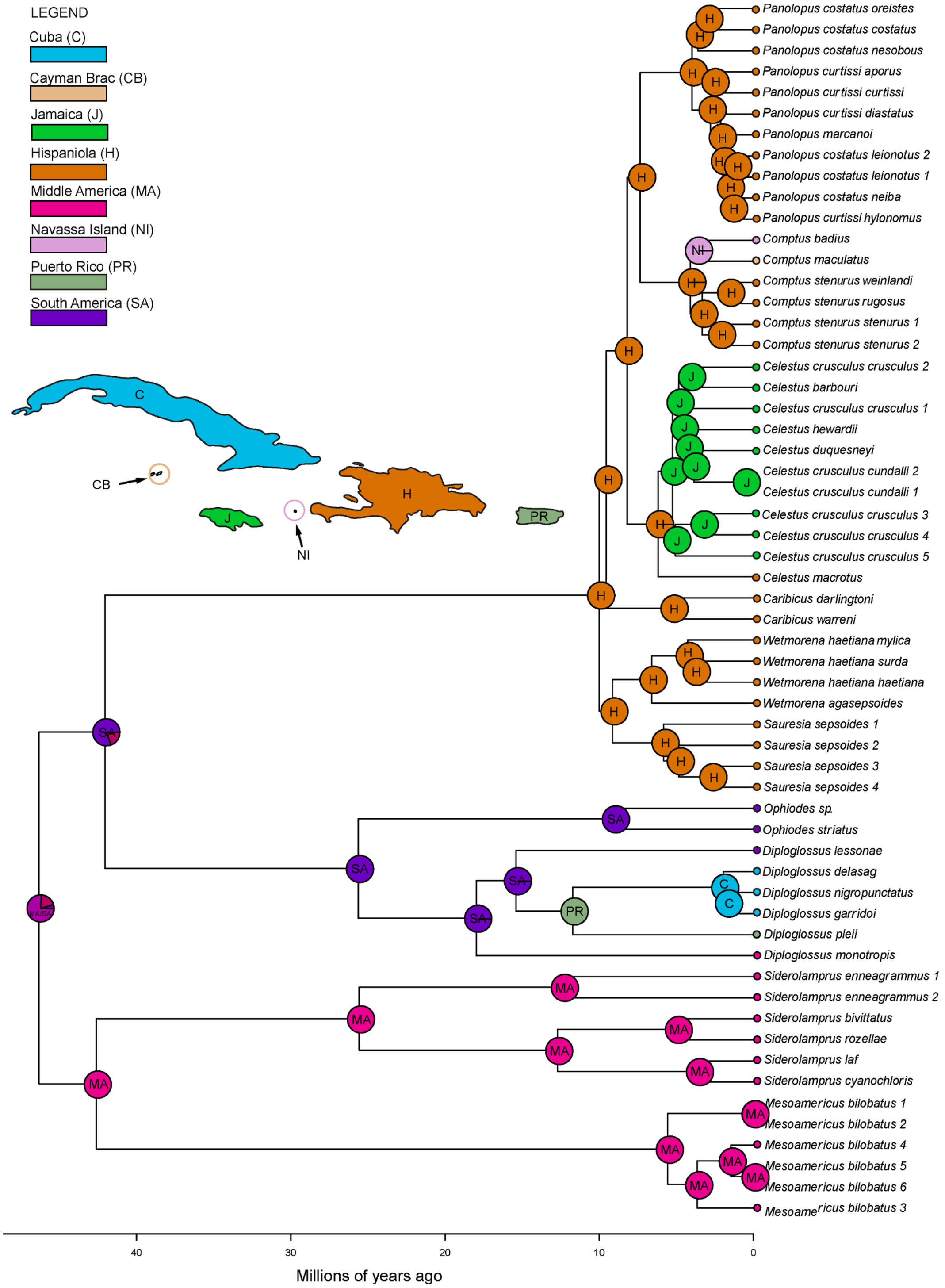

Fig. 2. Ancestral area reconstruction for diploglossid lizards under the DIVALIKE + J model, in BIOGEOBEARS with dispersal restricted to North and West based on ocean currents. The phylogeny shows estimated ancestral areas and their respective probabilities at each internal node. The center of each node displays the most likely states. A map of the Caribbean islands used in the analysis is included for reference.

support values ≥95% while Siderolamprinae had a support value of 87%. Of the 10 genera present in our analyses, all had Bayesian support values ≥95%. In ML analyses, nine had support values ≥95%, with *Ophiodes* having a support value of 79%. The low value in the latter could be explained by the presence of only one gene in one of the two representatives of that genus sampled. The genus is otherwise unquestionably monophyletic based on morphology.

3.2. Ancestral area estimation

The most likely model was the Constrained + Distance + Areas Adjacent model under the DIVALIKE + J scenario (AICc_wt = 0.711) (Table 3). In all six models, the DIVALIKE + J scenario was the most likely (Table 3). According to this model, major dispersal events include: (a) dispersal from South America to Hispaniola, giving rise to the Caribbean members of Celestinae, (b) dispersal from South America to Puerto Rico, giving rise to *Diploglossus pleii*, (c) dispersal from Puerto

Table 2
CONVEVOL and WHEATSHEAF results. The *p*-values are shown in parentheses under their respective C value, unless otherwise labeled.

Convergent Taxa	Ecomorph	C1	C2	C3	C4	C5
Diploglossus delasagra, D. nigropunctatus, D. pleii, Sauresia sepsoides, Wetmorena agasepsoides, W. haetiana haetiana, W. haetiana mylica, W. haetiana surda	soil	0.308	0.364	0.152	0.0163	12
		(0.0370)	(0.000)	(0.0370)	(0.0579)	(0.0140)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		0.848	0.799	0.938	0.493	
Celestus duquesneyi, Comptus stenurus stenurus, Panolopus costatus costatus, Panolopus costatus oreistes, S. laf, S. rozellae	tree	0.242	0.161	0.114	0.00720	10
		(0.290)	(0.299)	(0.209)	(0.495)	(0.0668)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		0.788	0.698	2.07	0.923	
Celestus duquesneyi, Comptus stenurus	tree	0.233	0.141	0.0964	0.0063	5
		(0.165)	(0.220)	(0.263)	(0.562)	(0.141)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		4.87	4.71	5.58	0.000	
Celestus duquesneyi, Panolopus costatus costatus, Panolopus, costatus nesobous, Panolopus costatus oreistes	tree	0.274	0.168	0.158	0.00753	4
		(0.103)	(0.0659)	(0.0450)	(0.344)	(0.0130)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		1.86	1.80	2.67	0.0725	
Celestus duquesneyi, Siderolamprus laf, Siderolamprus rozellae	tree	0.178	0.2	0.0775	0.00897	3
		(0.335)	(0.180)	(0.441)	(0.462)	(0.00700)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		0.788	0.698	2.07	0.928	
Comptus stenurus, Panolopus costatus costatus, Panolopus costatus nesobous, Panolopus costatus oreistes	tree	0.218	0.0657	0.12	0.00294	7
		(0.151)	(0.295)	(0.123)	(0.735)	(0.0970)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		1.83	1.77	1.95	0.00600	
Comptus stenurus, Sideolamprus laf, Siderolamprus rozellae	tree	0.233	0.141	0.0964	0.00631	6
		(0.159)	(0.202)	(0.241)	(0.553)	(0.138)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		1.62	1.43	2.19	0.181	
Panolopus costatus costatus, Panolopus costatus oreistes, Siderolamprus laf, Siderolamprus rozellae	tree	0.313	0.248	0.133	0.0111	5
		(0.829)	(0.829)	(0.139)	(0.313)	(0.00500)
		Wheatsheaf Index:	**Lower 95% CI:**	**Upper 95% CI:**	***p*-value:**	
		1.42	1.24	1.94	0.437	

Rico to Cuba, giving rise to *Diploglossus delasagra*, *D. garridoi*, and *D. nigropunctatus*, (d) dispersal from Hispaniola to Jamaica for all members of *Celestus* except *Celestus macrotus*, (e) dispersal from South America to Middle America, giving rise to *Diploglossus monotropis*, (f) dispersal from Hispaniola to Navassa Island, giving rise to *Comptus badius*, and (g) dispersal from Hispaniola to Cayman Brac, giving rise to *Comptus maculatus* (Fig. 2).

3.3. Ecomorph definition

3.3.1. Testing for an association between habitat use and morphology

Our phylogenetic MANOVA revealed that there was a significant association between morphology and habitat use in the four ecomorphs represented in our phylogeny (Wilks' $\lambda = 0.137$, df = 3, p-value = 0.002). Our post-hoc ANOVA analyses show that the first PC does not demonstrate a significant association between morphology and habitat use (PC1: $F_{3, 44} = 9.42$, p-value = 0.147). Our second PC does demonstrate a significant association between morphology and habitat use (PC2: $F_{3, 44} = 38.6$, p-value < 0.00799). PC1 loads strongly on limb measurements while PC2 loads strongly on eye length and lamellae counts.

3.3.2. Detecting significant levels of convergence

We calculated the C1–C5 metrics using groups identified as convergent based on ecological reports of the species and their morphology (tree and soil ecomorphs). We show the C1–C5 metrics based on PC1 and PC2 in Table 2. For our soil regime, all C values were significant except for C4 (p-value = 0.0579). The C1 and C3 values for this group indicate that evolution has closed 30.8% of the distance between these groups of taxa, with convergence accounting for 15.2% of the total evolution between the two lineages from the most recent common ancestor. For our tree regimes, none of the C values were significant. However, the pairwise comparisons shown in Table 2 indicate that the non-significance in the other C metrics may stem from the inclusion of a few lineages that do not converge with the others.

3.3.3. Testing the strength of convergence

Our soil group and the majority of our tree groups did not have a significant Wheatsheaf Index, suggesting the degree of similarity in these groups is not stronger than would be expected by chance (Table 2). The pairwise comparisons of *Celestus duquesneyi* and *Comptus stenurus* and *Comptus stenurus*, *Panolopus costatus costatus*, *Panolopus costatus nesobous*, and *Panolopus costatus oreistes* had significant Wheatsheaf Indices (p-value = 0.00 and p-value = 0.00294, respectively).

Table 3
Results comparing the six biogeographic models in BioGeoBEARS under the DEC, DEC + J, DIVALIKE, DIVALIKE + J, BAYAREALIKE, and BAYAREALIKE + J models.

Dispersal Model	BioGeoBEARS model	LnL	numparams	d	e	j	AICc	AICc_wt
1) Relaxed	DEC	-51.5958	2	2.06E-03	3.34E-03	0	107.4097	2.26E-06
	DEC + J	-38.6628	3	1.00E-12	1.00E-12	0.0102	83.77	3.07E-01
	DIVALIKE	-46.7375	2	2.14E-03	1.00E-12	0	97.69312	2.91E-04
	DIVALIKE + J	-37.8944	3	1.00E-12	1.00E-12	0.01026	82.23314	6.63E-01
	BAYAREALIKE	-64.064	2	2.71E-03	2.28E-02	0	132.3461	8.70E-12
	BAYAREALIKE + J	-40.9921	3	1.00E-07	1.00E-07	0.011629	88.42867	2.99E-02
		LnL	numparams	d	e	j	AICc	AICc_wt
2) Relaxed + Distance	DEC	-51.5958	2	2.06E-03	3.34E-03	0	107.4097	2.26E-06
	DEC + J	-38.6628	3	1.00E-12	1.00E-12	0.0102	83.77	3.07E-01
	DIVALIKE	-46.7375	2	2.14E-03	1.00E-12	0	97.69312	2.91E-04
	DIVALIKE + J	-37.8944	3	1.00E-12	1.00E-12	0.01026	82.23314	6.63E-01
	BAYAREALIKE	-64.064	2	2.71E-03	2.28E-02	0	132.3461	8.70E-12
	BAYAREALIKE + J	-40.9921	3	1.00E-07	1.00E-07	0.011629	88.42867	2.99E-02
3) Relaxed + Areas Adjacent	DEC	-55.7731	2	4.06E-03	7.79E-03	0	115.7644	5.53E-08
	DEC + J	-39.1532	3	1.00E-12	1.00E-12	0.010132	84.75089	3.00E-01
	DIVALIKE	-51.3428	2	4.13E-03	4.56E-03	0	106.9038	4.65E-06
	DIVALIKE + J	-38.3782	3	1.00E-12	1.00E-12	0.010298	83.20075	6.52E-01
	BAYAREALIKE	-67.0356	2	4.42E-03	2.49E-02	0	138.2893	7.11E-13
	BAYAREALIKE + J	-40.992	3	1.00E-07	1.00E-07	0.011628	88.42841	4.78E-02
		LnL	numparams	d	e	j	AICc	AICc_wt
4) Relaxed + Distance + Areas Adjacent	DEC	-55.7731	2	4.06E-03	7.79E-03	0	115.7644	5.53E-08
	DEC + J	-39.1532	3	1.00E-12	1.00E-12	0.010132	84.75089	3.00E-01
	DIVALIKE	-51.3428	2	4.13E-03	4.56E-03	0	106.9038	4.65E-06
	DIVALIKE + J	-38.3782	3	1.00E-12	1.00E-12	0.010298	83.20075	6.52E-01
	BAYAREALIKE	-67.0356	2	4.42E-03	2.49E-02	0	138.2893	7.11E-13
	BAYAREALIKE + J	-40.992	3	1.00E-07	1.00E-07	0.011628	88.42841	4.78E-02
		LnL	numparams	d	e	j	AICc	AICc_wt
5) Constrained + Distance + Areas Adjacent	DEC	-52.0618	2	1.05E-02	8.90E-03	0	108.3418	3.22E-09
	DEC + J	-32.7612	3	1.00E-12	1.00E-12	0.03523	71.9669	2.55E-01
	DIVALIKE	-47.6453	2	1.01E-02	6.45E-03	0	99.50871	2.67E-07
	DIVALIKE + J	-31.7364	3	1.00E-12	1.00E-12	0.034674	69.91724	7.11E-01
	BAYAREALIKE	-63.4375	2	1.14E-02	2.39E-02	0	131.0931	3.69E-14
	BAYAREALIKE + J	-34.7627	3	1.00E-07	1.00E-07	0.038961	75.96985	3.45E-02
		LnL	numparams	d	e	j	AICc	AICc_wt
6) Half constrained + Distance + Areas Adjacent	DEC	-54.4952	2	5.88E-03	8.03E-03	0	113.2086	4.10E-08
	DEC + J	-37.6692	3	1.00E-12	1.00E-12	0.01551	81.78276	2.73E-01
	DIVALIKE	-49.8784	2	5.86E-03	4.61E-03	0	103.9751	4.15E-06
	DIVALIKE + J	-36.7371	3	1.00E-12	1.00E-12	0.015546	79.91857	6.94E-01
	BAYAREALIKE	-65.4702	2	6.35E-03	2.47E-02	0	135.1586	7.02E-13
	BAYAREALIKE + J	-39.7957	3	1.00E-07	1.00E-07	0.017654	86.03593	3.26E-02

4. Discussion

4.1. *Diploglossid phylogeny*

Not unexpectedly, our updated phylogeny of diploglossid lizards from genomic data supports many of the same relationships as in our previous tree based on a smaller molecular data set (Schools and Hedges, 2021), but with increased nodal support. We report a comparison of nodal support between our new genomic phylogeny and the previously published nine-gene phylogeny for all subfamilies and genera in Table 4. In addition to those support values, the support value defining the sister relationship of *Sauresia* and *Wetmorena* was 81% in the ML analyses of the previous nine-gene dataset. This value increased to 99% in the ML analyses using our genomic data. In total, the average bootstrap value in ML analyses for the nine-gene phylogeny was 79.4% while in our genomic phylogeny the average is 92.6%. In Bayesian analyses, the average nodal support in the nine-gene tree was 94.2%, while this value in our genomic phylogeny is 94.6%. The one deep node that is still not highly supported in the ML tree, Siderolamprinae, may require increased species and gene sampling in the future, especially from taxa in Middle and South America, to resolve.

Table 4
Comparison of average nodal support of the nine-gene trees (Schools and Hedges 2021) and the tree using ultra-conserved elements (UCEs; this study).

Group	Nine-gene ML	UCEs ML	Nine-gene Bayesian	UCEs Bayesian
Subfamilies				
Celestinae	72.5	90.0	92.8	95.5
Diploglossinae	86.7	96.1	94.0	99.6
Siderolamprinae	97.5	98.9	97.9	87.7
Genera				
Caribicus	100	100	100	100
Celestus	60.0	80.0	83.2	88.4
Comptus	82.2	86.4	95.8	96
Diploglossus	86.0	98.8	91.6	99.4
Ophiodes	77.0	79.0	100	100
Panolopus	58.2	93.8	91.8	96.9
Mesoamericus	96.6	98.0	96.2	75.6
Sauresia	79.3	99.0	100	100
Siderolamprus	99.2	100	100	100
Wetmorena	98.3	89.0	100	100

The topology of the phylogeny produced from our genomic dataset shows several differences from our previous phylogeny of diploglossid lizards constructed using nine genes (Schools and Hedges, 2021). In the latter tree, the genera *Celestus* and *Panolopus* were sister groups, while our new phylogeny places *Comptus* and *Panolopus* as sister groups. In addition, the previous phylogeny had placed the genus *Caribicus* as the sister group to all other Caribbean celestines. Our new phylogeny indicates that, instead, the clade comprising genera *Sauresia* and *Wetmorena* is the sister group to other Caribbean celestines. As with the previous diploglossid phylogeny, our genomic phylogeny indicates that several species are not monophyletic, warranting the definition of new species in this family.

4.2. Ancestral area estimation

Previous studies that hypothesized about the historical biogeography of Caribbean diploglossids have relied on morphological characteristics (Savage and Lips, 1993; Strahm and Schwartz, 1977). Those characters supported different relationships than our genetic data. According to our analyses, a model that only allowed dispersal to the north and west (following the current patterns of the area) best explains the dispersal and colonization history of this family. This analysis, coupled with the recent divergence times for Caribbean diploglossid lizards, support the classical model that Caribbean colonization events in this family took place via dispersal on flotsam (Hedges et al., 1992; Hedges, 1996a; Schools and Hedges, 2021). While we did not include outgroups in our BioGeoBEARS analysis, all the groups that are close relatives of Diploglossidae (Anguinae, Gerrhonotinae, Anniellidae, Helodermatidae, and Xenosauridae) have members in Middle America. Because of these outgroup distributions, the last common ancestor of living diploglossids probably resided in Middle America, even though the node is shown as unresolved in Fig. 2.

When evaluating the results of our BioGeoBEARS analysis, the divergence times must be considered. The initial split between Siderolamprinae and Celestinae/Diploglossinae left the latter group in South America (Fig. 3). This split occurred 48.7–44.8 million years ago, Mya (midpoint, 46.8 Mya), during the Eocene. From South America, a dispersal to Hispaniola led to the Caribbean celestines, 44.1–10.3 Mya (midpoint, 27.2 Mya). A later dispersal from Hispaniola to Jamaica occurred 6.37–5.28 Mya (midpoint, 5.83 Mya) resulting in the members of *Celestus* that are distributed on Jamaica. Additional dispersals from Hispaniola to Navassa Island and to Cayman Brac (after 3.76 Mya) led to the current distributions of *Comptus badius* and *Comptus maculatus*, respectively.

Related to the dispersal of celestines to Caribbean islands is the phylogenetic position of *Advenus*, the only mainland celestine. Our molecular phylogeny does not include that rare taxon, known only from the holotype of the only species. It was placed in the subfamily based on morphology (Schools and Hedges, 2021). If it is the closest relative of all other celestine genera, it may represent the mainland stock of celestines that dispersed to Caribbean islands. Although the current geographic location of *Advenus*, at the intersection of Central America and South America, introduces some biogeographic ambiguity, distributions in the distant past, especially within a continent, are likely to have been much different. If, instead, *Advenus* is found to be nested within the celestine tree, it would represent a “reverse dispersal” from the Caribbean islands to the mainland, a pattern that is known in two other large Caribbean clades: landfrogs (Hedges, 1989b; Heinicke et al., 2018) and anoline lizards (Nicholson et al., 2005). Genetic data from *Advenus* are important to resolve these questions.

In Diploglossinae, an ancestor located in South America gave rise to the genus *Ophiodes* while a dispersal event to Middle America resulted in *Diploglossus monotropis* (after 17.0 Mya). Dispersal of a diploglossine from South America into the Caribbean occurred 14.9–11.5 Mya (midpoint, 13.2 Mya). Based on our results, which are supported by the direction of ocean currents today but similar to those in the past (Hedges 2006), this dispersal event was to Puerto Rico, leading to *Diploglossus pleii.* A later dispersal from Puerto Rico to Cuba (11.5–1.76 Mya, midpoint, 6.63 Mya) led to the Cuban diploglossines (*D. delasagra*, *D. garridoi*, and *D. nigropunctatus*). While not in our genetic tree, the species *Diploglossus montisserrati* represents another Caribbean member of *Diploglossus*. Fossils of a now extinct diploglossid that closely resembled *D. montisserrati* have also been discovered on Guadeloupe (Bochaton et al., 2016). Because of the proximity of Guadeloupe and Montserrat, in addition to the morphological similarities between the fossil remains and *D. montisserrati*, the same colonization event probably resulted in the Caribbean distribution of the two taxa. Genetic data are

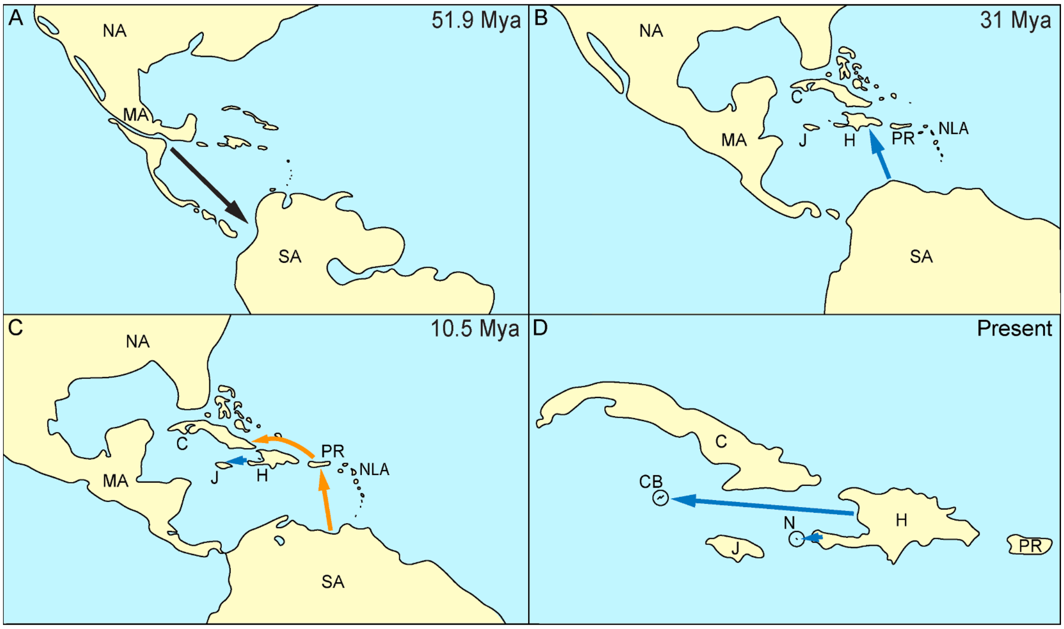

Fig. 3. Biogeographic model showing the origin of the South American and Caribbean clades of diploglossid lizards. Paleogeographic reconstructions were drawn from Scotese and Wright (2018). Arrows represent the midpoint of dispersal time ranges. The black arrow indicates the Celestinae + Diploglossinae dispersal event, the blue arrows indicate Celestinae dispersal events, and the orange arrows indicate Diploglossinae dispersal events. (A) Eocene, when a dispersal from Middle America to South America established Celestinae and Diploglossinae 48.7–44.8 Mya (46.8 Mya). (B) Oligocene, when a dispersal from northern South America to the Caribbean established the Caribbean celestines 44.1–10.3 Mya (27.2 Mya). (C) Miocene, when members of *Diploglossus* dispersed from Northern South America to Puerto Rico 14.9–11.5 Mya (13.2 Mya), from Puerto Rico to Cuba 11.5–1.76 Mya (6.63 Mya), and when Celestinae dispersed from Hispaniola to Jamaica 6.37–5.28 Mya (5.83 Mya). (D) Pliocene to Present, when recent dispersals from Hispaniola to Cayman Brac and Navassa Island (after 3.76 Mya) led to the current distribution of *Comptus maculatus* and *Comptus badius* (respectively). Landmasses are abbreviated as follows: Cuba (C), Cayman Brac (CB), Hispaniola (H), Jamaica (J), Middle America (MA), Navassa Island (N), Northern Lesser Antilles (NLA), Puerto Rico (PR), and South America (SA). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

needed to determine if this was the result of a second colonization event of *Diploglossus*, or if the distribution of these taxa is a result of the same colonization event that resulted in the Cuban and Puerto Rican members of *Diploglossus.* If this is the result of the same dispersal event, the Greater Antilles-Northern Lesser Antilles (GrANoLA) landmass may have been where *Diploglossus* first reached the Caribbean (Philippon et al., 2020). After this landmass separated, this would have led to the distribution of *Diploglossus montisserrati* and the fossil *Diploglossus* in the Northern Lesser Antilles and *Diploglossus pleii* on Puerto Rico.

4.3. Ecomorph definition

Similar to other adaptive radiations on Caribbean islands (Williams, 1972; Hedges, 1989a,b; Losos, 2011), diploglossid lizards have

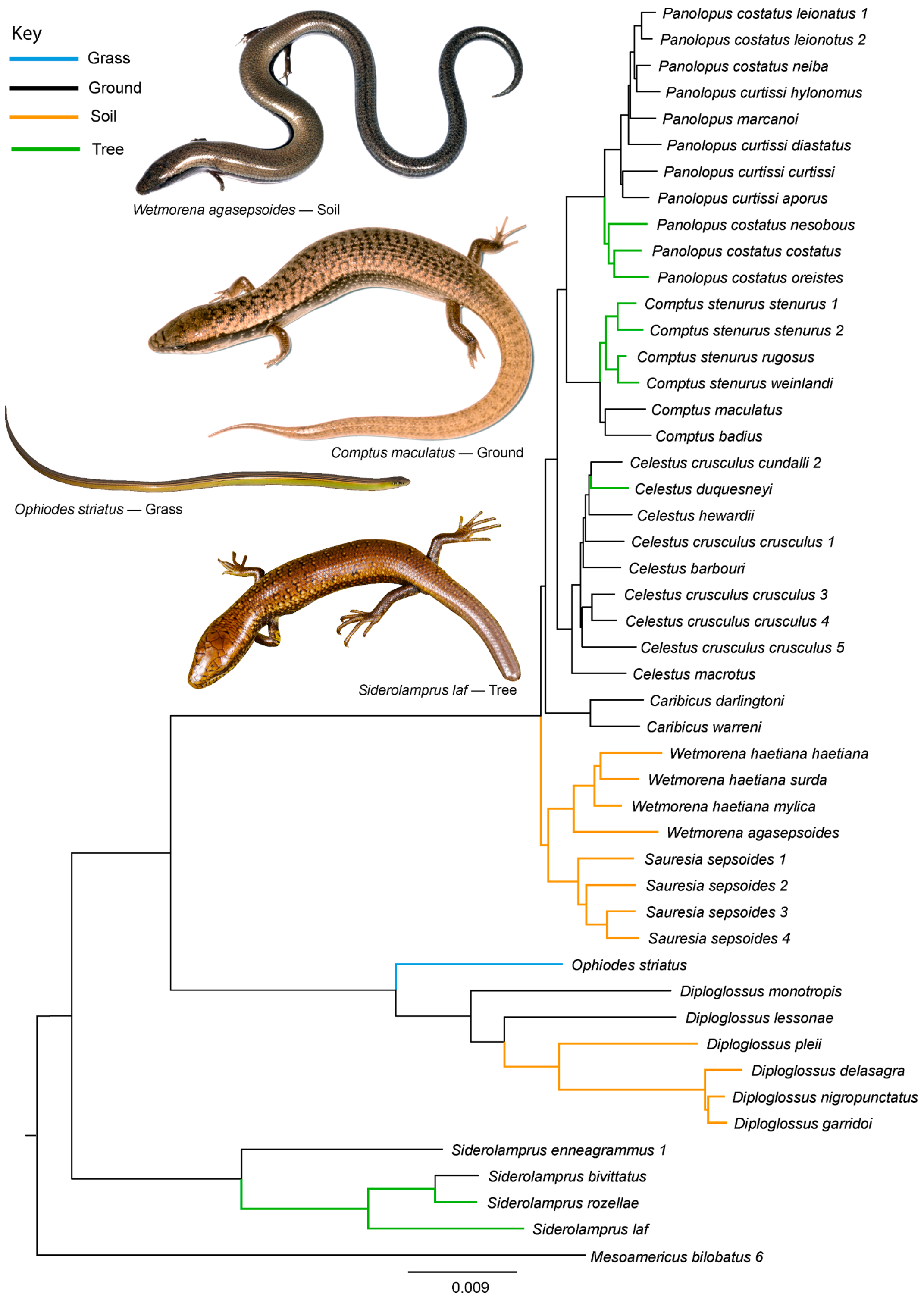

Fig. 4. The phylogeny used in our analyses of convergence with our proposed ecomorph CLASSES color coded. The images of diploglossid species represent four of the different ecomorphs (photographs of *Wetmorena agasepsoides* and *Comptus maculatus* by S.B.H.; that of *Ophiodes striatus* by Santiago Carreira; and that of *Siderolamprus laf* by Sebastian Lotzkat).

diversified and adapted to distinct ecological niches (Fig. 4). The soil and tree ecomorphs, each of which have convergent species, show that species have adapted to the same ecological niches in similar ways. Herein, we introduce and refine the names of the diploglossid ecomorphs to refer to their niches, as opposed to their behavior. We do this to be consistent with the general concept, and how it is applied to reptiles, specifically anoles (Williams, 1972; Losos, 2011). We use the term "ecomorph" whether or not it is associated with convergence (i.e., repeated, independently, in other species). Convergent representatives may be extinct or undiscovered, or may exist outside the family, and that should not bear on how we interpret the phenotypic association of a species and its ecological niche.

4.3.1. Convergent ecomorphs from our analyses

4.3.1.1. Soil ecomorph. The soil ecomorph that we define herein contains seven species of diploglossid lizards including the Hispaniolan species *Sauresia sepsoides*, *Wetmorena agasepsoides*, and *W. haetiana*, in addition to the Cuban and Puerto Rican species of *Diploglossus* (*D. delasagra*, *D. garridoi*, *D. nigropunctuatus*, and *D. pleii*). The traits of the 'soil ecomorph' include a reduction of external ear openings, limbs, and digits. A combination of these traits is found in the Hispaniolan species *Sauresia sepsoides*, *Wetmorena agasepsoides*, and *W. haetiana*. Similarly, the Caribbean diploglossids (*Diploglossus delasagra*, *D. garridoi*, *D. nigropunctatus,* and *D. pleii*) have greatly reduced limbs in comparison to most Neotropical forest lizard species. Furthermore, collectors have found many of these soil ecomorph species in rotten logs, underground, or while plowing (Cochran, 1927; Barbour and Shreve, 1937; Thomas, 1971; Thomas and Hedges, 1998). At times, they share habitat with members of the ground ecomorph, but even in those cases they tend to occupy areas that are moister and are more like soil (S.B.H., personal observations).

All species that we assigned to this ecomorph had genetic data available and were included in our statistical analyses. Although the Wheatsheaf index showed that the degree of similarity was not greater than would be expected by chance, this ecomorph had significant support in four of the five C metrics that we tested. Furthermore, the results from our MANOVA and second ANOVA tests demonstrate that there is an association between the morphology and habitat use of this ecomorph.

4.3.1.2. Tree ecomorph. The tree ecomorph that we define herein includes 15 species of diploglossid lizards, ten of which were included in our genetic analyses, however additional ecological reports warrant the assignment of additional species to this ecomorph. Long digits and high lamellae counts are traits that are associated with arboreality in other lizard species (Larson and Losos, 1996; Collins et al., 2013). These traits are exhibited by the Jamaican species *Celestus duquesneyi* and *Celestus fowleri* (Table S1), the latter of which is known exclusively from bromeliads (Schwartz, 1971). Furthermore, *C. duquesneyi*, which was included in our statistical analyses, may be a close relative of *C. fowleri* (Schwartz, 1971). It is possible that an arboreal nature is what allowed these two species to survive the introduction of the mongoose to the Caribbean islands in the 19th century, as the mongoose is not an adept climber (Pimentel, 1955). The same morphological traits recorded in the larger species, *Celestus striatus*, known only from a single nineteenth century specimen, led to the suggestion that it, also, was a tree-dwelling species (Schools and Hedges, 2021). Reports of large diploglossids observed in trees in the Cockpit Country of Jamaica (B. S. Wilson, personal communication), may correspond to either *C. fowleri* or *C. striatus*.

Similarly, the Hispaniolan species *Panolopus costatus* has been collected in trees (Schmidt, 1921) and has high lamellae counts relative to the other ecomorphs. High lamellae counts have also been recorded in *Comptus stenurus*, a species that was previously synonymized with *Panolopus costatus*. Several mainland species of *Siderolamprus* that share these arboreal traits have been collected from thatched roofs and tree trunks, indicating arboreal tendencies (Schmidt, 1933; Alvarez del Toro, 1982; Hidalgo, 1982; McCranie and Wilson, 1996; Lotzkat et al., 2016).

While not included in our analyses because of a lack of morphological and genetic data, we also place the Middle American species *Siderolamprus atitlanensis, S. cyanochloris, S. hyliaus, S. montanus, S. owenii,* and *S. scansorius* in the tree ecomorph based on ecological reports of them being arboreal or showing arboreal tendencies (Schmidt, 1933; Alvarez del Toro, 1982; Hidalgo, 1982; McCranie and Wilson, 1996). The only Middle American member of Celestinae, *Advenus montisilvestris*, was also collected from a tree trunk (Myers, 1973). This species also has high lamellae counts and long limbs, similar to other species in the tree ecomorph (Table S1).

Our convergence analyses included the Caribbean species *Panolopus costatus costatus*, *Panolopus costatus nesobus*, and *Panolopus costatus oreistes* (a monophyletic group) in the tree ecomorph and the results from our MANOVA and second ANOVA tests show that there is an association between their morphology and habitat use. However, other subspecies of *Panolopus costatus* are not a part of this monophyletic group, and future work should examine if the different subspecies of *P. costatus* should be placed in different ecomorphs. When testing the C metrics for our tree ecomorph, one pairwise comparisons yielded significant C values in a distance based (C3) metric of convergence, and three yielded C values in a frequency based (C5) metric of convergence. This suggest that convergence is present in this ecomorph, and two of our pairwise comparisons indicated that the level of convergence was greater than would be expected by chance.

4.3.2. Non-convergent ecomorphs from our analyses

4.3.2.1. Grass ecomorph. The traits of the 'grass ecomorph' resemble those of the soil ecomorph but are more extreme in nature. They are found in species of the snake-like genus *Ophiodes*, which lack external ear openings and forelimbs, in addition to having vestigial hind limbs. Members of this genus have been observed to live in grassy areas and "swim" through the grass (Barros and Teixeira, 2007; Cei, 1993). Previously, the genus *Ophiodes* was placed in a "large, long-tailed, grass swimmer" ecomorph (Wiens and Slingluff, 2001).

The results from our MANOVA and second ANOVA tests indicate that there is a significant relationship between habitat use and morphology for our ecomorph categories, further validating the assignment of this genus to an ecomorph.

4.3.2.2. Ground ecomorph. Most species of diploglossid lizards have the body type of a typical lizard and are ground-dwelling species, what we call here the 'ground ecomorph.' The traits of this ecomorph serve as a baseline for the how the traits of other ecomorphs differ (i.e. "reduced ears", "long limb", etc.). In total, there are 24 species that we classify as members of the ground ecomorph, including several for which genetic data were not available (Table 1). These species have a typical lizard body plan that is adapted to life on the ground, including robust limbs, limbs and digits of medium length, digital lamellae moderate in number, and they possess ear openings. While these species are not convergent in our phylogeny, the results from our MANOVA and second ANOVA tests demonstrate that there is an association between their morphology and habitat use. This indicates that they represent the organismal counterparts to their ecological niche, hence our classification of them as an ecomorph.

In future work, the ground ecomorph may be further subdivided. Several species that we classify as members of the ground ecomorph are reported to have been found in leaf litter. For example, the ecological habits of *Comptus badius*, endemic to Navassa Island, were described by Thomas (1966) and Powell (1999). Both authors found the species to be closely associated with leaf litter in dry forest. In particular, Powell noted that, "the most common encounter consisted of hearing a rustling in the litter, allowing one to locate an animal that would appear to 'swim' along, producing a 'wake' on the surface, and occasionally 'surfacing' to scan the vicinity. Frequently individuals would cover distances of as much as 15–20 m before slipping beneath rocks or into crevices." This type of locomotion, and occurrence in a dimly lit environment, might explain the reduced limbs and eye openings of the species. Similarly, *Celestus microblepharis* shows reduced limbs and eye openings. This Jamaican species is known only from the holotype collected in 1952 in a pile of coconut trash near the coast, bordering dry scrub forest (Underwood, 1959). Ecological accounts of the mainland species *Siderolamprus bivittatus* also report that the species has been captured actively foraging in leaf litter (Campbell and Camarillo, 1994). Similar reports exist for *Diploglossus monotropis*, *D. montisserrati*, and *Mesoamericus bilobatus* (Myers, 1973; Ogrodowczyk et al., 2006; Díaz-Ayala et al., 2015). Additional ecological and morphological data may help in the future to determine if these species represent a leaf litter ecomorph, distinct from the ground ecomorph.

We tentatively assign *Siderolamprus legnotus* and *S. owenii* to the ground ecomorph. Little is known of the ecology of *S. legnotus*, although previously it has been hypothesized to be a ground dweller because of its low lamellae counts (Savage et al., 2008). However, other species of *Siderolamprus* with similar lamellae counts have been identified as tree dwellers based on their ecology (Savage et al., 2008). Similarly, little is known about the ecology or the morphology of *Siderolamprus owenii*, and further studies are needed to identify the ecomorph to which it belongs.

4.3.3. Additional ecomorphs

4.3.3.1. Rock ecomorph. The species *Diploglossus millepunctatus* is the only member of what we call the 'rock ecomorph.' This species is endemic to Malpelo Island, which consists largely of exposed rock, where it stays close to rock crevices (Kiester, 1975). It is characterized by a spotted pattern, a feature that has been reported as being more pronounced in other rock-dwelling lizard species when compared to their relatives that have different ecologies (Bezy, 1967). While *D. millepunctatus* will occasionally enter the water as a means of escape, they spend the majority of their time on the rocks that make up Malpelo Island (Slevin, 1928). This species has a diet that includes insects, other invertebrates (including crabs), carrion, and Blue-faced Booby feces and vomitus (Kiester, 1975; Slevin, 1928). These food sources show its close tie to the rocky areas of Malpelo Island, hence its assignment to the rock ecomorph, although the specific morphological adaptations related to this ecomorph, other than its pattern, are unclear.

4.3.3.2. Swamp ecomorph. Two Jamaican species, *Celestus macrolepis* and *Celestus occiduus*, are the only members of the 'swamp ecomorph.' *Celestus macrolepis* was recently recognized as a valid species (Schools and Hedges, 2021) long after it had been synonymized with *Celestus occiduus* (Boulenger, 1885). Multiple ecological reports have tied both species to a swamp habitat (Sloane, 1725; Gosse, 1851; Cockerell, 1894). Crabs were also found in the stomach of *Celestus macrolepis* (incorrectly identified as *Celestus occiduus*) (Sloane, 1725). It is possible that the mammal-like molars of this species (as noted in Shaw, 1802) are an adaptation for eating hard invertebrates, an association noted in other species of lizards (Renesto and Dalla Vecchia, 2000). A laterally compressed tail was also reported in a subset of both *Celestus macrolepis* and *Celestus occiduus*, a trait that has been observed as an adaptation to an aquatic or semi-aquatic lifestyle in other lizards, such as marine iguanas (Bedford and Christian, 1996).

4.4. Conclusion

We presented a genomic phylogeny for Diploglossidae, a biogeographic hypothesis for how the family reached and radiated throughout the Caribbean islands, and evidence for the presence of ecomorphs in the family. Future studies with additional genetic data of species not included in our phylogeny may help to better resolve the deep node (Siderolamprinae) that was significantly supported in our likelihood analyses but not significantly supported (87%) in our Bayesian analyses. Similarly, additional genetic data could help to resolve the placement of *Advenus* and *Diploglossus montisserrati* to further clarify the dispersal events that led to the current distribution of diploglossids. Additional ecological and morphological data may also be able to further clarify the ecomorph assignments that we present.

Unfortunately, the introduction of the mongoose in the Caribbean islands in the late nineteenth century led to decimation of ground-dwelling reptiles, such as skinks and forest lizards (Hedges and Conn, 2012). Among those that may have disappeared are *Celestus macrolepis* and *Celestus occiduus*, the sole members of the swamp ecomorph, and *C. striatus*, a member of the tree ecomorph. No specimens of those three species have been found since the early- or mid-1800s. Other Caribbean members of the tree ecomorph, *C. duquesneyi* and *C. fowleri*, are rare, being known from seven and two specimens, respectively (GBIF 2021; Schwartz, 1971). For reasons such as this, studies similar to ours are critical in the face of declining biodiversity, particularly in biodiversity hotspots, such as the Caribbean islands.

Acronyms of museum collections

The Academy of Natural Sciences of Drexel University (ANSP), Centro Universitario de Riviera, Uruguay (CURC), Coleção Herpetológica da Universidade de Brasília, Brazil (CHUNB), Frozen tissue and voucher collection, S. Blair Hedges, Temple University, Philadelphia, Pennsylvania, USA (SBH), Museo Nacional de Historia Natural de Cuba, La Habana, Cuba (MNHNCU), National Museum of Natural History (USNM), Senckenberg Forschungsinstitut und Naturmuseum [alternatively Senckenberg Research Institute and Natural History Museum], Frankfurt am Main, Germany (SMF), University of California, Museum of Vertebrate Zoology, Berkeley (MVZ).

CRediT authorship contribution statement

Molly Schools: Conceptualization, Methodology, Formal analysis, Writing – original draft preparation. **Adrienne Kasprowicz:** Methodology, Writing – review & editing. **S. Blair Hedges:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Specimens and sequences used in the molecular analyses

In the following list we distinguish samples from a previously published nine-gene data set (Schools and Hedges, 2021), indicated with an asterisk (*), from newly sequenced samples for the genomic (UCE) data set reported here, indicated by a double asterisk (**). *Caribicus darlingtoni* (*: USNM 328806; Dom. Rep., La Vega Province, Constanza, 37 km SE of, via new road to San Jose de Ocoa; 18.7056, -70.5981; **: USNM 328807; Dom. Rep., La Vega Province, Constanza, 37 km SE of, via new road to San Jose de Ocoa; 18.7056, -70.5981), *Caribicus warreni* (*: Voucher not available, SBH 194521; Dom. Rep., Puerto Plata, presumably the region of Puerto Plata; **: ANSP 38501; Haiti, not available (pet trade)), *Celestus barbouri* (*: USNM 328153; Jamaica, Trelawny, Quick Step, vicinity of; **: ANSP 38503; Jamaica, Trelawny, Windsor, 0.5 km N of; 18.3579, -77.6482), *Celestus crusculus crusculus 1* (*: USNM 328169; Jamaica, St. Elizabeth, Knoxwood; **: USNM 328157; Jamaica, Westmoreland, Old Hope, 4.5 km W of, at Little Bay), *Celestus crusculus crusculus 2* (* and **: USNM 328158; Jamaica, Westmoreland, Old Hope, 7.0 km WSW of), *Celestus crusculus crusculus 3* (*: USNM 328154; Jamaica, Hanover, Content, 3.2 km SE of; **: USNM 328156, Jamaica, Westmoreland, Town Head, 5.3 km N of), *Celestus crusculus crusculus 4* (*: USNM 328174; Jamaica, St. Mary, Oracabessa, 6.2 km W of, **: USNM 328183; Jamaica, St. Mary, Port Maria, 6.4 km S of), *Celestus crusculus crusculus 5* (*: USNM 328160; Jamaica, Trelawny, Duncans, 0.3 km W of, at junction of Route A-1 with Silver Sands Road), *Celestus crusculus cundalli 1* (*: Voucher not available, SBH 274632; Jamaica, St. Thomas, Trinity Ville, 5.9 km W of by road), *Celestus crusculus cundalli 2* (* and **: USNM 328144; Jamaica, Portland, Section, 1.3 km WSW of, on road to Hardwar Gap), *Celestus duquesneyi* (* and **: Voucher not available, SBH 267952; Jamaica, St. Catherine, Hellshire Hills), *Celestus hewardii* (*: Voucher not available, SBH 267097; Jamaica, Manchester, Mandeville), *Celestus macrotus* (* and **: 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; **: SBH 194966; United States Caribbean, Navassa Island), *Comptus maculatus* (*: ANSP 38507; Cayman Islands, Cayman Brac, 0.7 km E Hawkesbill Bay on A7, ~10 km E West End, 1.7 km E Ashton Reid Drive; 19.7142, -79.7864; **: ANSP 38510; Cayman Islands, Cayman Brac, West End; 19.7192, -79.8263), *Comptus stenurus rugosus* (*: USNM 328830; Dom. Rep., Maria Trinidad Sanchez, Nagua, 4.0 km SE of; 19.3481, -69.8244; **: USNM 328832; Dom. Rep., Samana, Las Galeras, 6 km SSW of; 19.2433, -69.2053), *Comptus stenurus stenurus 1* (*: USNM 328836; Haiti, Grand'Anse, Marché Léon, 6.5–1.5 km S, 0.1–4.5 km E (airline) of, between Rampe des Lions and Bois Sec; 18.4805, -74.0782; **: USNM 328838; Haiti, Grand'Anse, Marché Léon, 6.5–1.5 km S, 0.1–4.5 km E (airline) of, between Rampe des Lions and Bois Sec; 18.4805, -74.0782), *Comptus stenurus stenurus 2* (* and **: ANSP 38540; Haiti, Grand'Anse, Belandier, Dame Marie [turn back locality], 5.0 km N of; 18.585683, -74.407617), *Comptus stenurus weinlandi* (*: USNM 328808; Dom. Rep., Barahona, Canoa, 16.0 km ESE of; 18.3125, -71.0417; **: SBH 102958; Unknown), *Diploglossus delasagra* (* and **: USNM 512238; Cuba, Pinar del Rio, San Vicente, 4.0 km NW, north base of Sierra de San Vicente; 22.7088, -83.7442), *Diploglossus garridoi* (* and **: MNHNCU 4420; Cuba, Granma, El Manguito), *Diploglossus lessonae* (*: CHUNB 62432; Brazil; **: CHUNB 62433; Brazil), *Diploglossus monotropis* (* and **: SMF 100420; Costa Rica), *Diploglossus nigropunctatus* (* and **: USNM 512240; Cuba, Guantanamo, San Luis de Potosi, 1 km SW of), *Diploglossus pleii* (*: ANSP 38556; United States, Puerto Rico, Reserva Forestal, Rio Abajo (8 km airline SSE Arecibo); 18.4000, -66.6913; **: ANSP 38557; United States, Puerto Rico, Reserva Forestal, Rio Abajo (8 km airline SSE Arecibo); 18.4000, -66.6913), *Mesoamericus bilobatus 1* (*: SMF 89546; Panama, Veraguas, PNSF, Cerro Mariposa: water supply hut near Alto de Piedra; 8.51607, -81.11849), *Mesoamericus bilobatus 2* (*: SMF 89549; Panama, Veraguas, PNSF, Cerro Mariposa: water supply hut near Alto de Piedra; 8.51607, -81.11849), *Mesoamericus bilobatus 3* (*: SMF 101026; Costa Rica, Limón, Finca Curré,northern limit, close to creek; 9.61823, -82.71195), *Mesoamericus bilobatus 4* (*: MVZ 207334; Costa Rica, Moravia), *Mesoamericus bilobatus 5* (*: SMF 94584; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), *Mesoamericus bilobatus 6* (* and **: SMF 94583; Costa Rica, Guanacaste, Volcan Miravalles; 10.70435, -85.11355), *Ophiodes* sp. (*: CURCR 94), *Ophiodes striatus* (*: MVZ 191047; Brazil, Edo. Sao Paulo), *Panolopus costatus costatus* (*: ANSP 38558; Haiti, Grand'Anse, Abricots [outskirts]; 18.64783, -74.307212; **: SBH 274063; Haiti; Nippes, Morne Bois Pangnol; 18.418689, -73.775122), *Panolopus costatus leionotus 1* (*: ANSP 38566; Dom. Rep., SanJuan, 1.6 mi NNE El Azul; 18.717, -71.413), *Panolopus costatus leionotus 2* (*: ANSP 38570; Haiti, Artibonite, Morne Boeuf; 19.072394, -72.250208; **: ANSP 38571; 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; **: SBH 194362; Dom. Rep., Baoruco, Apolinar Pelodroma, 5 km N of), *Panolopus costatus nesobous* (*: ANSP 38583; Haiti, Sud, Ile a Vache; 18.105163, -73.69288, **: ANSP 38581, Haiti, Sud, Caye Michel, previously called Caye Paul (10.7 km WNW Les Platons Citadel); 18.331598, -74.022442), *Panolopus costatus oreistes* (*: USNM 328792; Haiti, Sud-Est, Jacmel, 9.5 km E of; 18.2242, -72.4414; **: ANSP 38608, Haiti, Sud-Est, Morne D'Enfer, southwestern edge of plateau; 18.330052, -72.37095), *Panolopus curtissi aporus* (*: USNM 328800; Dom. Rep., Pedernales, Juancho, 6.4 km SW, 0.7 km SE by road SW of Enriquillo; 17.8358, -71.3439; **: ANSP 38628; Dom. Rep., Pedernales, Pedernales town, in palm grove; 18.029, -71.7471), *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; **: ANSP 38643; Haiti, Nord'Ouest, Mole St. Nicolas; 19.805831, -73.375556), *Panolopus curtissi hylonomus* (* and **: 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; **: ANSP 38648; Dom. Rep., Santiago, La Lagus; 19.1512, -71.0102), *Pseudopus apodus* (CAS 182911; Russia), *Sauresia sepsoides 1*

(*: ANSP 38675; Haiti, Grand'Anse, Grande Cayemite; 18.635615, -73.751749; **: ANSP 38674; Haiti, Grand'Anse, Grande Cayemite; 18.635615, -73.751749), *Sauresia sepsoides 2* (*: ANSP 38684; Haiti, Nippes, Morne Bois Pangnol; 18.418689, -73.775122; **: ANSP 38663; Haiti, Grand'Anse, Baraderes, 8.0 km SSW of; 18.44032, -73.667556), *Sauresia sepsoides 3* (*: ANSP 38667; Haiti, Ouest, Berry; 18.307945, -72.253894; **: ANSP 38687; Haiti, Sud-Est, Morne D'Enfer, southwestern edge of plateau; 18.330052, -72.37095), *Sauresia sepsoides 4* (* and **: USNM 328846; Dom. Rep., Hato Mayor, Sabana de la Mar, 9.5 km W [airline] in Los Haitises; 19.0606, -69.4758), *Siderolamprus bivittatus* (* and **: UTAR-46542; Guatemala, Jalapa, Cerro Tablon de las Minas), *Siderolamprus cyanochloris* (* and **: MVZ 204069; Costa Rica, Refugio National Tapanti), *Siderolamprus enneagrammus 1* (* and **: 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* (* and **: SMF 90177; Panama, Chiriquí, Lost and Found Ecohostel; 8.67462, -82.21958), *Siderolamprus rozellae* (* and **: UTA R-46107; Guatemala, Izabal, Morales, Finca Karen), *Wetmorena agasepsoides* (*: ANSP 38712; Dom. Rep., Barahona, Canoa, 0.3 km S, 13.5 kmE airline; 18.3448, -71.032; **: SBH 102690; Dom. Rep., Barahona, Canoa, 3.0 km E of), *Wetmorena haetiana haetiana* (*: ANSP 38745; Haiti, Ouest, Waterfall in Parc La Visite; 18.34014, -72.269826; **: ANSP 38734; Haiti, Sud-Est, Pic La Selle, Sud-Ouest; 18.32887, -72.021842), *Wetmorena haetiana mylica* (* and **: USNM 328858; Dom. Rep., Barahona, Cabral, 15.3 km S, 6.7 km E by road; 18.1094, -71.2292), *Wetmorena haetiana surda* (*: USNM 328899; Dom. Rep., Pedernales, El Aguacate, 10.3 km S, on Haitian border road; 18.2897, -71.7111; **: USNM 328900; Dom. Rep., Pedernales, El Aguacate, 6.6 km S of, on Haitian border road; 18.3008, -71.6944).

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2022.107577.

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