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Original Article

One if by land, two if by sea: molecular phylogeny and biogeography of the Neotropical leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*)

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ABSTRACT

The evolutionary histories of plant and animal species are often tightly linked to geological histories. A key example is the closure of the Isthmus of Panama, which facilitated widespread biotic dispersal between North and South America after independent faunal assemblages had evolved within each region. Likewise, Andean uplift accelerated and, consequently, created many barriers that led to numerous lineage diversifications. Leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*) represent an ideal model for exploring the impact of Isthmus of Panama closure and Andean uplift on their evolutionary history. We present the most complete time-calibrated phylogeny for this genus to date and reconstruct the biogeographical history of the group. Our phylogenetic hypotheses indicate that the North and Central American *Phyllodactylus* clade is older than the hypothesized time for the full Isthmus of Panama closure, and *Phyllodactylus* most probably dispersed over open ocean before full isthmus formation was complete. Andean uplift coincided with several divergence events, although not until the late Miocene, after many clades had already diverged. Associated instances of hidden diversity in the Andes were revealed in this reconstruction, indicating that the full extent of diversity is yet to be characterized fully. Identification of species complexes and paraphyly within *Phyllodactylus* has important conservation implications for the protection of these reptiles.

Keywords: Andes; biogeography; dispersal; Neotropical; phylogenetics; reptile

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INTRODUCTION

Geological events in the Central and South American tropics have heavily impacted biogeographical histories across this region and much of the Western Hemisphere (Simpson 1980, Hoorn *et al.* 2010, Leigh *et al.* 2014). With the increase in molecular phylogenies for taxa distributed across Central and South America, focus on assessing the relative timing of these events and their impact on the dispersal and vicariance of different groups has continued to grow (Lessios 2008, O'Dea *et al.* 2016, Silliman *et al.* 2021).

The formation of the Isthmus of Panama facilitated the Great American Biotic Interchange, drastically transforming biotic assemblages across both North and South America (Simpson 1980, Marshall *et al.* 1982, Webb 1991). More recent evidence suggests that an older and more prolonged formation (origin 23–25 Mya; Farris *et al.* 2011, Bacon *et al.* 2015a, 2015b, Montes *et al.* 2015) occurred instead of a later, rapid period of formation (origin 3.5 Mya), which was often cited in older literature as a calibration point for other dating analyses. However, debate is abundant on the appropriate interpretation of the molecular evidence and timing of isthmus formation (Coates and Stallard 2013, Lessios 2015, Marko *et al.* 2015). Instances of dispersal between land masses prior to the land bridge have been hypothesized based on the fossil record, thus the association of isthmus formation and biotic interchange is less clear for some groups (Vanzolini and Heyer 1985).

Andean uplift also drove speciation in Neotropical fauna by forming new geographical barriers to previously connected landscapes and new habitats (Hazzi *et al.* 2018). The North and Central Andes are some of the most biodiverse regions in the world, serving as hotspots for vertebrates, invertebrates, and plants, with many threats to extinction anticipated in the near future (Moura *et al.* 2016, Hazzi *et al.* 2018). Molecular phylogenetics, in addition to palaeontological and geological evidence, suggest that Andean uplift was also a gradual process beginning as early as 40 Mya (Gregory-Wodzicki 2000, Hoorn *et al.* 2010, Esquerré *et al.* 2019). The South American fauna is hypothesized to have been heavily impacted by rapid Northern and Central Andean uplift ~7–10 Mya, but testing this with biogeographical data is difficult because of widespread hyperdiversity in the area (Pérez-Escobar *et al.* 2022) and the dynamic nature of mountain building (Esquerré *et al.* 2019).

Although Isthmus of Panama formation and Andean uplift are largely accepted as significant events in the evolutionary history of many terrestrial vertebrate groups, the American herpetofauna often displays complex biogeographical histories, defying geographical barriers and dispersing over water (Vanzolini 1968, Vanzolini and Heyer 1985, Poe *et al.* 2017). The integration of new insight on geological processes and molecular phylogenies is needed for better assessment of the alignment of geological and biogeographical histories across the Americas.

The Phyllodactylidae (leaf-toed geckos) are a trans-Atlantic family in Gekkota distributed across northern Africa, the Arabian Peninsula, central Asia, and the Americas (Dixon 1964, Dixon and Huey 1970, Vanzolini and Heyer 1985, Gamble *et al.* 2008). *Phyllodactylus*, the most species-rich genus in the family with almost 70 species described to date, occupies coastal and near-coastal habitats in North and South America, including surrounding islands (Uetz *et al.* 2021). The description of 10 new species since 2008 (Venegas *et al.* 2008, Murphy *et al.* 2009, McCranie and Hedges 2013, Torres-Carvajal *et al.* 2013, Koch *et al.* 2016, Ramírez-Reyes and Flores-Villela 2018, Arteaga *et al.* 2019, Ramírez-Reyes *et al.* 2021) indicates that endemism is high, particularly on islands and in the Marañón River Valley of Peru (Venegas *et al.* 2008, Torres-Carvajal *et al.* 2016, Koch *et al.* 2018). Unfortunately, 17 species are currently International Union for Conservation of Nature (IUCN) Red Listed as Near Threatened, Vulnerable, Endangered, and Critically Endangered (IUCN 2025). Previous research on this group has focused on regional phylogenetic and biogeographical reconstructions, while uncovering hidden species diversity (Weiss and Hedges 2007, Blair *et al.* 2009, 2015, Torres-Carvajal *et al.* 2014, Koch *et al.* 2016). Additional studies have found numerous instances of long-range overseas dispersal and island colonization in this genus and other phyllodactylid genera (Gamble *et al.* 2011, Torres-Carvajal *et al.* 2014, 2016). However, the extent to which overseas dispersal contributed to the evolutionary history of this group, and in particular, how and when interchange between North and South America occurred, has yet to be explored fully. Whether the formation of the Isthmus of Panama and Andean uplift are associated with divergence events in *Phyllodactylus* is unknown without a genus-wide molecular phylogeny across its entire distribution. Thus, this group serves as a good test case to assess the impacts of geographical history on speciation and dispersal patterns of herpetofauna across this high-diversity region.

In this study, we present the most complete time-calibrated molecular phylogeny for this genus to date and use this tree and species distribution data to reconstruct a biogeographical hypothesis for *Phyllodactylus*. We tested our phylogeny against two biogeographical models corresponding to the key geological events occurring during the evolutionary history of *Phyllodactylus*: (i) Central Andean uplift acceleration beginning 10 Mya; and (ii) formation of the Isthmus of Panama 23–25 Mya. Additionally, we identified several cases of mitonuclear discordance and instances of potential introgression within *Phyllodactylus*. Our results suggest an early dispersal into North America prior to Isthmus of Panama formation, followed by multiple instances of overseas dispersal within *Phyllodactylus* from South America to other landmasses. Furthermore, Andean uplift aligns with the divergence of several lineages endemic to the Marañón Valley.

MATERIALS AND METHODS

Taxon sampling and molecular data

Tissue samples were obtained from specimens across the range of *Phyllodactylus* and closely related phyllodactylid species. DNA was extracted using Qiagen DNEasy Blood and Tissue kits following the spin column protocol, and sequences for portions of five nuclear protein-coding genes [recombination-activating gene 1 (*RAG1*), recombination-activating gene 2 (*RAG2*), oocyte maturation factor MOS (*C-MOS*), acetylcholinergic receptor M4 (*ACM4* or *CHRM4*), and brain-derived neurotrophic factor (*BDNF*)] and two mitochondrial markers [16S rRNA and NADH dehydrogenase subunit 4 (*ND4*)] were amplified with PCR and Sanger sequenced using primers and protocols detailed elsewhere

(Gamble *et al.* 2008, 2011, 2012; Supporting Information, Table S1).

We assigned identifications to specimens based on current taxonomy (Dixon 1962, 1964, Dixon and Huey 1970, Koch *et al.* 2018). In instances of high intraspecific diversity in a species complex, taxa were designated as such in the species tree (i.e. *Phyllodactylus reissii* mountain/coast corresponds to the *P. reissii* clade IIIb/c in the study by Koch *et al.* 2016). *Phyllodactylus microphyllus* (North/South) and *Phyllodactylus sentosus* (Lima/South) were found to exhibit strong structuring into population-specific clades and were noted as such for subsequent analysis (see Results). We also included 12 specimens representing nine outgroup taxa from the closely related genera *Garthia*, *Phyllopezus*, and *Homonota*. We used publicly available data from GenBank for 62 specimens of *Phyllodactylus* and outgroups to supplement our specimens, for a taxon sampling matrix totalling 147 specimens representing 52 taxa (Gamble *et al.* 2008, 2011, 2012, Blair *et al.* 2009, Torres-Carvajal *et al.* 2014, Koch *et al.* 2016, Daza *et al.* 2017). New GenBank accessions are listed in the Supporting Information (Table S2). This dataset contains 588 newly generated sequences, which added substantially to the available 347 sequences that were analysed in geographical and taxonomic coverage. Eighty-five specimens were newly sequenced and another 18 were sequenced for additional loci. Of the 52 taxa, 18 are from this newly generated data (35%), 14 are currently named as distinct species, and another four taxa were split into geographical populations based on genetic diversity. The full matrix that was analysed is missing data for 94 sequences (9.14%), where each specimen had data for at least two genes, and each taxon was represented by both mitochondrial genes and at least two nuclear genes.

Sequences were assembled in Geneious Prime v.2022.2.1 (Kearse *et al.* 2012) and aligned with GenBank sequences using MUSCLE v.3.8.425 (Edgar 2004). Subsequently, we visualized and manually trimmed alignments in Geneious to minimize missing data across sequences. The two mitochondrial genes were aligned separately, then concatenated and analysed together for all downstream analyses (Brennan *et al.* 2016). We used SeqPHASE (Flot 2010) and PHASE v.2.1.1 (Stephens *et al.* 2001, Stephens and Scheet 2005) for phasing of allelic variants in nuclear markers *ACM4*, *CMOS*, *RAG1*, and *RAG2*. *BDNF* did not have any heterozygous sites. One phased sequence was chosen randomly for each individual in the maximum likelihood analyses, and both phased sequences were included in the Bayesian species tree analyses.

Phylogenetic analysis and divergence time estimation

Maximum likelihood (ML) and Bayesian inference (BI) methods were used to infer phylogeny using Marquette University's Raj HPC clusters. We used IQ-TREE 2 (Minh *et al.* 2020) for a maximum likelihood phylogenetic reconstruction of the full concatenated dataset. The ModelFinder (Kalyaanamoorthy *et al.* 2017) option selected best substitution models for each locus with partition modelling (Chernomor *et al.* 2016) using the -m -TESTMERGE option and -p option for edge-linked branch lengths with different rates between partitions. Node support was assessed with 1000 ultrafast bootstrap replicates (Hoang *et al.* 2018) and the SH-like approximate likelihood ratio test (Guindon *et al.* 2010), where support is considered strong at values ≥95 and ≥80, respectively (Guindon *et al.* 2010, Minh *et al.* 2013). Bootstrap trees were optimized using the nearest neighbour interchange search option -bnni to reduce the risk of overestimating branch support.

Divergence times were estimated simultaneously with the species tree in a Bayesian framework using the multispecies coalescent model StarBeast3 in BEAST v.2.6.7 (Bouckaert *et al.* 2019, Douglas *et al.* 2022). No fossils are known within this group, hence secondary calibrations were used from Gamble *et al.* (2015), who used fossil and biogeographical data, as was done by Torres-Carvajal *et al.* (2014) and Ramírez-Reyes *et al.* (2020). Calibration priors were uniformly distributed, with a lower and upper bound corresponding to the 95% confidence interval found by Gamble *et al.* (2015). Calibrations for shallower nodes obtained from previous works were not used because taxon sampling varied substantially across studies, and deeper node calibrations are more accurate (Mello and Schrago 2014, Ramírez-Reyes *et al.* 2020; Supporting Information, Table S3).

Given that not all models available in IQ-TREE 2 are also available in BEAST2, we used MEGA11 (Stecher *et al.* 2020, Tamura *et al.* 2021) for substitution model selection for each of the five nuclear loci and the concatenated mitochondrial markers (mtDNA). Models were chosen using the lowest Bayesian information criterion among available models implemented in BEAST2 (Nei and Kumar 2000). Appropriate site substitution models were implemented in the StarBeast3 template, with HKY+G as the best-fitting model for all nuclear loci and GTR+G for the mtDNA dataset. The template used a relaxed clock and Yule model with site, clock, and tree models all unlinked. Three independent Markov chain Monte Carlo analyses were run for 2×10^8 generations, storing every 50000 samples, with 10% burn-in. Tracer was used to assess convergence of the independent runs and whether appropriate effective sample size values had been reached (>200; Rambaut *et al.* 2018). TreeAnnotator and LogCombiner from the BEAST v.2.6.7 package were used to create a maximum clade credibility tree, with 50% burn-in removed and with mean heights as node heights.

Topology hypothesis testing

In instances where support in the full species trees was weak (see Results) and population structuring revealed high genetic diversity, we tested alternative topologies with monophyletic constraints. Trees were estimated again using only concatenated mitochondrial markers and only concatenated nuclear markers. These were used to assess phylogenetic discordance and identify cases of potential introgression or incomplete lineage sorting where mitochondrial and nuclear markers conflicted. The posterior distribution of BI species trees from nuclear-only, mitochondrial-only, and full dataset runs were filtered through PAUP* v.4.0a168 (Swofford 1998) using a monophyletic constraint to assess posterior probability of the alternative topology in each dataset. We also tested tree topologies using the full concatenated ML tree and implemented constraints on monophyly of groups. Constraint trees were generated using the R package ape (Paradis and Schliep 2019) and were run in IQ-TREE 2 using the same parameters as the unconstrained trees. Approximately unbiased (AU) (Shimodaira 2002), KH (Kishino and Hasegawa

1989), and SH (Shimodaira and Hasegawa 1999) hypothesis tests were run in IQ-TREE 2, with 10000 RELL replicates (Kishino *et al.* 1990) to compare the log-likelihood scores of the constrained trees with the unconstrained tree for each incident of discordance.

Biogeography

Taxa were assigned to one of five biogeographical regions that encompass the full range of *Phyllodactylus* + *Homonota*: North America and Central America (N); Galápagos Islands (G); northern South America and Caribbean Islands (C); west of Andes, including inter-Andean valleys (W); and east of Andes (E). These regions were chosen based on their relevance to geological processes (i.e. isthmus formation and Andean uplift) and *a priori* assignment to major clades, in addition to previous designations in regional works (Vallejos-Garrido *et al.* 2023). This scheme also aimed to maximize model efficiency while addressing questions about these specific geographical features with adequate resolution (Matzke 2014). For example, we combined North and Central America regions for *Phyllodactylus* species that occur north of the Isthmus of Panama, like other studies whose objective was to determine the timing of dispersal from South America (Dacosta and Klicka 2008, Burns and Racicot 2009, Pinto-Sánchez *et al.* 2012). Likewise, we had only one species from northern South America, *Phyllodactylus ventralis*, hence we included that species/region along with the geographically proximate Caribbean. Each taxon, with the exception of *P. reissii*, occupies one of these regions, and given that *P. reissii* is a recent invader of the Galápagos (Hoogmoed 1989, Swash and Still 2005), *P. reissii* specimens were included only from west of Andes and assigned to that region only. In addition to specimen locality data, historical data from the literature were used for the region assignment (Dixon 1962, 1964, Dixon and Huey 1970).

Biogeographical model testing and ancestral area reconstructions were implemented in the R package BIOGEOBEARS v.1.1.3 (Matzke 2013) using the species tree from the STARBEAST3 analysis, with the outgroups pruned. Event-based ML estimation of ancestral area was tested with three models: dispersal–extinction–cladogenesis (DEC; Ree and Smith 2008), DIVALIKE (Ronquist 1997), and BAYAREALIKE (Landis *et al.* 2013), all with and without founder event speciation (+J; Matzke 2014). An additional time-stratified analysis of DEC and DEC+J was done with a dispersal rate constraint at the time point of 25 Mya, which pre-dates Isthmus of Panama formation and closure, and 10 Mya, which pre-dates Central Andean uplift. The manually adjusted dispersal rate of North/Central America (N) to and from all other regions was assigned a decreased value prior to 25 Mya, and dispersal rates to and from N were equal after 25 Mya until the present. The west (W) to east (E) of Andes dispersals were assigned decreased values between each other after 10 Mya (Supporting Information, Table S4). Constrained dispersal rates were tested independently to ensure that each time point and dispersal matrix was not significantly worsening the model likelihood. Taxa were allowed to occupy a maximum of two areas and were assigned to one region each in a presence–absence matrix. A corrected Akaike information criterion (AICc) score was calculated for all models to determine the best-fitting model, which was used to estimate ancestral geographical areas with 50 stochastic mappings onto the species tree (Dupin *et al.* 2017).

RESULTS

Phylogenetic analysis with divergence time estimation

Our complete concatenated dataset and coalescent species tree analysis produced phylogenetic reconstructions that were congruent for all well-supported nodes (Fig. 1; Supporting Information, Figs S1–S2). Tree topologies estimated with only mitochondrial or nuclear data differ in relationships involving species complexes with hypothesized incomplete lineage sorting (*P. reissii* and *Phyllodactylus gilberti*) and potential introgression (*P. microphyllus*, *P. lepidopygus*, and *Phyllodactylus inaequalis*), which were not well supported in the BI coalescent species trees or ML trees (Supporting Information, Figs S3–S6). Relationships among outgroups had strong nodal support except for placement of *Garthia gaudichaudii*, which ultimately did not affect further analyses and conclusions. Relationships among species within *Phyllodactylus* in this analysis were largely concordant with those in previous analyses (Blair *et al.* 2009, 2015, Torres-Carvajal *et al.* 2014, Koch *et al.* 2016, Ramírez-Reyes *et al.* 2020). However, for the first time in any study, *Phyllodactylus* was not recovered as monophyletic, with *Phyllodactylus gerrhopygus* and *Phyllodactylus angustidigitus* forming a clade sister to *Garthia* + *Homonota* + remaining *Phyllodactylus* species with high nodal support. Both the concatenated and coalescent species trees (using all the available data) find *Phyllodactylus delsolari* from the Marañón Valley as sister to the remaining *Phyllodactylus* species, exclusive of the *P. gerrhopygus* and *P. angustidigitus* clade. Divergence dates were estimated simultaneously with species tree reconstruction in STARBEAST3, and all runs converged with effective sample size values of >200 for all relevant parameters (Supporting Information, Fig. S7). Divergence timing estimates overlapped with previous estimates for the Galápagos (Torres-Carvajal *et al.* 2014, 2016, Myers *et al.* 2025) and Mexican clades (Ramírez-Reyes *et al.* 2020).

Biogeography model testing and ancestral area reconstruction

DEC+J had the highest likelihood of the unconstrained models tested, although DIVALIKE+J and BAYAREALIKE+J also compared well (Table 1). The founder event (+J) parameter improved model fit for each of the three base models tested (but see Ree and Sanmartín 2018, Matzke 2022). The constrained model at 25 Mya did not improve model fit compared with an unconstrained model, but the constrained model at 10 Mya had the highest likelihood (by a slight margin) of all models and was used for subsequent ancestral area reconstruction (Fig. 2; Supporting Information, Fig. S8). Although the DEC+J constrained likelihood was slightly higher than DEC+J unconstrained, the reconstructed states were nearly identical in both cases, with very few ambiguously reconstructed nodes in the tree. All models tested with the +J parameter converged on highly similar biogeographical scenarios. The analysis estimated a South American origin for the *Phyllodactylus* + *Garthia* + *Homonota* group, most probably in the modern area west of the Andes. *Phyllodactylus* (excluding the *P. angustidigitus* + *P. gerrhopygus* clade and *P. delsolari*) comprises three major clades corresponding to, but not exclusively, the

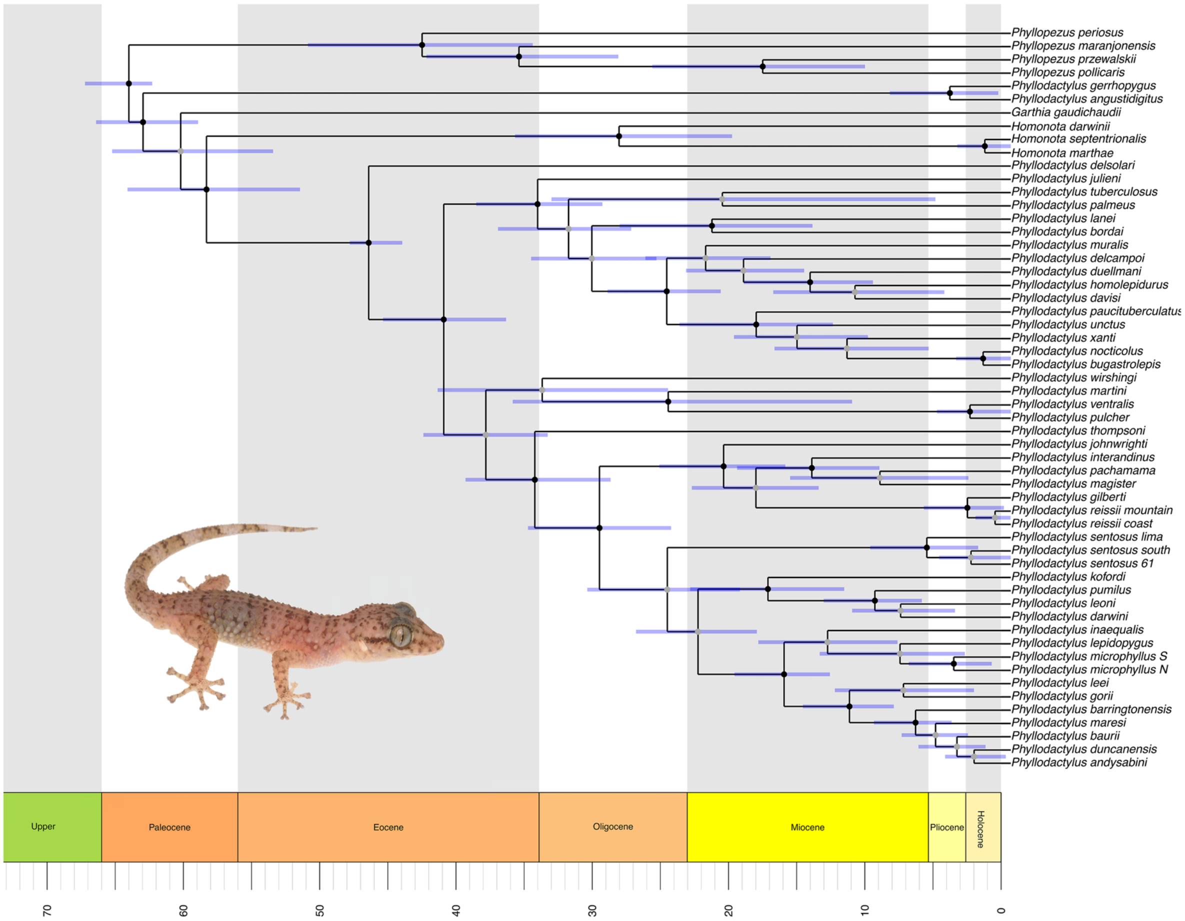

Figure 1. A time-calibrated species tree inferred using seven secondary calibrations from Gamble *et al.* (2015), implemented in the StarBeast3 template in BEAST v.2.6. Bars represent 95% highest posterior density intervals for mean node ages. Node colours indicate the Bayesian posterior probability (BPP) for each clade (black > .90; grey < .90). Image of *Phyllodactylus wirshingi* from Stu Nielsen.

Table 1. Biogeographical model testing for ancestral area reconstruction with relative likelihood and Akaike information criterion scores.

Model	LnL	numparams	d	e	j	AICc	AICc_wt
DECc10+J	−34.03	3	1.00×10^{-12}	$1.00 \times 10^{-12} \times 10^{-12}$	.021	74.55	.25
DEC+J	−34.42	3	1.00×10^{-12}	1.00×10^{-12}	.020	75.34	.17
DIVALIKE+J	−34.74	3	1.00×10^{-12}	1.00×10^{-12}	.020	75.98	.12
BAYAREALIKE+J	−34.75	3	1.00×10^{-7}	1.00×10^{-7}	.020	76.01	.12
DECc25+J	−45.69	3	.0002	4.00×10^{-4}	.019	97.88	2.20×10^{-6}
DEC	−47.79	2	.0013	1.00×10^{-12}	0	99.82	8.20×10^{-7}
DIVALIKE	−48.51	2	.0017	2.80×10^{-11}	0	101.30	4.00×10^{-7}
BAYAREALIKE	−66.98	2	.0019	.01	0	138.20	3.80×10^{-15}

Abbreviations: LnL, natural log likelihood; numparams, number of parameters estimated in model; d, rate of dispersal; e, rate of extinction; j, founder event speciation; AICc, corrected Akaike Information Criterion; AICc_wt, weighted AICc.

North/Central American, Caribbean/northern South American, and western Andean/Galápagos regions, with no history of presence in the southeastern lowlands of South America. The reconstruction for the most species-rich clade in western South America and the Galápagos is concordant with previous work revealing multiple colonizations from South America to the Galápagos (Torres-Carvajal *et al.* 2014, Myers *et al.* 2025). One dispersal event from South America to North America most probably occurred between 37 and 46 Mya, rather than an initial dispersal north with subsequent reinvasion of South America. At least two dispersal events to the Caribbean occurred in a similar time frame in the late Eocene to Oligocene from a Central American ancestor and another from a South American ancestor.

Topology tests and mitonuclear discordance

Instances of mitonuclear discordance occur in the *Phyllodactylus johnwrighti*, *Phyllodactylus interandinus*, *Phyllodactylus magister*, and *Phyllodactylus pachamama* clade, the *P. microphyllus*, *P. lepidopygus*, and *P. inaequalis* clade, and within the *P. reissii* + *P. gilberti* clade (Fig. 3; Supporting Information, Fig. S9). Sister

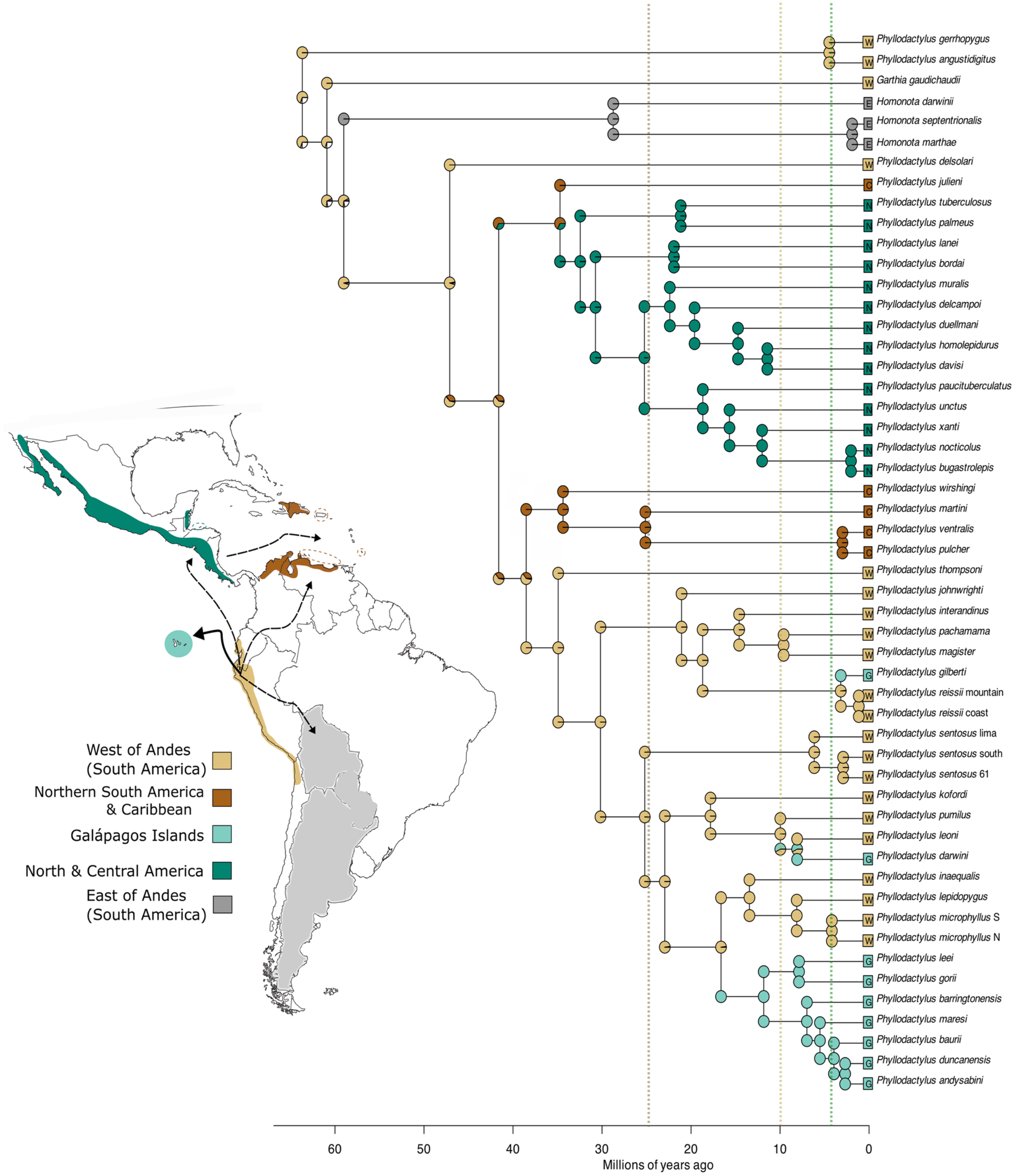

Figure 2. BioGeoBEARS ancestral area reconstruction using the DEC+J biogeographical model with dispersal constraint at 10 Mya (yellow dotted line). Isthmus of Panama closure (brown dotted line) and Galápagos Islands emergence (green dotted line) are designated at 25 and 4 Mya, respectively. Pie chart colours correspond to geographical ranges, and white represents both west of Andes and east of Andes areas. Map of biogeographical regions and hypothesized dispersal routes are represented by arrows; solid arrows represent multiple dispersal events and dashed arrows single dispersal events.

relationships within the *P. johnwrighti*, *P. interandinus*, *P. magister*, and *P. pachamama* clade were not considered strongly supported (PP of <.90) in either mitochondrial or nuclear coalescent trees and were not evaluated in topology tests.

Although *P. microphyllus* was recovered as monophyletic in the full BI species tree and the nuclear-only tree, the mitochondrial-only tree split *P. microphyllus* into a northern lineage that was sister to *P. inaequalis* and a southern lineage that clustered together with *P. lepidopygus*. Mitonuclear discordance was the same across the BI gene trees and ML trees (Supporting Information, Figs S10–S15); however, the BI and ML methods recovered different topologies when using the full dataset, because the coalescent method better accounts for discordant gene trees in the species tree (Leavitt *et al.* 2017). The mitochondrial- and nuclear-only BI posterior tree distributions were filtered in PAUP* using the monophyletic constraint for *P. microphyllus* (North+South), which the full species tree recovered with a PP of .91 (Table 2). The nuclear dataset had a similar PP of .89 that supported the monophyly constraint, while the mitochondrial dataset contained 152 of 12003 trees (PP = .01) that met the constraint. Additionally, the ML trees were used for hypothesis testing the monophyly of *P. microphyllus* using the full concatenated dataset (Table 2). The constrained tree log-likelihood (logL) was significantly worse than the unconstrained tree in two hypothesis tests (p-value for KH test (p-KH) = .001 and p-value for AU test (p-AU) = .01), therefore rejecting the monophyly of the *P. microphyllus* group even when incorporating nuclear markers in the ML tree.

The full concatenated, mitochondrial, and nuclear-only BI trees were filtered in PAUP* using the monophyletic constraint for *P. reissii* (coast+mountain), which is the topology in the nuclear species tree with a PP of .66 (Table 2). The mitochondrial dataset contained 45 of 12003 trees that met the constraint ($PP < .01$), and the full dataset contained 4863 of 12003 trees (PP = .40). The filter retained 4959 of 12003 trees (PP = .41) with a constraint for the *P. reissii* mountain individuals as sister to the *P. gilberti* + *reissii* coast taxa in the full dataset. The mitochondrial gene tree generated in the full dataset StarBeast3 run has the same topology as the mitochondrial coalescent tree and was used to assess the placement of *P. gilberti* with respect to *P. reissii*. No trees from the mitochondrial gene tree distribution met the constraint for *P. gilberti* and *P. reissii* coast as reciprocally monophyletic sister groups. Most of the nuclear gene trees were poorly resolved in this group, hence discordance analyses between nuclear and mitochondrial markers were not possible. Hypothesis testing of the full ML tree with constraints for *P. reissii* (coast+mountain) monophyly and *P. reissii* coast monophyly were rejected. Poorly resolved species boundaries within this group have been identified previously, and further work will be required to disentangle the relationships among these taxa (Koch *et al.* 2016). The relative age estimate suggests a recent split of *P. reissii* mountain and coast populations, and incomplete lineage sorting potentially causes this discordance.

DISCUSSION

Phylogenetic relationships within Phyllodactylidae

We estimated the most complete (46 of 68; 67% of described species) and well-resolved phylogeny for *Phyllodactylus* to date, expanding taxon sampling to cover the entire known range of the group. Our analyses are largely concordant with other recent works focused on regional diversity (Torres-Carvajal *et al.* 2014, Koch *et al.* 2016, Ramírez-Reyes *et al.* 2020), and we identified multiple cases of hidden diversity within the genus. Based on our analyses, the genus *Phyllodactylus* is not monophyletic, and all reconstructions have high support for the *P. angustidigitus* + *P. gerrhopygus* clade as sister to *Homonota* + *Phyllodactylus s.s.* Reconstructions placed *Garthia gaudichaudii* as either sister to the *Homonota* + *Phyllodactylus s.s.* clade or to (*P. angustidigitus* + *P. gerrhopygus*) + *Homonota* + *Phyllodactylus*, but there was no support for a monophyletic *Phyllodactylus* when *Homonota* was included in the analysis. Hidden diversity within species groups, particularly in the Andes, indicates that the total diversity of this group is still yet to be documented fully. Niche partitioning and climatic barriers might be driving differentiation across western South America between the Pacific coast and the Andes (Hazzi *et al.* 2018, Esquerré *et al.* 2019). Although instances of sympatry are known for most of these Andean species, complete range data are increasingly difficult to obtain, with ongoing habitat destruction and human development of the Andean dry forest (Koch *et al.* 2018); therefore, the extent of geographical overlap and boundaries between species remain difficult to characterize.

Mitonuclear discordance

Individuals in the widespread species complex *P. reissii* showed unclear placement with the Galápagos endemic *P. gilberti*. *Phyllodactylus reissii* is distributed along the Pacific coast of Ecuador and Peru and in low and high elevations across the Andes (Uetz *et al.* 2021). The montane *P. reissii* population, albeit with only two samples available, showed increased differentiation from the remaining coastal individuals of this species, probably indicating reproductive isolation between these populations. The estimated divergence of the lineage in the Huancabamba river valley from the *P. gilberti* and coastal *P. reissii* group is between .5 and 6.5 Mya. This might be a case of incomplete lineage sorting, whereby the populations are geographically separated and now on divergent evolutionary pathways, but genetic similarity is still relatively high. Alternatively, there might have been instances of ancient hybridization in the ancestor of *P. gilberti* and *P. reissii* contributing to discordance among gene trees for different populations today (Brennan *et al.* 2016). Ramírez-Reyes *et al.* (2017) found mitonuclear discordance in the *Phyllodactylus lanei* complex, which also consists of many island endemics on the Western Pacific coast of Mexico and a widespread sister species. Owing to the relevance for conservation of *P. gilberti* on the Galápagos, further sampling and monitoring of the *P. reissii* complex is warranted.

Introgression

We propose that the mitonuclear discordance within the *P. microphyllus* clade is a result of mitochondrial capture and introgression of *P. lepidopygus* by the southern population of *P. microphyllus*. These two species are known to overlap at the southern limit of the *P. microphyllus* range (i.e. coastal central Peru; Dixon and Huey 1970), and the hypothesis tests support a distinct evolutionary pathway in the nuclear vs. mitochondrial genetic markers in this clade. Mitochondrial average genetic distance between these three groups is fairly high (~10%), and no shared mitochondrial haplotypes were found, which is unlikely to be the case if hybridization is recent (McCormack and Venkatraman 2013). Additionally, the morphological distinction between the terrestrial *P. microphyllus* group and scansorial *P. lepidopygus* also suggests that today both species are adapted to different habitats, with little gene flow and strong niche partitioning (Dixon and Huey 1970). Mitochondrial capture can occur as a mechanism for adaptation (Pardo-Diaz *et al.* 2012), and in this case the split between *P. microphyllus* and *P. lepidopygus* is estimated to be 2.6–7.5 Mya, which coincides with Andean uplift and rapidly changing climatic conditions. After this split, while the southern *P. microphyllus* population was still in contact with *P. lepidopygus*, mitochondrial introgression could have occurred and provided some adaptive benefit to changes in elevation or climate (Morales *et al.* 2018, Myers *et al.* 2022).

Divergence timing and biogeography

This study is the first to recover a paraphyletic *Phyllodactylus* within a time-calibrated species tree. The split between the main *Phyllodactylus* clade and sister *Homonota* was much earlier than

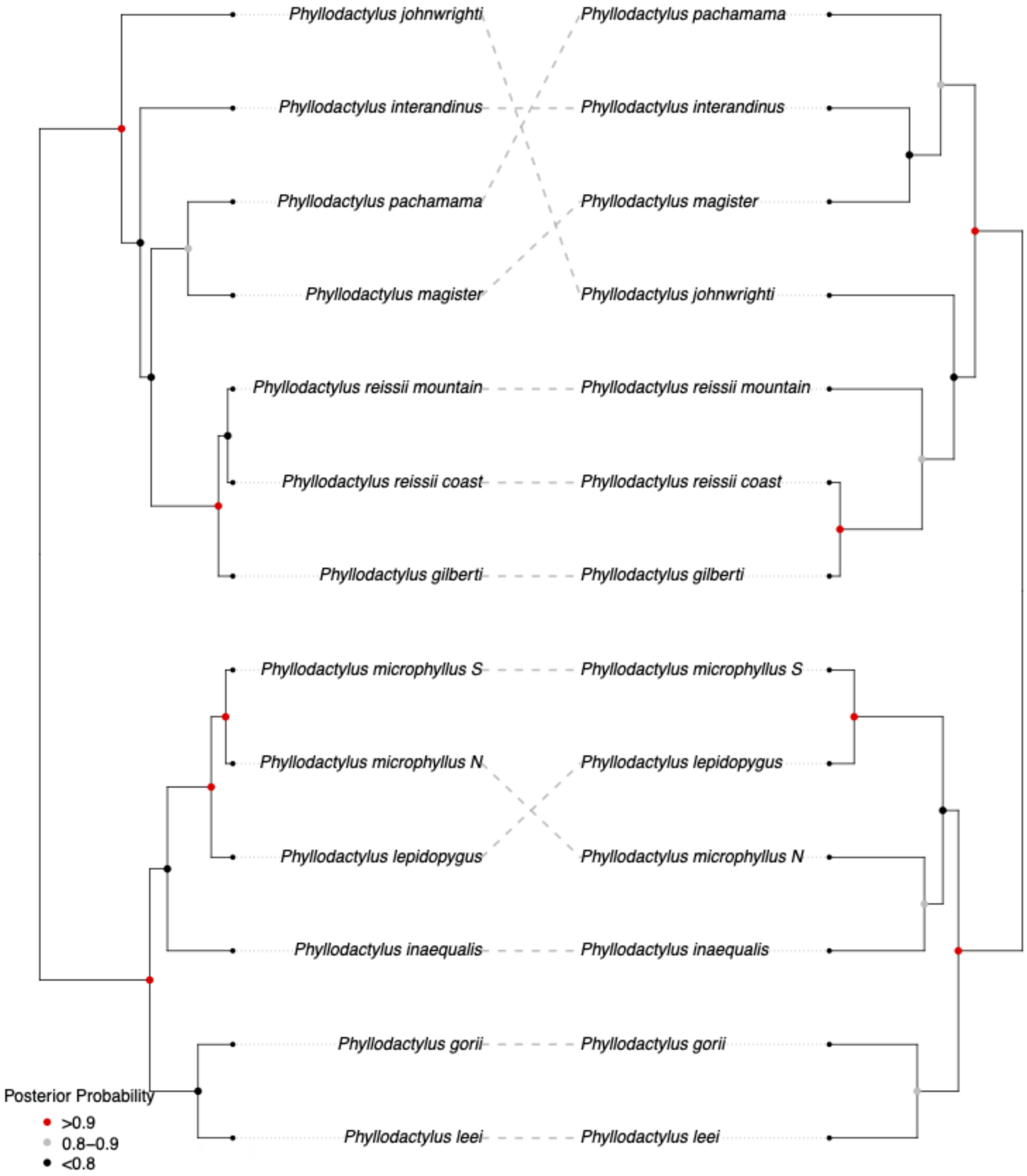

Figure 3. Cophylogram of species trees showing mitonuclear discordance within the West of Andes *Phyllodactylus* clade pruned for visualization. The nuclear-only tree is on the left and the mitochondrial-only tree on the right. Grey dashed lines show relative phylogenetic position compared across datasets to show discordance. Nodes are coloured by Bayesian posterior probability values.

the main period of Andean uplift, although the southern Patagonian Andes began accelerated uplift earlier than the Central Andes, which might be concordant with an early divergence scenario (Folguera *et al.* 2011). Subsequent formation of inter-Andean river valleys has separated *Homonota* from *Phyllodactylus* for ≥15 Myr, but older climatic events in southern South America potentially restricted the ancestral *Homonota* range from *Phyllodactylus* prior to Andean formation (Ortiz-Jaureguizar and Cladera 2006, Malleret *et al.* 2023). In the late Miocene, during which the Paranean Sea isolated much of the southeastern portion of the continent (Pascual *et al.* 1996), we found support for divergence of the two main clades of *Homonota* corresponding to these separate regions, as also suggested by Morando *et al.* (2014) and Malleret *et al.* (2023). Placement of *Garthia* does not change the estimate for a South American ancestral origin of the Neotropical Phyllodactylidae as most likely in the proto-west of Andes region. The split of either *P. gerrhopygus* + *P. angustidigitus* or *Garthia gaudichaudii* from *Homonota* + *Phyllodactylus* pre-dates major tectonic activity (~60 Mya), but both *G. gaudichaudii* and *P. gerrhopygus* + *P. angustidigitus* are found in near-coastal habitats in western

Table 2. Hypothesis testing of *Phyllodactylus microphyllus* monophyly and relationships between *Phyllodactylus reissii* populations and *Phyllodactylus gilberti* with maximum likelihood topology tests and PAUP.[*]

Hypothesis	logL	deltaL	bp-RELL	p-KH	p-SH	p-AU	PP-nuclear	PP-mito	PP-full
Best unconstrained ML tree	−45321.645	0	.979 (+)	.974 (+)	1(+)	.996 (+)			
P. microphyllus monophyly	−45353.512	31.867	0.011 (−)	.013 (−)	.112 (+)	.010 (−)	.887	.013	.910
P. reissii monophyly (coast + mountain)	−45350.758	29.113	.010 (−)	.027 (−)	.146 (+)	.007 (−)	.640	.004	.405
P. gilberti + *P. reissii* (coast)	−45392.871	71.226	0 (−)	2.00×10^{-4} (−)	.001 (−)	8.68×10^{-5} (−)	.177	.988	.413
P. reissii coast monophyly	−45392.875	71.230	1.00×10^{-4} (−)	2.00×10^{-4} (−)	.001 (−)	8.68×10^{-5} (−)		0[*]	

[*] Abbreviations: logL, log likelihood; deltaL, difference from the maximal logL in the ML tree set; bp-RELL, bootstrap proportion of RELL replicates; p-KH, p-value for KH test; p-SH, p-value for SH test; p-AU, p-value for AU test; PP, posterior probability calculated from BEAST and filtered in PAUP* to meet constraints; (+), the 95% confidence sets; (−), significant exclusion.

[*] For gene tree.

Chile and Peru, which is within the likely ancestral distribution. Furthermore, the phylogenetic position of *P. delsolari*, from the Marañón Valley, as sister to the remaining *Phyllodactylus* species exclusive of the *P. gerrhopygus* + *P. angustidigitus* clade, suggests the distribution of the most recent common ancestor of the group was relatively widespread in western South America.

The probable impact of extinction and lack of fossils in our tree makes the Caribbean biogeographical scenario difficult to reconstruct and interpret. The split between *P. wirshingi* (Puerto Rico endemic) and the other species of the region occurred 26–43 Mya, which is consistent with the GAARlandia hypothesis, in which the Greater Antilles and Aves Ridge briefly formed a near-contiguous land bridge to South America ~35 Mya (Iturralde-Vinent and MacPhee 1999, Iturralde-Vinent 2006, Tong *et al.* 2019). In this scenario, the ancestor of the Caribbean clade dispersed from mainland South America across a land bridge into modern-day Puerto Rico and Hispaniola. Close relatives *Phyllodactylus hispaniolae* and *Phyllodactylus sommeri* (Hispaniola) were not represented in this analysis but would probably be placed in the same lineage based on a previous revision of the Greater Antilles group (Weiss and Hedges 2007). Our estimate of the *Phyllodactylus* crown mean age does fall within the hypothesized time interval at 35 Mya, but debate over support for the GAARlandia hypothesis exists, and overseas dispersal is also plausible (Weiss and Hedges 2007, Ali and Hedges 2021). The *Phyllodactylus pulcher* (Barbados) and *P. ventralis* (northern South America) split is consistent with the emergence of the Lesser Antilles in the last 10 Myr, and a mainland South American ancestor probably dispersed over water to the newly formed volcanic islands (Tong *et al.* 2019).

The placement of *Phyllodactylus julieni* (Aruba) as a long branch sister to *Phyllodactylus tuberculosus* and *Phyllodactylus palmeus* (Central America/Mexico) while the remaining Caribbean Island species form a separate clade is consistent with a potential reinvasion scenario in which a Central American ancestor dispersed either directly to Aruba or to the northern coast of South America, with a subsequent dispersal to the island. Instances of other squamate taxa exhibiting similar dispersal patterns, including *Anolis* lizards and *Bothrops* pit vipers, that belong to a Central American and Southern Antilles assemblage have been found, but the mechanism has seldom been discussed (Savage 1982, Poe *et al.* 2017, Hamdan *et al.* 2020). Depending on the timing of the divergence of the *P. julieni* and *P. tuberculosus* + *P. palmeus* ancestor (95% highest posterior density = 29–38 Mya), marine currents travelling from the southern tip of the proto-isthmus could have facilitated overseas dispersal to Aruba (Iturralde-Vinent and MacPhee 1999, Schweitzer *et al.* 2006). Alternatively, if divergence was in the more recent range, after the isthmus was fully formed, a mainland reinvasion was possible; however, with no other members of that clade in South America, there is little support for that hypothesis. Dixon (1962) suggested that *P. julieni*, although geographically closer to other members of the Caribbean *Phyllodactylus* clade, might be a distant relative based on morphological features more closely resembling the North American *P. tuberculosus* clade (Dixon 1962). Although the relative position of *P. julieni* to sister taxa *P. tuberculosus* + *P. palmeus* is not well supported, the support for *P. julieni* within the North/Central American clade is high, and the biogeographical reconstruction with multiple dispersal events into the Caribbean was also recovered. The main Caribbean clade might have had multiple overseas dispersal events from the mainland or between other islands; however, additional surveying of species in the region and/or a fossil record would need to be included to test further biogeographical scenarios.

Our reconstruction also found support for three independent colonizations of the Galápagos archipelago that have been reported previously (Wright 1983, Torres-Carvajal *et al.* 2014, 2016, Myers *et al.* 2025). We estimate divergence timing of the western Galápagos clade with the mainland ~13.5–21.2 Mya, which is slightly earlier than previous estimates of 8–20 Mya for the stem age of the *Phyllodactylus leei* clade (Torres-Carvajal *et al.* 2014, 2016). Our estimate for the *Phyllodactylus darwini* divergence was also older than previous estimates, between 4.5 and 12 Mya, supporting that both colonizations of the southeastern archipelago probably occurred in a similar time frame (Torres-Carvajal *et al.* 2016). Additionally, the *P. darwini* timing estimate supports an additional 'older than the islands' scenario, which may or may not reflect the phenomenon of terrestrial vertebrates pre-dating the Galápagos by initially colonizing landmasses that are now underwater (Ali and Fritz 2024). The recent human-mediated introduction of *P. reissii* to the Galápagos was not factored into the analysis; however, future work on this species complex should include this island population because it has been present since the 1970s and poses a threat to the endemic species (Hoogmoed 1989). Because of the positioning of *P. gilberti* within the *P. reissii* complex and conservation implications, further work should be done to assess genetic structure within these island populations.

The biogeographical reconstruction involving the North and Central American clade supported the topology and relative timings found in a previous analysis for three Mexican subclades (i.e. *Phyllodactylus homolepidurus* and *Phyllodactylus nocticolus* in the Gulf of California and *P. tuberculosus* along the western Pacific coast; Ramírez-Reyes *et al.* 2020). There is high support for one dispersal event from South America into North America, which would be earlier than our current understanding of the timing of the Isthmus of Panama closure but potentially overlapping with the earliest formation steps (Bacon *et al.* 2015a). Similar early age estimates for biotic interchange and dispersal between the two continents have been found in other squamates [e.g. *Anolis* lizards, ~30 Mya (Poe *et al.* 2017) and diploglossid lizards, ~45 Mya (Schools *et al.* 2022)]. Additionally, the propensity for long-distance overseas dispersal in geckos supports a timing that well pre-dates the isthmus closure as plausible (Fisher 1997, Gamble *et al.* 2011, Tonione *et al.* 2016, Daza *et al.* 2019).

Multiple divergence events within the west of Andes clade overlap with the hypothesized timing of accelerated Northern and Central Andean uplift between 3 and 10 Mya (*Phyllodactylus pumilus*, *P. leoni* + *P. darwini*; *P. pachamama* + *P. magister*; *P. angustidigitus* + *P. gerrhopygus*; *P. lepidopygus* + *P. microphyllus*; and *P. reissii* complex). The *P. pumilus* clade contains the Galápagos endemic species *P. darwini*, mainland high-elevation *P. leoni*, and coastal *P. pumilus* in Ecuador. A split between *P. pumilus* and the *P. darwini* + *P. leoni* clade coincides with the start of Andean uplift and changing climatic conditions. The divergence of *P. leoni* and *P. darwini* was ~8 Mya, during the period of the most rapid mountain building in the Ecuadorian Andes. This ancestor could have been in the early and relatively low Andes, which became an isolated mountain population and lowland population during rapid uplift, followed by the ancestral *P. darwini* lineage dispersing to the Galápagos. Torres-Carvajal *et al.* (2014) suggested that the ancestor of *P. darwini* could also have arisen from the Andes, in contrast to the other two colonizations where the ancestors were on the proximate coast of South America. Two other instances of divergence west of the Andes involve the *P. reissii* complex and the *P. microphyllus* + *P. lepidopygus* clade, which potentially hybridized/introgressed with other species in the region and require additional sampling to delimit species boundaries and assess biogeographical hypotheses. The *P. pachamama* + *P. magister* clade origin aligns with the formation of the Marañón River Valley, which might have acted as a barrier at various times to facilitate allopatric speciation (Espurt *et al.* 2009). Especially considering the high degree of endemism in the region and the rate of newly discovered species, there is likely to be much more uncharacterized diversity yet to be incorporated into this reconstruction (Koch *et al.* 2016).

Long-distance dispersal

Our analysis revealed support for several long-distance dispersal hypotheses in *Phyllodactylus*. In addition to previously known instances of dispersal from the South American mainland to the Galápagos and from Baja California to surrounding islands, we found overseas dispersal to be the most likely mechanism for dispersal events from South America to North America and from Central America to the Caribbean. Geckos have experienced long-distance dispersal both 'naturally' via rafting and by human-mediated transport (Carranza *et al.* 2002, Austin *et al.* 2004, Gamble *et al.* 2008, Agarwal *et al.* 2021). The divergence dating estimates support all dispersal events in *Phyllodactylus* as natural island colonizations rather than anthropogenic introductions.

Dispersal between different regions and even biomes in the Neotropics is common in squamates. In particular, the interchange between North and South America is often not a straightforward history, with many regions acting as a source for clades now present in Mesoamerica (Antonelli *et al.* 2018). Although land bridges are responsible for facilitating migration in some instances, climate and environmental factors must also be sufficient for interchange, and Isthmus of Panama formation itself is not reliable for dating migratory events (Bacon *et al.* 2016). We found that although *Phyllodactylus* probably used land connections for some dispersal events, long-distance overseas dispersal occurred multiple times between various island groups and most probably between the North and South American continents prior to the formation of a complete land bridge. Overseas dispersal cannot be ruled out for the movements between the Caribbean islands and continents, owing to the history of island hopping or 'seeding' at very early time points in island formation in the Antilles in other squamates (Thorpe *et al.* 2008, Pinto-Sánchez *et al.* 2015, Poe *et al.* 2017).

Although this dispersal pre-dates the major migration of many other vertebrates in the Great American Biotic Interchange, most other herpetofaunal histories point to dispersals that pre-date the land bridge, and very few can be placed confidently after isthmus closure (Vanzolini and Heyer 1985). Our reconstruction analyses support a single unidirectional dispersal of *Phyllodactylus* from South America to North America, with a Central American intermediate facilitating invasion of North America to Baja California, as opposed to a direct overseas dispersal between North and South America, which is rarely seen in reptiles (Vanzolini and Heyer 1985, Fritz *et al.* 2012, Head *et al.* 2012, Bona *et al.* 2018). Additionally, this provides another example of asymmetric dispersal from south to north for squamates (Poe *et al.* 2017), which counters the pattern seen in mammals (Carrillo *et al.* 2020) and salamanders (Elmer *et al.* 2013), but reflects the pattern seen in birds (Weir *et al.* 2009) and frogs (Pinto-Sánchez *et al.* 2012).

Andean uplift as a driver of diversification

The role of Andean uplift during the *Phyllodactylus* radiation within western South America is still unclear, because this analysis uncovered hidden diversity, and sampling across complete species ranges is lacking. High rates of endemism and diversification in the Andes region for the past 50 Myr make it difficult to attribute Andean uplift specifically as a driver of speciation in some of these lineages, particularly given that divergence times of most *Phyllodactylus* lineages in Peru (e.g. *Phyllodactylus thompsoni*, most of the species in the *P. johnwrighti* + *P. interandinus* clade, and particularly *P. delsolari*), pre-date Central Andean uplift 7–10 Mya. Some divergence events, however, do align with the time period of most active mountain building. Although our most strongly supported biogeographical model had a constrained dispersal parameter after Andean uplift, there was little difference between this model and one without any constraints, suggesting that the Andes as a geographical barrier between western and eastern South America is not particularly important to overall model fit. However, it seems most plausible that mountain building created new niche space that drove higher diversification and ecological specialization in the inter-Andean valleys as uplift accelerated. Allopatric speciation within biogeographical regions was not tested in the BioGeoBears model with current distribution data at the species level. The role of the Andes as a geographical barrier to facilitate allopatric speciation is well known in many other groups within the Marañón River Valley (Venegas *et al.* 2008, Patterson and Costa 2012, Winger and Bates 2015), but further work must be done to determine the full extent of *Phyllodactylus* species ranges for better understanding of the processes within the Andes. Additionally, cryptic diversity might affect other taxa in the main *Phyllodactylus* clade, which should be investigated with additional sampling before assessing Andean relationships any further.

Range expansion is correlated with increased diversification rates and richness in squamates; although range expansion over time is greater in Phyllodactylidae than in most other gecko families, the diversification rate is comparatively lower (Li and Wiens 2022). Our biogeographical reconstruction suggests that climatic niche change and subsequent divergence might be more important to diversification rather than range expansion alone, because the region with highest diversity is also the source for the group, which provides many variable microhabitats. Additionally, this might highlight a lack of described diversity in this group, underscoring the need for additional sampling (Nachman *et al.* 2023). This centre of micro-endemism in the Andes warrants further exploration as anthropogenic threats continue to loom.

CONCLUSION

We present the most complete time-calibrated phylogeny for *Phyllodactylus* to date and reconstruct the biogeographical history of the group. We found support for a South American ancestor for *Phyllodactylus* that subsequently dispersed across the continent and overseas multiple times to the Galápagos, North/Central America, and the Caribbean. The systematic analyses reveal an unstable taxonomy within *Phyllodactylus*, and placement of *Homonota* and *Garthia* render *Phyllodactylus* paraphyletic, because the *P. angustidigitus* + *P. gerrhopygus* clade is deeply divergent from *Phyllodactylus s.s.* Future work will seek to resolve taxonomic issues with genetic and geographical diversity highlighted in this study, particularly in the west Andean species, which should be integrated with previous studies (Torres-Carvajal *et al.* 2014, Koch *et al.* 2016, Ramírez-Reyes *et al.* 2020), in addition to paraphyly in the genus through additional morphological and molecular data. Conservation efforts should focus on these lizards as a model example of prolific dispersal capabilities, island endemism, and niche differentiation within a group (Dixon and Huey 1970, Venegas *et al.* 2008).

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SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

Sequences are available on the GenBank Nucleotide Database at accessions PV645394–PV645669, PV656227–PV656371, and PV631910–PV631992.

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