Swept ashore: Transoceanic dispersals and the biogeographic origins of Australian gekkonid lizards

Authors: Wesley J. Read[1*], Ian G. Brennan[2,1], Sarin Tiatragul[1], Paul, M. Oliver[3,2], R. Alex Pyron[4], Aaron M. Bauer[5], Todd R. Jackman[5], Alan R. Lemmon[6], Emily M. Lemmon[6], Christopher C. Austin[7], Craig C. Moritz[1], J. Scott Keogh[1], and Stephen M. Zozaya[1]

Affiliations: [1]Division of Ecology & Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia
[2]Biodiversity and Geosciences, Queensland Museum, PO Box 3300, South Brisbane BC, Queensland 4101, Australia
[3] School of Environment and Science, Griffith University, 170 Kessels Rd, Nathan 4111, QLD, Australia
[4]Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, DC 20052, USA
[5]Department of Biology, Villanova University, Villanova, Pennsylvania, United States of America
[6] Department of Biological Science, Florida State University, Tallahassee FL 32306, USA
[7]Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, United States of America
*Corresponding author: wesley.read@anu.edu.au

Data Accessibility: All data and code are available on GitHub at:

www.github.com/W-Read/Gekkonidae_biogeography

ABSTRACT

Oceanic dispersal is a rare mode of long-distance dispersal where taxa colonize disconnected islands or continents, sometimes resulting in new radiations. Australia has been isolated from other continental landmasses during the last 45 million years, and overwater colonisation has played a critical role in shaping its contemporary biota. Here, we investigate the biogeographic origins of Australian gekkonid lizards. Previous work has attributed the polyphyly of Australian gekkonids to multiple independent colonizations, some potentially via oceanic dispersal. To test this, we estimated phylogenetic relationships and divergence times using a genome-wide dataset for this globally distributed family and reconstructed ancestral biogeographic ranges. Our phylogeny reveals rapid diversification near the K-Pg boundary, coinciding with the crown origin of the family. Remarkably, ancestral range estimates indicate that gekkonids colonized Australia across eight independent events, the highest number by any non-volant vertebrate family. Most notably, the genus *Christinus* likely rafted at least 6,400 kilometres across the Indian Ocean—among the longest documented oceanic dispersals by a non-volant vertebrate. These findings emphasise the dominant role of oceanic dispersal in shaping the exceptionally diverse Australian squamate biota.

Keywords: BioGeoBEARS; diversification; Gekkonidae; long-distance dispersal; oceanic dispersal; phylogenomics; rafting

INTRODUCTION

Oceanic dispersal is a mechanism by which non-marine taxa colonize distant, disconnected landmasses, sometimes resulting in new radiations. The disjunct distributions of organisms across continents can be explained by this process, or ancient vicariance (de Queiroz, 2005). For species capable of flight or dispersal via wind or ocean currents, oceanic dispersal may be common, but non-volant organisms face greater challenges. For the latter, dispersal is most typically achieved through passive rafting on vegetation or flotsam (Censky et al., 1998; Gillespie et al., 2012). Despite successful rafting events likely being rare, studies documenting oceanic dispersal in vertebrates are now numerous (e.g., Ali & Hedges, 2025; Godinot, 2020; Melo et al., 2022; Reilly et al., 2019; Weil et al., 2022). Among non-volant vertebrates, squamates provide especially compelling examples of oceanic dispersal (Blom et al., 2019; Keogh et al., 2008; Gamble et al., 2010; Scarpetta et al., 2025a; Vidal et al., 2007; Welt & Raxworthy, 2022), making them a powerful system for investigating how oceanic dispersal may shape the assembly of diverse regional biotas.

Australia has remained isolated for much of the last ~45 Ma (Bijl et al., 2013) and is renowned for its highly endemic biota that contains a striking mix of lineages with vicariant and dispersalist origins. This raises an obvious question: where did this biodiversity originate? Some of this diversity can be attributed to ancient Gondwanan lineages that originated via vicariance and diversified *in situ*, including the marsupial (Black et al., 2012) and monotreme mammals (Flannery et al., 2022), myobatrachoid frogs (Brennan et al., 2024b), chelid turtles (Todd et al., 2013), pygopodoid geckos (Brennan & Oliver, 2017; Skipwith et al., 2019; Tiatragul et al., 2026), and passerine birds (McCullough et al., 2022; Moyle et al., 2016). However, much of Australia's biodiversity is derived from taxa that have colonized the landmass within the last 35 Ma, typically, but not always, from Asia (Lohman

et al., 2011; Oliver & Hugall, 2017; Skeels et al., 2023), including radiations such as the murine rodents (Rowe et al., 2019; Roycroft et al., 2022), bats (Tsang et al., 2019), scincid lizards (Chapple et al., 2023; Skinner et al., 2013) and varanid lizards (Brennan et al., 2021), and elapid snakes (Keogh, 1998; Sanders et al., 2008), typhlopid snakes (Tiatragul et al., 2023), and pythonid snakes (Esquerré et al., 2020). Although this period saw extensive island formation, amalgamation, and subsidence throughout the south-western Pacific (Hall, 1997; Hall, 2013), no continuous land connection between mainland south-east Asia and Australia has ever been established. As such, these lineages must have traversed marine barriers to colonize Australia and other Pacific islands (Skeels et al., 2023; Upchurch, 2008), indicating that the striking turnover at Wallace's line cannot always be attributed to vicariance.

Among non-volant vertebrates, gekkonid lizards (infraorder Gekkota) are notably adept at crossing vast marine distances, and numerous instances of oceanic dispersal are inferred from their biogeographic patterns (Carranza & Arnold, 2006; Fisher, 1997; Gamble et al., 2008, 2010; Oliver et al., 2016; Šmíd et al., 2013; Tonione et al., 2016). Four gecko families occur in Australia, of which three—Carphodactylidae (34 species), Diplodactylidae (202 species), and Pygopodidae (50 species)—are Gondwanan lineages that have been present on the continent for at least 60 Ma, with two independent transoceanic dispersals of Diplodactylidae to New Caledonia and Aotearoa/New Zealand (Brennan & Oliver, 2017; Skipwith et al., 2019; Tiatragul et al., 2026). The fourth, Gekkonidae, is far more species-rich at a global scale (1727 species) and pantropically distributed (Feng et al., 2007; Uetz et al., 2020). Only six of ~60 gekkonid genera occur naturally in Australia, and these have consistently been recovered as polyphyletic with respect to the broader family (Gamble et al., 2015; Grismer et al., 2021; Heinicke et al., 2010, 2011, 2014; Oliver et al., 2024). Of these, at least two—*Christinus* and *Gehyra*—are thought to have reached Australia via oceanic dispersal

(Heinicke et al., 2011, 2014). *Christinus* is a particularly striking case: its closest relatives are restricted to southern Africa, suggesting a transoceanic crossing of the Indian Ocean that would be one of the longest inferred for any non-volant vertebrate (Heinicke et al., 2014; Scarpetta et al. 2025a). The remaining four Australian gekkonid genera are thought to have dispersed to Australia from Asia within the last 10 Ma (Fujita et al., 2010; Worthington Wilmer & Couper, 2016), with *Nactus* and *Cyrtodactylus* each colonising Australia independently on two occasions, via either land bridges with New Guinea or rafting events (Jackman et al., 2008; Oliver et al., 2024; Wood et al., 2012; Zug & Fisher, 2012). Taken together, these patterns point to at least eight independent dispersal events to Australia by Gekkonidae—the most documented for any non-volant Australian vertebrate family—including several instances of oceanic dispersal. Despite this, no biogeographic study has treated Australian Gekkonidae as a whole, and broader phylogenomic analyses have been limited in their genus-level or Australian species-level sampling. Addressing both gaps with a near-species complete genome-wide dataset allows us to better constrain timing, pathways, and mode of colonisation across distantly related Australian lineages, within one of the most dispersive non-volant vertebrate families.

Here we identify how many times and by what routes gekkonid lizards colonized Australia. To do this, we used a genome-wide dataset of ~5,400 loci—with near-complete taxon sampling of Australian lineages and genus-level sampling for the family—to estimate phylogenetic relationships among 50 gekkonid genera and 214 described and putative species. Subsequently, we estimated divergence times and reconstructed the biogeographic history of the globally distributed family. We tested the hypothesis that Australian gekkonids dispersed to the continent via a combination of long-distance oceanic dispersal and stepwise island hopping through Wallacea and Melanesia. We further tested two competing

hypotheses about how *Christinus* dispersed to Australia: (1) via direct oceanic dispersal from Africa, or (2) stepping-stone dispersal via Antarctica. Our results highlight rapid divergence at the Gekkonid crown radiation and support eight independent colonizations of Australia, including one of the longest known overwater dispersals by a non-volant vertebrate.

METHODS

Molecular sampling, sequencing and assembly

We assembled a sequence-capture data set with near-complete sampling of both described and putative Australian gekkonid species (68 species and 40 additional putative species; 108 total), as well as additional gekkonids throughout the Pacific region to test the monophyly of Australian groups (a further 17 species). Sample selection for Australian species was based on previous work by Ashman et al. (2018), Kay (2008), Laver et al. (2017), Moritz et al. (2018), Oliver et al. (2020b, 2024), and Zozaya et al. (2023, 2025). In total, liver, heart, or muscle tissue was obtained from 189 samples. Three representative outgroup samples of Pygopodoidea were also included (*Lucasium iris*, QM J96406; *Ophidiocephalus taeniatus*, SAMA R28366; *Saltuarius eximius*, QM J92379). Tissues were sourced from the following institutions: Museum and Art Gallery of the Northern Territory, Queensland Museum, South Australian Museum, and Western Australian Museum.

Genomic DNA was extracted at the Australian National University (ANU) using a salt precipitation method before being diluted to 16.5 ng/μL in 110 μL. DNA was then sonicated into 200–600 base pair (bp) fragments using a Bioruptor NGS (Diagenode, Inc,). Subsequently, double-ended size selection was performed using Cytiva Sera-mag SpeedBead Magnetic Carboxylate beads at a 0.5x ratio to bind fragments over 600 bp in length. After transferring the supernatant to a new plate, DNA was bound by adding a 0.7x ratio of beads

prior to washing with 70% ethanol twice, before drying and then being eluted in 16 µL molecular grade water. Post size selection, DNA was enzymatically fragmented and simultaneously tagged with Illumina-compatible adapter sequences using a NextFlex Rapid DNA-Seq Kit 2.0 (PerkinElmer). Fragments were then barcoded using Unique Dual Index Barcodes prior to fragment amplification via six cycles of PCR using Eppendorf Mastercycler Nexus and Applied Biosystems ProFlex PCR System thermocyclers. Subsequently, nuclear exons were targeted using the Squamate Conserved Loci (SqCL) probes (Singhal et al., 2017), which target a combination of 386 Anchored Hybrid Enrichment (AHE; Lemmon et al., 2012), 4995 Ultra Conserved Elements (UCE; Faircloth et al., 2012), and 38 legacy exons for a total of 5,462 unique loci. Capture success was evaluated by comparing targeted and non-targeted loci levels both pre- and post-hybridisation using an Applied Biosystems QuantStudio3 qPCR machine. Finally, hybridised libraries were pooled on a single lane of Illumina HiSeq 2500 at the Biomolecular Resource Facility at the ANU. This sample collection and preparation was completed as part of the Australian Amphibian and Reptile Genomics initiative (AusARG) under the Phylogenomics Working Group.

To increase coverage of non-Australian genera, we sourced SqCL alignments for a further 89 taxa from the following projects: Skipwith, Bi & Oliver (2019)—four samples; Singhal et al. (2021)—1 sample; Title et al. (2024)—37 samples; and a pre-existing dataset of 367 of the 386 AHE loci described above (Lemmon et al., 2012) targeting a range of gekkonid genera—44 samples. Finally, outgroup samples for Eublepharidae (*Coleonyx switaki*; MVZHerp189994), Sphaerodactylidae (*Gonatodes humeralis*; GRCOLLI24011) and Phyllodactylidae (*Gymnodactylus darwinii*; CHUNB56644, and *Thecadactylus rapicauda*; JAC20992) were also sourced from these projects. In total, our sampling scheme covered 278 samples across 214 described and putative species and included most recognised gekkonid

genera (50/60). Sample identification, source, summary statistics, and analysis use can be found in supplementary material.

Sequence assembly

Sequence assembly and alignment was accomplished using a combination of custom scripts developed for the SqCL pipeline (see github.com/IanGBrennan/AusARG_Phylogenomics) and *pipesnake* (Brennan et al., 2024c) for the entire dataset. Briefly, this process involves assembly via deduplicating with BBMAP (Bushnell, 2014), trimming of adaptors and barcodes using TRIMMOMATIC (Bolger et al., 2014), and then mapping against reference sequences via BBMAP prior to assembly of contigs with SPAdes (Bankevich et al., 2012). Contigs are then mapped to target sequences via BLAT (Kent, 2002) before Pseudo-Reference Genomes (PRGs) are constructed from the highest quality contig-to-target matches. The resulting PRGs are then aligned with MAFFT (Katoh et al., 2002). This produced a total of 5,419 loci. Finally, we removed all UCEs below 600 bp in length (nine loci) and ran ClipKIT (Steenwyk et al., 2020) at an informativeness threshold of 0.80 to remove poorly informative sites.

Phylogenomics

Phylogenetic analyses

We estimated maximum likelihood gene trees for all SqCL markers using IQ-TREE v2.2.6 (Minh et al., 2020a). Modelfinder (Kalyaanamoorthy et al., 2017) was used to identify the best molecular evolution model and branch support was assessed via 1000 ultrafast bootstrap (UFB) replicates implemented using ufboot2 (Hoang et al., 2018). We then estimated the species tree using hybrid weighted-ASTRAL (wASTRAL; Zhang & Mirarab, 2022) implemented in the package ASTER (Zhang et. al., 2025). To investigate discordance among

gene trees, we also calculated gene concordance factors (gCF) in IQ-TREE (Minh et al., 2020b). As our subsequent dating analyses were conducted using only the AHE subset (see 'Divergence dating' for justification), we ran further wASTRAL analyses using only the following subsets of the AHE loci: (1) all AHE loci, (2) 100 fastest-evolving, (3) 100 longest, and (4) 100 most parsimony-informative (PIS), to assess whether locus selection influenced topology and to evaluate potential effects on our divergence time estimates.

Divergence dating

To estimate divergence times for taxa on the wASTRAL species tree, we used the software MCMCTree implemented in the PAML package (v4.7; Rannala & Yang, 2007). We relied on a set of five secondary node calibrations (dating scheme 1; Table S1) informed by the posterior estimates of Brennan et al. (2024a), as no fossil calibration points can be placed unequivocally within Gekkonidae at ages older than ~20 Ma (see Daza et al., 2014; Vasilyan et al., 2017). All priors were applied with SkewT distributions. The first four were placed on the divergence of the outgroups Sphenodontidae, Pygopodoidea, Eublepharidae, and Phyllodactylidae, with the final prior placed on the divergence between the gekkonid genera *Gekko* and *Gehyra*. As MCMCTree has been demonstrated to over- or underestimate divergence times when using different node calibration strategies (dos Reis et al., 2015; dos Reis et al., 2018), we conducted a secondary analysis (dating scheme 2) where we removed the priors on the pygopodoid, eublepharid, and *Gekko* + *Gehyra* splits to determine whether posterior estimates converged on similar ages. Further justification of prior usage and specifications is included in the Supplementary Material.

The input topology was specified using the wASTRAL species tree constructed using the whole dataset. We pruned to a single sample per Australian species/putative species, or a

single tip per genera that did not include Australian representatives. This resulted in a total of 188 tips. We used only the AHE dataset for dating analyses as UCE data were unavailable for most non-Australian genera (37/50 genera; 46/188 total tips) and rates are known to vary significantly within and among UCEs (Tagliacollo & Lanfear, 2018). We further accounted for potential rate heterogeneity within the AHE subset by using AMAS (Borowiec, 2016) to remove the third codon position and split the alignment (total 539,997 bp) into four rate-quartile partitions based on rate estimates previously established for AHE loci (Brennan et al., 2024a). We then used baseml to estimate branch lengths, gradient, and the Hessian for each of the four partitions, before running MCMCTree on the concatenated outputs (gradient and Hessian (in.BV file)) and the concatenated alignment for a total of four independent analyses. The output mcmc files from MCMCTree were combined using LogCombiner (Bouckaert et al., 2014) and rerun using option "print = -1" in the .ctl file, before being checked for convergence (ESS > 200) using Tracer V1.7.2 (Rambaut et al., 2018).

Biogeography

To investigate the frequency, origin, and dispersal mode of gekkonid colonizations of Australia, we modelled the biogeography of the family using the R package BioGeoBEARS V1.1.3 (Matzke, 2013). We divided the distribution of Gekkonidae into nine geographic regions: Africa, Madagascar (including the Seychelles), eastern Asia (mainland south-east Asia including China, Mongolia and Nepal), western Asia, India (including Sri Lanka), Sundaland (islands of south-east Asia west of Wallace's line), Melanesia (islands of south-east Asia and the Pacific east of Wallace's line), Australia, and Antarctica. While somewhat unusual to separate Australia and New Guinea in continental biogeographic analyses, this was done as few gekkonid species are shared between them (one *Gehyra* and *Lepidodactylus* respectively), and this study focuses on the colonisation of Australia by the family. The

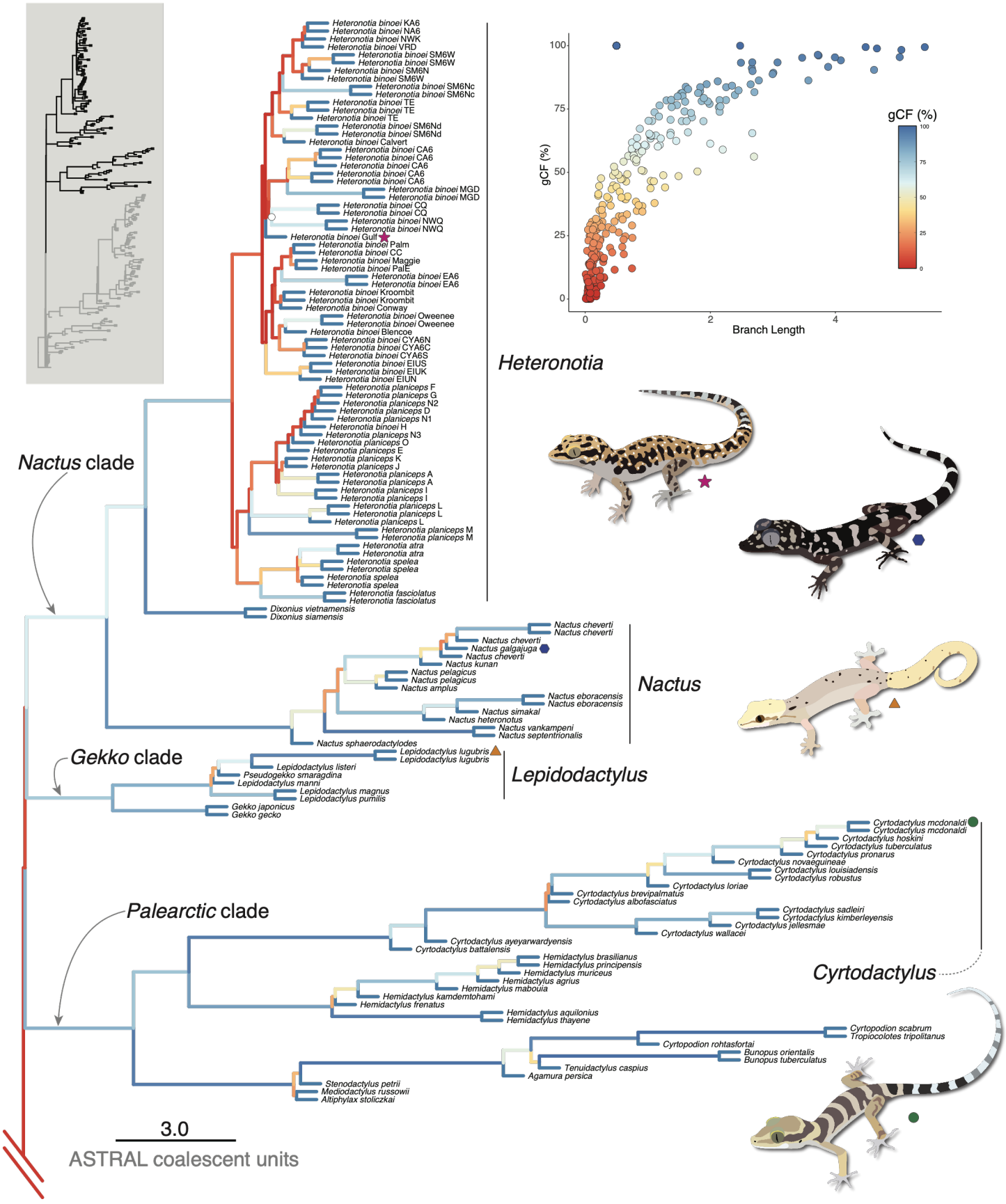
Americas were excluded based on the six species occurring there being deeply embedded within their respective Old World genera, which are only distantly related to Australian lineages (Carranza & Arnold, 2006; Ceríaco & Passos, 2023; Lanna et al., 2018). For non-Australian genera, we included a single tip encoded as the range of its respective genus (e.g., the representative tip for *Stenodactylus* was encoded as occurring in both Africa and West Asia). Where a genus included both Australian and non-Australian species, we also retained the deepest split among Australian representatives (the Australian crown group) and their closest non-Australian relative—these tips were assigned the range of their respective species, not genus. To investigate any potential biases introduced by our region encoding strategy, we ran two sensitivity analyses where we 1) included the Americas as an additional region, and 2) encoded each tip to reflect the distribution of the retained species. We stratified the MCMCTree phylogeny in 5 Ma increments and recorded the closest pairwise distances between the nine geographic areas at these time slices using GPlates (Müller et al., 2018) to construct dispersal distance (x) and dispersal probability (w) matrices; the dispersal distance matrix penalised overwater dispersals exceeding 200 km. We first fitted the DEC (Ree & Smith, 2008), DIVALIKE (Ronquist, 1997), and BAYAREALIKE (Landis et al., 2013) models as well as the free parameter j (Matzke, 2014). After initial model fit was found to strongly favour DEC and DEC + j, we fit the dispersal scalers x and w, including all combinations, to these two models. We assessed model fit using AIC and AICc values and conducted additional likelihood ratio tests to test whether free parameters improved model performance. Using the model with the best fit (DEC + j + x), we then compared an alternate stepping-stone mode of dispersal for *Christinus* by incorporating a hypothetical ancestral taxon distributed in Antarctica into the tree, prior to comparing model fit between this and the standard DEC + j + x implementation. Finally, we ran 200 biogeographic stochastic maps using the best model and combined the outputs using custom scripts to account for

uncertainty in ancestral range reconstructions and to estimate the frequency and direction of dispersal events between areas (Matzke, 2014). Full model specifications, justifications, and further discussion is included in the supplementary material (see also Matzke, 2014; Van Dam & Matzke, 2016).

RESULTS

Phylogenomics and divergence time estimation

The full wASTRAL analysis recovered Australian gekkonids as polyphyletic with respect to the broader family. Relationships of Australian genera to their closest relatives are consistent with previous studies: *Christinus* is sister to the clade containing the southern African genera *Afrogecko*, *Cryptactites*, and *Ramigekko*; Australian *Gehyra* form a monophyletic group sister to *G. rohan* and *G. vorax* of New Guinea and the south-west Pacific; *Heteronotia* is sister to the mainland south-east Asian *Dixonius*, which together are sister to *Nactus*; Australian *Nactus* are polyphyletic, with both clades sister to different Melanesian lineages; Australian *Cyrtodactylus* are also polyphyletic—northeast Australian species form a clade nested within New Guinea relatives, while *C. kimberleyensis* is sister to *C. sadleiri* of Christmas Island, south of Java; and *Lepidodactylus pumilus* is sister to the New Guinean *L. magnus* (Figure 1a, 1b). Many of the earliest divergences within Gekkonidae are characterised by exceptionally short branch lengths, low gene tree concordance (gCF < 30) (Figure S3), and sometimes low support (pp < 0.7). Most relationships with low support occur among the earliest diverging clades, and topologies constructed using the AHE subsets show some variation in these relationships (Figures S4–S7). Critically, however, Australian clades are recovered in consistent positions with high support across all phylogenies. Further discussion of generic-level relationships and topological discordance is provided in the Supplementary Results.


Heteronotia binoei KA6
Heteronotia binoei NA6
Heteronotia binoei NWK
Heteronotia binoei VRD
Heteronotia binoei SM6W
Heteronotia binoei SM6W
Heteronotia binoei SM6N
Heteronotia binoei SM6W
Heteronotia binoei SM6Nc
Heteronotia binoei SM6Nc
Heteronotia binoei TE
Heteronotia binoei TE
Heteronotia binoei TE
Heteronotia binoei SM6Nd
Heteronotia binoei SM6Nd
Heteronotia binoei Calvert
Heteronotia binoei CA6
Heteronotia binoei CA6
Heteronotia binoei CA6
Heteronotia binoei CA6
Heteronotia binoei CA6
Heteronotia binoei MGD
Heteronotia binoei MGD
Heteronotia binoei CQ
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Heteronotia binoei NWQ
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Heteronotia binoei Gulf
Heteronotia binoei Palm
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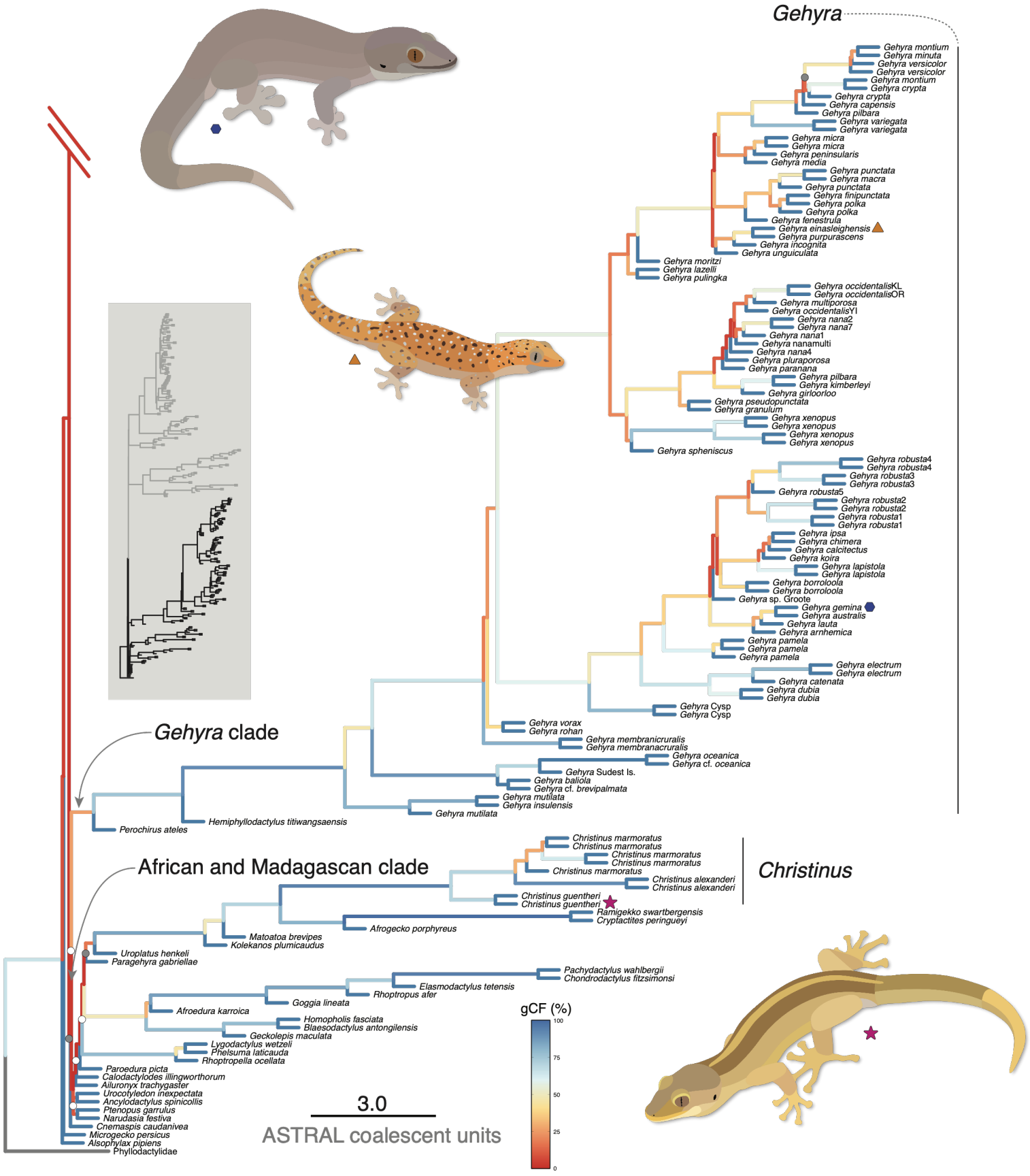
Heteronotia binoei Kroombit
Heteronotia binoei Conway
Heteronotia binoei Oweenee
Heteronotia binoei Oweenee
Heteronotia binoei Blencoe
Heteronotia binoei CYA6N
Heteronotia binoei CYA6C
Heteronotia binoei CYA6S
Heteronotia binoei EIUS
Heteronotia binoei EIUK
Heteronotia binoei EIUN
Heteronotia planiceps F
Heteronotia planiceps G
Heteronotia planiceps N2
Heteronotia planiceps D
Heteronotia planiceps N1
Heteronotia binoei H
Heteronotia planiceps N3
Heteronotia planiceps O
Heteronotia planiceps E
Heteronotia planiceps K
Heteronotia planiceps J
Heteronotia planiceps A
Heteronotia planiceps A
Heteronotia planiceps I
Heteronotia planiceps I
Heteronotia planiceps L
Heteronotia planiceps L
Heteronotia planiceps L
Heteronotia planiceps M
Heteronotia planiceps M
Heteronotia atra
Heteronotia atra
Heteronotia spelea
Heteronotia spelea
Heteronotia spelea
Heteronotia spelea
Heteronotia fasciolatus
Heteronotia fasciolatus
Dixonius vietnamensis
Dixonius siamensis
Nactus clade
Heteronotia
gCF (%)
Branch Length
Nactus cheverti
Nactus cheverti
Nactus cheverti
Nactus galgajuga
Nactus kunan
Nactus pelagicus
Nactus pelagicus
Nactus amplus
Nactus eboracensis
Nactus eboracensis
Nactus simakal
Nactus heteronotus
Nactus vankampeni
Nactus septentrionalis
Nactus sphaerodactylodes
Nactus
Gekko clade
Lepidodactylus lugubris
Lepidodactylus lugubris
Lepidodactylus listeri
Pseudogekko smaragdina
Lepidodactylus manni
Lepidodactylus magnus
Lepidodactylus pumilis
Gekko japonicus
Gekko gecko
Lepidodactylus
Palearctic clade
Cyrtodactylus mcdonaldi
Cyrtodactylus mcdonaldi
Cyrtodactylus hoskini
Cyrtodactylus tuberculatus
Cyrtodactylus pronarus
Cyrtodactylus novaeguineae
Cyrtodactylus louisiadensis
Cyrtodactylus robustus
Cyrtodactylus loriae
Cyrtodactylus brevipalmatus
Cyrtodactylus albofasciatus
Cyrtodactylus sadleiri
Cyrtodactylus kimberleyensis
Cyrtodactylus jellesmae
Cyrtodactylus wallacei
Cyrtodactylus ayeyarwardyensis
Cyrtodactylus battalensis
Hemidactylus brasilianus
Hemidactylus principensis
Hemidactylus muriceus
Hemidactylus agrius
Hemidactylus mabouia
Hemidactylus kamdemtohami
Hemidactylus frenatus
Hemidactylus aquilonius
Hemidactylus thayene
Cyrtodactylus
Cyrtopodion scabrum
Tropiocolotes tripolitanus
Cyrtopodion rohtasfortai
Bunopus orientalis
Bunopus tuberculatus
Tenuidactylus caspius
Agamura persica
Stenodactylus petrii
Mediodactylus russowii
Altiphylax stoliczkai
3.0
ASTRAL coalescent units


Gehyra
Gehyra montium
Gehyra minuta
Gehyra versicolor
Gehyra versicolor
Gehyra montium
Gehyra crypta
Gehyra crypta
Gehyra capensis
Gehyra pilbara
Gehyra variegata
Gehyra variegata
Gehyra micra
Gehyra micra
Gehyra peninsularis
Gehyra media
Gehyra punctata
Gehyra macra
Gehyra punctata
Gehyra tinipunctata
Gehyra polka
Gehyra polka
Gehyra fenestrula
Gehyra einasleighensis
Gehyra purpurascens
Gehyra incognita
Gehyra unguiculata
Gehyra moritzi
Gehyra lazelli
Gehyra pulingka
Gehyra occidentalisKL
Gehyra occidentalisOR
Gehyra multiporosa
Gehyra occidentalisYI
Gehyra nana2
Gehyra nana7
Gehyra nana1
Gehyra nanamulti
Gehyra nana4
Gehyra pluraporosa
Gehyra paranana
Gehyra pilbara
Gehyra kimberleyi
Gehyra girloorloo
Gehyra pseudopunctata
Gehyra granulum
Gehyra xenopus
Gehyra xenopus
Gehyra xenopus
Gehyra xenopus
Gehyra spheniscus
Gehyra robusta4
Gehyra robusta4
Gehyra robusta3
Gehyra robusta3
Gehyra robusta5
Gehyra robusta2
Gehyra robusta2
Gehyra robusta1
Gehyra robusta1
Gehyra ipsa
Gehyra chimera
Gehyra calcitectus
Gehyra koira
Gehyra lapistola
Gehyra lapistola
Gehyra borroloola
Gehyra borroloola
Gehyra sp. Groote
Gehyra gemina
Gehyra australis
Gehyra lauta
Gehyra arnhemica
Gehyra pamela
Gehyra pamela
Gehyra pamela
Gehyra electrum
Gehyra electrum
Gehyra catenata
Gehyra dubia
Gehyra dubia
Gehyra Cysp
Gehyra Cysp
Gehyra vorax
Gehyra rohan
Gehyra membranicruralis
Gehyra membranacruralis
Gehyra oceanica
Gehyra cf. oceanica
Gehyra Sudest Is.
Gehyra baliola
Gehyra cf. brevipalmata
Gehyra mutilata
Gehyra insulensis
Gehyra mutilata
Gehyra clade
Perochirus ateles
Hemiphyllodactylus titiwangsaensis
African and Madagascan clade
Christinus marmoratus
Christinus marmoratus
Christinus marmoratus
Christinus marmoratus
Christinus marmoratus
Christinus alexanderi
Christinus alexanderi
Christinus guentheri
Christinus guentheri
Christinus
Ramigekko swartbergensis
Cryptactites peringueyi
Afrogecko porphyreus
Matoatoa brevipes
Kolekanos plumicaudus
Uroplatus henkeli
Paragehyra gabriellae
Pachydactylus wahlbergii
Chondrodactylus fitzsimonsi
Elasmodactylus tetensis
Rhoptropus afer
Goggia lineata
Afroedura karroica
Homopholis fasciata
Blaesodactylus antongilensis
Geckolepis maculata
Lygodactylus wetzeli
Phelsuma laticauda
Rhoptropella ocellata
Paroedura picta
Calodactylodes illingworthorum
Ailuronyx trachygaster
Urocotyledon inexpectata
Ancylodactylus spinicollis
Ptenopus garrulus
Narudasia festiva
Cnemaspis caudanivea
Microgecko persicus
Alsophylax pipiens
Phyllodactylidae
gCF (%)
100
75
50
25
0
3.0
ASTRAL coalescent units

298 **Figure 1.** Gekkonidae species tree constructed using weighted ASTRAL (wASTRAL) shows
299 extensive gene tree discordance around the crown of the family and the polyphyletic
300 placement of Australian clades. Nodes denoted by grey (local posterior probability [pp]
301 values $0.90 > x > 0.70$) and white circles ($pp \leq 0.70$) are considered equivocal; all other
302 nodes $pp > 0.90$. Branch colours correspond to gene concordance factors (gCF) and represent
303 the percent (%) of gene trees that decisively support the respective bifurcation. Scale bar
304 shows branch length in coalescent units: terminal (tip) branch lengths are not estimated by
305 wASTRAL and are arbitrary. Inset plot in part 1 show that gCF values increase with
306 increasing branch lengths. Major clade branches indicated by labels with arrows, genera with
307 Australian representatives are indicated by labels on the right. Illustrations depict taxa
308 indicated by coloured symbols.
309
310 Both divergence dating analyses using MCMCTree produced similar date estimates (Figures
311 2, S10) and, consequently, we present the results from dating scheme 1 (all calibrations) here.
312 Our results indicate that the crown split of living Gekkonidae occurred 63.3 Ma (95%
313 Highest Posterior Density (HPD): 58.3–68.6) and that subsequent splits followed in short
314 succession, with the establishment of all major clades by 59.0 Ma (54.2–63.9; Figure 2).
315 These deep, clade level splits, as well as many subsequent genus-level splits, occurred rapidly
316 with extensive HPD overlap. Of the 50 genera included in our sampling scheme, 40 (80%)
317 diverged prior to 30 Ma based on mean estimates. The crown age of Australian *Gehyra* is
318 also relatively old at 26.11 Ma (23.3–29.0). In contrast, crown ages for the remaining
319 Australian genera and clades are younger: 17.2 Ma (HPD: 14.7–20.0) for *Christinus*; 8.1 Ma
320 (6.7–9.5) for north-east Queensland *Cyrtodactylus*; 9.3 Ma (8.4–10.3) for *Heteronotia*; and
321 7.0 (5.7–8.4) and 7.2 (5.7–8.8) Ma for the two *Nactus* clades. This is particularly notable
322 within the *H. binoei* and *H. planiceps* species groups, where all lineage splits (36 species and

species-level lineages; Zozaya et al., 2023, 2025) have occurred within the last 8.5 Ma based on mean estimates (Figure S10).

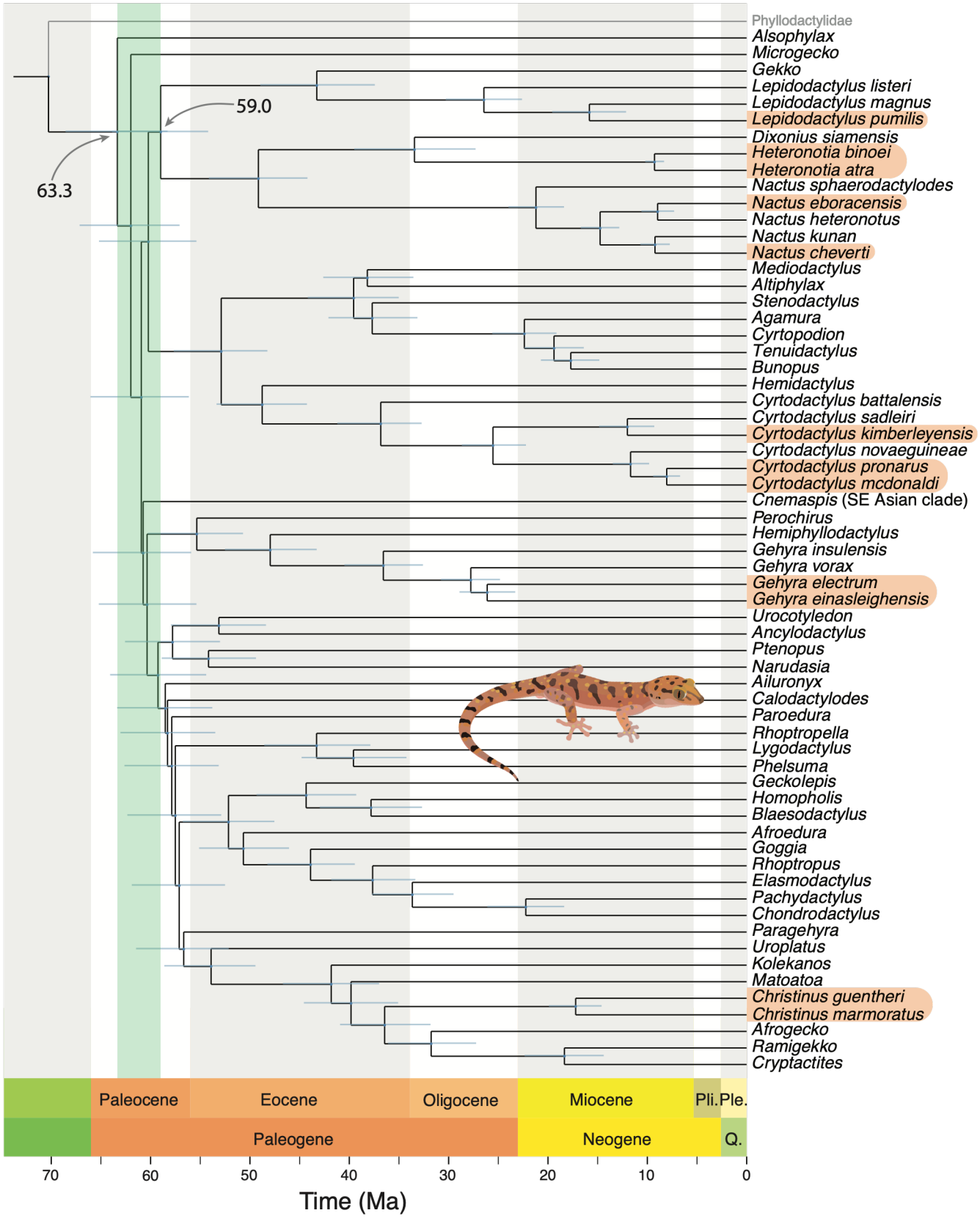


Figure 2. Time-calibrated phylogenetic tree of Gekkonidae, showing rapid diversification around the crown age of the family. Divergence times were estimated with MCMCTree, using 368 Anchored Hybrid Enrichment (AHE) loci and five secondary calibration points. The tree has been pruned to a single tip per genus for visual purposes, except where the genus includes both Australian and non-Australian representatives. Australian lineages are outlined in orange. The light green bar highlights the ~4 Ma period during which all major clades of Gekkonidae diverged. The input topology was specified as the weighted ASTRAL tree in Figure 1. The fully-sampled ultrametric tree is available as Figure S9. Illustration depicts *Gehyra unguiculata.*

Biogeography

Reconstruction of gekkonid ancestral ranges estimated eight independent colonizations of mainland Australia and nearby islands (including islands of the Torres Strait and Kimberley region). Model comparison favoured the overwater dispersal model over the stepping-stone model via Antarctica for *Christinus* (LnL overwater = -177.4; LnL stepping-stone = -186.7; Δ AICc =18.7; AICc weight overwater = 0.76; AICc weight stepping-stone < 0.01). The DEC + *j* + *x* and DEC + *j* + *x* + *w* overwater models were the most heavily favoured and differed only in AICc weighting (LnL for both models = -177.4; Δ AICc =2.3; AICc weight DEC + *j* + *x* = 0.76; AICc weight DEC + *j* + *x* = 0.24) (Table S2). Including the free parameter *j* (founder events) and the distance scalar *x* (the value of the exponent applied to the distance matrix, i.e., distance between biogeographic areas) significantly improved the performance of models (*D*-statistic > 34.46, df = 1, *p*-value < 0.001), but the dispersal scalar *w* (the value of the distance applied to environmental distance matrix, i.e., overland *vs*. oceanic dispersal) did not (*D*-statistic < 0.001, df = 1, *p*-value = 1) (Table S3). The parameter estimates for *j* (= 0.02) and *x* (= -0.29) from the best performing model (Table S2) indicate that founder-event

speciation is moderately important during the diversification of Gekkonidae, and that geographic distance has played a significant role in constraining dispersal. That the dispersal scalar *w* did not improve model fit is indicative of environment (land *vs*. water) not inhibiting gekkonid dispersal. The two sensitivity analyses showed no variation in ancestral ranges for Australian lineages (Figures S12, S13).

Regarding Australian gekkonid lineages, the most favoured model reconstructed the ancestors of *Christinus* dispersing to Australia from Africa; *Gehyra* from Melanesia; *Heteronotia* from eastern Asia; *Nactus* from Melanesia (both lineages); *Lepidodactylus* from Melanesia; and *Cyrtodactylus* from Melanesia (both lineages). For the broader clades defined in Figure 1, the Palearctic group was reconstructed as originating in eastern and western Asia, the *Gehyra* and *Nactus* groups in Melanesia, the *Gekko* group in Sundaland or Melanesia, and the African and Madagascan group in Madagascar. No single area was recovered as the most likely ancestral area for crown Gekkonidae; rather, support was split roughly equally among western and eastern Asia—a result likely influenced by the placement of *Alsophylax pipiens* and *Microgecko persicus* as the two earliest diverging lineages in the tree.

Stochastic mapping using the DEC + *j* + *x* model estimated an average of 92.8 ± 1.46 (mean ± SD) total shifts between biogeographic areas across the entire phylogeny. Of these, the majority (65.0 ± 0; 70.0% of total events) were inferred as cladogenetic events, versus a smaller number (27.8 ± 1.46; 30.0% of total events) of anagenetic events. Eastern Asia was the biggest source of outward dispersal (11.6 ± 0.6), followed closely by Melanesia (10.1 ± 0.7) (Figure 3b). Africa (9.7 ± 0.6), followed by eastern Asia (8.8 ± 0.8), were the largest sinks for inward dispersal and, unsurprisingly, the majority of dispersal to Australia was

dominated by the geographically adjacent Melanesia (6.1 ± 0.8), followed by Africa (0.7 ± 0.4) and eastern Asia (0.6 ± 0.7) (Figure 3c).

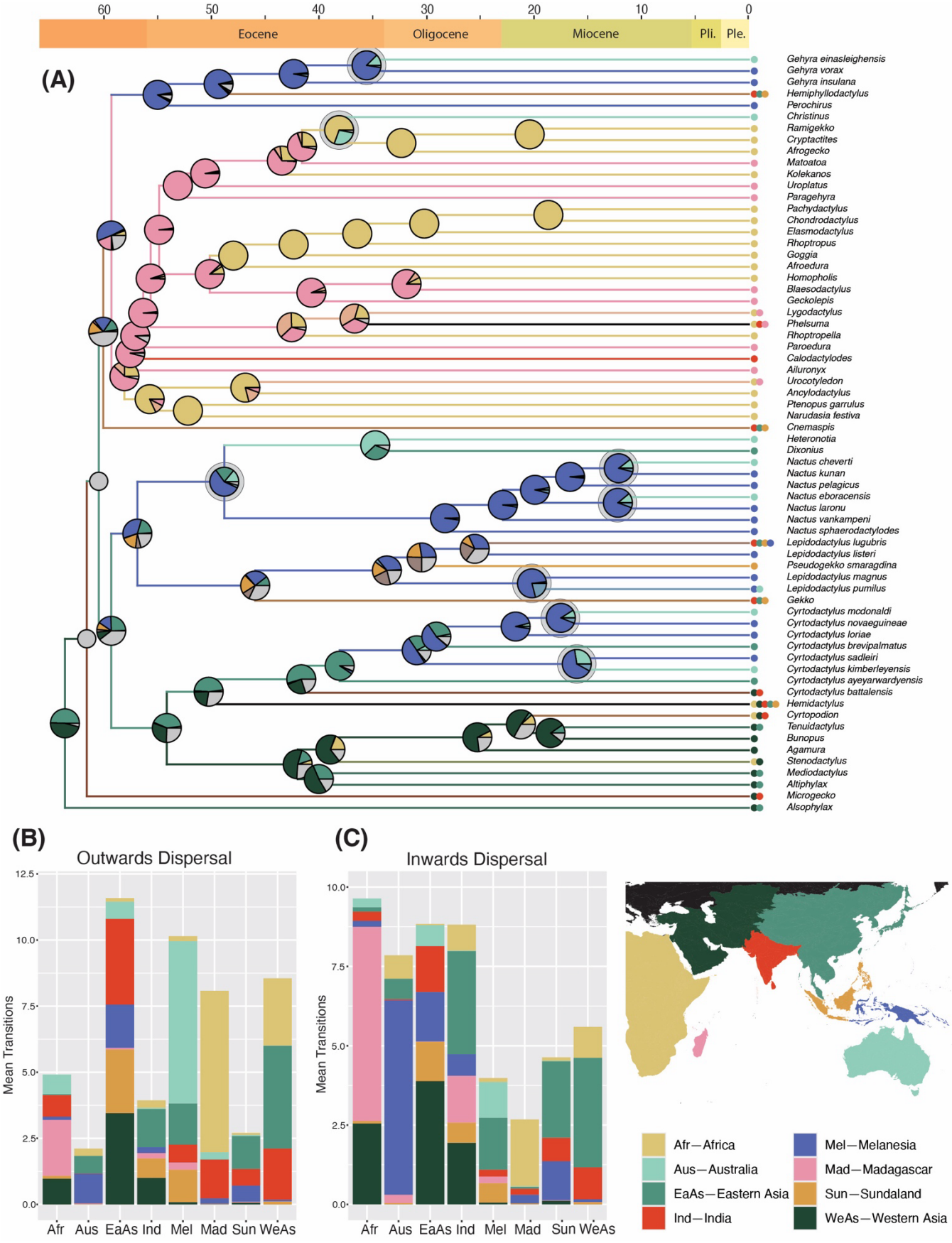


Figure 3. Gekkonid biogeographic history favours long-distance dispersal events, multiple independent colonizations of Australia, and an ancestral range of eastern and western Asia for the family. (A) Ancestral biogeographic ranges estimated for Gekkonidae in BioGeoBEARS using the DEC + *j* + *x* model. Pie charts display ancestral area probabilities based on 200 biogeographic stochastic maps (BSM). States accounting for less than 20% of BSMs at all nodes are collapsed into 'other' (grey). Two ancestral nodes show no single state exceeding 20% and are shown entirely in grey. Tip circles correspond to assigned biogeographic area—these areas are coloured in the global map in the lower right. Nodes that lead to Australian lineages are outlined by grey circle edges. Biogeographic areas were assigned based on their respective genera, except for Australian clades and relatives where they instead correspond to species distributions. Colours present in pie charts but not in the legend (i.e., mixed colours) indicate presence across multiple continental areas. Bar plots visualise frequency and composition of both (B) outward and (C) inward transitions for each area—the highest number of outwards dispersals occurred from eastern Asia, and most dispersals to Australia originated from Melanesia.

DISCUSSION

The origin of Australian gekkonid lizards is an intriguing biogeographical puzzle due to their phylogenetic relationships within the broader, pantropically distributed family, with some of their closest relatives occurring thousands of kilometres away. Here we use a genome-wide dataset, integrative phylogenomics, and ancestral range estimates to resolve the biogeographic history of all Australian gekkonid clades. Our results highlight eight independent dispersals to the continent, the most to Australia by any non-volant vertebrate family, and several instances of oceanic dispersal. In the case of *Christinus*, this involved its ancestors dispersing the width of the Indian Ocean from southern Africa—a distance of

~6,400 km—among the longest recorded for any non-volant vertebrate (Scarpetta et al. 2025a). Collectively, these results underscore a family that underwent rapid diversification ~60 Ma and has since been able to repeatedly overcome marine barriers, potentially more frequently than any other non-volant vertebrate clade (Carranza & Arnold, 2006).

Phylogenomics & divergence dating

Our divergence estimates indicate that crown Gekkonidae began diversifying soon after the K-Pg boundary (65 Ma), a period of massive faunal turnover following the Cretaceous mass-extinction (McInerney & Wing, 2011; Schulte et al., 2010). Subsequent diversification occurred rapidly, as evidenced by the short internodes and low gene concordance, with the establishment of all major clades by 59.0 Ma (54.2–63.9). These estimates are younger but broadly consistent with those of Burbrink et al. (2020; gekkonid crown age 72.6 Ma), Singhal et al. (2021; 74.3 Ma), and Title et al. (2024; 68.3 Ma). This rapid cladogenesis immediately following a mass extinction event is consistent with an ecological opportunity hypothesis (Wellborn & Langerhans, 2014), whereby extinction opened niche space and promoted elevated rates of diversification. Rapid diversification near the K-Pg boundary has also been identified in Placentalia (Álvarez-Carretero et al., 2022), and ecological opportunity has been posited to explain the diversification of groups such as the Neoaves (Stiller et al., 2024) and angiosperms (Dimitrov et al. 2023). Gekkonids may have been predisposed to exploit this opportunity, as they are noted to flourish in disturbed and novel environments due to generalist diets, broad thermal niches, and rapid generation times (Hoskin 2011; Kraus 2009; Montaña et al., 2025; Rato et al., 2021).

Such rapid accumulation of lineages can obscure evolutionary relationships due to the proliferation of incomplete lineage sorting (ILS) and introgression, as reflected in the

426 extensive gene discordance and low support for some relationships in our results (Degnan &
427 Rosenberg, 2006, 2009; Mallet et al., 2016; Tan et al., 2023). True phylogenetic relationships
428 are difficult to disentangle for some nodes due to this extensive gene tree discordance, and
429 this was likely compounded by the reduced number of loci available for many of our non-
430 Australian taxa (Fig. S1). The inclusion of more loci, specifically from intergenic regions,
431 may help resolve these recalcitrant nodes, as has been demonstrated in other groups (e.g.,
432 Chen et al., 2017; Stiller et al. 2024).
433
434 We found strong support for most relationships in Gekkonidae and corroborate previous
435 studies in finding that Australian gekkonids are not monophyletic. *Christinus* is recovered as
436 deeply embedded within an African and Madagascan clade and sister to a group confined
437 entirely to the southern coastline of South Africa. The split between *Christinus* and these
438 African genera is relatively old (36.4 Ma; 31.9–41.0) and supports the out-of-Africa rafting
439 hypothesis of Heinicke et al. (2014). Our results also highlight the monophyly of Australian
440 *Gehyra*—which are closely related to the Melanesian *G. vorax* and *G. rohan*—supporting a
441 single colonization of the continent by Melanesian ancestors around 26 Ma (Heinicke et al.,
442 2011). *Gehyra* has subsequently diversified to become the most species-rich gekkotan genus
443 in Australia with nearly 60 species (Wilson & Swan, 2025).
444
445 *Heteronotia*, *Nactus*, and *Dixonius* form a strongly supported clade with deep divergences
446 among genera (Jackman et al., 2008) despite morphological conservatism. Notably,
447 *Heteronotia* is sister to *Dixonius* rather than the geographically adjacent—and sometimes
448 sympatric—*Nactus*, a relationship we discuss further in the 'Biogeography' section below.
449 Our divergence estimates for *Heteronotia* are considerably older than those of Fujita et al.
450 (2010)—9.3 Ma *vs*. 4 Ma—likely reflecting differences in molecular datasets and calibration

strategies. Australian *Cyrtodactylus* comprise two clades: north-eastern Queensland taxa are sister to New Guinean species (Grismer et al., 2021; Tallowin et al., 2018) and *C. kimberleyensis* is allied with *C. sadleiri* from Christmas Island, south of Java. These latter two species belong to the *C. laevigatus* complex, for which our sampling was limited, but *C. kimberleyensis* is known to be most closely related to Timorese taxa (Kathriner, 2015; Reilly et al., 2023). Finally, *Lepidodactylus pumilus* and *L. magnus* are sister to the remainder of *Lepidodactylus* (including *Pseudogekko*), reinforcing the finding that the *pumilus* group represents an old lineage with considerable body size variation (Oliver et al., 2018).

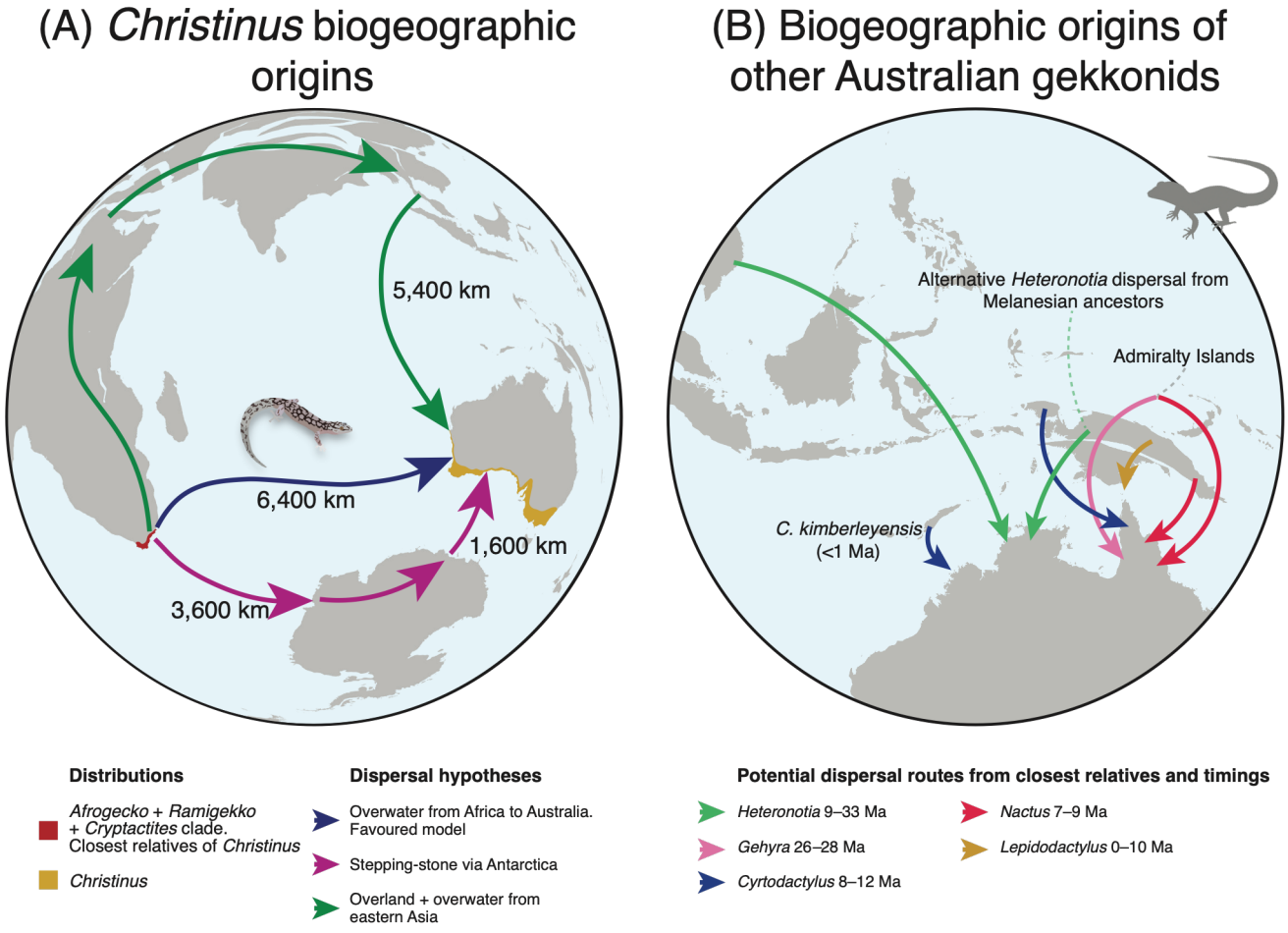


Figure 4. Hypothesised geographic origins and dispersal routes consistent with phylogenetic relationships and results of biogeographic analyses (Figures 2, 3), which highlight repeated overwater dispersal during the colonization of Australia by gekkonid lizards. (A) Proposed

dispersal routes of *Christinus* to Australia, with overwater distances indicated. (B) Potential dispersal routes linking all other Australian gekkonid lineages to their closest relatives. Ages denote estimated divergence time ranges, with the younger age representing the Australian clade crown age and the older age representing the divergence from the closest relative; lineages are inferred to have dispersed to Australian sometime within these ranges. Each arrow indicates an independent colonization event, except for *Heteronotia*. Note that the divergence timing of *Lepidodactylus pumilus* is taken from Oliver et al. (2018) whose sampling included more species from the *L. pumilus* group. Maps generated in GPlates (Müller et al., 2018) at 30 Ma (A) and 10 Ma (B) following Landis (2017).

Biogeography

Squamates are prolific long-distance overwater dispersers (Blom et al., 2019; Carranza & Arnold, 2003; Scarpetta et al., 2025a), likely because of their low dehydration rates, slow metabolisms, high salinity tolerance, and precocial young (Hsu et al., 2021). However, gekkotans stand out as exceptional oceanic dispersers even among squamates, and hypotheses invoking oceanic dispersal to explain the disjunct distributions of geckos are correspondingly well-established—particularly among *Hemidactylus* and *Gehyra* (Agashe et al., 2025; Agarwal et al., 2021; Carranza & Arnold, 2006; Heinicke et al., 2011; Oliver et al., 2026; Tonione et al., 2016). The dispersal propensity of gekkotans may reflect a suite of traits common to many lineages: small body size, adhesive toepads, hard-shelled and sometimes sticky eggs, and in some taxa, parthenogenesis (Cuellar, 1977). This is most clearly demonstrated by the massive range expansions of the Asian House Gecko (*Hemidactylus frenatus*) and the parthenogenic Mourning Gecko (*Lepidodactylus lugubris*), with many non-deliberate introductions occurring due to human-mediated cargo shipping (Carranza & Arnold, 2006; Chance et al., 2024; Nania et al., 2020; Rödder et al., 2008). A similar pattern

has been identified in Bufonidae, where a range-expansion phenotype has been linked to global colonization, including transoceanic dispersals, and rapid diversification (Fonte et al., 2019; Pramuk et al., 2007; Van Bocxlaer et al., 2010; Wu et al., 2025), although bufonids failed to colonize Australia without the assistance from people in the sugar cane industry.

Modelling the biogeography of Australian clades reveals a total of eight independent dispersal events to the continent, more than any other family of non-volant vertebrates—the next closest being Scincidae with at least three colonisations (Brennan et al., 2024a; Chapple et al., 2023; Skinner et al., 2011). Most remarkably, the ancestors of *Christinus* likely rafted ~6,400 km across the Indian Ocean (Figure 4a). At a more global scale, our biogeographic reconstruction reveals additional instances of oceanic dispersal, including repeated interchange between Madagascar and Africa (see also Gippner et al., 2021), and an inferred ancestral range for the family spanning eastern and western Asia. However, given our sparse sampling of non-Australian taxa, we focus on Australian gekkonids here.

The single-step transoceanic dispersal by *Christinus* is only known to be surpassed by *Brachylophus* iguanas (>8,000 km; Keogh et al., 2008; Scarpetta et al., 2025a) and potentially by *Cryptoblepharus* skinks (6,600–7,000 km; Blom et al., 2019), oplurid iguanas (6,500–6,800 km; Welt & Raxworthy, 2022), and possibly Mascarene *Nactus* geckos (5,300–8,000 km; Heinicke et al., 2010). For *Christinus*, oceanic dispersal from Africa to Australia post-Gondwana breakup is, to our knowledge, the first recorded for a non-flying vertebrate; although a matching pattern has been identified in plants (Barker et al., 2007; Crisp & Cook, 2013; Skeels et al., 2025) and mygalomorph spiders (Harrison et al., 2017). It is not surprising that the direct overwater model was favoured over the stepping-stone model; dispersal via Antarctica would still require a similar total rafting distance (~5,200 km), and

highly dispersive taxa are thought to have a greater probability of dispersing via a singular long-distance event rather than via successive, stepping-stone events (Crisp et al., 2011). Despite this, we note here that an Antarctic hypothesis cannot be rejected on this basis, and future fossil evidence may disprove the evidence presented here. Finally, the only remaining alternative—land-based dispersal across Asia followed by oceanic dispersal to Australia—is implausible as it would require both long-distance overland (~14,000 km) and overwater dispersal (5,200 km), as well as the extinction of all geographically intermediate ancestors.

The feasibility of rafting the width of the Indian Ocean is further supported by the high dispersibility noted in several other gekkonid species (Carranza & Arnold, 2006; Grismer et al., 2022; Heinicke et al., 2011; Šmíd et al., 2013; Weiss & Hedges 2007), the presence a proto-Antarctic circumpolar current that developed sometime around 30 Ma (Evangelinos et al., 2024; Feldmann & Schweitzer, 2006)—circulating in an easterly direction from Africa towards Australia—and the temperate climes of south-western Australia and southern Africa (Lamont & He, 2017; Rundel et al., 2016) that may have aided successful establishment post dispersal. The ancestors of *Christinus* must have arrived sometime between when the genera split from its African relatives 36.4 (31.9–41.0) Ma and the crown age of the genus 17.2 (14.7–20.0) Ma. Despite this long period of separation, both *Christinus* and its closest African relatives display evidence of niche conservatism in retaining similar phenotypes and a close association with Mediterranean climates in both continents. Analyses of biome conservatism in plants have also found evidence for exchange between the arid and sclerophyll biomes in Africa and Australia (Crisp et al. 2009), emphasising that dispersal across thousands of kilometres of water can in some cases be less challenging than making a major shift in climatic niche. Since arriving in Australia, *Christinus* have also made further long-distance overwater dispersals to the Lord Howe Island (580 km to the east of the

continent) and Norfolk Island (1,400 km east), despite now being largely absent from the Australian east coast. These two island groups only surfaced ~3 and ~7 Ma, respectively, and have never been connected to other landmasses (Jones & McDougall, 1973; McDougall et al., 1981).

The remaining Australian genera and clades present broadly similar but independent dispersals to the continent via a combination of rafting, island hopping, and potential land bridges through south-east Asia and Melanesia during the last ~30 Ma (Figure 4b). The geological history of the south-western Pacific from the Oligocene to present is complex, with extensive periods of island building and immersions resulting from the interactions between four continental plates (Davies, 2012; Hall, 1997). Such complexity is difficult to capture within the discrete biogeographic categories of BioGeoBEARS, and our incomplete sampling of non-Australian taxa further limits the precision of these reconstructions. Nonetheless, our topology and dating analyses offer some insight.

Our dating analyses place the first split within the Melanesian distributed *Gehyra* clade (the split with *Perochirus*) at 55.4 (50.7–60.3) Ma. This predates the Australia-Eurasian plate collision (~25 Ma; Hall, 1997), suggesting the *Gehyra* clade ancestor crossed >1,500 km of ocean from south-east Asia to islands in the Pacific. Subsequently, the Australian clade of *Gehyra* split from the remainder of the genus sometime around 26 Ma, again likely via oceanic dispersal from Melanesian ancestors. Northern Australia's more mesic conditions during this period could have favoured the mesic-adapted non-Australian *Gehyra*, before subsequent diversification into the interior. Colonising Australia during this time is broadly consistent with several other squamate groups, notably agamid (Brennan et al., 2026a; Scarpetta et al., 2025b) and varanid lizards (Brennan et al., 2021), as well as pythonid

(Esquerré et al., 2020) and typhlopid snakes (Tiatragul et al., 2023). *Gehyra* may have accomplished the most non-mediated oceanic dispersals of any gekkotan genus (Heinicke et al., 2011; Oliver et al., 2026; Tonione et al., 2016), having colonized islands as far east as French Polynesia (Fisher, 1997; Tonione et al., 2016). Despite this, our results indicate that the Australian clade has not contributed to outward dispersal events. Oliver et al. (2026) also recovered exceptionally little interchange between Australia and elsewhere, and our tree further strengthens this inference by providing much stronger support for the monophyly of Australian *Gehyra*.

Australian lineages of *Nactus* and north-eastern *Cyrtodactylus* are far younger than *Gehyra*, and dispersal to the continent from New Guinea likely occurred sometime between 5.5–9.5 Ma for all clades. Lower sea levels during this period may have facilitated dispersal (Miller et al., 2020), though the exact timing of when land bridges formed between Australia and the New Guinea region remains poorly understood. Interchange between Australia and New Guinea during the middle to late Miocene was extensive and included marsupial mammals (Mitchell, 2014), microhylid frogs (Brennan et al., 2026b), murine rodents (Roycroft et al., 2022) and planorbid snails (Gauffre-Autelin et al., 2021). *Cyrtodactylus kimberleyensis* likely arrived more recently given it is very closely related to an undescribed member of the *C. laevigatus* complex in Timor (Chan et al., 2023; Kathriner, 2015). As the species is known only from its holotype and subsequent surveys have failed to locate further specimens, this individual may represent a contemporary dispersal event rather than an established population. Australia's only native *Lepidodactylus* (*L. pumilis*) is not endemic and restricted to the northern Torres Strait, which it presumably colonized from southern New Guinea. Records of *L. lugubris* from mainland Australia are the result of human-mediated introductions (Fitzsimons, 2011), and it remains unclear whether *L. lugubris* is naturally

present in the Torres Strait. Though currently only a minor fraction of Australia's gekkonid diversity, further human-mediated introductions may continue to increase the distributional ranges and diversity of *Lepidodactylus*—as well as the entirely non-native genus *Hemidactylus* (Hoskin, 2011).

Unlike these previous examples, our analyses did not recover a continuous eastwards expansion from Asian ancestors for the *Nactus* clade. Instead, our biogeographic estimation favoured Melanesia as the ancestral range of the clade at 49.2 (44.2–54.2) Ma, predating most estimates for the formation of the proto-Papuan Archipelago (Hall, 2017). Subsequently, the ancestor of *Heteronotia* and *Dixonius* dispersed to Australia, before *Dixonius* finally dispersed back to mainland south-east Asia. A similar sister taxon relationship between Indochinese and Australasian lineages is observed in agamids (Scarpetta et al., 2025b), suggesting potential dispersal predated extensive land formation in Sundaland and Wallacea. Deeply divergent lineages across Pacific islands are also noted in frogmouth birds (Oliver et al., 2020a), varanid lizards (Pavón-Vázquez et al., 2022), Tiliquini skinks (Brennan et al., 2024a), and the aforementioned *Gehyra* clade. These lineages potentially represent greatly attenuated remnants of radiations linked to ancient but unstable and extinction-prone arc systems in the south-west Pacific.

Alternatively, a more parsimonious reconstruction might maintain an ancestral range of the *Nactus* clade as east Asian, with subsequent independent dispersals of *Nactus* to Melanesia—and then twice to Australia—and *Heteronotia* to Australia. Regardless of their true biogeographic history in the broader region, *Heteronotia* likely arrived in Australia at a similar time to *Nactus* and *Cyrtodactylus* but has since spread across the continent and undergone far more rapid lineage accumulation in the last ~9 Ma (Grismer et al., 2022;

Oliver et al., 2024; Zozaya et. al., 2025). As with *Cyrtodactylus*, *Nactus* colonized Australia on two independent occasions, with the Australian lineages separated by Melanesian taxa (Heinicke et al., 2010). Intriguingly, these Melanesian taxa are lowland-restricted species found north of the now continuous New Guinean Central Cordillera, and one, *N. kunan*, is found only on the Bismarck Archipelago, a series of islands that have never been connected to other land masses (Oliver et al., 2024). These patterns suggest oceanic dispersal has also played a role in the diversification of these lineages.

Conclusion

Resolving the biogeographic origins of clades at a global scale remains challenging, and our study has limitations characteristic of the field more broadly. Firstly, many species remain genetically unsampled or have poorly resolved distributions, and native ranges are further clouded by recent human introductions. This can mislead ancestral state reconstructions, and even with perfect sampling, extinction remains an issue (Crisp et al., 2011). Ancestral biogeographic reconstructions using BioGeoBEARS necessitate drawing discrete biogeographic boundaries that do not fully capture the subtleties of the distributions of real organisms. For example, the geologically complex island chains of south-east Asia and Melanesia were here classified into two regions, yet they represent one of the most complex geological systems on Earth that could defensibly be subdivided further. Finer discretisation of south-east Asia and Melanesia—which would also necessitate further sampling of missing taxa—would no doubt better resolve the complex dispersal history of gekkonids in this region. Irrespective of these limitations, our study clearly highlights a dramatic pattern of eight independent colonisations of Australian by gekkonid lizards, including long-distance oceanic dispersals. This reinforces the significance of oceanic dispersals in explaining the global distribution and radiation of this diverse family.

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Supplementary material for:

Swept ashore: Transoceanic dispersals and the biogeographic origins of Australian gekkonid lizards

Supplementary Tables

Table S1.

Node calibrations used in the MCMCTree dating analyses. The node numbers these were applied to are visualised in Figure S9.

Node	Scheme1	Scheme2	*xi*	*omega*	*alpha*	*nu*
189	y	y	2.55271205	0.02396999	-10.691342	9.34681611
190	y	n	0.99013548	0.09889148	1.49926774	331.915734
191	y	n	0.93509969	0.09806964	1.57217349	118.134835
193	y	y	0.65565628	0.09235249	2.33676518	402.915707
196	y	n	0.56685653	0.09234561	2.53116602	294.84316

Table S2. BioGeoBEARS model comparisons and maximum likelihood parameter estimates. Models ordered according to AICc, low AICc indicates better fit to data. LnL = log likelihood, # of parameters = number of parameters of the model, d = rate of anagenetic dispersal, e = rate of anagenetic extinction, j = rate of cladogenetic long-distance dispersal, x = the value of exponent applied to the distance matrix, w = the value of the exponent applied to the dispersal matrix.

Model	LnL	# parameters	*d*	*e*	*j*	*x*	*w*	AICc	AICc weights
DEC+X+J	-177.4	4	4.63E-4	1.00E-12	0.02	-0.29	1	363.4	0.76
DEC+X+W+J	-177.4	5	4.64E-4	1.00E-12	0.02	-0.29	0	365.7	0.24
DEC+X+J (Stepping-stone)	-186.7	4	5.03E-4	4.76E-4	0.02	-0.28	1	382.1	6.64E-05
DEC+J	-195.3	3	1.15E-3	1.00E-12	0.04	0	1	397.0	3.86E-08
DEC+X	-199.6	3	6.64E-4	2.54E-4	0	-0.28	1	405.7	5.04E-10
DEC+X+W	-199.6	4	6.64E-4	2.54E-4	0	-0.28	0	407.9	1.62E-10
BAYAREALIKE	-216.9	2	1.64E-3	2.74E-05	0	0	1	437.7	4.12E-12

DEC	-216.9	2	1.64E-3	2.74E-5	0	0	1	437.9	4.96E-17
DIVALIKE+J	-216.8	3	1.43E-3	1E-12	0.04	0	1	439.6	1.81E-17
BAYAREALIKE+J	-230.3	2	8.69E-4	2.19E-2	0	0	1	464.6	7.16E-23
DIVALIKE	-244.9	2	2.62E-3	3.22E-3	0	0	1	493.7	3.47E-29

Table S3. BioGeoBEARS likelihood ratio tests for nested models. Alt = alternate model, null = null model, and LnL = log likelihood.

alt	null	LnL alt	LnL null	*D*-statistic	*p*-value
DEC+J	DEC	-195.3	-216.9	43.14	5.10E-11
DEC+J+X	DEC+X	-177.4	-199.6	44.54	2.50E-11
DEC+J+X+W	DEC+X+W	-177.4	-199.6	44.54	2.50E-11
DEC+X	DEC	-199.6	-216.9	34.46	4.30E-9
DEC+J+X+W	DEC+J+X	-177.4	-177.4	-3.60E-5	1
DIVALIKE+J	DIVALIKE	-216.8	-244.9	56.15	6.70E-14
BAYAREALIKE+J	BAYAREALIKE	-204.4	-230.3	51.75	6.30E-13

Table S4. Summary of events from 200 Biogeographic Stochastic Maps with the DEC + *j* + *x* model.

	founder	a	d	e	subset	vicariance	sympatry	all_disp	ana_disp	all_ana	all_clado	total_events
means	24.24	0	27.79	0	7.17	3.48	30.11	52.02	27.79	27.79	65	92.78
stdevs	2.77	0	1.46	0	2.7	1.7	2.49	2.73	1.46	1.46	0	1.46
sums	4848	0	5557	0	1435	695	6022	10405	5557	5557	13000	18557

Table S5. Total mean dispersal events and mean standard deviations for 200 SBM using the DEC + J + X model.

	Source	SD	Sink	SD
Africa	4.90	0.62	9.65	0.57
West Asia	8.56	0.52	5.59	0.65
India	3.94	0.65	8.83	0.73
East Asia	11.60	0.93	8.83	0.79

Sundaland	2.72	0.49	4.64	0.56
Melanesia	10.14	0.71	3.97	0.64
Madagascar	8.09	0.43	2.68	0.38
Australia	2.11	0.37	7.85	0.40

1223

Supplementary Figures

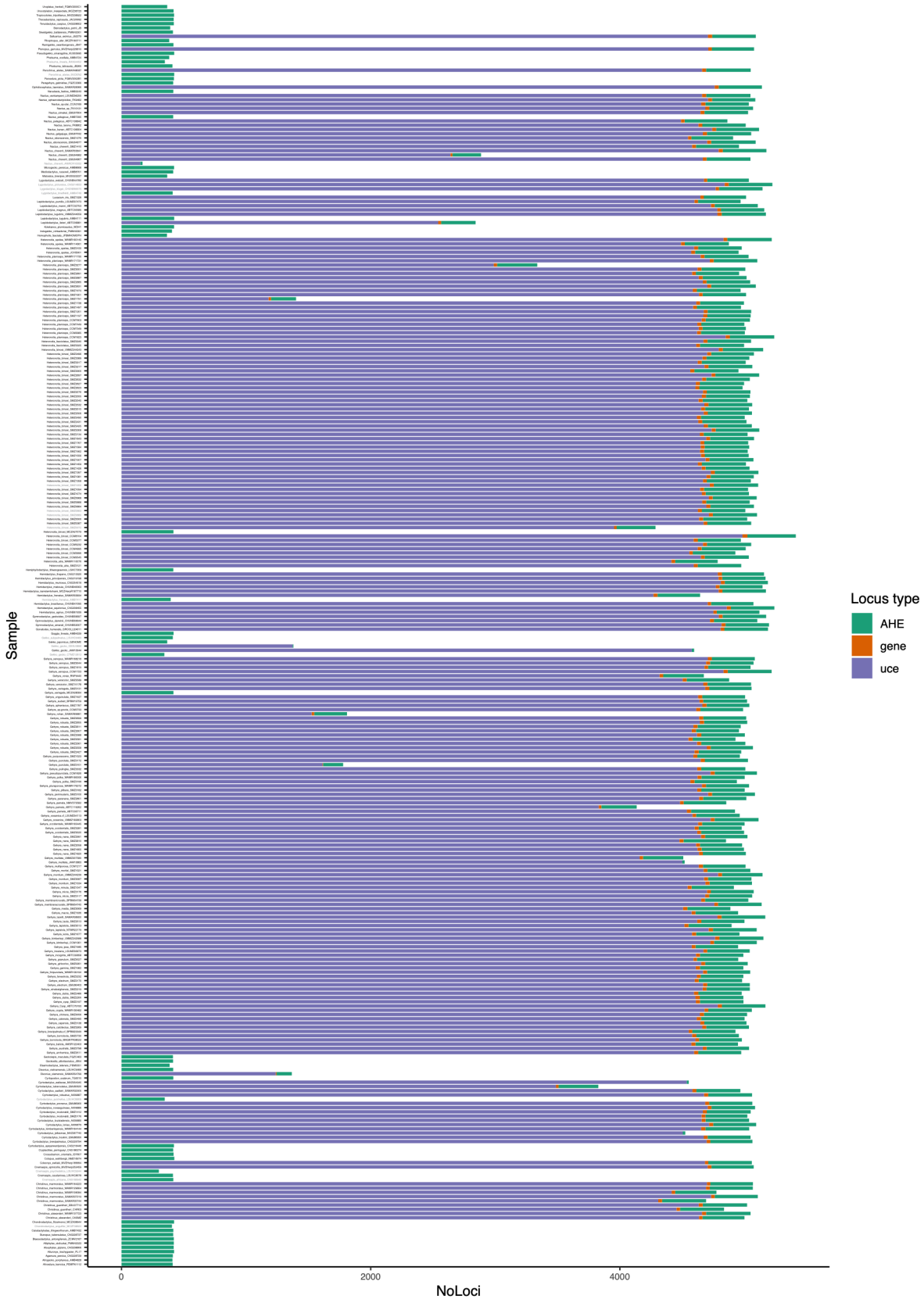


Figure S1. Locus type and number summarized by sample included in this study. Samples in grey text at left were not included in any final analyses. Sample inclusion across different analyses is list in the 'sample_inclusion.csv' file in the online repository.

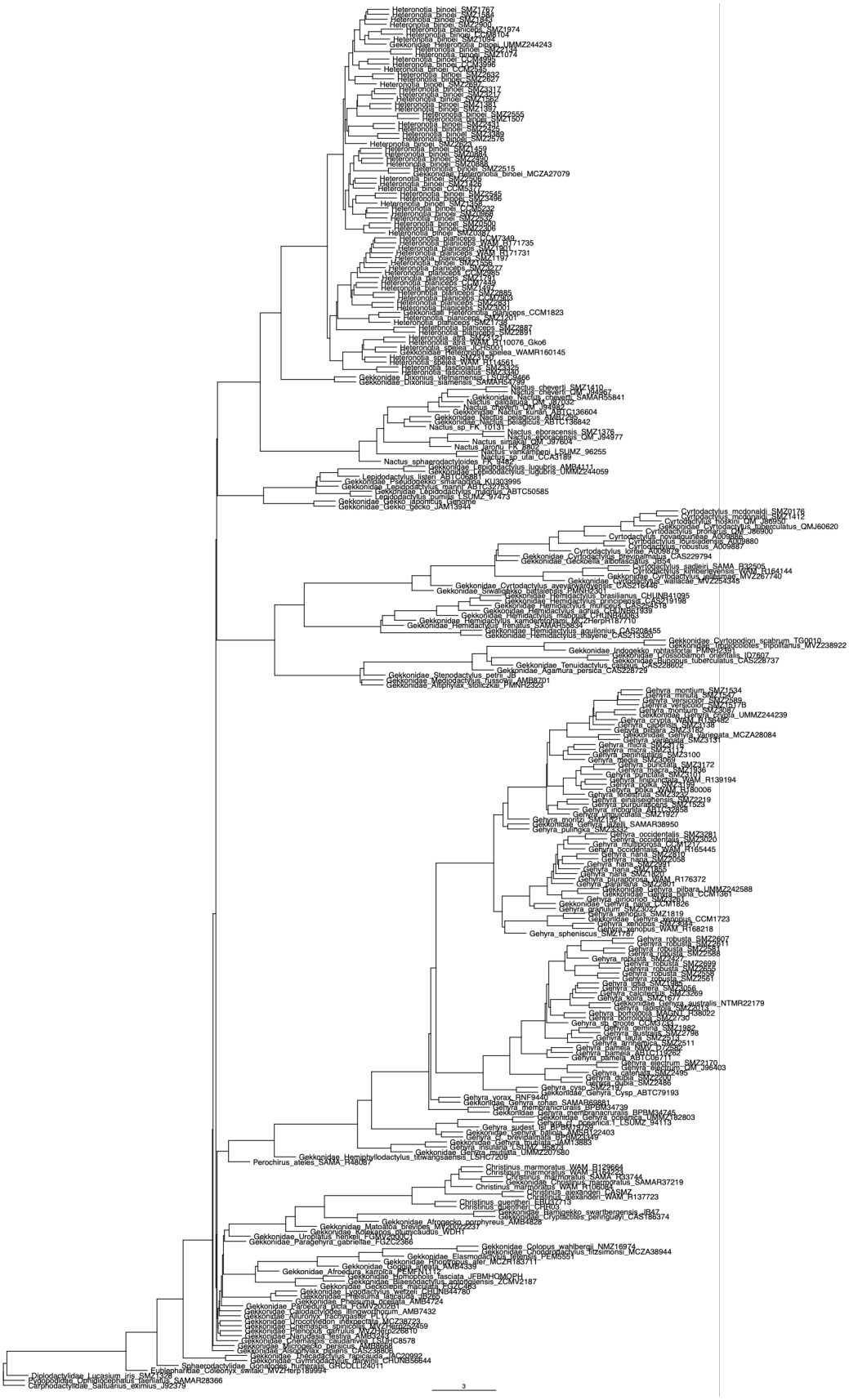


Figure S2. Species tree from weighted ASTRAL-hybrid constructed using the whole genomic dataset. Scale bar shows branch length in coalescent units: terminal (tip) branch

lengths are not estimated by wASTRAL and are arbitrary. Tree files for all phylogenetic analyses are available in the online repository.

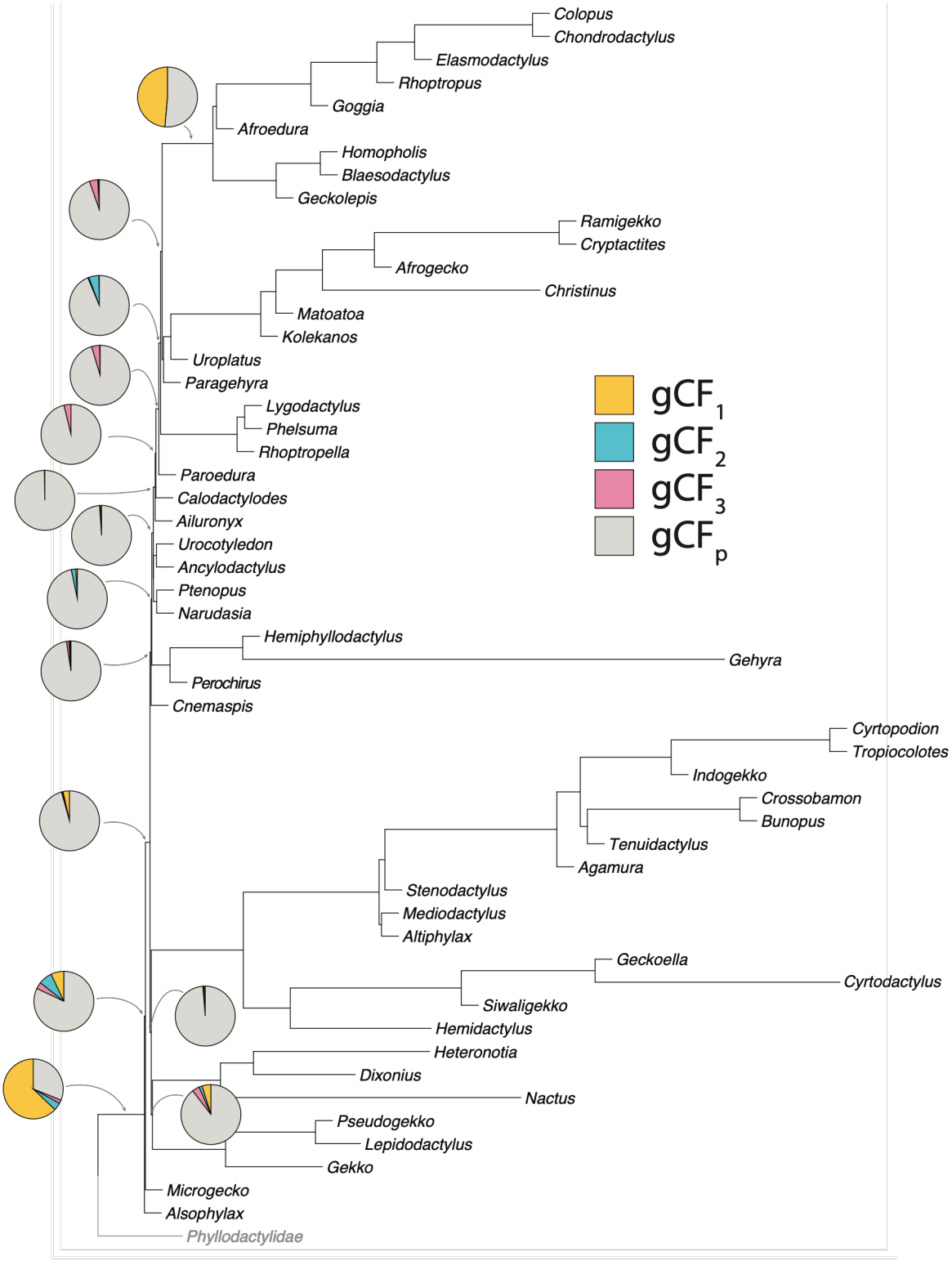


Figure S3. Weighted ASTRAL phylogeny of Gekkonidae constructed using the whole genomic dataset (Fig. S2) and pruned to show intergeneric relationships and gene concordance factors (gCF) along the tree's backbone. gCF values represent the proportion of gene trees that support a given bifurcation. Pie charts on branches indicate the percent of loci that support the presented bifurcation

(gCF$_1$, orange), one of each of the two other most common resolutions (gCF$_2$, blue; gCF$_3$, pink) or all other possibilities (gCF$_p$, grey). Areas of low concordance (i.e., the family backbone) indicate topological uncertainty, likely due to high levels of incomplete lineage sorting.

Figure S4. Species tree from weighted ASTRAL-hybrid constructed using all AHE loci. Scale bar shows branch length in coalescent units.

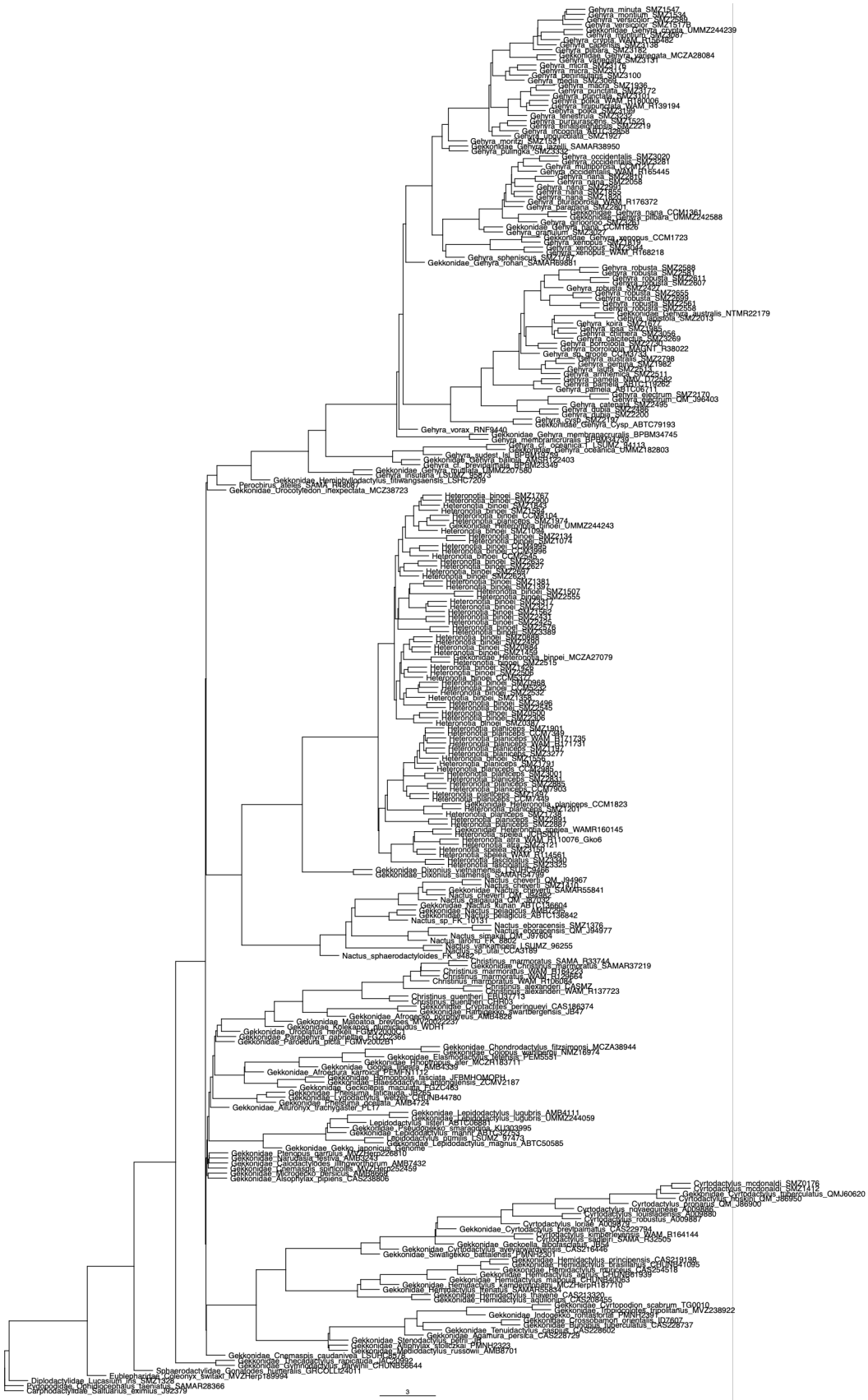
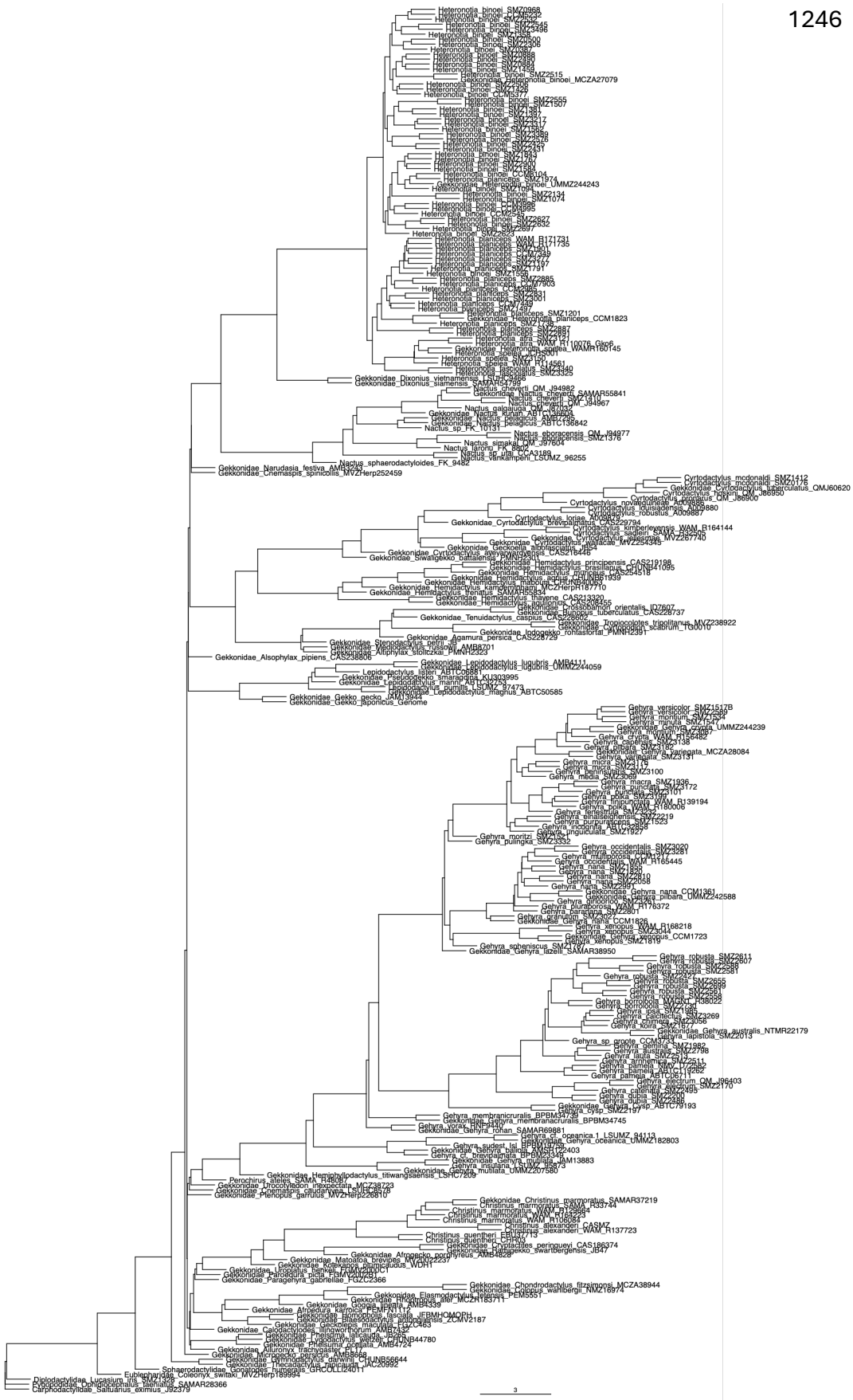


Figure S5. Species tree from weighted ASTRAL-hybrid constructed using the 100 AHE loci with the highest number of parsimony informative sites. Scale bar shows branch length in coalescent units.



1247 **Figure S6.** Species tree from weighted ASTRAL-hybrid constructed using the 100 fastest
1248 evolving AHE loci. Scale bar shows branch length in coalescent units.

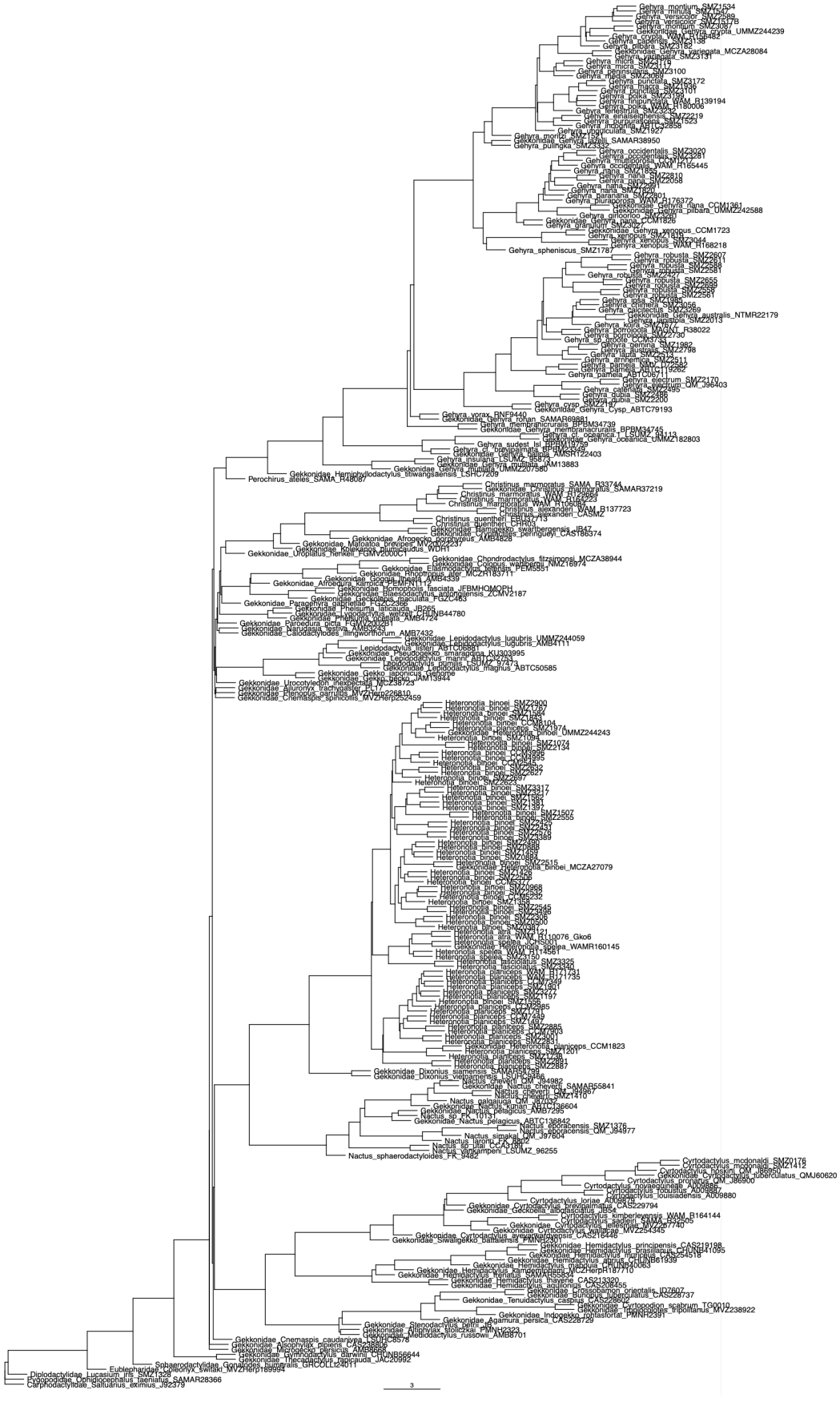


Figure S7. Species tree from weighted ASTRAL-hybrid constructed using the 100 longest AHE loci. Scale bar shows branch length in coalescent units.

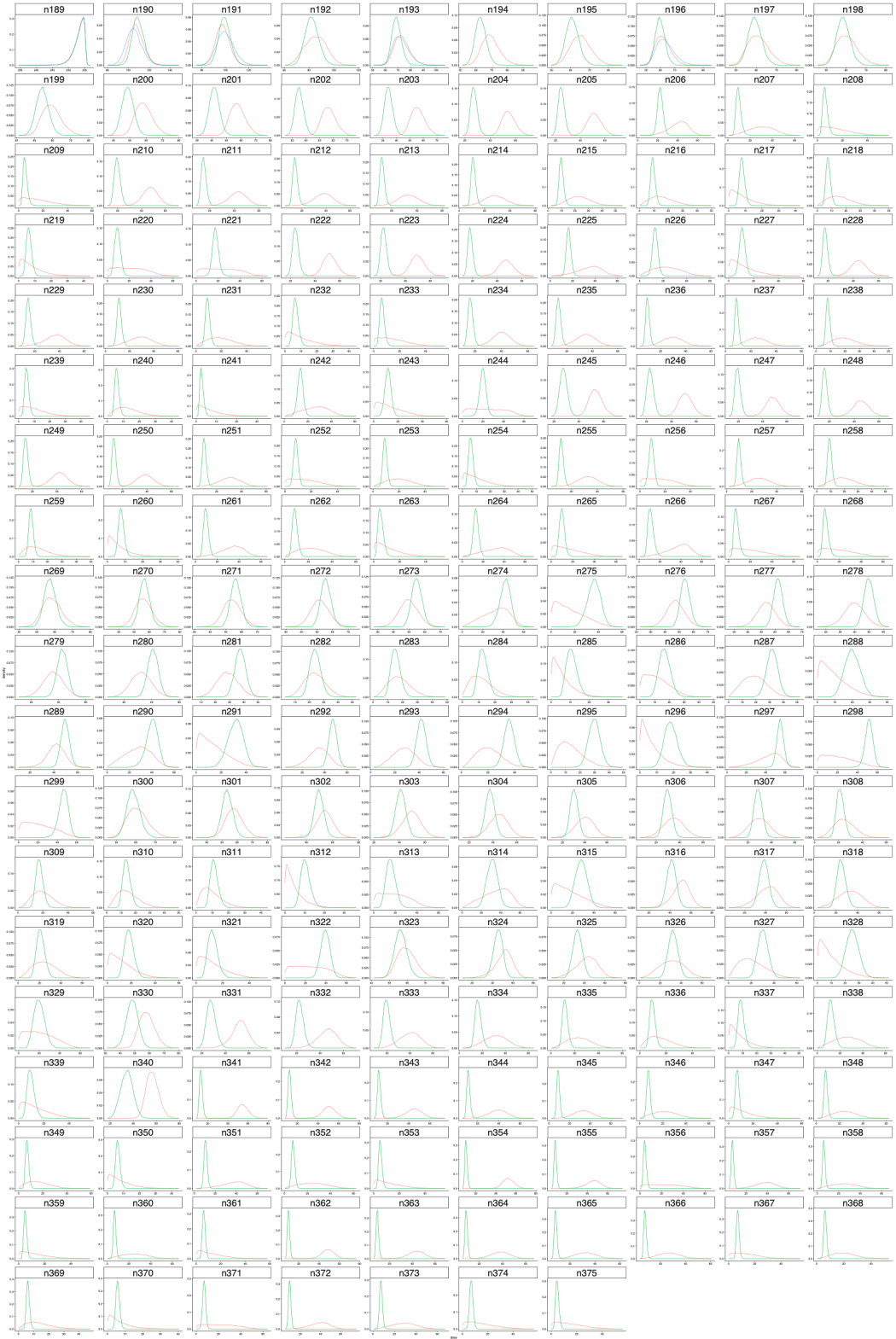


Figure S8. Plots of applied priors (blue), effective priors (pink), and posteriors (green) for each node in MCMCTree using all five priors. Node numbers correspond to the phylogeny plotted in Fig. S9, where n189 is the root node. The effective prior (pink) shows how the interaction of multiple priors can shape the expected ages for a given node. This can be seen when comparing input (blue) and effective (pink) priors on calibrated nodes (n189, n190, n191, n193, and n196).

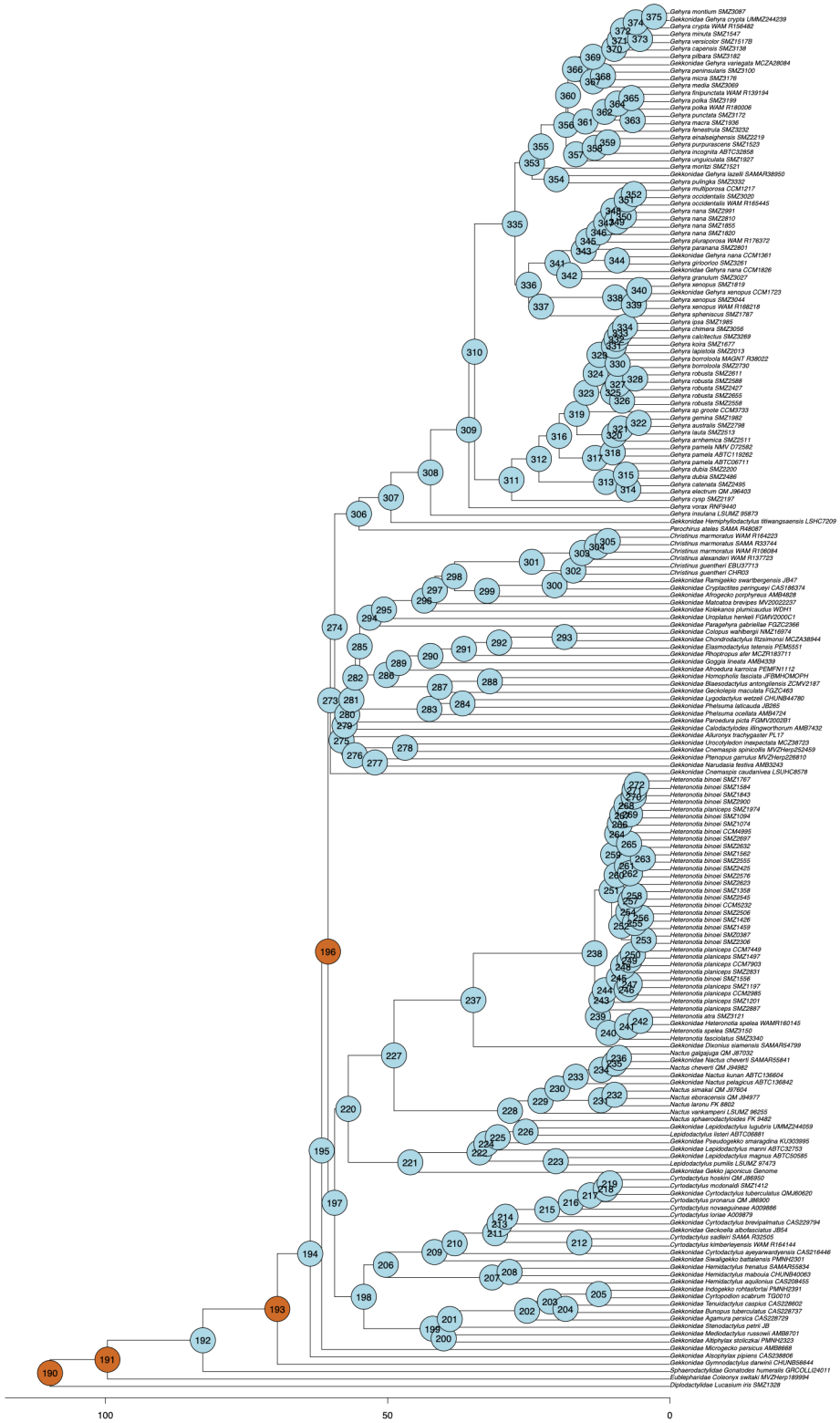


Figure S9. Time calibrated phylogenetic tree of Gekkonidae constructed with MCMCTree using 368 Anchored Hybrid Enrichment (AHE) loci and five secondary calibration points. The input topology specified as the weighted ASTRAL tree in Fig. 1. Node labels are supplied for reference to Fig. S8, orange nodes are calibrated — n189 (Sphenodon_punctatus_SAMN08038466; the fifth calibration) omitted for graphical clarity.

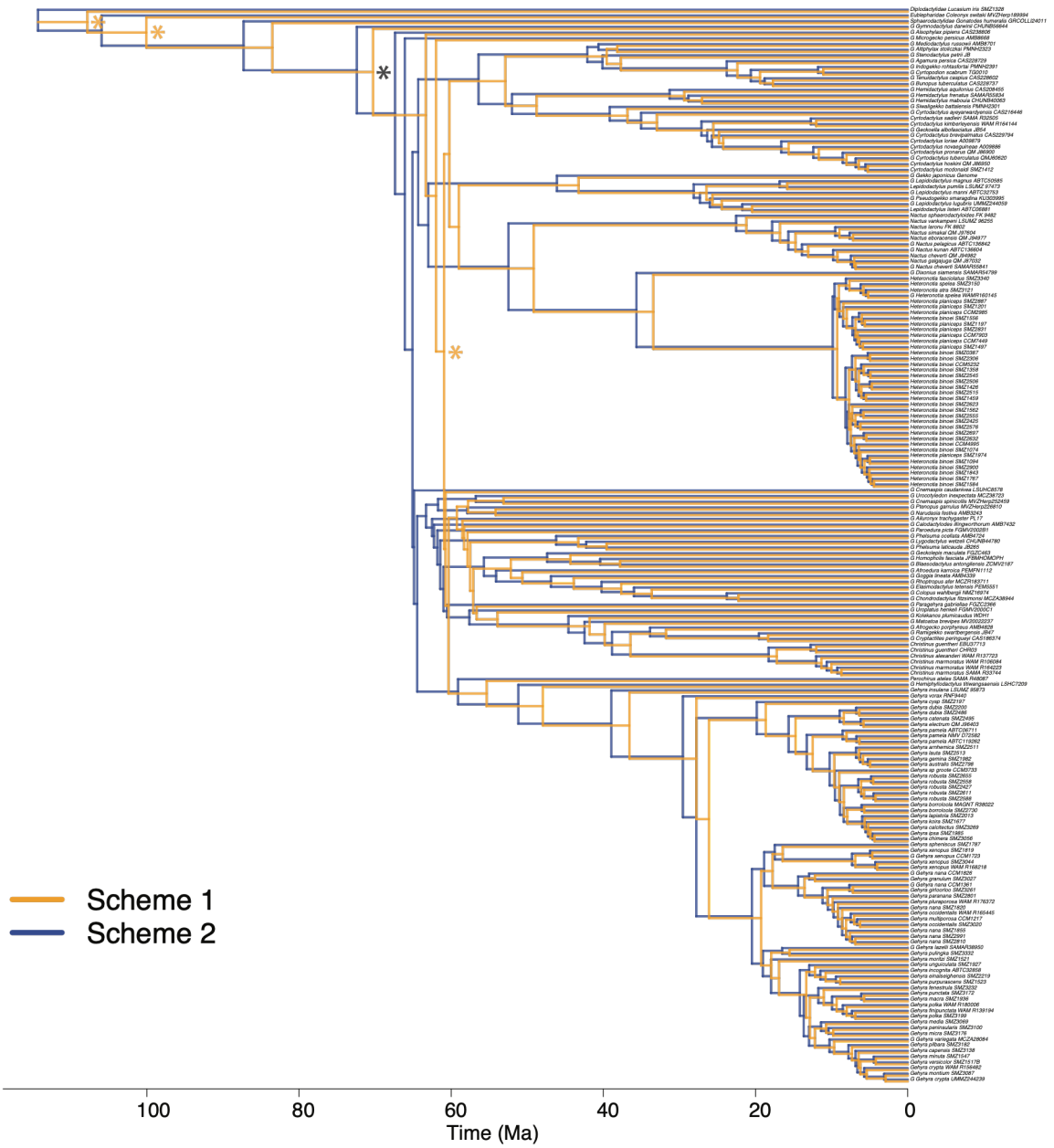
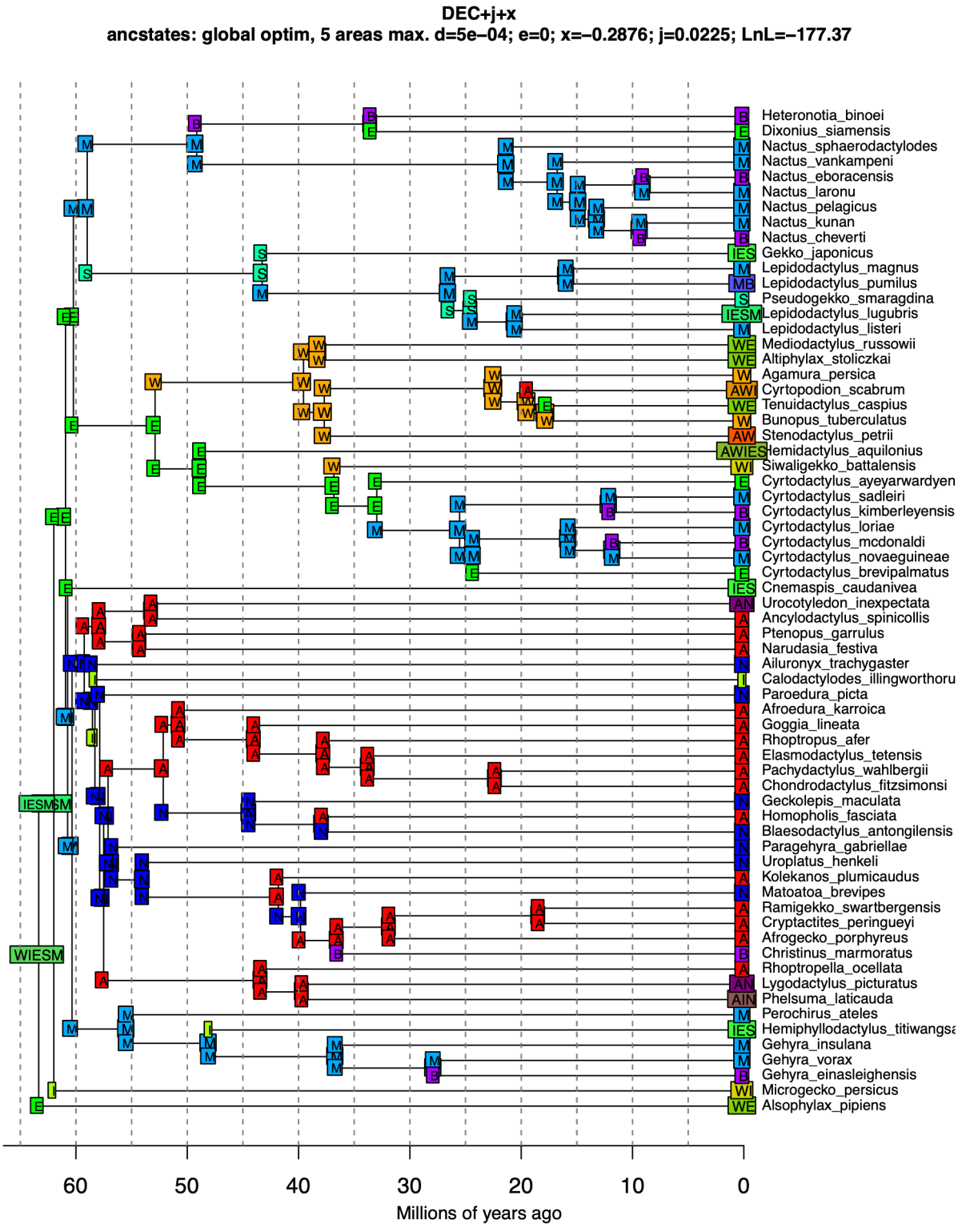


Figure S10. The influence of node prior usage on posterior estimates of divergence in Gekkonidae. The orange-coloured tree shows divergence times estimated using five SkewT calibration priors (strategy 1), indicated by orange and black asterisks (*). The blue-coloured tree shows divergence estimates using only two of these SkewT calibration priors (strategy 2), indicated by black asterisks. The root, Sphenodon_punctatus_SAMN08038466, omitted for graphical clarity but used as a calibration node in both analyses. The tree estimated using five node priors (strategy 1) is used for all downstream analyses. Note calibrations are supplied in Table S1.



1271 **Figure S11.** Ancestral area estimation of Gekkonidae in BioGeoBEARS, using the favoured
1272 DEC+*j*+*x* model. Tip boxes correspond to assigned biogeographical areas: A = Africa, B =
1273 Australia, E = East Asia, I = India, M = Melanesia, N = Madagascar, S = Sundaland, W =
1274 West Asia.

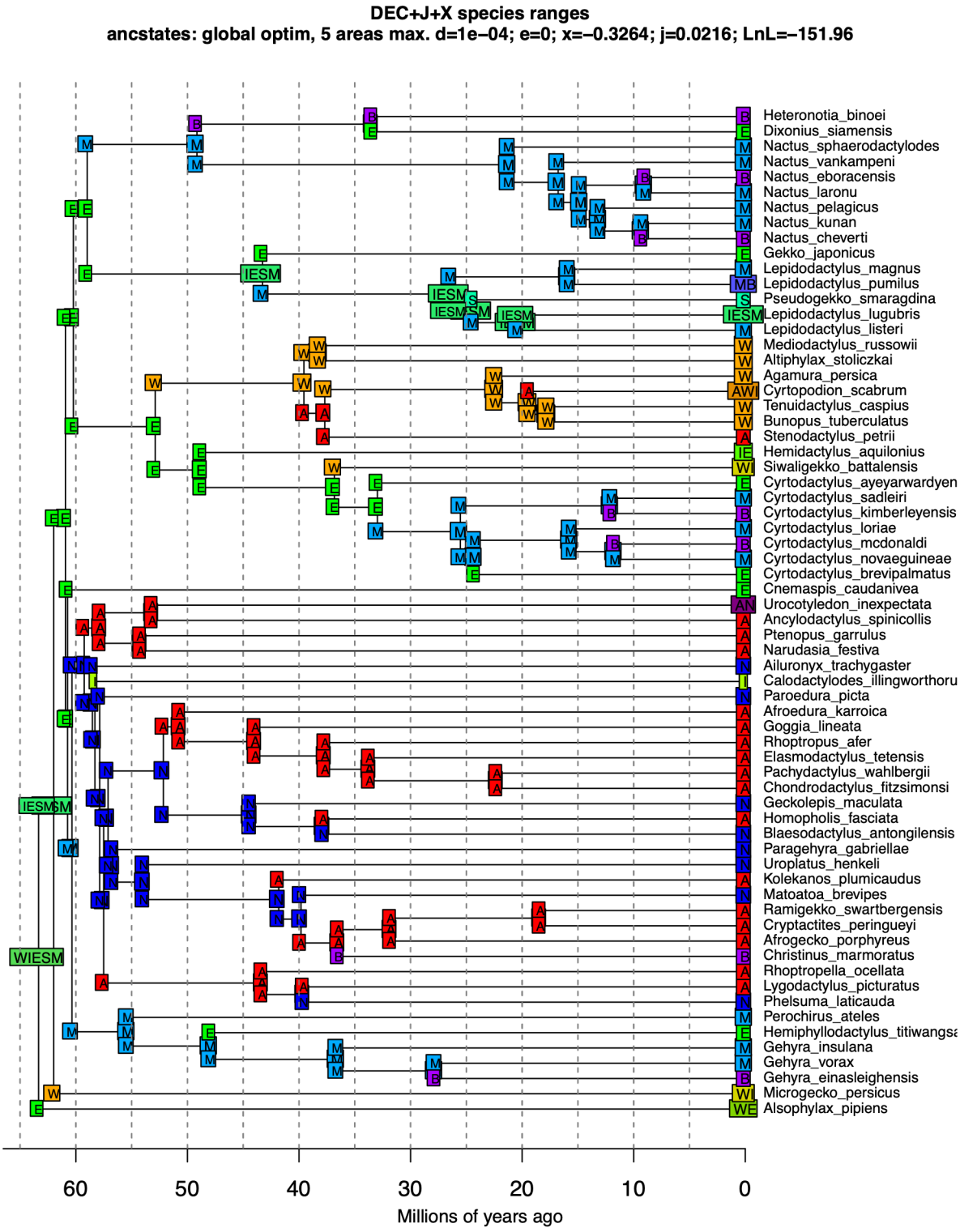


Figure S12. Sensitivity test for ancestral area estimation of Gekkonidae in BioGeoBEARS, using the favoured DEC+*j*+*x* model and encoding the tips as the representative species range, rather than the genus/clade. Tip boxes correspond to assigned biogeographical areas: A = Africa, B = Australia, E = East Asia, I = India, M = Melanesia, N = Madagascar, S = Sundaland, W = West Asia.

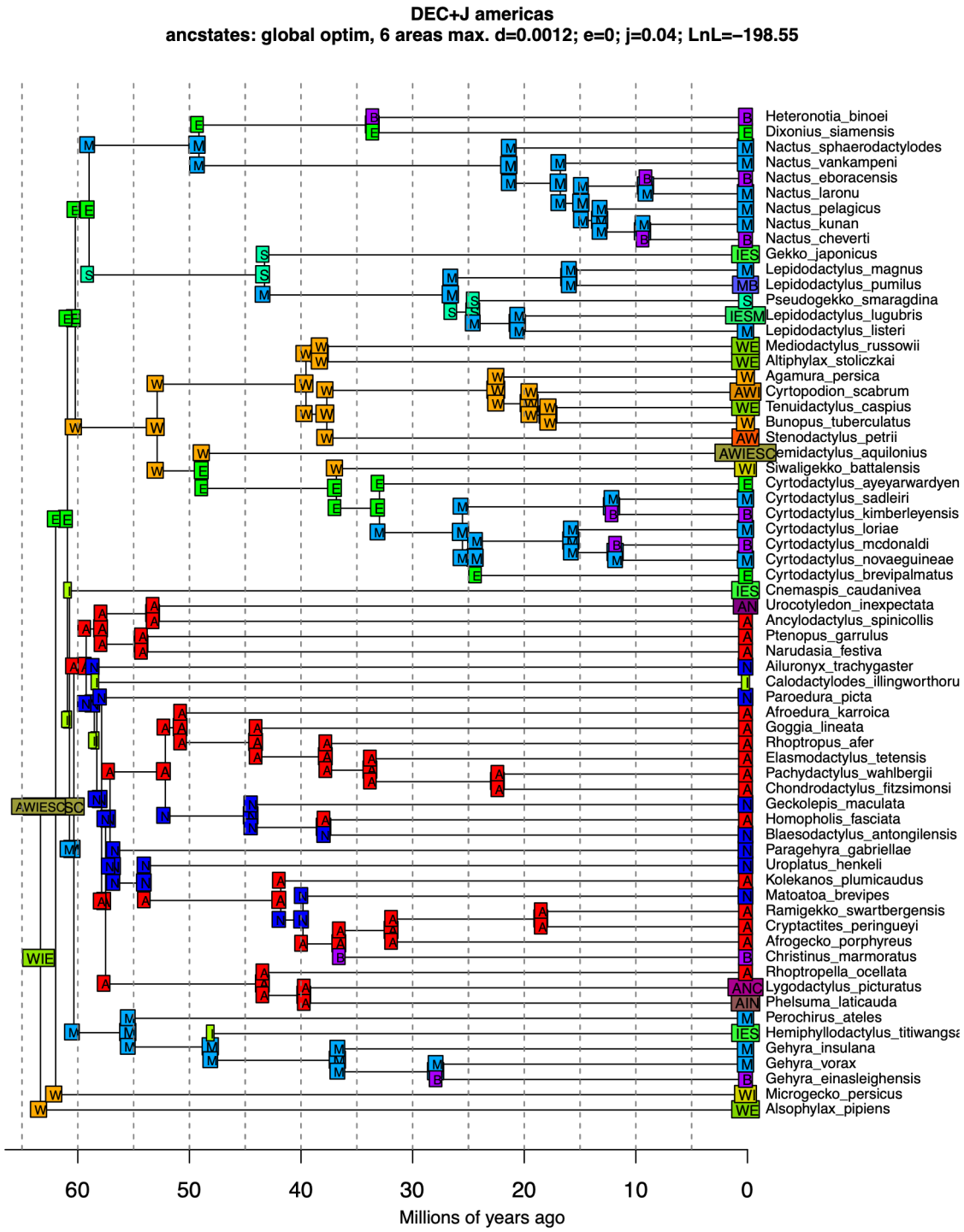


Figure S13. Sensitivity test for ancestral area estimation of Gekkonidae in BioGeoBEARS, using the favoured DEC+*j* model and including the Americas for encoding of *Hemidactylus* and *Lygodactylus*. Tip boxes correspond to assigned biogeographical areas: A = Africa, B = Australia, E = East Asia, I = India, M = Melanesia, N = Madagascar, S = Sundaland, W = West Asia, C = Americas.

Supplementary methods

Dating analyses

Accurately estimating divergence dates within Gekkonidae is complicated by two factors. Firstly, the early splits in the family occur in rapid succession, resulting in short internode lengths and low confidence in among-clade relationships, which is reflected in the many conflicting gene tree topologies (Figure S3). Rapid divergence and low resolution among older relationships has been previously identified within the family (e.g., Gamble et al., 2015). Given this extensive discordance, we specify the input topology in MCMCTree as that constructed using wASTRAL and the whole genomic dataset, as we regard this as our most accurate phylogenetic reconstruction. Secondly, while there exists several gekkotan fossils from our period of interest (i.e., ~20–100 mya), none can be confidently placed within Gekkonidae (see Daza et al., 2014). Though these taxa may indeed be true gekkonids and therefore of great value as priors, we instead choose a cautious approach to not misassign taxa (Martin, 1993). The only fossil gekkotans that can be confidently placed within Gekkonidae are relatively modern, e.g., *Hemidactylus turcicus* from the Holocene (Delfino, 2006) and an *Alsophylax* sp. from the Neogene (Vasilyan et al., 2017), and are uninformative for our dating scheme. To account for the absence of fossil calibration points, we applied two methods to estimate divergence times among Gekkonidae, and test for differences in estimates using two calibration strategies in MCMCTree and a set of priors that were developed for the whole of squamata (Brennan et al. 2024).

Biogeographical modelling

We estimated the ancestral biogeography of Gekkonidae using the R package BioGeoBEARS (Matzke, 2013). BioGeoBEARS allows for the testing of multiple flexible models of biogeographical history, incorporating both anagenetic (range expansion and contraction along branches) and cladogenetic processes (sympatric, vicariant, and founder-event "speciation" at nodes) across discrete geographical regions. We divided the distribution of Gekkonidae into 9 geographically relevant regions: Africa, Madagascar (including the Seychelles), eastern Asia (mainland south-east Asia including China, Mongolia and Nepal), western Asia, India (including Sri Lanka), Sundaland (islands of south-east Asia west of Wallace's line), Melanesia (islands of south-east Asia, New Guinea, and the Pacific east of Wallace's line), Australia, and Antarctica. We did not include the Americas within our main model comparisons as only six species from the genera *Lygodactylus* and *Hemidactylus* occur there (three from each). These species are deeply embedded within their respective genera that occur in Africa and Eurasia, and these genera are themselves only distantly related to Australian clades (Carranza & Arnold, 2006; Ceríaco & Passos, 2023; Lanna et al., 2018). We accounted for the potential biases introduced by this by running a sensitivity analysis where we included the Americas, and encoded the tips for *Lygodactylus* and *Hemidactylus* as occurring there. This alteration did not change the estimated ancestral areas Australian lineages (Figure S13). It did alter the estimated ancestral areas of the paleartic clade (which includes *Hemidactylus*) to include the Americas, as well as the node containing all major clades, but excluding the first splits of *Alsophylax pipiens* and *Microgecko persicus,* to include the Americas.

Due to the unevenness of sampling in our study (almost all Australian species were present, while most non-Australian genera included only 1–3 samples), unbalanced inclusion of taxa

would likely bias ancestral range reconstruction to those which were disproportionately represented within the tree. To account for this, we pruned the tree to a single tip per non-Australian genera, and where a genus included both Australian and non-Australian species, we instead retained the deepest split among Australian representatives (the Australian crown group) and their closest non-Australian relative, allowing us to bound the interval during which the lineage likely arrived in Australia. Genera that did not include Australian lineages were encoded as the range of the whole genus (e.g., the representative tip for *Stenodactylus* was encoded as occurring in both Africa and West Asia). In genera that included both Australian and non-Australian taxa, the tips were instead encoded as the distribution of their respective species (e.g. *Cyrtodactylus loriae* was encoded as occurring in Melanesia, and *Cyrtodactylus mcdonaldi* as occurring in Australia, rather than a singular *Cyrtodactylus* tip encoded for the whole genus range). To investigate any potential biases introduced by this strategy, we also reran the best performing model, encoding each tip as only where that species is distributed. No changes were detected for ancestral areas of Australian lineages (Figure S12). Some minor changes were observed where the encoded area shrunk from multiple areas to a single one due to the species occupying a smaller number of biogeographic regions than its genus — these did not alter the ancestral area for crown Gekkonidae.

To incorporate the movement of continents during the last ~65 Ma, we stratified the MCMCTree phylogeny in 5 Ma increments to account for changes in areas of continental adjacency and dispersal distance. to construct dispersal distance (x) and dispersal probability (w) matrices. X values were calculated by dividing distance over the longest possible distance recorded; w values of 0.25 were assigned to landmasses that were adjacent or separated by less than 200 km of water, while a value of 1 was assigned where dispersal required crossing more than 200 km of open ocean. We acknowledge that dispersal over any oceanic distance is likely exceptionally rare for a terrestrial vertebrate but, given the proclivity for gekkonids to overcome such barriers, we chose to penalise only oceanic dispersals greater than 200 km.

There has been notable criticism of the application of DEC and DEC + j models in BioGeoBEARS (see Ree & Sanmartin, 2018 and citing literature). This is because cladogenetic events are not modelled as probabilistic with respect to time by these models, giving cladogenetic events greater explanatory power. Ree and Sanmartin also argue that model comparison is therefore invalidated as more weight is allocated to jump dispersal, i.e., DEC + j has an 'unfair' advantage in explaining the dataset. However, Matzke (2022) demonstrated that simulations with larger datasets do not necessarily favour DEC + j, and that likelihoods allow us to reject a statistical unfairness argument. Regardless, given that all models are 'wrong' to some degree (Box, 1976), their application and support should always be carefully interrogated. Here, we test hypotheses of oceanic dispersal using a group where such feats are regarded as common and intuitive given their geographically disjunct distributions (Carranza & Arnold, 2006; Šmíd et al. 2013; Grismer et al. 2022). Additionally, where dispersal occurs across such vast distances to isolated landmasses, speciation is essentially not time dependent (Matzke 2022). Our use of DEC and DEC + j models is therefore valid.

Supplementary Results

Phylogenomics

Here, we first present our phylogenetic hypothesis estimated using the complete dataset before highlighting the discordances between it and our AHE-only derived topologies. Phylogenetic estimation using weighted ASTRAL supports the monophyly of Gekkonidae with respect to Phyllodactylidae (posterior probability [pp] = 1, gCF = 65.7, Fig. 1). Broadly, our analyses recovered several clades (Fig. 1): a palearctic group (*Altiphylax, Stenodactylus, Mediodactylus, Agamura, Tenuidactylus, Crossobamon, Bunopus, Indogekko, Cyrtopodion, Cyrtodactylus,* and *Hemidactylus*); a *Gekko* group (*Lepidodactylus* and *Gekko*); a *Nactus* group (*Nactus, Heteronotia,* and *Dixonius*); a *Gehyra* group (*Gehyra, Hemiphyllodactylus,* and *Perochirus*); and a large, predominantly African and Madagascan group (*Narudasia*, *Ptenopus*, *Ancylodactylus*, *Urocotyledon*, *Ailuronyx*, *Calodactylodes*, *Paroedura*, *Rhoptropella*, *Phelsuma*, *Lygodactylus*, *Geckolepis*, *Blaesodactylus*, *Homopholis*, *Afroedura*, *Goggia*, *Rhoptropus*, *Elasmodactylus*, *Chondrodactylus*, *Pachydactylus*, *Paragehyra*, *Uroplatus*, *Kolekanos*, *Matoatoa*, *Afrogecko*, *Cryptactites*, *Ramigekko,* and the Australian *Christinus*) (Fig. 1). The topology recovered the *Gekko* and *Nactus* clades as sister, which were in turn sister to the palearctic clade. This three-clade combination was estimated as sister to the combined *Gehyra* + African & Madagascan clades — ((palearctic clade, (*Gekko* clade, *Nactus* clade)), (*Gehyra* clade, African & Madagascan clade)). The genera *Alsophylax* and *Microgecko* were estimated as the first and second splits in the family, respectively, and *Cnemaspis* as sister to the *Gehyra* + African & Madagascan clades.

Many of the earliest divergences within the family are characterised by exceptionally short branch lengths, low gCF (Fig. S3), and sometimes low support (i.e., pp < 0.7). Most relationships with low support occur among the earliest splits in the family, as well as the early relationships within the African and Madagascan clade. This uncertainty is reflected in the movement of some of these taxa between our data subset trees (Figs. S2, S4) — the most notable changes being the placement of the *Gekko* clade and *Alsophylax pipiens.* While the all-loci dataset topology places the *Gekko* clade as sister to the *Nactus* clade, and *A. pipiens* as the first split in the family, the AHE dataset places the *Gekko* clade as the second split within the African and Madagascan clade (inside *Cnemaspis*) and *A. pipiens* as the third split. Topologies vary more severely amongst the AHE subsets, with notable movement of *Narudasia festiva, Ancylodactylus spinicollis, Cnemaspis caudanivea*, and *Urocotyledon inexpectata* (Figs. S5–S7).

Divergence dating

Divergence estimates by MCMCTree using our two dating schemes varied moderately, with the largest differences within Gekkonidae concentrated towards the crown age (crown age split scheme 1, 63.3; 95% HPD: 58.3–68.6 Ma, *vs.* scheme 2, 67.4; 95% HPD: 58.6–77.0; Fig. S10). Gekkotan outgroups, with the exception of Sphenodontidae, varied slightly due to the absence of informative priors (e.g., the greatest difference between two nodes was the Diplodactylidae split; scheme 1, 107.8, 95% HPD 99.7–116.6 Ma *vs.* scheme 2, 114.3; 95%

HPD 97.7–132.2 Ma). The difference between estimates within Gekkonidae gradually declined towards the present, with the youngest nodes diverging by only ~0.5–1 Ma. Given the concordance between the two dating schemes, and the greater value of using more informative node calibrations, we used the dated tree produced using scheme 1 for our subsequent biogeographic analyses.

Supplementary Discussion

Phylogenomics and divergence dating

Our phylogenetic estimates are largely consistent with those of previous studies (e.g., Agarwal et al. 2014; Gamble et al. 2012, 2015, Heinicke et al. 2010, 2011, 2014; Jackman et al. 2008; Oliver et al. 2024; Pyron et al. 2013; Title et al., 2024; Wood et al. 2020), although we note that with the exception of Title et al. (2024), all of these use either a smaller numbers of markers or include fewer taxa. The most notable discrepancies concern the placement of *Alsophylax*, *Microgecko*, and the South-east Asian clade of *Cnemaspis* (no samples of the South Asian clade were included in our study). Pyron et al. (2013) recovered *Alsophylax* as sister to the Palearctic clade and South-east Asian *Cnemaspis* as sister to *Tropiocolotes* (which together were sister to the Palearctic clade, inside *Alsophylax*); their sampling did not include *Microgecko*. Gamble et al. (2015) and Title et al. (2024) placed both *Alsophylax* and *Microgecko* as sister to the Palearctic clade. Gamble et al. (2015) estimated the South-east Asian *Cnemaspis* as sister to the *Gehyra* clade, while Title et al. (2024) found them to be sister to the *Gekko* clade. The true evolutionary relationships of these three genera remain uncertain, though the geographic distributions of *Alsophylax* and *Microgecko* in Central Asia are consistent with membership in the Palearctic clade. The broader topological differences between our results and those of Feng et al. (2007) are unsurprising given that study's reliance on two gene fragments. Like other studies, our results show that the earliest splits within the family (i.e., between major clades) occurred rapidly and are characterised by exceptionally short internode lengths and high gene tree discordance, resulting in low confidence for some relationships and potentially artefactual support for others. Nevertheless, our results recover *Alsophylax* and *Microgecko* as the first splits, followed by a sister relationship between the African and Madagascan clade and all remaining taxa. Given that *Alsophylax* and *Microgecko* are distributed across Central and West Asia, and that the subsequent deepest split separates African and Asian lineages, this pattern is consistent with a western Asian origin of Gekkonidae (Bauer et al. 2013; Agarwal et al. 2014).

Ten gekkonid genera are not represented in our dataset. However, these contain few taxa (total 27 species) and three are monotypic. Seven of these belong to either the Palearctic or African clades (de Pous et al., 2016; Fujita et al., 2011; Jackman et al., 2008; Lobon-Rovira et al., 2022; Pola et al., 2021; Yousefkhani et al. 2019) and the phylogenetic placement of *Parsigecko* (Safaei-Mahroo et al., 2016) and *Lakigecko* (Torki, 2020) has never been assessed. Their inclusion would be unlikely to clarify the more poorly resolved, clade-level relationships within the family.

Our crown age estimates for individual genera are generally consistent with previous studies (Agarwal et al. 2014; Agashe et al. 2025; Grismer et al. 2022; Oliver et al. 2018, 2024; Tallowin et al. 2018; Title et al., 2024). Title et al. (2024), the most recently published dated gekkonid phylogeny, estimated on average slightly younger estimates for most genera crown

ages: (e.g., for Australian genera/clades, Title et al. (2024) estimated the following; *Heteronotia* = 6.5 *vs.* 9.3 Ma; *Nactus* = 18.5 *vs.* 21.2 Ma; *Christinus* = 11.69 *vs.* 17.2 Ma; and *Gehyra* = 21.11 *vs.* 26.1 Ma). The only instance where their estimates exceeded those presented here was for the north-eastern Australian *Cyrtodactylus* clade (11.07 *vs.* 8.05 Ma). Except for *Gehyra* (26.1 Ma), the crown ages of Australian clades are considerably younger than most genus-level splits in the family. Some studies recover even younger estimates than ours — for example, *Heteronotia* (4 Ma; Fujita et al. 2010) and *Gehyra* (11.2 Ma; Sistrom et al. 2014). In these instances, divergence estimates were based on a small number of markers, older substitution rate estimates (Macey et al. 1998), and no primary or secondary fossil prior calibrations, which likely accounts for their significantly younger estimates. Regardless of their true crown age, *Heteronotia* is comparatively young and has seen high rates of lineage diversification in the last 10 Ma. Australia has undergone significant aridification during this period, and particularly since the onset of the Pleistocene ~2.5 Ma (Byrne et al. 2008; Fujioka et al. 2009). This is suggestive of a potential relationship between increasing aridification and diversification (Fujita et al. 2010).

The older divergence estimates by dating scheme 2 (Fig. S10; blue phylogenetic tree) are unsurprising given the absence of a constraining prior within Gekkonidae. The lack of primary fossil calibration points within Gekkonidae (Daza et al., 2014) makes it difficult to validate which of these two schemes produced the most accurate divergence time estimates. However, given the concordance between estimates from dating scheme 1 (Fig. S10; orange phylogenetic tree) and other studies, we regard these results as the most accurate reconstruction of the family's divergence times. If further fossil evidence did suggest dating scheme 2 to be more accurate, the crown age of Gekkonidae would predate the K-Pg boundary. Furthermore, many of the earliest splits within the family would also occur in a ~5 Ma period before the Cretaceous mass extinction event, precluding an ecological opportunity hypothesis.

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