**Very limited dispersal and differing evolutionary trajectories across proximate continental and insular regions in a widespread lizard radiation (*Gehyra*).**

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**Abstract.**

The probability of biotic dispersal between regions is likely to be mediated by a suite of geographic, environmental and biotic factors, and may vary greatly across taxa. Australia and Melanesia, centred on New Guinea, are geographically proximate regions that show broadly differing environments and histories, providing an opportunity to document how environmental variation may interact with geographic proximity in shaping dispersal and evolution. Here, we present a phylogenomic framework and analysis of dispersal history for geckos in the genus *Gehyra*, a radiation of ~70 species that occur across Australia, Melanesia, and other nearby regions. Despite an evident history and ability to disperse over water in at least some species groups, we find evidence for very low rates of historical dispersal between Australia and Melanesia and no evidence of a Pliocene or later uptick as putative land bridges formed between Australia and New Guinea. Analyses of body size evolution suggest that 'giant' large-bodied forms have evolved on islands, but rather than evolving repeatly *in-situ*, are mostly members of a single old clade that dispersed across multiple islands. These data suggest that, in striking contrast to some other Australasian vertebrate radiations, for *Gehyra* geckos, environmental variation has strongly impeded dispersal between Australia and Melanesia, and also favoured differing evolutionary trajectories.

**Keywords.** Australia, New Guinea,niche conservatism, overwater dispersal, phylogenomics, Sahul

**Introduction**

In biogeographic comparisons between islands and continents, the former have often been characterised as either biogeographic dead ends or hotspots of ecological release and innovation (MacArthur & Wilson, 1967; Whittaker, Fernández-Palacios, Matthews, Borregaard & Triantis, 2017). However, although researchers often seek such general trends, real-world patterns of dispersal and diversification across islands and continents show considerable nuance and often challenge neat characterisation. For instance, islands, and especially geologically complex and large islands, may be important sources of diversity for nearby continents (upstream colonisation or reverse colonisation) (Bellemain & Ricklefs, 2008; Jønsson, Fabre, Ricklefs & Fjeldså, 2011). Likewise, comparisons of key traits such as body size and shape, and ecological niche breadth across related insular and continental radiations have emphasised both divergence and overlap, sometimes even within the same radiation (Huie, Prates, Bell & de Queiroz, 2021; Patton, Harmon, del Rosario Castañeda, Frank, Donihue, Herrel & Losos, 2021). The dynamic, complex, and poorly understood geological histories of many island systems can further obscure their role in shaping regional biotas (Whittaker et al., 2017).

The “island continent” of Australia, and nearby Melanesia—centred on the world’s largest and highest tropical island of New Guinea—provide opportunities for focused comparison of patterns of biotic radiation and dispersal across geographically proximate continental and insular regions. These two regions share many lineages (Heinsohn & Hope, 2006; Letsch, Balke, Kusy, McKenna, Pramesa Narakusumo, Sagata, Toussaint, White & Riedel, 2023; Mitchell, Pratt, Watson, Gibb, Llamas, Kasper, Edson, Hopwood, Male & Armstrong, 2014; Pavón-Vázquez, Brennan, Skeels & Keogh, 2022; Tallowin, Meiri, Donnellan, Richards, Austin & Oliver, 2020), but are also each characterised by their own rich and highly endemic biotas (Joyce, Thiele, Slik & Crayn, 2021; Prasetya, Moritz, Joseph, Stelling & Oliver, 2023). Australia and Melanesia are also dominated by strongly contrasting environments—the former is predominantly arid, flat and more temperate; while the islands of Melanesia (and especially New Guinea) are wet, more mountainous, and tropical. These two broad areas provide an opportunity to examine the extent to which increasing geographic proximity may, or may not, enable taxa to overcome environmental differentiation and niche conservatism and disperse between regions.

The geological history of the islands of Melanesia is complex, and their proximity to the main landmass of Australia has varied greatly through time (Harrington, Zahirovic, Flament & Müller, 2017; Norvick, 2003). During the Plio-Pleistocene, land bridges repeatedly formed across the Arafura Shelf and linked northern Australia with southern New Guinea, forming the paleocontinent of Sahul and potentially allowing overland dispersal (Heinsohn & Hope, 2006; Jones & Torgersen, 1988). Many taxa, especially in rainforest and savannah lineages, show divergences consistent with dispersal across these land bridges (Liang, Nunes, Leong, Carvalho, Müller, Braby, Pequin, Hoshizaki, Morinaka & Peggie, 2024; Oliver, Rittmeyer, Torkkola, Donnellan, Dahl & Richards, 2021; Peñalba, Joseph & Moritz, 2019; Roycroft, Fabre, MacDonald, Moritz, Moussalli & Rowe, 2022). However, this Plio-Pleistocene connectivity likely masks a deeper history of geological differentiation. Although the southern portions of New Guinea are comprised of the uplifted northern edge of the northwards-moving Australian plate, northern and eastern New Guinea, and many nearby islands, are derived from accreted island arc terranes and associated archipelagos that have likely been at tropical latitudes, and thus some distance from Australia, for more than 30 million years (Harrington et al., 2017). Biogeographic analyses of many Australasian radiations dating back to the Miocene or earlier also show marked differentiation between Australia and islands to the north (Joyce et al., 2021; Oliver, Bower, McDonald, Kraus, Luedtke, Neam, Hobin, Chauvenet, Allison, Arida, Clulow, Gunther, Nagombi, Tjaturadi, Travers & Richards, 2022), and evidence for long time periods with limited or no dispersal (Pavón-Vázquez et al., 2022)**.**

Environmental differences between Australia and mesic tropical Melanesia may also have presented an important barrier to successful dispersal, especially from the mid-Miocene to the present as Australia became substantially more arid (Heinsohn & Hope, 2006). Even radiations that do occur across both regions may show divergent patterns of ecological differentiation. For instance, in agamid lizards, certain ecological niches such as terrestriality (ground-dwelling) are absent in New Guinea but common in Australia (Tallowin et al., 2020), while in dasyurid marsupials, it has been suggested that low seasonality and resource-rich environments in New Guinea have mediated the evolution of larger brains (Weisbecker, Blomberg, Goldizen, Brown & Fisher, 2015). If signatures of divergent evolution are found to be pervasive, this would support the hypothesis that environmental differentiation between these two regions may have played a key role in limiting biotic dispersal (Heinsohn & Hope, 2006). However, for most taxa shared between Australia and Melanesia, patterns of evolutionary diversification in the two regions, including eco-morphology, have not been compared.

*Gehyra* is a genus comprising around 70 species of scansorial gecko lizards that is widespread across both Australia (~55 species) and the islands of Melanesia and the Pacific (~17 recognised species). It has been hypothesised that Southeast Asia is the origin for this genus (Heinicke, Greenbaum, Jackman & Bauer, 2011), although the contemporary fauna of this region includes just five species (Uetz, 2025). The diversity, biogeography, and macroevolutionary dynamics of *Gehyra* in Australia have been investigated by numerous recent studies (Ashman, Bragg, Doughty, Hutchinson, Bank, Matzke, Oliver & Moritz, 2018; Oliver, Ashman, Bank, Laver, Pratt, Tedeschi & Moritz, 2019; Sistrom, Donnellan & Hutchinson, 2013; Sistrom, Hutchinson, Hutchinson & Donnellan, 2009). These have revealed two moderately diverse radiations with Miocene origins and both characterised by high levels of cryptic lineage diversity (Kealley, Doughty, Pepper, Keogh, Hillyer & Huey, 2018; Oliver, Prasetya, Tedeschi, Fenker, Ellis, Doughty & Moritz, 2020; Sistrom et al., 2013), morphological conservatism in most aspects except body size (Moritz, Pratt, Bank, Bourke, Bragg, Doughty, Keogh, Laver, Potter & Teasdale, 2018),and limited ability to disperse between monsoonal and arid biomes (Ashman et al., 2018).

In contrast, lineage diversity and biogeographic patterns in Melanesian *Gehyra* remain much more poorly known. Recent taxonomic work has increased known species diversity (Kraus, 2024; Kraus, Vahtera & Weijola, 2024) and preliminary estimates of divergence times point to the presence of deeply divergent lineages dating back well into the Miocene (Heinicke et al., 2011; Oliver, Clegg, Fisher, Richards, Taylor & Jocque, 2016). A notable feature of Melanesian *Gehyra* is a suite of species that show relatively large body sizes, especially when compared against *Gehyra* from Australia and Asia (SVL >130 mm and up to nearly 160 mm, versus a maximum of usually <90 mm). The evolution of particularly large-sized taxa has occurred in several island radiations of gekkonids (Böhme, 2006; Heinicke, Nielsen, Bauer, Kelly, Geneva, Daza, Keating & Gamble, 2023; Oliver, Skipwith & Lee, 2014; Skipwith & Oliver, 2023), raising the possibility that large insular *Gehyra* may be showing a differing evolutionary regime to their continental relatives.

Here we aim to: a) understand patterns of dispersal in *Gehyra* across continental Australia and insular Melanesia, with a particular focus on assessing support for contrasting broader biogeographic narratives of high or low connectivity between these two regions, and b) to contrast patterns of evolutionary diversification in body size, with a particular focus on the evolution of the “giant” species of Melanesia. To undertake these analyses, we first assembled an expanded mitochondrial genetic sampling of taxa from the poorly known Melanesian region and used this to identify divergent lineages. We then collected exon-capture data for representative samples and combined this with recently published data for Australian taxa to generate a robust tree for Australasian *Gehyra*. This tree was then used to infer and contrast patterns of dispersal and body-size evolution across Australasia using Bayesian biogeographic approaches.

**Material and Methods**

*Taxon sampling and lineage diversity in Melanesia*

Australian *Gehyra* have been the focus of extensive taxonomic work over the last decade, resulting in the description of numerous new species, and the elucidation of additional lineage diversity within nominal species. A phylogenomic tree including the vast majority of recognised species of Australian *Gehyra,* plus divergent intraspecific lineages based on exon-capture data, has also recently been made available (Lau, Christian, Fenker, Laver, O'Hara, Zozaya, Moritz & Roycroft, 2024).

Melanesian *Gehyra* have also been the focus of some recent taxonomic work (Kraus, 2024; Kraus et al., 2024; Oliver et al., 2016; Skipwith & Oliver, 2014), however they remain less well known. For an initial assessment of evolutionary diversity in Melanesian *Gehyra* we sequenced the full mitochondrial ND2 gene. For these analyses our sampling of *Gehyra* from Melanesia and other regions outside of Australia included 154 unique individuals, of which the majority were newly sequenced in this study (Appendix S1). Within the mitochondrial dataset, we used the divergence level between lineages in the *Gehyra oceanica* group that have elsewhere been identified as candidate species based on population genetic approaches (Tonione, Fisher, Zhu & Moritz, 2016) as a yardstick for selecting lineages to include in downstream exon-capture and macroevolutionary analyses. We emphasise that our priority was to ensure that we sampled the maximum possible diversity of Melanesian *Gehyra*. Further work is required to test hypotheses that these lineages warrant recognition as distinct species. Where possible, we matched these lineages to recognised species; however, for unnamed candidate species or taxonomically ambiguous lineages, we used code names. There are already codenames available for some lineages in the *Gehyra oceanica* complex (Kraus et al., 2024; Tonione et al., 2016); however, given the ongoing discovery of additional lineages in this group, we reverted to a simple numbering system here (i.e., oceanica 1 and so forth).

*Exon-capture, alignment, and selection*

Where possible, we selected multiple geographically dispersed individuals from each candidate lineage for genomic analysis via exon-capture. The final exon-capture dataset included 51 samples from outside Australia. These data were integrated with exon-capture data for Australian *Gehyra* that have already been published (65 samples) (Ashman et al., 2018; Lau et al., 2024; Moritz et al., 2018; Oliver et al., 2019) (Appendix S2). Methods for generating and processing exon-capture data, and consequently constructing phylogenetic trees from these data, largely follow those outlined in the afore-mentioned papers. To briefly summarise, raw sequencing reads were cleaned and trimmed using the pre-cleanup and scrubReads scripts of the SCPP pipeline (Peñalba, Smith, Tonione, Sass, Hykin, Skipwith, McGuire, Bowie & Moritz, 2014). Cleaned reads were assembled into contigs using a pipeline described elsewhere (Bragg, Potter, Bi & Moritz, 2016), filtered to base quality >20 and sequence coverage >20, and then individually assembled, phased, aligned, and concatenated as described in Moritz et al. (2018).

*Species-tree estimation*

When possible, two representative individuals with the highest average read coverage were selected for each species/operation taxonomic unit (OTU), and h0 haplotypes were produced for use in multi-species coalescent analyses via the EAPhy pipeline v1.2 (Blom, 2015). In cases where only one sample was available for a particular OTU and the sample had >20x average coverage, both the h0 and h1 haplotypes from EAPhy were included for the sample to try to ensure two representatives for all taxa. Single exon alignments (1473 in total) were then produced for the representative samples using EAPhy, after which neighbour-joining (NJ) trees were created for each exon in PAUP\* v4.0.b10 (Swofford, 2002) using the HKY substitution model. From these NJ trees, we randomly selected 100 loci that satisfied criteria appropriate for a StarBEAST2 analysis (200–500 bp, sequences with at least 90% complete alignments and at least 95% taxa, no paralogs). These loci were then concatenated, and initial trees were created using maximum likelihood as implemented in RAxML (Stamatakis, 2014). These initial trees used the GTR-G model and bootstrapping to check topological support and were not rooted. In addition, alignment of each locus was also checked by eye in Geneious v6.1.8 (http://www.geneious.com, Kearse, Moir, Wilson, Stones-Havas, Cheung, Sturrock, Buxton, Cooper, Markowitz, Duran, Thierer, Ashton, Mentjies & Drummond, 2012) and cleaned―among the remaining loci, gene paralogs, low-quality individuals (high rates of Ns due to low sample coverage), chimeric/contaminated individuals (haplotypes of incorrect species, often associated with chimeras)―were removed from the data. Post-cleaning, the top-ranked 100 loci were again concatenated, and initial trees were estimatd using both Maximum Likelihood (RAxML) and Bayesian approaches as implemented in BEAST2 v2.4.8 (Bouckaert, Heled, Kühnert, Vaughan, Wu, Xie, Suchard, Rambaut & Drummond, 2014; Drummond & Bouckaert, 2015).

To conduct the multi-species coalescent analyses, we used the algorithms implemented in BEAST2 v2.4.8 (Bouckaert et al., 2014; Drummond & Bouckaert, 2015), as StarBEAST2 v0.14 (Ogilvie, Bouckaert & Drummond, 2017), with all xml files set up using BEAUti v2.4.8 (Bouckaert et al., 2014). Following Ashman et al. 2018 and to overcome the computational limits on taxa numbers, we employed a “divide-and-conquer” strategy (sensu Antonelli, Hettling, Condamine, Vos, Nilsson, Sanderson, Sauquet, Scharn, Silvestro, Töpel, Bacon, Oxelman & Vos, 2016). We identified five strongly-supported subclades with many closely related lineages from initial RAxML concatenated trees, and removed them for smaller, subclade-specific StarBEAST2 analyses. When a subclade was removed, at least two lineages delimiting the subclade were retained in order to represent the subclade’s root node; any lineages that were phylogenetically isolated, or had highly uncertain placement, were also left in the remaining “skeleton tree” analysis.

Each subclade analysis and the skeleton tree analysis were set up to run using a linked strict-clock model across all exons with a 1/X prior setting, and estimated the clock of each gene relative to the overall mean clock. The data were partitioned by locus with substitution models set to HKY+G, an overall constant-populations model, and a Birth-Death speciation model. Each subclade analysis was set with a relative date for tree height by placing a tight Normal(1,0.001) prior on the root node to facilitate easy integration back into the skeleton tree. Two independent MCMC runs were conducted for each subclade and the skeleton tree, with a chain length of 1.0x109, logging every 1.0x105, and results were combined after 20% burn-in was removed. The largest internal clade required four independent runs to ensure adequate effective sample size (ESS) values (>200) for all parameters (assessed using Tracer v1.7; Rambaut, Drummond, Xie, Baele & Suchard, 2018).

After the StarBEAST2 analyses were completed, the trees sampled from the posterior of each subclade analysis were integrated with trees sampled from the posterior of the skeleton tree analysis by replacing each pair of subclade-delimiting lineages with a sampled full subclade tree, with branch lengths scaled to match the subclade root date of the sampled skeleton tree. The new collection of dated trees contained all lineages, was treated (with caveats) as a posterior distribution of dated species trees, and was summarised as a Maximum-Clade Credibility tree calculated with TreeAnnotator v2.4.8 (Rambaut & Drummond, 2002-2017).

For all macroevolutionary analyses, we used the coalescent species tree as the basic framework. We calibrated the Maximum-Clade Credibility tree into a timeframe of millions of years before present by assigning a crown age of 24 million years to the well-supported node comprising the two main Australian radiations and the two large-bodied Melanesian radiations (see results below). This age constraint broadly matches with ages estimated for the same node by fossil-calibrated nuclear-gene-based dating analyses (e.g., ~24 mya (Oliver, Brown, Kraus, Rittmeyer, Travers & Siler, 2018); ~22 mya (Title, Singhal, Grundler, Costa, Pyron, Colston, Grundler, Prates, Stepanova & Jones, 2024)).

Four additional taxa for which exon sequences were not available were imputed into the dated tree based on their inferred phylogenetic position and inferred divergence dates in mitochondrial analyses. Specifically, these were two divergent lineages within a currently unrecognised clade that occur across Cape York and far southern New Guinea ‒ CYsp2A and CYspB, *Gehyra corona* from an island north of New Guinea, and *Gehyra fehlmanni* from mainland Asia (Heinicke et al., 2011; Kraus et al., 2024; Oliver et al., 2019). This resulted in a phylogeny with a total of 96 terminal taxa.

*Bayesian biogeographic analyses*

Given the overall small number of lineages in many regions, we caution that all biogeographic analyses are likely to lack power with respect to estimating ancestral areas or precise absolute rates of dispersal. For these reasons we did not follow recent analyses of other Melanesian geckos (Oliver, Kraus, Austin, Tedeschi, O’Brien & Maddock, 2024) and divide New Guinea into its constituent regions, such as the East Papuan Composite Terrane and Northern Terranes. While some *Gehyra* taxa do appear to be associated with some of these regions, the low number of lineages makes our dataset suboptimal for testing for regions of origin and patterns of dispersal at this finer scale. In a similar vein, in the absence of outgroups, and given poor sampling of the small number of Asian *Gehyra* (only one out five described species), we refrain from making any comments about the ancestral area for the entire *Gehyra* radiation. Rather, our analyses are focused on understanding relative patterns of dispersal and diversification across insular Melanesia and continental Australia.

Patterns of dispersal across Australasia and the Pacific were initially estimated on the fixed 96-taxon tree using BEAST X (Baele, Ji, Hassler, McCrone, Shao, Zhang, Holbrook, Lemey, Drummond & Rambaut, 2025), treating distribution area as a discrete general-time-irreversible character (i.e., with separate forward and reverse relative rates between areas). This biogeographic model is analogous to the GTI DNA substitution model, which has 12 relative rates for forward and reverse changes between nucleotides and an absolute substitution rate. The ancestral areas for each node, and the number of transitions of each type, were recorded for each Markov chain Monte Carlo (MCMC) sample (using the ancestralTreeLikelihood and MarkovJumps functions); convergence was monitored in Tracer v1.7, and results were collated and visualised using LogCombiner and TreeAnnotator in the BEAST X v10.5 package (Baele et al., 2025). In total, four runs of each analysis were performed, and the details of the MCMC parameters are in the supplied xml scripts, with relevant annotations (Table S1).

To test whether dispersal probability between Australia and New Guinea varied across time periods, a 2-epoch clock was employed, with overall dispersal rates estimated separately for two time slices: 0–10 and >10 million years (see justification below). Ten million years ago was chosen as the breakpoint as it roughly corresponds with the estimated end of the most extensive recent widespread inundation of the New Guinea region (Harrington et al. 2017). Over the period from 10 million years until the present, New Guinea was increasing in areal extent, with the width of sea barriers between New Guinea and Australia diminishing, and at multiple times these were completely severed by land bridges (Heinsohn & Hope, 2006; Norvick, 2003). If land area and barrier permeability are primary determinants of dispersal probability, it would be predicted that dispersal rates between Australia and New Guinea should be much higher in the more recent time period, after correcting for extant lineage diversity in each timeslice.

To visualise histories of dispersal and diversification across contemporary geographical regions, we used a six-region coding system as follows: 1) Australia―corresponding to the boundary of contemporary Australia and not including New Guinea (Oliver, Hugall, Prasteya, Slavenko & Zahirovic, 2023); 2) New Guinea―the contemporary islands of New Guinea and nearby land-bridge islands; 3) Asia and the Sunda Shelf; 4) East Melanesia―the islands of the Southwest Pacific that are largely underpinned by the Vitiaz Arc, namely Manus, New Britain, Solomons, Fiji and Vanuatu; 5) Wallacea―broadly referring to the islands between Wallace’s Line and Lydekker’s Line; and 6) Pacific―more isolated islands in the Southwest Pacific that are not part of the Vitiaz Arc systems, including parts of Micronesia (Palau) and Polynesia (e.g., Tonga and Samoa).

*BioGeoBEARS and Phybears*

To determine congruence across methods for inferring biogeographic history we ran additional analyses on the six geographic state division in the R packages BioGeoBEARS (Matzke, 2013) version 1.1.4 (Matzke, 2025) and the Julia package PhyBEARS.jl (Matzke & Bland, 2024). Across these two programs, we sought to identify the biogeographic model that best fit the available data using AICc, and then compare estimates of ancestral states for that model with those from the BEAST analyses. These methods are described in detail in the supplementary material, but briefly: in BioGeoBEARS we implemented and compared a set of six standard models, while in PhyBEARS.jl we tested if inclusion of more complex models including extinction and speciation parameters significantly changed likelihood and inference.

*Comparing macroevolutionary regimes for body size*

Body-size analyses were performed on a pruned version of the 96-taxon species tree: thirteen lineages or species for which we were unable to obtain body-size data were pruned for the phylogeny used in this analysis. Maximum body size (snout-vent length) data were obtained from published literature (most species) or through direct measurements of museum material (Table S1).

Shifts in body-size optima (OU theta parameter) were estimated using a relaxed Ornstein–Uhlenbeck (OU) model (Uyeda & Harmon, 2014) as implemented in RevBayes (May & Hoehna, 2022). Snout-vent length was log10-transformed before all analyses to reduce potential impacts of skewed data. The settings in the model RevBayes script (May & Hoehna, 2022) were used with the following modifications: i) The burnin, MCMC run length, and sampling interval were increased tenfold, to ensure convergence and stationarity; ii) The lower bound of the prior on the sigma2 distribution was lowered to 10-5, because the sampled parameter estimates abutted the original lower limit of 10-3. Four runs were performed, convergence was monitored using Tracer 1.7, and a maximum-clade-credibility tree was computed using TreeAnnotator in the BEAST X v 10.5 package (see above).

**Results**

*Species groups in* Gehyra *and lineage diversity in Melanesia*

All analyses of both mtDNA (ND2) and exon-capture data identified six major lineages of *Gehyra* (Fig. 1). The *G.* *variegata* group (here expanded to include *G. xenopus*) and *G. australis* groups are endemic, or nearly endemic, to Australia, with only a single taxon (CYsp) within the *G. australis* group occurring in the savannahs of the Trans-Fly region of southernmost New Guinea. Within CYsp, mitochondrial diversity is strongly concentrated in northern Australia and low in southern New Guinea. Diversity and relationships within these Australian groups are discussed in more detail elsewhere (Moritz et al. 2018; Ashman et al. 2018; Oliver et al. 2019).

The remaining four lineages consist of: 1) the *G. mutilata* group, including at least three species (only two sampled here for exons) that together have a huge distribution spanning across Asia, the Pacific, and the Indian Ocean; 2) the *G. vorax* group―three described species and one candidate taxon distributed from Manus Island to Fiji; 3) the *G. membranacruralis* group―three recognised species known from across eastern New Guinea and Sudest Island in the Louisiade Archipelago; and 4) the *G. oceanica* group―at least nine recognised species (plus several candidate species) distributed from Wallacea, across New Guinea, and much of the tropical west Pacific (Fig. 1).

Mitochondrial and exon-capture-based analyses highlighted the presence of additional lineage diversity not captured by current taxonomy (Fig. S1). Particularly striking are divergent (e.g., ~ late-Miocene origins) lineages in the *G. oceanica* group from Maluku and the Solomon Islands. Conversely, several previously recognised taxa or candidate taxa in the *G. oceanica* group were found to be less divergent (e.g., *G. baliola* and *G. barea,* and lineages within the *G. oceanica* species complex from across the Pacific).

*Phylogenetic relationships*

Topological relationships of the exon-capture data were broadly similar across RAxML, BEAST2 (concatenated), and StarBEAST (coalescent) analyses, although there were some key differences (Figs. 1, S2–4). We only focus on relationships between the six major species groups here. Although they were deeply divergent, a sister-taxon pairing of the larger-bodied insular taxa in the *G. membranacruralis* and *G. vorax* groups was strongly supported in concatenated and coalescent Bayesian analyses. In maximum-likelihood analyses of the concatenated data, the basal relationship of the two giant lineages was retrieved but less strongly supported. These two large-bodied insular species groups also always formed a strongly supported clade with the *G. australis* and *G.* *variegata* groups from Australia. In concatenated (maximum likelihood and Bayesian) datasets, the two Australian lineages tended to form a clade, while in coalescent analyses, the two Australian lineages and the large-bodied clade essentially formed a trichotomy. In all analyses of exon-capture data, the *G. mutilata* and *G. oceanica* groups clustered together with strong support.

*Biogeographic analyses*

Biogeographic analyses revealed limited numbers of shifts between Australia and islands to the north (Figs. 2, S5), with an especially low number of jumps over the most recent time period (i.e., the last ten million years). In BEAST, BioGeoBEARS, and PhyBEARS, the most probable ancestral states suggest that Australia was colonised either twice, or only once, with a subsequent dispersal into Melanesia shortly thereafter, with the latter model tending to receive stronger support (Figs. 2, S5). This uncertainty around basal states is unaffected by variation in extinction rate as implemented PhyBears. Our data cannot robustly distinguish between these two options due to uncertainty around the basal state (ancestral area) for all *Gehyra*. The only other well-supported shift between Australia and nearby regions occurred much more recently in CYsp in the *G. australis* group and involves a species that occurs across both Australia and the savannahs of far southern New Guinea, with the inferred shift being robustly inferred to be out of Australia.

The Markov-Jumps shift counts result in slightly higher average numbers of shifts, due to a scattering of low-probability shifts occurring in any single MCMC sample; these are distributed across different branches in different samples (always at low probability) and thus do not appear in the consensus ancestral reconstructions. Ancestral reconstructions on the detailed 6-state analysis infer ~2.8 shifts between Australia and islands to the north, and 1.9 shifts from islands into Australia. In contrast, at least 12.3 dispersals between island systems to the north of Australia that have likely never been connected by land are inferred, with the most frequent shifts being from East Melanesia into New Guinea, and from New Guinea into East Melanesia and Wallacea.

*Body size*

The relaxed OU analyses on the StarBEAST phylogeny found the biggest shift in body optima between the clade comprising the *G. vorax* (East Melanesia) plus *G. membranacruralis* (New Guinea) groups and all other taxa (Fig. S6). This is consistent with the larger body sizes observed in all members of these two species groups (max SVL between 129–155 mm; Fig. 3). There was also a subtler increase within the *G.* *oceanica* group, and nested within this clade, a further increase in the lineage leading to *marginata* from Wallacea (SVL 142 mm). The Australian lineages show no evidence of marked shifts in optima either when compared against each other or against the basal nodes for the genus.

**Discussion**

We present a phylogeny that includes nearly all recognised species of Australasian *Gehyra* based on a large (100-locus) nuclear gene dataset and concatenated as well as coalescent analyses. This phylogeny emphasises that *Gehyra* radiations from Australia are highly discrete from those from New Guinea and other islands of Melanesia. Furthermore, successful dispersal has been very rare between these regions despite their proximity, especially since the mid-Miocene when Australia was moving northwards into the Melanesian region (Hall, 2002). Some, but not all, lineages of Melanesian *Gehyra* also show evidence of a shift in body-size optima towards very large size. Below, we discuss the significance of these results both for understanding the biogeographic history of Australasia and the factors that may mediate patterns of dispersal and ecological diversification across insular and continental regions.

**Phylogeny of *Gehyra***

This study represents the most complete and gene-comprehensive phylogeny of *Gehyra* available to date. The six major species groups of *Gehyra* identified here are well-supported and robust, as are most shallower relationships, although the latter were not the primary focus of this paper (see (Ashman et al., 2018; Oliver et al., 2019)). Our sampling supports the distinctiveness of recognised Melanesian species, although some, such as *G. baliola* and *G. barea*, are only shallowly divergent. Our data also highlight divergent lineages that are either unnamed or for which the correct name is uncertain. Resolving the status and ecology of these potentially unnamed taxa is a priority for ongoing taxonomic work; however, documentation of this Melanesian diversity is unlikely to change our broadscale understanding of the biogeography of *Gehyra* in Australasia.

In contrast, the shortage of genetic (and especially genomic) data for the small number of *Gehyra* endemic to Asia, and the absence of matching genomic data for probable outgroups in the genera *Hemiphyllodactylus* and *Perochirus* (Heinicke et al., 2011) impose major constraints on our understanding of the deep-scale relationships and biogeography of *Gehyra*. Most notably, relationships of the *G.* *oceanica* and *G.* *mutilata* groups vary in our analyses when compared against phylogenies (using concatenation) including more outgroups (Heinicke et al., 2011; Title et al., 2024). Alternative positions for these species groups and the addition of missing Asian taxa may also be the difference between inferring whether *Gehyra* has deep Oligocene origins on island arcs in the Southwest Pacific (like some other co-occurring Australasian squamate taxa (Oliver et al., 2018)), or conversely, are more recent colonists from the Asian continental shelf (Oliver & Hugall, 2017). Filling these data gaps should be a priority area for further research, although we re-emphasise that new data are unlikely to change our interpretation that the well-sampled Australian and Melanesian radiations of *Gehyra* have largely independent and distinctive histories (see below).

**Island-to-continent dispersals in Australasia**

Understanding the degree to which the biotas of Australia and Melanesia (and especially New Guinea) are shared has been a theme in Australasian biogeography for over 150 years (Heinsohn & Hope, 2006; Wallace, 1876). Our data indicate that dispersals between Australia and islands have played a limited role in shaping the contemporary diversity of *Gehyra*. Furthermore, the probability of dispersal is inferred to be lower in the last ten million years, despite the increasing proximity of Australia and New Guinea, increasing extent of land in the New Guinean region, and sporadic formation of land bridges through this time (Harrington et al., 2017). In contrast, frequent and often long-distance overwater dispersals have clearly occurred in several Melanesian lineages of *Gehyra* (Oliver et al., 2016; Tonione et al., 2016). We particularly emphasise that New Guinea and East Melanesia have been important sources of lineages for nearby islands, especially in the *G.* *oceanica* group (Figs. 2, S5). Furthermore, our coding for regions across Melanesia and Wallacea certainly underestimates the historical number of inter-island overwater dispersals because some regions consist of islands that have never been connected by land (e.g., Manus versus Fiji/Vanuatu within East Melanesia) or landmasses such as New Guinea that are comprised of formerly discrete islands (Pigram & Davies, 1987). These data indicate that, at least for the Melanesian *Gehyra*, an inability to disperse overwater cannot be invoked to explain the low rate of dispersal into northern Australia, especially over the last ten million years.

Possible explanations for limited dispersal by *Gehyra* between Australia and Melanesia (and especially New Guinea) are niche conservatism (Crisp, Arroyo, Cook, Gandolfo, Jordan, McGlone, Weston, Westoby, Wilf & Linder, 2009) and biotic interactions such as competition. It is very difficult to distinguish between these two potential processes, and it is even possible that both are playing a role. However, with respect to niche conservatism, studies of Australian *Gehyra* have emphasised that even within this moderately old radiation, only one lineage has been able to shift from monsoonal to arid environments (Ashman et al., 2018), despite having hard-shelled eggs and considerable lability in thermal and hydric physiology (Skelton, Moritz, Day, Weitzman, Schlesinger, Zozaya & Christian, 2024). Melanesian *Gehyra* are strongly associated with tropical rainforest habitats, whereas the two Australian *Gehyra* lineages are almost completely absent from rainforest areas. Analyses of other families of Australasian reptiles, including diverse and relatively old radiations associated with arid and savannah environments in Australia, have also found limited or no evidence for dispersal into New Guinea (Pavón-Vázquez et al., 2022; Skipwith, Bi & Oliver, 2019; Tallowin et al., 2020). This suggests that for many taxa, and perhaps for ectothermic reptiles in particular, the increasingly close proximity of Australia and New Guinea has not been sufficient to overcome environmental differences and the constraints of niche conservatism.

The rarity of recent dispersal between Australia and New Guinea within *Gehyra* strikingly contrasts with some other components of the Australasian biota, including some other lizard radiations (Blom, Matzke, Bragg, Arida, Austin, Backlin, Carretero, Fisher, Glaw & Hathaway, 2019; Probst, Frandsen & Whiting, 2025), rats (Roycroft et al., 2022), pigeons (Oliver et al., 2023), some groups of parrots (Schweizer, Wright, Peñalba, Schirtzinger & Joseph, 2015), and even tropical rainforest plants (Sniderman & Jordan, 2011). These studies have all inferred numerous and recent colonisations between Australia and islands to the north, centred on, but not exclusive to, New Guinea. In most cases, these lineages are much more closely associated with mesic environments than are typically inhabited by Australian *Gehyra*. Many of these groups are also likely to be either more physiologically labile (over evolutionary timescales) and/or better dispersers than *Gehyra.* Ecological, taxonomic, and environmental variation likely all mediate varying probabilities of dispersal between Australia and islands to the near north. Comparative analyses that control for these factors across multiple taxa are a logical next step towards a more holistic understanding of how biotic exchange has occurred between Australia and Melanesia.

**Single origin of most island ‘giants’**

*Gehyra* do not show a general shift to gigantism (as optimal body size) on all islands of Melanesia. Rather, there is a single marked shift in body size in a clade comprising the *G.* *membranacruralis* and *G.* *vorax* groups (which are sister taxa), which then dispersed across multiple islands. One other lineage in the *G.* *oceanica* group from Wallacea (where the afore-mentioned two species groups are not present) has also evolved large body size. Most other species on islands (*G.* *mutilata* and *G.* *oceanica* groups) tend to be similar, or at most *slightly* larger in size than Australian and Asian continental forms (max SVL usually between 60–100 mm). This overall conservatism of large body size contrasts with the widely known pattern in *Anolis* lizards, where large-bodied ecomorphs have evolved repeatedly on different islands (e.g., Losos et al. 1998). It also differs from emerging signal that geographically localised and evolutionarily rapid shifts in body size have played an important role in the assemblance species communities in some other insular radiations in Melanesian taxa, most notably various lineages of bats (Almeida, Helgen, Simmons & Giannini, 2025; Lavery, DeRaad, Holland, Olson, DeCicco, Seddon, Leung & Moyle, 2024).

The limited number of shifts in body size makes it difficult to test whether the larger body size in some island *Gehyra* is due to contingency (large species evolved by chance on islands) or determinism (island environments favour the evolution of large species) (Losos, Jackman, Larson, Queiroz & Rodrı́guez-Schettino, 1998). A trend towards large body size in *Gehyra* does, however, mirror large body sizes observed in other lineages of forest-associated geckos with distributions occurring across south-east Asia (Das, 2010) and throughout the south-west Pacific (Heinicke et al., 2023; Skipwith & Oliver, 2023). In as much as their ecology is understood, these lineages are mostly highly arboreal and often found resting on the trunks or branches of trees. This combination of large size and a highly arboreal ecology also suggests parallels with the crown-giant ecomorphs in scansorial *Anolis* lizards that occur in both insular and continental regions of tropical America (Huie et al., 2021). On this basis we suggest that large body size in geckos may be correlated with a highly arboreal ecology, but we emphasise that a lineages comprehensive global comparative analysis is needed to test this idea further. Leaving aside the uncertainty around evolutionary drivers, we also argue the absence of large (SVL < 130) arboreal geckos from most of Australia provides further support for the idea that despite their proximity, Australia and nearby Melanesia have - for some taxa - fostered distinct radiations showing differing patterns of diversification.

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**Data accessibility.** All phylogenetic data and tree files will be made available in The Dryad depository upon publication of this manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website.

Supplementary biogeographic methods and references.

**Table S1.** Area state and maximum body size data for species and OTUs of *Gehyra* included in analyses.

**Table S2.** Results of statistical model comparison of the six standard BioGeoBEARS models.

**Table S3**. Statistical model comparison of 12 biogeographic models run in the Julia package PhyBEARS.jl

**Figure S1.** Maximum Likelihood tree showing major species groups and summary of ND2 sampling for Melanesian *Gehyra.*

**Figure S2.** Maximum likelihood tree for *Gehyra* estimated from concatenated 100 nuclear loci dataset using RAxML.

**Figure S3.** Bayesian chronogram for *Gehyra* estimated using BEAST and a concatenated 100 nuclear loci dataset.

**Figure S4.** StarBEAST “divide and conquer” tree for *Gehyra* estimated from 100 loci.

**Figure S5.** Ancestral area estimations for *Gehyra* based on model with highest AICc value in PhyBears (DEC+J+D=e=D).

**Figure S6.** Ancestral area estimations for *Gehyra* based on DEC+J+D+B=D model as implemented in PhyBears.

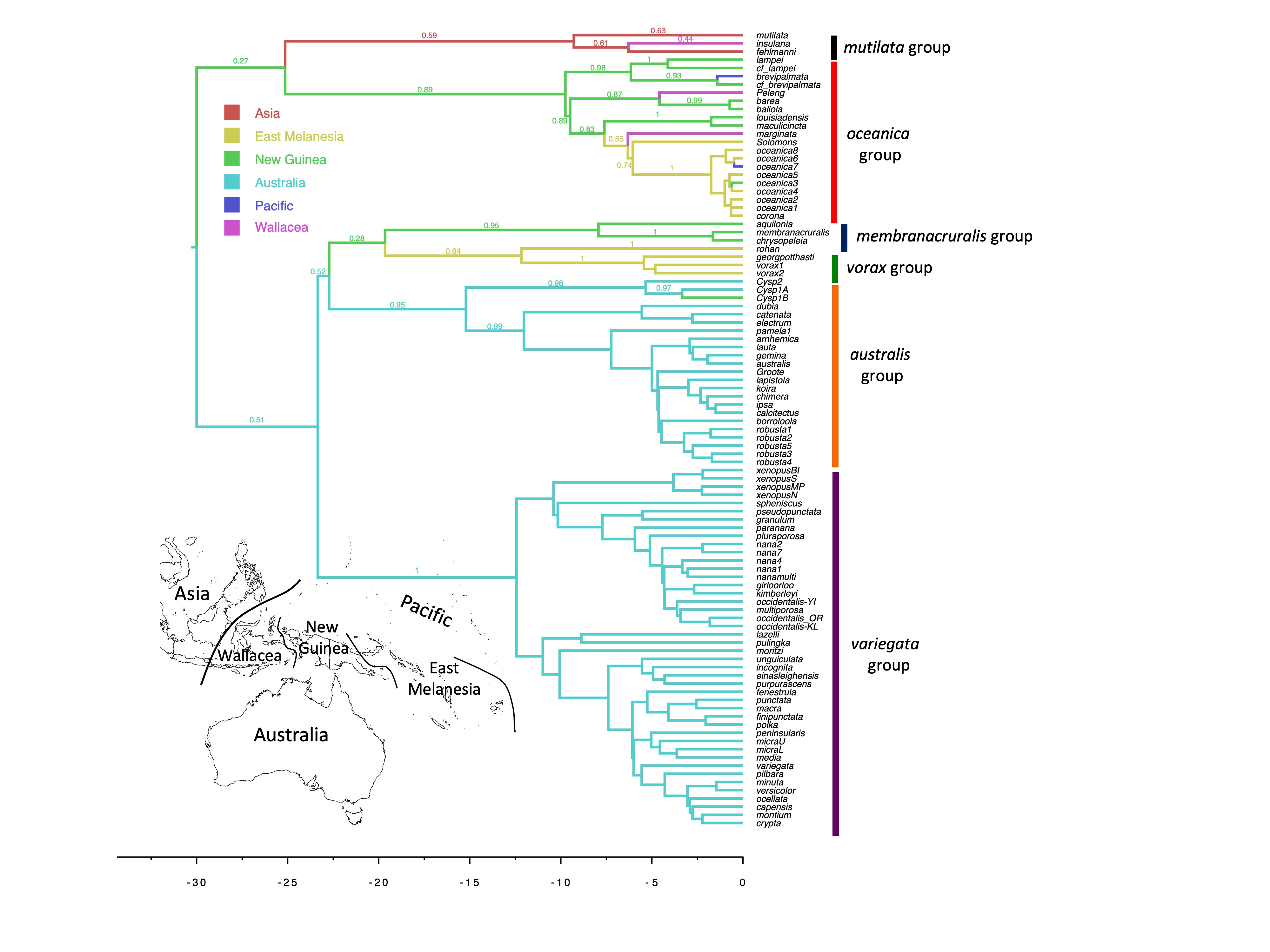
**Figure S7.** Ancestral area estimations for *Gehyra* based on DEC+J+B=D-e model as implemented in PhyBears.

**Figure S8.** Estimation of values for body-size optima (OU theta parameter) estimated using a relaxed Ornstein–Uhlenbeck (OU) model.

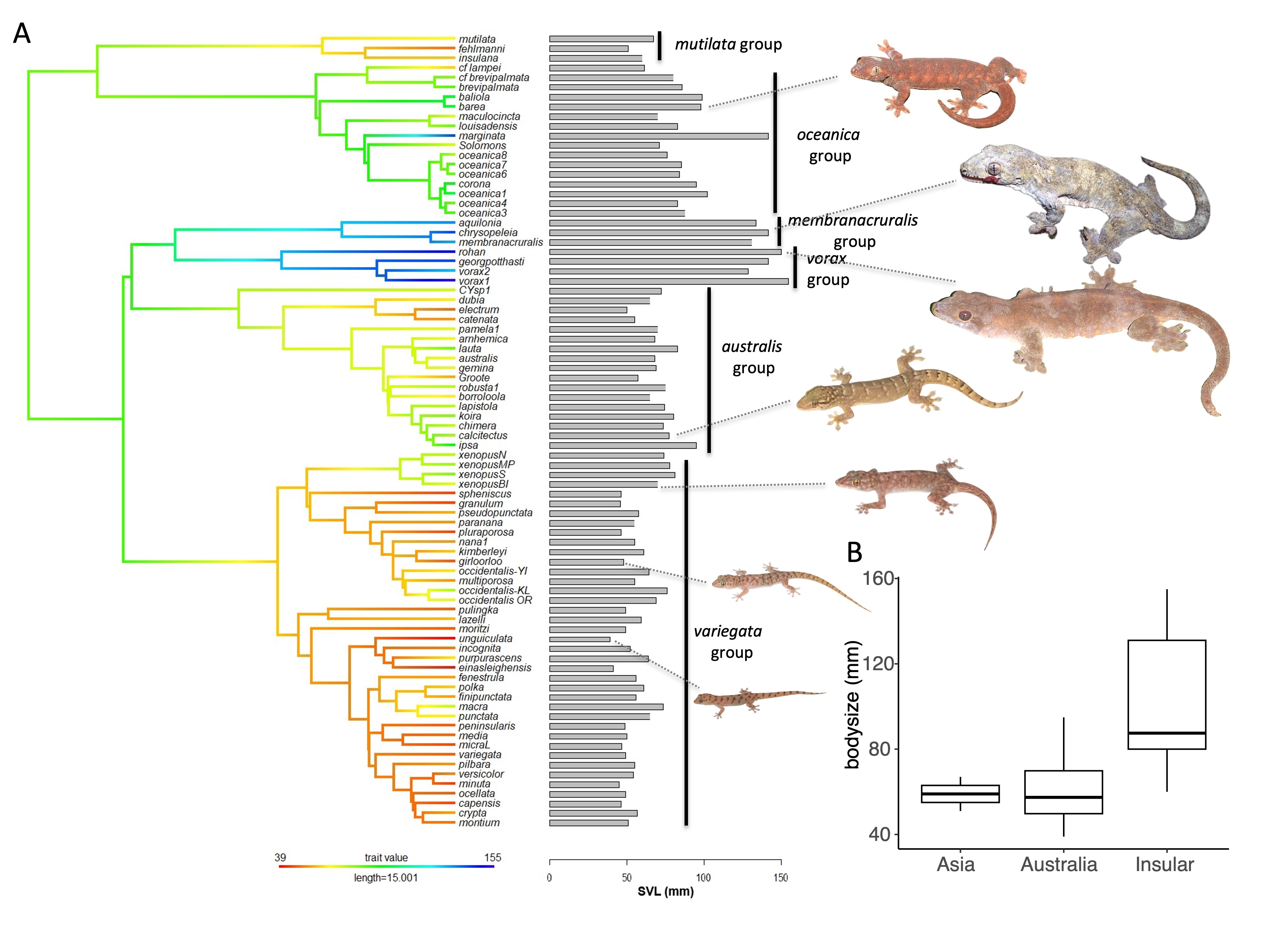
A map of different groups of people

AI-generated content may be incorrect.

**Figure 1.** StarBEAST topology for *Gehyra* estimated using 100 loci. Nodes with Bayesian support values above 0.90 indicated. Maps on right show distribution of the main *Gehyra* groups that occur east of Wallace’s Line. The distribution of the *G. mutilata* group (Asia through the Pacific region) is not shown because the extent of the natural versus introduced range of that very widespread species group is unclear.



**Figure 2.** Biogeographic reconstructions for Australasian *Gehyra*. Phylogeny estimated using 100 loci in \*BEAST with imputed positions for four taxa for which genetic data were missing. Ancestral states estimated on a fixed topology using BEAST. Values on branches indicate the probability of the most frequent geographic state (not shown for tip branches or unequivocally Australian sub-radiations). The ancestral area for the entire radiation is ambiguous. Despite the close proximity of Australia and islands to the north, few shifts into or out of Australia are inferred. In contrast, multiple transmarine dispersals across Wallacea, Melanesia, and the Pacific are inferred.



**Figure 3.** Summary data on body-size evolution in *Gehyra*. A) Evolution of body size along a time-calibrated phylogeny for all species and divergent OTUs for which we were able to obtain maximum body-size data. Smallest sizes are in red while largest sizes are in blue. B) Boxplots showing median and ranges of maximum snout-to-vent length in Asia, Australia, and insular regions. Images of exemplar *Gehyra* showing size variation courtesy of Scott Maccor, Glenn Shea, and Stephen Richards.