



## Early insularity and subsequent mountain uplift were complementary drivers of diversification in a Melanesian lizard radiation (Gekkonidae: *Cyrtodactylus*)

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### ABSTRACT

Regions with complex geological histories present a major challenge for scientists studying the processes that have shaped their biotas. The history of the vast and biologically rich tropical island of New Guinea is particularly complex and poorly resolved. Competing geological models propose New Guinea emerged as a substantial landmass either during the Mid-Miocene or as recently as the Pliocene. Likewise, the estimated timing for the uplift of the high Central Cordillera, spanning the length of the island, differs across models. Here we investigate how early islands and mountain uplift have shaped the diversification and biogeography of *Cyrtodactylus* geckos. Our data strongly support initial colonisation and divergence within proto-Papuan islands in the Early- to Mid-Miocene, with divergent lineages and endemic diversity concentrated on oceanic island arcs in northern New Guinea and the formerly isolated East-Papuan Composite Terrane. At least four lineages are inferred to have independently colonised hill- and lower-montane forests, indicating that mountain uplift has also played a critical role in accumulating diversity, even in this predominantly lowland lineage. Our findings suggest that substantial land in northern New Guinea and lower-montane habitats date back well into the Miocene and that insular diversification and mountain colonisation have synergistically generated diversity in the geologically complex Papuan region.

### 1. Introduction

The Australo-Papuan region – encompassing Australia, New Guinea and immediately adjacent islands – is a centre of global vertebrate and plant species endemism (Grenyer et al., 2006; Kreft and Jetz, 2007; Kier et al., 2009; Givnish et al., 2015). New Guinea, the world's second largest (785,753 km<sup>2</sup>) and highest (4884 m) island comprises less than 0.2% of the Earth's land surface yet is estimated to contain ~5% of the world's terrestrial vertebrate species (Allison, 2009), including a number of spectacular, near-endemic radiations (e.g., Birds-of-paradise - *Paradisaeidae* [Irestedt et al., 2009] and narrow-mouthed frogs – *Asoterophryinae* [Zweifel, 1972; Rivera et al., 2017]). This high diversity has been attributed to the combination of New Guinea's wet and warm

tropical climate, exceedingly complex geological history of arc accretion and mountain uplift, and consequent extreme topographic complexity (Heads et al., 2002; Givnish et al., 2015; Oliver et al., 2017a; Tallowin et al., 2017). Molecular phylogenetic studies have provided key insights into the origin, timing, and history of tropical radiations in regions such as the Andes, Philippines, and Himalayas (e.g., Hoorn et al., 2010; Brown et al., 2013; Price et al., 2014). However, fewer equivalent studies (i.e. attempting to integrate across different processes for diverse components of the biota) have been conducted in the Melanesian region (Toussaint et al., 2014; Oliver et al., 2018b).

Following the onset of Australian-Antarctic continental breakup around the late Cretaceous, the Australian plate moved through almost 30° of latitude (Baldwin et al., 2012). In the complex Australian-Pacific

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plate boundary zone to the north, New Guinea and the mobile oceanic Admiralty, Bismarck, and Solomon island archipelagos emerged (Baldwin et al., 2012). Small portions of present-day New Guinea likely formed during the Eocene to early Oligocene (~45–30 million years ago [Ma]; Audley-Charles, 1991; Hall, 2002; van Ufford and Cloos, 2005; Hall, 2009). Subsequent dynamic tectonic uplift events coupled with a drop-in sea level (Hall, 2002; ) exposed ever-increasing portions of a proto-Papuan archipelago (van Ufford and Cloos, 2005). Around 25 Ma, oblique west-to-east island-arc accretion across the leading edge of the Australian Craton began (AC; Pigram and Davies, 1987; Hall, 2002; Baldwin et al., 2012). While the precise timings, and extent of subaerial terranes in the ‘proto-Papuan’ region remains ambiguous (Hall, 2009), geological and biogeographical studies suggest that substantial land in the New Guinean area only existed after 15 Ma (van Ufford and Cloos, 2005; Cloos et al., 2005; Moyle et al., 2016) or as recently as 10 Ma (Hall, 2002; Toussaint et al., 2014).

Collisional delamination of the continental Australian Craton also initiated the uplift of the most striking geological feature of contemporary New Guinea – a continuous Central Cordillera that runs nearly the length of the island. On the one hand van Ufford and Cloos (2005) predicted uplift initiated around 12 Ma, with much of the east–west extent of the highlands being attained by 5 Ma. Conversely Hill and Hall (2003) suggested the emergence of the Central Range occurred more recently after 5 Ma. The temporal emergence of the East-Papuan Composite Terrane (EPCT, comprising the Papuan Peninsula and nearby islands) orogeny has also been contested. Its uplift was reported to have initiated during the Oligocene (~35–30 Ma; Pigram and Davies, 1982; van Ufford and Cloos, 2005) contrasting with models predicting a more recent development during the Mid-Miocene (14–12 Ma; Hall, 2002; Hill and Hall, 2003).

Phylogenetic analyses can provide complementary datasets to verify and refine hypotheses stemming from geology (Crisp et al., 2011). However, care is required when contrasting palaeographic reconstructions with biogeographic models, as the former often omit whether landforms were subaerial or submarine (Hall, 2009). In the context of New Guinea’s exceptionally complex history, three broad geological and biological processes have dominated discussion as to what underpins the origin and diversity of the resident biota. One hypothesis is that there was extensive initial speciation and diversification on ‘proto-Papuan’ archipelagos, prior to the accretion of these terranes along the northern edge of the Australian plate (Polhemus, 2007; Jönsson et al., 2011; Aggerbeck et al., 2014; Strickland et al., 2016; Oliver et al., 2018b). Under this scenario, major lineages would have originated before the accretion of the island arcs (40–10 Ma) and may be concentrated in regions to the north of the Australian Craton (see Fig. 1). A related prediction is that major geological entities that comprise northern New Guinea, broadly the Vogelkop Composite Terrane, Oceanic Arc Terranes, and the East-Papuan Composite Terrane (see Fig. 1) may have their own distinct biotas.

A contrasting, and long-standing hypothesis is that the biota of New Guinea, especially the montane-biota, is dominated by lineages with Australian origins whose ranges have contracted northwards in the face Australia’s severe aridification since the Miocene (Schodde and Calaby, 1972; Crisp et al., 1995). This would predict older divergences and ancestral-state origins within the Australian Craton (mainland Australia and southern New Guinea; see Fig. 1) and younger divergences and colonisation within island-arc complexes that have more recently accreted onto New Guinea (Mitchell et al., 2014).

Finally, the rapid mountain uplift is also proposed to have played a central role in generating species diversity in New Guinea. First, by initiating vicariant divergence among lowland taxa (Unmack et al., 2013; Georges et al., 2014), and second by providing novel habitats for lineages to adapt to and exploit, first the hill forest, and more recently lower-, mid-, and upper-montane habitats (Toussaint et al., 2014; Marki et al., 2017; Oliver et al., 2017a).

A growing body of phylogenetic and phylogeographic work has

focused on teasing apart the role of these processes in shaping divergent New Guinean taxa, including beetles (Toussaint et al., 2014), birds (Jönsson et al., 2011; Moyle et al., 2016), fish (Unmack et al., 2013), frogs (Oliver et al., 2017a; Rivera et al., 2017), skinks (Austin et al., 2010), geckos (Oliver et al., 2018b), and freshwater turtles (Georges et al., 2014). These studies have uncovered a strong signature of geological history on the genetic structure of the region’s biota. However, the total number of clades examined remains low. Furthermore, many studies have focused on a subset of key hypotheses for what may have shaped the New Guinean fauna, and fewer have used comprehensive species/lineage phylogenies of diverse radiations. Here we complement existing work by presenting a species-level biogeographic analysis of a moderately diverse endemic Melanesian radiation of bent-toed geckos (*Cyrtodactylus*).

*Cyrtodactylus* is the most species-rich gecko genus in both the Australo-Papuan region and the world (31 and 233 species respectively, Uetz et al., 2018). Dispersing eastwards from a continental-Asian origin (Wood et al., 2012), two distantly related *Cyrtodactylus* lineages have independently colonized the Australo-Papuan region (Oliver et al., 2014). One lineage is represented by a single recognised species, *C. papuensis*. All other species are placed in the other lineage, which has dispersed and diversified throughout the region, including northern Australia and the Solomon Islands (see Fig. 1). Knowledge of Papuan *Cyrtodactylus* diversity has increased rapidly in recent years (Rösler et al., 2007; Kraus, 2007; Oliver et al., 2011; Shea et al., 2011; Oliver et al., 2012; Oliver and Richards, 2012; Oliver et al., 2016), providing a much-improved taxonomic framework for biogeographic analyses. Diversification among these geckos has been attributed to ecological plasticity and evolutionary divergence in traits such as body size and shape (Oliver et al., 2014) and habitat preference (e.g., limestone karst and cave formations, Wilmer and Couper, 2016; Nielsen and Oliver, 2017). Non-ecological processes such as climatic change (Wilmer and Couper, 2016) and sporadic overwater dispersal (Oliver et al., 2018a) are also implicated in *Cyrtodactylus* diversification. Most *Cyrtodactylus* in New Guinea (and indeed elsewhere) occur in lowland habitats (< 500 m above sea level – a.s.l.), but several inhabit hill forests (500–1000 m a.s.l.), or lower montane areas (1000–1500 m a.s.l., highest recorded Australo-Papuan *Cyrtodactylus* at 1448 m a.s.l.) (habitat categorization after Shearman and Bryan, 2015). This indicates elevational gradients may also have played a role in their diversification (Oliver et al., 2012, 2016).

We examine the timing and role of putative key drivers of Papuan diversification using a newly assembled near-complete phylogeny for Australo-Papuan *Cyrtodactylus* (missing only three recognised species, *Cyrtodactylus aaroni*, *C. derongo* and *C. irianjayaensis*). We (1) compare time-constrained biogeographic analyses to test if there is stronger support for early evolutionary processes on the Australian Craton or former islands to the North; (2) examine whether *Cyrtodactylus* biogeographical patterns correlate with the distinct Australo-Papuan geological regions (see Fig. 1); (3) quantify infra-regional phylogenetic structure to identify if there is evidence of non-random phylogenetic clustering, indicative of shared geographical histories, or over-dispersal resulting from repeated inter-regional dispersal and colonisation; and (4) estimate the number and timing of shifts into uplifted / mountain habitats and the number of north–south lineage pairs separated by high elevation habitats (see Fig. 1) to better understand the role of mountain uplift in the accumulation of species diversity.

## 2. Methods and methods

### 2.1. Sampling, sequencing and datasets

New genetic data were taken from whole specimens and tissue samples stored at museums in Australia, the United States of America and Europe (see Table S1 for complete list of samples, field/voucher specimen and GenBank accession codes). Our total dataset of aligned

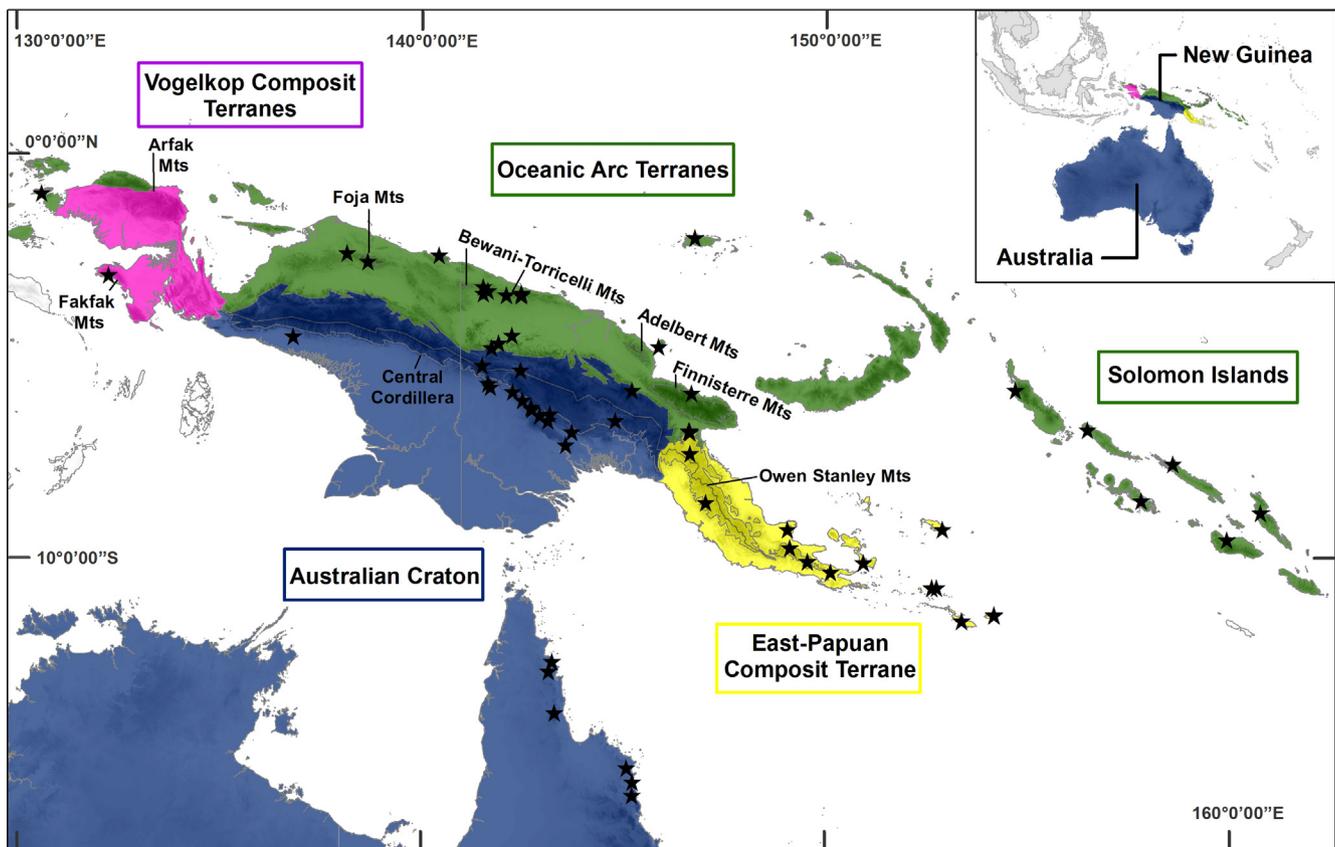


Fig. 1. Map of the present-day Australo-Papuan region, with four major geological areas denoted by color. Mountains ranges are illustrated with darker shading and Australo-papuan *Cyrtodactylus* specimen localities are illustrated with star symbols.

sequences included 136 Australo-Papuan *Cyrtodactylus* (including 40 newly sequenced specimens), 77 extralimital *Cyrtodactylus*, and 16 other gecko species used for fossil calibrations. Our sample included 28 of the 31 Australo-Papuan *Cyrtodactylus* species (lacking *C. aaroni*, *C. derongo* and *C. irianjayaensis*, see Table S1 for full species list). Sequencing protocols and targeted genes followed Wood et al. (2012). Our alignment included portions of the mitochondrial gene, nicotinamide adenine dinucleotide dehydrogenase subunit 2 (*ND2*, 1044 base pairs [bp]), and three nuclear genes: recombination activating gene-1 exon (*RAG1*, 1062 bp), phosphocyanin (*PHOS*, 378 bp), and matrix-remodelling associated 5 (*MXRA5*, 834 bp). Chromatographs were checked manually, assembled and edited using Geneious v.7.1.9 (Biomatter Ltd.). For the nuclear genes heterozygous positions were identified and coded according to the IUPAC ambiguity codes. Sequences were aligned, for each gene independently, using the online application of MAFFT v.7.3 (Katoh and Standley, 2013) with default parameters. All genes were translated to amino acids and no stop codons were detected. We treated alignment gaps as missing data. Nuclear gene sequences were not phased.

Three different subsets of data were used to evaluate lineage diversity, relationships and biogeography within Australo-Papuan *Cyrtodactylus*: alignment (a) an *ND2* complete dataset of all specimens for initial assessments of lineage diversity; alignment (b) a complete concatenated dataset of single representatives of each species and candidate species identified from alignment (a) for dating and biogeographical analyses; alignment (c) a complete concatenated dataset of all specimens for phylogenetic assessments.

We partitioned the data and determined nucleotide-substitution models with PartitionFinder v.2.1.1 (Lanfear et al., 2016), with the following parameters: linked branch length; BEAST models; BIC model selection; greedy schemes search; partition by codon for all four genes. A summary of DNA partitions and relevant models is presented in Table

S2.

## 2.2. Species delimitation

As well as the recognised Australo-Papuan *Cyrtodactylus* species, additional candidate species of *Cyrtodactylus* have been diagnosed through morphological comparisons by the authors (AA, FK, SJR, and PMO). To build on these observations, genetic divergence among the Australo-Papuan *Cyrtodactylus* in alignment (a) were assessed using a multi-rate Poisson Tree Processes (mPTP; Kapli et al., 2016) carried out through a webserver (<http://mptp.h-its.org/>). The mPTP analysis method uses single-locus data—in this case the *ND2* alignment—and fits the branching events of each delimited species to a particular exponential distribution (Kapli et al., 2016). Recent studies have highlighted that multi-species coalescent methods detect population structure which, in alignments where terminal units are poorly defined, may result in misleadingly high posterior ‘speciation’ probabilities for those lineages (Sukumaran and Knowles, 2017). The mPTP method was found to be the most reliable single-locus delimitation method, especially among alignments with highly uneven sampling or large differences in effective population sizes of species (Blair and Bryson, 2017). However, the candidate species delimited by this approach should be considered only tentative hypotheses of species, requiring confirmation or rejection through subsequent analyses or using other types of data (Sukumaran and Knowles, 2017).

We carried out mPTP analysis on the Australo-Papuan *Cyrtodactylus* *ND2* gene tree estimated through ML analysis of alignment (a), described above (Table S2). The putative species—henceforth referred to as operational taxonomic units (OTU's)—were further assessed using uncorrected pairwise genetic divergence. We chose a minimum of 10% as the measure that particular lineages may have long histories of isolation from each other. Other *Cyrtodactylus* genetic studies have also used this

value as a starting point for identifying distinctive lineages (Welton et al., 2016; Oliver et al., 2012). Inter- and intra-specific uncorrected  $p$ -distances were calculated in MEGA v.7.0.14 (Kumar et al., 2016; see Table 4).

### 2.3. Phylogenetic analysis

We estimated phylogenetic relationships using Maximum Likelihood (ML), and Bayesian Inference (BI) methods implemented on the CIPRES Science Gateway v.3.3 (Miller et al., 2010). Maximum Likelihood analyses were performed with RAxML v.8.1.2 (Stamatakis, 2014) using RAxMLGUI v.1.5 (Silvestro and Michalak, 2012). ML analyses were carried out on alignments (a) and (c) with a GTR+G model of evolution used for both. Partitioning strategy selected was by codons for alignment (a) and Partitionfinder for alignment (c) (Table S2). The best ML trees were determined from 1000 randomized maximum-parsimony starting trees, with four independent runs used to assess tree topology. Bootstrap support was estimated from 1000 replicates. We also inferred Maximum Likelihood trees with IQ-TREE v.1.6.1 (Nguyen et al., 2015) implementing 1000 ultrafast bootstrap replicates (Hoang et al., 2017) and using default parameters for partition models (Chernomor et al., 2016; see Table S2).

Bayesian inference of topology was performed in BEAST v.1.8.2 (Drummond et al., 2012) on the full species-level alignment (c). Information on the models, priors and calibrations are presented in Table S2. Posterior trace plots and effective sample-size (ESS) values of parameters ( $> 200$ ) of each run were assessed in Tracer v.1.6 (Rambaut and Drummond, 2009), and LogCombiner and TreeAnnotator were used to infer the ultrametric tree (both in BEAST package; Drummond et al., 2012). Nodes are reported if they received ML bootstrap values  $\geq 70\%$  and posterior probability (pp) support values  $\geq 0.95$  (Wilcox et al., 2002; Huelsenbeck and Rannala, 2004).

Diversification times were estimated in BEAST v.1.8.2 (see priors in Table S3) using the reduced phylogenetic alignment (b) incorporating one representative for each *Cyrtodactylus* species and candidate species (from the mPTP and pairwise genetic distance analyses), as well as outgroup taxa (see Tables S1, S4). These analyses were calibrated using three fossil calibrations in other gekkotan lineages (Heinicke et al., 2011) and a fourth calibration at the base of the *Cyrtodactylus* tree derived from a fossil-calibrated analysis of five nuclear genes for the majority of gecko genera (see Gamble et al., 2015; Oliver et al., 2018a; see Table S3). Studies have noted that a high number of partitions on divergence time analyses can lead to poor estimations due to aberrant narrow credibility intervals (Dos Reis et al., 2014; Jin and Brown, 2017). As the effect is detectable above four partitions (Jin and Brown, 2017), in addition to our dating analyses using six partitions we ran additional analyses with two partitions and contrasted the divergence time estimates (see Table S2). We used a random starting tree and Yule speciation prior to run 4 independent analyses for 100 million generations, sampling every 10,000 generations. Convergence of the four runs was assessed in Tracer v.1.6 (Rambaut et al., 2014), and ESS values above 200 were used to determine adequate convergence. The first 10% of generations were discarded as burn-in using LogCombiner, and TreeAnnotator was used to infer the ultrametric tree (both in BEAST package; Drummond et al., 2012).

### 2.4. Ancestral area estimation

We ran three different ancestral-state-estimation analyses focusing on: (a) an Australian Craton versus proto-Papuan island-arc origin for Australo-Papuan *Cyrtodactylus*; (b) geographic structuring within the three major geological regions of Australo-Papuan region (see Fig. 1); and (c) the frequency and timing of both upslope colonization of montane habitats and north/south divisions across the Central Dividing Ranges (see Section 2.5).

Ancestral ranges and elevational states were inferred using

BioGeoBEARS v.0.2.1 (Matzke, 2013a; Matzke, 2013b). We compared three commonly used models: Dispersal-Extinction-Cladogenesis (DEC; Ree et al., 2005; Ree and Smith, 2008), Dispersal-Vicariance Analysis (DIVA; Ronquist, 1997), and Bayesian Analysis of Biogeography (BayArea; Landis et al., 2013). We also ran all three models, with and without modelling founder-effect jump dispersal (the J-parameter), which specifies the probability of a jump dispersal event at cladogenesis, conditional on the ancestral range (Matzke, 2014). Long-range dispersal is widely recognised as an important process that has shaped organismal distributions and founder-event speciation, being particularly important for increasing model fit when estimating the evolutionary history of island radiations (Zhang et al., 2017). We conducted these analyses on the time-calibrated chronogram from BEAST including only representatives of the main Australo-Papuan *Cyrtodactylus* radiation (alignment b).

To test whether early *Cyrtodactylus* diversification occurred on either the Australian Craton or adjacent islands to the north and east (the 'proto-Papuan' region; see Fig. 1), all species and candidate species were assigned to one of these two regions based on their extant distributions (see Table S5). Range data were obtained from Tallowin et al. (2017; see Fig. 1 and Table S1). To test support for geological model suggesting no or little land was present north of Australia before the Mid-Miocene (or even later), we ran equivalent models placing time-constraints of 15 Ma (Moyle et al., 2016) and 10 Ma (Hill and Hall, 2003; Toussaint et al., 2014) on *Cyrtodactylus* diversification in the geological regions north of Australia.

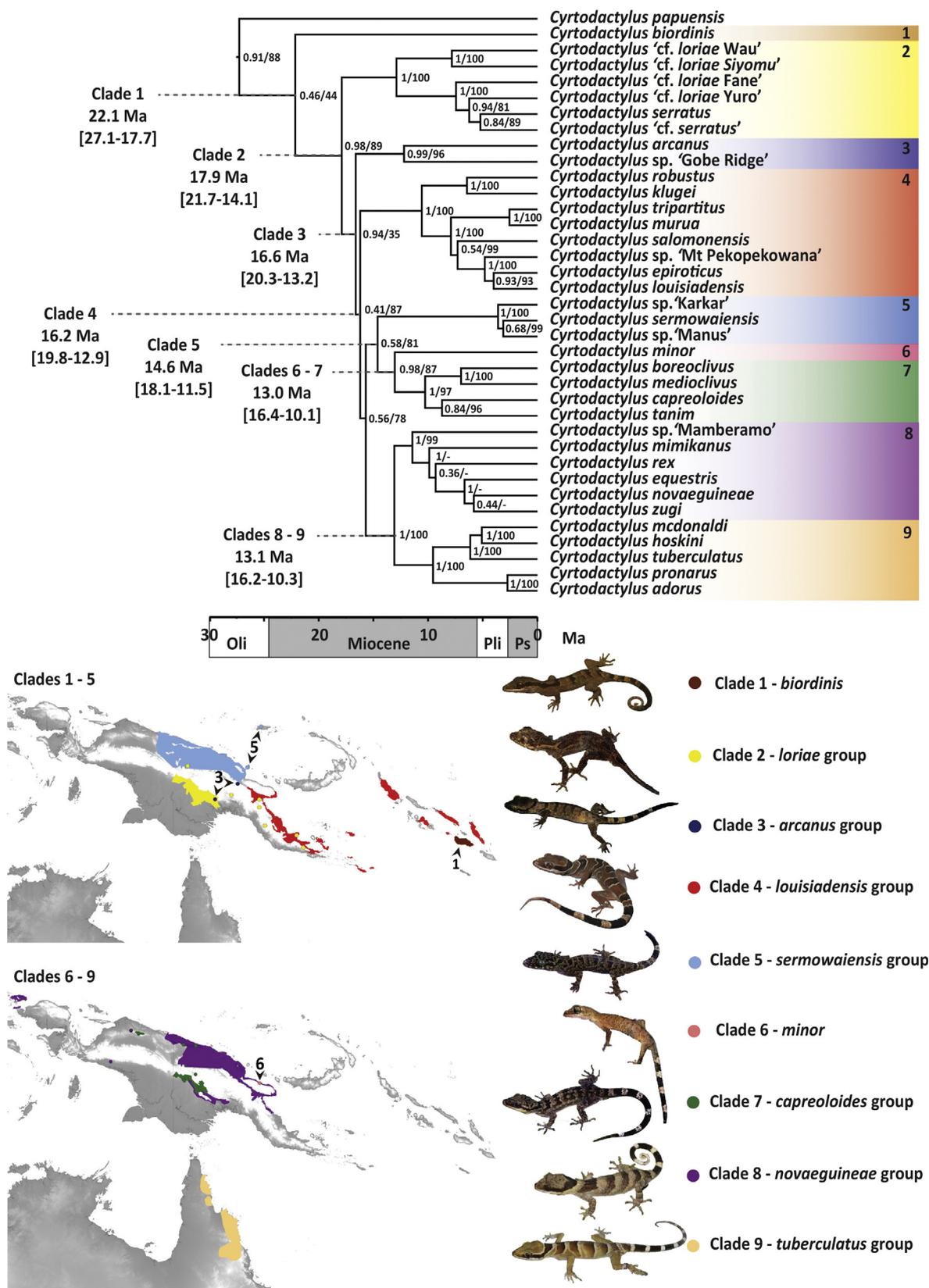
To test whether Australo-Papuan *Cyrtodactylus* exhibit phylogenetic regionalisation associated with broadly distinct geological areas of New Guinea (Fig. 1), each species and candidate species was assigned to one of three regions based on current distributions (see Table S5). A majority of species and candidate species are endemic to a single region, except for three known from two regions (*C. epiroticus*, *C. novaeguineae* and *C. rex*). These were assigned to the region containing the highest proportion of each species' distribution.

### 2.5. Mountain uplift and diversification

Mountain uplift can generate taxonomic diversity in two main ways: (a) ecological diversification and colonisation of newly forming higher-elevation habitats; and (b) isolation of formerly continuous lowland taxa. Both means can operate simultaneously. All Australo-Papuan *Cyrtodactylus* species and candidate species were coded as lowland ( $< 500$  m a.s.l.), hill-forest (500–1000 m a.s.l.) or lower montane (1000–1500 m a.s.l.), in accordance with the forest-categorisation scheme described by Shearman and Bryan (2015). *Cyrtodactylus* species and candidate species representatives were coded according to their minimum elevational extent (see Table S5). Minimum elevation was used in favour of other elevational metrics, such as mid-elevation, as it better indicates whether a taxon's range is truly montane rather than simply wide-ranging. To estimate the number of upslope colonisation events we ran both unconstrained and time-constrained ancestral-state analyses using BioGeoBEARS v.0.2.1, as described in Section 2.4. In the time-constrained analyses we assumed the emergence of the Central Cordillera, and thus *Cyrtodactylus* occupation of hill-forest and lower montane habitats, occurred after 15 Ma (van Ufford and Cloos, 2005; Baldwin et al., 2012) and after five Ma (Toussaint et al., 2014). These analyses also provided information on the number of north-south sister lineages, their elevational distribution, and the timing of their divergences. We conducted these analyses on the chronogram from BEAST, derived from the alignment (b) containing representatives of each Australo-Papuan *Cyrtodactylus* species and candidate species.

### 2.6. Phylogenetic structure

To test for evidence of endemic diversification, as opposed to recent dispersal between major regions of New Guinea, we also quantified



**Fig. 2.** Time-calibrated Bayesian-inference gene tree of Australo-Papuan *Cyrtodactylus*. Tree inferred from the reduced concatenated (four gene fragments) dataset with representatives of each species and candidate species. BI posterior-probability and ML bootstrap values (IQ-TREE and alignment (c) analysis; see Figure S4) are shown at nodes, with node age and HPD 95% confidence intervals in brackets shown for the nine major lineages. Geographic distribution of each of the nine major lineages are illustrated with corresponding colors on the two maps, and specimen representatives of each lineage shown on the right. *Cyrtodactylus arcanus* image provided by Terry Reardon, *Cyrtodactylus biordinis* by Scott Travers, *Cyrtodactylus pronarus* in the *tuberculatus* group by Conrad Hoskin, and all other images provided by the authors.

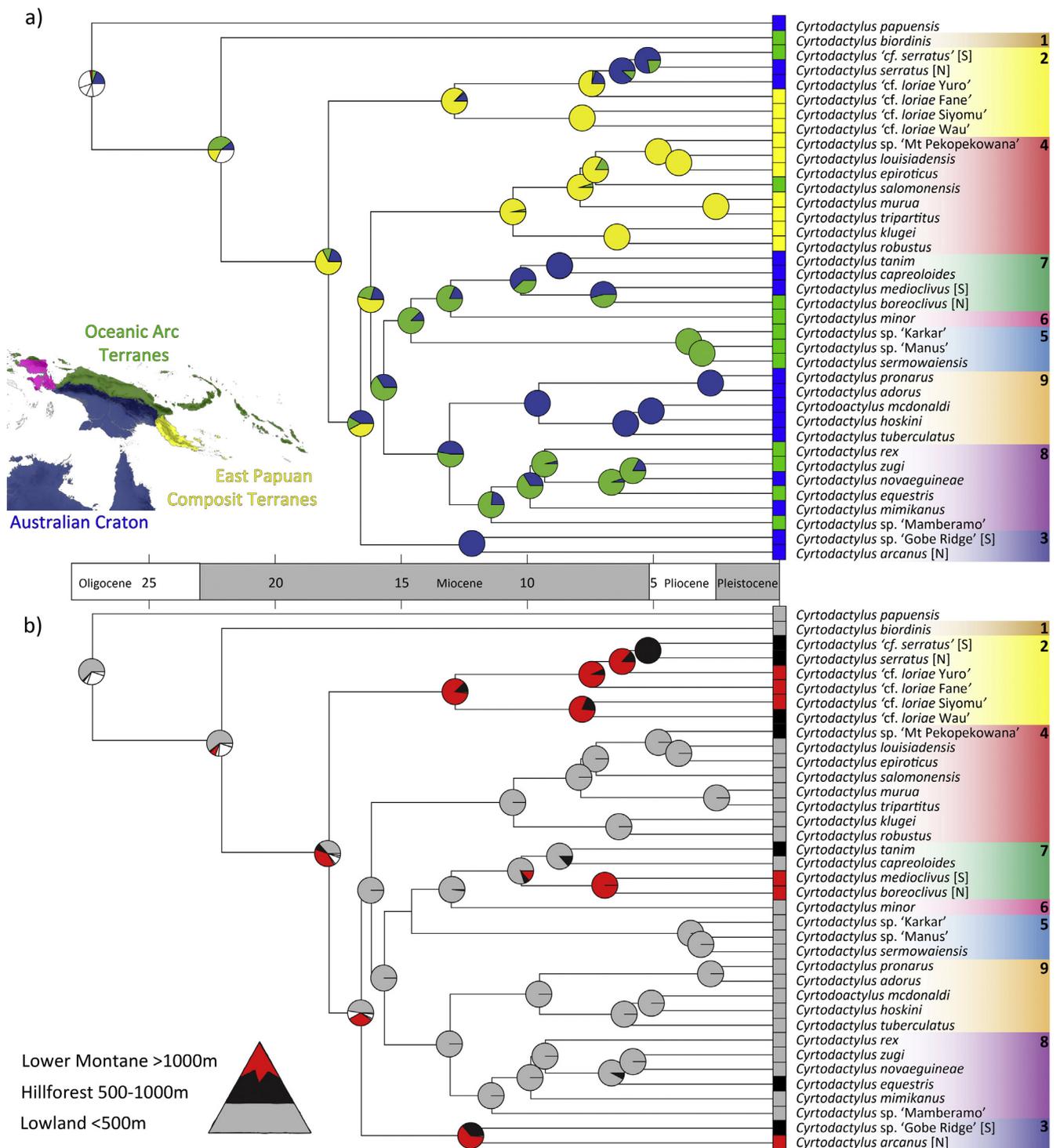


Fig. 3. Chronogram with ancestral state estimation for Australo-papuan *Cyrtodactylus* using BioGeoBEARS to reconstruct a) three-state regional (Australian Craton, East Papuan Composite Terrane and Oceanic Arc Terranes) DIVALIKE+J model, b) three-state elevational (Lowland, Hillforest and Lower Montane) DEC+J model. The pie diagrams at nodes illustrate the estimated probability of each state (biogeographic region/elevation combinations). Well-supported sister lineages and lineage groups with distributions on opposing sides of the New Guinean Central Dividing Range are denoted with [N] for northern lineages and [S] for southern lineages.

infra-regional phylogenetic structure using the R package *picante* v.1.6 (Kembel et al., 2010). We calculated two commonly used indices: Faith's phylogenetic diversity (PD; Faith, 1992) and the mean pairwise phylogenetic distances (MPD; Webb, 2000). The standardised effect size of these metrics (SES.PD and SES.MPD) were used to test the significance of observed patterns against null expectations, generated from 100,000 runs. Positive SES values indicate phylogenetic over-dispersion (i.e., more distantly related than expected, given the regions species

richness), whereas negative SES values indicate phylogenetic clustering (endemic diversification). We conducted these analyses on the chronogram from BEAST, derived from the alignment (b) containing representatives of each Australo-Papuan *Cyrtodactylus* species and candidate species.

### 3. Results

#### 3.1. Genetic diversity and phylogenetic relationships

In addition to 28 recognized Australo-Papuan *Cyrtodactylus* species (Uetz et al., 2018), we identified ten distinct lineages that we consider candidate species (see Fig. 2 and Table S4). The candidate species (Fig. 2) include: four lineages within the *C. loriae* species-group; a taxon allied to *C. serratus* from the northern versant of the Central Cordillera; a candidate species, ‘Gobe-Ridge’, previously identified by Rösler et al. (2007); a candidate species in the *C. louisadensis* species-group from the southeastern Papua New Guinea (Mt Pekopekowana); two candidate species in the *C. sermowaiensis* species-group: one on the northern New Guinea volcanic island of Karkar and another on Manus Island in the Admiralty Archipelago; and finally a candidate species ‘Mamberamo’ in the *C. novaeguineae* species-group from northwestern New Guinea.

We identified nine major lineages within the Australo-Papuan *Cyrtodactylus* taxa (clades 1–9 in Fig. 2), as well as the phylogenetically divergent *C. papuensis* clade. This accords with previous phylogenetic analyses of Australo-Papuan *Cyrtodactylus* (Wood et al., 2012; Oliver et al., 2014; Wilmer and Couper, 2016; Oliver et al., 2018a). Two of the nine major lineages are monotypic (*C. biordinis* and *C. minor*), whereas the others are comprised of two to six taxa / OTUs. Five of the nine major lineages are strongly supported in the BI analysis of the reduced concatenated alignment (alignment b; posterior probability values  $\geq 0.95$ ; see Fig. 2). Seven clades are strongly supported in the ML analysis performed in IQ-TREE (alignment a and c; bootstrap values  $\geq 70\%$ ; see Figs. S1–S2), while, only two of the nine clades are strongly supported in the ML analysis performed in RAxML (alignment a and c; bootstrap values  $\geq 70\%$ ; see Figs. S3–S4). *Cyrtodactylus biordinis* was found to be the sister to all other lineages in all ML analyses but with low support (bootstrap values  $< 70\%$ ; see Figs. S1–S4) and sister to a South-East Asian clade in the BI analysis (alignment c) but again with low support (posterior probability value 0.15, see Fig. S5). Placement of the *C. arcanus* clade was marginally unsupported in the BI (posterior probability value 0.94; see Fig. 2) and poorly supported in the ML IQ-TREE analyses (bootstrap value 35%; see Fig. 2).

#### 3.2. Divergence dating

Contrasting the divergence time estimates from the dating analyses using either two or six partitions, revealed equivalent 95% HPD dating ranges (see Figs. S6–S7). All further reference to dating estimates will thus relate to the six partition analysis. Divergence-time estimates suggest the major Papuan *Cyrtodactylus* lineage split from its nearest relatives in Asia (a lineage from central Indochina) during the early Miocene (24.3 Ma; 95% HPD: 29.6–19.5 Ma). Diversification of the Australo-Papuan *Cyrtodactylus* clade into nine major lineages occurred during the Mid-Miocene (Fig. 2). The deepest split amongst the nine major lineages initiated with the *C. biordinis* lineage against the other eight lineages 22.1 Ma (95% HPD: 27.1–17.7 Ma; see Fig. 2 clade 1); however, this node was not well supported (posterior probability value 0.46). The most recent split was the *C. novaeguineae* and *C. tuberculatus* species groups 13.1 Ma (95% HPD: 16.2–10.3 Ma; see Fig. 2 clades 8–9). There was an approximately equal division of inferred divergence ages for species and candidate species before and after the end of the Miocene (~5.3 Ma).

#### 3.3. Ancestral-area estimation

Evaluating whether *Cyrtodactylus* exhibited Australian Craton or proto-Papuan origins revealed a DIVA + J model had the highest likelihood ( $\ln L = -23.12$ ; AICc = 53.0, see Table S6 and Figs. 3 and S8). However, all three biogeographic models incorporating the jump dispersal parameter had comparable AICc values and predicted equivalent range estimations (see Table S6). All best-fit models estimated the

proto-Papuan region as the origin of the entire major Australo-Papuan *Cyrtodactylus* clade, and seven of its nine constituent lineages (Fig. S8). Subsequent analyses constraining *Cyrtodactylus* diversification in the proto-Papuan region to 15 Ma (Moyle et al., 2016) and 10 Ma (Hill and Hall, 2003; Toussaint et al., 2014), had lower model likelihoods (10 Ma:  $\ln L = -56.84$ , AICc = 120.4; 15 Ma:  $\ln L = -37.6$ ; AICc = 81.9) than the unconstrained model (see Table S6).

In a three-state ancestral-state regional analysis, the DIVA + J model had the highest likelihood ( $\ln L = -33.3$ ; AICc = 73.2) and inferred a high degree of intra-regional phylogenetic clustering within the East-Papuan Composite Terrane region and *C. loriae* and *C. louisadensis* clades (see Fig. 3 and Table S7). None of the nine major lineages occurred over all four geological regions; most were found in only one or two, and only one clade (i.e., the *C. loriae* species group) occurred across three regions (see Fig. 3). Within the nine major Papuan *Cyrtodactylus* lineages four were estimated to have originated on the Oceanic Arc Terranes (*biordinis*, *sermowaiensis*, *minor* and *novaeguineae*), three on the Australian Craton (*arcanus*, *capreoloides* and *tuberculatus*), and two on the EPCT (*loriae* and *louisadensis*). Two dispersal events out of the EPCT were inferred, one in each of the *C. louisadensis* and *C. loriae* species-groups. Shifts between the Oceanic Arc Terranes and Australian Craton were more common, specifically within the *C. arcanus*, *C. capreoloides* and *C. novaeguineae* lineages.

#### 3.4. Mountain uplift and diversification

In the three-state elevational analyses, the DEC + J model had the highest likelihood ( $\ln L = -27.9$ ; AICc = 62.5; see Table S6), but all three biogeographic models incorporating the jump dispersal parameter have equivalent AICc values and range estimations (see Table S6 and Fig. 3). Seven of the nine major Papuan lineages are estimated to have originated in lowlands, with the other lineages (i.e., *C. loriae* and *C. arcanus* species-groups) originated in the lower montane area during the Miocene. Placing time constraints of 12 Ma or 5 Ma on *Cyrtodactylus* divergence in the hill forest and lower montane regions, sequentially, reduced model likelihood (12 Ma– $\ln L = -48.5$ ; AICc = 103.7; 5 Ma– $\ln L = -75.3$ ; AICc = 155.0).

We inferred three upslope elevational shifts from lowland to hill forest, six shifts into lower-montane regions (three of them from hill forests), and three downward shifts from lower montane to hill forest (two in the *C. loriae* clade and one in the *C. arcanus* clade). The estimated timing of upslope shifts ranged from around the Mid-Miocene (16.6 Ma, 95% HPD: 20.3–13.2 Ma) to the early Pliocene (5.2 Ma, 95% HPD: 7.0–3.8 Ma). Four of the inferred upslope shifts were on the Central Cordillera, four in the Owen Stanley Mts., and one in the North Papuan Mountains. The downslope shifts inferred in the *C. loriae* and *C. arcanus* clades were distributed on the northern and southern flanks of the Central Cordillera in central New Guinea.

Across the 38 *Cyrtodactylus* species and candidate species we identified only three sister-lineage pairs that are known from opposing sides of the Central Cordillera. These are: a) *C. arcanus* and *Cyrtodactylus* sp. Gobe-Ridge; b) *C. serratus* and *C. cf. serratus*; and c) *C. boreoclivus* and *C. medioclivus*. These taxa are higher-elevation forms occurring in either the hill forest or lower montane zones. Mean age estimates for these north–south splits varied from 12.2 Ma to 5.2 Ma (see Fig. 3).

#### 3.5. Phylogenetic structure

Analysis of phylogenetic structure based on the three-state regional model inferred phylogenetic clustering within the East-Papuan Composite Terrane (SES.PD = -2.38, SES.MPD = -2.74, both  $P < 0.005$ ; see Table S7). No significant structure was observed in the Australian Craton or Oceanic Arc Terranes assemblages.

#### 4. Discussion

The Papuan region has an exceptionally complex geological history, and there remain major uncertainties associated with the geological reconstructions (Hall, 2002; Hill and Hall, 2003; van Ufford and Cloos, 2005; Baldwin et al., 2012). There is also a paucity of comprehensive time-calibrated phylogenies with which to test hypotheses relating to geological origins and ecological states of ancestral lineages. Here we provide phylogenetic evidence for lineage diversity and present-day regionalisation supporting a Mid-Miocene colonisation and diversification on formerly discrete proto-Papuan island's north and east of the Australian continental plate, especially on the East Papuan Composite Terrane. From the same data, we infer multiple, independent, upslope elevational range shifts, suggesting that orogeny has played a complementary role in generating regional diversity.

##### 4.1. Early colonisation and divergence on proto-Papuan islands

Early origins and diversification of New Guinean biota on formerly isolated proto-Papuan islands, has received support from Amphibia (Rivera et al., 2017), Aves (Jönsson et al., 2011; Aggerbeck et al., 2014), Reptilia (Strickland et al., 2016; Oliver et al., 2018b) and aquatic Heteroptera (Polhemus and Polhemus, 1998). Other studies, on birds (Moyle et al., 2016) and diving beetles (Toussaint et al., 2014), have however suggested this inference is inconsistent with the geological chronology. However, these respective studies focused either on vagile lineages with either southern (Gondwanan) origins (birds) or that have radiated primarily within the Pliocene-Pleistocene, perhaps limiting their ability to detect endemic diversity patterns in the proto-Papuan region.

Ancestral-state analyses for the Melanesian *Cyrtodactylus* radiation support initial colonisation and diversification on the former proto-Papuan islands to the north of the main Australian landmass. Applying a younger ( $\leq 15$  Ma) age constraint on the emergence of the proto-Papuan islands markedly reduced model likelihood. Although some of the exact branching patterns among the deeper nodes for the Papuan *Cyrtodactylus* clade are poorly supported, several lineages originating during the mid-Miocene are restricted to such former islands (Figs. 2 and 3). Divergent but species-poor lineages having restricted ranges on the Oceanic Arc Terranes region – such as the *C. sermowaiensis* and *C. minor* clades (clades 5 and 6, respectively) – suggest these were once insular taxa that arrived to New Guinea when their associated islands accreted onto its northern margin. Conversely, only the *C. tuberculatus* group (clade 9) is unambiguously endemic to the Australian Craton, and it is estimated to have diverged from a Papuan lineage during the Mid-Miocene (13.1 Ma).

The presence of two near-endemic Late-Miocene radiations of *Cyrtodactylus* on the East-Papuan Composite Terrane (or Papuan Peninsula and adjacent offshore islands) is particularly compelling evidence that this region has been subaerial since at least this time. Some recent studies have discounted or not supported an important role for the East-Papuan Composite Terrane in shaping Melanesian diversity (Toussaint et al., 2014; Moyle et al., 2016). However, some geological models suggest formation of the East-Papuan Composite Terrane as long ago as the Paleogene, with the emergence of the Owen-Stanley fault zone caused as ophiolites obducted over Owen-Stanley metamorphics at the far northern edge of the Australian plate (Baldwin et al., 2012). Our phylogenetic data, and similar deep phylogenetic structure and ancient divergences in other taxa, especially in vertebrates with low vagility (Oliver et al., 2013; Rivera et al., 2017), lend increasingly strong support to the long-term importance of the EPCT as a centre for the initial accumulation and diversification of New Guinean biota. Indeed, we found evidence of outwards colonisations from the EPCT, eastward to the Solomon Islands, and westward into Central New Guinea. This is consistent with the claim that the EPCT was formed several million years before the Central Dividing Range (Cloos et al.,

2005).

##### 4.2. Orogeny and diversity

Tropical mountains are home to some of the world's most diverse regional biotas and are often dominated by recent endemic lineages (Price et al., 2014; Merckx et al., 2015). We identified 14 *Cyrtodactylus* lineages associated with mountain ranges (including both hill and lower montane forest), representing 36% of the Australo-Papuan *Cyrtodactylus* diversity. This supports other recent studies linking mountain uplift to diversification in both New Guinea (Toussaint et al., 2014; Rivera et al., 2017; Oliver et al., 2017a; Meredith et al., 2010) and elsewhere in the tropics (Price et al., 2014; Smith et al., 2014). However, the focal taxa in most of these studies show a clear mid-elevational peak in diversity. In contrast, lizards are generally most diverse and exhibit species-richness peaks at lower elevations in Australia and New Guinea (Powney et al., 2010; Tallowin et al., 2017). Indeed, despite their diversity, the maximum recorded elevation for Australo-Papuan *Cyrtodactylus* species is less the 1500 m. a.s.l. (1448 m ~ *C. cf. lorae* Yuro). Nonetheless while they are predominantly a lowland group, the formation of complex elevational gradients in New Guinea has clearly facilitated endemism and increased diversity among the major Australo-Papuan *Cyrtodactylus*, and may also have played an important role elsewhere (just over half of the *Cyrtodactylus* species for which have elevational data [90 of 170] are known only from below 500 m (S. Meiri unpublished data).

Estimates for the age and timing of major mountain uplift in New Guinea vary. Hall (2002) and Hill and Hall (2003) suggested a change in motion of the Australian and Pacific plates during the Pliocene resulted in the formation of the New Guinean fold-and-thrust belt and the rise of the Central Range around five million years ago. In contrast, van Ufford and Cloos (2005) proposed an older uplift of the Central Range, around 12 Ma in the west and five Ma in the east, reaching its current extent around five Ma. Our analyses suggest that the *Cyrtodactylus lorae* clade, centred on the East-Papuan Composite Terrane, colonised montane habitats by the Mid- to Late-Miocene (12.9 Ma, 95% HPD: 16.1–9.9 Ma). Other montane lineages centred on the main Central Cordillera farther to the west also date back to the Miocene, but are either more poorly sampled (*C. arcanus* group) or more recent (7.0 Ma; *C. boreoclivus* and *C. medioclivus*). While there is strong evidence that some areas have seen massive and relatively recent uplift (especially from Late-Miocene marine deposits found high in the Star and Snow mountains, [Fitzgerald et al., 2013]), our data from *Cyrtodactylus* suggest that at least lower montane habitats have a history dating back well into the Miocene.

In addition to providing novel montane habitats and ecological opportunities for speciation, the mountain uplift also could potentially have isolated formerly continuous taxa inhabiting lower-elevation habitats. Most of New Guinea is currently divided into northern and southern lowlands by a high Central Cordillera that reaches elevations well above those from which *Cyrtodactylus* has been reported (1448 m a.s.l.) – indicating that it is likely to be a contemporary barrier to gene flow. Here we identified several north–south sister lineages, all in lower montane/hill forest taxa and all dated to the Late-Miocene. This suggests that Late-Miocene mountain uplift may have been responsible for isolation of north–south variants amongst taxa already adapted to upland environments. The two shallowest north–south splits were identified towards the west, suggesting substantial uplift there around the end of the Miocene. Dates for the north–south splits give potential maximum ages for when uplift could have first isolated lineages. While it is possible that these vicariant events may have occurred more recently, they are unlikely to pre-date the estimated divergent times. Phylogenetic and phylogeographic analyses of other Papuan taxa have recovered north–south sister lineages with divergence dates ranging from the Pliocene in birds (Deiner et al., 2011; Irestedt et al., 2015) to the Paleocene in turtles (Georges et al., 2014) and fish (Unmack et al.,

2013). These contrasting dates suggest that the uplift of the Central Cordillera has played a role in isolating north–south variants in many lineages, but that the timing of this varies greatly across taxa with differing ecologies, and also in different parts of New Guinea.

## 5. Conclusions

Our lineage-level time-calibrated phylogeny indicates a combination of geological processes that have shaped regional diversification of Australo-Papuan *Cyrtodactylus* lizards. Following dispersal from Southeast Asia during the Early-Miocene, *Cyrtodactylus* diversified within proto-Papuan islands, and, at least in the East-Papuan Composite Terrane–formed distinct regional assemblages that were subsequently incorporated into present-day New Guinea. Subsequent diversification and shifts up elevational gradients indicate that uplift of major mountain ranges during the Late-Miocene mediated further accumulation of diversity, in a manner similar to tropical mountains across the tropics (Price et al., 2014). Surprisingly, few previous studies have explicitly inferred that these two processes have acted in concert to generate New Guinean diversity. This emphasizes the need for complete species-level alignments spanning taxa with a diversity of origins, ages, and ecologies in order to generate a more holistic understanding of the history of the diverse New Guinean biota.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jympev.2018.03.020>.

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