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ORIGINAL ARTICLE

Old but not ancient: coalescent species tree of New Caledonian geckos reveals recent post-inundation diversification

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ABSTRACT

Aim New Caledonia is a remnant of the land mass Tasmantis that harbours high levels of endemism. Two primary hypotheses have been proposed for the origin of such endemic lineages; the first suggests a vicariant origin arising from the sundering of eastern Gondwana in the Cretaceous. The second posits more recent dispersal and colonization. We use concatenated and coalescent time-calibrated phylogenies to test whether New Caledonian diplodactylid geckos diversified steadily following an ancient vicariance event or experienced an early burst of diversification followed by a decline in net diversification after long-distance dispersal.

Location New Caledonia, Gondwana.

Methods Phylogenetic relationships were elucidated from a multilocus DNA data set. Divergence times were inferred using relaxed clock Bayesian methods on the concatenated data set and in a multispecies coalescent framework using *BEAST. In order to elucidate patterns of diversification for the New Caledonian clade we tested models of diversification using LASER and DDD.

Results The divergence of the New Caledonian clade from its Australian sister clade occurred well after Gondwanan fragmentation, and the age of the crown clade is younger than the proposed drowning period of the island. Diversification analyses strongly suggest that the group experienced an early burst of diversification, which has slowed towards the present.

Main conclusions We demonstrate that the species-rich diplodactylid geckos endemic to New Caledonia are of recent origin and that the diversification of the clade is consistent with the expectations of a recent radiation. Diversification in this clade does not conform to a constant-rate model, but rather experienced an initial burst followed by a decline in net diversification. This pattern is consistent with a decline in diversification as ecological niche space was filled. Our results add to the growing body of evidence that recent adaptive radiations have contributed to the remarkable endemism of New Caledonia.

Keywords
Diplodactylidae, dispersal, diversity dependence, New Caledonia, species tree, Tasmantis

INTRODUCTION

New Caledonia is part of the continental fragment Tasmantis, along with New Zealand, which separated from eastern Gondwana during the late Cretaceous with the opening of the Tasman and Coral Seas (~83 Ma) (Smith *et al.*, 2007; Grandcolas *et al.*, 2008; Chapple *et al.*, 2009). The presence of limestone formations from marine sedimentation offers strong evidence that the region of Tasmantis that now supports New Caledonia was submerged during the Palaeocene. New Caledonia came to its current position about 45 Ma and geological evidence suggests that the Grande Terre did not become emergent until the Oligocene during an uplifting of ultramafic covered lithosphere (Grandcolas *et al.*, 2008).

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Its biota has long been regarded as ancient, with high endemism and a presumed vicariant origin (Bauer & Sadlier, 2000; Heads, 2010). This view has been supported by the presence of seemingly ancient taxa such as *Amborella* (Amborellaceae), the possible sister taxon to all other flowering plants (Qiu *et al.*, 1999).

Despite having separated from eastern Gondwana in the Cretaceous, there is growing evidence suggesting that New Caledonia was submerged intermittently or completely until the late Eocene (~37 Ma) (Grandcolas *et al.*, 2008; Cluzel *et al.*, 2012). The extent of submergence has been a topic of debate (Waters & Craw, 2006; Espeland & Johanson, 2010; Giribet & Boyer, 2010), and is of great relevance to the biogeography of the region. Several studies have demonstrated that most, if not all, terrestrial groups colonized the island and other regions in Tasmantis during the Cenozoic via overwater dispersal (Swofford, 2002; Smith *et al.*, 2007; Espeland *et al.*, 2008; Grandcolas *et al.*, 2008; Chapple *et al.*, 2009; Murienne, 2009; Espeland & Murienne, 2011; Nielsen *et al.*, 2011; Barrabé *et al.*, 2014).

We investigate the relationships and divergence times of the endemic New Caledonian diplodactylid gecko clade which, along with a diverse assemblage of *Eugongylus* group lygosomine skinks (Smith *et al.*, 2007; Chapple *et al.*, 2009), constitute the only terrestrial non-flying New Caledonian vertebrate radiations. This clade is unambiguously monophyletic with 36 described species distributed among eight morphologically divergent genera entirely endemic to New Caledonia (*Bavayia, Paniegekko, Oedodera, Dierogekko, Eurydactylodes, Mniarogekko, Correlophus* and *Rhacodactylus*) (Bauer *et al.*, 2006a,b; Bauer *et al.*, 2012). It is an ecologically diverse group with taxa that exhibit unusual traits such as saurophagy (lizard eating) in *Rhacodactylus auriculatus*, secondary diurnality in *Eurydactylodes* and gigantism (*Rhacodactylus*, *Correlophus*, and *Mniarogekko*) (Bauer & Sadlier, 2000; Bauer *et al.*, 2009, 2012; Snyder *et al.*, 2010). The New Caledonian taxa are collectively sister to the Australian *Pseudothecadactylus,* and this group is, in turn sister to all remaining diplodactylids (seven New Zealand and an additional nine Australian genera) (Nielsen *et al.*, 2011).

There is presently little statistical support for the monophyly of *Bavayia* and *Rhacodactylus*, and there remains taxonomic uncertainty, as evidenced by the on-going description of cryptic species (Bauer & Jackman, 2006; Bauer *et al.*, 2006a,b; Bauer *et al.*, 2012). Although the age and exact mechanisms of dispersal and diversification within this clade remain poorly understood, it is highly likely that it is significantly older than the current gekkonid gecko assemblage (*Hemidactylus*, *Hemiphyllodactylus*, *Lepidodactylus*, *Nactus* and *Gehyra*), some members of which may have anthropogenic origins on this archipelago (Grant-Mackie *et al.*, 2003). If the gekkonid fauna arrived only recently, it is likely that the colonizing ancestors of the New Caledonian diplodactylids would have been largely without competitors upon arrival in New Caledonia, as they would have been the only primarily nocturnal squamates on the island. In open ecological space, the ancestors of this group may have been able to diversify rapidly, a pattern that has been suggested for other New Caledonian taxa (Espeland & Murienne, 2011) and other Tasmantis diplodactylids (Garcia-Porta & Ord, 2013).

We use concatenation and multispecies coalescent methods, the first for a lineage endemic to New Caledonia, to date the crown group as well as its divergence from its sister taxon. In order to test hypotheses regarding the mode of diversification in this diverse clade of geckos, we use likelihood methods to estimate net rates of diversification. We test alternative models using our Bayesian concatenated and coalescent species trees to determine if diversification in this clade follows a constant-rate pure-birth model, as would be expected for an old clade with steady lineage accumulation (Murienne, 2009; Espeland & Murienne, 2011), or if there has been a burst of rapid diversification followed by a decline towards the present as ecological space is filled. The latter has been found in invertebrates, scincid lizards and plants that recently colonized New Caledonia via long-distance dispersal or island-hopping (Murienne, 2009; Espeland & Murienne, 2011). While other studies have attempted to estimate diversification rates for diplodactylids, none have used a large multilocus data set, included all described species or have tried to account for gene-tree heterogeneity (Garcia-Porta & Ord, 2013), which is well known to influence the inference phylogenetic relationships and divergence times (McCormack *et al.*, 2011; Oaks, 2011).

MATERIALS AND METHODS

Taxonomic and molecular sampling

We included representatives of all 36 described species of New Caledonian diplodactylid, as well as 27 outgroup taxa, totalling 191 individuals (Table S1). We compiled a mitochondrial data set (1533 bp) representing *ND2* (NADH dehydrogenase subunit 2) and five tRNAs (WANCY). Five independent nuclear exons that have been useful in resolving deeper squamate relationships were also included (Portik *et al.*, 2012), including *RAG1* (recombination activating gene 1: 1054 bp), *MXRA5* (matrix-remodelling associated 5: 855 bp), *KIAA1549* (823 bp), *KIF24* (kinesin family member 24: 575 bp) and *PDC* (phosducin: 395 bp) for a total of 5235 bp. Primers were developed from *Gallus, Anolis* and *Python* (Table S2 in Supporting information). We extracted, amplified, and sequenced DNA following the protocols of Nielsen *et al.* (2011) (Appendix S2). Gene sequences have been made available on GenBank (KU157229–KU158095).

Concatenated phylogenetic analyses

Sequences were aligned by hand and GENEIOUS 4.7 was used to assess the presence of stop codons (Drummond *et al.*, 2006). Phylogenetic relationships were inferred using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). Maximum parsimony was run in

PAUP* 4.0b10a (Swofford, 2002) through a stepwise addition heuristic search with 10 addition replicates under tree bisection-reconnection branch swapping with 10 random addition replicates. Node support was determined using 1000 nonparametric bootstrap replicates from which a 50% majority rule consensus tree was constructed. Individual genes were analysed using ML alone while the concatenated nucDNA and mtDNA + nucDNA data sets were analysed with MP, ML, and BI.

Each locus was partitioned by codon (tRNAs were treated as a separate partition) and models were selected using MODELTEST 3.5 (Posada & Crandall, 1998) under the Akaike information criterion (AIC) (Table S3). Maximum likelihood analyses for individual gene trees and the concatenated data set were run in RAxML 7.2.6 (Stamatakis, 2006) with the best tree being found with 1000 full likelihood searches and support determined using 1000 nonparametric traditional bootstrap replicates. The GTR + G model was used for all partitions as it is not possible to specify different models to different partitions in RAxML. Bayesian analyses were run in MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001) under the same partitioning scheme as the ML analyses for the mtDNA only, nucDNA only and combined data sets. However, the original model specified by MODELTEST for the appropriate partition was implemented. All Bayesian analyses were run for 20,000,000 generations sampling every 1000 generations. The first 25% of samples were removed from the Bayesian analyses as burn-in, with stationarity determined by checking ESS values using TRACER 1.5.0 (Drummond & Rambaut, 2007), and using the online program AWTY (Nylander *et al.*, 2008). The results from MRBAYES were used to generate 50% majority rule consensus trees for the mtDNA, nucDNA, and combined mtDNA + nucDNA data sets. The ML mtDNA only, nucDNA only and concatenated mtDNA + nucDNA trees are available in Appendix S3 (Figs S1–S5). The final concatenated alignment and corresponding ML phylogram are available on Treebase (http://purl.org/phylo/treebase/phylows/study/TB2:S18521). Given the phylogenetic uncertainty of this clade, we also tested alternative phylogenetic hypotheses from the literature for the New Caledonian clade and these are described in Appendix S2.

Divergence dating and species tree estimation

A time-calibrated ultrametric phylogeny was generated in BEAST 1.6.2 (Drummond & Rambaut, 2007) under an uncorrelated lognormal relaxed clock and a Yule tree prior. Our data set was pruned down to a single exemplar for each species for the concatenated BEAST analyses and run for 80,000,000 generations. Data sets were partitioned in the same fashion as for the ML and BI analyses and the same substitution models were used as in the BI analyses. The first 25% of samples were treated as burn-in and removed before individual runs were combined in LOGCOMBINER 1.6.2. Stationarity was assessed using the program TRACER 1.5.0 with ESS values > 200 taken as evidence for convergence. A final MCC maximum clade credibility tree was generated from the cumulative post-burn-in sample of the combined analyses in the program TREEANNOTATOR 1.6.2 (Drummond & Rambaut, 2007).

Root age was determined by a secondary calibration between gekkotans and toxicoferans (*Anolis* and *Python*) (normal: $\mu = 200$, $\sigma = 20$) based on the results of Vidal & Hedges (2009). Previous studies have estimated dates in other gekkotan groups under a relaxed Bayesian clock by assigning putative gecko fossils to constrain the crown age of gekkotans (normal: $\mu = 110$, $\sigma = 15$) (Gamble *et al.*, 2008a,b, 2011; Oliver & Sanders, 2009; Nielsen *et al.*, 2011). The clade containing *Sphaerodactylus torrei* and *S. roosevelti* was constrained with the amber preserved *S. dommeli* (exponential: $\mu = 3$, offset = 15) while the *Euleptes-Sphaerodactylus* split was calibrated using a fossil *Euleptes* (exponential: $\mu = 25$, offset = 22.5) (Gamble *et al.*, 2008b). Miocene diplodactylid fossils from St. Bathans, New Zealand (Lee *et al.*, 2009) represent the closest node t o the New Caledonian clade for which a calibration was available. The node containing the three New Zealand forms was calibrated with a minimum constraint using these fossils (exponential: $\mu = 17$, offset = 16). We ran another BEAST analysis of the concatenated data set without the New Zealand diplodactylid calibration as was done with New Caledonian eneopterine crickets to determine if its inclusion biased a young crown age for the New Caledonian clade (Nattier *et al.*, 2011).

Preliminary analyses suggested some genealogical discordance between the mitochondrial and nuclear phylogenies of the New Caledonian clade (Figs S1–S4). To account for incomplete lineage sorting, we inferred the species tree of the partitioned dataset under a Bayesian multispecies coalescent framework using the program *BEAST v1.7.4 (Heled & Drummond, 2010), an extension of the BEAST package. Rather than treating all the loci as a single concatenated gene region, *BEAST reconstructs each gene tree individually while making inferences about the genealogical history of each locus (i.e. effective population size). Two individuals per species were included for the ingroup when possible while each of the outgroup taxa were represented by a single exemplar. We did not phase our nuclear sequences as all of the outgroup taxa and some of the ingroup only had single individuals available. The analysis was run using a Yule tree prior for 2.5 billion generations, sampled every 150,000 generations, with the first 45% discarded as burn-in TRACER and TREEANNOTATOR. A large burn-in was needed as these analyses required considerable time to reach near-stationarity. A dozen parallel analyses were run to improve MCMC mixing and to boost ESS values. To complement the concatenated dating analysis, we inferred divergence dates and species trees simultaneously as gene divergences may pre-date species divergences (McCormack *et al.*, 2011). The same fossil and secondary calibrations from the concatenated BEAST analyses were included here.

Diversification analyses

All diversification analyses were performed with all outgroup taxa removed using single representatives for the ingroup taxa. We first estimated whether net diversification followed a constant-rate pure-birth model using the γ-statistic on the MCC tree and 1000 trees from the posteriors of BEAST AND *BEAST (Pybus & Harvey, 2000) in LASER 2.4.1 (Rabosky, 2006). We further tested rate-constant, rate-variable and diversity dependent models of diversification using the MCC trees of BEAST and *BEAST in LASER. All analyses assumed that the phylogeny was completely sampled. To test whether our data set deviated significantly from the null Yule model, 1000 trees were simulated with the yuleSim function implementing the speciation (λ) rates inferred from fitdAICrc in LASER. Model choice for LASER was done using the ΔAIC criterion. Constant-rate pure-birth, birth-death, and diversity dependent with and without extinction models were run using the dd_ML function in DDD 2.4 (Etienne *et al.*, 2012) while assuming that the clade was completely sampled. Each of these four models were run iteratively over 100 random trees from the post-burn-in posteriors of BEAST and *BEAST and model choice was done by calculating the AIC weights (AICw) from the mean parameter estimates for each model.

RESULTS

Concatenated topology

Despite compiling and analysing a data set composed of more than 5000 bp of sequence data, the intergeneric relationships of the New Caledonian clade remained poorly resolved in the combined mtDNA-nucDNA analyses and topology testing failed to distinguish between alternative intergeneric topologies (Fig. S5; see Figs S1–S4 for mtDNA and nucDNA phylogenies; Appendix S2). The combined mitochondrial and nuclear tree included two primary clades, one uniting *Oedodera* and *Dierogekko* and the other containing all other genera, although the latter clade was only moderately supported in the ML analyses (bootstrap proportion = 62, versus posterior probability = 1.0). Within *Dierogekko* we failed to resolve the phylogenetic position of *D. insularis,* and we found a cryptic lineage of *D.* cf. *koniambo* that was consistently allied to the *D. kaalaensis* + *D. thomaswhitei* clade rather than with putatively conspecific *D. koniambo* samples (Skipwith *et al.*, 2014).

Bavayia fell out in a polytomy with *Paniegekko* and a clade containing *Eurydactylodes* and the large bodied forms formerly placed within *Rhacodactylus*. Two well-supported, reciprocally monophyletic groups were recovered within *Bavayia*, a small-bodied *B. sauvagii* complex and a larger bodied *B. cyclura* complex. All analyses of the combined data place *B. septuiclavis* and *B. ornata* in a clade sister to the *B. cyclura* complex. As with the individual gene trees, the concatenated analysis did not support the collective monophyly of the giant geckos (*Rhacodactylus*, *Correlophus, Mniarogekko*). Our MP, ML and BI analyses were largely congruent topologically. However, the MP analysis of the concatenated data set failed to recover the basal split between *Oedodera* + *Dierogekko* and all other taxa or a giant gecko + *Eurydactylodes* clade. These were groupings that received moderate to strong support in the model-based ML and BI runs.

Divergence dating

The BEAST topology is virtually identical to that recovered in the MRBAYES and RAxML analyses, although support is greatly increased, particularly at the base of the tree (Fig. 1). In this concatenated analysis, the New Caledonian taxa appear to have diverged from their nearest diplodactylid sister taxon (*Pseudothecadactylus*) in the early Eocene (μ = 48.3, CI = 39.9–56.9) (Table 1). However, divergence within the New Caledonian taxa did not occur until the late Oligocene or early Miocene (μ = 22.4, CI = 18.4–26.5). Removal of the New Zealand calibration did not affect divergence date estimation within New Caledonia or in the outgroup taxa (Table S4).

Species tree estimation

The estimation of the time-calibrated species tree was exceedingly difficult as some MCMC parameters mixed poorly across runs. Most notable of these were speciation.likelihood, speciesTree.rootheight and the treemodel.rootheights for each locus (as viewed in TRACER). Decreasing species number, removing outgroups and extending runs failed to improve MCMC mixing as did combining multiple runs with better parameter estimates. However, all other parameters attained stationarity and, after the removal of the burn-in samples, had high ESS values. Species tree estimation without divergence dates and *Pseudothecadactylus* as the only outgroup yielded an identical topology to the calibrated species tree and the best time-calibrated species tree had basal node dates largely congruent with our concatenated analysis. Thus, we are reasonably confident that our species tree is topologically and temporally reliable when compared to our other analyses. The MCC tree received strong support for the placements of most outgroup taxa with the exception of *Euleptes* and *Crenadactylus*. The monophyly of the New Caledonian clade received strong support, as did the monophyly of most genera within, the sole exception being *Rhacodactylus* (*sensu stricto* Bauer *et al.*, 2012). Intergeneric relationships largely received very poor support and conflicted directly with the findings of the concatenated analyses (Fig. 2, Table 1). Rather than recovering a *Dierogekko* + *Oedodera* clade at the base of the tree (an arrangement with moderate to strong support in the concatenated analyses), the *BEAST analysis placed a strongly monophyletic *Bavayia* as sister to a weakly supported clade containing the remaining genera. Intrageneric relationships are largely consistent with the concatenated tree, with conflicts only for those that received weak or moderate support in the concatenated tree. The most notable incongruence was the extremely low support that the *Mniarogekko* + *Eurydacty-*

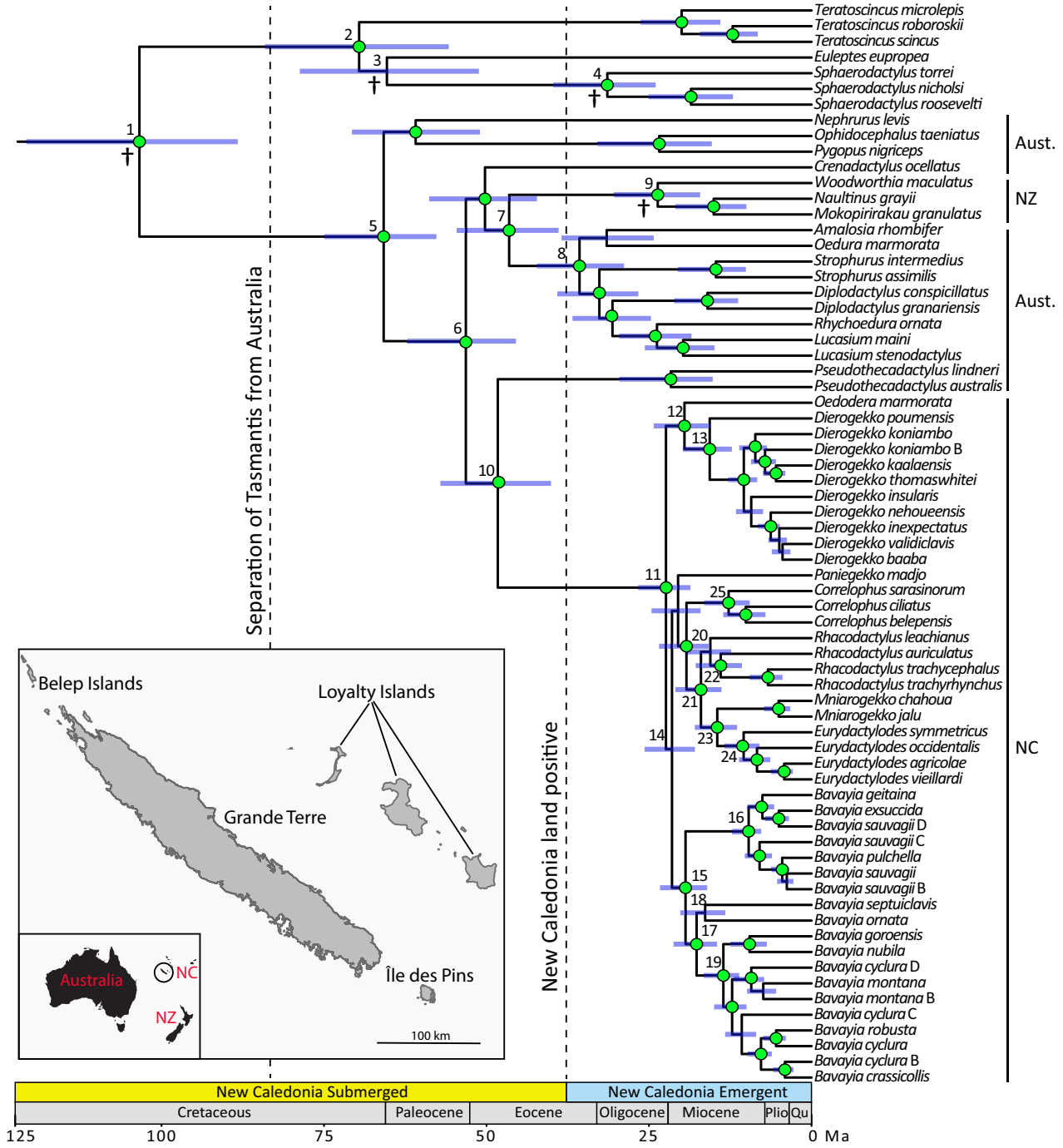

Figure 1 Concatenated BEAST MCC timetree of gekkotans (*Python* and *Anolis* not shown). Green circles indicate posterior probabilities ≥ 0.95 and error bars are 95% credibility intervals. Dashed vertical lines indicate the separation of Tasmantis from Australia and the emergence of New Caledonia. † = node with calibration. Node numbers correspond to those in Table 1. Aust. = Australia, NZ = New Zealand, NC = New Caledonia.

lodes relationship received in the *BEAST analysis (pos. prob. = 0.69 vs. BI pos. prob. = 1.0 and ML bootstrap = 82 in concatenated analyses).

Divergence time estimates are younger than those obtained in previous studies and in our own concatenated BEAST run (Table 1), with our *BEAST analysis yielding a *Pseudothecadactylus*-New Caledonia split of 43.2 Ma (CI = 37.5–48.6). The New Caledonian crown age was inferred as extremely young at 15.5 Ma (CI = 13.9–17.1).

Phylogenetic diversification analyses

Estimating diversification rates under different models in LASER strongly suggests a non-constant rate of diversification

Table 1 Mean divergence dates (Ma) for nodes represented in the *BEAST and BEAST trees of gekkotans. Support shown for all model-based phylogenetic estimates (parsimony not shown). Node numbers correspond to those of Figs 1 and 2 and those not recovered in an analysis are represented by a '–'. Nodes with calibrations are denoted with a '†'. Strong support is taken as posterior probabilities (pos. prob.) ≥ 0.95 and bootstrap values ≥ 70%. Bold numbers indicate support values that were high in concatenated analyses but low in the coalescent species tree.

	*BEAST			BEAST (with NZ calibration)			RAxML	MrBayes
Node	Mean	95% HPD	pos. prob.	Mean	95% HPD	pos. prob.	bootstrap	pos. prob.
1) Gekkota†	109.5	94.5–123.8	1	103.4	88.5–120.6	1	100	1
2) Sphaerodactylidae	70.3	57.9–81.9	1	69.6	55.6–83.8	1	100	1
3) *Sphaerodactylus* + *Euleptes*†	66.4	53.8–77.9	0.71	65.3	50.9–78.5	0.5	56	0.69
4) *Sphaerodactylus*†	24.3	17.4–30.9	1	31.4	23.8–39.5	1	100	1
5) Diplodactyloidea	63.9	56.6–70.7	1	65.8	57.5–74.8	1	100	1
6) Diplodactylidae	47	42.2–51.6	1	53.2	45.3–61.9	1	100	1
7) NZ + Aust. Diplodactylidae	42.5	37.6–47.6	0.99	46.5	38.7–54.4	1	85	1
8) Aust. Diplodactylidae	39.8	26.2–34.4	1	35.7	28.6–42	1	100	1
9) NZ†	19	16.2–24	1	23.7	16.9–30.2	1	100	1
10) *Pseudothecadactylus* + NC	43.2	37.5–48.6	0.95	48.3	39.9–56.9	1	92	1
11) NC	15.5	13.9–17.1	1	22.4	18.4–26.5	1	100	1
12) *Dierogekko* + *Oedodera*	–	–	–	19.5	15.4–24.1	**1**	**83**	**1**
13) *Dierogekko*	9.5	7.5–11.6	1	15.7	12–19.6	1	99	1
14) NC excluding *Dierogekko* + *Oedodera*	–	–	–	22.4	18.4–26.4	0.68	62	**1**
15) *Bavayia*	13.6	12.1–15.1	0.98	19.4	15.8–23.1	1	94	1
16) *B. sauvagii* clade	4.8	3.8–5.9	1	9.7	7.5–11.9	1	100	1
17) *B. ornata/B. septuiclavis* + *B. cylura* clade	11.9	10.4–13.4	0.99	17.7	14.3–21	1	87	1
18) *B. ornata* + *B. septuiclavis*	10.4	8.2–12.3	0.87	16.4	13–19.9	0.92	**72**	**0.99**
19) *B. cyclura* clade	8.7	7.3–10	1	13.6	10.9–16.4	1	100	1
20) giant forms + *Eurydactylodes*	13.1	11.3–14.7	0.2	19.2	15.5–23.2	**0.95**	37	0.6
21) *Rhacodactylus* + *Eurydactylodes*	12.2	10.3–13.9	0.52	17	13.6–20.7	**0.98**	57	**1**
22) *R. auriculatus* + *R. trachyrhynchus*	10.5	7.9–12.5	0.5	13.97	10.5–17.6	**0.99**	48	–
23) *Eurydactylodes* + *Mniarogekko*	10.2	8.4–12	0.69	14.5	11.2–17.7	**0.98**	**82**	**1**
24) *Eurydactylodes*	7.1	5.3–9	1	10.4	7.8–13.18	1	100	1
25) *Correlophus*	8.7	6.6–10.9	1	12.8	9.3–16.3	1	100	1

NZ, New Zealand; NC, New Caledonia, and Aust., Australia.

for this clade (Fig. 3a). The fitdAICrc function in LASER yielded a positive ΔAIC_{rc} ($\Delta AIC_{rc} = AIC_{rc}–AIC_{rv}$) for both the coalescent and concatenated trees. This was shown to be significantly different from the null expectation of constant speciation in the Yule pure-birth simulations for both the concatenated tree ($P = 0$) and the species tree ($P = 0.003$) (Fig. 3b). The best rate-variable model selected by fitdAICrc was the Yule 3-rate model for both trees (*BEAST: AIC = −0.06, $\Delta AIC_{rc} = 10.31$; BEAST: AIC = 20.8, $\Delta AIC_{rc} = 28.5$), which is a Yule model with three speciation rates (*BEAST: $r_1 = 0.55$, $r_2 = 0.17$, $r_3 = 0.03$; BEAST: $r_1 = 0.48$, $r_2 = 0.12$, $r_3 = 0.05$) that decrease at two time intervals (*BEAST: $st_1 = 13.05$ Ma, $st_2 = 2.19$ Ma; BEAST: $st_1 = 19.23$ Ma, $st_2 = 4.1$ Ma). Results from analysis of both trees suggest a downshift in diversification (Table S5). Furthermore, evaluation of this data set using the γ-statistic rejected the hypothesis that diversification has been constant; instead indicating that diversification has decreased over time (*BEAST MCC: $\gamma = -2.92$, $P = 0.002$; *BEAST posterior: mean $\gamma = -2.78$, $P = < 0.001$; BEAST MCC: $\gamma = -4.54$, $P < 0.001$, BEAST posterior: mean $\gamma = -4.45$, $P = < 0.001$). Model testing using the dd_ML function in DDD on 100 trees from *BEAST recovered a diversity dependent with extinction (DDD+E) model ($\lambda = 0.28$, $\mu = 4.45e^{-5}$) under AICw and a species carrying capacity that was slightly greater than our estimate of 44 putative extant species (mean ± SD: $K = 56.8 \pm 3.2$) (Table S6). Model choice from DDD for the concatenated BEAST trees was identical to that of *BEAST, with a DDD+E model being selected ($\lambda = 0.28$, $\mu = 7.67e^{-12}$, mean estimates ± SD: $K = 57.2 \pm 3.1$).

DISCUSSION

Phylogeny of the New Caledonian clade

Intergeneric and intrageneric relationships within the New Caledonian clade are mostly consistent with previous studies (Bauer *et al.*, 2012), but often receive increased statistical support with our additional data in the concatenated analyses. Given the overall lack of support in the individual gene trees, we attribute these boosts in support in the concatenated trees to hidden phylogenetic information content (Gatesy & Baker, 2005; Edwards, 2009). Our topology testing (Appendix S2) rejected all trees that placed non-New Caledonian lineages within the New Caledonian clade, but failed to reject alternative arrangements within our focal taxon.

As in the mitochondrial tree and in the findings of Bauer *et al.* (2009, 2012), *Eurydactylodes* was recovered as sister to

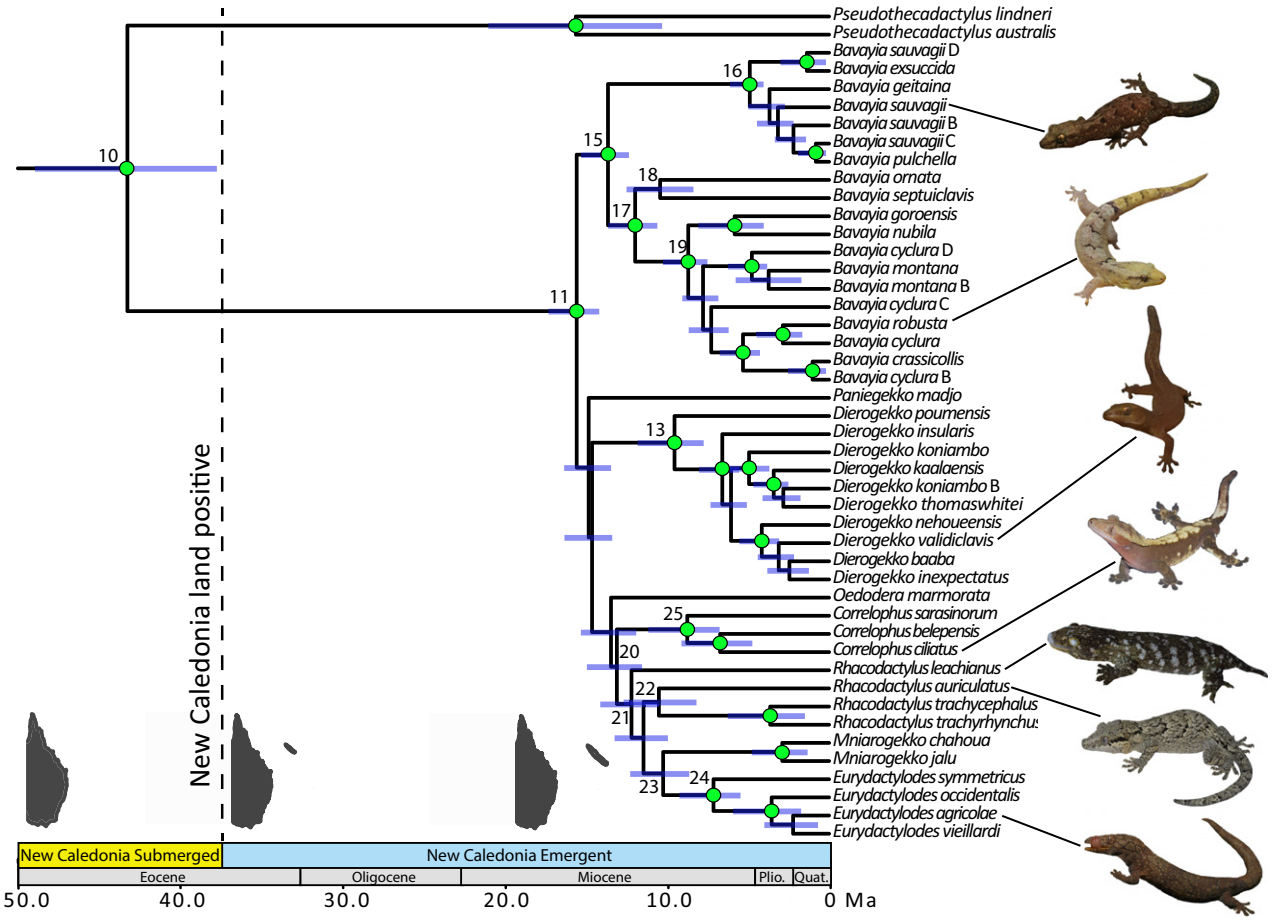

Figure 2 *BEAST MCC timetree of *Pseudothecadactylus* + New Caledonia (remaining outgroups not shown). Green circles indicate posterior probabilities ≥ 0.95 and error bars are 95% credibility intervals. Dashed vertical line indicates the emergence of New Caledonia. Small inset images represent eastern Australia (left) and the gradual emergence of New Caledonia (right). Node numbers correspond to those in Table 1.

Mniarogekko. The fact that our species tree fails to recover strong support for a giant gecko clade (node 20 (Figs 1 & 2) or the sister relationship between *Mniarogekko* and *Eurydactylodes* suggests that the concatenated topology is driven almost entirely by mtDNA (Figs 1 & 2, S1 & S2; Table 1). Overall support in the species tree is substantially lower than in some of the concatenated analyses (Table 1), and this is likely to be due to the lack of informativeness of the individual nuclear genes and incongruence between genes (Edwards, 2009; McCormack *et al.*, 2011). If this is the case, the recovery of clades, such as nodes 12, 14 and 20 in the concatenated analyses may result from a combination of insufficient data and a strong, but ultimately incorrect, phylogenetic signal (Edwards, 2009).

Nevertheless, some nodes are strongly supported by both methods, namely the monophyly of *Bavayia*, a genus that has previously received low support (Bauer *et al.*, 2012). This suggests that the loci here, despite being uninformative when analysed alone, possess some hidden phylogenetic signal. Although hidden support has been demonstrated and is fairly well understood for concatenated analyses, it has not been previously reported for species tree methods (Townsend *et al.*, 2011). Both analyses have high support for the presence of a small-bodied *B. sauvagii* clade and a large bodied *B. cyclura* clade. Our additional data unambiguously place the enigmatic *B. septuiclavis* and *B. ornata* as sister to the *B. cyclura* complex. Both species have been allied to superficially similar species in *Bavayia* and *Dierogekko*. Many of the wide-ranging species (i.e. *B. sauvagii*, *B. cyclura*, *B. montana*, *B. crassicollis*), identified based on external morphology were non-monophyletic as previously suggested by Bauer & Jackman (2006). Within *Dierogekko,* the strong support we recovered for the *D. koniambo* and *D. inexpectatus* complexes agrees with previous studies (Bauer *et al.*, 2006b; Skipwith *et al.*, 2014). All of our analyses recover two lineages on Massif Koniambo attributed to *D. koniambo*, one restricted to the type locality (Massif Koniambo) and another from Taavo Pointe de Vavouto (*D. koniambo* B in Figs 1 & 2) to the north-west. This study fully resolves the relationships within *Eurydactylodes*, recovering *E. agricolae* and *E. viellardi* as sister taxa, which is in agreement with Bauer *et al.* (2009).

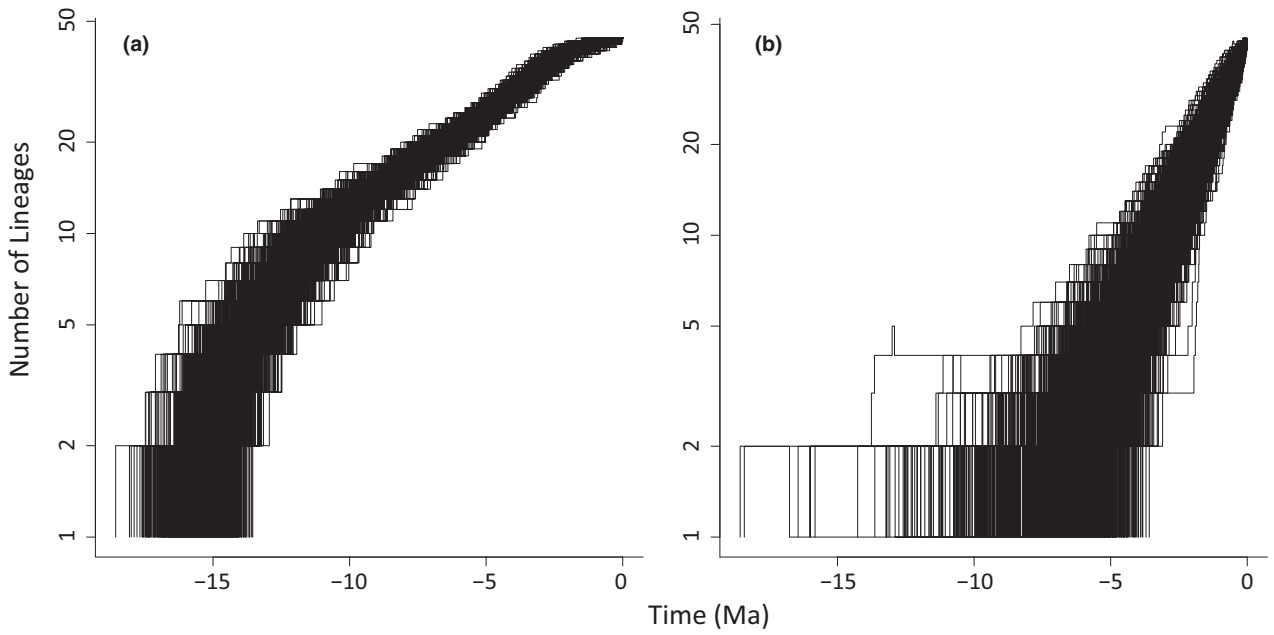

Figure 3 (a) Lineage through time plot (LTT) of 1000 trees from empirical *BEAST data showing a diversity dependent diversification pattern with an early burst of speciation followed by declining lineage accumulation of the gekkotans. (b) LTT of 1000 simulated trees under a constant-rate pure-birth model (lack of diversity dependence).

Divergence times and biogeography

Results from our dating analysis using a relaxed molecular clock were largely congruent with previous analyses focusing on gekkotans (Gamble *et al.*, 2008b; Oliver & Sanders, 2009; Oliver *et al.*, 2010). Both the concatenated and coalescent dating analyses support a post-Cretaceous New Caledonian-*Pseudothecadactylus* divergence (concatenated: 48.3 Ma, CI = 39.9–56.9; coalescent: 43.2 Ma, CI = 37.5–48.6), with divergence within the crown New Caledonian group being as recent as the Miocene (Figs 1 & 2). Our analyses thus reject the hypothesis of a Cretaceous origin for this clade of geckos and rather imply long-distance overwater dispersal, well after the fragmentation of eastern Gondwana. Although some authors have suggested that there may have been emergent refugia in the New Caledonian region prior to 37 Ma (Mefre *et al.*, 2006), evidence for persistent land in the area during the early Cenozoic is lacking, and we favour a dispersal scenario dating closer to the emergence of New Caledonia followed by recent diversification (Grandcolas *et al.*, 2008). As there are no long branches in the New Caledonian clade predating 37 Ma, we propose that this clade diverged from the ancestors of *Pseudothecadactylus* during the Eocene while still in Australia and dispersed to New Caledonia after its re-emergence. This hypothesis, of course, requires the extinction of the Australian stem lineages.

Our study is the first to use a time-calibrated coalescent species tree to infer the age of a New Caledonian taxon. There is strong evidence demonstrating that the accuracy of divergence dates using coalescent methods exceeds that of concatenation, as the latter may overestimate divergence times (McCormack *et al.*, 2011). Our species tree yielded divergence dates that are substantially younger than those obtained in previous studies for other Tasmantis taxa relying on concatenation (Smith *et al.*, 2007; Chapple *et al.*, 2009; Espeland & Johanson, 2010; Espeland & Murienne, 2011; Nielsen *et al.*, 2011; Barrabé *et al.*, 2014). This suggests that crown ages for other Tasmantis taxa may be younger than previously reported (Espeland *et al.*, 2008; Pillon *et al.*, 2009; Espeland & Murienne, 2011; Nielsen *et al.*, 2011). Furthermore, rapid speciation may increase gene-tree species tree discordance, making coalescent approaches particularly appropriate (McCormack *et al.*, 2011).

Some members of the New Caledonian diplodactylid clade have managed to colonize the nearby satellite islands of the Grande Terre (mainland) such as the Beleps, Île des Pins and the Loyalties. The first two of these were largely submerged prior to the Plio-Pleistocene, before becoming emergent and intermittently connected to the Grande Terre via narrow land bridges during the Pleistocene (Bauer & Sadlier, 2000). As their divergences from their respective sister taxa pre-date the emergence of these land bridges, the species present on the Beleps and other northern offshore islands (i.e. *Correlophus belepensis*, *Mniarogekko jalu*, *Dierogekko baaba*, *D. insularis* and *Bavayia cyclura* group sp.) must have dispersed either via a land bridge or overwater during the Plio-Pleistocene. We propose the same scenario to explain the presence of *Rhacodactylus trachycephalus*, *R. leachianus*, *Correlophus ciliatus, B. sauvagii* and *B. robusta* on the Île des Pins. Unlike the Grande Terre, the Loyalties are volcanic in origin, topped by Miocene reefs, and were not emergent until the Pleistocene (Bauer & Sadlier, 2000). As these islands were never

contiguous with the Grande Terre, it is most likely that both *B. crassicollis* and *B. sauvagii* dispersed over water to the Loyalties during the Pleistocene.

Several lineages, primarily the small-bodied *Oedodera, Paniegekko, Dierogekko* and *Bavayia*, demonstrate high levels of microendemism, with representative species being restricted to various vegetation types and isolated mountain ranges. The erosion of the ultramafic nape across the Grande Terre during the Eocene has left several areas of floral endemism in the northern and southern portions of the island (Cluzel *et al.*, 2001; Bauer *et al.*, 2006a). This patchy substrate combined with climatic oscillations during the Neogene and topographic complexity may have influenced the formation and maintenance of microendemism in these groups. This combination of factors is likely when considering that all of the speciation events within this clade occurred well after the initial erosion of the ultramafic nape (Nattier *et al.*, 2013). Based on the species tree, divergences between *C. ciliatus–C. belepensis* and *Mniarogekko chahoua–M. jalu* occurred in the late Miocene and late Pliocene respectively. Both groups are present in the northern and southern portions of the Grande Terre, with no known samples from central Grande Terre. This pattern suggests that climate change in the Neogene played a major role in the isolation of these lineages as suitable habitat was reduced on the mainland.

Patterns of diversification

Our diversification analyses are largely congruent with our proposed recent origination hypothesis, as net diversification was initially rapid before declining towards the present (Fig. 3a). This pattern has been documented in invertebrates, plants, and Tasmantis geckos (Espeland & Murienne, 2011; Garcia-Porta & Ord, 2013). While it is extremely unlikely that this clade has experienced zero extinction, and a number of factors can produce a signature of decline, diversity dependence is probable when considering the young age and rapid diversification of these geckos (Quental & Marshall, 2011). While our DDD analyses suggest that extinction was a factor, the failure to estimate a realistic extinction rate (i.e. -μ near 0 in our analyses) may be an artefact of small clade size. However, it is clear that there was an early burst of speciation in both the concatenated and species trees, as is evident by the short internal branches, and this may have coincided with phenotypic diversification. The slightly higher speciation rates seen in the *BEAST LASER analyses may reflect the overall shorter branch lengths and timeframe of this tree when compared to the concatenated tree (Table S5). While there are allopatric, morphologically conservative species present in this clade, there are many phenotypically divergent taxa that occur in sympatry. The proposed recent overwater dispersal of this clade and the fact that it was almost certainly the first gecko lineage to arrive on the island (Grant-Mackie *et al.*, 2003) may have resulted in rapid *in situ* adaptive diversification. This study contributes to the growing body of literature supporting the recent dispersal of taxa to the emergent areas of Tasmantis and further demonstrates that these lineages diversified rapidly soon after colonization.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary table: Specimen locality details and GenBank accession numbers (Table S1).

Appendix S2 Supplementary methods, results, and tables: Detailed methods on molecular, phylogenetic, and diversification analyses. Table with BEAST divergence dates (Table S2) without New Zealand calibration and results from LASER and DDD (Tables S3 & S4).

Appendix S3 Supplementary figures: Maximum likelihood phylograms of mtDNA (Figs S1 & S2), nucDNA (Figs S3 & S4), and combined mtDNA and nucDNA (Figs S5).

BIOSKETCH

The authors study the phylogenetics, biogeography and taxonomy of Australian and Tasmantis squamates. Of particular interest is testing the divergence times and modes of diversification for various lineages.

Author contributions: Project ideas were conceived of by P.S.S. and A.M.B. P.S.S. did the lab work, data analysis and manuscript writing, with other authors contributing to editing and approving the final manuscript. All the authors conducted fieldwork and collected the samples used in all subsequent analyses. A.M.B., R.A.S. and T.R.J. acquired funding and permitting for fieldwork and molecular lab work.

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