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Cryptic diversity and non-adaptive radiation of montane New Guinea skinks (*Papuascincus*; Scincidae)

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ABSTRACT

New Guinea, the world's largest and highest tropical island, has a rich but poorly known biota. *Papuascincus* is a genus of skinks endemic to New Guinea's mountain regions, comprising two wide-ranging species and two species known only from their type series. The phylogeny of the genus has never been examined and the relationships among its species – as well as between it and closely related taxa – are hitherto unknown. We performed the first large-scale molecular-phylogenetic study of *Papuascincus*, including sampling across the genus' range in Papua New Guinea. We sequenced three mitochondrial and two nuclear markers from 65 specimens of *Papuascincus* and reconstructed their phylogenetic relationships. We also performed species-delimitation analyses, estimated divergence times and ancestral biogeography, and examined body-size evolution within the genus. *Papuascincus* was strongly supported as monophyletic. It began radiating during the mid-Miocene in the area now comprising the Central Cordillera of New Guinea, then dispersed eastward colonising the Papuan Peninsula. We found evidence of extensive cryptic diversity within the genus, with between nine and 20 supported genetic lineages. These were estimated using three methods of species delimitation and predominantly occur in allopatry. Distribution and body-size divergence patterns indicated that character displacement in size took place during the evolutionary history of *Papuascincus*. We conclude that the genus requires comprehensive taxonomic revision and likely represents a species-rich lineage of montane skinks.

1. Introduction

Cryptic species are distinct taxa with discrete evolutionary trajectories that have typically been classified as a single species due to morphological similarities precluding correct identification and assignment of taxonomic status (Bickford et al., 2007; Jörger and Schrödl, 2013; Pante et al., 2015). Although the advent of molecular phylogenetic methods has advanced our understanding and description of cryptic diversity, several regions and taxa remain woefully understudied in this regard. This is particularly true of tropical rainforest taxa (Bickford et al., 2007). Tropical regions are usually among the most species-rich areas on the planet (Willig et al., 2003), and many are considered as hotspots for conservation priorities (Myers et al., 2000; Brooks et al., 2006).

New Guinea is the world's largest tropical island and is one of the most biologically diverse regions on Earth, with high levels of vertebrate species richness and endemism (Allison, 2009). The island's size, topography, geological history, and tropical climate are all factors thought to contribute to its high level of biodiversity (Allison, 2009), and much of the island's diversity patterns closely align with elevational gradients across the island's massive mountain ranges (Diamond, 1973; Allison, 1982; Tallowin et al., 2017). Recent molecular phylogenetic studies have uncovered extensive cryptic diversity on New Guinea from various taxa (birds: Marki et al., 2017; fishes: McGuigan et al., 2000; Kadarusman et al., 2012; frogs: Oliver et al., 2013; Oliver et al., 2017; Lepidoptera: Craft et al., 2010; reptiles: Donnellan and Aplin, 1989; Rawlings and Donnellan, 2003; Metzger et al., 2010; Tallowin et al., 2018).

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The mountains of New Guinea reach as high as 4884 m above sea level (a.s.l; the summit of Puncak Jaya in Papua Province, Indonesia) and cover a vast extent of the island, with over a third of its land area lying above 1000 m (Allison, 2009). The formation of contemporary New Guinea and its montane topography arose through the progressive northward movement of the Australian Plate and its collision with the Pacific Plate, along with extensive island-arc accretion along the plate margin (Hall, 2002; Quarles van Ufford and Cloos, 2005; Baldwin et al., 2012). Despite controversy regarding the exact timing of geological events, accretion along the leading edge of Australian Craton is thought to have begun in the early Miocene (Pigram and Davies, 1987; Hall, 2002; Baldwin et al., 2012), eventually giving rise to several mountain chains along the northern coast of contemporary New Guinea. Montane uplift of the Central Cordillera that runs along the long (W-E) axis of the island is thought to have begun much more recently, likely to have arisen no earlier than the mid-Miocene (Hall, 2002; Hill and Hall, 2003; Quarles van Ufford and Cloos, 2005). The exact timing of the orogeny of the East-Papuan Composite Terrane – comprising the Papuan Peninsula in the southeast of New Guinea – is equally contentious, with estimates ranging from initiation during the Oligocene (Pigram and Davies, 1987; Quarles van Ufford and Cloos, 2005) to more recent orogeny during the mid-Miocene (Hall, 2002; Hill and Hall, 2003). Irrespective of the exact timing, the uplift of these mountain ranges has evidently influenced New Guinea's natural diversity, by promoting speciation of lowland taxa through the formation of barriers to gene flow (Georges et al., 2013; Tallowin et al., 2018; Tallowin et al., 2019) and through generation of novel, highly dissected montane habitats for lineages to colonize (Toussaint et al., 2014; Marki et al., 2017; Oliver et al., 2017; Tallowin et al., 2018).

The genus *Papuascincus* Allison and Greer, 1986 is endemic to the montane regions of New Guinea, occurring only at elevations above 1000 m (Allison, 1982; Allison and Greer, 1986; Fig. 1). The genus is thought to be a part of a group of mostly, but not exclusively, high-elevation skinks that includes *Lipinia*, *Prasinohaema* and *Lobulia* (Greer et al., 2005). Based on shared derived characteristics Greer (1974) suggested that these four genera are closely related. This result has recently been corroborated by molecular studies – albeit with the monophyly of *Lipinia* and *Prasinohaema* not supported (Rodriguez et al., 2018). *Papuascincus* is unique among the montane skinks of New Guinea in its reproductive mode. Whereas montane species of *Lobulia* and *Prasinohaema* are ovoviviparous, *Papuascincus* is oviparous, laying a fixed clutch of two eggs (Allison and Greer, 1986). This is unusual for lizards inhabiting cold, montane habitats (Meiri et al., 2012) and likely creates an upper barrier on their elevational distribution due to thermoregulatory limitations on egg development (Allison, 1982).

Four species are currently described in *Papuascincus*. Two – *P. stanleyanus* (Boulenger, 1897) and *P. morokanus* (Parker, 1936) – are considered widespread, whereas two (*P. buergersi* and *P. phaeodes*) are only known from their original 1932 descriptions (Vogt, 1932; Meiri et al., 2018). All four species, however, are phenotypically similar in general colouration and body shape. They mainly differ from each other in body size and in their elevational distribution, but at least *P. stanleyanus* and *P. morokanus* are otherwise ecologically and morphologically similar (Allison, 1982). The body-size variation, along with variation in some aspects of colour patterns (*e.g.,* continuous vs. fragmented dorsolateral stripes) and various scale counts across the range, points towards the existence of undescribed diversity in the genus.

In this study, we present the first large-scale genetic sampling of *Papuascincus* throughout its range in Papua New Guinea, enabling us to explore phylogeographic relationships and genetic diversity in the genus. We used a multilocus approach including both mitochondrial and nuclear DNA sequences and performed phylogenetic analyses based on concatenated datasets. Furthermore, we conducted species-delimitation analyses, biogeographical reconstructions, and estimated the divergence times and genetic diversity between and within delimited lineages. We thus provide data concerning the diversity and distribution within *Papuascincus*, its evolution, and historical biogeography in this under-studied region of the world.

2. Material and methods

2.1. Genetic sampling, DNA extraction, amplification, and sequence analysis

We collected 63 tissue samples of *Papuascincus* specimens from

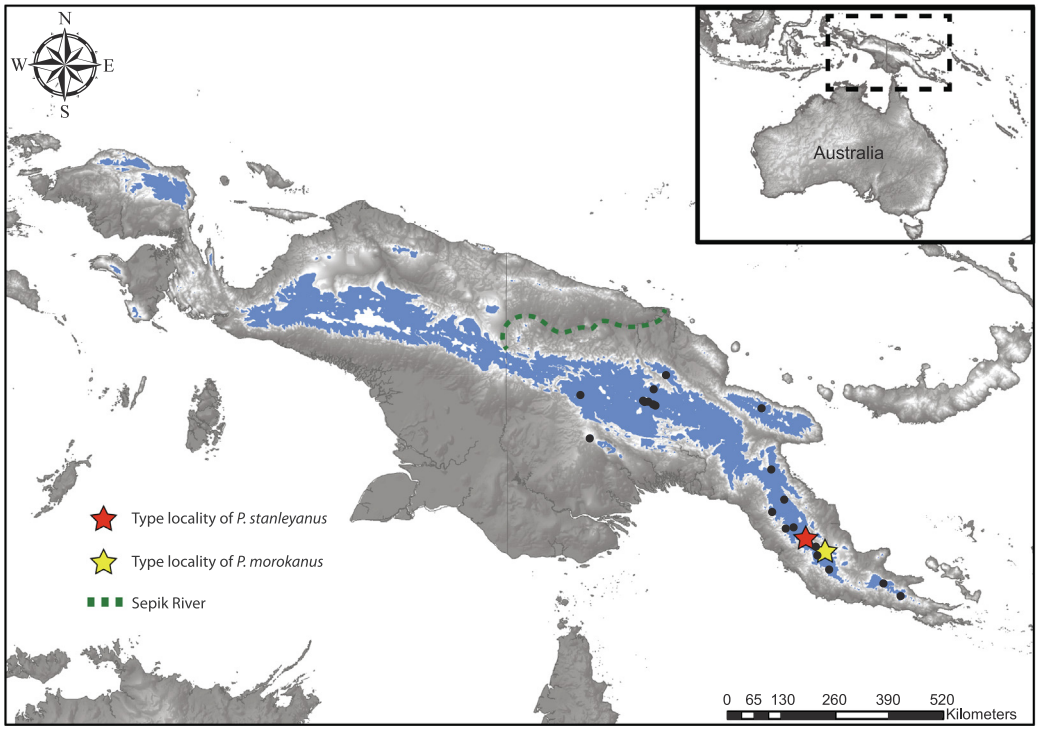
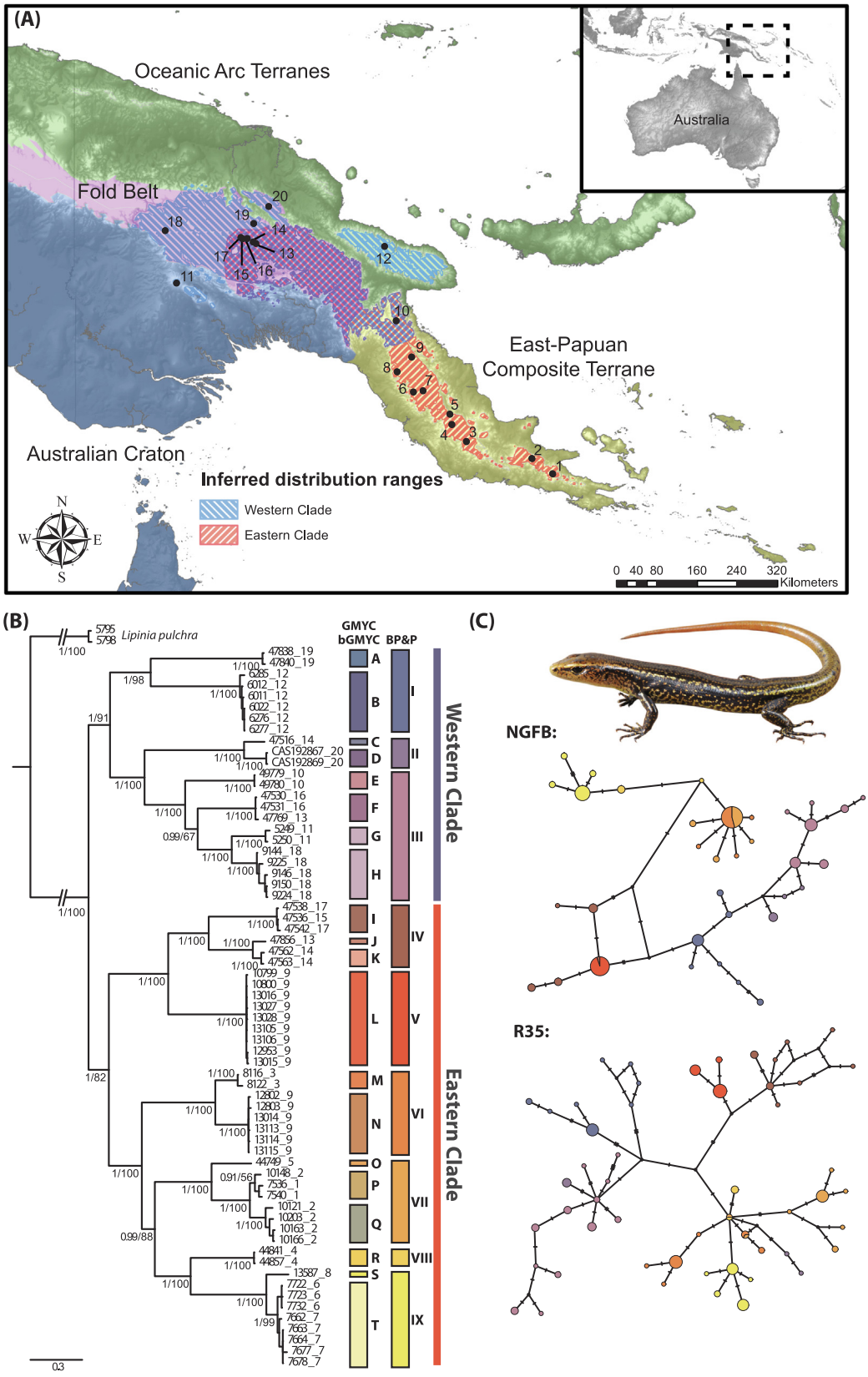


Fig. 1. Map of New Guinea showing the distribution of samples analysed herein and the type localities of recognized species of *Papuascincus*. The blue polygon includes all areas encompassing the elevational range of samples in this study (1190–3282 m), representing potential distribution for *Papuascincus*. Black dots denote sampled localities in this study. The red star denotes the type locality of *Papuascincus stanleyanus* (Mt. Victoria), the yellow star denotes the type locality of *Papuascincus morokanus* (Moroka), and the green dashed line follows the path of the Sepik River, the type locality for *Papuascincus buergersi* and *P. phaeodes*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



(caption on next page)

Fig. 2. (A) a map of specimen localities used in the study. Overlaid on top of the map are polygons showing the distribution ranges of the Eastern and the Western clades in the phylogeny, inferred based on the sampled localities and their elevational range (1190–3282 m). The four different geological regions of Papua New Guinea are coloured blue (Australian Craton), purple (Fold Belt), green (Oceanic Arc Terranes), and yellow (East-Papuan Composite Terrane). (B) Bayesian Inference phylogenetic tree based on the concatenated dataset of three mitochondrial and two nuclear markers, with BI posterior probabilities and ML bootstrap support values shown at each node, respectively. On each label, the sample code of the specimen detailed in Table S1 is followed by a locality number presented in the map in panel A. Next to the tree are lineages as delimited by species delimitation methods: GMYC/bGMYC and BP&P. (C) Nuclear haplotype networks for two markers, *NGFB* (top) and *R35* (bottom). The colours correspond to the nine BP&P lineages as shown in panel B. Photo of *Papuascincus* courtesy of Allen Allison. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

across its range in Papua New Guinea (Fig. 2A; Table S1) and retrieved sequences from GenBank of two additional specimens (from Linkem et al., 2011). Two tissue samples of *Lipinia pulchra* – currently estimated as the phylogenetically closest species to *Papuascincus* (Rodriguez et al., 2018) – were used as an outgroup. We used the dataset comprised of *Papuascincus* and *Lipinia* sequences to understand the genetic structure within *Papuascincus*. To obtain calibrations for the time-calibrated phylogenetic analyses, we generated another dataset adding retrieved sequences from GenBank of more-distant relatives, based on previous studies of Australasian skinks: one specimen each of *Lipinia noctua*, *Lerista lineopunctulata*, *Lerista neander*, *Notoscincus ornatus*, *Scincella lateralis* and *Sphenomorphus solomonis*, and two specimens each of *Scincella assatus* and *Lipinia pulchella* (Rabosky et al., 2007; Skinner et al., 2011; Rodriguez et al., 2018). A total of 77 specimens was used for the analyses (Table S1).

We extracted DNA from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kits (Qiagen, Valencia, CA, USA). We sequenced a total of three mitochondrial markers – the ribosomal 12S rRNA (*12S*), the NADH dehydrogenase subunit 2 (*ND2*) and the NADH dehydrogenase subunit 4 (*ND4*) – and two nuclear markers – RNA fingerprint protein 35 (*R35*), and the nerve growth factor β polypeptide (*NGFB*). Primers and PCR conditions used for the amplification and sequencing of all markers are as detailed in Linkem et al. (2011). Chromatographs were assembled and edited using Geneious v.11.0.5 (Biomatter Ltd). For the nuclear markers, we identified heterozygous positions and coded them according to the standard IUPAC ambiguity codes. We translated protein-coding genes into amino acids, and we detected no stop codons, suggesting that they were not pseudogenes. We aligned sequences for each marker using MAFFT v.7.3 (Katoh and Standley, 2013) with default parameters. We tested the occurrence of recombination for the two phased nuclear-gene alignments using the Pairwise Homoplasy Index (PhiTest; Bruen et al., 2006) implemented in SplitsTree v.4.14.5 (Huson and Bryant, 2006), and we detected no evidence of recombination ($P > 0.6$ for the two genes).

2.2. Phylogenetic analyses

We partitioned our dataset for phylogenetic analyses with PartitionFinder v.2 (Lanfear et al., 2016), using the following parameters: linked branch lengths; BEAST models; BIC model selection; "greedy schemes" search algorithm; single partition for *12S* and by codons for the protein-coding genes *ND2*, *ND4*, *R35*, and *NGFB*. For the dataset of *Papuascincus* and *Lipinia*, we performed phylogenetic analyses under Maximum Likelihood (ML) and Bayesian Inference (BI) frameworks. We analysed the complete, mitochondrial, and nuclear concatenated datasets separately with the following partitions and relevant substitution models: *12S* + *ND2*_1 + *ND4*_1 (HKY + I + G), *ND2*_2 + *ND4*_2 (HKY + I + G), *ND2*_3 + *ND4*_3 (TRN + G), *NGFB*_1 + *NGFB*_2 + *NGFB*_3 + *R35*_1 + *R35*_2 (K80 + I), *R35*_3 (HKY + I). We conducted ML analyses in RAxML v.8.1.2, as implemented in raxmlGUI v.1.5 (Silvestro and Michalak, 2012), with the GTRGAMMA model of sequence evolution and 100 random-addition replicates. We assessed nodal support with 1000 bootstrap replicates. We conducted BI analyses with MrBayes v.3.2.6 (Ronquist et al., 2012). Nucleotide substitution model parameters were unlinked across partitions, and we allowed the different partitions to evolve at different rates. We performed two simultaneous parallel runs with four chains per run (three heated, one cold) for 10^7 generations, sampling every 1000 generations for the complete concatenated dataset, and for 3×10^6 generations with a sampling frequency of every 3000 generations for the mitochondrial and nuclear concatenated datasets. We examined the standard deviation of the split frequencies between the two runs and the Potential Scale Reduction Factor (PSRF) diagnostic, and we assessed convergence by confirming that all parameters had reached stationarity and had sufficient effective sample sizes (> 200) using Tracer v.1.6 (Rambaut et al., 2014). We discarded the first 25% of trees as burn-in. We considered nodes well-supported if they received ML bootstrap values $\geq 80\%$ and posterior probability (pp) support values ≥ 0.95.

With the aim of exploring patterns of intra-specific diversity and nuclear allele sharing within *Papuascincus*, we inferred statistical parsimony networks on the two individual nuclear genes with the program TCS v.1.21 (Clement et al., 2000) implemented in PopART (Leigh and Bryant, 2015) using default settings (connection limit of 95%) and including only full length sequences. To infer haplotypes, we used the online web tool SeqPHASE (Flot, 2010) to convert the input and output files, and we used the software PHASE v.2.1.1 (Stephens et al., 2001; Stephens and Scheet, 2005) to resolve heterozygous single-nucleotide polymorphisms in the phased alignments, with a probability threshold of 0.7 for *NGFB* and 0.5 for *R35*.

We calculated inter- and intra-specific uncorrected *p*-distances of the mitochondrial (based on GMYC/bGMYC analyses) and nuclear (based on BP&P analyses) delimited *Papuascincus* lineages (see below) for each sequenced mitochondrial marker in MEGA v.7.0.14 (Kumar et al., 2016).

2.3. Species-delimitation analyses

We delimited distinct lineages within *Papuascincus* using two datasets: mitochondrial and nuclear. At the first stage we evaluated mitochondrial divergence using the ML and BI functions of the Generalized Mixed Yule-Coalescent analysis (GMYC and bGMYC, respectively; Pons et al., 2006; Reid and Carstens, 2012) implemented in R v.3.4.2 (R Core Team, 2017). For these analyses we inferred a concatenated ultrametric mitochondrial haplotype tree using BEAST v.1.8.4 (Drummond et al., 2012) with the following priors (otherwise by default): partitions and models as selected by PartitionFinder, 12S + ND2_1 + ND4_1 (HKY + I + G), ND2_2 + ND4_2 (HKY + I), ND2_3 + ND4_3 (TRN + G); Yule process tree model; random starting tree; alpha prior uniform (0–10), strict clock prior (uniform distribution; mean 1, 0–1). We carried out three individual runs of 10^7 generations, sampling at intervals of 1000 generations. We evaluated convergence, posterior trace plots, effective sample sizes (ESS > 200), and burn-in in Tracer v.1.6 (Rambaut et al., 2014). We combined the tree runs in LogCombiner, discarded the first 10% of trees as burn-in, and generated an ultrametric tree with TreeAnnotator (both provided with the BEAST package). For the GMYC analysis we used the *splits* R package (Ezard et al., 2009), applying a single threshold algorithm. For the bGMYC analysis we used the *bGMYC* R package (Reid and Carstens, 2012) to calculate marginal posterior probabilities of lineage limits from a subsample of 250 trees; we ran MCMC chains for each tree for 10^4 generations with 10% burn-in.

As a second step of species delimitation, we evaluated nuclear divergence and tested the mitochondrial GMYC/bGMYC candidate species with Bayesian Phylogenetics and Phylogeography v.3.4 (BP&P; Rannala and Yang, 2003; Yang and Rannala, 2010) using the full phased nuclear loci only. As prior distributions on the ancestral population size (θ) and root age (τ) can affect the posterior probabilities for models (Yang and Rannala, 2010; Zhang et al., 2011), we performed a preliminary analysis estimating the two parameters under the MSC model with a given species phylogeny (A00 configuration, with the topology obtained using the concatenated dataset; Rannala and Yang, 2003). We parameterized these priors through Inverse Gamma distributions setting $\alpha = 3$ and two values of β (0.002, 0.2) that cover different alternative scenarios for ancestral population size and root age. The suggested values were (Inv-Gamma(α,β)): θ = Inv-Gamma(2, 0.2) and τ = Inv-Gamma(2, 0.01), with which we carried out two types of analyses, setting the initial number of lineages to 20 (recovered from the GMYC/bGMYC analysis, see Results): (i) A10 configuration – conducting Bayesian species delimitation analysis using a user-specified guide tree (with the topology obtained using the concatenated dataset; Yang and Rannala, 2010; Rannala and Yang, 2013), and (ii) A11 configuration – implementing a joint analysis conducting Bayesian species-delimitation while estimating the species tree (Yang and Rannala, 2014; Yang, 2015). For these analyses we used algorithms 1 and 0, assigning each species-delimitation model equal prior probability. We estimated the locus rate parameter that allows variable mutation rates among loci with a Dirichlet prior (α = 2). We set the heredity parameter that allows θ to vary among loci as default, due to our dataset being autosomal. Each rjMCMC analysis ran for 5×10^5 generations with 10% discarded as burn-in. We considered probability values ≥0.95 in all the different alternative scenarios for ancestral population size and root age as strong evidence for delimited lineages.

2.4. Estimation of divergence times and biogeographic analyses

We estimated divergence times with BEAST and the concatenated dataset containing one sample per GMYC/bGMYC-delimited lineage (see Results) and one sequence for each of the outgroups (see Table S1). We set the following divergence times, as previously estimated in other studies: (a) between the clade containing *Lerista*, *Notoscincus,* and *Sphenomorphus*, and the clade containing *Scincella*, *Papuascincus*, and *Lipinia*, to 29.4–55.8 Mya (normal distribution; mean 37 Mya, sd = 4) (Skinner et al., 2011), (b) between *Scincella lateralis* and the clade containing *Papuascincus* and *Lipinia* to 20.6–43.9 Mya (normal distribution; mean 32 ± 7 Mya) (Skinner et al., 2011), (c) between *Sphenomorphus solomonis* and the clade containing *Lerista* and *Notoscincus* to 24.3–48.5 Mya (normal distribution; mean 33 ± 4 Mya) (Skinner et al., 2011), (d) between *Notoscincus ornatus* and the clade containing *Lerista* to 19.1–53.6 Mya (lognormal distribution; mean 28.2; log(sd) = 0.35, offset 5) (Rabosky et al., 2007), and (e) between *Lerista lineopunctulata* and *Lerista neander* to 12.9–22.1 Mya (normal distribution; mean 17.5 ± 2.8 Mya) (Rabosky et al., 2014).

We conducted biogeographic analyses using Bayesian Stochastic Search Variable Selection (BSSVS; Lemey et al., 2009) implemented in BEAST. For these analyses we used the same dataset as in the divergence-time estimates mentioned above, but for one GMYC/bGMYC lineage that was distributed in more than one discrete elevational region, we added a single specimen to represent all regions occupied by that lineage (*i.e.*, adding specimen 7662 to lineage T). We performed the biogeographic analyses twice, assigning all specimens to geological and elevational regions based on the current distribution of the genus. In one analysis we assigned the lineages to one of four discrete geological regions: (1) AC – Australian Craton; (2) FB – Fold Belt; (3) EPCT - East-Papuan Composite Terrane; and (4) OAT – Oceanic Arc Terranes. In the second analysis we assigned the lineages to one of four discrete elevational regions: (1) A – alpine (> 3000 m); (2) SA – subalpine (2500–3000 m); (3) HM - higher montane (1500–2500 m); and (4) LM – lower montane (1000–1500 m) based on the habitat categorization of Bryan and Shearman (2015).

We conducted the calibration and the two biogeographical analyses in BEAST v.1.8.4 with the following partitions and relevant models as determined by PartitionFinder: 12S + ND2_1 + ND4_1 (GTR + I + G), ND2_2 + ND4_2 (GTR + I + G), ND2_3 + ND4_3 (TRN + G), NGFB_1 + NGFB_2 + NGFB_3 + R35_1 + R35_2 (K80 + G), R35_3 (HKY + G). Other priors were as detailed above, apart from base-substitution parameter (0–100), and uncorrelated relaxed-clock model for the mitochondrial genes (uniform distribution; 0–1). For the ancestral-area reconstruction analyses additional priors were: symmetric discrete-trait substitution model, strict-clock model for the location trait, and exponential prior for the discrete-location state rate (locations.clock.rate) with mean of 1.0 and offset of 0. We conducted three individual runs of 10^8 generations for each of the three analyses, with sampling at intervals of every 10^4 generations. We evaluated convergence, posterior trace plots, effective sample sizes (ESS > 200), and burn-in with Tracer. We combined the tree runs in LogCombiner, discarding the first 10% as burn-in, and generated an ultrametric tree with TreeAnnotator.

2.5. Body-size evolution

We used the time-calibrated phylogenetic tree constructed in Section 2.4 to map adult body size onto the phylogeny. We used digital calipers to measure snout-vent-lengths (SVLs) to the nearest 0.1 mm of 533 adult specimens representing the various lineages, including 62 specimens vouchered with tissues (Table S2). We assigned the specimens that were not sampled genetically to the different delimited lineages based on sampling localities and dates and general morphological similarity in colour patterns and size. Thus, specimens that were collected from the same population, and during the same collecting expedition as voucher specimens that were sampled genetically, were assigned to the same lineage of similar-sized genetic vouchers with a similar colour pattern. We excluded juveniles and subadults – as determined based on dissection and visual examination of gonads – from this analysis. We then calculated the mean SVL for each GMYC/bGMYC and BP&P-delimited lineage. We mapped the mean SVL onto the tips of the time-calibrated phylogeny and used the *fancyTree* and *phenogram* functions in the *phytools* package (Revell, 2012), implemented in R v.3.4.2 (R Core Team, 2017), to visualize body-size evolution along the phylogeny. We compared SVLs between the different GMYC/bGMYC-delimited lineages using ANOVA with *post-hoc* Tukey tests, and we generated boxplots to visualize differences in SVL between lineages.

3. Results

Our dataset comprised 65 specimens of *Papuascincus* and 12 outgroup specimens, together with a concatenated length of 3302 bp divided into three mitochondrial gene fragments (*12S*, 392 bp; *ND2*, 1020 bp; *ND4*, 708 bp) and two nuclear gene fragments (*NGFB*, 546 bp; *R35*, 636 bp).

Both the ML and BI phylogenetic trees of the complete concatenated dataset recovered the same topologies, with high support values for most nodes (Fig. 2B & S1). The topology of the phylogenetic tree based on the complete concatenated dataset is highly congruent with the topology based on the mitochondrial concatenated dataset only (Fig. S2A), although less so for the topology based on the nuclear concatenated dataset alone (Fig. S2B). We recovered *Papuascincus* as monophyletic. The GMYC and bGMYC species-delimitation analyses recovered 20 delimited mitochondrial lineages within *Papuascincus* (labelled A-T; Fig. 2B & S3). Using these 20 lineages the BP&P analyses of the nuclear data recovered only nine delimited lineages (numbered I-IX), mostly representing clustering of several GMYC/bGMYC-delimited lineages into single BP&P-delimited lineages (Fig. 2B). Only BP&P lineages V and VIII represent a single GMYC/bGMYC lineage each (L

and R, respectively).

Based on the complete concatenated phylogenetic tree, the earliest split in *Papuascincus* separated the genus into two clades: (1) a "western" clade containing BP&P lineages I-III (GMYC/bGMYC lineages A-H), distributed on the Central Cordillera, the Finisterre Mts and the westernmost Owen Stanley Mts (localities 10–20 in Fig. 2A), and (2) an "eastern" clade containing BP&P lineages IV-IX (GMYC/bGMYC lineages I-T), distributed on the Central Highlands portion of the Central Cordillera and throughout the Owen Stanley Mts (localities 1–10, 13–15 and 17 in Fig. 2A).

Genetic distances among the nine BP&P-delimited lineages were greater than the genetic distances within the lineages for all three mitochondrial gene fragments (Table S3). The lowest genetic divergence among lineages in the *ND2* and *ND4* markers was found between BP&P lineages VIII and IX (*12S*: 3.2%; *ND2*: 9.4%; *ND4*: 9.7%), whereas in the *12S* marker, the distance between BP&P lineages VI and VIII was the lowest (*12S*: 3%; *ND2*: 12.8%; *ND4*: 12.5%). Similarly, genetic distances between the 20 GMYC/bGMYC-delimited lineages (Table S4) were mostly greater than the genetic distances within lineages, although the between-lineage distances of some lineage pairs were much lower than the average between-lineage distances and even comparable to some within-lineage distances (*e.g.*, in the *12S* marker the distance between GMYC/bGMYC lineages S and T was 0.3%).

We recovered 35 unique haplotypes in the *NGFB* gene fragment and 53 unique haplotypes in the *R35* gene fragment. Of the BP&P-delimited lineages (Fig. 2C), lineages IV and V shared alleles in the *NGFB* network, lineages VII and VIII shared alleles in the *R35* network, and lineages VI and VII shared alleles in both *NGFB* and *R35* networks. No other lineages shared any alleles. More of the GMYC/bGMYC-delimited lineages shared alleles, but similarly to the BP&P lineages, few lineages shared alleles in both the *NGFB* and *R35* networks (Fig. S4).

The time-calibrated phylogenetic tree based on the dataset containing only a single representative from each GMYC/bGMYC-delimited lineage had a similar topology to the concatenated ML and BI trees (Fig. S5). We recovered the split of *Papuascincus* from its sister taxon, *Lipinia pulchra*, to have occurred roughly 14.4 Mya (95% highest posterior density [HPD]: 11.15–17.52). The sampled lineages within the genus *Papuascincus* then began radiating roughly 11.6 Mya (HPD: 9.25–14.15) in the mid-Miocene, with most of our sampled lineages arising during the late Miocene and Pliocene, between ~10 and 3 Mya. While some of the GMYC/bGMYC-delimited lineages arose during the Pleistocene, all the BP&P-delimited lineages had arisen by the end of the Pliocene.

According to the BSSVS analyses of geological ancestral reconstruction, *Papuascincus* originated with high probability on the Fold Belt (Fig. 3A). This was then followed by at least two independent colonisations of the East-Papuan Composite Terrane – once in the late Miocene by the clade giving rise to GMYC/bGMYC lineages M–T, distributed throughout the Papuan Peninsula (locations 1–9 in Fig. 2A), and a second time in the Pliocene by GMYC/bGMYC lineage E, which is restricted to Mt Missim (location 10 in Fig. 2A). There was also a single colonization event of the Oceanic Arc Terranes in the late Miocene – by GMYC/bGMYC lineage B, which is restricted to the Huon Peninsula (location 12 in Fig. 2A) – and a single colonization event of the Australian Craton in the early Pleistocene – by GMYC/bGMYC lineage G, which is restricted to Mt Bosavi (location 11 in Fig. 2A).

Our BSSVS reconstruction of *Papuascincus* according to elevational regions indicates that the ancestral population of the genus had, with a high probability, a higher montane elevational distribution (1500–2500 m in today's biome elevations – although the exact elevations that make up the same climatic conditions might well have been different in earlier geological periods; Fig. 3B). Based on this analysis, at least three independent transitions occurred from higher montane to lower montane (1000–1500 m) elevational distributions – by GMYC/bGMYC lineages E, M and T – and at least one transition each to subalpine (2500–3000 m) and alpine (> 3000 m) elevational distributions, by lineages I and S, respectively.

Adult SVLs of *Papuascincus* varied between 36.3 mm and 67.8 mm (Table S2; Figs. 4 & S6). The subclade containing GMYC/bGMYC lineages A-H is comprised of mostly small-sized lineages, with mean SVLs of 50.8 mm or less (the "small" morph). The subclade containing GMYC/bGMYC lineages I-T was comprised of mostly large-sized lineages, with mean SVLs of 52.5 mm or higher (the "large" morph), except GMYC/bGMYC lineage L (mean SVL 48.8 mm). Almost all lineages from the "large" morph were significantly larger than almost all lineages from the "small" morph (exceptions were almost all in cases where sample sizes were exceedingly small; Table S5).

4. Discussion

4.1. Cryptic diversity and evolutionary history

Our study provides the first large-scale time-calibrated phylogenetic

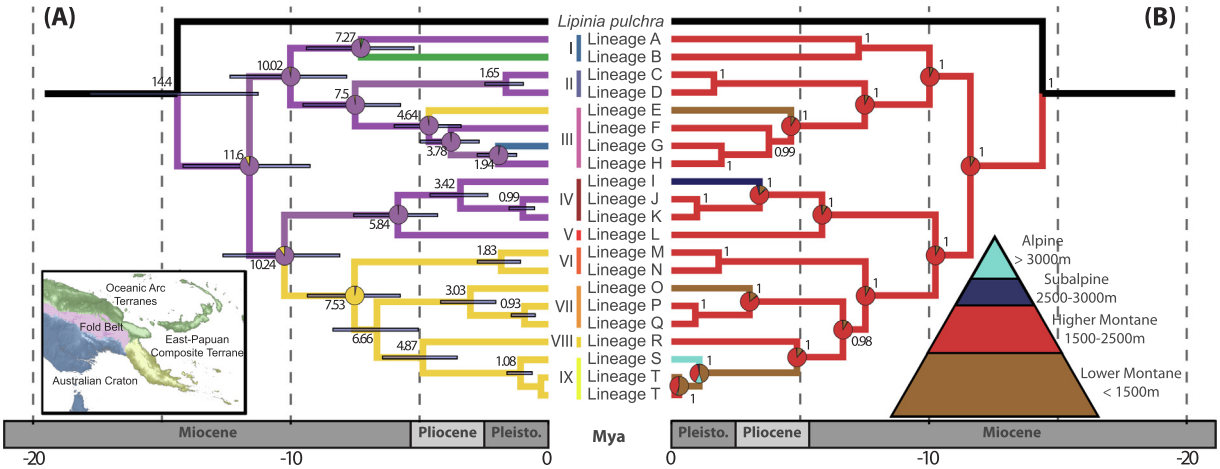


Fig. 3. Time-calibrated phylogenetic trees and the ancestral biogeographical reconstruction analyses of *Papuascincus*. The analyses were based on the reduced concatenated dataset, containing a single sample per GMYC/bGMYC lineage, and an additional sample for lineage T (with a different elevational distribution). Branch colours and pie charts near the major nodes describe the probability of each inferred character state. (A) Reconstruction according to geological regions: blue (Australian Craton), purple (Fold Belt), green (Oceanic Arc Terranes), and yellow (East-Papuan Composite Terrane). Mean age estimates are provided above the nodes with horizontal bars representing the 95% highest posterior densities. (B) Reconstruction according to elevational distribution: brown (lower montane, 1000–1500 m), red (higher montane, 1500–2500 m), dark blue (subalpine, 2500–3000 m), and light blue (apine, > 3000 m). Posterior probability values are indicated above the nodes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analyses of the genus *Papuascincus*, currently endemic to montane regions in New Guinea. Our results confirm that *Papuascincus* is a valid, monophyletic genus, as previously considered based on its unique synapomorphy: pustulate surface structures on the egg shells (Allison and Greer, 1986). This corroborates previous preliminary results based on two samples each in the molecular studies of Linkem et al. (2011) and Rodriguez et al. (2018).

Using three different species-delimitation approaches based on both nuclear and mitochondrial datasets, we uncovered as little as nine and as many as 20 distinct genetic lineages, many of which may merit evaluation as separate species. Genetic divergence in mitochondrial markers between both GMYC/bGMYC and BP&P-delimited lineages was high (Tables S3 and S4), and they shared few nuclear haplotypes (Fig. 2C & S4; although shared haplotypes may be indicative of gene flow or of incomplete lineage sorting). Furthermore, our time-calibrated phylogeny revealed deep splits between BP&P-delimited lineages, mostly occurring during the late Miocene and Pliocene.

The different lineages, however, are difficult to tell apart via general morphometric proportions, colouration patterns and scalation (A.S., pers. obs.) – although less so in size (Figs. 4 & S6). As far as is known, all members of *Papuascincus* have many similarities in their ecologies: they are all diurnal, insectivorous, oviparous, mostly terrestrial lizards, occurring in open habitats such as tree-fall gaps, cliff faces, forest clearings and alpine grasslands (Allison, 1982; Allison and Greer, 1986). Closely related lineages within *Papuascincus* are mostly distributed allopatrically (*e.g.*, the non-overlapping distributions of the "eastern" clade *Papuascincus* lineages in the Papuan Peninsula; Fig. 2). A lack of suitable habitat between the open habitat patches *Papuascincus* favours could appear in two forms: either as low-elevation barriers between montane regions (but see below), such as the Kokoda Gap in the Owen Stanley Mts, or continuous dense forest canopy without open habitats that precludes basking opportunities. Both would generate geographic barriers that could maintain reproductive isolation, and without divergence in ecological specialization by the different lineages, phylogenetic inertia or stabilizing selection could maintain niche conservatism and phenotypic similarity (Wiens and Graham, 2005; Losos, 2008).

4.2. Biogeographic history

The precise timing of the uplift of New Guinea's Central Cordillera is still debated. The formation of these mountains, spanning New Guinea's W-E axis, resulted from a complex geological history involving the northern movement of the Australian Plate margin and collision with the Pacific Plate, and repeated events of subduction, orogenic uplift and terrane accretion (Pigram and Davies, 1987; Hall, 2002; Baldwin et al., 2012). Whereas some studies time the uplift of the Central New Guinea Highlands to have occurred in the mid-Miocene, ~12 Mya (Quarles van Ufford and Cloos, 2005), others have suggested this uplift to have begun as recently as 5 Mya (Hill and Hall, 2003) or as early as 25 Mya (Pigram and Davies, 1987). This uplift was complemented by docking of numerous accreted terranes, forming several isolated mountain ranges on New Guinea's north coast, as well as the docking of the entire East-Papuan Composite Terrane, forming the Papuan Peninsula with its Owen Stanley Mountain Range.

Our results support a relatively old, mid-Miocene origin of New Guinea's Central Cordillera, with a 11.6 Mya origin of the montane *Papuascincus* skinks on the Fold Belt (Fig. 3), congruent with previous phylogenetic studies suggesting similar dates for the orogenic events (Toussaint et al., 2014; Oliver et al., 2017; Tallowin et al., 2018). The uplift of the central mountain ranges likely drove the radiation of these skinks, with the likely ancestral range of the Central Cordillera occupied by 10 of the GMYC/bGMYC-delimited lineages (A, C-D, and G-L) and five of the BP&P-delimited lineages (I-V). Due to a lack of fossil data for the studied taxa, we used secondary calibrations which may give erroneous divergence time estimates (Schenk, 2016), and the true divergence times may therefore be different than estimated here.

A second radiation of *Papuascincus* then occurred ~7.5 Mya, following dispersal to the East-Papuan Composite Terrane and colonization of the Owen Stanley Mts. These mountains may have arisen during the mid-Miocene (Hill and Hall, 2003), or even earlier during the Oligocene or Eocene, followed by docking with the remainder of New Guinea during the mid-Miocene (Pigram and Davies, 1987), before possibly experiencing renewed uplift and exhumation during the Pliocene (Quarles van Ufford and Cloos, 2005).

Finally, there is GMYC/bGMYC lineage B, the sole representative of the genus on the Huon Peninsula (location 12 in Fig. 2A). The Huon Peninsula is part of the accreted Finisterre Terrane, estimated to have begun colliding with northern New Guinea during the late Miocene (Hill and Raza, 1999; Baldwin et al., 2012) or Pliocene (Weiler and Coe, 2000). The dearth of high-elevation frogs in the Huon Peninsula has been suggested as evidence that the region is isolated from source areas in the Central Highlands (Zweifel, 1980). Zweifel (1980) also suggested that the Huon Peninsula is geologically young due to low rates of endemism. Geological evidence likewise suggests the Huon Peninsula to have only been subaerially connected to New Guinea very recently, during the late Pliocene (Abbott et al., 1994; Abbott, 1995; Hill and Raza, 1999). We recovered the divergence between the Huon lineage and its closest relative (within BP&P lineage I) – GMYC/bGMYC lineage A from Baiyer Gorge – to have occurred ~7.3 Mya, much earlier than the proposed subaerial connection between the Huon Peninsula and New Guinea. However, there is a pronounced gap in our sampling in the eastern Central Highlands (Fig. 1), raising the possibility that the closest lineage to the Huon Peninsula animals wasn't sampled in this study. It is likely that *Papuascincus* colonized the Huon Peninsula from the Central Highlands following the collision and uplift of the mountain ranges, bridging the low-elevation Ramu-Markham Valley between the Finisterre Mts and the Central Cordillera (Fig. 1). While this gap currently represents inhospitable habitat for *Papuascincus*, several studies have suggested depressions of habitat boundaries in the mountains of New Guinea by hundreds of meters during glaciation periods (Hope and Golson, 1995; Porter, 2000). Data on the dispersal capabilities of *Papuascincus* are lacking, and ecological studies of them are sorely needed to fully answer this question.

4.3. Body-size evolution

Papuascincus lineages seem to differentiate based on size, with seemingly two "morphs" – small (SVL ≤ 51 mm) and large (SVL ≥ 52.5 mm). There appears to be a strong phylogenetic signal in SVL, with the "western" clade (GMYC/bGMYC lineages A-H; BP&P lineages I-III) comprised of the small morph, whereas the "eastern" clade (GMYC/bGMYC lineages I-T; BPP lineages IV-IX) is comprised mostly of the large morph, with the exception of the relatively small-sized GMYC/bGMYC lineage L from Mt Strong (BP&P lineage V; mean SVL 48.8 mm). The two size morphs also seem to differ in colour pattern (Fig. 4A), with lizards of the small morph typically having continuous dorsolateral stripes, whereas those belonging to the large morph typically have fragmented dorsolateral stripes (juveniles of the large morph, although similar in SVL to adults of the small morph, also have fragmented dorsolateral stripes; A.S., pers. obs.). The differences in size between lineages from the large and small morphs were almost always significant (Table S5), with the exceptions mostly being in comparisons with lineages C, M and S, all three of which only have a single specimen each.

The spatial distribution of the two lineages may help explain the differences in body size. Whereas most lineages occur in allopatry, a few lineage pairs are sympatric: lineage C is sympatric with lineage K in Keltiga (near Mt Hagen), lineage F is sympatric with lineage J in Rondon Ridge (also near Mt Hagen), and lineage L is sympatric with lineage N on Mt Strong. In all three cases, one lineage in each pair (C, F, and L) is of the small morph, whereas the other lineage (J, K, and N) is

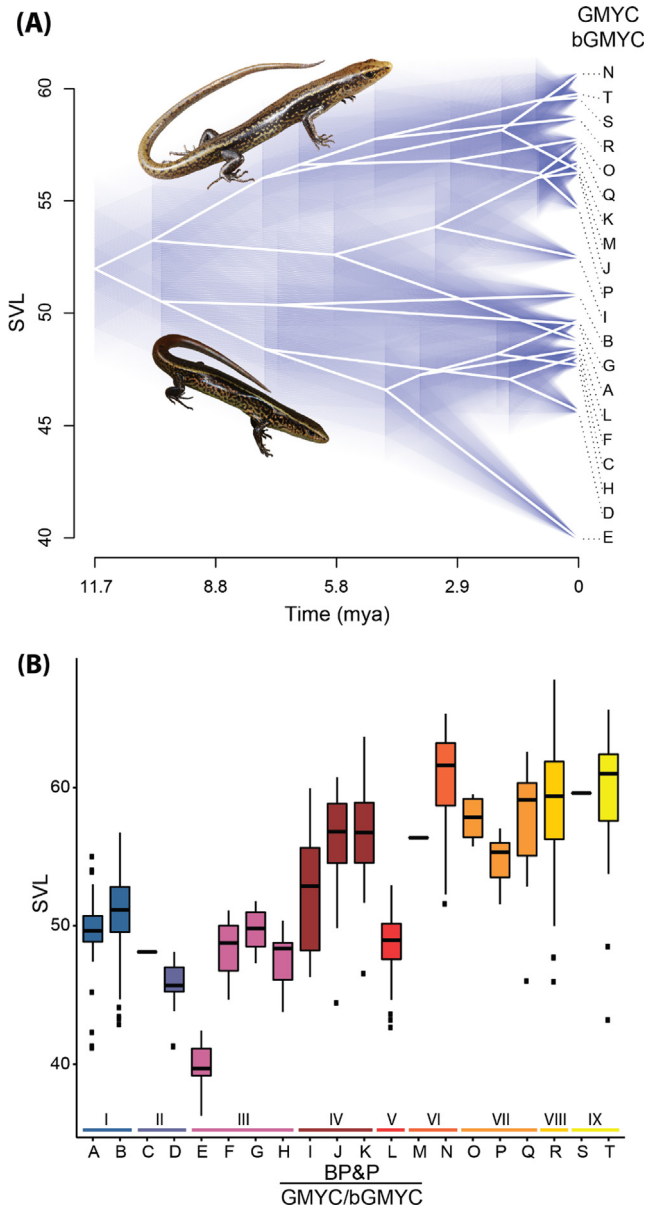


Fig. 4. Body size differentiation within *Papuascincus*. (A) Phenogram showing evolution of SVL along the time-calibrated phylogeny of 20 GMYC/bGMYC delimited lineages of *Papuascincus*, with blue colouration representing 95% confidence intervals. Photos of *Papuascincus* specimens from the 'large' morph (top) and 'small' morph (bottom) courtesy of Allen Allison. (B) Boxplots of SVL for each GMYC/bGMYC delimited lineage. The boxplots are coloured based on BP&P delimited lineages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the large morph. Although under-sampling may result in us missing other cases of sympatry between different lineages, a more conservative interpretation using the wider-ranging BP&P lineages (II and III sympatric with IV in the vicinity of Mt Hagen; V sympatric with VI on Mt Strong) reveals the same general pattern: no two lineages of similar size occur in sympatry. The likelihood to get three cases of sympatry of different morphs by chance from a pool of 20 lineages is only 14%, lending credence to a scenario whereby this distributional pattern was generated by a biological mechanism.

Such a spatial distribution, with no overlap in size between sympatric lineages, can arise by character displacement (Brown and Wilson, 1956; Slatkin, 1980; Dayan and Simberloff, 2005; Grant and Grant, 2006) or through species sorting (Grant, 1972; Davies et al., 2007). Discerning between the two mechanisms from present distributions can be difficult, and they are not mutually exclusive. However, we offer three lines of evidence in support of character displacement. First, BP&P lineage IV is comprised of GMYC/bGMYC lineages I-K. The smallest of the three, lineage I, occurs on high elevations by Mt Hagen and seemingly not in sympatry with any other lineage. However, the two larger lineages J and K occur in sympatry with the small-sized lineages F and C, respectively, both in localities in the vicinity of Mt Hagen. Second, the smallest lineage in our sample, GMYC/bGMYC lineage E (significantly smaller than all other lineages apart from lineage C; Table S5), occurs in sympatry with a large morph on Mt Missim for which we were unable to obtain tissues for molecular analyses (A.A., pers. obs.). Third, lineage B, which occurs on the Huon Peninsula with no congeners, is the largest of the small-sized lineages, even when compared to its sister lineage A (Fig. 4), possibly suggestive of character release allowing lineage B to achieve a comparatively larger size (Simberloff et al., 2000).

Several unanswered questions regarding size evolution in this group remain, with the foremost being why most of the large-sized lineages are distributed in the Papuan Peninsula, seemingly without small-sized congeners occurring in sympatry (Figs. 1 and 2)? What drove the evolution of large size particularly in this clade remains to be examined.

4.4. Taxonomic implications

There are currently four described species in the genus *Papuascincus*: *P. stanleyanus* (the type species), *P. morokanus*, *P. buergersi* and *P. phaeodes* (Allison and Greer, 1986; Uetz et al., 2019). The genus was diagnosed based on a combination of derived traits, including fused frontoparietals, lower eyelid with a clear or semi-translucent window, slightly expanded basal subdigital lamellae, smooth body scales, and pustulate egg-shell surfaces (Allison and Greer, 1986) – traits which all occur in our measured specimens (apart from the poorly sampled GMYC/bGMYC lineages C, G and S, all other lineages had female specimens with oviductal eggs; A.S., pers. obs.). Our analyses, based on broad genetic sampling, recovered *Papuascincus* as a monophyletic genus, congruent with preliminary results from previous phylogenetic studies (Linkem et al., 2011; Rodriguez et al., 2018). However, our phylogenetic reconstruction and estimates of divergence times and genetic distances strongly suggest the existence of currently unrecognized diversity in the genus, with multitudes of lineages potentially meriting recognition as different species.

Papuascincus stanleyanus (Boulenger, 1897) was originally described as *Lygosoma stanleyanum*, based on collections made from Mt Victoria (Fig. 1) in the Owen Stanley Mts by Mr A.S. Anthony (Boulenger, 1897). It is a medium-sized skink (holotype SVL = 57 mm; Boulenger, 1897) that has since been reported from montane regions throughout New Guinea. It has been recorded to occur in high elevations, above 1700 m, but not higher than 3000 m. At those elevations *P. stanleyanus* likely reaches physiological limits on egg development imposed by low temperatures, and it is replaced by ovoviviparous species from other genera (Allison, 1982). Based on SVL and proximity to the type locality, Mt Victoria, we infer three BP&P lineages (VII, VIII and IX) as candidates to represent 'true' *P. stanleyanus*. However, the relatively restricted distributions of these lineages suggest that *P. stanleyanus* is distributed only in the Owen Stanley Mts, with similar-sized animals from other parts of New Guinea, particularly the distantly related Central Highlands lineage IV, representing yet to be described distinct species.

Papuascincus morokanus (Parker, 1936) is a smaller (SVL of the type specimens = 43–47 mm; Parker, 1936) skink. It was described from two specimens collected by Dr L. Loria from Moroka, a locality in the eastern Owen Stanley Mts (Fig. 1). It has since been reported throughout most of the lower montane regions of New Guinea (Parker, 1936; Allison and Greer, 1986), ostensibly being replaced by *P. stanleyanus* above 1700 m (Allison, 1982). Despite many of our sampled lineages having similar SVLs to *P. morokanus*, none of them is from the

vicinity of Moroka, and the type specimens of *P. morokanus* exhibit a unique dorsal colour pattern that is absent from all specimens we examined (two longitudinal dorsal stripes; A.S., pers. obs.). We therefore think it unlikely that we have representatives of this species sampled in this study, and we suspect its true distribution is much narrower than previously believed.

Papuascincus buergersi and *Papuascincus phaeodes* (Vogt, 1932) are two poorly known species collected by Dr J. Bürgers during the 1912–13 Kaiserin-Augusta-Fluss expedition to the Sepik River Basin. The two species were described by Vogt (1932), with no specific locality data given. They are not known from any collections since (Meiri et al., 2018), and little is known of their biology or natural history, apart from *P. buergersi* (52–60 mm; Vogt, 1932) having similar SVL to *P. stanleyanus*, and *P. phaeodes* (45 mm; Vogt, 1932) having similar SVL to *P. morokanus*. The expedition likely reached high elevations typical of *Papuascincus* (Fig. 1) in the Hunstein and Schrader ranges (Sauer, 1915), making those likely candidates for the *terra typica* of either species. The small-sized BP&P lineage II, from the Kaironk Valley (locality 20 in Fig. 2A), is therefore a possible candidate for *P. phaeodes*, but confirmation of this hypothesis will require careful comparison to type material and further research into Bürgers' itinerary to identify the type localities of these two enigmatic species.

Animals that fit the generic description of *Papuascincus* have also been collected in the Indonesian New Guinea mountains of Papua Province (A.A., pers. obs.), and are currently housed in the collections of the Bernice P. Bishop Museum in Honolulu, Hawaii. They are phenotypically similar in SVL and colour morph to members of the large morph (A.S., pers. obs.). Unfortunately, we were unable to obtain tissue samples for molecular analyses for these animals, and so we are unable to assign them to any genetic lineages.

Although our molecular analyses recovered between nine and 20 distinct lineages of *Papuascincus*, the species-delimitation methods we used have been criticized as being sensitive to incomplete geographic sampling and delimiting only genetic structure, and so to be of limited use for assignment of lineages to species (*e.g.*, Olave et al., 2014; Jackson et al., 2017; Sukumaran and Knowles, 2017; Hillis, 2019; Leaché et al., 2019). We therefore avoid making any taxonomic suggestions yet, as a revision of *Papuascincus*, together with descriptions of new species, will require thorough morphological examination and comparisons to type material, work which we are currently undertaking. However, since we suspect there are no available samples for genetic analyses from the *terra typica* of at least three of the four currently recognized species, focused field expeditions to the type localities will be of great value in resolving the taxonomy within this endemic genus.

4.5. Conclusions

We have uncovered considerable genetic diversity in an endemic radiation of New Guinean montane skinks. This further exemplifies the importance of mountains in tropical regions as cradles and generators of biodiversity (Weir, 2006; Elias et al., 2009; Santos et al., 2009; Sedano and Burns, 2010; Hutter et al., 2013; Chazot et al., 2016), and should the different lineages described here be elevated to species status, this would place *Papuascincus* as one of the richest lineages of lizards on the New Guinean mountains.

Despite New Guinea's lizard fauna being most diverse in lowland regions (Tallowin et al., 2017), our results showcase the high-elevation habitats of the island to house unique, endemic radiations, comparable to what is found in other New Guinea taxa such as birds (Mayr and Diamond, 1976; Fritz et al., 2012), amphibians (Oliver et al., 2017), plants (Givnish et al., 2015), and insects (Toussaint et al., 2014). This emphasizes the importance of New Guinea's mountains as unique centres of biodiversity deserving particular conservation attention.

CRediT authorship contribution statement

Alex Slavenko: Conceptualization, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Karin Tamar:** Formal analysis, Investigation, Data curation, Writing - review & editing. **Oliver J.S. Tallowin:** Investigation, Resources, Writing - review & editing. **Allen Allison:** Conceptualization, Investigation, Resources, Writing - review & editing, Funding acquisition. **Fred Kraus:** Investigation, Resources, Writing - review & editing, Funding acquisition. **Salvador Carranza:** Resources, Writing - review & editing, Funding acquisition. **Shai Meiri:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106749.

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