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**Article:**

Slavenko, A. orcid.org/0000-0002-3265-7715, Tamar, K., Tallowin, O.J.S. et al. (4 more authors) (2020) Cryptic diversity and non-adaptive radiation of montane New Guinea skinks (Papuascincus; Scincidae). *Molecular Phylogenetics and Evolution*, 146. 106749. ISSN 1055-7903

<https://doi.org/10.1016/j.ympev.2020.106749>

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

3

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15 **ABSTRACT**

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

35

36 **KEYWORDS:** island diversity; molecular phylogeny; mountains; species-delimitation; tropics

37

38 **HIGHLIGHTS:**

- 39 • *Papuascincus* is a genus of skinks endemic to montane regions of New Guinea  
40 • *Papuascincus* contains up to 20 previously undescribed distinct genetic lineages  
41 • High degrees of cryptic diversity highlight the need for taxonomic revision  
42 • Divergent body sizes of sympatric lineages are suggestive of character displacement

43     **1. INTRODUCTION**

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

53       New Guinea is the world's largest tropical island and is one of the most biologically  
54       diverse regions on Earth, with high levels of vertebrate species richness and endemism  
55       (Allison, 2009). The island's size, topography, geological history, and tropical climate are all  
56       factors thought to contribute to its high level of biodiversity (Allison, 2009), and much of the  
57       island's diversity patterns closely align with elevational gradients across the island's massive  
58       mountain ranges (Diamond, 1973; Allison, 1982; Tallowin *et al.*, 2017). Recent molecular  
59       phylogenetic studies have uncovered extensive cryptic diversity on New Guinea from  
60       various taxa (birds: Marki *et al.*, 2017; fishes: McGuigan *et al.*, 2000; Kadarusman *et al.*,  
61       2012; frogs: Oliver *et al.*, 2013; Oliver *et al.*, 2017; Lepidoptera: Craft *et al.*, 2010; reptiles:  
62       Donnellan & Aplin, 1989; Rawlings & Donnellan, 2003; Metzger *et al.*, 2010; Tallowin *et al.*,  
63       2018).

64       The mountains of New Guinea reach as high as 4884 m above sea level (a.s.l; the  
65       summit of Puncak Jaya in Papua Province, Indonesia) and cover a vast extent of the island,  
66       with over a third of its land area lying above 1000 m (Allison, 2009). The formation of  
67       contemporary New Guinea and its montane topography arose through the progressive  
68       northward movement of the Australian Plate and its collision with the Pacific Plate, along  
69       with extensive island-arc accretion along the plate margin (Hall, 2002; Quarles van Ufford &  
70       Cloos, 2005; Baldwin *et al.*, 2012). Despite controversy regarding the exact timing of  
71       geological events, accretion along the leading edge of Australian Craton is thought to have  
72       begun in the early Miocene (Pigram & Davies, 1987; Hall, 2002; Baldwin *et al.*, 2012),  
73       eventually giving rise to several mountain chains along the northern coast of contemporary

74 New Guinea. Montane uplift of the Central Cordillera that runs along the long (W-E) axis of  
75 the island is thought to have begun much more recently, likely to have arisen no earlier than  
76 the mid-Miocene (Hall, 2002; Hill & Hall, 2003; Quarles van Ufford & Cloos, 2005). The exact  
77 timing of the orogeny of the East-Papuan Composite Terrane – comprising the Papuan  
78 Peninsula in the southeast of New Guinea – is equally contentious, with estimates ranging  
79 from initiation during the Oligocene (Pigram & Davies, 1987; Quarles van Ufford & Cloos,  
80 2005) to more recent orogeny during the mid-Miocene (Hall, 2002; Hill & Hall, 2003).  
81 Irrespective of the exact timing, the uplift of these mountain ranges has evidently  
82 influenced New Guinea's natural diversity, by promoting speciation of lowland taxa through  
83 the formation of barriers to gene flow (Georges *et al.*, 2013; Tallowin *et al.*, 2018; Tallowin  
84 *et al.*, 2019) and through generation of novel, highly dissected montane habitats for  
85 lineages to colonize (Toussaint *et al.*, 2014; Marki *et al.*, 2017; Oliver *et al.*, 2017; Tallowin *et*  
86 *al.*, 2018).

87 The genus *Papuascincus* Allison & Greer, 1986 is endemic to the montane regions of  
88 New Guinea, occurring only at elevations above 1000 m (Allison, 1982; Allison & Greer,  
89 1986; Fig. 1). The genus is thought to be a part of a group of mostly, but not exclusively,  
90 high-elevation skinks that includes *Lipinia*, *Prasinohaema* and *Lobulia* (Greer *et al.*, 2005).  
91 Based on shared derived characteristics Greer (1974) suggested that these four genera are  
92 closely related. This result has recently been corroborated by molecular studies – albeit with  
93 the monophyly of *Lipinia* and *Prasinohaema* not supported (Rodriguez *et al.*, 2018).  
94 *Papuascincus* is unique among the montane skinks of New Guinea in its reproductive mode.  
95 Whereas montane species of *Lobulia* and *Prasinohaema* are ovoviparous, *Papuascincus* is  
96 oviparous, laying a fixed clutch of two eggs (Allison & Greer, 1986). This is unusual for lizards  
97 inhabiting cold, montane habitats (Meiri *et al.*, 2012) and likely creates an upper barrier on  
98 their elevational distribution due to thermoregulatory limitations on egg development  
99 (Allison, 1982).

100 Four species are currently described in *Papuascincus*. Two – *P. stanleyanus* (Boulenger,  
101 1897) and *P. morokanus* (Parker, 1936) – are considered widespread, whereas two (*P.*  
102 *buergeri* and *P. phaeodes*) are only known from their original 1932 descriptions (Vogt,  
103 1932; Meiri *et al.*, 2018). All four species, however, are phenotypically similar in general  
104 colouration and body shape. They mainly differ from each other in body size and in their  
105 elevational distribution, but at least *P. stanleyanus* and *P. morokanus* are otherwise

106 ecologically and morphologically similar (Allison, 1982). The body-size variation, along with  
107 variation in some aspects of colour patterns (e.g., continuous vs. fragmented dorsolateral  
108 stripes) and various scale counts across the range, points towards the existence of  
109 undescribed diversity in the genus.

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

119

## 120 **2. MATERIAL AND METHODS**

### 121 **2.1. Genetic sampling, DNA extraction, amplification, and sequence analysis**

122 We collected 63 tissue samples of *Papuascincus* specimens from across its range in  
123 Papua New Guinea (Fig. 2A; Table S1) and retrieved sequences from GenBank of two  
124 additional specimens (from Linkem *et al.*, 2011). Two tissue samples of *Lipinia pulchra* –  
125 currently estimated as the phylogenetically closest species to *Papuascincus* (Rodriguez *et*  
126 *al.*, 2018) – were used as an outgroup. We used the dataset comprised of *Papuascincus* and  
127 *Lipinia* sequences to understand the genetic structure within *Papuascincus*. To obtain  
128 calibrations for the time-calibrated phylogenetic analyses, we generated another dataset  
129 adding retrieved sequences from GenBank of more-distant relatives, based on previous  
130 studies of Australian skinks: one specimen each of *Lipinia noctua*, *Lerista lineopunctulata*,  
131 *Lerista neander*, *Notoscincus ornatus*, *Scincella lateralis* and *Sphenomorphus solomonis*, and  
132 two specimens each of *Scincella assatus* and *Lipinia pulchella* (Rabosky *et al.*, 2007; Skinner  
133 *et al.*, 2011; Rodriguez *et al.*, 2018). A total of 77 specimens was used for the analyses (Table  
134 S1).

135 We extracted DNA from ethanol-preserved tissue samples using the Qiagen DNeasy  
136 Blood & Tissue Kits (Qiagen, Valencia, CA, USA). We sequenced a total of three

137 mitochondrial markers – the ribosomal 12S rRNA (*12S*), the NADH dehydrogenase subunit 2  
138 (*ND2*) and the NADH dehydrogenase subunit 4 (*ND4*) – and two nuclear markers – RNA  
139 fingerprint protein 35 (*R35*), and the nerve growth factor  $\beta$  polypeptide (*NGFB*). Primers and  
140 PCR conditions used for the amplification and sequencing of all markers are as detailed in  
141 Linkem *et al.* (2011). Chromatographs were assembled and edited using Geneious v.11.0.5  
142 (Biomatter Ltd). For the nuclear markers, we identified heterozygous positions and coded  
143 them according to the standard IUPAC ambiguity codes. We translated protein-coding genes  
144 into amino acids, and we detected no stop codons, suggesting that they were not  
145 pseudogenes. We aligned sequences for each marker using MAFFT v.7.3 (Katoh & Standley,  
146 2013) with default parameters. We tested the occurrence of recombination for the two  
147 phased nuclear-gene alignments using the Pairwise Homoplasy Index (PhiTest; Bruen *et al.*,  
148 2006) implemented in SplitsTree v.4.14.5 (Huson & Bryant, 2006), and we detected no  
149 evidence of recombination ( $P > 0.6$  for the two genes).

150

## 151       **2.2. Phylogenetic analyses**

152       We partitioned our dataset for phylogenetic analyses with PartitionFinder v.2 (Lanfear  
153 *et al.*, 2016), using the following parameters: linked branch lengths; BEAST models; BIC  
154 model selection; “greedy schemes” search algorithm; single partition for *12S* and by codons  
155 for the protein-coding genes *ND2*, *ND4*, *R35*, and *NGFB*. For the dataset of *Papuascincus* and  
156 *Lipinia*, we performed phylogenetic analyses under Maximum Likelihood (ML) and Bayesian  
157 Inference (BI) frameworks. We analysed the complete, mitochondrial, and nuclear  
158 concatenated datasets separately with the following partitions and relevant substitution  
159 models: *12S+ND2\_1+ND4\_1* (HKY+I+G), *ND2\_2+ND4\_2* (HKY+I+G), *ND2\_3+ND4\_3* (TRN+G),  
160 *NGFB\_1+NGFB\_2+NGFB\_3+R35\_1+R35\_2* (K80+I), *R35\_3* (HKY+I). We conducted ML  
161 analyses in RAxML v.8.1.2, as implemented in raxmlGUI v.1.5 (Silvestro & Michalak, 2012),  
162 with the GTRGAMMA model of sequence evolution and 100 random-addition replicates. We  
163 assessed nodal support with 1000 bootstrap replicates. We conducted BI analyses with  
164 MrBayes v.3.2.6 (Ronquist *et al.*, 2012). Nucleotide substitution model parameters were  
165 unlinked across partitions, and we allowed the different partitions to evolve at different  
166 rates. We performed two simultaneous parallel runs with four chains per run (three heated,  
167 one cold) for  $10^7$  generations, sampling every 1000 generations for the complete  
168 concatenated dataset, and for  $3 \times 10^6$  generations with a sampling frequency of every 3000

169 generations for the mitochondrial and nuclear concatenated datasets. We examined the  
170 standard deviation of the split frequencies between the two runs and the Potential Scale  
171 Reduction Factor (PSRF) diagnostic, and we assessed convergence by confirming that all  
172 parameters had reached stationarity and had sufficient effective sample sizes (> 200) using  
173 Tracer v.1.6 (Rambaut *et al.*, 2014). We discarded the first 25% of trees as burn-in. We  
174 considered nodes well-supported if they received ML bootstrap values  $\geq$  80% and posterior  
175 probability (pp) support values  $\geq$  0.95.

176 With the aim of exploring patterns of intra-specific diversity and nuclear allele sharing  
177 within *Papuascincus*, we inferred statistical parsimony networks on the two individual  
178 nuclear genes with the program TCS v.1.21 (Clement *et al.*, 2000) implemented in PopART  
179 (Leigh & Bryant, 2015) using default settings (connection limit of 95%) and including only full  
180 length sequences. To infer haplotypes, we used the on-line web tool SeqPHASE (Flot, 2010)  
181 to convert the input and output files, and we used the software PHASE v.2.1.1 (Stephens *et*  
182 *al.*, 2001; Stephens & Scheet, 2005) to resolve heterozygous single-nucleotide  
183 polymorphisms in the phased alignments, with a probability threshold of 0.7 for *NGFB* and  
184 0.5 for *R35*.

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

189

### 190 **2.3. Species-delimitation analyses**

191 We delimited distinct lineages within *Papuascincus* using two datasets: mitochondrial  
192 and nuclear. At the first stage we evaluated mitochondrial divergence using the ML and BI  
193 functions of the Generalized Mixed Yule-Coalescent analysis (GMYC and bGMYC,  
194 respectively; Pons *et al.*, 2006; Reid & Carstens, 2012) implemented in R v.3.4.2 (R Core  
195 Team, 2017). For these analyses we inferred a concatenated ultrametric mitochondrial  
196 haplotype tree using BEAST v.1.8.4 (Drummond *et al.*, 2012) with the following priors  
197 (otherwise by default): partitions and models as selected by PartitionFinder,  
198 12S+ND2\_1+ND4\_1 (HKY+I+G), ND2\_2+ND4\_2 (HKY+I), ND2\_3+ND4\_3 (TRN+G); Yule  
199 process tree model; random starting tree; alpha prior uniform (0–10), strict clock prior  
200 (uniform distribution; mean 1, 0–1). We carried out three individual runs of  $10^7$  generations,

201 sampling at intervals of 1000 generations. We evaluated convergence, posterior trace plots,  
202 effective sample sizes (ESS > 200), and burn-in in Tracer v.1.6 (Rambaut *et al.*, 2014). We  
203 combined the tree runs in LogCombiner, discarded the first 10% of trees as burn-in, and  
204 generated an ultrametric tree with TreeAnnotator (both provided with the BEAST package).  
205 For the GMYC analysis we used the *splits* R package (Ezard *et al.*, 2009), applying a single  
206 threshold algorithm. For the bGMYC analysis we used the *bGMYC* R package (Reid &  
207 Carstens, 2012) to calculate marginal posterior probabilities of lineage limits from a  
208 subsample of 250 trees; we ran MCMC chains for each tree for  $10^4$  generations with 10%  
209 burn-in.

210 As a second step of species delimitation, we evaluated nuclear divergence and tested  
211 the mitochondrial GMYC/bGMYC candidate species with Bayesian Phylogenetics and  
212 Phylogeography v.3.4 (BP&P; Rannala & Yang, 2003; Yang & Rannala, 2010) using the full  
213 phased nuclear loci only. As prior distributions on the ancestral population size ( $\theta$ ) and root  
214 age ( $\tau$ ) can affect the posterior probabilities for models (Yang & Rannala, 2010; Zhang *et al.*,  
215 2011), we performed a preliminary analysis estimating the two parameters under the MSC  
216 model with a given species phylogeny (A00 configuration, with the topology obtained using  
217 the concatenated dataset; Rannala & Yang, 2003). We parameterized these priors through  
218 Inverse Gamma distributions setting  $\alpha=3$  and two values of  $\beta$  (0.002, 0.2) that cover  
219 different alternative scenarios for ancestral population size and root age. The suggested  
220 values were (Inv-Gamma( $\alpha, \beta$ )):  $\theta = \text{Inv-Gamma}(2, 0.2)$  and  $\tau = \text{Inv-Gamma}(2, 0.01)$ , with  
221 which we carried out two types of analyses, setting the initial number of lineages to 20  
222 (recovered from the GMYC/bGMYC analysis, see Results): (i) A10 configuration – conducting  
223 Bayesian species delimitation analysis using a user-specified guide tree (with the topology  
224 obtained using the concatenated dataset; Yang & Rannala, 2010; Rannala & Yang, 2013),  
225 and (ii) A11 configuration – implementing a joint analysis conducting Bayesian species-  
226 delimitation while estimating the species tree (Yang & Rannala, 2014; Yang, 2015). For these  
227 analyses we used algorithms 1 and 0, assigning each species-delimitation model equal prior  
228 probability. We estimated the locus rate parameter that allows variable mutation rates  
229 among loci with a Dirichlet prior ( $\alpha = 2$ ). We set the heredity parameter that allows  $\theta$  to vary  
230 among loci as default, due to our dataset being autosomal. Each rjMCMC analysis ran for  
231  $5 \times 10^5$  generations with 10% discarded as burn-in. We considered probability values  $\geq 0.95$  in

232 all the different alternative scenarios for ancestral population size and root age as strong  
233 evidence for delimited lineages.

234

235 **2.4. Estimation of divergence times and biogeographic analyses**

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

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

262 We conducted the calibration and the two biogeographical analyses in BEAST v.1.8.4  
263 with the following partitions and relevant models as determined by PartitionFinder:

264 12S+ND2\_1+ND4\_1 (GTR+I+G), ND2\_2+ND4\_2 (GTR+I+G), ND2\_3+ND4\_3 (TRN+G),  
265 NGFB\_1+NGFB\_2+NGFB\_3+R35\_1+R35\_2 (K80+G), R35\_3 (HKY+G). Other priors were as  
266 detailed above, apart from base-substitution parameter (0–100), and uncorrelated relaxed-  
267 clock model for the mitochondrial genes (uniform distribution; 0–1). For the ancestral-area  
268 reconstruction analyses additional priors were: symmetric discrete-trait substitution model,  
269 strict-clock model for the location trait, and exponential prior for the discrete-location state  
270 rate (`locations.clock.rate`) with mean of 1.0 and offset of 0. We conducted three individual  
271 runs of  $10^8$  generations for each of the three analyses, with sampling at intervals of every  
272  $10^4$  generations. We evaluated convergence, posterior trace plots, effective sample sizes  
273 (ESS > 200), and burn-in with Tracer. We combined the tree runs in LogCombiner, discarding  
274 the first 10% as burn-in, and generated an ultrametric tree with TreeAnnotator.

275

276 **2.5. Body-size evolution**

277 We used the time-calibrated phylogenetic tree constructed in Section 2.4 to map adult  
278 body size onto the phylogeny. We used digital calipers to measure snout-vent-lengths (SVLs)  
279 to the nearest 0.1 mm of 533 adult specimens representing the various lineages, including  
280 62 specimens vouchered with tissues (Table S2). We assigned the specimens that were not  
281 sampled genetically to the different delimited lineages based on sampling localities and  
282 dates and general morphological similarity in colour patterns and size. Thus, specimens that  
283 were collected from the same population, and during the same collecting expedition as  
284 voucher specimens that were sampled genetically, were assigned to the same lineage of  
285 similar-sized genetic vouchers with a similar colour pattern. We excluded juveniles and  
286 subadults – as determined based on dissection and visual examination of gonads – from this  
287 analysis. We then calculated the mean SVL for each GMYC/bGMYC and BP&P-delimited  
288 lineage. We mapped the mean SVL onto the tips of the time-calibrated phylogeny and used  
289 the *fancyTree* and *phenogram* functions in the *phytools* package (Revell, 2012),  
290 implemented in R v.3.4.2 (R Core Team, 2017), to visualize body-size evolution along the  
291 phylogeny. We compared SVLs between the different GMYC/bGMYC-delimited lineages  
292 using ANOVA with *post-hoc* Tukey tests, and we generated boxplots to visualize differences  
293 in SVL between lineages.

294

295 **3. RESULTS**

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

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

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

319 Genetic distances among the nine BP&P-delimited lineages were greater than the  
320 genetic distances within the lineages for all three mitochondrial gene fragments (Table S3).  
321 The lowest genetic divergence among lineages in the *ND2* and *ND4* markers was found  
322 between BP&P lineages VIII and IX (*12S*: 3.2%; *ND2*: 9.4%; *ND4*: 9.7%), whereas in the *12S*  
323 marker, the distance between BP&P lineages VI and VIII was the lowest (*12S*: 3%; *ND2*:  
324 12.8%; *ND4*: 12.5%). Similarly, genetic distances between the 20 GMYC/bGMYC-delimited  
325 lineages (Table S4) were mostly greater than the genetic distances within lineages, although

326 the between-lineage distances of some lineage pairs were much lower than the average  
327 between-lineage distances and even comparable to some within-lineage distances (e.g., in  
328 the *12S* marker the distance between GMYC/bGMYC lineages S and T was 0.3%).

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

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

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

355 Our BSSVS reconstruction of *Papuascincus* according to elevational regions indicates  
356 that the ancestral population of the genus had, with a high probability, a higher montane  
357 elevational distribution (1500-2500 m in today's biome elevations – although the exact

358 elevations that make up the same climatic conditions might well have been different in  
359 earlier geological periods; Fig. 3B). Based on this analysis, at least three independent  
360 transitions occurred from higher montane to lower montane (1000-1500 m) elevational  
361 distributions – by GMYC/bGMYC lineages E, M and T – and at least one transition each to  
362 subalpine (2500-3000 m) and alpine (> 3000 m) elevational distributions, by lineages I and S,  
363 respectively.

364 Adult SVLs of *Papuascincus* varied between 36.3 mm and 67.8 mm (Table S2; Figs. 4 &  
365 S6). The subclade containing GMYC/bGMYC lineages A-H is comprised of mostly small-sized  
366 lineages, with mean SVLs of 50.8 mm or less (the "small" morph). The subclade containing  
367 GMYC/bGMYC lineages I-T was comprised of mostly large-sized lineages, with mean SVLs of  
368 52.5 mm or higher (the "large" morph), except GMYC/bGMYC lineage L (mean SVL 48.8  
369 mm). Almost all lineages from the "large" morph were significantly larger than almost all  
370 lineages from the "small" morph (exceptions were almost all in cases where sample sizes  
371 were exceedingly small; Table S5).

372

## 373 **4. DISCUSSION**

### 374 **4.1. Cryptic diversity and evolutionary history**

375 Our study provides the first large-scale time-calibrated phylogenetic analyses of the  
376 genus *Papuascincus*, currently endemic to montane regions in New Guinea. Our results  
377 confirm that *Papuascincus* is a valid, monophyletic genus, as previously considered based on  
378 its unique synapomorphy: pustulate surface structures on the egg shells (Allison & Greer,  
379 1986). This corroborates previous preliminary results based on two samples each in the  
380 molecular studies of Linkem *et al.* (2011) and Rodriguez *et al.* (2018).

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

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

404

#### 405       **4.2. Biogeographic history**

406       The precise timing of the uplift of New Guinea's Central Cordillera is still debated. The  
407 formation of these mountains, spanning New Guinea's W-E axis, resulted from a complex  
408 geological history involving the northern movement of the Australian Plate margin and  
409 collision with the Pacific Plate, and repeated events of subduction, orogenic uplift and  
410 terrane accretion (Pigram & Davies, 1987; Hall, 2002; Baldwin *et al.*, 2012). Whereas some  
411 studies time the uplift of the Central New Guinea Highlands to have occurred in the mid-  
412 Miocene, ~12 Mya (Quarles van Ufford & Cloos, 2005), others have suggested this uplift to  
413 have begun as recently as 5 Mya (Hill & Hall, 2003) or as early as 25 Mya (Pigram & Davies,  
414 1987). This uplift was complemented by docking of numerous accreted terranes, forming  
415 several isolated mountain ranges on New Guinea's north coast, as well as the docking of the  
416 entire East-Papuan Composite Terrane, forming the Papuan Peninsula with its Owen Stanley  
417 Mountain Range.

418       Our results support a relatively old, mid-Miocene origin of New Guinea's Central  
419 Cordillera, with a 11.6 Mya origin of the montane *Papuascincus* skinks on the Fold Belt (Fig.  
420 3), congruent with previous phylogenetic studies suggesting similar dates for the orogenic

421 events (Toussaint *et al.*, 2014; Oliver *et al.*, 2017; Tallowin *et al.*, 2018). The uplift of the  
422 central mountain ranges likely drove the radiation of these skinks, with the likely ancestral  
423 range of the Central Cordillera occupied by 10 of the GMYC/bGMYC-delimited lineages (A,  
424 C-D, and G-L) and five of the BP&P-delimited lineages (I-V). Due to a lack of fossil data for  
425 the studied taxa, we used secondary calibrations which may give erroneous divergence time  
426 estimates (Schenk, 2016), and the true divergence times may therefore be different than  
427 estimated here.

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

434 Finally, there is GMYC/bGMYC lineage B, the sole representative of the genus on the  
435 Huon Peninsula (location 12 in Fig. 2A). The Huon Peninsula is part of the accreted Finisterre  
436 Terrane, estimated to have begun colliding with northern New Guinea during the late  
437 Miocene (Hill & Raza, 1999; Baldwin *et al.*, 2012) or Pliocene (Weiler & Coe, 2000). The  
438 dearth of high-elevation frogs in the Huon Peninsula has been suggested as evidence that  
439 the region is isolated from source areas in the Central Highlands (Zwiefel, 1980). Zwiefel  
440 (1980) also suggested that the Huon Peninsula is geologically young due to low rates of  
441 endemism. Geological evidence likewise suggests the Huon Peninsula to have only been  
442 subaerially connected to New Guinea very recently, during the late Pliocene (Abbott *et al.*,  
443 1994; Abbott, 1995; Hill & Raza, 1999). We recovered the divergence between the Huon  
444 lineage and its closest relative (within BP&P lineage I) – GMYC/bGMYC lineage A from Baiyer  
445 Gorge – to have occurred ~7.3 Mya, much earlier than the proposed subaerial connection  
446 between the Huon Peninsula and New Guinea. However, there is a pronounced gap in our  
447 sampling in the eastern Central Highlands (Fig. 1), raising the possibility that the closest  
448 lineage to the Huon Peninsula animals wasn't sampled in this study. It is likely that  
449 *Papuascincus* colonized the Huon Peninsula from the Central Highlands following the  
450 collision and uplift of the mountain ranges, bridging the low-elevation Ramu-Markham  
451 Valley between the Finisterre Mts and the Central Cordillera (Fig. 1). While this gap  
452 currently represents inhospitable habitat for *Papuascincus*, several studies have suggested

453 depressions of habitat boundaries in the mountains of New Guinea by hundreds of meters  
454 during glaciation periods (Hope & Golson, 1995; Porter, 2000). Data on the dispersal  
455 capabilities of *Papuascincus* are lacking, and ecological studies of them are sorely needed to  
456 fully answer this question.

457

#### 458       **4.3.       Body-size evolution**

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

473       The spatial distribution of the two lineages may help explain the differences in body  
474 size. Whereas most lineages occur in allopatry, a few lineage pairs are sympatric: lineage C is  
475 sympatric with lineage K in Keltiga (near Mt Hagen), lineage F is sympatric with lineage J in  
476 Rondon Ridge (also near Mt Hagen), and lineage L is sympatric with lineage N on Mt Strong.  
477 In all three cases, one lineage in each pair (C, F, and L) is of the small morph, whereas the  
478 other lineage (J, K, and N) is of the large morph. Although under-sampling may result in us  
479 missing other cases of sympatry between different lineages, a more conservative  
480 interpretation using the wider-ranging BP&P lineages (II and III sympatric with IV in the  
481 vicinity of Mt Hagen; V sympatric with VI on Mt Strong) reveals the same general pattern:  
482 no two lineages of similar size occur in sympatry. The likelihood to get three cases of  
483 sympatry of different morphs by chance from a pool of 20 lineages is only 14%, lending

484 credence to a scenario whereby this distributional pattern was generated by a biological  
485 mechanism.

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

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

506

#### 507 **4.4. Taxonomic implications**

508 There are currently four described species in the genus *Papuascincus*: *P. stanleyanus*  
509 (the type species), *P. morokanus*, *P. buergersi* and *P. phaeodes* (Allison & Greer, 1986; Uetz  
510 *et al.*, 2019). The genus was diagnosed based on a combination of derived traits, including  
511 fused frontoparietals, lower eyelid with a clear or semi-translucent window, slightly  
512 expanded basal subdigital lamellae, smooth body scales, and pustulate egg-shell surfaces  
513 (Allison & Greer, 1986) – traits which all occur in our measured specimens (apart from the  
514 poorly sampled GMYC/bGMYC lineages C, G and S, all other lineages had female specimens  
515 with oviductal eggs; A.S., pers. obs.). Our analyses, based on broad genetic sampling,

516 recovered *Papuascincus* as a monophyletic genus, congruent with preliminary results from  
517 previous phylogenetic studies (Linkem *et al.*, 2011; Rodriguez *et al.*, 2018). However, our  
518 phylogenetic reconstruction and estimates of divergence times and genetic distances  
519 strongly suggest the existence of currently unrecognized diversity in the genus, with  
520 multitudes of lineages potentially meriting recognition as different species.

521       *Papuascincus stanleyanus* (Boulenger, 1897) was originally described as *Lygosoma*  
522 *stanleyanum*, based on collections made from Mt Victoria (Fig. 1) in the Owen Stanley Mts  
523 by Mr A.S. Anthony (Boulenger, 1897). It is a medium-sized skink (holotype SVL = 57 mm;  
524 Boulenger, 1897) that has since been reported from montane regions throughout New  
525 Guinea. It has been recorded to occur in high elevations, above 1700 m, but not higher than  
526 3000 m. At those elevations *P. stanleyanus* likely reaches physiological limits on egg  
527 development imposed by low temperatures, and it is replaced by ovoviparous species  
528 from other genera (Allison, 1982). Based on SVL and proximity to the type locality, Mt  
529 Victoria, we infer three BP&P lineages (VII, VIII and IX) as candidates to represent 'true' *P.*  
530 *stanleyanus*. However, the relatively restricted distributions of these lineages suggest that *P.*  
531 *stanleyanus* is distributed only in the Owen Stanley Mts, with similar-sized animals from  
532 other parts of New Guinea, particularly the distantly related Central Highlands lineage IV,  
533 representing yet to be described distinct species.

534       *Papuascincus morokanus* (Parker, 1936) is a smaller (SVL of the type specimens = 43-47  
535 mm; Parker, 1936) skink. It was described from two specimens collected by Dr L. Loria from  
536 Moroka, a locality in the eastern Owen Stanley Mts (Fig. 1). It has since been reported  
537 throughout most of the lower montane regions of New Guinea (Parker, 1936; Allison &  
538 Greer, 1986), ostensibly being replaced by *P. stanleyanus* above 1700 m (Allison, 1982).  
539 Despite many of our sampled lineages having similar SVLs to *P. morokanus*, none of them is  
540 from the vicinity of Moroka, and the type specimens of *P. morokanus* exhibit a unique  
541 dorsal colour pattern that is absent from all specimens we examined (two longitudinal  
542 dorsal stripes; A.S., pers. obs.). We therefore think it unlikely that we have representatives  
543 of this species sampled in this study, and we suspect its true distribution is much narrower  
544 than previously believed.

545       *Papuascincus buergersi* and *Papuascincus phaeodes* (Vogt, 1932) are two poorly known  
546 species collected by Dr J. Bürgers during the 1912-13 Kaiserin-Augusta-Fluss expedition to  
547 the Sepik River Basin. The two species were described by Vogt (1932), with no specific

548 locality data given. They are not known from any collections since (Meiri *et al.*, 2018), and  
549 little is known of their biology or natural history, apart from *P. buergeri* (52–60 mm; Vogt  
550 1932) having similar SVL to *P. stanleyanus*, and *P. phaeodes* (45 mm; Vogt 1932) having  
551 similar SVL to *P. morokanus*. The expedition likely reached high elevations typical of  
552 *Papuascincus* (Fig. 1) in the Hunstein and Schrader ranges (Sauer, 1915), making those likely  
553 candidates for the *terra typica* of either species. The small-sized BP&P lineage II, from the  
554 Kaironk Valley (locality 20 in Fig. 2A), is therefore a possible candidate for *P. phaeodes*, but  
555 confirmation of this hypothesis will require careful comparison to type material and further  
556 research into Bürgers' itinerary to identify the type localities of these two enigmatic species.

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

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

574

#### 575 **4.5. Conclusions**

576 We have uncovered considerable genetic diversity in an endemic radiation of New  
577 Guinean montane skinks. This further exemplifies the importance of mountains in tropical  
578 regions as cradles and generators of biodiversity (Weir, 2006; Elias *et al.*, 2009; Santos *et al.*,  
579 2009; Sedano & Burns, 2010; Hutter *et al.*, 2013; Chazot *et al.*, 2016), and should the

580 different lineages described here be elevated to species status, this would place  
581 *Papuascincus* as one of the richest lineages of lizards on the New Guinean mountains.

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

589

## 590 **ACKNOWLEDGEMENTS**

591 We thank Molly Hagemann (Bernice P. Bishop Museum), Lauren Scheinberg (California  
592 Academy of Sciences), Steve Donellan and Alejandro Velasco Castrillon (South Australian  
593 Museum), and Erez Maza (Steinhardt Museum of Natural History), for facilitating generous  
594 loans of tissue samples and voucher specimens used in this study. This work was supported  
595 by BSF grants no. 2012143 to S.M. and A.A., NSF grants no. DEB-0103794 and 0743890 to  
596 F.K., and by the Naomi Foundation through the Tel Aviv University GRTF programme grant  
597 no. 064181317 to A.S. K.T. and S.C. were supported by grants CGL2015-70390-P and  
598 PGC2018-098290-B-I00 (co-funded by FEDER) from the Spanish government. Fieldwork in  
599 Papua New Guinea and research permits were approved by the respective provincial  
600 governments, PNG National Research Institute, and the PNG Conservation and Environment  
601 Protection Authority. Finally, and most importantly, this work could not have been done  
602 without the generous assistance of many local communities in Papua New Guinea. We  
603 extend our deepest gratitude to the numerous landowners and field assistants who  
604 provided us with access to their lands and aided us in collections in the field.

605

606 **FIGURE LEGENDS**

607

608 **Figure 1.** Map of New Guinea showing the distribution of samples analysed herein and the  
609 type localities of recognized species of *Papuascincus*. The blue polygon includes all areas  
610 encompassing the elevational range of samples in this study (1190-3282 m), representing  
611 potential distribution for *Papuascincus*. Black dots denote sampled localities in this study.  
612 The red star denotes the type locality of *Papuascincus stanleyanus* (Mt. Victoria), the yellow  
613 star denotes the type locality of *Papuascincus morokanus* (Moroka), and the green dashed  
614 line follows the path of the Sepik River, the type locality for *Papuascincus buergeri* and *P.  
615 phaeodes*.

616

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

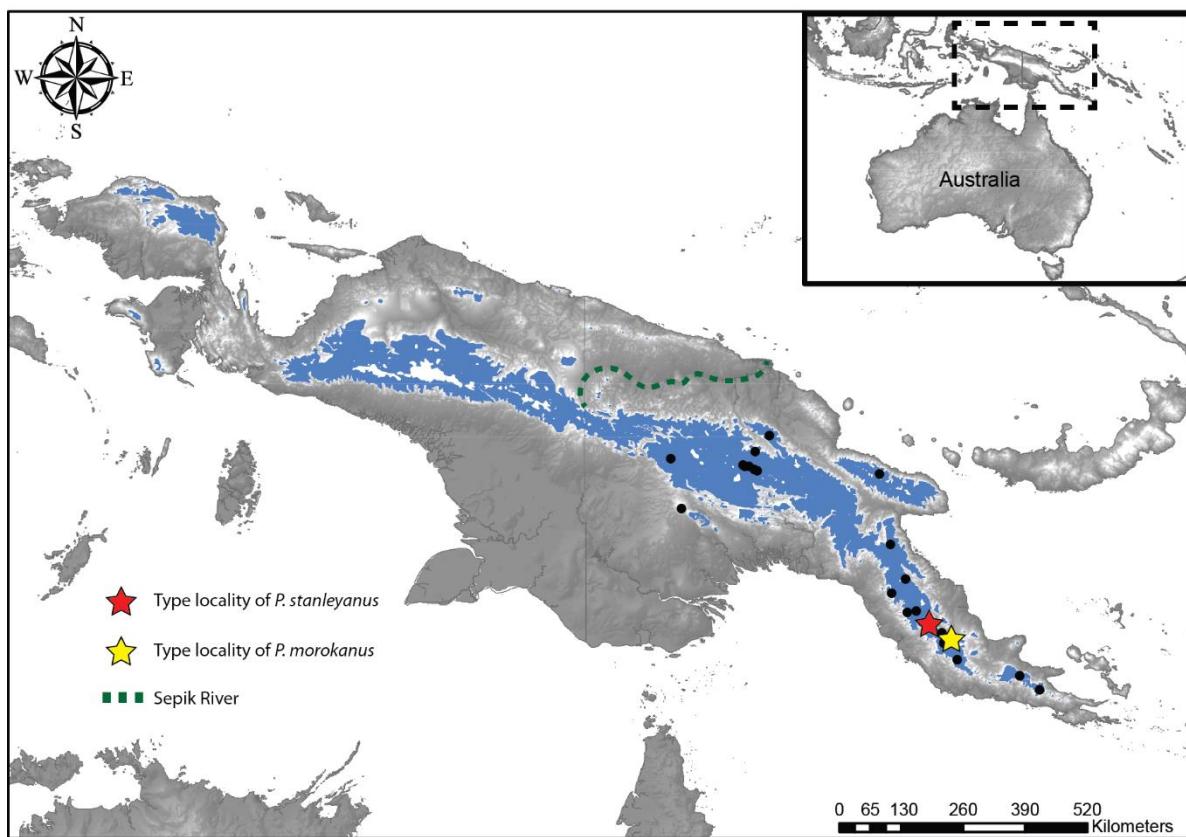
630

631 **Figure 3.** Time-calibrated phylogenetic trees and the ancestral biogeographical  
632 reconstruction analyses of *Papuascincus*. The analyses were based on the reduced  
633 concatenated dataset, containing a single sample per GMYC/bGMYC lineage, and an  
634 additional sample for lineage T (with a different elevational distribution). Branch colours  
635 and pie charts near the major nodes describe the probability of each inferred character  
636 state. (A) Reconstruction according to geological regions: blue (Australian Craton), purple  
637 (Fold Belt), green (Oceanic Arc Terranes), and yellow (East-Papuan Composite Terrane).  
638 Mean age estimates are provided above the nodes with horizontal bars representing the  
639 95% highest posterior densities. (B) Reconstruction according to elevational distribution:  
640 brown (lower montane, 1000-1500 m), red (higher montane, 1500-2500 m), dark blue  
641 (subalpine, 2500-3000 m), and light blue (apine, > 3000m). Posterior probability values are  
642 indicated above the nodes.

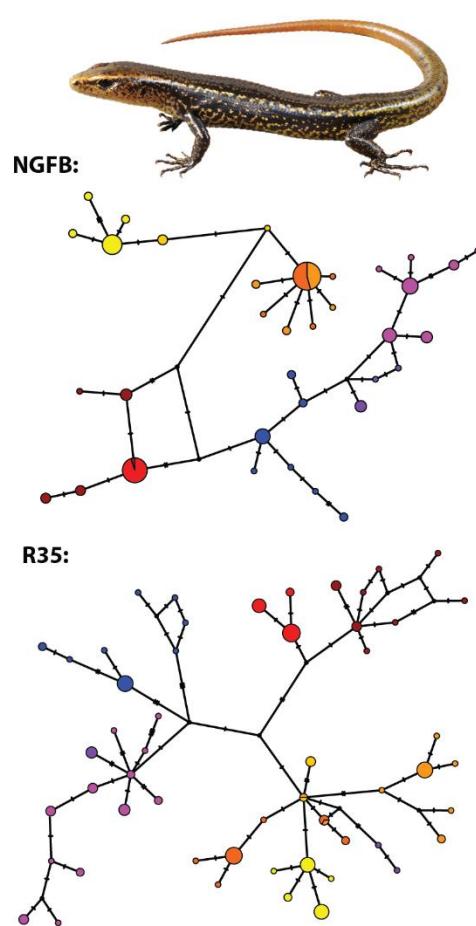
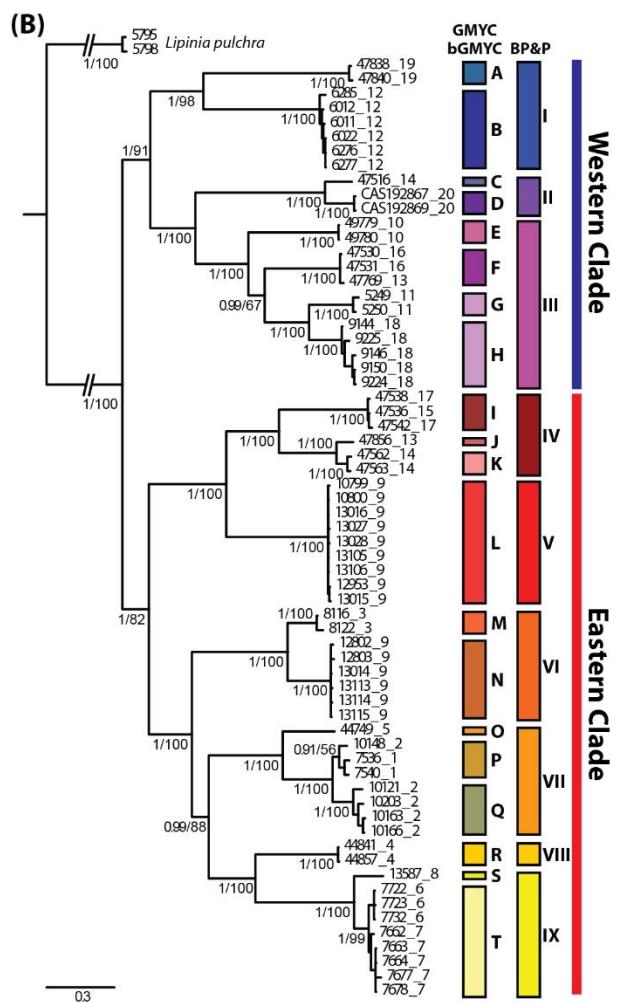
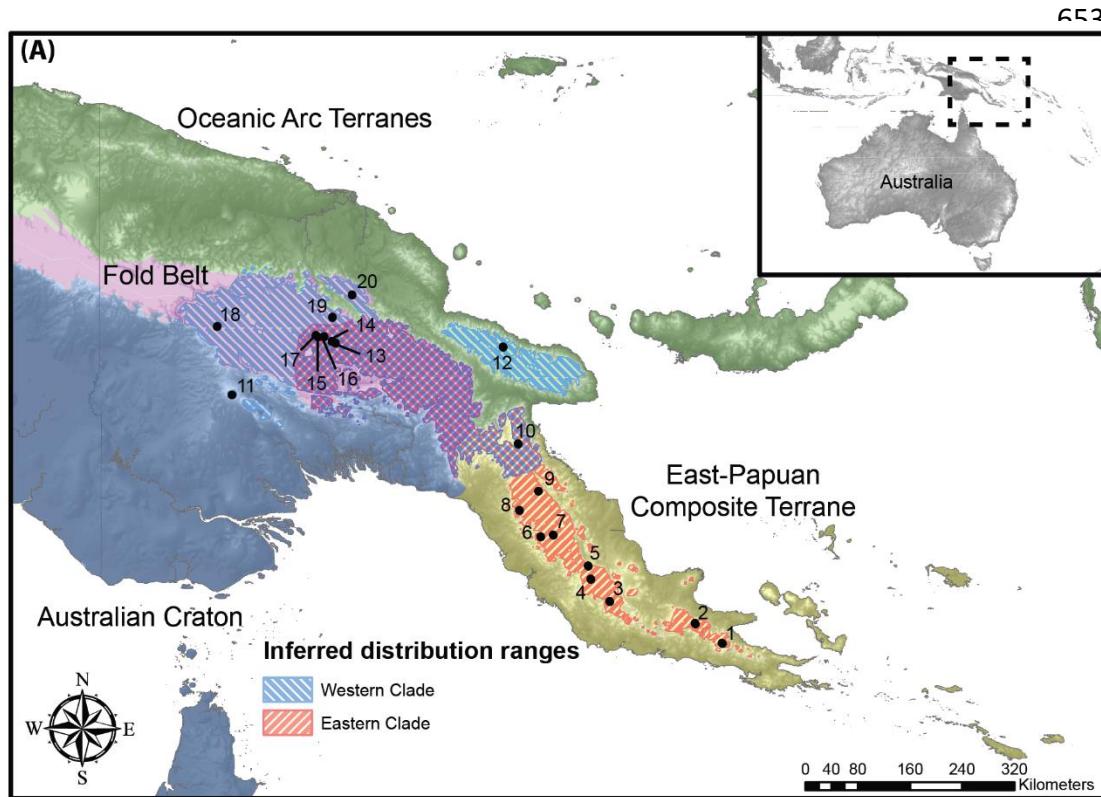
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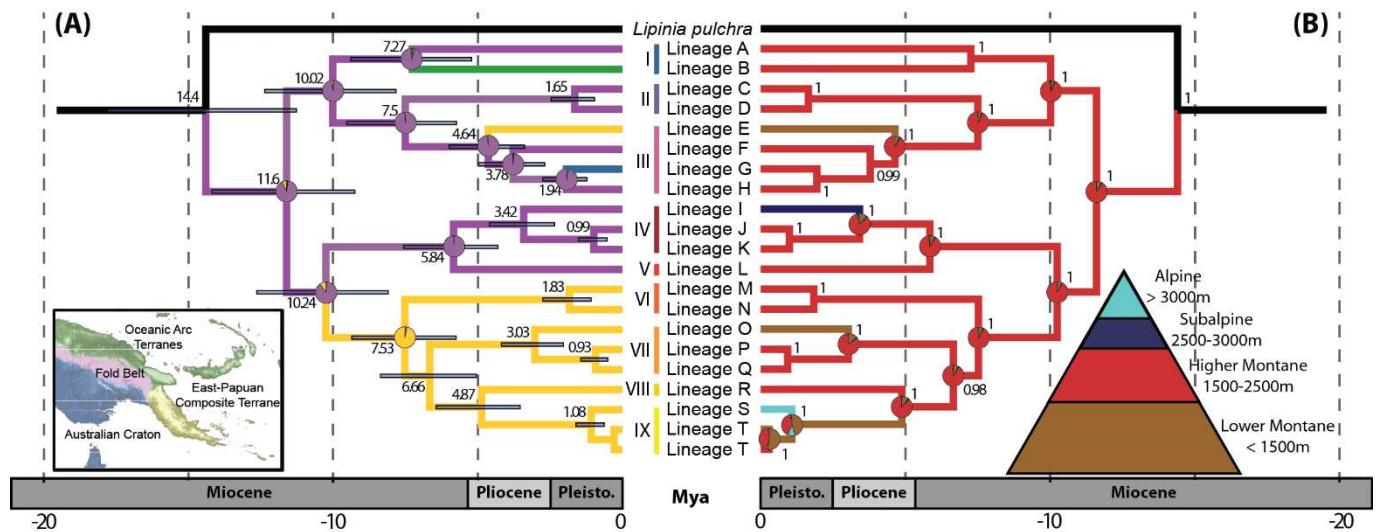
644 **Figure 4.** Body size differentiation within *Papuascincus*. (A) Phenogram showing evolution of  
645 SVL along the time-calibrated phylogeny of 20 GMYC/bGMYC delimited lineages of  
646 *Papuascincus*, with blue colouration representing 95% confidence interval. Photos of  
647 *Papuascincus* specimens from the ‘large’ morph (top) and ‘small’ morph (bottom) courtesy  
648 of Allen Allison. (B) Boxplots of SVL for each GMYC/bGMYC delimited lineage. The boxplots  
649 are coloured based on BP&P delimited lineages.

650 **Figure 1.**



651

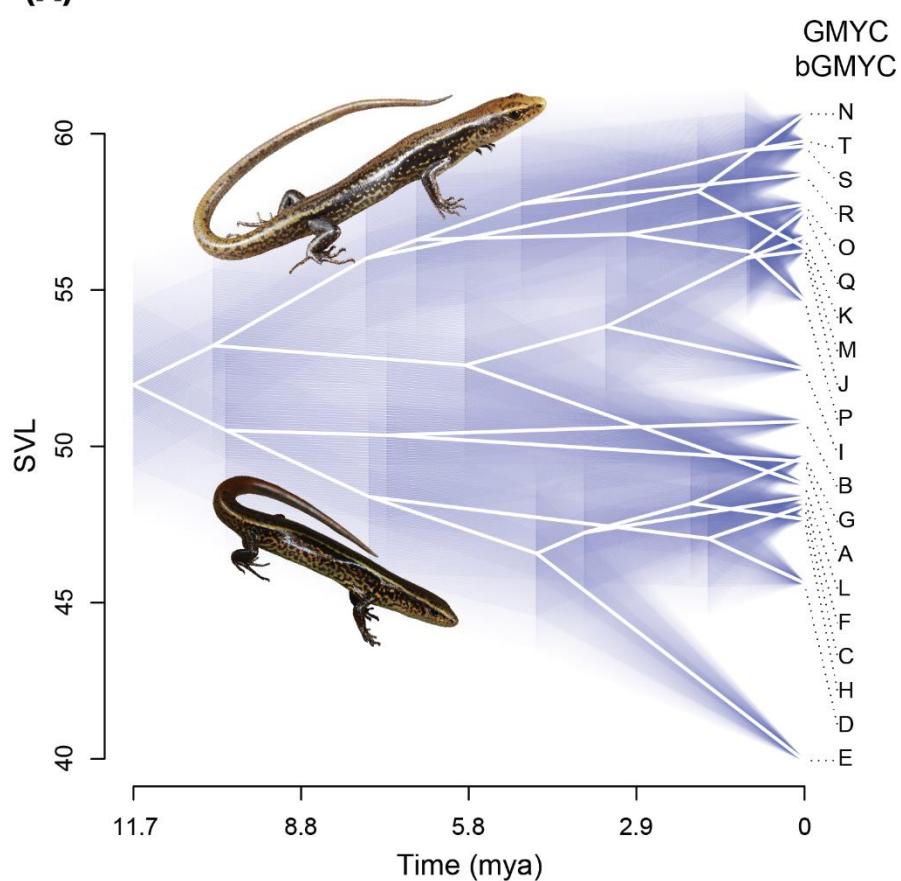
**Figure 2.**

**Figure 3.**

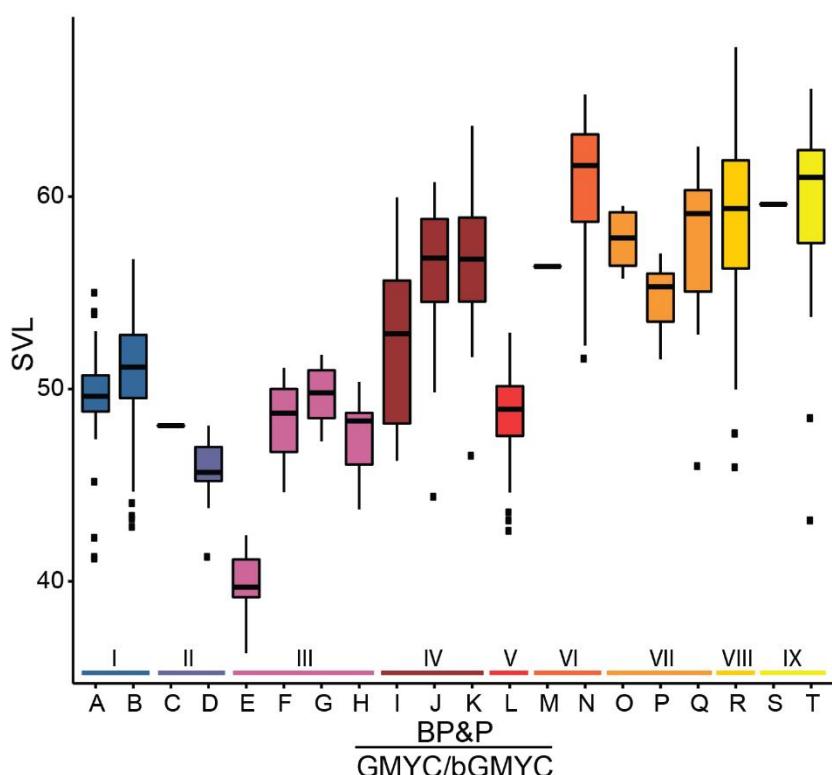
656  
657

**Figure 4.**

**(A)**



**(B)**



658 **SUPPLEMENTARY FILES**

659

660 **Figure S1.** Maximum-likelihood phylogenetic tree based on the concatenated dataset of  
661 three mitochondrial and two nuclear markers, with BI posterior probabilities and ML  
662 bootstrap support values shown at each node, respectively. On each label, the number  
663 following the underscore corresponds to a locality in the map in Fig. 1A. Next to the tree are  
664 lineages as delimited by species delimitation methods: GMYC/bGMYC and BP&P.

665

666 **Figure S2.** Bayesian-inference phylogenetic trees based on the (A) concatenated  
667 mitochondrial dataset, and (B) concatenated nuclear dataset. BI posterior probabilities and  
668 ML bootstrap support values shown at each node, respectively. On each label, the number  
669 following the underscore corresponds to a locality in the map in Fig. 1A. Next to the trees  
670 are lineages as delimited by species delimitation methods: GMYC/bGMYC and BP&P.

671

672 **Figure S3.** Results of the GMYC and bGMYC analyses. (A) Clustering of samples into lineages  
673 according to GMYC, with each red clade representing a separate lineage. (B) Likelihood  
674 values produced by GMYC analysis to estimate the transition between interspecific  
675 diversification and allele intraspecific coalescence along the branches. (C) Lineage through  
676 time plot by GMYC analysis show in vertical red line the sharp increase in branching rate  
677 (threshold separating a Yule process from a Coalescent process). (D) Posterior distribution  
678 of lineage numbers according to bGMYC. The highest posterior probability is for 20 lineages.

679

680 **Figure S4.** Nuclear haplotype networks for two markers, *NGFB* (top) and *R35* (bottom). The  
681 colours correspond to the 20 GMYC/bGMYC lineages.

682

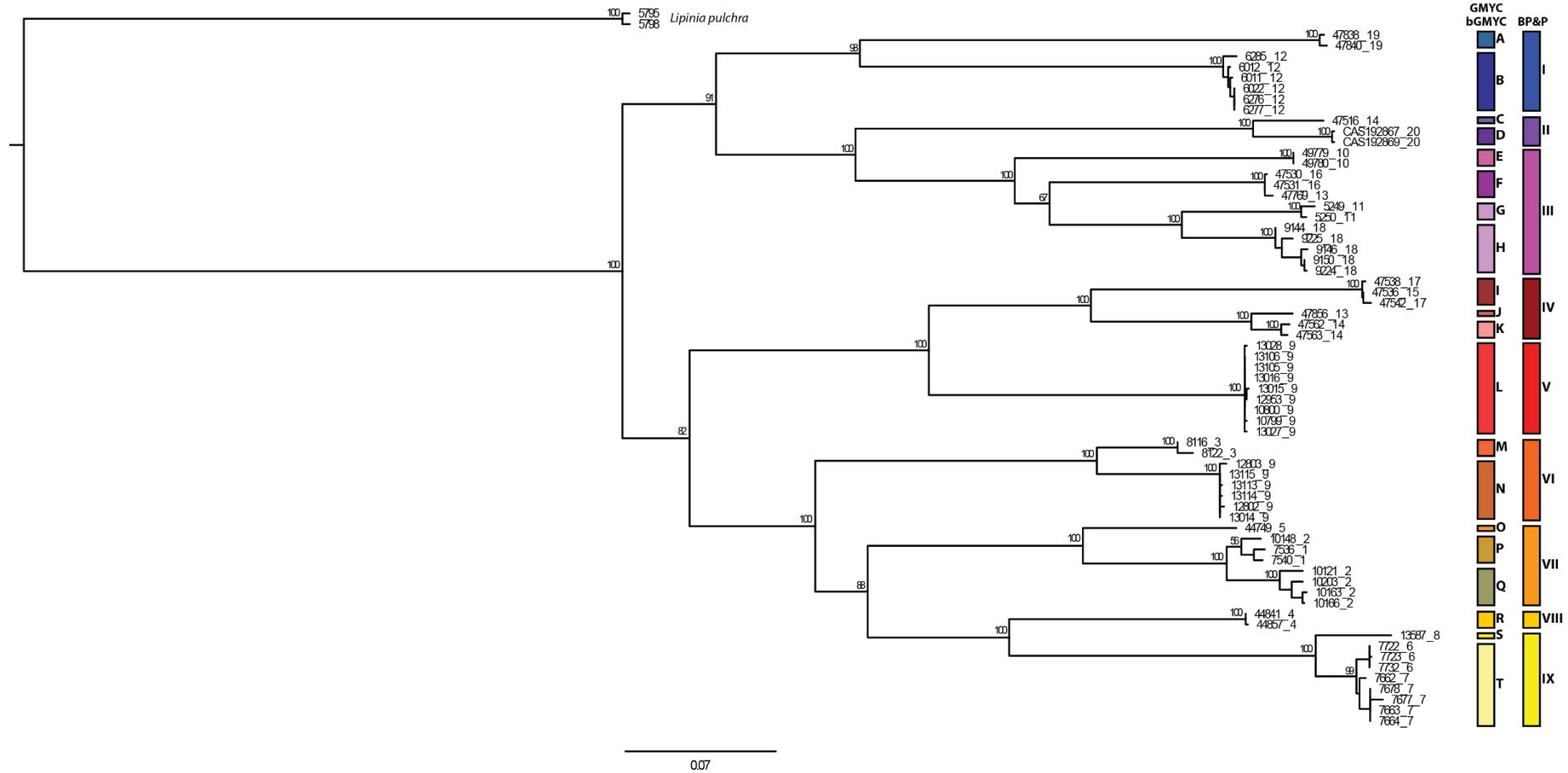
683 **Figure S5.** Time-calibrated phylogeny of *Papuascincus*. Mean age estimates are provided  
684 above the nodes with horizontal bars representing the 95% highest posterior densities.  
685 Posterior probability values are indicated next to the nodes. Details of the samples are  
686 presented in Table S1.

687

688 **Figure S6.** Phenogram showing evolution of SVL along the time-calibrated phylogeny of nine  
689 BP&P delimited lineages of *Papuascincus*, with blue colouration representing 95%  
690 confidence interval.

691

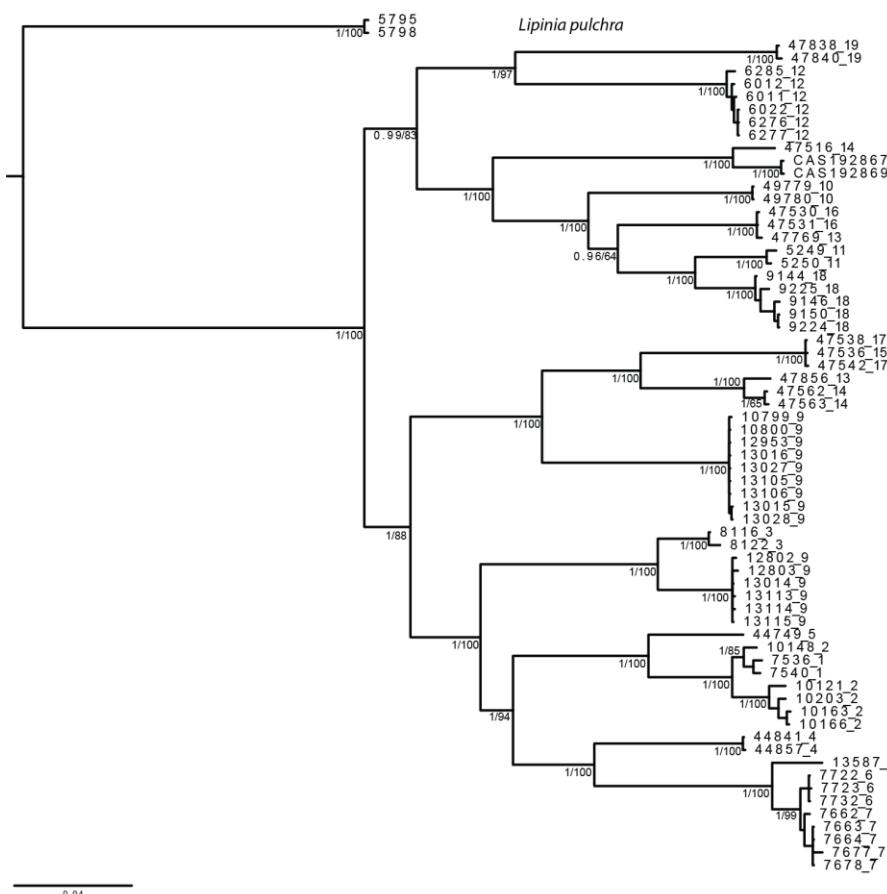
692 **Figure S1.**



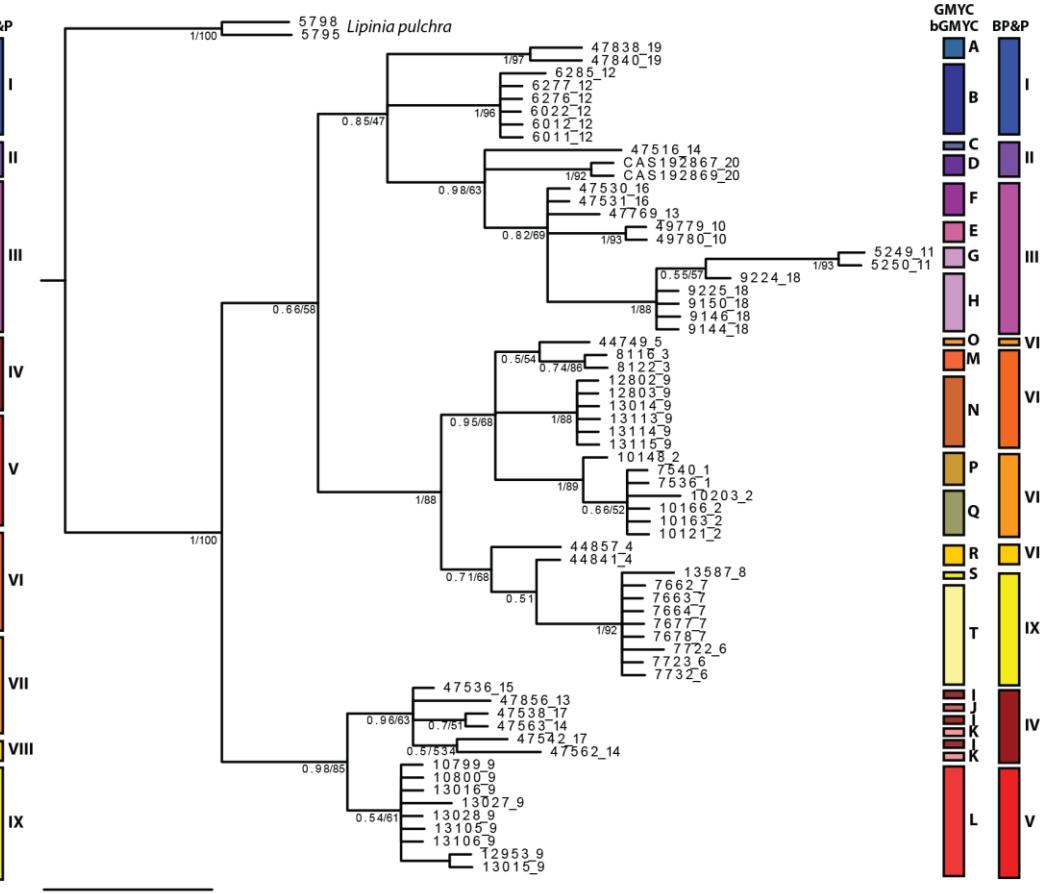
693

694 **Figure S2.**

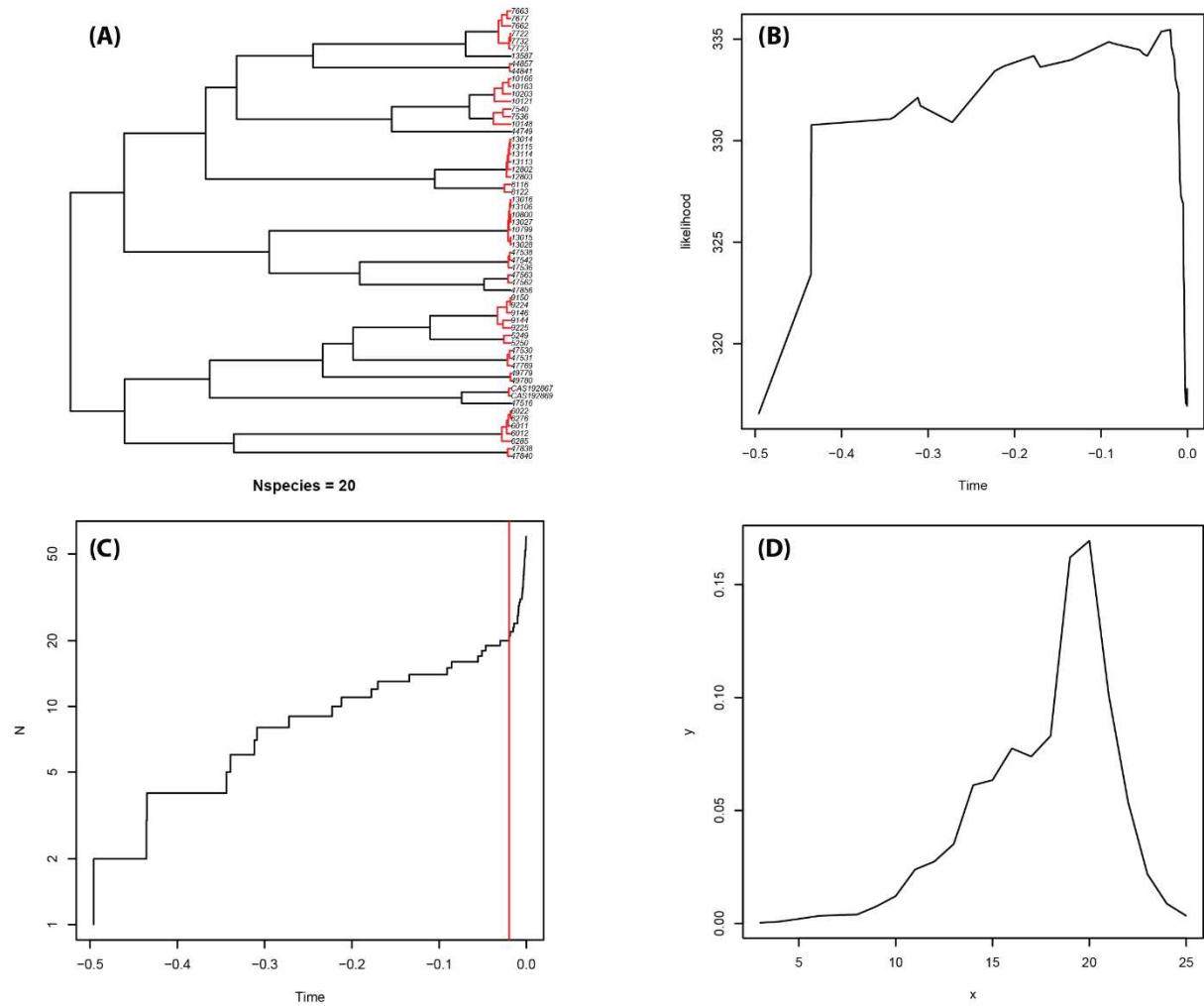
**(A)**



**(B)**



696 **Figure S3.**

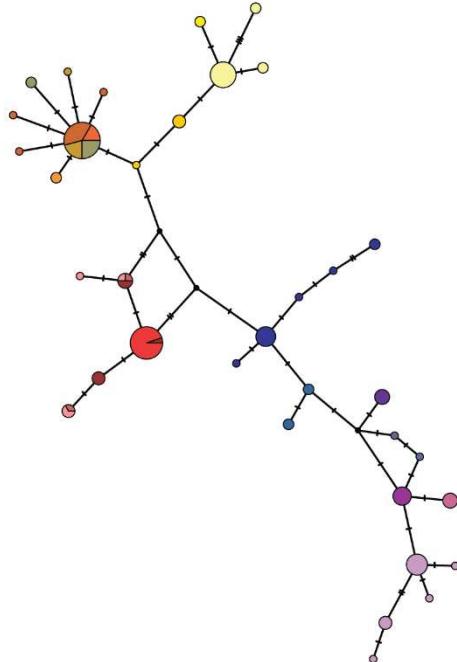


697

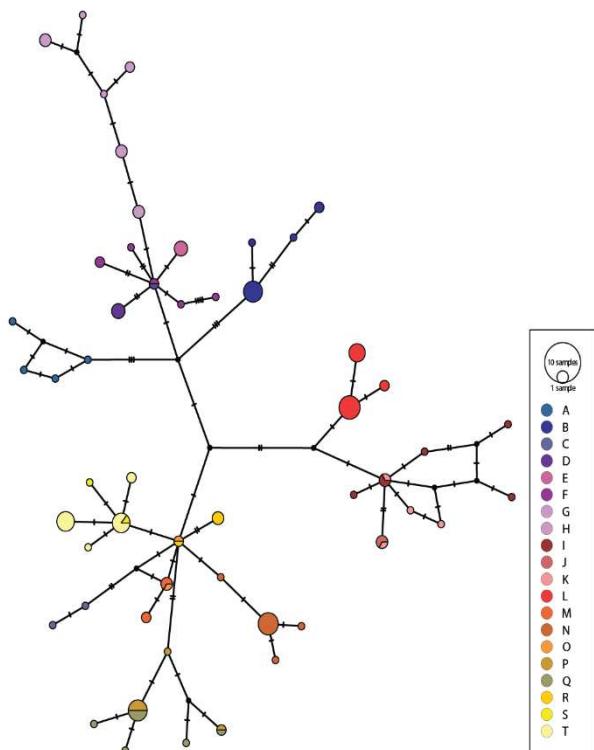
698

**Figure S4.**

NGFB:

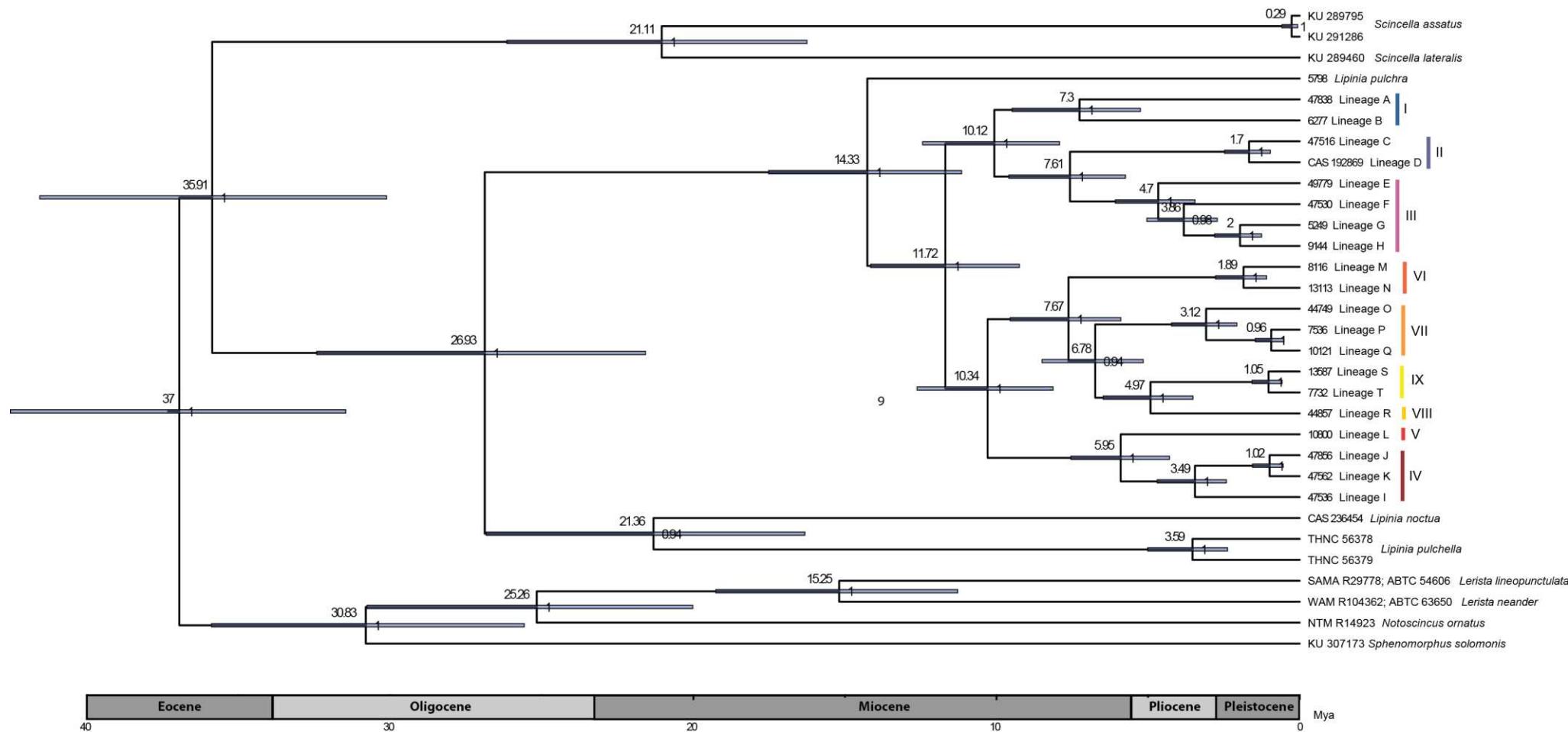


R35:

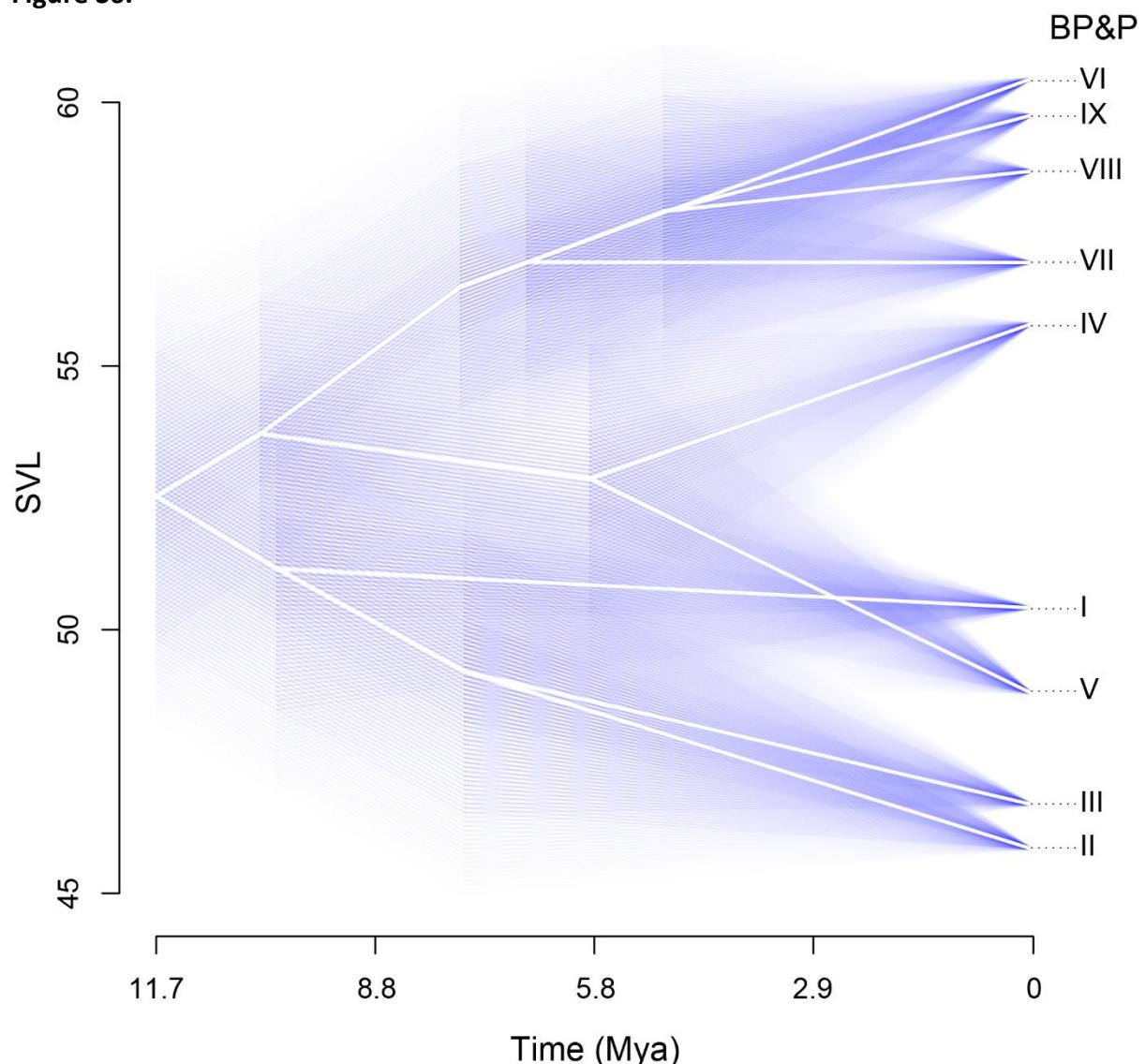


699

700 **Figure S5.**



701 **Figure S6.**



702  
703

704 **Table S1. Information on the specimens included in this study and related GenBank accession numbers.** Tissue codes correspond to the  
 705 labels assigned to each sample in the phylogenetic analyses. For *Papuascincus* specimens, information in the “species” column is given  
 706 regarding phylogenetic clades denoted by species delimitation methods (GMYC/bGMYC: letters A-T, BP&P: Roman numerals I-IX, respectively)  
 707 and locality data (as shown in Figure 1A). SVL (in mm) of voucher specimens and elevation (in m) of the locality are listed for specimens used in  
 708 biogeographic reconstruction and size evolution analyses. <sup>a</sup> Mitochondrial Haplotypes used for the GMYC and bGMYC species delimitation  
 709 analyses (n=60). <sup>b</sup> Representatives used for estimation of divergence times and ancestral state reconstructions (n=32). <sup>\*</sup> Juvenile specimen  
 710 omitted from body size comparisons (n=3).  
 711

Tissue Code	Voucher Code	Species	SVL	Elevation	Locality	Latitude	Longitude	12S	ND2	ND4	NGFB	R35
5249 <sup>a,b</sup>	BPBM 34851	<i>Papuascincus</i> G III	50.7	2443	11	-6.6143	142.8267	MN870695	MN870760	MN870825	MN870890	MN870955
5250 <sup>a</sup>	BPBM 34852	<i>Papuascincus</i> G III	48.9	2443	11	-6.6143	142.8267	MN870696	MN870761	MN870826	MN870891	MN870956
6011 <sup>a</sup>	BPBM 40404	<i>Papuascincus</i> B I	48.6	2173	12	-5.9552	146.5595	MN870699	MN870764	MN870829	MN870894	MN870959
6012 <sup>a</sup>	BPBM 40405	<i>Papuascincus</i> B I	50.4	2173	12	-5.9552	146.5595	MN870700	MN870765	MN870830	MN870895	MN870960
6022 <sup>a</sup>	BPBM 40397	<i>Papuascincus</i> B I	50.8	2655	12	-5.9372	146.5503	MN870701	MN870766	MN870831	MN870896	MN870961
6276 <sup>a</sup>	BPBM 40450	<i>Papuascincus</i> B I	56.7	2556	12	-5.9392	146.5523	MN870702	MN870767	MN870832	MN870897	MN870962
6277 <sup>b</sup>	BPBM 40449	<i>Papuascincus</i> B I	51.6	2556	12	-5.9392	146.5523	MN870703	MN870768	MN870833	MN870898	MN870963
6285 <sup>a</sup>	BPBM 40445	<i>Papuascincus</i> B I	54.8	2646	12	-5.9358	146.5574	MN870704	MN870769	MN870834	MN870899	MN870964
7536 <sup>a,b</sup>	BPBM 16767	<i>Papuascincus</i> P VII	56	2480	1	-10.0364	149.5749	MN870705	MN870770	MN870835	MN870900	MN870965
7540 <sup>a</sup>	BPBM 16769	<i>Papuascincus</i> P VII	53.5	2480	1	-10.0364	149.5749	MN870706	MN870771	MN870836	MN870901	MN870966
7662 <sup>a</sup>	BPBM 18858	<i>Papuascincus</i> T IX	60.9	1620	7	-8.5378	147.2423	MN870707	MN870772	MN870837	MN870902	MN870967
7663 <sup>a</sup>	BPBM 18859	<i>Papuascincus</i> T IX	57.1	1620	7	-8.5378	147.2423	MN870708	MN870773	MN870838	MN870903	MN870968
7664	BPBM 18860	<i>Papuascincus</i> T IX	41.1*	1650	7	-8.5291	147.2345	MN870709	MN870774	MN870839	MN870904	MN870969
7677 <sup>a</sup>	BPBM 18861	<i>Papuascincus</i> T IX	52.2	1604	7	-8.5448	147.2505	MN870710	MN870775	MN870840	MN870905	MN870970
7678	BPBM 18862	<i>Papuascincus</i> T IX	57.4	1604	7	-8.5448	147.2505	MN870711	MN870776	MN870841	MN870906	MN870971
7722 <sup>a</sup>	BPBM 18875	<i>Papuascincus</i> T IX	52.4	1800	6	-8.5693	147.0768	MN870712	MN870777	MN870842	MN870907	MN870972
7723 <sup>a</sup>	BPBM 18876	<i>Papuascincus</i> T IX	57.4	1800	6	-8.5693	147.0768	MN870713	MN870778	MN870843	MN870908	MN870973
7732 <sup>a,b</sup>	BPBM 18881	<i>Papuascincus</i> T IX	58.2	1340	6	-8.5683	147.0851	MN870714	MN870779	MN870844	MN870909	MN870974
8116 <sup>a,b</sup>	BPBM 19591	<i>Papuascincus</i> M VI	56.4	1822	3	-9.4571	148.0258	MN870715	MN870780	MN870845	MN870910	MN870975
8122 <sup>a</sup>	BPBM 19593	<i>Papuascincus</i> M VI	43.8*	1822	3	-9.4571	148.0258	MN870716	MN870781	MN870846	MN870911	MN870976
9144 <sup>a,b</sup>	BPBM 34179	<i>Papuascincus</i> H III	48.6	2177	18	-5.6695	142.6233	MN870717	MN870782	MN870847	MN870912	MN870977
9146 <sup>a</sup>	BPBM 34180	<i>Papuascincus</i> H III	44.6	1910	18	-5.6431	142.6342	MN870718	MN870783	MN870848	MN870913	MN870978
9150 <sup>a</sup>	BPBM 34181	<i>Papuascincus</i> H III	48.3	1910	18	-5.6431	142.6342	MN870719	MN870784	MN870849	MN870914	MN870979
9224 <sup>a</sup>	BPBM 34186	<i>Papuascincus</i> H III	47	2351	18	-5.6668	142.6163	MN870720	MN870785	MN870850	MN870915	MN870980
9225 <sup>a</sup>	BPBM 34187	<i>Papuascincus</i> H III	48.7	2351	18	-5.6668	142.6163	MN870721	MN870786	MN870851	MN870916	MN870981
10121 <sup>a,b</sup>	BPBM 39060	<i>Papuascincus</i> Q VII	52.8	1730	2	-9.7651	149.2176	MN870662	MN870727	MN870792	MN870857	MN870922
10148 <sup>a</sup>	BPBM 39061	<i>Papuascincus</i> P VII	57	1860	2	-9.7580	149.1822	MN870663	MN870728	MN870793	MN870858	MN870923
10163 <sup>a</sup>	BPBM 39063	<i>Papuascincus</i> Q VII	62.6	1860	2	-9.7580	149.1822	MN870664	MN870729	MN870794	MN870859	MN870924
10166 <sup>a</sup>	BPBM 39071	<i>Papuascincus</i> Q VII	59.7	1790	2	-9.7626	149.2021	MN870665	MN870730	MN870795	MN870860	MN870925
10203 <sup>a</sup>	BPBM 39089	<i>Papuascincus</i> Q VII	60.6	1730	2	-9.7651	149.2176	MN870666	MN870731	MN870796	MN870861	MN870926
10799 <sup>a</sup>	BPBM 38211	<i>Papuascincus</i> L V	49.2	1737	9	-7.9188	147.0843	MN870667	MN870732	MN870797	MN870862	MN870927

Tissue Code	Voucher Code	Species	SVL	Elevation	Locality	Latitude	Longitude	12S	ND2	ND4	NGFB	R35
10800 <sup>a,b</sup>	BPBM 38206	<i>Papuascincus</i> L V	47.1	1737	9	-7.9188	147.0843	MN870668	MN870733	MN870798	MN870863	MN870928
12802 <sup>a</sup>	BPBM 41228	<i>Papuascincus</i> N VI	62.5	1856	9	-7.9210	147.0802	MN870669	MN870734	MN870799	MN870864	MN870929
12803 <sup>a</sup>	BPBM 41229	<i>Papuascincus</i> N VI	61.2	1856	9	-7.9210	147.0802	MN870670	MN870735	MN870800	MN870865	MN870930
12953	BPBM 41253	<i>Papuascincus</i> L V	51.3	1856	9	-7.9210	147.0802	MN870671	MN870736	MN870801	MN870866	MN870931
13014 <sup>a</sup>	BPBM 41245	<i>Papuascincus</i> N VI	51.6	1733	9	-7.9372	147.0544	MN870672	MN870737	MN870802	MN870867	MN870932
13015 <sup>a</sup>	BPBM 41256	<i>Papuascincus</i> L V	48.8	1733	9	-7.9372	147.0544	MN870673	MN870738	MN870803	MN870868	MN870933
13016 <sup>a</sup>	BPBM 41257	<i>Papuascincus</i> L V	48.2	1733	9	-7.9372	147.0544	MN870674	MN870739	MN870804	MN870869	MN870934
13027 <sup>a</sup>	BPBM 41267	<i>Papuascincus</i> L V	48.6	1965	9	-7.9380	147.0458	MN870675	MN870740	MN870805	MN870870	MN870935
13028 <sup>a</sup>	BPBM 41268	<i>Papuascincus</i> L V	49.2	1965	9	-7.9380	147.0458	MN870676	MN870741	MN870806	MN870871	MN870936
13105	BPBM 41300	<i>Papuascincus</i> L V	49.4	2161	9	-7.9325	147.0399	MN870677	MN870742	MN870807	MN870872	MN870937
13106 <sup>a</sup>	BPBM 41301	<i>Papuascincus</i> L V	52.9	2161	9	-7.9325	147.0399	MN870678	MN870743	MN870808	MN870873	MN870938
13113 <sup>a,b</sup>	BPBM 41246	<i>Papuascincus</i> N VI	63.7	1965	9	-7.9380	147.0458	MN870679	MN870744	MN870809	MN870874	MN870939
13114 <sup>a</sup>	BPBM 41247	<i>Papuascincus</i> N VI	61.4	2161	9	-7.9325	147.0399	MN870680	MN870745	MN870810	MN870875	MN870940
13115 <sup>a</sup>	BPBM 41248	<i>Papuascincus</i> N VI	57.3	2161	9	-7.9325	147.0399	MN870681	MN870746	MN870811	MN870876	MN870941
13587 <sup>a,b</sup>	BPBM 44306	<i>Papuascincus</i> S IX	59.6	3282	8	-8.2069	146.7848	MN870682	MN870747	MN870812	MN870877	MN870942
44749 <sup>a,b</sup>	BPBM 44749	<i>Papuascincus</i> O VII	59.5	1262	5	-8.9646	147.7327	MN870722	MN870787	MN870852	MN870917	MN870982
44841 <sup>a</sup>	BPBM 44841	<i>Papuascincus</i> R VIII	63.6	1936	4	-9.1288	147.7264	MN870723	MN870788	MN870853	MN870918	MN870983
44857 <sup>a,b</sup>	BPBM 44857	<i>Papuascincus</i> R VIII	64.8	2076	4	-9.1509	147.7675	MN870724	MN870789	MN870854	MN870919	MN870984
47516 <sup>a,b</sup>	BPBM 22896	<i>Papuascincus</i> C II	48.1	1800	14	-5.8735	144.2003	MN870683	MN870748	MN870813	MN870878	MN870943
47530 <sup>a,b</sup>	BPBM 22902	<i>Papuascincus</i> F III	45.9	2200	16	-5.8120	144.0950	MN870684	MN870749	MN870814	MN870879	MN870944
47531 <sup>a</sup>	BPBM 22903	<i>Papuascincus</i> F III	50	2200	16	-5.8120	144.0950	MN870685	MN870750	MN870815	MN870880	MN870945
47536 <sup>a,b</sup>	BPBM 22908	<i>Papuascincus</i> I IV	60	2600	15	-5.8193	144.0144	MN870686	MN870751	MN870816	MN870881	MN870946
47538 <sup>a</sup>	BPBM 22910	<i>Papuascincus</i> I IV	46.3	2800	17	-5.7935	143.9799	MN870687	MN870752	MN870817	MN870882	MN870947
47542 <sup>a</sup>	BPBM 22914	<i>Papuascincus</i> I IV	43.6*	2800	17	-5.7935	143.9799	MN870688	MN870753	MN870818	MN870883	MN870948
47562 <sup>a,b</sup>	BPBM 22934	<i>Papuascincus</i> K IV	57	1800	14	-5.8735	144.2003	MN870689	MN870754	MN870819	MN870884	MN870949
47563 <sup>a</sup>	BPBM 22935	<i>Papuascincus</i> K IV	56.7	1800	14	-5.8735	144.2033	MN870690	MN870755	MN870820	MN870885	MN870950
47769 <sup>a</sup>	BPBM 47769	<i>Papuascincus</i> F III	44.6	1960	13	-5.8991	144.2521	MN870726	MN870791	MN870856	MN870921	MN870986
47838 <sup>a,b</sup>	BPBM 23082	<i>Papuascincus</i> A I	50.1	1650	19	-5.5423	144.2091	MN870691	MN870756	MN870821	MN870886	MN870951
47840 <sup>a</sup>	BPBM 23084	<i>Papuascincus</i> A I	48.7	1650	19	-5.5423	144.2091	MN870692	MN870757	MN870822	MN870887	MN870952
47856 <sup>a,b</sup>	BPBM 47856	<i>Papuascincus</i> J IV	60.1	1960	13	-5.8991	144.2521	MN870725	MN870790	MN870855	MN870920	MN870985
49779 <sup>a,b</sup>	BPBM 23713	<i>Papuascincus</i> E III	41.1	1190	10	-7.2885	146.7654	MN870693	MN870758	MN870823	MN870888	MN870953
49780 <sup>a</sup>	BPBM 23714	<i>Papuascincus</i> E III	42.1	1190	10	-7.2885	146.7654	MN870694	MN870759	MN870824	MN870889	MN870954
CAS 192867 <sup>a</sup>	CAS 192687	<i>Papuascincus</i> D II	48.1	1830	20	-5.2376	144.4805	JF497876	JF498128	JF498479	JF498234	JF498355
CAS 192869 <sup>a,b</sup>	CAS 192869	<i>Papuascincus</i> D II	43.8	1830	20	-5.2376	144.4805	JF497877	JF498129	JF498480	JF498235	JF498356
CAS 236454 <sup>b</sup>	CAS 236454	<i>Lipinia noctua</i>	-	-	-	-	-	JF497868	JF498120	JF498473	-	JF498348
THNC 56378 <sup>b</sup>		<i>Lipinia pulchella</i>	-	-	-	-	-	JF497869	JF498121	JF498474	JF498228	JF498349
THNC 56379 <sup>b</sup>		<i>Lipinia pulchella</i>	-	-	-	-	-	JF497870	JF498122	JF498475	JF498229	-
5795 <sup>b</sup>	BPBM 38789	<i>Lipinia pulchra</i>	-	-	-	-	-	MN870697	MN870762	MN870827	MN870892	MN870957
5798 <sup>b</sup>	BPBM 38792	<i>Lipinia pulchra</i>	-	-	-	-	-	MN870698	MN870763	MN870828	MN870893	MN870958
SAMA R29778; ABTC 54606 <sup>b</sup>		<i>Lerista lineopunctulata</i>	-	-	-	-	-	EF672792	JQ517871	EF673004	-	-
WAM R104362;		<i>Lerista neander</i>	-	-	-	-	-	EF672796	-	EF673008	-	-

Tissue Code	Voucher Code	Species	SVL	Elevation	Locality	Latitude	Longitude	12S	ND2	ND4	NGFB	R35
ABTC 63650 <sup>b</sup>												
NTM R14923		<i>Notoscincus ornatus</i>	-	-	-	-	-	AY169594	-	AY169669	-	-
KU 289795 <sup>b</sup>		<i>Scincella assatus</i>	-	-	-	-	-	JF497946	-	JF498548	JF498302	JF498427
KU 291286 <sup>b</sup>		<i>Scincella assatus</i>	-	-	-	-	-	-	JF498186	JF498549	JF498303	JF498428
KU 289460 <sup>b</sup>		<i>Scincella lateralis</i>	-	-	-	-	-	JF497948	JF498187	AY169673	JF498305	JF498430
KU 307173 <sup>b</sup>		<i>Sphenomorphus solomonis</i>	-	-	-	-	-	JF497964	JF498203	JF498567	JF498321	JF498446

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**Table S2.** Specimens used for body size analyses. Tissue code is given for voucher specimens of samples used in the molecular analyses. SVL was recorded to the nearest 0.1 mm.

Voucher Code	Collection Code	Tissue Code	GMYC/bGMYC	BP&P	SVL (mm)	Latitude	Longitude
BPBM 23071	AA 12174		A		49.7	-5.542282	144.209116
BPBM 23072	AA 12175		A		47.9	-5.542282	144.209116
BPBM 23073	AA 12176		A		49.3	-5.542282	144.209116
BPBM 23074	AA 12177		A		49.5	-5.542282	144.209116
BPBM 23075	AA 12178		A		50.9	-5.542282	144.209116
BPBM 23076	AA 12179		A		49.1	-5.542282	144.209116
BPBM 23077	AA 12180		A		49.5	-5.542282	144.209116
BPBM 23078	AA 12181		A		41.2	-5.542282	144.209116
BPBM 23079	AA 12182		A		51.5	-5.542282	144.209116
BPBM 23080	AA 12183		A		50.8	-5.542282	144.209116
BPBM 23081	AA 12184		A		50.6	-5.542282	144.209116
BPBM 23082	AA 12185	47838	A		50.1	-5.542282	144.209116
BPBM 23083	AA 12186		A		48.2	-5.542282	144.209116
BPBM 23084	AA 12187	47840	A		48.7	-5.542282	144.209116
BPBM 23085	AA 12188		A		50.2	-5.542282	144.209116
BPBM 23086	AA 12189		A		49.7	-5.542282	144.209116
BPBM 23087	AA 12190		A		48.9	-5.542282	144.209116
BPBM 23088	AA 12191		A		50.7	-5.542282	144.209116
BPBM 23089	AA 12192		A		45.2	-5.542282	144.209116
BPBM 30503	AA 10899		A		54.0	-5.533	144.15
BPBM 30504	AA 10900		A		48.9	-5.533	144.15
BPBM 30505	AA 10901		A		42.3	-5.533	144.15
BPBM 30506	AA 10902		A		50.1	-5.533	144.15
BPBM 30556	AA 10958		A		49.4	-5.509057999	144.1621552
BPBM 30605	AA 11025		A		52.1	-5.542282	144.209116
BPBM 30606	AA 11026		A		47.8	-5.542282	144.209116
BPBM 30607	AA 11027		A		50.2	-5.542282	144.209116

BPBM 30610	AA 11030		A		41.3	-5.542282	144.209116
BPBM 30611	AA 11031		A		49.5	-5.542282	144.209116
BPBM 30612	AA 11032		A		50.0	-5.542282	144.209116
BPBM 30613	AA 11033		A		48.8	-5.542282	144.209116
BPBM 30614	AA 11034		A		55.0	-5.542282	144.209116
BPBM 30615	AA 11035		A		49.6	-5.542282	144.209116
BPBM 30616	AA 11036		A		53.0	-5.542282	144.209116
BPBM 30617	AA 11037		A		50.4	-5.542282	144.209116
BPBM 30618	AA 11038		A		48.8	-5.542282	144.209116
BPBM 30619	AA 11039		A		50.8	-5.542282	144.209116
BPBM 30620	AA 11040		A		48.3	-5.542282	144.209116
BPBM 30621	AA 11041		A		50.1	-5.542282	144.209116
BPBM 30622	AA 11042		A		53.0	-5.542282	144.209116
BPBM 30623	AA 11043		A		53.9	-5.542282	144.209116
BPBM 30624	AA 11044		A		47.4	-5.542282	144.209116
BPBM 30625	AA 11045		A		49.0	-5.542282	144.209116
BPBM 30626	AA 11046		A		49.6	-5.542282	144.209116
BPBM 30627	AA 11047		A		50.7	-5.542282	144.209116
BPBM 30628	AA 11048		A		52.3	-5.542282	144.209116
BPBM 40378	AA 20321		B		48.7	-5.95517	146.55952
BPBM 40379	AA 20316		B		50.7	-5.95517	146.55952
BPBM 40380	AA 20323		B		49.7	-5.95517	146.55952
BPBM 40381	AA 20325		B		44.1	-5.95517	146.55952
BPBM 40383	AA 20322		B		50.7	-5.95517	146.55952
BPBM 40384	AA 20443		B		51.7	-5.95517	146.55952
BPBM 40385	AA 20320		B		53.3	-5.95517	146.55952
BPBM 40386	AA 20319		B		52.0	-5.95517	146.55952
BPBM 40387	AA 20327		B		49.4	-5.95517	146.55952
BPBM 40388	AA 20317		B		49.6	-5.95517	146.55952

BPBM 40391	AA 20314		B		47.0	-5.95517	146.55952
BPBM 40392	AA 20313		B		52.7	-5.95517	146.55952
BPBM 40394	AA 20311		B		43.4	-5.95517	146.55952
BPBM 40395	AA 20310		B		48.7	-5.95517	146.55952
BPBM 40396	AA 20284		B		45.7	-5.95517	146.55952
BPBM 40397	AA 20294	6022	B		50.8	-5.93721	146.55032
BPBM 40400	AA 20358		B		49.8	-5.95517	146.55952
BPBM 40401	AA 20357		B		50.6	-5.95517	146.55952
BPBM 40402	AA 20356		B		52.1	-5.95517	146.55952
BPBM 40404	AA 20282	6011	B		48.6	-5.95517	146.55952
BPBM 40405	AA 20283	6012	B		50.4	-5.95517	146.55952
BPBM 40407	AA 20326		B		53.3	-5.95517	146.55952
BPBM 40408	AA 20344		B		51.0	-5.95517	146.55952
BPBM 40409	AA 20436		B		52.7	-5.95517	146.55952
BPBM 40414	AA 20337		B		51.1	-5.95517	146.55952
BPBM 40417	AA 20329		B		51.2	-5.95517	146.55952
BPBM 40418	AA 20345		B		44.7	-5.95517	146.55952
BPBM 40419	AA 20484		B		54.0	-5.95517	146.55952
BPBM 40421	AA 20496		B		54.8	-5.95517	146.55952
BPBM 40422	AA 20495		B		53.3	-5.95517	146.55952
BPBM 40423	AA 20494		B		50.2	-5.95517	146.55952
BPBM 40424	AA 20493		B		52.5	-5.95517	146.55952
BPBM 40425	AA 20491		B		54.8	-5.95517	146.55952
BPBM 40428	AA 20488		B		51.5	-5.95517	146.55952
BPBM 40431	AA 20485		B		53.9	-5.95517	146.55952
BPBM 40433	AA 20483		B		55.0	-5.95517	146.55952
BPBM 40434	AA 20482		B		46.6	-5.95517	146.55952
BPBM 40435	AA 20481		B		52.2	-5.95517	146.55952
BPBM 40436	AA 20480		B		53.4	-5.95517	146.55952

BPBM 40437	AA 20479		B		47.8	-5.95517	146.55952
BPBM 40438	AA 20478		B		53.3	-5.95517	146.55952
BPBM 40439	AA 20477		B		50.2	-5.95517	146.55952
BPBM 40440	AA 20476		B		54.1	-5.95517	146.55952
BPBM 40441	AA 20441		B		54.5	-5.95517	146.55952
BPBM 40442	AA 20474		B		48.3	-5.95517	146.55952
BPBM 40443	AA 20486		B		52.1	-5.95517	146.55952
BPBM 40445	AA 20575	6285	B		54.8	-5.93577	146.55735
BPBM 40448	AA 20568		B		51.7	-5.93919	146.55229
BPBM 40449	AA 20567	6277	B		51.6	-5.93919	146.55229
BPBM 40450	AA 20566	6276	B		56.7	-5.93919	146.55229
BPBM 40454	AA 20492		B		42.8	-5.95517	146.55952
BPBM 40457	AA 20473		B		51.4	-5.95517	146.55952
BPBM 40459	AA 20454		B		46.4	-5.95517	146.55952
BPBM 40461	AA 20506		B		46.7	-5.95517	146.55952
BPBM 40462	AA 20505		B		47.2	-5.95517	146.55952
BPBM 40463	AA 20504		B		49.8	-5.95517	146.55952
BPBM 40464	AA 20503		B		47.1	-5.95517	146.55952
BPBM 40465	AA 20502		B		47.4	-5.95517	146.55952
BPBM 40466	AA 20501		B		50.3	-5.95517	146.55952
BPBM 40469	AA 20431		B		47.5	-5.95517	146.55952
BPBM 40473	AA 20442		B		50.6	-5.95517	146.55952
BPBM 40474	AA 20440		B		52.0	-5.95517	146.55952
BPBM 40475	AA 20439		B		50.1	-5.95517	146.55952
BPBM 40476	AA 20438		B		46.3	-5.95517	146.55952
BPBM 40477	AA 20437		B		52.8	-5.95517	146.55952
BPBM 40478	AA 20435		B		48.2	-5.95517	146.55952
BPBM 40480	AA 20472		B		51.6	-5.95517	146.55952
BPBM 40482	AA 20446		B		43.3	-5.95517	146.55952

BPBM 40483	AA 20430		B		51.1	-5.95517	146.55952
BPBM 40484	AA 20429		B		47.5	-5.95517	146.55952
BPBM 40485	AA 20428		B		50.0	-5.95517	146.55952
BPBM 40486	AA 20427		B		49.7	-5.95517	146.55952
BPBM 40487	AA 20426		B		52.8	-5.95517	146.55952
BPBM 40488	AA 20425		B		54.3	-5.95517	146.55952
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BPBM 40490	AA 20423		B		53.1	-5.95517	146.55952
BPBM 40494	AA 20459		B		45.8	-5.95517	146.55952
BPBM 40495	AA 20471		B		52.6	-5.95517	146.55952
BPBM 40496	AA 20470		B		51.1	-5.95517	146.55952
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BPBM 40498	AA 20468		B		50.2	-5.95517	146.55952
BPBM 40499	AA 20467		B		52.4	-5.95517	146.55952
BPBM 40500	AA 20466		B		49.5	-5.95517	146.55952
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BPBM 40502	AA 20464		B		50.4	-5.95517	146.55952
BPBM 40503	AA 20463		B		49.9	-5.95517	146.55952
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BPBM 40506	AA 20444		B		50.7	-5.95517	146.55952
BPBM 40507	AA 20460		B		54.6	-5.95517	146.55952
BPBM 40509	AA 20458		B		55.1	-5.95517	146.55952
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BPBM 40512	AA 20455		B		51.5	-5.95517	146.55952
BPBM 40513	AA 20453		B		53.0	-5.95517	146.55952
BPBM 40514	AA 20452		B		48.6	-5.95517	146.55952
BPBM 40515	AA 20451		B		52.1	-5.95517	146.55952

BPBM 40516	AA 20450		B	I	52.7	-5.95517	146.55952
BPBM 40517	AA 20449		B	I	51.8	-5.95517	146.55952
BPBM 40518	AA 20448		B	I	53.9	-5.95517	146.55952
SAM R69660	2159		B	I	54.0	-6.079	146.575
SAM R69663	2174		B	I	55.3	-6.079	146.575
SAM R69664	2192		B	I	49.9	-6.079	146.575
SAM R69668	2202		B	I	53.4	-6.097	146.559
SAM R69670	2214		B	I	54.2	-6.097	146.559
SAM R69671	2215		B	I	51.4	-6.097	146.559
BPBM 22896	AA 11485	47516	C	II	48.1	-5.87345413	144.2003064
CAS 192866	RNF 0064		D	II	47.1	-5.2376	144.4805
CAS 192867	RNF 0065	CAS192867	D	II	48.1	-5.2376	144.4805
CAS 192868	RNF 0066		D	II	47.3	-5.2376	144.4805
CAS 192869	RNF 0067	CAS192869	D	II	43.8	-5.2376	144.4805
CAS 192870	RNF 0068		D	II	45.1	-5.2376	144.4805
CAS 192871	RNF 0069		D	II	45.4	-5.2376	144.4805
CAS 192872	RNF 0070		D	II	46.0	-5.2376	144.4805
CAS 192874	RNF 0075		D	II	45.7	-5.2376	144.4805
CAS 192875	RNF 0076		D	II	46.8	-5.2376	144.4805
CAS 192876	RNF 0078		D	II	45.4	-5.2376	144.4805
CAS 192877	RNF 0080		D	II	41.3	-5.2376	144.4805
BPBM 23647	AA 12801		E	III	39.2	-7.2789858	146.7744565
BPBM 23682	AA 12951		E	III	39.5	-7.2826087	146.7690217
BPBM 23713	AA 13047	49779	E	III	41.1	-7.2884963	146.7653985
BPBM 23714	AA 13048	49780	E	III	42.1	-7.2884963	146.7653985
BPBM 23715	AA 13049		E	III	40.6	-7.2884963	146.7653985
BPBM 24060	AA 12760		E	III	38.8	-7.2826087	146.7690217
BPBM 24061	AA 12761		E	III	39.7	-7.2826087	146.7690217
BPBM 24063	AA 12767		E	III	36.3	-7.2826087	146.7690217
BPBM 24064	AA 12772		E	III	42.4	-7.2826087	146.7690217

BPBM 22902	AA 11505	47530	F	III	45.9	-5.812	144.095
BPBM 22903	AA 11506	47531	F	III	50.0	-5.812	144.095
BPBM 22904	AA 11507		F	III	51.1	-5.812	144.095
BPBM 22905	AA 11508		F	III	51.1	-5.812	144.095
BPBM 22906	AA 11509		F	III	46.0	-5.812	144.095
BPBM 22907	AA 11510		F	III	48.7	-5.812	144.095
BPBM 22966	AA 11606		F	III	48.8	-5.812	144.095
BPBM 22967	AA 11607		F	III	48.7	-5.812	144.095
BPBM 22968	AA 11608		F	III	50.7	-5.812	144.095
BPBM 22969	AA 11609		F	III	48.5	-5.812	144.095
BPBM 22970	AA 11610		F	III	46.7	-5.812	144.095
BPBM 22971	AA 11611		F	III	50.3	-5.812	144.095
BPBM 22972	AA 11612		F	III	46.3	-5.812	144.095
BPBM 22973	AA 11613		F	III	49.1	-5.812	144.095
BPBM 22974	AA 11614		F	III	49.1	-5.812	144.095
BPBM 22975	AA 11615		F	III	46.9	-5.812	144.095
BPBM 47769	AA 24811	47769	F	III	44.6	-5.8991	144.2521
BPBM 34851	AA 19399	5249	G	III	50.7	-6.614342	142.826652
BPBM 34852	AA 19400	5250	G	III	48.9	-6.614342	142.826652
BPBM 34853	AA 19401		G	III	47.3	-6.614342	142.826652
BPBM 34854	AA 19402		G	III	51.8	-6.614342	142.826652
BPBM 34179	FK 12506	9144	H	III	48.6	-5.66954	142.62334
BPBM 34180	FK 12508	9146	H	III	44.6	-5.6431	142.6342
BPBM 34181	FK 12512	9150	H	III	48.3	-5.6431	142.6342
BPBM 34182	FK 12513		H	III	50.4	-5.6431	142.6342
BPBM 34183	FK 12514		H	III	43.7	-5.6431	142.6342
BPBM 34184	FK 12544		H	III	48.6	-5.65915	142.63538
BPBM 34185	FK 12545		H	III	48.7	-5.65915	142.63538
BPBM 34186	FK 12721	9224	H	III	47.0	-5.66681	142.61625
BPBM 34187	FK 12722	9225	H	III	48.7	-5.66681	142.61625

BPBM 34189	FK 12746		H	III	48.0	-5.65915	142.63538
BPBM 34192	FK 12775		H	III	49.4	-5.68381	142.61012
BPBM 34193	FK 12776		H	III	48.9	-5.68381	142.61012
BPBM 34194	FK 12777		H	III	46.1	-5.68381	142.61012
BPBM 34195	FK 12778		H	III	45.4	-5.68381	142.61012
BPBM 34203	FK 12811		H	III	45.8	-5.67075	142.62553
BPBM 34204	FK 12812		H	III	48.4	-5.67075	142.62553
BPBM 34206	FK 12814		H	III	47.2	-5.67075	142.62553
BPBM 34207	FK 12815		H	III	46.0	-5.67075	142.62553
BPBM 34215	FK 12905		H	III	50.2	-5.66465	142.61949
	FK 12543		H	III	49.4	-5.6592	142.635
BPBM 22908	AA 11511	47536	I	IV	60.0	-5.819347	144.014407
BPBM 22910	AA 11515	47538	I	IV	46.3	-5.793534	143.979889
BPBM 22915	AA 11520		I	IV	55.4	-5.793534	143.979889
BPBM 22916	AA 11521		I	IV	55.7	-5.793534	143.979889
BPBM 22920	AA 11525		I	IV	51.0	-5.793534	143.979889
BPBM 22921	AA 11526		I	IV	47.7	-5.793534	143.979889
BPBM 22924	AA 11529		I	IV	47.6	-5.793534	143.979889
BPBM 22925	AA 11530		I	IV	46.9	-5.793534	143.979889
BPBM 22928	AA 11533		I	IV	50.6	-5.793534	143.979889
BPBM 22979	AA 11621		I	IV	49.9	-5.793534	143.979889
BPBM 22981	AA 11623		I	IV	56.9	-5.793534	143.979889
BPBM 22983	AA 11625		I	IV	54.7	-5.793534	143.979889
BPBM 22985	AA 11627		I	IV	54.7	-5.793534	143.979889
BPBM 22986	AA 11628		I	IV	57.7	-5.793534	143.979889
BPBM 22898	AA 11501		J	IV	59.5	-5.812	144.095
BPBM 22901	AA 11504		J	IV	57.6	-5.812	144.095
BPBM 22911	AA 11516		J	IV	54.3	-5.793534	143.979889
BPBM 22913	AA 11518		J	IV	44.4	-5.793534	143.979889

BPBM 22918	AA 11523		J	IV	55.3	-5.793534	143.979889
BPBM 22919	AA 11524		J	IV	53.7	-5.793534	143.979889
BPBM 22922	AA 11527		J	IV	56.7	-5.793534	143.979889
BPBM 22923	AA 11528		J	IV	51.2	-5.793534	143.979889
BPBM 22926	AA 11531		J	IV	58.3	-5.793534	143.979889
BPBM 22936	AA 11546		J	IV	60.3	-5.87345413	144.2003064
BPBM 22944	AA 11584		J	IV	56.3	-5.812	144.095
BPBM 22946	AA 11586		J	IV	60.8	-5.812	144.095
BPBM 22947	AA 11587		J	IV	54.8	-5.812	144.095
BPBM 22949	AA 11589		J	IV	56.3	-5.812	144.095
BPBM 22950	AA 11590		J	IV	56.8	-5.812	144.095
BPBM 22954	AA 11594		J	IV	60.3	-5.812	144.095
BPBM 22955	AA 11595		J	IV	50.8	-5.812	144.095
BPBM 22956	AA 11596		J	IV	59.4	-5.812	144.095
BPBM 22959	AA 11599		J	IV	55.3	-5.812	144.095
BPBM 22960	AA 11600		J	IV	57.7	-5.812	144.095
BPBM 22963	AA 11603		J	IV	58.0	-5.812	144.095
BPBM 22964	AA 11604		J	IV	55.1	-5.812	144.095
BPBM 22978	AA 11620		J	IV	52.8	-5.793534	143.979889
BPBM 22984	AA 11626		J	IV	58.3	-5.793534	143.979889
BPBM 22987	AA 11629		J	IV	49.8	-5.793534	143.979889
BPBM 23023	AA 11879		J	IV	58.7	-5.827355	144.045508
BPBM 23025	AA 11881		J	IV	53.1	-5.615138	143.880914
BPBM 23030	AA 11886		J	IV	57.2	-5.615138	143.880914
BPBM 23031	AA 11887		J	IV	59.4	-5.615138	143.880914
BPBM 23032	AA 11888		J	IV	58.3	-5.615138	143.880914
BPBM 23033	AA 11889		J	IV	54.1	-5.615138	143.880914
BPBM 23036	AA 11892		J	IV	59.0	-5.615138	143.880914
BPBM 23043	AA 11899		J	IV	56.1	-5.615138	143.880914

BPBM 23044	AA 11900		J	IV	59.4	-5.615138	143.880914
BPBM 47856	AA 24898	47856	J	IV	60.1	-5.899058	144.252075
BPBM 22900	AA 11503		K	IV	55.8	-5.812	144.095
BPBM 22934	AA 11544	47562	K	IV	57.0	-5.87345413	144.2003064
BPBM 22935	AA 11545	47563	K	IV	56.7	-5.87345413	144.2003064
BPBM 22938	AA 11578		K	IV	54.8	-5.812	144.095
BPBM 22939	AA 11579		K	IV	59.2	-5.812	144.095
BPBM 22940	AA 11580		K	IV	56.1	-5.812	144.095
BPBM 22941	AA 11581		K	IV	59.4	-5.812	144.095
BPBM 22942	AA 11582		K	IV	58.4	-5.812	144.095
BPBM 22943	AA 11583		K	IV	56.0	-5.812	144.095
BPBM 22945	AA 11585		K	IV	63.7	-5.812	144.095
BPBM 22948	AA 11588		K	IV	51.9	-5.812	144.095
BPBM 22951	AA 11591		K	IV	58.5	-5.812	144.095
BPBM 22953	AA 11593		K	IV	63.7	-5.812	144.095
BPBM 22957	AA 11597		K	IV	53.4	-5.812	144.095
BPBM 22958	AA 11598		K	IV	56.2	-5.812	144.095
BPBM 22965	AA 11605		K	IV	59.1	-5.812	144.095
BPBM 23018	AA 11874		K	IV	62.8	-5.827355	144.045508
BPBM 23019	AA 11875		K	IV	54.7	-5.827355	144.045508
BPBM 23020	AA 11876		K	IV	62.0	-5.827355	144.045508
BPBM 23021	AA 11877		K	IV	51.9	-5.827355	144.045508
BPBM 23022	AA 11878		K	IV	56.8	-5.827355	144.045508
BPBM 23028	AA 11884		K	IV	60.1	-5.615138	143.880914
BPBM 23037	AA 11893		K	IV	53.5	-5.615138	143.880914
BPBM 23038	AA 11894		K	IV	59.9	-5.615138	143.880914
BPBM 23039	AA 11895		K	IV	46.5	-5.615138	143.880914
BPBM 23040	AA 11896		K	IV	57.1	-5.615138	143.880914
BPBM 23045	AA 11901		K	IV	51.7	-5.615138	143.880914

BPBM 2575			K	IV	52.9	-5.869196	144.763327
BPBM 30564	AA 10979		K	IV	58.1	-5.8269016	144.0205562
BPBM 30565	AA 10980		K	IV	57.2	-5.8269016	144.0205562
BPBM 30566	AA 10981		K	IV	58.8	-5.8269016	144.0205562
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BPBM 30572	AA 10989		K	IV	55.9	-5.8269016	144.0205562
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BPBM 38206	AA 20771	10800	L	V	47.1	-7.91876	147.08429
BPBM 38210	AA 20772		L	V	43.6	-7.91876	147.08429
BPBM 38211	AA 20770	10799	L	V	49.2	-7.91876	147.08429
BPBM 41250	AA 21175		L	V	49.7	-7.921	147.08015
BPBM 41251	AA 21177		L	V	48.5	-7.921	147.08015
BPBM 41253	AA 21310	12953	L	V	51.3	-7.921	147.08015
BPBM 41254	AA 21311		L	V	48.9	-7.921	147.08015
BPBM 41255	AA 21316		L	V	47.3	-7.921	147.08015
BPBM 41256	AA 21404	13015	L	V	48.8	-7.93721	147.05444
BPBM 41257	AA 21405	13016	L	V	48.2	-7.93721	147.05444
BPBM 41258	AA 21407		L	V	45.4	-7.93721	147.05444
BPBM 41259	AA 21408		L	V	50.3	-7.93721	147.05444
BPBM 41260	AA 21409		L	V	48.8	-7.93721	147.05444
BPBM 41262	AA 21411		L	V	43.2	-7.93721	147.05444
BPBM 41263	AA 21412		L	V	46.5	-7.93721	147.05444
BPBM 41264	AA 21413		L	V	50.3	-7.93721	147.05444
BPBM 41265	AA 21414		L	V	49.7	-7.93803	147.04582
BPBM 41266	AA 21415		L	V	51.4	-7.93803	147.04582
BPBM 41267	AA 21416	13027	L	V	48.6	-7.93803	147.04582
BPBM 41268	AA 21417	13028	L	V	49.2	-7.93803	147.04582
BPBM 41269	AA 21418		L	V	48.6	-7.93803	147.04582
BPBM 41271	AA 21420		L	V	50.1	-7.93803	147.04582

BPBM 41272	AA 21421		L	V	51.3	-7.93803	147.04582
BPBM 41273	AA 21422		L	V	47.5	-7.93803	147.04582
BPBM 41274	AA 21423		L	V	51.7	-7.93803	147.04582
BPBM 41275	AA 21424		L	V	49.9	-7.93803	147.04582
BPBM 41276	AA 21456		L	V	50.8	-7.93803	147.04582
BPBM 41277	AA 21457		L	V	50.2	-7.93803	147.04582
BPBM 41278	AA 21458		L	V	49.5	-7.93803	147.04582
BPBM 41279	AA 21459		L	V	42.6	-7.93803	147.04582
BPBM 41281	AA 21461		L	V	50.1	-7.93803	147.04582
BPBM 41284	AA 21464		L	V	46.4	-7.93803	147.04582
BPBM 41285	AA 21465		L	V	48.8	-7.93803	147.04582
BPBM 41286	AA 21466		L	V	49.6	-7.93803	147.04582
BPBM 41287	AA 21467		L	V	50.1	-7.93803	147.04582
BPBM 41289	AA 21469		L	V	46.5	-7.93803	147.04582
BPBM 41290	AA 21470		L	V	48.6	-7.93803	147.04582
BPBM 41291	AA 21471		L	V	45.9	-7.93803	147.04582
BPBM 41292	AA 21472		L	V	48.7	-7.93803	147.04582
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BPBM 41294	AA 21474		L	V	48.9	-7.93803	147.04582
BPBM 41295	AA 21475		L	V	45.0	-7.93803	147.04582
BPBM 41297	AA 21477		L	V	50.5	-7.93803	147.04582
BPBM 41298	AA 21478		L	V	47.0	-7.93803	147.04582
BPBM 41300	AA 21495	13105	L	V	49.4	-7.93251	147.03993
BPBM 41301	AA 21496	13106	L	V	52.9	-7.93251	147.03993
BPBM 41303	AA 21526		L	V	49.0	-7.93803	147.04582
BPBM 41304	AA 21527		L	V	44.6	-7.93803	147.04582
BPBM 41306	AA 21529		L	V	48.3	-7.93803	147.04582
BPBM 41308	AA 21531		L	V	50.9	-7.93803	147.04582
BPBM 41309	AA 21532		L	V	48.4	-7.93803	147.04582

BPBM 41310	AA 21533		L	V	48.8	-7.93803	147.04582
BPBM 41311	AA 21534		L	V	47.2	-7.93803	147.04582
BPBM 41312	AA 21535		L	V	47.6	-7.93803	147.04582
BPBM 41314	AA 21542		L	V	45.4	-7.93721	147.05444
BPBM 41315	AA 21560		L	V	52.3	-7.93721	147.05444
BPBM 41316	AA 21561		L	V	49.5	-7.93721	147.05444
BPBM 41317	AA 21562		L	V	49.3	-7.93721	147.05444
BPBM 41318	AA 21563		L	V	49.7	-7.93721	147.05444
BPBM 41319	AA 21564		L	V	51.8	-7.93721	147.05444
BPBM 41320	AA 21565		L	V	50.0	-7.93721	147.05444
BPBM 41321	AA 21566		L	V	51.0	-7.93721	147.05444
BPBM 41322	AA 21567		L	V	51.9	-7.93721	147.05444
BPBM 41323	AA 21406		L	V	48.3	-7.93721	147.05444
BPBM 19591	FK 8959	8116	M	VI	56.4	-9.45711	148.0258
BPBM 38212	AA 20733		N	VI	61.9	-7.91876	147.08429
BPBM 41227	AA 21136		N	VI	61.0	-7.921	147.08015
BPBM 41228	AA 21144	12802	N	VI	62.5	-7.921	147.08015
BPBM 41229	AA 21145	12803	N	VI	61.2	-7.921	147.08015
BPBM 41230	AA 21171		N	VI	58.5	-7.921	147.08015
BPBM 41231	AA 21172		N	VI	52.3	-7.921	147.08015
BPBM 41232	AA 21173		N	VI	63.7	-7.921	147.08015
BPBM 41233	AA 21174		N	VI	61.5	-7.921	147.08015
BPBM 41234	AA 21179		N	VI	63.4	-7.921	147.08015
BPBM 41235	AA 21202		N	VI	55.1	-7.921	147.08015
BPBM 41236	AA 21303		N	VI	65.3	-7.921	147.08015
BPBM 41237	AA 21304		N	VI	62.3	-7.921	147.08015
BPBM 41238	AA 21305		N	VI	61.7	-7.921	147.08015
BPBM 41239	AA 21306		N	VI	65.1	-7.921	147.08015
BPBM 41240	AA 21307		N	VI	64.1	-7.921	147.08015

BPBM 41241	AA 21308		N	VI	62.6	-7.921	147.08015
BPBM 41242	AA 21312		N	VI	58.1	-7.921	147.08015
BPBM 41243	AA 21313		N	VI	63.2	-7.921	147.08015
BPBM 41244	AA 21314		N	VI	59.1	-7.921	147.08015
BPBM 41245	AA 21403	13014	N	VI	51.6	-7.93721	147.05444
BPBM 41246	AA 21503	13113	N	VI	63.7	-7.93803	147.04582
BPBM 41247	AA 21504	13114	N	VI	61.4	-7.93251	147.03993
BPBM 41248	AA 21505	13115	N	VI	57.3	-7.93251	147.03993
BPBM 41249	AA 21506		N	VI	58.8	-7.93251	147.03993
BPBM 44747	AA 23018		O	VII	55.7	-8.9650667	147.73275
BPBM 44748	AA 23079		O	VII	56.6	-8.964611	147.732717
BPBM 44749	AA 23080	44749	O	VII	59.5	-8.964611	147.732717
BPBM 44750	AA 23134		O	VII	59.1	-8.96438	147.731923
BPBM 16767	FK 7409	7536	P	VII	56.0	-10.0364	149.5749
BPBM 16769	FK 7417	7540	P	VII	53.5	-10.0364	149.5749
BPBM 39061	FK 15334	10148	P	VII	57.0	-9.75802	149.18218
PM 25118	FK 7418		P	VII	51.5	-10.0364167	149.5748833
PM 25119	FK 7419		P	VII	55.3	-10.0364167	149.5748833
BPBM 39060	FK 15282	10121	Q	VII	52.8	-9.76505	149.21764
BPBM 39063	FK 15379	10163	Q	VII	62.6	-9.75802	149.18218
BPBM 39064	FK 15380		Q	VII	59.1	-9.75802	149.18218
BPBM 39069	FK 15385		Q	VII	46.0	-9.76258	149.20211
BPBM 39071	FK 15387	10166	Q	VII	59.7	-9.76258	149.20211
BPBM 39072	FK 15388		Q	VII	56.2	-9.76258	149.20211
BPBM 39081	FK 15409		Q	VII	61.0	-9.75802	149.18218
BPBM 39082	FK 15410		Q	VII	60.1	-9.75802	149.18218
BPBM 39083	FK 15411		Q	VII	60.9	-9.75802	149.18218
BPBM 39085	FK 15428		Q	VII	59.4	-9.75802	149.18218
BPBM 39086	FK 15429		Q	VII	58.6	-9.75802	149.18218
BPBM 39087	FK 15430		Q	VII	58.7	-9.75802	149.18218

BPBM 39088	FK 15431		Q	VII	53.2	-9.75802	149.18218
BPBM 39089	FK 15578	10203	Q	VII	60.6	-9.76505	149.21764
	FK 15397		Q	VII	54.0	-9.76258	149.20211
BPBM 44751	AA 23146		R	VIII	61.7	-9.05596	147.7368
BPBM 44754	AA 23149		R	VIII	56.5	-9.05451	147.75782
BPBM 44755	AA 23150		R	VIII	52.6	-9.05451	147.75782
BPBM 44756	AA 23151		R	VIII	60.8	-9.05451	147.75782
BPBM 44757	AA 23152		R	VIII	54.3	-9.05451	147.75782
BPBM 44758	AA 23153		R	VIII	61.1	-9.05451	147.75782
BPBM 44759	AA 23154		R	VIII	51.9	-9.05451	147.75782
BPBM 44760	AA 23155		R	VIII	59.5	-9.05451	147.75782
BPBM 44762	AA 23157		R	VIII	65.2	-9.071289	147.735211
BPBM 44763	AA 23158		R	VIII	53.7	-9.0448833	147.74095
BPBM 44766	AA 23170		R	VIII	55.8	-9.033287	147.739861
BPBM 44767	AA 23171		R	VIII	57.8	-9.033287	147.739861
BPBM 44770	AA 23174		R	VIII	50.2	-9.033287	147.739861
BPBM 44771	AA 23181		R	VIII	57.3	-9.0378167	147.74085
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BPBM 44775	AA 23185		R	VIII	56.6	-9.0366	147.7410667
BPBM 44777	AA 23198		R	VIII	54.6	-9.05451	147.73782
BPBM 44778	AA 23199		R	VIII	59.3	-9.05451	147.73782
BPBM 44779	AA 23200		R	VIII	61.0	-9.05451	147.73782
BPBM 44780	AA 23201		R	VIII	62.6	-9.05451	147.73782
BPBM 44781	AA 23202		R	VIII	57.9	-9.05451	147.73782
BPBM 44783	AA 23204		R	VIII	50.7	-9.04782	147.73505
BPBM 44787	AA 23208		R	VIII	55.3	-9.05596	147.7368
BPBM 44788	AA 23209		R	VIII	61.9	-9.07094	147.7348
BPBM 44789	AA 23210		R	VIII	64.0	-9.06744	147.73532
BPBM 44790	AA 23211		R	VIII	65.0	-9.08285	147.76342

BPBM 44791	AA 23212		R	VIII	57.2	-9.08285	147.76342
BPBM 44792	AA 23215		R	VIII	58.1	-9.091225	147.734361
BPBM 44793	AA 23216		R	VIII	59.2	-9.091225	147.734361
BPBM 44794	AA 23217		R	VIII	59.5	-9.091225	147.734361
BPBM 44795	AA 23218		R	VIII	52.1	-9.091225	147.734361
BPBM 44797	AA 23220		R	VIII	59.5	-9.091225	147.734361
BPBM 44798	AA 23221		R	VIII	62.2	-9.091225	147.734361
BPBM 44799	AA 23222		R	VIII	59.3	-9.091225	147.734361
BPBM 44801	AA 23224		R	VIII	51.3	-9.091225	147.734361
BPBM 44802	AA 23225		R	VIII	55.0	-9.091225	147.734361
BPBM 44812	AA 23235		R	VIII	55.1	-9.091225	147.734361
BPBM 44813	AA 23236		R	VIII	50.0	-9.091225	147.734361
BPBM 44815	AA 23238		R	VIII	56.2	-9.091225	147.734361
BPBM 44817	AA 23242		R	VIII	63.1	-9.091225	147.734361
BPBM 44820	AA 23246		R	VIII	57.1	-9.091225	147.734361
BPBM 44821	AA 23247		R	VIII	55.2	-9.091225	147.734361
BPBM 44822	AA 23248		R	VIII	61.5	-9.091225	147.734361
BPBM 44824	AA 23250		R	VIII	52.0	-9.092002	147.7379
BPBM 44825	AA 23251		R	VIII	60.6	-9.092002	147.7379
BPBM 44826	AA 23252		R	VIII	66.4	-9.092002	147.7379
BPBM 44827	AA 23253		R	VIII	59.1	-9.092002	147.7379
BPBM 44828	AA 23254		R	VIII	57.3	-9.092002	147.7379
BPBM 44829	AA 23255		R	VIII	59.2	-9.092002	147.7379
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BPBM 44834	AA 23261		R	VIII	59.7	-9.092002	147.7379
BPBM 44835	AA 23262		R	VIII	63.4	-9.092002	147.7379
BPBM 44836	AA 23294		R	VIII	61.9	-9.10536	147.73794

BPBM 44838	AA 23296		R	VIII	65.5	-9.112397	147.726369
BPBM 44839	AA 23297		R	VIII	59.4	-9.218797	147.726369
BPBM 44840	AA 23298		R	VIII	63.9	-9.218797	147.726369
BPBM 44841	AA 23340	44841	R	VIII	63.6	-9.218797	147.726369
BPBM 44845	AA 23347		R	VIII	59.4	-9.218797	147.726369
BPBM 44846	AA 23348		R	VIII	56.9	-9.218797	147.726369
BPBM 44847	AA 23349		R	VIII	45.9	-9.218797	147.726369
BPBM 44848	AA 23350		R	VIII	62.5	-9.218797	147.726369
BPBM 44849	AA 23351		R	VIII	57.9	-9.218797	147.726369
BPBM 44853	AA 23355		R	VIII	59.7	-9.218797	147.726369
BPBM 44854	AA 23356		R	VIII	57.5	-9.218797	147.726369
BPBM 44857	AA 23390	44857	R	VIII	64.8	-9.150945	147.767477
BPBM 44860	AA 23397		R	VIII	47.7	-9.150945	147.767477
BPBM 44861	AA 23427		R	VIII	60.8	-9.118136	147.734361
BPBM 44863	AA 23437		R	VIII	64.6	-9.218797	147.726369
BPBM 44864	AA 23439		R	VIII	60.8	-9.14217	147.72617
BPBM 44865	AA 23443		R	VIII	59.8	-9.150646	147.767192
BPBM 44866	AA 23453		R	VIII	62.1	-9.150793	147.768331
BPBM 44867	AA 23454		R	VIII	59.7	-9.150793	147.768331
BPBM 44868	AA 23455		R	VIII	60.0	-9.150793	147.768331
BPBM 44869	AA 23458		R	VIII	51.2	-9.128795	147.726369
BPBM 44871	AA 23460		R	VIII	56.5	-9.14068	147.74244
BPBM 44872	AA 23475		R	VIII	58.9	-9.178219	147.767188
BPBM 44873	AA 23476		R	VIII	67.3	-9.178219	147.767188
BPBM 44874	AA 23482		R	VIII	55.5	-9.218797	147.726369
BPBM 44875	AA 23487		R	VIII	67.3	-9.11242	147.73806
BPBM 44876	AA 23488		R	VIII	64.3	-9.11242	147.73806
BPBM 44877	AA 23489		R	VIII	61.9	-9.11242	147.73806
BPBM 44878	AA 23490		R	VIII	47.7	-9.11242	147.73806

BPBM 44879	AA 23491		R	VIII	67.8	-9.11242	147.73806
BPBM 44880	AA 23492		R	VIII	62.0	-9.11242	147.73806
BPBM 44306	AA 22424	13587	S	IX	59.6	-8.20692	146.78476
BPBM 10935			T	IX	62.3	-8.576	147.072
BPBM 10936			T	IX	62.3	-8.576	147.072
BPBM 10937			T	IX	58.1	-8.576	147.072
BPBM 10938			T	IX	58.5	-8.576	147.072
BPBM 10939			T	IX	61.4	-8.576	147.072
BPBM 10940			T	IX	59.5	-8.576	147.072
BPBM 10941			T	IX	60.2	-8.576	147.072
BPBM 10942			T	IX	61.3	-8.576	147.072
BPBM 10943			T	IX	65.6	-8.576	147.072
BPBM 10944			T	IX	64.8	-8.576	147.072
BPBM 10945			T	IX	48.5	-8.576	147.072
BPBM 10946			T	IX	43.2	-8.576	147.072
BPBM 10947			T	IX	64.9	-8.576	147.072
BPBM 10948			T	IX	53.7	-8.576	147.072
BPBM 18858	FK 7896	7662	T	IX	60.9	-8.5377666	147.2423166
BPBM 18859	FK 7897	7663	T	IX	57.1	-8.5377666	147.2423166
BPBM 18861	FK 7928	7677	T	IX	62.2	-8.5448369	147.2504528
BPBM 18862	FK 7929	7678	T	IX	57.4	-8.5448369	147.2504528
BPBM 18863	FK 7939		T	IX	60.6	-8.5448369	147.2504528
BPBM 18864	FK 7940		T	IX	56.6	-8.5448369	147.2504528
BPBM 18865	FK 7941		T	IX	61.1	-8.5448369	147.2504528
BPBM 18866	FK 7959		T	IX	63.1	-8.45538	147.26301
BPBM 18867	FK 7960		T	IX	65.2	-8.45538	147.26301
BPBM 18868	FK 7961		T	IX	54.6	-8.5448369	147.2504528
BPBM 18869	FK 7962		T	IX	61.2	-8.5448369	147.2504528
BPBM 18870	FK 7963		T	IX	65.6	-8.5448369	147.2504528
BPBM 18871	FK 7964		T	IX	64.3	-8.5448369	147.2504528

BPBM 18872	FK 7965		T	IX	63.5	-8.5448369	147.2504528
BPBM 18875	FK 8039	7722	T	IX	62.4	-8.56933	147.07675
BPBM 18876	FK 8040	7723	T	IX	57.4	-8.56933	147.07675
BPBM 18877	FK 8041		T	IX	61.6	-8.56789	147.07777
BPBM 18881	FK 8056	7732	T	IX	58.2	-8.56825	147.08509
BPBM 18882	FK 8057		T	IX	58.9	-8.5668056	147.0861111
BPBM 18883	FK 8059		T	IX	56.0	-8.5668056	147.0861111

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717 **Table S3.** Pairwise uncorrected mitochondrial sequence divergence (*p*-distances) between and within lineages of *Papuascincus* as delimited by  
 718 BP&P analyses (I-IX) for the three mitochondrial gene markers (12S, ND2 and ND4). The lower diagonal cells are *p*-distances and the upper  
 719 diagonal cells are the corresponding SE values.  
 720

	I	II	III	IV	V	VI	VII	VIII	IX	Within Lineage <i>p</i> -distance	Within Lineage SE
<b>12S</b>											
I		1.0	0.8	1.1	1.1	0.9	0.9	0.9	1.0	1.94	0.49
II	5.2		1.1	1.2	1.3	1.2	1.1	1.2	1.2	0.54	0.30
III	3.9	5.9		1.1	1.1	1.0	0.9	0.9	1.0	1.77	0.44
IV	7.2	7.3	7.3		0.8	1.0	1.1	1.0	1.1	2.39	0.61
V	6.1	7.7	6.4	4.2		1.0	1.1	1.0	1.1	0.00	0.00
VI	4.5	7.0	5.2	6.0	5.1		0.8	0.8	0.9	0.58	0.23
VII	4.7	6.5	4.9	6.7	5.6	3.2		0.9	1.0	0.79	0.27
VIII	4.2	6.6	4.3	5.4	4.2	3.0	3.7		0.8	0.00	0.00
IX	5.3	7.1	5.3	6.0	4.8	3.8	4.6	3.2		0.06	0.06
<b>ND2</b>											
I		1.0	0.9	1.0	1.0	0.9	1.0	1.0	0.9	1.94	0.49
II	14.6		0.9	1.0	1.1	1.0	1.1	1.0	1.0	0.54	0.30
III	14.6	12.8		0.9	1.0	1.0	1.0	1.0	1.0	1.77	0.44
IV	15.9	15.3	14.5		0.9	0.9	0.9	0.9	1.0	2.39	0.61
V	15.3	15.8	15.1	11.1		1.0	1.0	1.0	1.1	0.00	0.00
VI	16.0	15.3	15.0	15.2	14.2		0.9	0.9	1.0	0.58	0.23
VII	16.0	14.9	15.6	14.6	14.1	12.4		0.9	0.9	0.79	0.27
VIII	15.2	14.8	14.6	13.6	13.1	12.8	10.6		0.9	0.00	0.00
IX	14.5	15.1	15.2	14.6	14.5	12.2	12.1	9.4		0.06	0.06
<b>ND4</b>											
I		1.2	1.1	1.1	1.2	1.1	1.1	1.3	1.3	5.90	0.54
II	15.1		1.0	1.2	1.3	1.3	1.3	1.3	1.4	2.28	0.47

<b>III</b>	14.4	11.9		1.0	1.1	1.1	1.1	1.2	1.2	6.14	0.59
<b>IV</b>	15.2	15.7	13.9		1.0	1.1	1.2	1.2	1.2	5.00	0.59
<b>V</b>	15.9	16.1	14.4	11.3		1.2	1.2	1.3	1.3	0.09	0.06
<b>VI</b>	14.8	14.3	14.1	13.4	14.4		1.1	1.2	1.1	1.95	0.33
<b>VII</b>	14.7	15.8	13.9	14.7	14.3	12.2		1.1	1.2	2.89	0.37
<b>VIII</b>	15.6	14.8	14.1	14.0	13.9	12.5	11.7		1.1	0.00	0.00
<b>IX</b>	15.7	14.9	14.1	14.7	15.1	11.6	12.4	9.7		1.29	0.24

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723 **Table S4.** Pairwise uncorrected mitochondrial sequence divergence (*p*-distances) between and within lineages of *Papuascincus* as delimited by  
 724 GMYC and bGMYC analyses (A-T) for the three mitochondrial gene markers (*12S*, *ND2* and *ND4*). The lower diagonal cells are *p*-distances and  
 725 the upper diagonal cells are the corresponding SE values.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	Within Lineage <i>p</i> -distance	Within Lineage SE
<b>12S</b>																						
<b>A</b>		1.1%	1.4%	1.5%	1.2%	1.2%	1.2%	1.2%	1.6%	1.6%	1.5%	1.4%	1.2%	1.1%	1.2%	1.2%	1.2%	1.1%	1.3%	1.2%	0.00%	0.00%
<b>B</b>	4.5%		1.0%	1.1%	1.0%	0.8%	0.9%	0.9%	1.2%	1.2%	1.2%	1.1%	1.1%	1.0%	1.1%	1.0%	1.0%	1.0%	1.1%	1.0%	0.00%	0.00%
<b>C</b>	6.8%	4.2%		0.4%	1.2%	1.1%	1.2%	1.2%	1.3%	1.3%	1.3%	1.3%	1.3%	1.2%	1.3%	1.2%	1.2%	1.2%	1.2%	1.2%	-	-
<b>D</b>	7.4%	4.6%	0.8%		1.3%	1.2%	1.2%	1.2%	1.3%	1.3%	1.4%	1.3%	1.3%	1.3%	1.3%	1.2%	1.2%	1.2%	1.3%	1.3%	0.00%	0.00%
<b>E</b>	5.8%	4.2%	6.3%	6.8%		0.8%	0.9%	0.8%	1.4%	1.4%	1.4%	1.3%	1.2%	1.2%	1.2%	1.1%	1.1%	1.1%	1.1%	1.1%	0.00%	0.00%
<b>F</b>	5.3%	2.5%	5.1%	5.5%	2.7%		0.7%	0.7%	1.2%	1.2%	1.2%	1.1%	1.1%	1.0%	1.1%	1.0%	0.9%	1.1%	1.0%	0.18%	0.17%	
<b>G</b>	5.5%	3.7%	5.5%	6.0%	3.4%	2.5%		0.6%	1.4%	1.3%	1.4%	1.3%	1.2%	1.1%	1.1%	1.0%	1.0%	1.1%	1.1%	0.00%	0.00%	
<b>H</b>	5.2%	3.7%	5.6%	6.0%	2.7%	1.9%	1.6%		1.3%	1.3%	1.3%	1.2%	1.1%	1.1%	1.1%	1.0%	1.0%	1.0%	1.1%	0.00%	0.00%	
<b>I</b>	9.3%	7.1%	7.7%	7.5%	8.5%	6.7%	8.4%	8.0%		0.5%	0.9%	1.0%	1.3%	1.2%	1.2%	1.2%	1.2%	1.2%	1.2%	1.2%	-	-
<b>J</b>	8.8%	6.6%	7.2%	7.2%	7.9%	6.1%	7.9%	7.4%	1.2%		1.0%	0.9%	1.3%	1.2%	1.2%	1.2%	1.2%	1.1%	1.1%	0.26%	0.26%	
<b>K</b>	8.7%	6.4%	7.1%	7.5%	7.7%	6.0%	7.8%	7.4%	3.6%	3.7%		1.0%	1.2%	1.1%	1.3%	1.2%	1.2%	1.1%	1.2%	1.2%	0.17%	0.12%
<b>L</b>	7.1%	5.8%	7.4%	7.9%	7.4%	5.4%	6.8%	6.4%	4.5%	3.8%	4.3%		1.2%	1.0%	1.2%	1.1%	1.1%	1.0%	1.1%	1.1%	0.00%	0.00%
<b>M</b>	5.0%	4.9%	7.2%	7.6%	6.7%	5.3%	5.9%	5.5%	7.3%	7.3%	6.5%	5.9%		0.5%	1.0%	0.9%	0.9%	0.9%	1.1%	1.0%	0.26%	0.25%
<b>N</b>	4.4%	4.3%	6.6%	6.9%	6.1%	4.7%	5.3%	4.8%	6.1%	6.1%	5.3%	4.8%	1.2%		0.9%	0.8%	0.8%	0.8%	0.9%	0.9%	0.09%	0.08%
<b>O</b>	5.2%	5.5%	6.8%	7.0%	6.6%	5.6%	5.0%	5.0%	7.1%	7.0%	7.1%	5.8%	4.1%	3.5%		0.6%	0.6%	1.0%	1.1%	1.0%	-	-
<b>P</b>	5.4%	4.7%	6.6%	6.8%	6.1%	5.2%	4.5%	4.8%	7.2%	6.9%	6.5%	5.8%	3.8%	3.2%	1.5%		0.4%	0.9%	1.0%	1.0%	0.70%	0.33%
<b>Q</b>	5.0%	4.3%	6.1%	6.3%	5.8%	4.9%	4.3%	4.3%	6.9%	6.6%	6.3%	5.3%	3.4%	2.7%	1.4%	0.8%		0.8%	1.0%	1.0%	0.13%	0.12%
<b>R</b>	4.2%	4.2%	6.3%	6.8%	5.0%	3.8%	4.7%	4.2%	6.1%	5.5%	5.1%	4.2%	3.8%	2.7%	4.2%	3.9%	3.5%		0.8%	0.8%	0.00%	0.00%
<b>S</b>	5.8%	5.5%	6.6%	7.0%	6.3%	5.4%	5.8%	5.3%	6.3%	5.8%	6.0%	5.0%	4.9%	3.7%	5.2%	5.0%	4.5%	3.4%	0.2%	-	-	
<b>T</b>	5.5%	5.2%	6.8%	7.3%	6.0%	5.1%	5.5%	5.0%	6.3%	5.8%	6.0%	4.7%	4.6%	3.5%	5.0%	4.7%	4.3%	3.1%	0.3%		0.00%	0.00%
<b>ND2</b>																						
<b>A</b>		0.93%	1.05%	1.10%	1.11%	1.06%	1.06%	1.09%	1.09%	1.08%	1.09%	1.08%	1.10%	1.11%	1.13%	1.06%	1.10%	1.08%	1.03%	1.08%	0.29%	0.17%
<b>B</b>	11.86%		1.05%	1.15%	1.07%	1.06%	1.07%	1.15%	1.10%	1.08%	1.09%	1.11%	1.01%	1.05%	1.10%	1.08%	1.14%	1.04%	0.95%	0.96%	0.34%	0.12%
<b>C</b>	14.12%	13.90%		0.59%	1.00%	1.04%	1.02%	1.05%	1.04%	1.06%	1.07%	1.11%	1.07%	1.05%	1.07%	1.07%	1.08%	1.06%	1.05%	1.06%	-	-
<b>D</b>	14.71%	15.02%	3.35%		1.05%	1.06%	1.09%	1.04%	1.07%	1.07%	1.11%	1.11%	1.14%	1.11%	1.09%	1.12%	1.14%	1.11%	1.11%	1.09%	0.22%	0.15%

E	15.29%	13.19%	11.57%	12.47%		0.87%	0.84%	0.91%	1.06%	1.07%	1.06%	1.08%	1.13%	1.07%	1.06%	1.10%	1.07%	1.03%	1.09%	1.06%	0.00%	0.00%
F	15.46%	14.26%	13.50%	12.99%	8.69%		0.84%	0.83%	1.08%	1.08%	1.08%	1.04%	1.05%	1.02%	1.08%	1.04%	1.05%	1.09%	1.06%	1.00%	0.13%	0.09%
G	15.05%	14.36%	12.84%	13.23%	9.71%	8.55%		0.61%	1.07%	1.07%	1.08%	1.10%	1.09%	1.02%	1.12%	1.08%	1.07%	1.06%	1.06%	1.05%	0.49%	0.22%
H	15.14%	14.87%	12.43%	12.82%	9.26%	8.52%	4.49%		1.15%	1.17%	1.16%	1.10%	1.09%	1.09%	1.15%	1.12%	1.14%	1.09%	1.12%	1.13%	0.56%	0.17%
I	16.52%	15.40%	14.61%	15.45%	14.41%	14.41%	14.07%	13.72%		0.40%	0.83%	0.95%	1.13%	1.10%	1.04%	1.09%	1.10%	1.00%	0.99%	1.03%	-	-
J	16.62%	15.84%	15.10%	15.97%	14.71%	14.74%	14.31%	14.48%	1.76%		0.84%	0.94%	1.10%	1.08%	1.03%	1.06%	1.06%	0.99%	1.00%	1.03%	0.20%	0.14%
K	16.13%	15.90%	14.80%	15.35%	14.31%	14.77%	14.56%	14.68%	8.33%	8.92%		0.96%	1.15%	1.10%	1.06%	1.08%	1.09%	1.01%	1.10%	1.07%	0.00%	0.00%
L	14.59%	15.55%	15.60%	15.97%	15.59%	15.09%	15.40%	14.87%	11.09%	11.20%	10.98%		1.07%	1.05%	1.10%	1.04%	1.10%	0.99%	1.09%	1.11%	0.00%	0.00%
M	16.29%	15.72%	14.95%	15.85%	14.73%	14.18%	15.00%	15.53%	14.25%	14.57%	15.27%	14.62%		0.60%	0.99%	1.00%	1.00%	0.98%	1.00%	0.99%	0.54%	0.23%
N	16.62%	15.94%	14.90%	15.38%	14.68%	14.50%	14.95%	15.44%	14.55%	15.01%	15.89%	14.05%	4.64%		0.94%	1.01%	1.03%	1.00%	0.96%	0.97%	0.14%	0.07%
O	16.13%	15.38%	14.61%	15.14%	14.22%	15.26%	15.64%	15.13%	13.92%	13.82%	13.82%	13.69%	11.94%	11.62%		0.73%	0.76%	0.95%	0.95%	-	-	-
P	15.13%	15.40%	13.97%	14.70%	14.17%	15.09%	15.48%	15.23%	14.45%	14.31%	14.39%	13.67%	12.19%	12.16%	6.09%		0.48%	0.94%	0.95%	0.98%	0.64%	0.21%
Q	16.18%	16.67%	14.99%	15.48%	15.02%	16.13%	16.26%	16.38%	15.28%	15.05%	14.67%	14.56%	13.01%	12.77%	7.00%	2.92%		0.98%	0.94%	1.00%	0.83%	0.20%
R	15.39%	15.19%	14.26%	15.04%	13.58%	14.92%	15.59%	14.36%	14.17%	14.66%	12.79%	13.09%	12.42%	12.97%	10.64%	10.13%	11.01%		0.88%	0.89%	0.10%	0.10%
S	14.46%	13.42%	14.71%	15.55%	13.53%	14.67%	15.54%	15.54%	14.71%	15.29%	14.31%	14.30%	12.04%	12.13%	10.98%	11.09%	11.87%	9.17%		0.47%	-	-
T	15.13%	14.36%	14.70%	15.20%	14.27%	14.55%	15.51%	15.87%	14.55%	15.24%	14.15%	14.55%	12.47%	12.10%	11.42%	12.07%	12.36%	9.42%	2.75%		0.48%	0.15%

#### ND4

A		1.2%	1.4%	1.3%	1.4%	1.2%	1.4%	1.4%	1.3%	1.3%	1.3%	1.3%	1.2%	1.3%	1.3%	1.3%	1.3%	1.4%	1.4%	1.4%	0.14%	0.14%	
B	13.4%		1.4%	1.3%	1.3%	1.2%	1.3%	1.4%	1.4%	1.4%	1.3%	1.3%	1.3%	1.3%	1.3%	1.3%	1.3%	1.4%	1.3%	1.4%	0.27%	0.12%	
C	15.5%	15.7%		0.7%	1.2%	1.2%	1.2%	1.1%	1.2%	1.3%	1.4%	1.4%	1.4%	1.3%	1.4%	1.4%	1.4%	1.4%	1.3%	1.4%	1.4%	-	-
D	15.2%	14.7%	3.4%		1.2%	1.1%	1.1%	1.1%	1.2%	1.3%	1.3%	1.4%	1.4%	1.3%	1.3%	1.3%	1.4%	1.3%	1.3%	1.3%	1.3%	0.00%	0.00%
E	15.8%	14.8%	11.8%	11.8%		1.0%	1.1%	1.0%	1.2%	1.3%	1.4%	1.3%	1.3%	1.3%	1.3%	1.3%	1.3%	1.4%	1.3%	1.3%	1.3%	0.00%	0.00%
F	15.2%	13.9%	12.2%	11.8%	8.3%		1.0%	1.0%	1.2%	1.2%	1.3%	1.3%	1.3%	1.3%	1.3%	1.3%	1.4%	1.3%	1.3%	1.3%	1.3%	0.09%	0.09%
G	15.6%	14.3%	12.2%	12.4%	8.8%	8.4%		0.8%	1.3%	1.2%	1.3%	1.2%	1.3%	1.3%	1.3%	1.3%	1.3%	1.4%	1.3%	1.3%	1.3%	0.60%	0.28%
H	15.2%	14.0%	11.8%	11.8%	8.1%	8.3%	5.8%		1.2%	1.2%	1.2%	1.3%	1.2%	1.3%	1.2%	1.2%	1.3%	1.3%	1.3%	1.3%	1.3%	0.58%	0.22%
I	15.9%	15.2%	14.0%	14.4%	13.2%	13.4%	14.3%	12.0%		0.4%	1.0%	1.1%	1.2%	1.2%	1.2%	1.2%	1.2%	1.3%	1.3%	1.3%	1.3%	-	-
J	15.5%	14.8%	14.2%	14.9%	14.2%	13.3%	14.2%	12.0%	1.4%		0.9%	1.1%	1.2%	1.2%	1.2%	1.2%	1.3%	1.3%	1.3%	1.3%	1.3%	0.00%	0.00%
K	16.3%	15.0%	17.1%	16.8%	16.0%	14.6%	15.5%	14.1%	8.6%	7.7%		1.2%	1.3%	1.2%	1.2%	1.3%	1.3%	1.4%	1.4%	1.4%	1.4%	0.10%	0.09%
L	15.6%	16.0%	16.1%	16.1%	15.6%	14.9%	14.6%	13.6%	10.6%	10.5%	12.1%		1.2%	1.3%	1.2%	1.2%	1.3%	1.3%	1.2%	1.3%	1.3%	0.09%	0.06%
M	14.8%	14.9%	14.3%	14.4%	14.2%	14.3%	15.2%	13.8%	11.6%	12.4%	14.6%	13.7%		0.8%	1.1%	1.2%	1.2%	1.1%	1.2%	1.2%	0.15%	0.14%	
N	14.5%	14.8%	13.9%	14.4%	14.0%	14.3%	15.4%	13.4%	12.2%	12.7%	14.4%	14.6%	4.4%		1.2%	1.3%	1.3%	1.3%	1.2%	1.2%	0.10%	0.07%	
O	14.9%	14.3%	15.4%	15.3%	14.1%	14.9%	13.5%	12.8%	12.1%	12.2%	14.6%	12.8%	11.2%	12.8%		0.8%	0.9%	1.1%	1.2%	1.2%	-	-	
P	15.7%	14.1%	16.0%	16.0%	13.5%	14.6%	13.5%	12.9%	13.6%	13.7%	15.7%	13.9%	11.2%	12.2%	5.8%		0.5%	1.1%	1.2%	1.2%	0.94%	0.29%	
Q	15.4%	14.7%	16.0%	15.8%	13.8%	14.9%	14.4%	13.9%	14.1%	14.3%	15.8%	14.9%	11.5%	12.5%	6.7%	2.4%		1.2%	1.2%	1.2%	0.87%	0.25%	

R	15.9%	15.5%	14.2%	15.1%	15.0%	13.9%	15.0%	13.4%	13.6%	13.1%	14.8%	13.9%	11.3%	12.9%	11.2%	11.5%	12.0%		1.1%	1.1%	0.00%	0.00%
S	16.3%	15.7%	14.5%	15.0%	14.2%	13.8%	15.3%	13.8%	13.1%	13.5%	16.4%	14.6%	11.7%	11.5%	11.7%	12.6%	12.6%	10.2%		0.7%	-	-
T	16.0%	15.6%	14.5%	15.1%	14.3%	14.1%	15.3%	13.7%	13.7%	13.9%	15.5%	15.1%	11.7%	11.6%	12.1%	12.3%	12.4%	9.6%	3.6%		0.63%	0.19%

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728 **Table S5.** Pairwise comparisons of SVL between different GMYC/bGMYC lineages, performed using a *post-hoc* Tukey test. The upper triangle  
 729 shows the adjusted p values for each pair of lineages, from the corresponding row and column. Significant p values, with an alpha of 0.05, are  
 730 marked in bold. Cells shaded light grey represent comparisons between lineages of the small morph, cells shaded dark grey represent  
 731 comparisons between lineages of the large morph, and unshaded cells represent comparisons between lineages of different morphs. The two  
 732 right-most columns show the mean SVL (in mm)  $\pm$  standard error, and the sample size for each lineage.

GMYC/bGMYC Lineage	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	Mean SVL	n		
A		0.851	1	0.095	<b>0</b>	1	1	0.902	0.347	<b>0</b>	<b>0</b>	1	0.915	<b>0</b>	<b>0.001</b>	0.153	<b>0</b>	<b>0</b>	0.3	<b>0</b>	49.5 $\pm$	46		
B			1	<b>0.001</b>	<b>0</b>	0.44	1	<b>0.03</b>	0.977	<b>0</b>	<b>0</b>	<b>0.032</b>	0.989	<b>0</b>	<b>0.013</b>	0.619	<b>0</b>	<b>0</b>	0.556	<b>0</b>	50.8 $\pm$	106		
C				1	0.776	1	1	1	1	0.711	0.618	1	0.979	0.051	0.584	0.972	0.473	0.207	0.693	0.1	48.1	1		
D					<b>0.036</b>	0.877	0.902	0.991	<b>0</b>	<b>0</b>	<b>0</b>	0.362	0.248	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0.017</b>	<b>0</b>	45.6 $\pm$	11		
E						<b>0</b>	<b>0.001</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0.001</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	0.57	9		
F							1	1	0.111	<b>0</b>	<b>0</b>	1	0.767	<b>0</b>	<b>0</b>	<b>0.046</b>	<b>0</b>	<b>0</b>	0.16	<b>0</b>	0.48	17		
G								1	0.997	0.041	0.018	1	0.973	<b>0</b>	0.107	0.818	<b>0.009</b>	<b>0</b>	0.525	<b>0</b>	49.7 $\pm$	4		
H									<b>0.011</b>	<b>0</b>	<b>0</b>	0.999	0.615	<b>0</b>	<b>0</b>	<b>0.009</b>	<b>0</b>	<b>0</b>	0.089	<b>0</b>	0.99	20		
I										<b>0.07</b>	<b>0.019</b>	<b>0.04</b>	1	<b>0</b>	0.442	1	<b>0.014</b>	<b>0</b>	0.905	<b>0</b>	52.5 $\pm$ 1.2	14		
J											1	<b>0</b>	1	1	1	1	0.056	1	<b>0.005</b>	56.3 $\pm$ 0.6	35			
K												<b>0</b>	1	<b>0.003</b>	1	1	1	0.294	1	<b>0.032</b>	56.7 $\pm$	35		
L													0.811	<b>0</b>	<b>0</b>	<b>0.034</b>	<b>0</b>	<b>0</b>	0.182	<b>0</b>	0.62	48.8 $\pm$	64	
M														<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0.28	1		
N															0.992	0.06	0.402	0.645	1	1	1	56.4	24	
O																<b>0.999</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0.75	50.6 $\pm$	4	
P																	<b>0.99</b>	0.56	0.999	0.197	0.92	54.7 $\pm$	5	
Q																		<b>1</b>	<b>1</b>	0.855	0.97	1.13	57.5 $\pm$	15
R																			<b>1</b>	0.994	0.51	58.7 $\pm$	86	
S																			<b>1</b>	59.6	0.82	59.8 $\pm$	1	
T																					59.8 $\pm$	34		

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