

Arrival and diversification of mabuyine skinks (Squamata: Scincidae) in the Neotropics based on a fossil-calibrated timetree

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Background: The evolution of South American Mabuyinae skinks holds significant biogeographic interest because its sister lineage is distributed across the African continent and adjacent islands. Moreover, at least one insular species, *Trachylepis atlantica*, has independently reached the New World through transoceanic dispersal. To clarify the evolutionary history of both Neotropical lineages, this study aimed to infer an updated timescale using the largest species and gene sampling dataset ever assembled for this group. By extending the analysis to the Scincidae family, we could employ fossil information to estimate mabuyinae divergence times and carried out a formal statistical biogeography analysis. To unveil macroevolutionary patterns, we also inferred diversification rates for this lineage and evaluated whether the colonization of South American continent significantly altered the mode of Mabuyinae evolution.

Methods: A time-calibrated phylogeny was inferred under the Bayesian framework employing fossil information. This timetree was used to (i) evaluate the historical biogeography of mabuyines using the statistical approach implemented in BioGeoBEARS; (ii) estimate macroevolutionary diversification rates of the South American Mabuyinae lineages and the patterns of evolution of selected traits, namely, the mode of reproduction, body mass and snout-vent length; (iii) test the hypothesis of differential macroevolutionary patterns in South American lineages in BAMM and GeoSSE; and (iv) re-evaluate the ancestral state of the mode of reproduction of mabuyines.

Results: Our results corroborated the hypothesis that the occupation of the South American continent by Mabuyinae consisted of two independent dispersion events that occurred between the Oligocene and the Miocene. We found significant differences in speciation rates between the New World and the remaining Mabuyinae clades only in GeoSSE. The influence of phenotypic traits on diversification rates was not supported by any method. Ancestral state reconstruction suggested that the ancestor of South American mabuyine was likely viviparous.

Discussion: Our analyses further corroborated the existence of a transoceanic connection between Africa and South America in the Eocene/Oligocene period (Atlantogea). Following colonization of the isolated South America and subsequent dispersal through the continent by the ancestral mabuyine stock, we detected no difference in macroevolutionary regimes of New World clades. This finding argued against the ecological opportunity model as an explanation for the diversity of living mabuyines.

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20 **Abstract**

21

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49 colonization of the isolated South America and subsequent dispersal through the continent by the
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51 World clades. This finding argued against the ecological opportunity model as an explanation for
52 the diversity of living mabuyines.

53 Introduction

54

55 The subfamily Mabuyinae comprises 22 genera and approximately 190 species of lizards
56 and belongs to the highly diverse and worldwide spread Scincidae family (Lepidosauria;
57 Squamata) (Uetz and Hosek, 2015). The Mabuyinae, as well as the Scincidae, are distributed on
58 nearly all continents. Approximately one-third of the species in this subfamily are from the
59 Neotropical region, and they are the only representatives of scincids in this area.

60 The entire diversity of mabuyine species was traditionally assigned to the single genus,
61 *Mabuya*, but a previous analysis proposed four new monophyletic genera with well-defined
62 geographical distributions (Mausfeld *et al.*, 2002): (1) *Trachylepis* (previously *Euprepis*),
63 comprising African and Madagascan species with one South American representative (*T.*
64 *atlantica*); (2) *Eutropis*, containing Asian species; (3) *Chioninia*, from the Cape Verde islands;
65 and (4) *Mabuya*, containing New World species, recently rearranged into 16 new genera by
66 Hedges and Conn (2012). Hedges and Conn (2012) treated South American Mabuyinae as a
67 clade of family Mabuyidae, within the superfamily Lygosomoidea. The new Mabuyidae
68 consisted of four new subfamilies: Mabuyinae, Chioniniinae, Dasiinae and Trachylepidinae.
69 Hedges and Conn's arrangement disregarded many genera previously related to Mabuyinae, such
70 as *Eutropis*, *Lankaskincus*, and *Ristella* (Pyron *et al.*, 2013), and recent papers have questioned
71 this classification (e.g. Pyron *et al.*, 2013, Pinto *et al.*, 2015, Karin *et al.*, 2016). Recently,
72 alternative classifications were suggested. For instance, Karin *et al.* (2016) placed the Middle-
73 Eastern *Trachylepis* (*T. aurata*, *T. vittatus* and *T. septemtaeniatus*) into the genus *Heremites* and
74 *Eutropis novemcarinata* into *Toenayar novemcarinata*. Moreover, Pinto *et al.* (2015) assigned
75 species from the genera *Maracaiba* and *Alinea* back to genus *Mabuya* and Metallinou *et al.*

76 (2016) reclassified *Trachylepis ivensii* as *Lubuya ivensii*. In this study, we followed the Reptile
77 Database (Uetz and Hosek, 2015) taxonomy as of January 2017, which classified this clade as
78 subfamily Mabuyinae of the family Scincidae.

79 Therefore, at least two phylogenetically distinct lineages of Mabuyinae are distributed in
80 the New World, namely, *T. atlantica* and the Continental American Mabuyinae (CAM) clade.
81 These lineages are distinguished by both morphological features – presacral vertebrae counts,
82 keeled dorsal scales, coloration, and oviparity (Greer, 1970) – and molecular evidence (e.g.
83 Mausfeld and Vrcibradic, 2002; Carranza and Arnold, 2003; Whiting *et al.*, 2006). It is
84 customary to assume that the history of Mabuyinae in South American continent consisted of
85 two independent transoceanic dispersal events from the Old World (Mausfeld and Vrcibradic,
86 2002; Carranza and Arnold, 2003; Whiting *et al.*, 2006). The spatial distribution of the single
87 representative of the genus *Trachylepis* in an island closer to South America than to Africa, *T.*
88 *atlantica*, is of particular interest. This issue is so intriguing that it has reached the pages of
89 nontechnical literature (de Queiroz, 2014). *T. atlantica* is found in Fernando de Noronha, a small
90 volcanic archipelago in the Atlantic Ocean that lies 375 km from the northeastern coast of Brazil
91 and that was geologically formed from the Miocene (12.3 Ma) to the upper Pliocene, from 3.3 –
92 1.7 Ma (Almeida, 2002). Although other *Trachylepis* species have spread to several islands near
93 the African continent, the presence of *T. atlantica* in Fernando de Noronha likely represents the
94 farthest dispersal registered for the genus.

95 The CAM lineage, on the other hand, contains approximately 60 species of Mabuyinae.
96 Previous studies have suggested that the split between this clade and the African Mabuyinae
97 (genus *Trachylepis*) occurred from 28 – 34 Ma (Hedges and Conn, 2012; Karin *et al.*, 2016).
98 Additionally, the age of the last common ancestor (LCA) of the CAM was dated at 7 – 9 Ma

99 (Carranza and Arnold, 2003; Pinto-Sanchez et al., 2015) and 11 – 14 Ma (Miralles and Carranza,
100 2010; Hedges and Conn, 2012; Karin et al., 2016). Considering the present-day Atlantic Ocean
101 currents, Mausfeld *et al.* (2002) suggested that *T. atlantica* could have dispersed from the coast
102 of Southwest Africa to South America, but no work to date has comprehensively evaluated this
103 hypothesis. The older estimated ages could be consistent with the supposed faunal transoceanic
104 connection between Africa and South America during the Eocene/Oligocene (e.g. hystricognath
105 rodents, Loss-Oliveira *et al.*, 2012; Voloch *et al.*, 2013; anthropoid primates, Schrago *et al.*,
106 2012; 2013; amphisbaenians, Vidal *et al.*, 2008; emballonurid bats, Teeling, 2005; Leigh *et al.*,
107 2013; testudinid turtles, Le *et al.*, 2006), through a single or a series of islands constituting an
108 Atlantic Ocean Ridge (the Atlantogea paleo province) (Simpson, 1950; Poux *et al.*, 2006; de
109 Oliveira *et al.*, 2009; Ezcurra and Agnolin, 2012; de Queiroz, 2014). This transatlantic island
110 corridor, associated with a drop in the sea level in the Oligocene, could explain faunal exchanges
111 in this period (de Queiroz, 2014). Regarding *T. atlantica*, there is a lack of estimates of the age of
112 the separation between this species and its African sister lineage.

113 Chronological information is indispensable for a full understanding of the scenario
114 underlying the current geographic distribution and evolutionary history of extant lineages
115 (Sanmartín *et al.* 2008; Loss-Oliveira *et al.* 2012). However, estimates of divergence times
116 within the Mabuyinae have been hampered by the lack of fossils for Mabuyinae, which made
117 previous researchers rely on evolutionary rates borrowed from the literature (e.g., Carranza and
118 Arnold, 2003; Miralles and Carranza, 2010; Lima *et al.*, 2013; Barker et al., 2015; Karin *et al.*,
119 2016) or to employ biogeographic events as calibrations (Hedges and Conn, 2012; Pinto-Sanchez
120 et al., 2015) to derive the timescale of this lineage. The fossil record, however, has been
121 demonstrated to be much more informative than biogeographic events as a calibration tool

122 (Heads, 2011). The use of biogeographic events to time-calibrate phylogenies requires the
123 assumption of vicariant scenarios of diversification, which entails that the speciation is
124 synchronous with the breaking apart of landmasses, or that island colonization occurs
125 immediately following geological formation (Heads, 2011; Mello and Schrago, 2012).

126 Revealing the origin and diversification of the CAM clade and *T. atlantica* also requires a
127 robust phylogenetic hypothesis. Although it is generally accepted that *T. atlantica* is a member of
128 the genus *Trachylepis* and therefore excluded from the main diversification of the CAM, its
129 evolutionary affinity remains controversial (Mausfeld et al., 2002; Carranza and Arnold, 2003;
130 Whiting et al., 2006). Early proposed phylogenies of Mabuyinae used a maximum of 35 species,
131 a number that significantly underrepresents the diversity of this subfamily (Mausfeld et al., 2002;
132 Carranza and Arnold, 2003; Whiting et al., 2006). Hedges and Conn (2012) studied the CAM
133 clade exclusively and included 40 species, whereas the large-scale Squamata phylogeny of Pyron
134 et al. (2013), which contains 4,161 species, sampled 71 mabuyine skink species. Recently, Pinto
135 Sanchez et al. (2015) used 250 specimens to infer the phylogeny and species diversity of
136 neotropical mabuyinaes, focusing on Colombian populations. Karin et al. (2016) analyzed the
137 higher-order relationships of Mabuyinae using 22 species (24 specimens). Considering that
138 improvements in phylogenetic inference and divergence time estimation can be obtained by
139 increasing taxon sampling (Linder et al., 2005; Albert et al., 2009; Soares and Schrago, 2012),
140 this matter requires further investigation.

141 Moreover, the occupation of the South American mainland by the CAM motivates an
142 analysis of differential rates of diversification rates phenotypic traits evolution in this clade. It
143 has been broadly reported that the ecological opportunity of a new environment can induce
144 acceleration of macroevolutionary rates (Yoder et al., 2010; Liedtke et al., 2016). This

145 phenomenon was documented for insular vertebrates (Losos JB, Mahler DL. 2010; Jonsson KA
146 et al. 2012); but, as proposed by G.G. Simpson (1953), the occupation of a new continent also
147 could theoretically trigger evolutionary radiations (Yoder JB et al. 2010; Pires MM, Silvestro D,
148 Quental TB. 2015).

149 In this study, as a means of exploring the continental biogeographic and evolutionary
150 patterns associated with the occupation of South America by mabuyine skinks, we estimated the
151 molecular phylogeny and inferred the divergence times of its members employing fossil
152 information. The inferred time-tree was used to performed, for the first time, a formal statistical
153 historical biogeography analysis and macroevolutionary diversification rates inference of
154 Mabuyinae. To this end, by data-mining previously published data, we assembled the largest
155 dataset of species and gene sampling composed to date, with the aim of uncovering the evolution
156 of the Mabuyinae.

158 **Materials and Methods**

159

160 *Data collection, alignment and taxonomy*

161 We assembled a dataset containing sequence information for eight genetic loci from 117
162 species of Mabuyinae. Moreover, a representative number of terminals were collected from other
163 scincid subfamilies (102 genera), totaling 219 taxa. All sequences were downloaded from
164 GenBank. Two genera of the family Xantusiidae were used as outgroups. All seven genes
165 available from *Trachylepis atlantica* were used in our analysis: the mitochondrial ribosomal
166 genes *12S rRNA*, *16S rRNA* and the coding gene *cytochrome b (cytb)*; as well as the nuclear
167 genes alpha enolase (*enol*), oocyte maturation factor (*cmos*), glyceraldehyde-3-phosphate
168 dehydrogenase (*gapdh*), myosin heavy chain (*myh*), and G protein-coupled receptor
169 (*gpr149*). Detailed information on each locus was listed in Table 1 and accession numbers are
170 available in Supplementary File 2. When several sequences representative of each taxon were
171 available, the longest sequence was selected. We assumed genera and species as monophyletic.
172 Therefore, chimeric supermatrices were used. All protein-coding sequences were visually
173 checked for stop codons and aligned individually in SeaView v. 4.4.3 (Gouy *et al.*, 2010) using
174 the MUSCLE v3.8.31 (Edgar 2004) algorithm, whereas the ribosomal genes were aligned in
175 MAFFT v. 7 (Kato and Standley, 2013). Gblocks v. 0.91b (Castresana, 2000; Talavera and
176 Castresana, 2007) was used to exclude poorly aligned bases and divergent regions in the *12S*
177 *rRNA*, *16S rRNA* and *enol* genes. Individual genes were then concatenated into a single
178 supermatrix using the R package Phyloch (Heibl, 2015). RogueNarok (Aberer *et al.*, 2013) was
179 used to identify taxa without significant phylogenetic information using a ML tree and associated
180 bootstrapped topologies. These datasets were inferred under a rapid bootstrapping algorithm

181 analysis with 200 replicates (Stamatakis et al., 2008), followed by a thorough search of the ML
182 tree using the evolutionary model GTRGAMMA, performed in RAxML-HPC (8.1.24)
183 (Stamatakis, 2014). The terminal nodes *Larutia* and *Otosaurus*, which each presented relative
184 bipartition information criterion (RBIC) higher than 1.0, were removed from the analysis.
185 Another dataset, assembled with a more stringent (RBIC > 0.5) criterion, was composed for
186 comparison. Under this criterion, the genus *Lankascincus* and the mabuyine species *Eumecia*
187 *anchietae* and *Trachylepis acutilabris* were excluded from the analyses. The results, however,
188 were robust for both RBIC values, and we report the results under RBIC > 1.0 hereafter. The
189 final supermatrix consisting of 4,131 base pairs are available in Supplementary File 2.

190

191 *Evolutionary analyses*

192 We investigated 18 candidate partitioning schemes using PartitionFinder heuristic search
193 algorithm with the Bayesian information criterion (BIC) for model selection (Lanfear *et al.*,
194 2012). The partitioning schemes also tested codon positions of protein-coding genes. The
195 partitioning strategy with the best fit consisted of 7 partitions (Supplementary File 3), which
196 were used throughout the analyses. Maximum likelihood (ML) phylogenetic inference was
197 performed in RAxML-HPC (8.1.24) employing the evolutionary model GTRCAT. The GTR
198 substitution model was applied to each partition, as this is the only model supported in RAxML.
199 ML analyses used 200 initial searches for finding the optimal tree topology. Statistical support
200 for clades was assessed using 2,000 standard nonparametric bootstrap replicates (PB).

201 Inference of node ages was performed with the mcmctree program of the PAML 4.8a
202 package (Yang, 2007). For large alignments, the Bayesian inference of node ages via Markov
203 chain Monte Carlo is computationally intensive. To make the analyses feasible, we used an

204 approximate likelihood calculation modified from Thorne et al. (1998) and implemented in
205 mcmctree (Reis and Yang, 2011). Priors for the ρ gene and σ^2 parameters were set as $G(2,$
206 $200)$ and $G(1, 10)$, respectively. Markov chains were sampled every 1,000 generations until
207 50,000 trees were collected. The analysis was performed twice to check for convergence of the
208 chains. Effective sample sizes (ESS) of parameters were calculated in Tracer v. 1.5, and all
209 values were greater than 200.

210

211 *Calibration priors*

212 The age of the root, which corresponds to the split between the families Scincidae and
213 Xantusiidae, was calibrated at a minimum value of 70.6 Ma and a maximum age of 209.5 Ma.
214 The minimum was set according to the oldest scincid from the Late Cretaceous of North
215 America (Campanian, 83.5 – 70.6 Ma), as previously adopted by Mulcahy *et al.* (2012) (Rowe *et*
216 *al.*, 1992); while the maximum was set according to Benton *et al.* (2015), which proposed a
217 maximum age of the ancestral of Squamata. Additional calibration information was gathered
218 from the Paleobiology Database (paleobiology.org) and entered as minimum ages of the stem nodes of
219 clades. The minimum age of the Scincidae stem node was calibrated at 20.4 Ma, based on the
220 oldest crown scincid *Eumeces antiquus* classified as a member of the subfamily Scincinae
221 (Holman, 1981; Estes, 1983). The stem node of the clade containing the extant genus *Eumeces*
222 was calibrated at a minimum age of 13.6 Ma based on fossils from the Middle Miocene in North
223 America (Holman, 1966; Voorhies *et al.*, 1987; Joeckel, 1988). The age of an extinct *Egernia* sp.
224 from the Miocene of Hungary (>5 Ma) was used to calibrate the stem node of the clade
225 containing this extant genus (Venczel and Hír, 2013). According to Böhme (2010), the fossil
226 *Tropidophorus bavaricus* belongs to extant genus *Tropidophorus*, and it was used to calibrate the

227 stem node of this clade, setting its minimum age at 13.6 Ma (Böttcher *et al.*, 2009). Calibrate
228 nodes are shown in the Supplementary Figure 4.

229

230 *Ancestral area reconstruction*

231 A historical biogeographical reconstruction was performed for the subfamily Mabuyinae and its
232 sister clade (*Lankascincus* and *Ristella*). The R package BioGeoBEARS (Matzke 2013) was used
233 to run likelihood methods: DIVALIKE (a likelihood interpretation of DIVA that allows for the
234 same events as DIVA – Matzke, 2013) and DEC (Dispersal-Extinction-Cladogenesis, Ree and
235 Smith, 2008). In BioGeoBEARS, we used the likelihood ratio to test whether the null models
236 (DIVALIKE and DEC) fitted the data better than did the more sophisticated models
237 (DIVALIKE+J and DEC+J). The “J” in models represents the addition of the founder-event
238 speciation, thereby allowing dispersal without range expansion (Matzke 2014). The maximum
239 range size, which limits the number of areas defined by tips and nodes, was set to two, based on
240 the current geographic distribution of species. Constraints on dispersal or area availability were
241 not included. To make the biogeographic analysis computationally feasible, islands were not
242 considered independent regions. The rationale for choosing the seven biogeographic areas
243 follows the zoogeographical regions found in the herpetological and biogeographical literature
244 (Vitt and Caldwell, 2009; Lomolino, 2010; Morrone, 2014; Pyron, 2014): (1) Neotropical
245 Brazilian Subregion (B), (2) Neotropical Chacoan Subregion (C), (3) West Indies – Caribbean
246 Islands (W); (4) Oriental Region (O): Southeast Asia + Philippines + Indian Subcontinent
247 (Pakistan to Bangladesh, including Sri Lanka, Nepal, and Bhutan); (5) Afrotropical (A): Sub-
248 Saharan Africa; (6) Madagascar (M): Madagascar and adjacent islands (the Seychelles and the
249 Comoros); and (7) Saharo-Arabian (S): Europe + North Africa + the northern portion of the

250 Arabian Peninsula + Southwest Asia. Using online distributional data from the Reptile Database
251 (Uetz and Hosek, 2015), we classified the tips as belonging to one or more of these areas.

252

253 *Rate of species diversification and diversification-phenotype rate correlation*

254 Our dated phylogeny of Mabuyinae was used to infer the dynamics of species
255 diversification using BAMM 2.5 (Bayesian Analysis of Macroevolutionary Mixtures – Rabosky,
256 2014), which simultaneously accounts for variation in evolutionary rates through time and
257 among lineages using transdimensional (reversible-jump) Markov chain Monte Carlo (rjMCMC)
258 (Rabosky 2014). Markov chains were sampled every 1,000th generation until 37,500 trees were
259 collected after a burn-in of 25%. Prior distributions were set according to *setBAMMPriors*
260 function from the BAMMtools R package (Rabosky *et al.* 2014). The frequencies of the species
261 in each genus were considered.

262 We were also prompted to test for trait-dependent diversification. The following traits were
263 collated from the literature: (i) data on the reproductive mode for 60 species of the Mabuyinae –
264 39 species as viviparous, 17 as oviparous, and 3 as ovoviviparous (Meiri *et al.* 2013; Pyron and
265 Burbrink 2013); (ii) the SVL (snout–vent length) for 46 species (Meiri 2010; Miralles and
266 Carranza, 2010; Das 2010; Hedges and Conn, 2012; Meiri *et al.* 2013; Pyron and Burbrink
267 2013); and (iii) the body mass data for 35 species (Meiri 2010; Hedges and Conn, 2012).
268 Following previous works, we treated "ovoviviparity" as viviparity (Pyron and Burbrink 2013).

269 Differences in the rates of speciation (λ) and extinction (μ) between New World (*NW*)
270 and Old World (\overline{NW}) areas and between viviparous (*V*) and non-viviparous (\overline{V}) lineages were
271 tested using two approaches. Firstly, an ANOVA, implemented in the R package *diversitree*
272 (FitzJohn 2012), was used to compare different macroevolutionary regimes. In the NW/\overline{NW}

273 comparison, rates were calculated using the GeoSSE approach (Goldberg *et al.* 2011), whereas
274 BiSSE was used to test V/\bar{V} rates, with both tests of binary characters as implemented in
275 diversitree. In this sense, GeoSSE first optimised the parameters under an unconstrained full
276 model, in which ML estimates were obtained for (i) the speciation rate of the New World lineage
277 (λ_{NW}); (ii) the speciation rate of non-New World lineages ($\lambda_{\bar{NW}}$); (iii) the extinction rate of the
278 New World clade (μ_{NW}); (iv) the extinction rate of non-New World lineages ($\mu_{\bar{NW}}$); (v) the
279 intermediate speciation rate parameter ($\lambda_{NW,\bar{NW}}$); (vi) the dispersal rates from the New World
280 clade ($d_{NW\rightarrow\bar{NW}}$); and (vii) the dispersal rates of the sister lineages ($d_{\bar{NW}\rightarrow NW}$). Similarly, BiSSE
281 was used to infer (i) the speciation rate of the viviparous lineage (λ_V); (ii) the speciation rate of
282 non-viviparous lineages ($\lambda_{\bar{V}}$); (iii) the extinction rate of the viviparous clade (μ_V); (iv) the
283 extinction rate of non-viviparous lineages ($\mu_{\bar{V}}$); (v) transition rates from the viviparous clade (
284 $q_{V\rightarrow\bar{V}}$); and (vi) transition rates of the sister clade ($q_{\bar{V}\rightarrow V}$). Initial parametric values were set
285 according to the *starting.point* function from the diversitree package with an initial ratio of 0.5.
286 This preliminary step was required to build the likelihood function (the *make* command). In
287 BiSSE, species with unknown states were coded as ‘NA’ and assigned the sampling fraction of
288 the species of Mabuyinae used in this work (~61%), independent of the character state.
289 Subsequently, to perform the ANOVA test of the GeoSSE results, we chose to constrain the
290 intermediate speciation and the dispersal rate parameters to zero ($\lambda_{NW,\bar{NW}} = d_{NW\rightarrow\bar{NW}} =$
291 $d_{\bar{NW}\rightarrow NW} = 0$), in order to compare speciation and the extinction rates within regions exclusively.
292 Finally, we tested macroevolutionary alternative models against the full models (Table 2).
293 The second comparison between NW/\bar{NW} and V/\bar{V} macroevolutionary regimes used the
294 marginal posterior distributions of macroevolutionary parameters, inspected using the R package

295 diversitree. These distributions were obtained using the MCMC analyses, with samples taken in
296 diversitree every 1,000th generation until 1,000 samples were collected. A broad exponential
297 prior (mean of 0.5) for all parameters was used, as recommended, while the λ and μ rates were
298 set as the values obtained in the ML full model (FitzJohn 2012). For the NW/\overline{NW} relationship,
299 we also used the marginal posterior distributions obtained from BAMM, applying the
300 *getCladeRates* function of the BAMMtools R package. For all approaches, we calculated the
301 95% highest posterior density (HPD) interval for the difference between the means of the $NW/$
302 \overline{NW} and V/\overline{V} lineages (Bolstad 2007).

303 The diversification-phenotype rate correlation was performed in STRAPP (Rabosky and
304 Huang 2015), as implemented in BAMMtools. To run STRAPP, phylogenies were pruned to
305 match the available information for both tree terminals and traits. Diversification analysis results
306 previously obtained using BAMM were pruned to match the available trait information using the
307 function *subtreeBAMM* and were tested against the analyzed traits, using the Mann-Whitney
308 method for binary characters and both Pearson and Spearman methods for continuous traits.

309

310 *Rate of trait evolution and ancestral state reconstruction*

311 We inferred ancestral states of reproduction mode in the BayesTraits software (Pagel *et*
312 *al.* 2004) and in the R package BiSSE. Both approaches use the maximum likelihood method and
313 allow the use of species with unknown character states. Results were visualized in the R package
314 diversitree. The rates of trait evolution of the two continuous traits studied, namely, SVL and
315 body mass, were inferred in BAMM, using logarithms of both measures. Phylogenies were also
316 pruned to match the available information for both tree terminals and traits. We tested the
317 correlation between SVL and body mass using phylogenetic independent contrasts (PIC;

318 Felsenstein, 1985) as implemented in the R package ape. Prior distributions to these subtrees
319 were set according to *setBAMMPriors* function from the BAMMtools R package (Rabosky *et al.*
320 2014). Chains were sampled every 1,000 generations until 50,000 trees were collected. The
321 results were summarized and visualized in BAMMtools.

322 **Results**

323

324 Mabuyinae was recovered as a monophyletic group (BS = 76). The first split in this
325 subfamily isolated the genus *Dasia* from the remaining Mabuyinae and was inferred to have
326 occurred at 30 Ma, with an HPD interval ranging from 20 – 48 Ma (Supplementary File 4). The
327 biogeographical model with the highest likelihood was the DEC+J (lnL: -94.34). Therefore, the
328 addition of the J parameter for founder events significantly increased the likelihood of the DEC
329 model ($p = 1.2e^{-9}$, Table 3). Our results supported a model in which the genera *Lankascincus* and
330 *Ristella* split from Mabuyinae (BS = 20) in the Oriental region.

331 After dispersal from the Oriental region to Africa, the ancestor of the CAM clade split
332 from Saharo-Arabian *Trachylepis* approximately 25 Ma ($\pm 16 - 41$ Ma) (BS=60). Subsequently,
333 the stock that gave rise to New World Mabuyinae dispersed from the Saharo-Arabian region to
334 the Neotropical Brazilian Subregion (Figure 1). The New World Mabuyinae were recovered as
335 monophyletic (BS=97), and the age of their LCA was estimated as 19 Ma (12 – 31 Ma). Our
336 results supported the hypothesis that this lineage reached the Neotropics via the Brazilian
337 Subregion. From this region, the ancestor of *Spondylurus* and *Copeoglossum* dispersed to islands
338 of the West Indies. The continental clade later dispersed along the Brazilian Subregion.
339 Additional dispersal events to the West Indies were inferred to have occurred at least twice: in
340 the ancestor of *Mabuya* and in that of *Alinea* and *Marisora*. *Marisora* was not recovered as
341 monophyletic, with the Central American clade as sister to *Alinea* and the South American clade
342 as sister to *Aspronema*.

343 The origin of *Trachylepis atlantica* consisted of a different history. Firstly, the
344 monophyly of genus *Trachylepis* was not recovered. This genus was split into two lineages: one

345 sister lineage of the CAM clade and another major clade to which *T. atlantica* belongs. Our
346 analysis supported the phylogenetic position of *T. atlantica* as a sister lineage of the clade
347 including the Europa Island *T. infralineata*, the Madagascan *T. comorensis*, and the continental
348 African *T. maculilabris* (BS = 29). We found that the *T. atlantica* ancestor diverged from the
349 remaining *Trachylepis* in the Miocene, approximately 17 Ma (between 10 and 27 Ma) in tropical
350 Africa. The younger diversification of *T. atlantica* indicates that the crossing of this species to
351 Fernando de Noronha occurred more recently than did the occupation of South America by the
352 CAM clade. Our analyses also suggested that once the ancestors of this major *Trachylepis* clade
353 reached Africa, dispersal events from the African continent occurred to Madagascar and nearby
354 islands at least three times, in addition to the dispersion to the Neotropics (*T. atlantica*). Our
355 results showed that a monophyletic Madagascan *Trachylepis* (BS = 94) diverged from its sister
356 group approximately 19 Ma (12 – 32 Ma) (BS = 23).

357 The ANOVA was used to test whether the full four-parameter GeoSSE model of the *NW*/
358 \overline{NW} comparison (model 1) was statistically favored over simpler alternative models (models 2-
359 4). When we constrained speciation rates to be equal (model 2) and to present equal speciation
360 and extinction rates (model 4), the full model was supported over these alternative models ($p =$
361 0.00782 and $p = 0.02900$, respectively). The comparison with the model that constrained
362 extinction rates (model=3), however, was not significantly different ($p = 0.15575$).

363 GeoSSE analysis of the difference between the posterior distributions of speciation rates
364 in *NW*/ \overline{NW} lineages indicated a positive credible interval (CI) (0.005 – 0.113), indicating that the
365 speciation rates of South American clades (*NW*) were indeed higher than those of the remaining
366 lineages (\overline{NW}). In BAMM, however, we failed to find a significant difference between the
367 posterior distributions of speciation rates (CI: -0.030 – 0.031). We also found no evidence for

368 diversification shifts during mabuyine diversification. However, the macroevolutionary cohort
369 matrix suggested heterogeneous macroevolutionary rate regimes in the South American
370 Mabuyinae and the remaining clades (Figure 2a). In both GeoSSE and BAMM analyses, we
371 failed to find differences between the extinction rates (CI_{GeoSSE} : -0.036 – 0.074, CI_{BAMM} : -0.027 –
372 0.027) and between the net diversification rates (CI_{GeoSSE} : -0.010 – 0.090, CI_{BAMM} : -0.027 –
373 0.027) (Figure 2b).

374 Concerning the influence of viviparity on diversification rates, no submodels were
375 supported over the unconstrained model ($p > 0.05$). STRAPP analysis failed to find any
376 correlation between diversification rates and mode of reproduction ($p > 0.05$). We also found no
377 differences between the means obtained from the MCMC of the BiSSE (CI: -0.018 – 0.125, -
378 0.038 – 0.055, -0.051 – 0.049, respectively for speciation, extinction, and transition rates).

379 The ancestor of CAM and their *Trachylepis* sister clade was recovered as viviparous by
380 BayesTraits ($P_{\text{BTML}}=0.751$; $P_{\text{BTBA}}=0.787$) and as oviparous by BiSSE ($P_{\text{BiSSE}}=1$), while the
381 ancestor of CAM alone was recovered as viviparous by all approaches ($P_{\text{BiSSE}}=0.953$;
382 $P_{\text{BTML}}=0.992$; $P_{\text{BTBA}}=0.983$), suggesting that the ancestral species that colonised South America
383 was likely viviparous (Figure 2a). The ancestor of the subfamily Mabuyinae was inferred as
384 oviparous ($P_{\text{BiSSE}}=1$; $P_{\text{BTML}}=0.983$; $P_{\text{BTBA}}=0.980$). Viviparity seems to have emerged several
385 times in the genus *Trachylepis*, as well as in the ancestor of *Chioninia* ($P_{\text{BiSSE}}=0.952$;
386 $P_{\text{BTML}}=0.984$; $P_{\text{BTBA}}=0.971$).

387 According to PIC results, SVL measurement and body mass were correlated ($p_{\text{LRP}} <$
388 0.01), however, we had found differences in their evolutionary rates. The mean rates of trait
389 evolution of SVL and body mass were smaller in the New World clade than in the \overline{NW} lineages.
390 However, these differences were not significant. In BAMM, we found an increase in the rate of

391 SVL trait evolution in genus *Chioninia*. Only one clade presented an increase in the rate of body
392 mass trait evolution: the Seychelles *Trachylepis* (*T. wrightii* and *T. brevicollis*). STRAPP
393 analysis failed to find a significant correlation between the rate of species diversification and the
394 rate of SVL or body mass trait evolution ($p > 0.05$).

395 **Discussion**

396

397 Our analyses based on a fossil-calibrated timetree support the hypothesis that the
398 occupation of South America by the ancestors of the Continental America Mabuyinae (CAM)
399 clade occurred between the Eocene and the Oligocene from the Saharo-Arabian region,
400 corroborating recent estimates (e.g. Pinto-Sánchez *et al.* 2015; Karin *et al.*, 2016). This
401 colonization occurred independently of that of *Trachylepis atlantica*, which split from its tropical
402 African sister clade between the Oligocene and the Miocene. Therefore, our results corroborated
403 the hypothesis that the ancestor of *T. atlantica* dispersed from tropical Africa as suggested by
404 Mausfeld *et al.* (2002). The divergence between *T. atlantica* and its African ancestors was older
405 than the estimated age of the formation of the Fernando de Noronha archipelago (12.3 – 1.7 Ma;
406 Almeida, 2002). Thus, it is unlikely that the ancestors of *T. atlantica* reached South America in a
407 single transoceanic dispersal event. It is more probable to hypothesize a complex dispersal
408 scenario, with a series of dispersals through a transatlantic island corridor leading to Fernando de
409 Noronha, consistent with the Atlantogea model (Oliveira *et al.* 2009; Ezcurra and Agnolin,
410 2012). This stepping-stone mode of dispersal could explain the discrepancy between the ages of
411 genetic divergence and the formation of the archipelago because it would dissociate the
412 geological formation of the Fernando de Noronha archipelago from the genetic isolation of the
413 ancestor of *T. atlantica*. This result must be interpreted cautiously because choosing between
414 alternative biogeographical scenarios is influenced by the inferred timescale. The lack of extant
415 and extinct mabuyine species may have impacted divergence time estimates.

416 The age of the crown node of a living CAM species was inferred to be much older than
417 the previously reported estimates by Carranza and Arnold (2003), 7 – 9 Ma. However, the ages

418 inferred by Miralles and Carranza (2010); Hedges and Conn (2012) and Karin *et al.* (2016), at
419 approximately 14 Ma, lies within the range reported in our work (12 – 31 Ma). Nevertheless, all
420 previous estimates were also incompatible with single-event scenarios of New World
421 colonization. Note that a fossil of a putative species of Mabuyinae has been described in the mid-
422 Atlantic Ascension Island, although no recent systematic re-evaluation of this specimen is
423 available (Mausfeld and Vrcibradic, 2002). The direction of Atlantic Ocean currents from Africa
424 to South America would explain the scarcity of dispersals in the opposite direction (Houle,
425 1999). The evolution of the two American lineages of Mabuyinae also corroborates this faunal
426 connection and suggests that this dispersal may have occurred through island hopping, which is
427 more likely than a single sweepstake event across the Atlantic Ocean.

428 The arrival of Mabuyinae to South America seems to have changed the diversification
429 rate regime of this lineage. The evolution rates of both body mass and SVL traits were not
430 significantly altered after the arrival of the ancestors of New World clades, but the increases in
431 rates of both traits were found in island groups, such in Cape Verde's *Chioninia* and Seychelles'
432 *Trachylepis*. The viviparous CAM clade presents peculiar reproductive traits, such as a
433 specialized chorioallantoic placenta that provides the fetal nutrition, similarly to eutherian
434 mammals (Vrcibradic and Rocha, 2011). This character was suggested to be synapomorphic by
435 Mausfeld *et al.* (2002). According to our analysis, the CAM ancestor was already viviparous, in
436 agreement with the large-scale analysis of Squamates (Pyron and Burbrink, 2013). However,
437 Pyron and Burbrink (2013) analyses suggested an early origin of viviparity in Mabuyinae and
438 multiple reversions to oviparity, including the clade consisting of *Chioninia* and CAM +
439 *Heremites*. On the other hand, possibly because of topological differences, we estimated that the

440 ancestor of Mabuyinae was oviparous and multiple reversions to viviparity occurred later along
441 the evolution of the lineage.

442 Regarding the higher systematics of Mabuyinae, Greer (1970), based on the primitive
443 characteristics of Asian Mabuyinae, suggested that the ancestors of this subfamily first dispersed
444 from Asia. Other works reasserted this hypothesis, although no formal statistical analyses were
445 conducted (Honda *et al.*, 1999; 2003; Karin *et al.*, 2016). Our results suggested that the early
446 members of Mabuyinae dispersed to Africa and then reached South America and several oceanic
447 islands. The inferred time-dated phylogeny and biogeographic reconstruction similarly suggested
448 an Oriental ancestral distribution, as corroborated by the distribution of the genera *Lankascincus*
449 and *Ristella*, which were recovered as sister clades of Mabuyinae and are geographically
450 distributed in the Oriental region (Sri Lanka and the Indian, respectively). Karin *et al.*, 2016
451 inferred that *Eutropis*, instead of *Dasia*, was the first Mabuyinae offshoot. Nevertheless, as both
452 genera are distributed in the Oriental region, this topological rearrangement would not
453 significantly alter the ancestral area reconstruction.

454 Finally, this study provided an updated timescale and estimates of macroevolutionary
455 regimes of the diversification of the subfamily Mabuyinae. Our focus was the occupation of the
456 South American continent by the subfamily Mabuyinae through an Oligocene/Eocene
457 transoceanic connection (Atlantogea), which could be responsible for approximately 29% of the
458 South American mammal diversity, suggesting the importance of this event to the extant
459 vertebrate diversity in South America (Marshall *et al.*, 1982). *CAM* and *T. atlantica* are the only
460 representatives of the family Scincidae in South America accounting for 4% of the
461 approximately 1560 squamate species on this continent (Uetz, 2000). Although there are species
462 of other subfamilies of Scincidae in Central America, these species seem to have never crossed

463 the Isthmus of Panama. The converse also seems true because the only mabuyine genus
464 (*Marisora*) that partially occupied Central America based on our results had arrived via an
465 intermediate dispersion through the West Indies. If this is the case, no representative of Scincidae
466 would be found in present day South American fauna in the absence of this Atlantogea
467 connection. Our results presented an overall picture of the timing, biogeography and
468 macroevolutionary dynamics associated with the arrivals of the ancestors of the only vertebrate
469 clade known to have undergone transoceanic dispersal twice.

470

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472

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475 **References**

476

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Table 1 (on next page)

General information on the loci used in this study.

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	<i>12S</i>	<i>16S</i>	<i>enol</i>	<i>cytb</i>	<i>cmos</i>	<i>gapdh</i>	<i>myh</i>	<i>gpr149</i>	Total
Number of sequenced species	214	194	70	153	146	47	51	73	218
Alignment length	366	464	192	1,033	894	380	133	669	4,131
Frequency of sites with missing data	0.12	0.20	0.74	0.38	0.40	0.81	0.81	0.72	0.47
Frequency of indels	0.02	0.03	0.01	0.16	0.22	0.04	0.01	0.01	0.10

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Table 2 (on next page)

Model comparisons performed in 'diversitree'.

Constraints in the macroevolutionary models subjected to ANOVA for differences in the rates of speciation (λ) and extinction (μ) between New World (NW) and Old World (NW) areas (GeoSSE) and between viviparous (V) and non-viviparous (V) lineages (BiSSE).

Model	Approach	Constrains	Parameters
Reduced full	GeoSSE	NA	$\lambda_{NW}, \lambda_{\overline{NW}}, \mu_{NW}, \mu_{\overline{NW}}$
	BiSSE	NA	$\lambda_V, \lambda_{\overline{V}}, \mu_V, \mu_{\overline{V}}$
Equal speciation	GeoSSE	$\lambda_{NW} = \lambda_{\overline{NW}}$	$\lambda, \mu_{NW}, \mu_{\overline{NW}}$
	BiSSE	$\lambda_V = \lambda_{\overline{V}}$	$\lambda, \mu_V, \mu_{\overline{V}}$
Equal extinction	GeoSSE	$\mu_{NW} = \mu_{\overline{NW}}$	$\lambda_{NW}, \lambda_{\overline{NW}}, \mu$
	BiSSE	$\mu_V = \mu_{\overline{V}}$	$\lambda_V, \lambda_{\overline{V}}, \mu$
Equal diversification	GeoSSE	$\lambda_{NW} = \lambda_{\overline{NW}}$	λ, μ
	GeoSSE	$\mu_{NW} = \mu_{\overline{NW}}$	λ, μ
	BiSSE	$\lambda_V = \lambda_{\overline{V}}$	λ, μ
	BiSSE	$\mu_V = \mu_{\overline{V}}$	λ, μ

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2
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Table 3 (on next page)

Model comparisons performed in BioGeoBEARS

Likelihood-ratio tests between null models (DIVALIKE and DEC) and more sophisticated models with the addition of the founder-event speciation (+J) (DIVALIKE+J and DEC+J). (LnL) Likelihood value. (DF) Degrees of freedom for the chi-square test.

model	Null model	LnLalt	LnLnull	DF	pval
DEC+J	DEC	-94.34	-112.8	1	1.20E-09
DIVALIKE+J	DIVALIKE	-95.65	-119.2	1	6.70E-12

1

Figure 1

Time-dated phylogeny of the Mabuyinae with ancestral area reconstruction

Maps depict putative dispersals and vicariant events that culminated in the occupation of South America by this group. Ancestral area reconstruction was based on the results from DEC+J because this model produced a significantly higher log-likelihood score. The black regions in pie charts represent bootstrap supports.

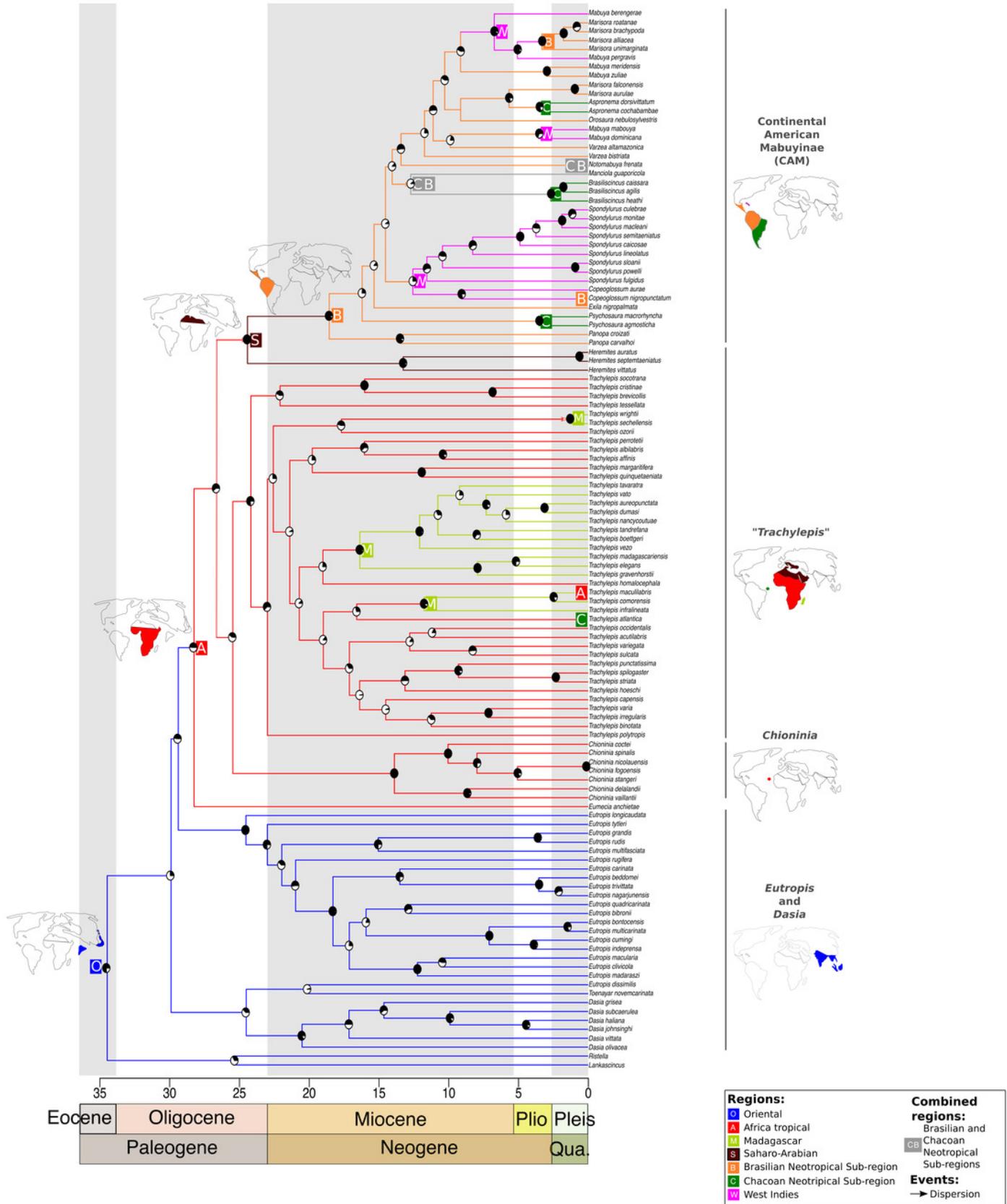


Figure 2

Macroevolutionary cohort matrix for the Mabuyinae subfamily.

A. Illustration of the macroevolutionary rates for the mabuyine lineage obtained using BAMB. For reference, the BAMB tree was plotted at the upper margin of the figure. The pairwise probability that any two species share a common macroevolutionary rate dynamic was indicated by the color of each individual cell. Color scale is indicated at the right. The coral and brown circles in the upper tree represent the shifts found with BAMB in the traits SVL and body mass, respectively. In the left most tree topology, pie charts at nodes indicate the mode of reproduction inferred by BayesTraits, according to the probability of occurrence of each character. Red represents viviparity, and black represents oviparity. **B.** Marginal distributions of macroevolutionary rates inferred in BAMB and GeoSSE were also depicted.

