Arrival and diversification of mabuyine skinks (Squamata: Scincidae) in the Neotropics

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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. Moreover, at least one insular species, *Trachylepis atlantica*, has independently reached the New World through transoceanic dispersal. In an effort to clarify the evolutionary history of this lineage, this study aimed to infer an updated timescale using the largest species and gene sampling dataset ever assembled for this group.

Methods: Our dated tree allowed the estimation of the 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. We also performed a historical-biogeographic analysis and a reconstruction of ancestral states of the mode of reproduction.

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, figures that are consistent with values estimated for other South American vertebrate colonisers from Africa.

Discussion: After reaching the isolated South American continent, dispersal events changed the macroevolutionary diversification regime of mabuyine skinks and favoured the evolution of viviparity in the lineage.

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Abstract

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Keywords: historical biogeography; Neotropics; transoceanic dispersal; Atlantic Ocean; Mabuyinae; South America

Introduction

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

The entire diversity of mabuyine species was traditionally assigned to the single genus, *Mabuya*, but a recent analysis proposed four new monophyletic genera with well-defined geographical distributions (Mausfeld *et al.*, 2002): (1) *Trachylepis* (previously *Euprepis*), comprising African and Madagascan species with one South American representative (namely, *T. atlantica*); (2) *Eutropis*, containing Asian species; (3) *Chioninia*, from the Cape Verde islands; and (4) *Mabuya*, containing New World species, recently rearranged into 16 new genera by Hedges and Conn (2012). Hedges and Conn (2012) treated South American Mabuyinae as a clade of family Mabuyidae, within the superfamily Lygosomoidea. The new Mabuyidae consisted of four new subfamilies, namely, Mabuyinae, Chioniniinae, Dasiinae and Trachylepidinae. Hedges and Conn's arrangement disregarded many genera previously related to Mabuyinae, such as *Eutropis*, *Lankaskincus*, and *Ristella* (Pyron *et al.*, 2013), although recent papers have questioned this classification (e.g. Pyron *et al*., 2013, Pinto *et al*., 2015, Karin *et al*., 2016).

Therefore, at least two phylogenetically distinct lineages of Mabuyinae are distributed in the New World, namely, *T. atlantica* and the Continental American Mabuyinae (CAM) clade. These lineages are distinguished by both morphological features – presacral vertebrae counts, keeled dorsal scales, coloration, and oviparity (Greer, '70) – and molecular evidence (Mausfeld and Vrcibradic, 2002; Carranza and Arnold, 2003; Whiting *et al.*, 2006). It is customary to assume that the history of Mabuyinae in South American continent consisted of two independent transoceanic dispersal events from the Old World (Mausfeld and Vrcibradic, 2002; Carranza and Arnold, 2003; Whiting et al., 2006). The spatial distribution of the single representative of the genus *Trachylepis* in South America, *T. atlantica*, is of particular interest. This issue is so intriguing that it has reached the pages of nontechnical literature (de Queiroz, 2014). *T. atlantica* is found in Fernando de Noronha, a small volcanic archipelago that lies 375 km from the

northeastern coast of Brazil in the Atlantic Ocean and was geologically formed from the Miocene (12.3 Ma) to the upper Pliocene, from 3.3-1.7 Ma (Almeida, 2002). Although other *Trachylepis* species have spread to several islands near the African continent, the presence of *T. atlantica* in Fernando de Noronha likely represents the farthest dispersal registered for the genus.

The CAM lineage, on the other hand, contains approximately 60 species of Mabuyinae. Previous studies have suggested that the split between this clade and the African Mabuyinae (genus *Trachylepis*) occurred from 28 Ma to 34 Ma (Hedges and Conn, 2012; Karin et al., 2016). Additionally, the age of the last common ancestor (LCA) of the CAM has been dated to 7-9 Ma (Carranza and Arnold, 2003; Pinto-Sanchez et al., 2015) and 11-14 Ma (Miralles and Carranza, 2010; Hedges and Conn, 2012; Karin et al., 2016). After analysis of the system dynamics of present-day Atlantic Ocean currents, Mausfeld *et al*. (2002) suggested that *T. atlantica* could have dispersed from the coast of Southwest Africa to South America, but no work to date has comprehensively evaluated this hypothesis.

Chronological information is indispensable for a full understanding of the scenario underlying the current geographic distribution and evolutionary history of extant (Sanmartín *et al.* 2008; Loss-Oliveira *et al.* 2012). However, estimates of divergence times within the Mabuyinae have been hampered by the lack of fossils for Mabuyinae, which made previous researchers rely on evolutionary rates borrowed from the literature (e.g., Carranza and Arnold, 2003; Miralles and Carranza, 2010; Lima *et al.*, 2013; Barker et al., 2015; Karin *et al.*, 2016) or to employ biogeographic events as calibrations (Hedges and Conn, 2012; Pinto-Sanchez et al., 2015) in order to derive the timescale of this lineage. The fossil record, however, has been demonstrated to be much more informative than biogeographic events as a calibration tool (Heads, 2011). These events require the assumption of vicariant scenarios of diversification, which entails that the speciation is synchronous with the breaking apart of landmasses or that island colonisation occurs immediately following geological formation (Heads, 2011; Mello and Schrago, 2012).

In addition to estimates of divergence time, revealing the origin and diversification of the CAM clade and *T. atlantica* requires a robust phylogenetic hypothesis. Although it is generally accepted that *T. atlantica* is a member of the genus *Trachylepis* and therefore excluded from the main diversification of the CAM, its evolutionary affinity remains controversial (Mausfeld et al., 2002; Carranza and Arnold, 2003; Whiting et al., 2006). Moreover, the occupation of the South

American mainland by the CAM motivates an analysis of differential diversification rates in this clade, as dispersal may influence the macroevolutionary dynamics of a lineage (e.g., Sigmodontinae rodents, (Leite et al., 2014)). Early proposed phylogenies of Mabuyinae used a maximum of 35 species, a number that significantly underrepresents the diversity of this subfamily (Mausfeld et al., 2002; Carranza and Arnold, 2003; Whiting et al., 2006). Recently, Hedges and Conn (2012) studied the CAM clade exclusively and included 40 species, whereas the large-scale Squamata phylogeny of Pyron *et al*. (2013), which contains 4,161 species, sampled 71 mabuyine skink species. Considering that improvements in phylogenetic inference and divergence time estimation can be obtained with increased taxon sampling (Linder et al., 2005; Albert et al., 2009; Soares and Schrago, 2012), this matter requires further investigation.

In this study, as a means of exploring the continental biogeographic and evolutionary patterns associated with the occupation of South America by mabuyine skinks, we estimated the molecular phylogeny of Scincidae, inferred the divergence times of its members, and performed, for the first time, a statistical historical-biogeographic analysis and diversification rate analysis of this group. To this end, we assembled a dataset for studying mabuyine evolution, which also included representatives of the rest of the Scincidae. This comprises the largest dataset of species and gene sampling composed to date, with the aim of uncovering the evolution of the Mabuyinae.

Materials and Methods

Data collection, alignment and taxonomy

We assembled a dataset containing sequence information for eight genetic loci from 117 species of Mabuyinae. Moreover, a representative number of terminals were collected from other scincid subfamilies (101 genera), totalling 227 taxa, that were downloaded from GenBank. Two genera of the family Xantusiidae were used as outgroups. All seven genes available from *Trachylepis atlantica* were used in our analysis: the mitochondrial ribosomal genes *12S* rRNA, *16S* rRNA and the coding gene cytochrome b (*cytb*); as well as the nuclear genes alpha enolase (*enol*), oocyte maturation factor (*cmos*), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), myosin heavy chain (*myh*), and G protein-coupled receptor 149 (GPR149). Accession numbers are available in Supplementary File 1. When several sequences representative of each taxon were available, the longest sequence was selected. All protein-coding sequences were aligned individually in SeaView (Gouy *et al.*, 2010) using the MUSCLE (Edgar 2004) algorithm, whereas the ribosomal genes were aligned in MAFFT (Katoh and Standley, 2013). Gblocks (Castresana, 2000; Talavera and Castresana, 2007) was used to exclude poorly aligned bases and divergent regions in the *12S* rRNA, *16S* rRNA and *enol* genes. Individual genes were then concatenated into a single supermatrix using the R package Phyloch (r-phylo.org). RogueNarok (Aberer *et al.*, 2013) was used to identify rogue taxa without significant phylogenetic information. To this end, a rapid bootstrapping algorithm analysis (Stamatakis *et al.*, 2008), followed by a thorough search of the ML tree using the evolutionary model GTRGAMMA, was performed in RAxML-HPC (8.1.24) (Stamatakis, 2014). The ML tree and bootstrap trees were analysed in the program. The terminal nodes *Larutia* and *Otosaurus*, which each presented a relative bipartition information criterion (RBIC) higher than 1.0, were removed from the analysis. Another dataset, assembled with a more stringent (RBIC > 0.5) criterion, was composed for comparison. Under this criterion, the genus *Lankascincus* and the mabuyine species *Eumecia anchietae* and *Trachylepis acutilabris* were excluded from the analyses. The results, however, were robust for both RBIC values, and we report the analyses under RBIC > 1.0 hereafter. The final supermatrix consisting of 4,131 base pairs are available in Supplementary File 2

In this study, we followed the current Reptile Database classification (as of October 2016), which adopts the genus-level taxonomical arrangement proposed by Hedges and Conn (2012), with the subfamily classification of Scincidae that includes Mabuyinae, Egerniinae, Sphenomorphinae, Eugongylinae, Lygosominae and Acontinae.

Evolutionary analyses

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

Inference of node ages was performed with the mcmctree program of the PAML 4.8a package (Yang, 2007). Priors for the rgene and sigma2 parameters were set as $G(2, 200)$ and $G(1, 10)$, respectively. Markov chains were sampled every 1,000 generations until 50,000 trees were collected. The analysis was performed twice to check for convergence of the chains. Effective sample sizes (ESS) of parameters were calculated in Tracer v. 1.5, and all values were greater than 200.

Calibration priors

The root age, which corresponds to the split between the families Scincidae and Xantusiidae, was calibrated at a minimum value of 70.6 Ma and a maximum age of 209.5 Ma. The minimum was set according to the oldest scincid from the Late Cretaceous in North America (Campanian, 83.5-70.6 Ma), as previously adopted by Mulcahy *et al.* (2012) (Rowe *et al.*, '92); while the maximum was set according to Benton *et al.* (2015), which proposed a maximum age of the ancestral of Squamata. Additional calibration information was gathered from the PaleoBioDB (paleobiodb.org) and entered as minimum ages of the stem nodes of clades. The minimum age of the Scincidae stem node was calibrated at 20.4 Ma, based on the oldest crown

scincid *Eumeces antiquus* classified as a member of the subfamily Scincinae (Holman, '81; Estes, '83). The clade containing the extant genus *Eumeces* was calibrated at a minimum age of 13.6 Ma based on fossils from the Middle Miocene in North America (Holman, '66; Voorhies *et al.*, '87; Joeckel, '88). An extinct *Egernia* sp. from the Miocene of Hungary was used to calibrate the part of Egerninae containing this extant genus (Venczel and Hír, 2013). According to Böhme (2010), the fossil *Tropidophorus bavaricus* belongs to extant genus *Tropidophorus*, and it was used to calibrate this clade (Böttcher *et al.*, 2009).

Ancestral area reconstruction

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

Rate of species diversification and diversification-phenotype rate correlation

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

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

Differences in the rates of speciation (λ) and extinction (μ) between New World (*NW*) and Old World ($\overline{NW}$) areas and between viviparous (*V*) and non-viviparous ($\overline{V}$) lineages were tested using two approaches. Firstly, an ANOVA, implemented in the R package diversitree (FitzJohn 2012), was used to compare different macroevolutionary regimes. In the *NW*/$\overline{NW}$ comparison, rates were calculated using the GeoSSE approach (Goldberg *et al.* 2011), whereas BiSSE was used to test *V*/$\overline{V}$ rates, with both tests of binary characters as implemented in diversitree. In this sense, GeoSSE first optimised the parameters under an unconstrained full model, in which ML estimates were obtained for (i) the speciation rate of the New World lineage (λ_{NW}); (ii) the speciation rate of non-New World lineages ($\lambda_{\overline{NW}}$); (iii) the extinction rate of the New World clade (μ_{NW}); (iv) the extinction rate of non-New World lineages ($\mu_{\overline{NW}}$); (v) the intermediate speciation rate parameter ($\lambda_{NW,\overline{NW}}$); (vi) the dispersal rates from the New World clade ($d_{NW\rightarrow\overline{NW}}$); and (vii) the dispersal rates of the sister lineages ($d_{\overline{NW}\rightarrow NW}$). Similarly, BiSSE was used to infer (i) the speciation rate of the viviparous lineage (λ_V); (ii) the speciation rate of

non-viviparous lineages ($\lambda_{\overline{V}}$); (iii) the extinction rate of the viviparous clade (μ_V); (iv) the extinction rate of non-viviparous lineages ($\mu_{\overline{V}}$); (v) transition rates from the viviparous clade ($q_{V\rightarrow\overline{V}}$); and (vi) transition rates of the sister clade ($q_{\overline{V}\rightarrow V}$). Initial parametric values were set according to the *starting.point* function from the diversitree package with an initial ratio of 0.5. This preliminary step was required to build the likelihood function (the *make* command). In BiSSE, species with unknown states were coded as 'NA' and assigned the sampling fraction of the species of Mabuyinae used in this work (~61%), independent of the character state. Subsequently, to perform the ANOVA test of the GeoSSE results, we chose to constrain the intermediate speciation and the dispersal rate parameters to zero ($\lambda_{NW,\overline{NW}} = d_{NW\rightarrow\overline{NW}} = d_{\overline{NW}\rightarrow NW} = 0$), in order to compare speciation and the extinction rates within regions exclusively. Finally, we tested macroevolutionary alternative models against the full models (Table 1).

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

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

Rate of trait evolution and ancestral state reconstruction

We inferred ancestral states of reproductive mode in the BayesTraits software (Pagel *et al.* 2004) and in the R package BiSSE. Both approaches use the maximum likelihood method and allow the use of species with unknown character states. Results were visualised in the R package diversitree. The rates of trait evolution of the two continuous traits studied, namely, SVL and body mass, were inferred in BAMM, using logarithms of both measures. Phylogenies were also pruned to match the available information for both tree terminals and traits. Prior distributions to these subtrees were set according to *setBAMMPriors* function from the BAMMtools R package (Rabosky *et al*. 2014). Chains were sampled every 1,000 generations until 50,000 trees were collected. The results were summarised and visualised in BAMMtools.

281 **Results**

282

283 Mabuyinae was recovered as a monophyletic group (BS = 76). The first split in this
284 subfamily isolated the genus *Dasia* from the remaining Mabuyinae and was inferred to have
285 occurred at 30 Ma, with an HPD interval ranging from 20 to 48 Ma (Supplementary File 4). The
286 biogeographical model with the highest likelihood was the DEC+J (lnL: -94.34). Therefore, the
287 addition of the J parameter for founder events significantly increased the likelihood of the DEC
288 model ($p = 1.2e^{-9}$, Table 2). Our results supported a model in which the genera *Lankascincus* and
289 *Ristella* split from Mabuyinae (BS = 20) in the Oriental region.

290 After dispersal from the Oriental region to Africa, the ancestor of the CAM clade split
291 from Saharo-Arabian *Trachylepis* approximately 25 Ma (± 16-41 Ma) (BS=60). Subsequently,
292 the stock that gave rise to New World Mabuyinae dispersed from the Saharo-Arabian region to
293 the Neotropical Brazilian Subregion (Figure 1). The New World Mabuyinae were recovered as
294 monophyletic (BS=97), and the age of their LCA was estimated as 19 Ma (12-31 Ma). Our
295 results supported the hypothesis that this lineage reached the Neotropics via the Chacoan
296 Subregion. From this region, the ancestor of *Spondylurus* and *Copeoglossum* dispersed to islands
297 of the West Indies. The continental clade later dispersed along the Brazilian Subregion.
298 Additional dispersal events to the West Indies were inferred to have occurred at least twice: in
299 the ancestor of *Mabuya* and in that of *Alinea* and *Marisora*. *Marisora* was not recovered as
300 monophyletic, with the Central American clade as sister to *Alinea* and the South American clade
301 as sister as *Aspronema.*

302 The origin of *Trachylepis atlantica* consisted of a different history. Firstly, the
303 monophyly of genus *Trachylepis* was not recovered. This genus was split into two lineages: one
304 sister lineage of the CAM clade and another major clade to which *T. atlantica* belongs. Our
305 analysis supported the phylogenetic position of *T. atlantica* as a sister lineage of the clade
306 including the Europa Island *T. infralineata*, the Madagascan *T. comorensis*, and the continental
307 African *T. maculilabris* (BS = 29). We found that the *T. atlantica* ancestor diverged from the
308 remaining *Trachylepis* in the Miocene, approximately 17 Ma (between 10 and 27 Ma) at tropical
309 Africa. The younger diversification of *T. atlantica* indicates that the crossing of this species to

Fernando de Noronha occurred more recently than did the occupation of South America by the CAM clade. Our analyses also suggested that once the ancestors of this major *Trachylepis* clade reached Africa, dispersal events from the African continent occurred to Madagascar and nearby islands at least three times, in addition to the dispersion to the Neotropics (*T. atlantica*). Our results showed that a monophyletic Madagascan *Trachylepis* (BS = 94) diverged from its sister group approximately 19 Ma (12 – 32 Ma) (BS = 23).

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

GeoSSE analysis of the difference between the posterior distributions of speciation rates in *NW*/$\overline{NW}$ lineages indicated a positive credible interval (CI) (0.005:0.113), indicating that the speciation rates of South American clades (*NW*) were indeed higher than those of the remaining lineages ($\overline{NW}$). In BAMM, however, we failed to find a significant difference between the posterior distributions of speciation rates (CI: -0.103:0.074). We also found no evidence for diversification shifts during mabuyine diversification. However, the macroevolutionary cohort matrix suggested heterogeneous macroevolutionary rate regimes in the South American Mabuyinae and the remaining clade (Figure 2). In both GeoSSE and BAMM analyses, we failed to find differences between the extinction rates (CI_{geoSSE}: -0.036:0.074, CI_{BAMM}: -0.103:0.110) and between the net diversification rates (CI_{geoSSE}: -0.010:0.090, CI_{BAMM}: -0.073:0.036).

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

337 According to the ancestral state reconstructions of the mode of reproduction, the ancestor
338 of CAM and their *Trachylepis* sister clade was recovered as viviparous by BayesTraits
339 (P_{BTML}=0.751; P_{BTBA}=0.787) and as oviparous by BiSSE (P_{BiSSE}=1), while the ancestor of CAM
340 alone was recovered as viviparous by all approaches (P_{BiSSE}=0.953; P_{BTML}=0.992; P_{BTBA}=0.983),
341 suggesting that the ancestral species that colonised South America was likely viviparous (Figure
342 2). The ancestor of the subfamily Mabuyinae was inferred as oviparous (P_{BiSSE}=1; P_{BTML}=0.983;
343 P_{BTBA}=0.980). Viviparity seems to have emerged several times in the genus *Trachylepis*, as well
344 as in the ancestor of *Chioninia* (P_{BiSSE}=0.952; P_{BTML}=0.984; P_{BTBA}=0.971).

345 We also analysed the differences in the SVL measurement and body mass of the *NW*
346 clade in comparison with the remainder $\overline{NW}$ lineages. The mean rates of trait evolution of SVL
347 and body mass were smaller in the New World clade than in the $\overline{NW}$ lineages. However, these
348 differences were not significant. In BAMM, we found an increase in the rate of SVL trait
349 evolution in genus *Chioninia*. Only one clade presented an increase in the rate of body mass trait
350 evolution: the Seychelles *Trachylepis* (*T. wrightii* and *T. brevicollis*). STRAPP analysis failed to
351 find a significant correlation between the rate of species diversification and the rate of SVL or
352 body mass trait evolution ($p > 0.05$).

353 **Discussion**
354
355 Our analyses support the hypothesis that the occupation of South America by the
356 ancestors of the Continental America Mabuyinae (CAM) clade occurred between the Eocene and
357 the Oligocene from the Saharo-Arabian region, corroborating recent estimates (e.g. Pinto-
358 Sánchez *et al.* 2015; Karin et al., 2016). This colonisation occurred independently of that of
359 *Trachylepis atlantica*, which split from its tropical African sister clade between the Oligocene
360 and the Miocene. Therefore, our results corroborated the hypothesis that the ancestor of *T.*
361 *atlantica* dispersed from tropical Africa as suggested by Mausfeld *et al.* (2002). The divergence
362 between *T. atlantica* and its African ancestors was older than the age of the formation of the
363 Fernando de Noronha archipelago. Thus, it is unlikely that the ancestors of *T. atlantica* reached
364 South America in a single transoceanic dispersal event. We must therefore assume a more
365 complex dispersal scenario, likely a series of dispersals through a transatlantic island corridor
366 leading to Fernando de Noronha. This stepping-stone mode of dispersal would explain the
367 discrepancy between the ages of genetic divergence and the formation of the archipelago because
368 it would dissociate the geological formation of the Fernando de Noronha archipelago from the
369 genetic isolation of the ancestor of *T. atlantica*.
370 The recurrent appearance of NW fossil forms related to Old Word vertebrate lineages in
371 the South American fossil record near the Eocene/Oligocene boundary, a period in which the
372 South American landmass was completely isolated from Africa, entails a transoceanic
373 connection between the two continents during this period (Simpson, '50; Poux *et al.*, 2006; de
374 Oliveira *et al.*, 2009). This transatlantic island corridor would also explain CAM clade
375 dispersion. Note that a fossil of a putative species of Mabuyinae has been described in the mid-
376 Atlantic Ascension Island, although no recent systematic re-evaluation of this specimen is
377 available (Mausfeld and Vrcibradic, 2002). In fact, studies have reported the existence of large
378 islands in the Atlantic Ocean (Ezcurra and Agnolin, 2012) that would have facilitated the
379 crossing from Africa to South America of lineages as diverse as the hystricognath rodents (Loss-
380 Oliveira *et al.*, 2012; Voloch *et al.*, 2013), anthropoid primates (Schrago *et al.*, 2012; 2013),
381 amphisbaenians (Vidal *et al.*, 2008), emballonurid bats (Teeling, 2005; Leigh *et al.*, 2013),
382 testudinid turtles (Le *et al.*, 2006), and others (Briggs, 2003; Renner, 2004; de Queiroz, 2005), all
383 taking place much later than the complete isolation of the two continents at approximately 100

Ma. The direction of Atlantic Ocean currents from Africa to South America would explain the scarcity of dispersals in the opposite direction (Houle, '99). The evolution of the two American lineages of Mabuyinae also corroborates this faunal connection and suggests that this dispersal may have occurred through island hopping, which is more likely than a single sweepstake event across the Atlantic Ocean.

The age of the first diversification of a living CAM species was inferred to be much earlier than the previously reported estimates by Carranza and Arnold (2003), 7-9 Ma. However, the ages inferred by Miralles and Carranza (2010); Hedges and Conn (2012) and Karin *et al*. (2016), approximately 14 Ma, lay within in the range found in this work (12-31 Ma). It is worth noting that previous estimates are also incompatible with single-event scenarios. Our molecular phylogeny was at odds with previous hypotheses on the relationships among the genera of Mabuyinae (Mausfeld, 2000; Mausfeld *et al.*, 2002; Carranza and Arnold, 2003; Whiting *et al.*, 2006; Pyron *et al.*, 2013). The evolutionary association between the Continental American Mabuyinae (CAM) and the (*T. vittata* + *T. aurata*) clade, a lineage that we herein propose to have emerged in the Oligocene, has already been reported in previous works (Carranza and Arnold, 2003; Sindaco *et al.*, 2012). As in this work, Pyron *et al*. (2013) also recovered *Trachylepis* as non-monophyletic but not directly related to the CAM. We also found that the (CAM + (*Trachylepis vittata* + *T. aurata* + *T. septaemtaeniata*) clade diverged from the lineage composed of the *Chioninia* and remaining *Trachylepis* in the Oligocene (~27 Ma). This estimate is older than the value reported by Hedges and Conn (2012), who placed the divergence in the Miocene (~18 Ma).

The arrival of Mabuyinae to South America seems to have changed the diversification rate regime of this lineage. The evolution rates of both body mass and SVL traits were not significantly altered after the arrival of the ancestors of New World clades, but the increases in rates of both traits were found in island groups, such in Cape Verde's *Chioninia* and Seychelles' *Trachylepis*. The viviparous CAM clade presents peculiar reproductive traits, such as a specialised chorioallantoic placenta that provides the foetal nutrition, similarly to eutherian mammals (Vrcibradic and Rocha, 2011). This character was suggested to be synapomorphous by Mausfeld *et al*. (2002). According to our analysis, the CAM ancestor was already viviparous, as was the ancestor of the genus *Chioninia*. Changes in reproductive mode seem to be correlated with dispersals or island occupation.

Regarding the higher systematics of Mabuyinae, Greer (‘70), based on the primitive characteristics of Asian Mabuyinae, suggested that the ancestors of this subfamily first dispersed from Asia. Other works reasserted this hypothesis, although no formal statistical analyses were conducted (Honda *et al.*, '99; 2003; Karin *et al.*, 2016). According to our results, early members of Mabuyinae dispersed to Africa and then reached South America and several oceanic islands. Our time-dated phylogeny and biogeographic reconstruction similarly suggested an Oriental ancestral distribution, as corroborated by the distribution of the genera *Lankascincus* and *Ristella*, which were recovered as sister clades of Mabuyinae and are geographically distributed in the Oriental region (Sri Lanka and the Indian, respectively). The age of the LCA of Mabuyinae and its sister clade was placed in the Eocene, and was likely distributed in the Oriental region. Additionally, we showed that the first genus of this group to diverge (*Dasia*, at 30 Ma) is from the Oriental region. Our time estimates overlap with the age of the collision between the Indian subcontinent and Southeast Asia at ca. 50 Ma (Chatterjee *et al.*, 2013). Therefore, the ancestor of the group may have reached the Asian continent through an Indian route and experienced a vicariant event with the uplift of the Himalayas.

Finally, this study provided an updated timescale and estimates of macroevolutionary regimes of the diversification of the subfamily Mabuyinae. Our focus was the occupation of the South American continent by the subfamily Mabuyinae through an Oligocene/Eocene transoceanic connection (E/O), which could be responsible for approximately 29% of the South American mammal diversity, suggesting the importance of this event to the extant vertebrate diversity in South America (Marshall *et al.*, '82). CAM and *T. atlantica* are the only representatives of the family Scincidae in South America accounting for 4% of the approximately 1560 squamate species on this continent (Uetz, 2000). Although there are species of other subfamilies of Scincidae in Central America, these species never crossed the Isthmus of Panama. The converse also seems true because the only mabuyine genus (*Marisora*) that partially occupied Central America based on our results had arrived via an intermediate dispersion through the West Indies. This suggests that no representative of Scincidae would be found in present day South American fauna in the absence of this E/O connection. Our results presented an overall picture of the timing, biogeography and macroevolutionary dynamics associated with the arrivals of the ancestors of the only vertebrate clade know to have undergone transoceanic dispersal twice.

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Figure 1

Time-dated phylogeny of the Mabuyinae with ancestral area reconstruction

Maps depict putative dispersals and vicariance 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.

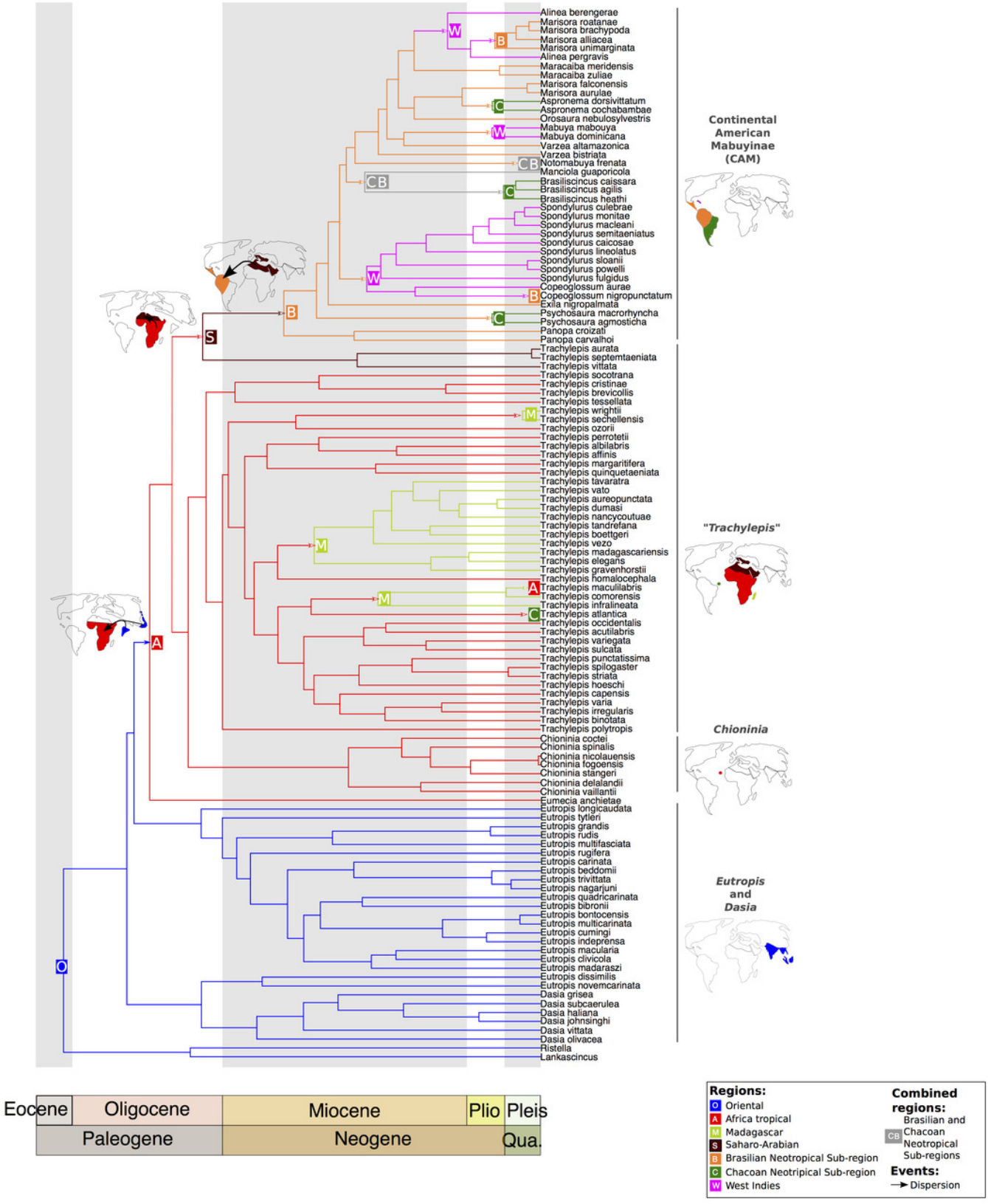
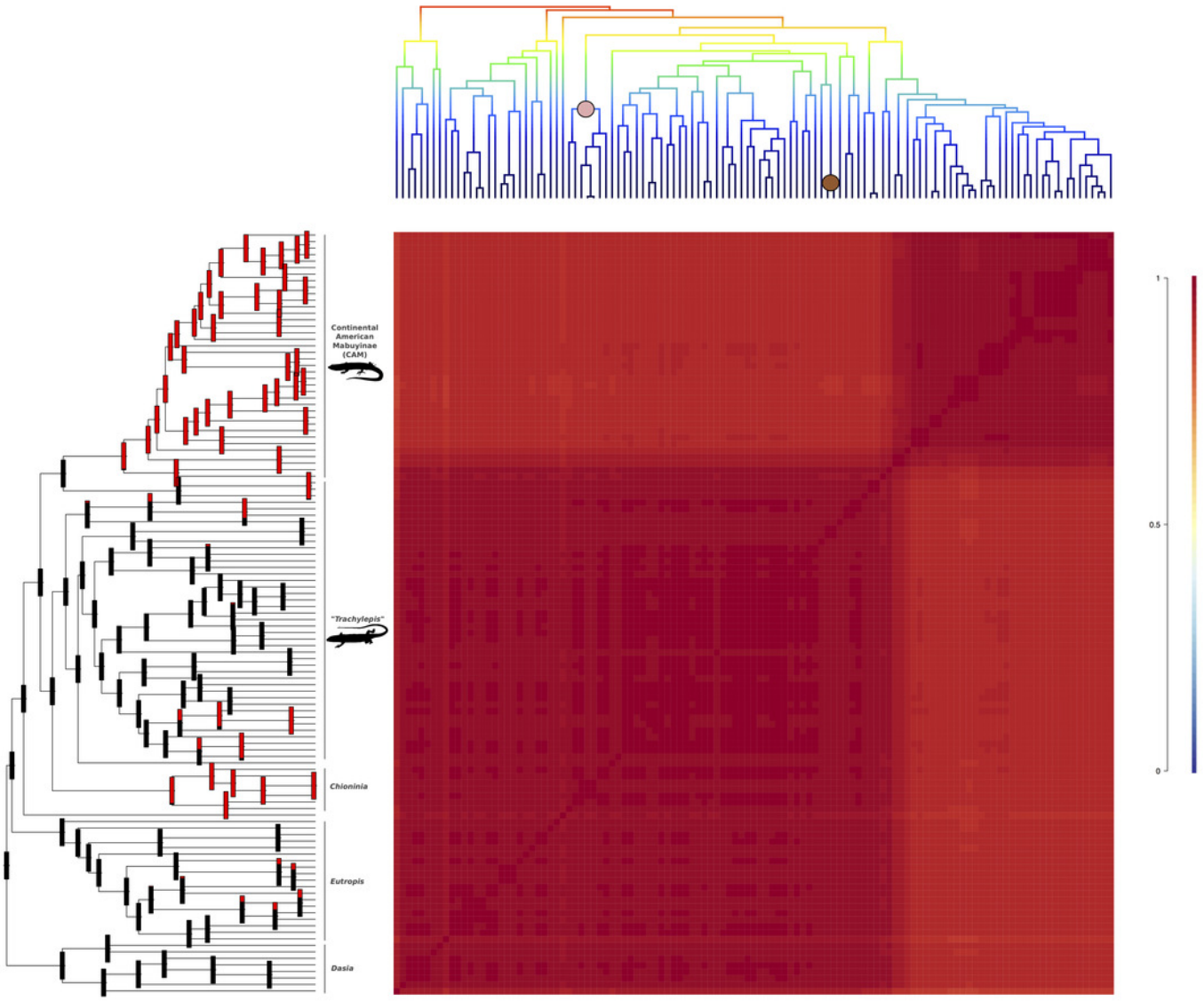

Alinea berengerae
Marisora roatanae
Marisora brachypoda
Marisora alliacea
Marisora unimarginata
Alinea pergravis
Maracaiba meridensis
Maracaiba zuliae
Marisora falconensis
Marisora aurulae
Aspronema dorsivittatum
Aspronema cochabambae
Orosaura nebulosylvestris
Mabuya mabouya
Mabuya dominicana
Varzea altamazonica
Varzea bistriata
Notomabuya frenata
Manciola guaporicola
Brasiliscincus caissara
Brasiliscincus agilis
Brasiliscincus heathi
Spondylurus culebrae
Spondylurus monitae
Spondylurus macleani
Spondylurus semitaeniatus
Spondylurus caicosae
Spondylurus lineolatus
Spondylurus sloanii
Spondylurus powelli
Spondylurus fulgidus
Copeoglossum aurae
Copeoglossum nigropunctatum
Exila nigropalmata
Psychosaura macrorhyncha
Psychosaura agmosticha
Panopa croizati
Panopa carvalhoi
Trachylepis aurata
Trachylepis septemtaeniata
Trachylepis vittata
Trachylepis socotrana
Trachylepis cristinae
Trachylepis brevicollis
Trachylepis tessellata
Trachylepis wrightii
Trachylepis sechellensis
Trachylepis ozorii
Trachylepis perrotetii
Trachylepis albilabris
Trachylepis affinis
Trachylepis margaritifera
Trachylepis quinquetaeniata
Trachylepis tavaratra
Trachylepis vato
Trachylepis aureopunctata
Trachylepis dumasi
Trachylepis nancycoutuae
Trachylepis tandrefana
Trachylepis boettgeri
Trachylepis vezo
Trachylepis madagascariensis
Trachylepis elegans
Trachylepis gravenhorstii
Trachylepis homalocephala
Trachylepis maculilabris
Trachylepis comorensis
Trachylepis infralineata
Trachylepis atlantica
Trachylepis occidentalis
Trachylepis acutilabris
Trachylepis variegata
Trachylepis sulcata
Trachylepis punctatissima
Trachylepis spilogaster
Trachylepis striata
Trachylepis hoeschi
Trachylepis capensis
Trachylepis varia
Trachylepis irregularis
Trachylepis binotata
Trachylepis polytropis
Chioninia coctei
Chioninia spinalis
Chioninia nicolauensis
Chioninia fogoensis
Chioninia stangeri
Chioninia delalandii
Chioninia vaillantii
Eumecia anchietae
Eutropis longicaudata
Eutropis tytleri
Eutropis grandis
Eutropis rudis
Eutropis multifasciata
Eutropis rugifera
Eutropis carinata
Eutropis beddomii
Eutropis trivittata
Eutropis nagarjuni
Eutropis quadricarinata
Eutropis bibronii
Eutropis bontocensis
Eutropis multicarinata
Eutropis cumingi
Eutropis indeprensa
Eutropis macularia
Eutropis clivicola
Eutropis madaraszi
Eutropis dissimilis
Eutropis novemcarinata
Dasia grisea
Dasia subcaerulea
Dasia haliana
Dasia johnsinghi
Dasia vittata
Dasia olivacea
Ristella
Lankascincus
Continental American Mabuyinae (CAM)
"Trachylepis"
Chioninia
Eutropis and Dasia
Eocene
Oligocene
Miocene
Plio
Pleis
Paleogene
Neogene
Qua.
Regions:
O Oriental
A Africa tropical
M Madagascar
S Saharo-Arabian
B Brasilian Neotropical Sub-region
C Chacoan Neotripical Sub-region
W West Indies
Combined regions:
CB Brasilian and Chacoan Neotropical Sub-regions
Events:
Dispersion

Figure 2

Macroevolutionary cohort matrix for the Mabuyinae subfamily.

Illustration of the macroevolutionary rates for the mabuyine lineage obtained using BAMM. For reference, the BAMM tree is plotted in the upper margin of the figure. The pairwise probability that any two species share a common macroevolutionary rate dynamic is indicated by the colour of each individual centre cell. The scale for the colour is indicated at the right. The coral and brown circles in the upper tree represent the shifts found with BAMM in the traits SVL and body mass, respectively. In the right tree, bars in the nodes show the mode of reproduction inferred by BayesTraits, according to the probability of occurrence of each character. Red represents viviparity, and black represents oviparity.


Continental American Mabuyinae (CAM)
"Trachylepis"
Chioninia
Eutropis
Dasia
1
0.5
0