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Slow and steady wins the race: Diversification rate is independent from body size and lifestyle in Malagasy skinks (Squamata: Scincidae: Scincinae)

Francesco Belluardo[a,b,c,*], A. Jesus Muñoz-Pajares[a,c,d], Aurélien Miralles[e], Daniele Silvestro[f,g,h], Walter Cocca[a,b,c], Fanomezana Mihaja Ratsoavina[i], Andrea Villa[j], Sam Hyde Roberts[k,l,m], Marcello Mezzasalma[a,c,n], Alexander Zizka[o], Alexandre Antonelli[g,h,p,q], Angelica Crottini[a,b,c]

[a] *CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal*
[b] *Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Praça Gomes Teixeira, 4099-002 Porto, Portugal*
[c] *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal*
[d] *Departamento de Genética, Universidad de Granada, Avenida de la Fuente Nueva S/N, 18071 Granada, Spain*
[e] *Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, Paris, France*
[f] *Department of Biology, University of Fribourg and Swiss Institute of Bioinformatics, Ch. du Musée 10, 1700 Fribourg, Switzerland*
[g] *Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, 405 30 Göteborg, Sweden*
[h] *Gothenburg Global Biodiversity Centre, Box 461, 405 30 Göteborg, Sweden*
[i] *Mention Zoologie et Biodiversité Animale, Domaine Sciences et Technologies, Université d'Antananarivo, B.P. 906, 101 Antananarivo, Madagascar*
[j] *Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, 08193 Cerdanyola del Vallès, Spain*
[k] *SEED Madagascar, Unit 7, Beethoven Street 1A, W10 4LG London, UK*
[l] *Oxford Brookes University, Headington Campus, 0X3 0BP Oxford, UK*
[m] *Operation Wallacea, Wallace House, Old Bolingbroke, PE23 4EX Spilsby, UK*
[n] *Department of Biology, Ecology and Earth Sciences, University of Calabria, Via P. Bucci 4/B, 87036 Rende, Italy*
[o] *Department of Biology, Philipps-University Marburg, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany*
[p] *Royal Botanic Gardens, Kew, TW9 3AE Richmond, UK*
[q] *Department of Biology, University of Oxford, South Parks Road, OX1 3RB Oxford, UK*

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ABSTRACT

Most of the unique and diverse vertebrate fauna that inhabits Madagascar derives from *in situ* diversification from colonisers that reached this continental island through overseas dispersal. The endemic Malagasy Scincinae lizards are amongst the most species-rich squamate groups on the island. They colonised all bioclimatic zones and display many ecomorphological adaptations to a fossorial (burrowing) lifestyle. Here we propose a new phylogenetic hypothesis for their diversification based on the largest taxon sampling so far compiled for this group. We estimated divergence times and investigated several aspects of their diversification (diversification rate, body size and fossorial lifestyle evolution, and biogeography). We found that diversification rate was constant throughout most of the evolutionary history of the group, but decreased over the last 6–4 million years and independently from body size and fossorial lifestyle evolution. Fossoriality has evolved from fully quadrupedal ancestors at least five times independently, which demonstrates that even complex morphological syndromes – in this case involving traits such as limb regression, body elongation, modification of cephalic scalation, depigmentation, and eyes and ear-opening regression – can evolve repeatedly and independently given enough time and eco-evolutionary advantages. Initial diversification of the group likely occurred in forests, and the divergence of sand-swimmer genera around 20 Ma appears linked to a period of aridification. Our results show that the large phenotypic variability of Malagasy Scincinae has not influenced diversification rate and that their rich species diversity results from a constant accumulation of lineages through time. By compiling large geographic and trait-related datasets together with the computation of a new time tree for the group, our study contributes important insights on the diversification of Malagasy vertebrates.

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* Corresponding author at: CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal.
E-mail address: france89belluardo@gmail.com (F. Belluardo).

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1. Introduction

Island biotas have played a significant role in the formulation of evolutionary theory (e.g., Darwin and Murray, 1859; Simpson, 1953; Gavrilets and Losos, 2009; Valente et al., 2020). Limited area and long-standing isolation are key features that make islands ideal settings to study evolutionary radiations and diversification (Losos and Ricklefs, 2009; Warren et al., 2015). The role of *in situ* diversification for island biodiversity was initially considered negligible for most islands systems (e.g., MacArthur and Wilson, 1963), but has gained increasing recognition in recent times (see e.g., Presgraves and Glor, 2010; Warren et al., 2015). *In situ* diversification is positively correlated with island size, and there appears to exist a minimum threshold in surface area above which local diversification becomes the primary source of diversity, with its contribution to local diversity increasing linearly with area (Heaney, 2000; Losos and Schluter, 2000; Kisel and Barraclough, 2010; Presgraves and Glor, 2010; Warren et al., 2015).

The geographic, geological, and environmental features that provide suitable conditions for *in situ* diversification differ amongst oceanic and continental islands. Yet, the study of island evolutionary radiations has been predominantly focused on oceanic archipelagos. The Galapagos and Hawaii provide amongst the best-known examples (e.g., Darwin and Murray, 1859; Lack, 1947; Warren et al., 2015; Meiri, 2017). The fact that oceanic islands emerge from the sea surface as blank slates can facilitate lineage diversification (i.e., providing new land and reduced competition for early colonisers; Toussaint et al., 2015; Ali, 2017). However, small sizes and young ages are features that can limit the extent of *in situ* diversification (McPeek and Brown, 2007; Kisel and Barraclough, 2010; Toussaint et al., 2015). In contrast, the rich bioclimatic and environmental diversity that can be available on large continental islands can provide ideal conditions for a multitude of diversification processes (Vences et al., 2009; Ali, 2017; Meiri, 2017; Ali and Meiri, 2019), and, if the islands are old enough, time may favour prolonged diversification. On the other hand, the presence of rich and structured biotas on continental islands may in turn limit the opportunities for the diversification of new colonisers (McPeek and Brown, 2007; Toussaint et al., 2015; Ali, 2017).

Madagascar is the fourth largest island in the world (ca. 587,000 km^2), initially part of the Gondwana supercontinent until it separated from Africa ca. 160–130 million years ago (Ma), it remained isolated from all other landmasses since ca. 80–65 Ma (Ali and Aitchison, 2008; Ali and Hedges, 2022). Madagascar's Cretaceous vertebrate biota was likely almost entirely depleted during the mass extinction at the boundary between the Cretaceous and Paleogene (K-T boundary) (Samonds et al., 2013) and time-calibrated phylogenies and biogeographic reconstructions suggest that most present-day biodiversity results from subsequent colonisation events rather than vicariance (Vences et al., 2003; Yoder and Nowak, 2006; Vences et al., 2009; Crottini et al., 2012; Samonds et al., 2012; Welt and Raxworthy, 2022). Biogeographic studies revealed a peak in successful colonisations through multiple overseas dispersal events around the K-T boundary that continued through most of the Cenozoic (Crottini et al., 2012; Samonds et al., 2012, 2013). The subsequent *in situ* diversification of these colonisers is responsible for most of present-day Malagasy vertebrate biota (Vences et al., 2003; Yoder and Nowak, 2006; Vences et al., 2009; Crottini et al., 2012; Samonds et al., 2012, 2013), which is composed of several endemic lineages, some of which represent high taxonomic ranks (e.g., genera, subfamilies, families).

The old age of Madagascar as an island (ca. 80–65 Ma), its rich environmental heterogeneity, and large size have favoured intense and prolonged diversification (Vences et al., 2009; Kisel and Barraclough, 2010; Crottini et al., 2012). In addition, the extinction of the Malagasy vertebrate assemblage at the end of the Cretaceous, when Madagascar was already isolated, has likely provided new colonisers with a depleted and much less-competitive environment where new lineages could widely diversify (Vences et al., 2003; Yoder and Nowak, 2006; Vences et al., 2009; Crottini et al., 2012). The combination of these circumstances makes Madagascar an ideal setting to study *in situ* diversification (Ali and Aitchison, 2008; Vences et al., 2009; Crottini et al., 2012; Samonds et al., 2012), and several Malagasy endemic lineages are salient examples of impressively species-rich evolutionary radiations (Ganzhorn et al., 2014; Goodman and Benstead, 2003). However, only a limited number of Malagasy vertebrate radiations have been investigated to unveil their processes of *in situ* diversification (e.g., vangid birds, Jønsson et al., 2012; lemurs, Herrera, 2017; pseudoxyrhophiine snakes, Burbrink et al., 2019).

Here we focus on the diversification of the species-rich Malagasy scincine lizards (subfamily Scincinae). This radiation endemic to Madagascar and neighbouring islands (see 2.1 Samples and dataset) has recently been the object of intensive systematic and taxonomic research, with several species described over the last three decades (e.g., Raxworthy and Nussbaum, 1993; Andreone and Greer, 2002; Köhler et al., 2009; Miralles et al., 2011a, 2011b, 2011c, 2012, 2016a, 2016b), and the knowledge of their phylogenetic relationships that has greatly improved (e.g., Crottini et al., 2009; Erens et al., 2017; Köhler et al., 2010; Miralles et al., 2015; Miralles and Vences, 2013; Schmitz et al., 2005; Whiting et al., 2004). Their richness and variety emphasise Madagascar's status as a global hotspot for skink diversity (Chapple et al., 2021). Nonetheless, part of the diversity of this group likely remains scientifically undescribed, as demonstrated by the large number of candidate species identified in recent years (Miralles et al., 2016b; Miralles and Vences, 2013; Nagy et al., 2012). Molecular phylogenies suggest that the most recent ancestor of all Malagasy Scincinae reached Madagascar from Africa 65–45 Ma (Whiting et al., 2004; Crottini et al., 2012; Miralles et al., 2015) and that *in situ* diversification is responsible for the large variety of species and forms observed today. Malagasy Scincinae have colonised most geographic and bioclimatic regions of the island, although species are differently distributed across Madagascar's regions (Brown et al., 2016). The eastern rainforest hosts the majority of the species of the group and the humid forest in northern Madagascar is the most relevant hotspot for scincines diversity (Brown et al., 2016). This distributional pattern, shared with other amphibian and reptile groups (Brown et al., 2016), would suggest that Madagascar's large environmental diversity and bioclimatic zonation played a role in the diversification of Malagasy Scincinae.

Malagasy Scincinae display an exceptional array of ecomorphological adaptations to the environments they inhabit (Fig. 1; Whiting et al., 2004; Glaw and Vences, 2007; Miralles et al., 2015, 2016a). Fully quadrupedal species (genera *Amphiglossus*, *Brachyseps*, *Flexiseps*, and *Madascincus*) mostly inhabit forested regions, with at least one genus (*Amphiglossus*) specialised to live in close association with freshwater. Limbless or limb-reduced species often exhibit several additional adaptations to a fossorial (burrowing) lifestyle, such as body elongation, modification of cephalic scalation, depigmentation, and regressed eyes and ear-openings (Glaw and Vences, 2007; Miralles et al., 2011b, 2012, 2015, 2016a). Fossorial species mostly inhabit either the forest litter (here termed 'litter-burrowers'; genera *Pseudoacontias* and *Paracontias* except for *Paracontias minimus* that is found in sandy soils) or sandy environments (here termed 'sand-swimmers'; genera *Grandidierina*, *Pygomeles*, and *Voeltzkowia*). The most recent investigation of the evolution of the body plan in Malagasy Scincinae suggested that the fully quadrupedal form (non-fossorial lifestyle) represents the plesiomorphic condition from which different morphological adaptations to a fossorial lifestyle have convergently evolved multiple times (Miralles et al., 2015). In addition, the almost concurrent divergence of fossorial sand-swimmer genera in different regions of the island during the Miocene was suggested as evidence for the establishment of dry and sandy environments in Madagascar during that period, although no biogeographic reconstruction was performed to support this hypothesis (Miralles et al., 2015).

Despite recent progress in the study of Malagasy Scincinae, we are still lacking a comprehensive characterisation of the *in situ* diversification of the group. Following the recent systematic and taxonomic advances outlined above and the availability of a large number of new samples, it is now possible to infer a new phylogenetic hypothesis of the group based on a more complete dataset (both in terms of number of included taxa and loci). The availability of this dataset makes the estimation of divergence times more reliable, which is, in turn, fundamental to performing informative macroevolutionary analyses within a robust phylogenetic and statistical framework. Using new macroevolutionary tools that have become available recently (e.g., Beaulieu and O'Meara, 2016; Harvey and Rabosky, 2018; Höhna et al., 2022; May et al., 2016; Rabosky, 2014; Rabosky and Huang, 2016), we can now explore the roles and contributions of intrinsic and extrinsic determinants of species diversification in the group by testing a variety of hypotheses on their *in situ* diversification. This contributes to the understanding of the evolution of Malagasy fauna and provides an accessible and replicable methodological framework that can be applied to study other radiations to identify possible shared patterns and improve our knowledge on the *in situ* diversification processes within Madagascar and other island systems. To achieve a comprehensive characterisation of the diversification of the Malagasy Scincinae we focussed on:

(1) Obtaining a robust phylogenetic framework. The phylogenetic relationships amongst major clades remain poorly resolved, and several undescribed taxa have not yet been included in molecular phylogenetic analyses (Erens et al., 2017). A new phylogenetic hypothesis encompassing most described and known candidate species and an estimation of their divergence times are needed to investigate the diversification of the group;

(2) Hypothesis testing:

(2a) Can an early burst in diversification rate, often observed in evolutionary radiations (Schluter, 2000; Gavrilets and Losos, 2009; Simões et al., 2016) as, for instance, in Madagascar's vangid birds (Jønsson et al., 2012), explain the pattern of diversity observed in this group? Alternatively, did diversification rate in Malagasy scincines increase towards the present (e.g., as previously identified in lemurs; Herrera, 2017), or followed a constant trend and a subsequent slowdown in the last million years as in pseudoxyrhophiine snakes from Madagascar (Burbrink et al., 2019)?

(2b) Is there an association between small body size and increased rate of diversification in Malagasy Scincinae, as reported for other taxa in Madagascar (e.g., Wollenberg et al., 2011)?

(2c) Is there an association between the several parallel transitions from quadrupedal to limb-regressed lineages (Miralles et al., 2015) and increased diversification rates?

(2d) Did the bioclimatic zonation of Madagascar play a role in the diversification of Malagasy Scincinae, and is it possible that past large-scale climatic changes favoured diversification, as in the case of the divergence of the fossorial sand-swimmer genera (Miralles et al., 2015)?

2. Material and methods

2.1. Samples and dataset

Malagasy Scincinae comprise 65 described species in nine genera: *Amphiglossus*, *Brachyseps*, *Flexiseps*, *Grandidierina*, *Madascincus*, *Paracontias*, *Pseudoacontias*, *Pygomeles*, and *Voeltzkowia* (Fig. 1; Supplementary Table S1; Glaw and Vences, 2007; Uetz et al., 2022). The genus *Mesomycterus* Cope 1892 has recently been proposed to be an older synonym of *Brachyseps* Erens et al., 2017 (Shea, 2021), but since it has not been used in the literature since its description, it qualifies as nomen oblitum (Uetz et al., 2022), and it is not considered in this study. Most species belonging to the Malagasy Scincinae are restricted to Madagascar, although two species of *Flexiseps* are endemic to the neighbouring islands of Mayotte and Glorioso (Glaw and Vences, 2007; Uetz et al., 2022).

Fig. 1. An overview of the Malagasy Scincinae diversity. (A) *Pseudoacontias menamainty*, Berara. (B) *Brachyseps macrocercus*, Ankaratra. (C) *Madascincus* CaNew Betampona (of the *Madascincus* "nanus" group), Betampona. (D) *Madascincus igneocaudatus*, Ifaty. (E) *Flexiseps ornaticeps*, Ifaty. (F) *Amphiglossus astrolabi*, Sainte Luce. (G) *Voeltzkowia yamagishii*, Ankarafantsika. (H) *Voeltzkowia mira*, Matsedroy. (I) *Paracontias vermisaurus*, Makira. (J, K) *Pygomeles braconnieri*, near Ifaty. (L) *Grandidierina* sp. aff. *rubrocaudata* Andranomaitso. (Credits: A - Franco Andreone; B - Frank Glaw and Miguel Vences; C, D, E, L - Gonçalo M. Rosa; F, H - Sam Hyde Roberts; G - Falk Eckhard; I - Miguel Vences; J, K - Aurélien Miralles).

We compiled a dataset comprising all individuals of Malagasy Scincinae whose tissue samples were available to us (Supplementary Table S2). These samples were sequenced for at least one of the three mitochondrial markers that are generally used for species identification of Malagasy Scincinae, which allowed us to identify and assign them unequivocally to a mitochondrial interspecific lineage: 16S rRNA 3′ terminus (16S), cytochrome oxidase I gene (COI), and NADH dehydrogenase subunit 1 (ND1) (with adjacent tRNAs) genes (see Supplementary Text S1 for details on laboratory work). To do this, we applied the skinks' standard interspecific threshold of 6.1–6.5% genetic distance at the COI marker, as proposed in Nagy et al. (2012), and used 16S and ND1 to refine species identification when necessary.

We compiled a phylogenetic multi-locus dataset using the matrix of Erens et al. (2017) as a starting point. This matrix contained 45 interspecific lineages (either nominal species or candidate species as defined by Vieites et al., 2009) and 13 loci. We augmented this matrix by adding one locus (COI) and sequences from 26 additional lineages (seven of which were identified for the first time; Supplementary Tables S2–S3) and removing three taxa corresponding to intraspecific lineages. Lineage identification in our phylogenetic multi-locus dataset was performed following the procedure described above. Our final molecular dataset included 68 ingroup taxa (47 of the 65 nominal species of Malagasy Scincinae and 21 candidate species; Supplementary Table S1) and 14 loci, which comprised four mitochondrial (12S rRNA, 16S, COI, and ND1 with adjacent tRNAs) and 10 nuclear markers (brain-derived neurotrophic factor (BDNF), oocyte maturation factor (CMOS), phosducin (PDC), recombination activating gene 1 and gene 2 (RAG1 and RAG2), alpha-enolase (ENO1), two non-overlapping segments of sacsin (SACS-A and SACS-B), leucine-rich repeat and WD repeat-containing protein (KIAA1239), and titin (TTN)) (Supplementary Table S3; Supplementary Text S1). To maximise the number of available loci, we used sequences of multiple congeneric species (chimera sequences) of *Cordylus*, *Eumeces*, *Tiliqua*, and *Scincella* as outgroups, as in Crottini et al. (2009) and Erens et al. (2017) (Supplementary Table S3). Newly generated sequences have been deposited in GenBank (OP256430–OP256524, OP263988–OP264059, OP271309–OP271456; Supplementary Table S3). For details on laboratory work and sample amplification see Supplementary Text S1.

2.2. Phylogenetic analyses

We performed phylogenetic analyses on a concatenated dataset composed of all mitochondrial and nuclear markers available in our dataset (Supplementary Table S3). We used PipeLogeny in R 4.0.2 (Muñoz-Pajares et al., 2019; R Core Team, 2021), which is a recently developed pipeline that automatises the preparation of the input files for several commonly used phylogenetic tools, which are then run separately in their standalone software applications. We aligned sequences with MAFFT 7.310 (Katoh and Standley, 2013), detected misaligned and hypervariable regions of the alignment to be excluded from the phylogenetic analyses with Gblocks 0.91b (Castresana, 2000), identified the best-fit partitioning scheme and models of evolution using PartitionFinder2 2.1.1 (Lanfear et al., 2017), and performed Bayesian analyses using MrBayes 3.2.7 (Ronquist et al., 2012). Due to the limited number of available gene fragments and the unavailability of recently collected tissue samples, we excluded *A. splendidus* and *P. menamainty* from the phylogenetic analyses (see Supplementary Table S3 for the phylogenetic dataset). After the preparation of the input files, we ran Gblocks on the GBlocks Server (Castresana, 2000) using the least stringent parameter settings. We used PartitionFinder2 on the CIPRES Science Gateway (Miller et al., 2010) to find the best-fit partitioning scheme and models of sequence evolution, which were tested under Bayesian Information Criterion (BIC). We ran MrBayes on CIPRES with two runs of 100-million generations each, setting four independent chains for each run with sampling at every 1,000th generation and 40% burn-in of the Markov Chain Monte Carlo (MCMC) chain. We assessed run convergence and posterior distributions with Tracer 1.7.1 (Rambaut et al., 2018) and considered a value of 200 Effective Sampling Size (ESS) as a minimum threshold to evaluate the fitness of each prior. We used FigTree 1.4.4 (Rambaut, 2009) to visualise the 50%-majority rule consensus tree.

Following the procedure described above, we inferred distinct topologies for the concatenated alignments of mitochondrial and nuclear markers, respectively. We ran two independent runs of 70-million generations each with MrBayes for both phylogenies and assessed topological congruence between the mitochondrial, nuclear and full concatenated (mitochondrial and nuclear) topologies with the Icong index (de Vienne et al., 2007; R script available on GitHub at https://github.com/damiendevienne/icong).

To explore the influence of alternative inference methods on tree topology, we inferred a maximum likelihood (ML) phylogeny with RAxML-HPC2 8.2.12 (Stamatakis, 2014) on the full multi-locus matrix (Supplementary Table S3). We used the same partition scheme estimated with PartitionFinder2 for Bayesian analyses (see above). We ran RAxML on CIPRES setting 1,000 replicates of rapid bootstrap and GTRCAT model. In addition, we inferred a species tree with ASTRAL 5.7.8 (Zhang et al., 2018) starting from gene trees of the 14 markers available in our dataset. We inferred the gene trees with MrBayes following the same procedure described above for concatenated datasets, with the only exception that we used jModeltest 2.1.10 (Darriba et al., 2012) on CIPRES to find the best model of sequence evolution for each gene. We performed two separate runs of 50-million generations. To estimate the species tree we ran ASTRAL with default parameters using the 50%-majority rule consensus trees for each gene.

2.3. Dated phylogeny

Given the absence of fossils in the ingroup, we used fossil-based calibrations on the outgroups. We compiled a reduced dataset including four Malagasy Scincinae and seven outgroups (Supplementary Table S5). We selected one species for each of the outgroups (*Cordylus*, *Eumeces*, *Tiliqua*, and *Scincella*) of the complete species-level dataset, and the remaining outgroups were selected based on the fossil calibrations that were used (Supplementary Table S5); phylogenetic placement and age of fossil calibrations were expert-verified (by A. Villa) (see Supplementary Table S6 for information on the selected fossils and justification of their use to calibrate the tree). We aligned the dataset with MAFFT 7.310 and inferred the best-fit partitioning scheme and models of evolution with PartitionFinder2 2.1.1, under BIC, on the CIPRES Science Gateway. We estimated divergence times with BEAST 2.6.0 (Bouckaert et al., 2019) (see Supplementary Text S1 for all analysis details). The height average and 95% Higher Posterior Density Interval (HPDI) of the crown node of the Malagasy Scincinae was used to calibrate the corresponding node on the complete species-level dataset, and we estimated divergence times on this dataset with BEAST (Supplementary Table S3; see Supplementary Text S1 for all analysis details).

2.4. Diversification rate analyses

We inferred diversification rates from the dated phylogeny pruned from all outgroups. Whenever possible we set a sampling fraction of 76%, corresponding to the percentage of taxa included in the phylogeny relative to the overall number of nominal species and candidate species recognised for the group. Since several models and methods that we employed in the following analyses assume rate homogeneity across lineages, we first checked for possible heterogeneity of diversification rate within the tree with BAMM 2.5.0 (Rabosky, 2014). BAMM identifies heterogeneity in the diversification process through time and across branches within a phylogeny using the reversible-jump MCMC (rjMCMC). The priors of the evolutionary rate parameters were set based on the function 'setBAMMpriors' of the package BAMMtools 2.1.7 (Rabosky et al., 2014b) available on R 4.0.2. We tested different priors for the values of the expected number of diversification rate shifts (0.1, 0.5, 1, 5, and 10) and for each value we ran two MCMC chains of 10-million steps to assess reciprocal convergence, while we ensured single-chain convergence through the ESS (minimum threshold of 200). We set a non-random incomplete taxon sampling, which accounts for the different numbers of included taxa amongst different genera of the group. The output was inspected with the R package BAMMtools 2.1.7. We evaluated the statistical support of the number of diversification rate shifts based on Posterior Probability (PP) and Bayes Factor after discarding 15% of the posterior samples as burn-in. Moore et al. (2016) criticised BAMM highlighting possible issues concerning the likelihood function and the prior models employed in the software. To account for these uncertainties in diversification rate analyses and the several other analyses in which we used this software (see 2.5 Trait evolution), we decided to run BAMM along with other tools to highlight potential discordance in the results that might be indicative of technical issues.

We further investigated the possible heterogeneity in diversification rates by examining the spectral density profile of the tree computed from the Laplacian graph of its branch lengths (Lewitus and Morlon, 2016). We obtained the eigenvalues and spectral density profile of the tree with the function ‘spectR’ implemented in the R package RPANDA 1.8 (Morlon et al., 2016). To test the number of modalities that characterise the tree, that can represent the number of heterogeneities in diversification rates, we used the function ‘BICompare’. We compared BIC values associated with the empirical tree and randomly bifurcating trees parametrised from this to provide a significance test for the number of modalities that were previously highlighted.

We investigated the occurrence and timing of mass extinction events and tree-wide diversification rate changes through time with the CoMET model within the R package TESS 2.1.0 (Höhna, 2013; May et al., 2016). This method implements a piecewise-constant speciation and extinction rate model with the number of rate shifts through time that is inferred through rjMCMC. We set the function ‘tess.analysis’ to account for empirical estimates of the hyperpriors of diversification-rates parameters. We ran the rjMCMC for 50-million steps of which the initial 14.5% was discarded as burn-in. We considered a minimum ESS of 200 to ensure convergence of the chains. The occurrence of mass extinction events and shifts in speciation and extinction rates was evaluated through Bayes Factor.

To further evaluate the TESS results, we investigated the possible time-dependence of diversification rates through a maximum likelihood model-fitting approach. We tested six models reported in Morlon et al. (2011) accounting for both time-independent and time-dependent variation of speciation and extinction rates as well as periods of expanding and declining diversity (Supplementary Table S7). These models were fitted with the function ‘fit_bd’ implemented in the R package RPANDA 1.8 (Supplementary Table S7). The best-fitting model was chosen based on the corrected Akaike Information Criterion (AICc) weights (Burnham and Anderson, 2002; Morlon et al., 2016).

After detecting evidence for time-dependence of diversification rates (see 3.3 Diversification rate), we investigated the possibility that time-variation was influenced by an accumulation of lineage diversity through time. We used the R package DDD 4.4 (Etienne et al., 2012, 2016), which implements a framework for adaptive radiations, modelling different aspects of diversity-dependence dynamics of diversification rate and accounting for possible time-dependent decreases in diversification rate that can follow an increase in species diversity and the presence of a diversity carrying capacity. Following Scantlebury (2013), we estimated the parameters (speciation rate, extinction rate, and carrying capacity) of different diversity-independent and diversity-dependent models with the function ‘dd_ML’ and evaluated the best-fitting model based on the AICc weights (Burnham and Anderson, 2002) (Supplementary Table S8). The estimated parameters of the best-fitting model were used in the function ‘dd_LR’, which implements a bootstrap likelihood ratio test of a diversity-dependent model against a constant-rates birth–death model (Etienne et al., 2016).

We tested the robustness of DDD results by investigating the possible relationships between diversification rates variation through time and lineage diversity accumulation through the nine models from Morlon et al. (2010) (Supplementary Table S9), whose maximum likelihood expressions are based on the coalescent process. We used the ‘fit_coal_cst’ and ‘fit_coal_var’ functions in the R package RPANDA 1.8. The tested models imply both saturated diversity scenarios with turnover rate (the rate at which an extinct lineage is substituted by an emerging one) and scenarios in which diversification is not diversity-dependent and diversity is not saturated (Supplementary Table S9). Model fitting was evaluated through the AICc weights (Burnham and Anderson, 2002).

Recently Louca and Pennell (2020) demonstrated that under a deterministic diversification process, infinite alternative homogeneous birth–death models could produce the same deterministic lineages-through-time curve and be equally probable of generating the same tree. This set of alternative congruent models is defined as a congruence class, characterised by the same identifiable variables of pulled diversification rate, product $\rho\lambda 0$ (between the fraction of sampled extant species and speciation rate at present) and pulled speciation rate, which is defined as the relative slope of the deterministic lineages-through-time curve. This approach differs from the hypothesis-driven model-fitting methods applied in some of the previous analyses and traditionally used in macroevolutionary studies (Morlon et al., 2020). Starting from diversification rate estimates from CoMET analyses, we used the R package ACDC (Höhna et al., 2022; Louca and Pennell, 2020) to construct the congruence class of all extinction and speciation rate functions with the same likelihood score and pulled diversification and speciation rates to explore the diversity of rate functions belonging to the class and uncover the array of potential diversification models underlying Malagasy Scincinae diversification. We tested a series of speciation and extinction rate functions (separately from each other) of different models and temporal trends towards the present (increasing and decreasing exponential, linear and episodically changing birth–death models). We computed speciation, extinction, relative extinction and net-diversification rates for each category of tested rate function and compared trends through time with the reference model (CoMET diversification rates estimates) to discern between functions belonging to the same congruence class and those that did not.

2.5. Trait evolution

2.5.1. Body size evolution

We investigated body size evolution using snout-vent length (SVL) as a proxy. We compiled a list of individual SVL measurements of specimens from museum collections and complemented it with published data to obtain a matrix of a total of 60 taxa and 341 SVL measures (Supplementary Table S10). SVL measures were not available for *Pseudoacontias* CaNew. Since *Pseudoacontias* spp. are the largest Malagasy Scincinae (Glaw and Vences, 2007), and their inclusion or exclusion may have an influence on the analyses, we ran a replicate of these analyses including the SVL of *P. menamainty* as a proxy value for the genus. We averaged SVL measures over conspecific individuals and log-transformed (Supplementary Table S11). We applied a global sampling fraction of 69% (with *Pseudoacontias* exclusion) and 70% (with *Pseudoacontias* inclusion) accounting for missing taxa to the following analyses, whenever possible.

We performed model-testing across different models of continuous trait evolution (Brownian motion, Ornstein-Uhlenbeck process, and Early Burst) with the function ‘fitContinuous’ in the R package geiger 2.0.7 (Pennell et al., 2014) (Supplementary Table S12). We performed the analyses on 100 trees randomly sampled from the posterior distribution of the dated phylogeny. We considered the number of trees in which a model resulted as the best-fitting (based on AICc weights; Burnham and Anderson, 2002) to evaluate the statistical support of each model over the entire posterior sample and over the phylogenetic inference uncertainty. In addition, we averaged AICc weights over the

100 trees for each tested model. We performed ancestral state reconstruction based on the best-fitting model on the 50%-majority rule consensus tree (see 2.2 Phylogenetic analyses) using the function 'contMap' in the R package phytools 0.7-70 (Revell, 2012).

We investigated possible rate shifts in SVL evolution with BAMM. We used the function 'setBAMMpriors' from BAMMtools to find a suitable set of priors for our dataset and tested different values of the expected number of rate shifts priors for the evolution of this trait (0.1, 0.5, 1, 5, and 10). We ran two MCMC chains of 10-million iterations. The output was processed with BAMMtools. We assessed multiple and single-chain convergence as described for BAMM diversification rate analyses (see 2.4 Diversification rate analyses). We selected the most supported number of trait evolution rate shifts based on the Bayes Factor and we chose the best configuration shift based on the highest Posterior Probability.

We tested the possible correlation between SVL and diversification rates with two tip-rate correlation methods: ES-sim (Harvey and Rabosky, 2018) and 'STructured RAte Permutations on Phylogenies' (STRAPP) (Rabosky and Huang, 2016). These methods are more robust compared to other approaches (e.g., QuaSSE; Fitzjohn, 2010) and in particular with small phylogenies (Harvey and Rabosky, 2018; Rabosky and Huang, 2016). ES-sim tests the correlation between trait variation across the tips of a phylogeny and diversification rates. It applies the Inverse Equal Splits as summary statistic of branching pattern and tests for deviations of the empirical phylogeny from a null distribution simulated with no evolutionary model (Harvey and Rabosky, 2018). We ran ES-sim with the R code provided in Harvey (2017) on the same 100 trees sampled from the posterior distribution used in previous SVL analyses (see above) and set 1,000 simulations for the null distribution. We assessed the number of trees over the total 100 for which the test was statistically significant (p-value < 0.05) or not (p-value > 0.05).

We ran STRAPP using the function 'traitDependentBAMM' in BAMMtools. In this analysis, a test statistic measuring the association between the trait and diversification rates estimated on a phylogeny is compared between the empirical values and a null distribution generated by structured permutations of rates across the phylogeny (Rabosky and Huang, 2016). We set 100,000 permutations on the posterior samples drawn from the output of previous BAMM analyses on diversification rate (see 2.4 Diversification rate analyses) for the expected number of diversification rate shifts 0.1, 0.5, 1, 5, and 10. We used Pearson's and Spearman's correlation coefficients as test statistics to test the correlation between trait evolution and speciation and extinction rates.

2.5.2. *Fossorial evolution*

We coded Malagasy Scincinae lifestyle as a binary character (fossorial or non-fossorial) based on the phenotype of each species. We included in the fossorial category limb-reduced species (which are characterised by a comprehensive body plan adaptation to this lifestyle including other apomorphic traits, e.g., body elongation, regressed eyes; Glaw and Vences, 2007; Miralles et al., 2011b, 2012, 2015, 2016a), while fully quadrupedal species were coded as 'non-fossorial': 0-fossorial (genera *Grandidierina*, *Paracontias*, *Pseudoacontias*, *Pygomeles*, and *Voeltzkowia*); 1-non-fossorial (genera *Amphiglossus*, *Brachyseps*, *Flexiseps*, and *Madascincus*) (Supplementary Table S13). Whenever possible, we accounted for incomplete taxon sampling (77%, computed separately for both states).

We explored fossorial evolution with the 'Hidden State Speciation and Extinction' (HiSSE) method implemented in the R package hisse 1.9.8 (Beaulieu and O'Meara, 2016), which estimates the effect of binary characters on diversification rate within a maximum-likelihood framework for model-testing. Unlike the 'Binary-State Speciation and Extinction' (BiSSE) and other SSE methods (Maddison et al., 2007; Fitzjohn, 2010), HiSSE accounts for additional unmeasured (hidden) states, which may potentially influence diversification and transitions rates amongst states, and implements more realistically complex character-independent null models. These aspects make HiSSE less prone to type I error compared with BiSSE and other SSE methods (Beaulieu and O'Meara, 2016; Caetano et al., 2018). We tested 29 models comprising BiSSE-like models (with no hidden trait; Maddison et al., 2007) and several additional models with the presence of one or two possible states of a hidden trait and considered both character-dependent and character-independent evolutionary models (Supplementary Table S14). We performed the analyses on the same 100 posterior trees used for testing body size evolution (see 2.5.1 Body size evolution) and each model statistical support over the 100 trees was evaluated as described therein. We fitted the most statistically supported model across the 100 trees to the 50%-majority rule consensus tree for ancestral state reconstruction. We tested the possible association between trait evolution and diversification rate with STRAPP in BAMMtools. The analysis was run on the consensus tree with identical settings as in previous analyses of body size evolution (see 2.5.1 Body size evolution). Unlike those, we used the Mann-Whitney U statistic to test the association with speciation and extinction rates.

2.6. *Historical biogeography*

We compiled a dataset of 391 geographic records relating to all species included in our phylogenetic analyses (Supplementary Table S15). We compiled these species distribution records from own field records, GenBank, taxonomic literature or from Glaw and Vences (2007). We revised all records following current Malagasy Scincinae taxonomy (Supplementary Table S15). We performed historical biogeography analyses using the 5-region bioclimatic classification (rainforest, dry deciduous forest, sub-humid forest, sub-arid spiny thicket, and montane thickets) modified from Yoder and Nowak (2006) by merging the Sambirano ecoregion with 'rainforest'. We categorised species into the regions with the R package speciesgeocodeR 2.0–10 (Töpel et al., 2016) and performed ancestral range reconstruction on the dated phylogeny pruned from outgroups with the R package BioGeoBEARS 1.1.2 (Matzke, 2018) using the R codes provided on the PhyloWiki webpage (https://phylo.wikidot.com/biogeobears) and from Antonelli et al. (2018). We tested three biogeographic models that are implemented in the package within a maximum likelihood framework to detect biases amongst tested methods: Dispersal-Extinction-Cladogenesis (DEC) (Ree and Smith, 2008), a likelihood interpretation of parsimony DIVA model ('DIVALIKE'; Ronquist, 1997), and a maximum likelihood interpretation of the Bayesian-framework model implemented in the software BayArea ('BAYAREALIKE'; Landis et al., 2013). While all three models use two free parameters of anagenetic change of range evolution (dispersal and extirpation rates), they differ in how they model cladogenetic inheritance of the ancestral ranges (Matzke, 2018). We did not include the null range and set the maximum range size to match the largest number of areas occupied by extant species.

3. Results

3.1. *Phylogenetic hypothesis*

We generated 168 sequences (Supplementary Table S3). The final multi-locus concatenated alignment contained 10,416 bp (2,456 bp from mitochondrial markers and 7,960 bp from nuclear markers), reduced to 9,573 after excluding the 843 positions identified as misaligned or hypervariable by Gblocks. The best-fitting partitioning scheme included 12 partitions (see Supplementary Table S16, which also provides the best model of sequence evolution for each partition).

Relationships amongst the different genera and all major clades retrieved full support (PP = 1), including the clades corresponding to the recently proposed genera *Amphiglossus*, *Brachyseps*, and *Flexiseps* (Fig. 2; see also Erens et al., 2017). *Pseudoacontias* sp. (clade C) was found to be sister to all other Malagasy Scincinae, which are organised in two additional main clades: clade A containing the genera *Madascincus* and

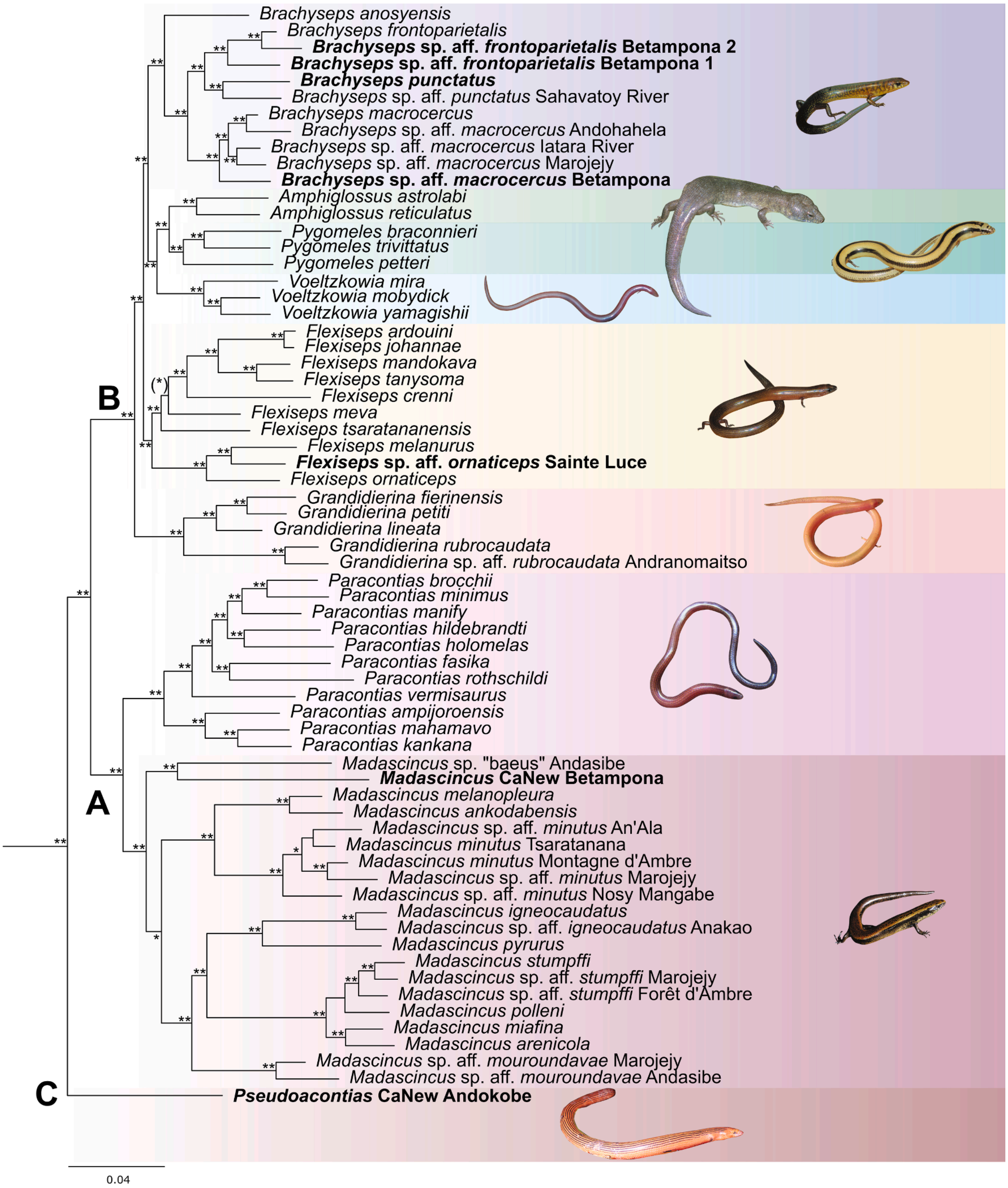

Fig. 2. 50%-majority rule consensus tree inferred with MrBayes on the species-level dataset (Supplementary Table S3). Posterior Probability values are reported before each node as follows: '**' = 1, '*' = 0.99, '(*)' = 0.95–0.98. Values below 0.95 not shown. Taxa analysed for the first time in an evolutionary context are highlighted in bold. Letters 'A', 'B', and 'C' indicate the three main clades of the group. The colours indicate genera. Outgroups are not shown. Representatives of each genus are displayed in photographs (in descending order): *Brachyseps frontoparietalis*, *Amphiglossus reticulatus*, *Pygomeles trivittatus*, *Voeltzkowia yamagishii*, *Flexiseps tanysoma*, *Grandidierina fierinensis*, *Paracontias ampijoroensis*, *Madascincus* sp. aff. *mouroundavae* Marojejy, and *Pseudoacontias menamainty*.

Paracontias, and clade B containing the genera *Amphiglossus*, *Brachyseps*, *Flexiseps*, *Grandidierina*, *Pygomeles*, and *Voeltzkowia*. The genus *Grandidierina* was found to be sister to the clade containing *Amphiglossus*, *Brachyseps*, *Flexiseps*, *Pygomeles*, and *Voeltzkowia*. In this clade, the genus *Flexiseps* was sister to *Amphiglossus*, *Brachyseps*, *Pygomeles*, and *Voeltzkowia*. In this other clade, *Voeltzkowia* was sister to the clade composed of *Amphiglossus* and *Pygomeles* and all together were sister of *Brachyseps*. Within the *Madascincus* clade, *Madascincus* sp. CaNew Betampona was sister to *Madascincus* sp. "baeus", and together they were sister to all other *Madascincus*.

Nearly all nodes at the intra-generic positions were fully supported (PP = 1). The few exceptions were: the position of *Flexiseps meva* as sister to the clade containing *F. crenni*, *F. tanysoma*, *F. mandokava*, *F. johannae*, and *F. ardouini* (PP = 0.96); the monophyly of the clade containing all *Madascincus* with the exception of *Madascincus* sp. CaNew Betampona and *Madascincus* sp. "baeus" (PP = 0.99); the sister relationship between the clade composed of *Madascincus* sp. aff. *minutus* Marojejy and *Madascincus minutus* Montagne d'Ambre with the clade of *Madascincus minutus* Tsaratanana and *Madascincus* sp. aff. *minutus* An'Ala (PP = 0.99); the sister relationship between *Madascincus minutus* Tsaratanana and *Madascincus* sp. aff. *minutus* An'Ala (PP = 0.79); the sister relationship of *Madascincus polleni* with the clade containing *Madascincus* sp.

aff. *stumpffi* Forêt d'Ambre, *Madascincus* sp. aff. *stumpffi* Marojejy, and *Madascincus stumpffi* (PP = 0.79). Interestingly, *Flexiseps crenni* was found to be sister to the clade made of *F. ardouini*, *F. johannae*, *F. mandokava*, and *F. tanysoma* (confirming the tentative position proposed by Erens et al., 2017). *Paracontias holomelas* had been excluded by Erens et al. (2017) and Miralles et al. (2016b) because of problems with the assignment of deposited sequences. After the revision of published sequences and the generation of new sequences from recently collected material for this taxon, we included *P. holomelas* in our phylogenetic analyses and found this taxon to be sister of *P. hildebrandti*.

The phylogenies inferred from the concatenated datasets of mitochondrial and nuclear markers showed some topological differences between each other and the full multi-locus concatenated dataset (mitochondrial with nuclear) (see Supplementary Figs S1–S2). However, the Icong index indicated a statistically significant overall topological congruence between all phylogenies (p-value < 0.01; 2.86 mitochondrial vs nuclear; 3.35 mitochondrial vs full; 3.63 nuclear vs full), suggesting that both phylogenetic signals of mitochondrial and nuclear markers contributed to the topology of the full dataset. The ML phylogeny inferred with RAxML on the full concatenated dataset (Supplementary Fig. S3) showed differences from the MrBayes tree in some inter-generic relationships (i.e., the position of the genus *Flexiseps* and

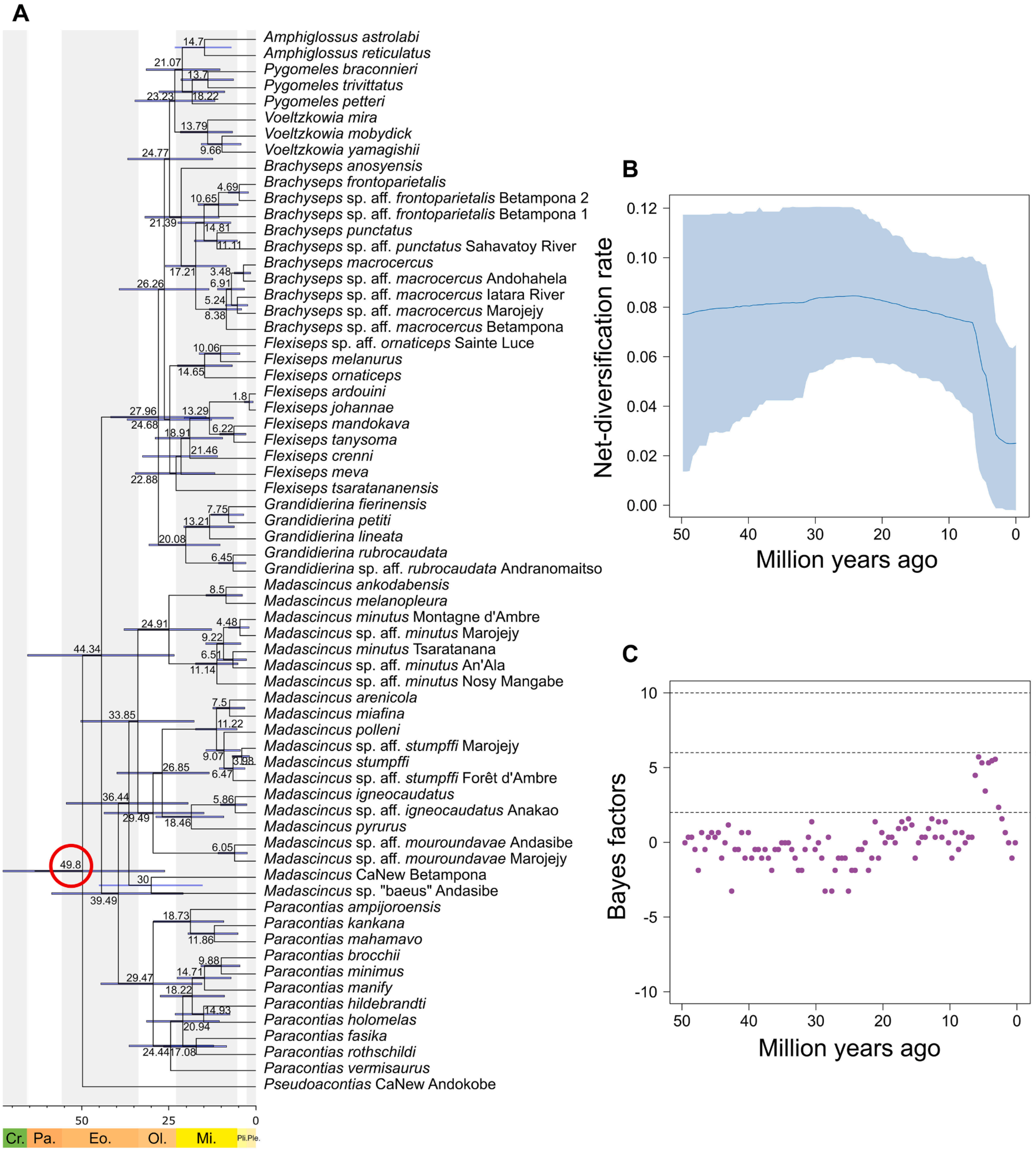

Fig. 3. Time-tree and diversification rates through time of Malagasy Scincinae. (A) Divergence times estimate performed on the species-level dataset (Supplementary Table S3). The red circle indicates the node that was calibrated based on divergence times estimated with primary fossils information on the reduced dataset (Supplementary Fig. S5; Supplementary Table S5). The analysis was performed in BEAST. Outgroups are not shown. Geological times were abbreviated as follows: Cr. (Cretaceous), Pa. (Paleocene), Eo. (Eocene), Ol. (Oligocene), Mi. (Miocene), Pli. (Pliocene), and Ple. (Pleistocene). (B) Net-diversification rate. (C) Bayes Factor of speciation shifts. B–C were inferred with the CoMET model implemented in the R package TESS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Grandidierina in clade B), although most relationships were congruent between the two phylogenies. However, differently from the Bayesian inference, this tree had overall lower statistical (bootstrap) support (e.g., most inter-generic relationships in Clade B received no statistical support). Similarly, the species tree inferred with ASTRAL showed some topological differences with the MrBayes phylogeny inferred from the full multi-locus concatenated dataset (Supplementary Fig. S4) and recovered limited statistical support: most inter-generic relationships and the monophyly of some genera (e.g., *Flexiseps*, *Madascincus*, *Pygomeles*) were not statistically supported. The normalised quartet score was 0.78 suggesting moderate concordance between gene trees. Considering the overall congruence between the trees inferred from the mitochondrial, nuclear, and full multi-locus datasets with MrBayes, the moderate concordance between gene trees, and the low statistical support of RAxML tree and ASTRAL species tree, we used the highly statistically supported topology inferred from the Bayesian analysis on the full multi-locus dataset (Fig. 2) in the following analyses.

3.2. Dated phylogeny

The concatenated alignment of the reduced dataset contained 11,147 bp, and the best-fitting partitioning scheme included 10 partitions (Supplementary Table S17). The 95% confidence intervals of divergence time estimates were not elongated and overlapping (Supplementary Fig. S5; Fig. 3A). The Scincoidea crown node was dated in the Late Jurassic (160.29 Ma) (Supplementary Fig. S5), while the diversification of the Scincidae family was inferred to be 111.65 Ma (142.83–79.47 Ma 95% HPDI) at the end of the Early Cretaceous. The crown node of the Scincinae subfamily was dated at 85.42 Ma (112.79–59.39 Ma 95% HPDI) in the Late Cretaceous, which also represents the stem node of the endemic Malagasy group relative to the considered outgroups. The crown node of Malagasy Scincinae was estimated at the boundary between Paleocene and Eocene epochs (55.14 Ma; 77.82–35.82 Ma 95% HPDI). The same node was dated at 49.8 Ma (72.67–26.16 Ma 95% HPDI), at the beginning of the Eocene, in the maximum clade credibility tree inferred from the complete dataset calibrated with secondary information (Fig. 3A). This estimate also represents the divergence of *Pseudoacontias* (clade C) from the rest of the group. The two other main clades diverged slightly after (44.34 Ma; 65.6–23.4 Ma 95% HPDI). The inter-generic diversification in clade A was complete by the mid-Oligocene (ca. 29 Ma), whereas the genera of clade B diverged more recently, between the mid-Oligocene and throughout the Miocene (ca. 28–13 Ma) (Fig. 3A). The genera with the most recent crown nodes were *Amphiglossus* (14.7 Ma; 23.24–6.92 Ma 95% HPDI) and *Voeltzkowia* (13.79 Ma; 21.61–6.62 Ma 95% HPDI). The most recent cladogenetic event (the only one that was estimated during the Pleistocene) was dated to 1.8 Ma (3.19–0.72 Ma 95% HPDI) and it represents the divergence between *Flexiseps ardouini* and *F. johannae*.

3.3. Diversification rates

BAMM analyses consistently supported a constant diversification rate across Malagasy Scincinae clades regardless of the choice of the expected number of rate shifts prior (Supplementary Figs S7–S9; see Supplementary Fig. S6 for multiple chains convergence). The Bayes factors comparing scenarios with number of rate shifts >0 with the null model (represented by the 0-rate shift scenario) were never above 1, meaning that the null model with no rate shifts could not be rejected and, consequently, supporting a unique evolutionary rate dynamic throughout the phylogeny. These results were confirmed by the analysis of the Laplacian spectrum of the tree in RPANDA (Lewitus and Morlon, 2016; Supplementary Fig. S10). The spectral density profile (principal eigenvalue = 11,960.49; asymmetry = −0.18; peakedness = 2.28) showed a single modality with eigengap between the first and second of the eigenvalues sorted in descending order (Supplementary Fig. S10). The BIC value of the tree (7,510,067) was lower than for randomly bifurcating trees (15,052,056), confirming the single modality of the spectral density profile, which indicates the presence of homogeneous diversification rates across the tree.

We investigated diversification rate through time and the possible occurrence of mass extinction events with the CoMET model (see Supplementary Figs S11–S12 for chain convergence). There was no evidence of mass-extinction events (Bayes Factor < 2.02; Supplementary Fig. S13). Net-diversification rate was found to be constant (0.02–0.12 lineages/myr) until ca. 6–4 Ma (Late Miocene-Pliocene), when it decreased to the present-day values of 0.00–0.06 lineages/myr (Fig. 3B). Bayes Factor values supported the slowdown (Bayes Factor = 3.43–5.72; average Bayes Factor = 5.13; Fig. 3C), corresponding to “substantial evidence” (Jeffreys, 1961). Extinction rate was constant throughout the evolution of the group and close to 0 (Supplementary Fig. S13), although this might reflect a general inability of phylogenetic models to infer extinction (Louca and Pennell, 2021; see below ACDC results). Speciation rate followed the trend that was recovered for net-diversification rate (Supplementary Fig. S13).

Time variation in diversification rate was confirmed by the maximum likelihood model-fitting approaches (Supplementary Table S7). Amongst the six models that were tested from Morlon et al. (2011), model 3 (speciation rate exponentially declining through time and null extinction rate) was the best-fitting (AICc weight = 0.61; speciation rate at present = 0.05 lineages/myr; exponential rate variation = 0.03) (Supplementary Table S7). The analyses performed with the DDD 4.4 package suggested diversity-dependent diversification in the group. The model DDLS (linear dependence of speciation rate with diversity carrying capacity and null extinction rate) fitted the data the best (AICc weight = 0.37) with parameters estimates of speciation and carrying capacity of 0.13 lineages/myr and 107, respectively (Supplementary Table S8). The bootstrap likelihood ratio test (Etienne et al., 2016) confirmed the prevalence of a diversity-dependence against a constant-rates model (Likelihood ratio = 3.69; p-value = 0.003; power of the test = 0.93). Amongst the tested models from Morlon et al. (2010), model 2 (saturated diversity with the turnover rate declining through time) provided the best-fit (AICc weight = 0.77; turnover rate at present = 0.03; exponential rate variation = 0.12; Supplementary Table S9). This model was followed by model 6 (non-saturated diversity, with declining speciation rate and null extinction rate) (AICc weight = 0.13), which is conceptually identical to model 3 from Morlon et al. (2011) (see above) (Supplementary Table S9).

With the exception of the episodically changing models and exponential models with decreasing trends towards the present (Supplementary Figs 18–20), the alternative extinction rate functions that we tested with ACDC produced speciation and net-diversification rates that were overall consistent with the reference model of CoMET diversification rate estimates, indicating that these models might be part of the congruence class computed from these (or be close to it) (Supplementary Figs 14–17). Models with increasing extinction rates towards the present seemed more congruent, suggesting that such temporal trends might have characterised Malagasy Scincinae diversification. These scenarios shared a slowdown in net-diversification rate that was parallel in time with the reference model (suggesting that the drop estimated with CoMET is robust), although for a few functions within some of the tested category models, such a decrease started slightly before, questioning their full congruence with the class (Supplementary Figs 14–17). These scenarios also showed speciation rate trends that were consistent with the reference, although in some models rate magnitudes were larger than in the reference, which is probably determined by higher extinction rates given similar net-diversification rates. Differently from the extinction rate, none of the speciation rate functions that we tested seemed to be part of the congruence class as they often produced incompatible net-diversification and speciation rate trends with the reference model and extinction rates that were unrealistically negative (Supplementary Figs 21–25).

3.4. *Trait evolution*

3.4.1. *Snout-vent length*

The inclusion or exclusion of an SVL proxy for the genus *Pseudoacontias* did not affect the analyses (Fig. 4A; Supplementary Fig. S26). We consequently report results for the analyses including *Pseudoacontias* (Fig. 4A), and the outputs of the analyses excluding the genus *Pseudoacontias* are provided in Supplementary material (Supplementary Figs S26, S31–S32). The Brownian motion model produced the best-fit over all 100 tested posterior trees (Supplementary Table S12). The ancestral state reconstruction performed on the 50%-majority rule consensus tree of the dated phylogeny reflected model testing results and suggested considerable body size variation within genera (Fig. 4A; Supplementary Fig. S26). In BAMM analyses, a model with a constant rate of trait evolution across clades was the most supported (based on both Bayes Factor and Posterior Probability values) regardless of the choice of the number of expected rate shifts prior (Supplementary Figs S28–S30; see Supplementary Fig. S27 for multiple chains convergence). ES-sim analyses were not significant (p-value > 0.05) for all 100 analysed posterior trees, suggesting the absence of correlation between SVL evolution and diversification rates. Similarly, the association between trait evolution and speciation and extinction rates investigated with STRAPP was not significant (p-value > 0.05) for any of the tested priors for the expected number of diversification rate shifts.

3.4.2. *Fossorial evolution*

There was no evidence of fossorial-dependent diversification from HiSSE analyses (Supplementary Table S14). BiSSE-like models received generally higher statistical support than HiSSE models, suggesting no evidence for the presence of hidden traits that may have influenced diversification. The model with no difference in speciation and extinction rates between the two states and null transition from fossorial to non-fossorial state resulted the best-fitting in 81/100 analysed posterior trees (Supplementary Table S14). The ancestral state reconstruction performed on this model fitted on the 50%-majority rule consensus tree of the dated phylogeny suggested that the common ancestor to Malagasy Scincinae was a quadrupedal and non-fossorial species, and that limb reduction and fossorial lifestyle evolved five independent times in the evolutionary history of the group (Fig. 4B). Character-independent evolution was also confirmed by STRAPP analyses, which showed no association (p-value > 0.05) between the fossorial lifestyle trait and the evolutionary rates estimated on the phylogeny for any of the tested rate shifts priors.

3.5. *Historical biogeography*

The results from BioGeoBEARS analyses were overall consistent between DEC (Fig. 5), DIVALIKE (Supplementary Fig. S33), and BAYAREALIKE (Supplementary Fig. S34) biogeographic models. Dry deciduous forest and rainforest biomes were reconstructed as ancestral ranges for the deepest nodes, suggesting a significant role of forested biomes in the early diversification of Malagasy Scincinae. The current distribution of most genera is predominantly restricted to individual biomes. For instance, species in the fossorial genera of Clade B (*Voeltzkowia*, *Grandidierina*, and *Pygomeles*) are restricted to either the sub-arid spiny thicket or dry deciduous forest, and quadrupedal non-fossorial genera of the same Clade B (*Flexiseps*, *Brachyseps*, and *Amphiglossus*) are mostly found in the forested humid biomes (rainforest and sub-humid forest) (Fig. 5). The 65 species included in our biogeographic analyses are not equally distributed across biomes. The rainforest hosts the largest number of species (34), followed by sub-humid forest (24), dry deciduous forest (23) and sub-arid spiny thicket and montane thickets with equal species numbers (10). Dry deciduous forest has the highest number of endemic species (i.e., with distributions exclusively restricted to individual biomes) (13), followed by rainforest (11), sub-humid forest (6), sub-arid spiny thicket (5), and montane thickets (3).

4. Discussion

The present study aimed to explore several facets of the *in situ*

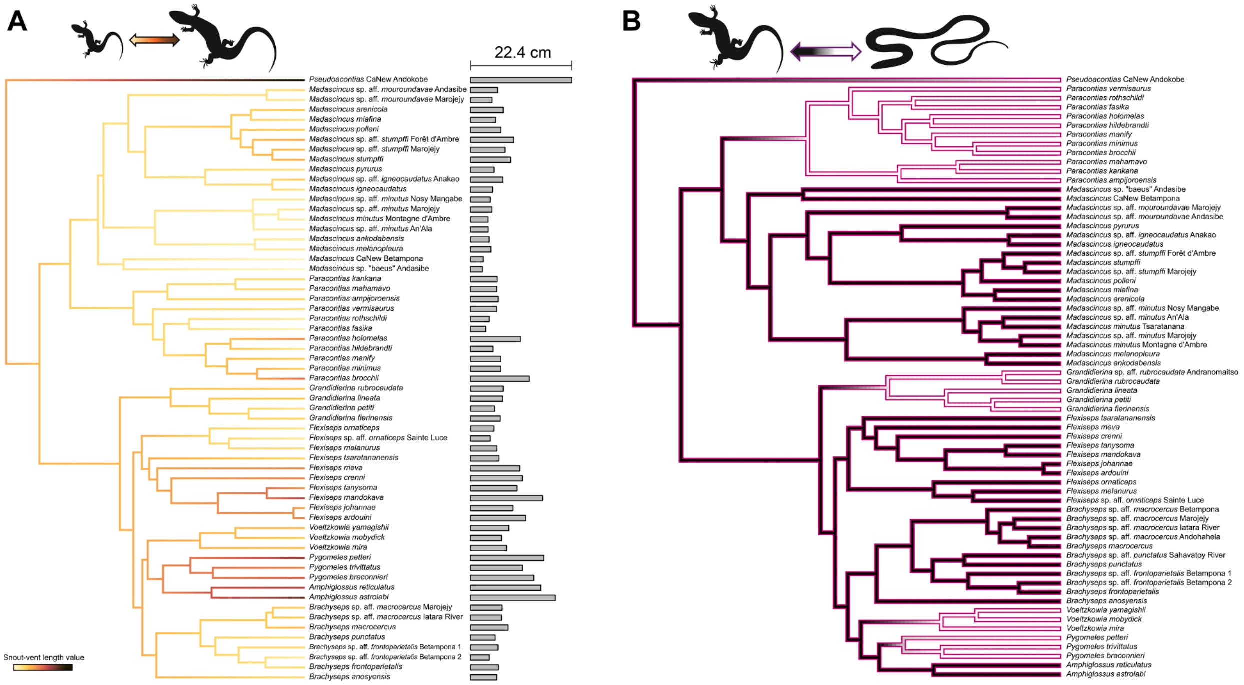

Fig. 4. Ancestral state reconstructions of traits evolution performed on the dated 50%-majority rule consensus tree. (A) Body size (snout-vent length (SVL)) evolution reconstructed with the R package phytools on the dataset including SVL measurement of *P. menamainty* as a proxy for the genus *Pseudoacontias* (Supplementary Table S11). The bars on the right represent SVL values of each species. (B) Fossorial lifestyle evolution reconstructed with the R package hisse. States are coded as follows: fossorial (white), non-fossorial (black) (Supplementary Table S13).

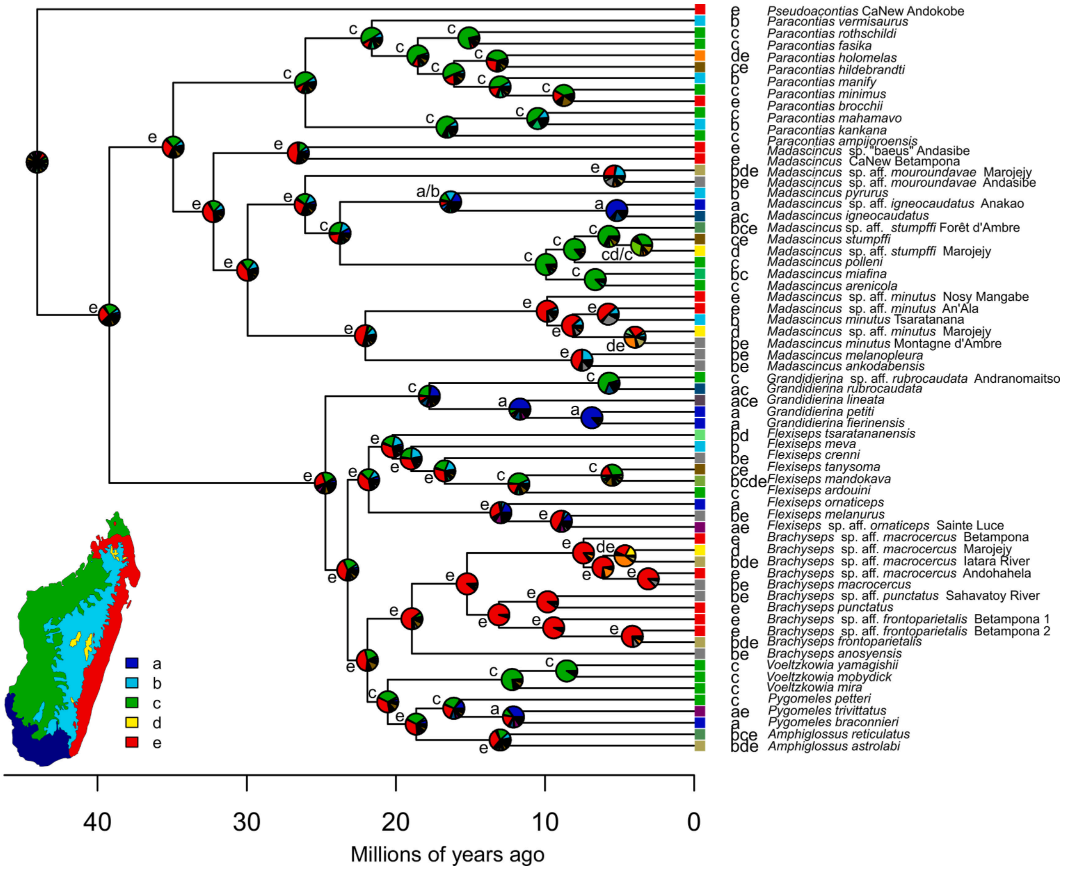

Fig. 5. Ancestral range reconstruction performed with the DEC model implemented in the R package BioGeoBEARS. Species distributions (Supplementary Table S15) were coded with the R package speciesgeocodeR based on Madagascar's bioclimatic classification modified from Yoder and Nowak (2006) (sub-arid spiny thicket (a, blue), sub-humid forest (b, light blue), dry deciduous forest (c, green), montane thickets (d, yellow), and rainforest (e, red)). Estimated dispersal and extirpation parameters were 0.0284 and 0.1275, respectively. Ancestral ranges with the highest marginal probabilities are letter-coded before each node. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversification (diversification rate, phenotypic evolution, and biogeography) of Malagasy scincine lizards. Based on diversification trends frequently observed in evolutionary radiations and especially in insular systems (e.g., Schluter, 2000; Wollenberg et al., 2011; Jønsson et al., 2012; Lee et al., 2013; Simões et al., 2016), a temporal trend in diversification rate displaying an early-burst pattern and increased diversification rates for small-sized species and fossorial lineages was expected. Our work also aimed to determine whether the rich bioclimatic diversity and possible past large-scale climatic changes of Madagascar influenced the diversification of the group, as expected from the asymmetric distribution of species richness across biomes (Brown et al., 2016) and the almost concurrent divergence of fossorial genera living in dry and sandy environments (sand-swimmers) (Miralles et al., 2015). Our findings revealed a contrasting scenario in which we recovered: (1) a constant diversification rate through most of the evolutionary history of the group, (2) a random pattern in the evolution of body size, which was found not to influence diversification rate, and (3) multiple evolutionary transitions from quadrupedal ancestors towards fossoriality that were not associated with shifts in diversification rate. Furthermore, we confirmed (4) a possible evolution of limb-regression in sand-swimmer genera as an adaptation to a period of general aridification of the Malagasy climate around 20 Ma (Wells, 2003), suggesting a potential influence of Madagascar's bioclimatic zonation on the diversification of the group. Altogether, these results support an evolutionary scenario in which the *in situ* diversification process of Malagasy Scincinae consisted of a constant accumulation of lineages through time and was determined by a combination of intrinsic and extrinsic factors, although none of them emerged as the main diversification driver of the group. In the following paragraphs we discuss such findings for each tested diversification hypothesis as well as the new phylogenetic hypothesis and time tree.

4.1. Systematics and time-tree

In contrast to previous published phylogenetic hypotheses (Whiting et al., 2004; Schmitz et al., 2005; Crottini et al., 2009; Miralles et al., 2015; Erens et al., 2017), the monophyly of major clades and their phylogenetic relationships received full support (Fig. 2). This was likely the result of a more complete data matrix, both in terms of a broader range of taxa and additional molecular loci included. However, the short internodes between Clade B genera might indicate that even a larger multi-locus dataset (e.g., obtained by a phylogenomic approach) will be needed to reconstruct evolutionary trajectories in the context of a rapid inter-generic divergence. This seems to be confirmed by the difficulty in retrieving well-supported phylogenetic hypotheses using alternative inference methods (see 3.1 Phylogenetic hypothesis).

Compared to previously published phylogenies, most differences are related to inter-generic relationships within clade B. Amongst these, the most remarkable are the recovery of the genus *Grandidierina* as the sister lineage to the clade containing *Amphiglossus*, *Brachyseps*, *Flexiseps*, *Pygomeles*, and *Voeltzkowia* (similarly to the phylogenetic hypothesis proposed in Schmitz et al., 2005), and the recovery of the genus *Voeltzkowia* as the sister lineage to the clade containing *Amphiglossus* and *Pygomeles*. This work also included 21 candidate species, some of which were molecularly characterised for the first time (Supplementary Tables S2–S3). Amongst these, *Madascincus* sp. CaNew from Betampona and *Madascincus* sp. "beaus" from Andasibe are likely representative of the *Madascincus nanus* group (Andreone and Greer, 2002), which might qualify to be considered as a separate genus based on their phylogenetic positions and marked genetic and morphological differences (Andreone and Greer, 2002; Miralles et al., 2016b; Miralles and Vences, 2013).

The Malagasy vertebrate fossil record of the Cenozoic is largely fragmented (Krause et al., 1997, 1999; Godfrey et al., 2020), limiting the use of fossil calibrations in dated phylogenies. To circumvent this limitation, either secondary calibrations from existing large and dated phylogenies (e.g., as from Crottini et al. 2012; Zheng and Wiens, 2016) or fossil data from outside Madagascar to calibrate selected outgroups could be used (as in Blair et al., 2015; Burbrink et al., 2019). We chose to use primary fossil calibrations on the outgroups of a reduced dataset (Supplementary Table S5) and used the resulting divergence time estimates of the ingroup crown age as secondary calibration on the full dataset. This approach received high statistical support and produced low uncertainty in the estimated divergence times (Fig. 3A), as also demonstrated by the consistency of our time estimates with estimates available from other dated phylogenies that used different calibration points (e.g., we estimated the crown node of the group at 49.8 Ma vs 47 Ma in Crottini et al., 2012 and 44.17 Ma in Zheng and Wiens, 2016). The 95% HPDI for the same node also overlaps with the range reported in the only other species-level dated phylogeny of the Malagasy Scincinae and that used a secondary calibration approach to infer the crown age from the divergence times estimated in Crottini et al. (2012) (Miralles et al., 2015). The average value estimated in that study is more recent (37.4 Ma), probably due to the absence of any representative of the basal genus *Pseudoacontias*. Similarly, the average values of divergence times at the inter-generic level reported in Miralles et al. (2015) are slightly younger, although in agreement with the timing of the cladogenetic events reported in our dated phylogeny (Fig. 3A).

4.2. *Diversification rates*

The diversification rate was found to be constant with the exception of a sharp decrease around 6–4 Ma (Fig. 3B), at the boundary between the Miocene and Pliocene, towards the present. The extinction rate remained stable and almost null throughout the evolutionary history of the group (Supplementary Fig. S13). In the absence of a fossil record, molecular phylogenies including only extant species are known to produce unrealistically low estimates of extinction rate (see Quental and Marshall, 2010; Rabosky, 2010; Stadler, 2013; Silvestro et al., 2018; Louca and Pennell, 2021). The analyses we performed with ACDC suggested that alternative extinction rate scenarios of higher rate magnitudes and with mostly constant or increasing trends towards the present might be part of the set of congruent models of our diversification hypothesis given, however, the same temporal trend and magnitude in net-diversification rate (Supplementary Figs 14–17). Such analyses demonstrate the importance of exploring alternative congruent models following the theoretical concepts introduced by Louca and Pennell (2020) to identify diversification dynamics that would be difficult to uncover using other approaches. The stable diversification rate observed across most of the evolutionary history of this group stands in contrast with empirical evidence and theoretical assumptions of an initial burst in speciation that is expected in evolutionary radiations, especially in island systems where the access to novel geographic areas and habitats could trigger diversification (Schluter, 2000; Gavrilets and Losos, 2009; Jønsson et al., 2012; Simões et al., 2016). Interestingly, a recent study focusing on the evolutionary history of the most diverse Malagasy squamate radiation (snakes of the endemic Pseudoxyrhophiinae subfamily; Burbrink et al., 2019), using a similar methodological approach, also found a constant trend in diversification rate from the origin of the group, followed by a sharp decline. Tellingly, this decrease in diversification rate is concurrent in time to the slowdown we detected for Malagasy Scincinae. Patterns of declining speciation rate towards the present are often recovered in molecular phylogenies and are frequently ascribed to diversity-dependent dynamics (Morlon, 2014; Morlon et al., 2010). Limited ecological resources may cause speciation and extinction rates to become equal and stabilise diversity to the carrying capacity of the system (Etienne et al., 2012, 2016). Similar to what has been observed in Malagasy pseudoxyrhophiine snakes, we consistently detected diversity-dependence in the evolutionary history of Malagasy Scincinae across all three tested methods (Morlon et al., 2010; Etienne et al., 2012, 2016; Burbrink et al., 2019). However, considering that slowdowns in macroevolutionary rates due to diversity-dependent dynamics can be mistaken with alternative mechanisms (see Condamine et al., 2019; Etienne et al., 2016; Etienne and Rosindell, 2012; Harmon and Harrison, 2015; Moen and Morlon, 2014; Morlon, 2014; Pannetier et al., 2020), future studies accounting for additional non-phylogenetic data types (e.g., geographical and ecological data) may help clarify the clade diversity dynamics (Moen and Morlon, 2014; Pannetier et al., 2020).

Alternative factors explaining this slowdown may be related to environmental and climatic changes that Madagascar underwent over the last million years. For instance, it has been proposed that Malagasy grasslands originated during the Late Miocene and Pliocene (Hackel et al., 2017). This suggests that a major change in Malagasy biota is concordant in time with the decreasing diversification rate observed for Malagasy Scincinae. Considering that most species of this group are forest dwellers (Glaw and Vences, 2007), the hypothesised expansion of grasslands may have had a significant impact on their diversification. A recent decline in diversification rates might also be consistent with a protracted speciation model (Rosindell et al., 2010) whereby recent speciation events might not have reached a sufficient level of differentiation to be reflected in current taxonomy. However, lineages included in the phylogenetic dataset were identified based on the interspecific genetic distance thresholds proposed for Malagasy skinks (Nagy et al., 2012; see 2.1 Samples and dataset; Supplementary Tables S2–S3). This approach likely helped to capture several incipient and recent speciation events even for taxa that, after a thorough investigation of their taxonomic status with the generation of additional data (e.g., morphological analyses and surveys of the genetic structure based on a denser individuals' sampling) will not qualify to be formally described as new species (i.e., Miralles et al., 2016b).

Finally, and differently from what has been observed in other groups (Raxworthy and Nussbaum, 1995; Wilmè et al., 2006; Yoder and Heckman, 2006; Boumans et al., 2007; Wollenberg et al., 2008; Vences et al., 2009), the estimation of divergence times (Fig. 3A) suggested that Pleistocene climatic oscillations did not play a strong role in the diversification of Malagasy Scincinae. A possible explanation for this might be that a relevant part of the diversification of the group (i.e., at the inter-generic level) was influenced by ancient large-scale climatic changes that occurred over the long 50-million evolutionary history of the group, as our biogeographic reconstruction and the observation that most genera are currently restricted to single biomes would suggest (Fig. 5; see 4.4 Fossorial evolution and biogeography). An ancient influence of climate on diversification could have determined climatic niche specialisation following adaptive mechanisms and smaller distributional ranges of species as a consequence of non-adaptive allopatric mechanisms. These conditions might have made these animals less susceptible to Pleistocene climatic oscillations compared to other Malagasy radiations for what concerns novel opportunities of speciation, although an influence on phylogeographic patterns within species cannot be excluded (Everson et al., 2020).

4.3. *Body size evolution*

Our analyses suggested that body size of Malagasy Scincinae evolved homogeneously across clades, and we found no support for an influence of body size on diversification rate in this group (Fig. 4A; Supplementary Figs S26–S32). With the exception of some species-poor genera (e.g., *Amphiglossus* and *Pygomeles*), the other clades did not evolve unidirectionally towards larger or smaller sizes and exhibit large variability ranging from small to relatively large body sizes (Fig. 4A; Supplementary Table S12).

Body size frequency distributions in amphibians and squamates show considerable variation both at continental and global scales (e.g., Meiri, 2008; Feldman et al., 2016; Amado et al., 2021). Small-sized species are usually more frequent than large-sized species (e.g., Meiri, 2008; Feldman et al., 2016; Amado et al., 2021) and associated with higher species richness in analysed clades (Zimkus et al., 2012). However, a relationship between body size evolution and diversification rate has rarely been found (e.g., Feldman et al., 2016), while in most cases such a relationship was not proven (Burbrink et al., 2012; Rabosky et al., 2014a; Zimkus et al., 2012; Wollenberg Valero et al., 2019). This might be because in phylogenies with extensive taxonomic and geographic sampling the effect of body size evolution on diversification can be masked by major ecomorphological differences that can arise at the beginning of the evolutionary history of a group, with a strong impact on their early diversification but with limited variation added subsequently (e.g., Crouch and Ricklefs, 2019).

In the large anuran family of mantellid frogs from Madagascar, clades with small body sizes were the most species-rich, tended to have higher mitochondrial substitution rates and smaller range sizes (Wollenberg et al., 2011), and the lower vagility of these smaller species could have favoured inter-populational divergence and speciation (Pabijan et al., 2012; Wollenberg Valero, 2015; Wollenberg Valero et al., 2019). Given the correlation between body size and range size in Malagasy squamates (Brown et al., 2016), a similar pattern could also be expected for the Scincinae, although we did not identify a relationship between body size evolution and diversification rate. Similarly, we can exclude a correlation between SVL and a specific ecomorphological adaptation (i.e., fossorial lifestyle evolution), due to the occurrence of body size extremes in both analysed ecomorphological adaptations (i.e., fossorial and non-fossorial lifestyle).

4.4. *Fossorial evolution and biogeography*

Our analyses suggested multiple, independent origins for limb regression (Fig. 4B) and similar diversification rates between fossorial and non-fossorial species (Supplementary Table S14). Our ancestral state reconstruction is consistent with previous findings in suggesting multiple parallel transitions from fully quadrupedal to limb-reduced forms (Miralles et al., 2015). The opposite scenario has been rarely hypothesised within squamates (Ebel et al., 2020) and normally consists in re-evolution of digits rather than the entire limbs (e.g., Kohlsdorf and Wagner, 2006; Wagner et al., 2018). These findings are also consistent with Wiens et al. (2006), who found that, at the global level, most limb-reduced fossorial clades evolved from fully quadrupedal ancestors rather than from species with a similar body plan and non-fossorial lifestyle (arboreal, aquatic, saxicolous), which would imply a lower number of evolutionary steps. In addition, Wiens et al. (2006) found that colonisations of new landmasses by limb-reduced taxa are extremely rare, probably due to their lower dispersal abilities.

The low vagility of fossorial species might be related to the generally small distribution ranges of these animals (Wiens et al., 2006; Lee et al., 2013), a condition that has been suggested to facilitate inter-populational genetic differentiation and increase diversification rates within clades (Pabijan et al., 2012; Lee et al., 2013; Wollenberg et al., 2011; Wollenberg Valero, 2015; Wollenberg Valero et al., 2019). Other evidence from large-scale macroecological studies suggests that fossorial evolution is linked to slowdowns in diversification rate because of the high ecomorphological specialisations associated with this lifestyle, which make fossorial species more susceptible to environmental oscillations (Bars-Closel et al., 2017; Cyriac and Kodandaramaiah, 2018). However, in our model system, the transition to a fossorial lifestyle was not found to be associated with changes in diversification rates.

Limb reduction and fossoriality are frequently associated with adaptations to arid and sandy environments where limbless species show faster subterranean locomotion than quadrupedal species (Grizante et al., 2012; Bergmann et al., 2020; Morinaga and Bergmann, 2020). Interestingly the three sand-swimmer genera of clade B (*Grandidierina*, *Voeltzkowia*, and *Pygomeles*; Fig. 1G–H; Fig. 1J–L) all evolved during the Early-Middle Miocene (between ca. 23 and 14 Ma; as previously observed by Miralles et al., 2015), while the origin of the litter-burrower genera *Pseudoacontias* and *Paracontias*, which are restricted to humid forests, is older (ca. 50–30 Ma). Different divergence times of these two groups may reflect the age of the environments they colonised, as suggested by our ancestral range reconstruction (Fig. 5). Forested biomes (dry deciduous and rainforest) were reconstructed as the oldest ancestral ranges, where the diversification of the group likely started. The oldest reconstruction of the sub-arid spiny thicket biome dated to ca. 18 Ma (Fig. 5), which could therefore match a time of general aridification of Malagasy climate. It is during this time that the south-western sub-arid spiny thicket biome (where most *Grandidierina* species occur) may have established, and with arid sandy environments appearing within the dry deciduous biome, where the genus *Voeltzkowia* and some species of the other two sand-swimmer genera (*Grandidierina* and *Pygomeles*) are now distributed. Due to the latitudinal position of Madagascar in the high-pressure arid belt at the boundary between the Cretaceous and Paleogene, the Malagasy climate was suggested to have been mostly arid at that time, with the sub-arid spiny thicket considered the oldest contemporary biome of the island (Wells, 2003). As Madagascar drifted north, it has been proposed that the island climate became more humid, and this climatic change triggered the rise of forested biomes and the contraction of the spiny thicket biome to its current extension in the southern part of the country (Wells, 2003). However, evidence from divergence time estimates in plants suggests an older origin of dry and humid forests (see Buerki et al., 2013 for a review). In line with this proposal, Ohba et al. (2016) suggested that mesic habitats (similar to the climatic conditions of the extant subhumid forest of the central highlands) were spread over most of the island during the early Paleogene, and that dry deciduous forests were present only in parts of the west and north-west of Madagascar, while the sub-arid spiny thicket and the rainforest were likely not yet existing (Ohba et al., 2016). Assuming that our study group is indicative of the environment in which it currently occurs, our results support the hypothesis that the arid biome may be younger, and that the rainforest biome may be older than traditionally thought (Wells, 2003; Ohba et al., 2016)

Overall, our ancestral range reconstruction suggested that Madagascar's biomes and past large-scale climatic changes played a role in the diversification of Malagasy Scincinae (Fig. 5). Today's asymmetric distribution of species across the island bioclimatic zonation supports the hypothesis that different biomes contributed differently to the *in situ* diversification of the group. Forested biomes were reconstructed as the oldest ranges (Fig. 5), and based on current knowledge they host most of present-day diversity and endemism. Rainforest habitats are currently home to 34 species (52% of total analysed diversity), 11 of which are found only in this biome. Considering that a distributional pattern with most species richness concentrated in the eastern rainforest is common across several Malagasy vertebrates (Lees and Colwell, 2007; Brown et al., 2016), different authors hypothesised a role of this biome as species pump (Crottini et al., 2012; Brown et al., 2016), although such a role has not been yet proved in a robust statistical framework. For instance, pseudoxyrhophiine snakes display a similar distributional pattern to Malagasy scincines relative to the island bioclimatic zonation (Burbrink et al., 2019). However, phylogenetic diversity of species assemblages was randomly dispersed across biomes, suggesting that all biomes contributed with the same extent to the *in situ* diversification of the group (Burbrink et al., 2019). Again, the limited knowledge on Madagascar's climate at the time it became isolated (ca. 80–65 Ma, Ali and Aitchison, 2008) and its evolution until the present hampers a better understanding of the influence of climatic changes and bioclimatic regions on the diversification of Malagasy Scincinae and other endemic radiations of the island.

4.5. Comparison with diversification patterns in other radiations

Examples of decoupled phenotypic evolution and diversification rate suggested from our exploration of the *in situ* diversification of Malagasy Scincinae have been previously described for Malagasy pseudoxyrhophiine snakes and mantellid frogs (Burbrink et al., 2019; Moen et al., 2021). The constant diversification rate for most of the evolutionary history of Malagasy pseudoxyrhophiine snakes was not influenced by the evolution of their large variety of dietary and habitat preferences (Glaw and Vences, 2007; Burbrink et al., 2019). Similarly, a recent investigation of the radiation of mantellid frogs found a decoupling between an accelerating body shape rate and similar diversification rates relative to other analysed frog radiations from outside Madagascar (Moen et al., 2021). At the same time, diversification of Malagasy Scincinae is discordant with the patterns proposed for lemurs and vangid birds (Jønsson et al., 2012; Herrera, 2017). In lemurs, a steady and slightly increasing diversification rate towards the present is coupled with an early burst pattern in body mass evolution and a parallel expansion in the ecological space, concordant with the expectations of adaptive evolution (Herrera, 2017). Vangid birds are a textbook example of adaptive radiation (Jønsson et al., 2012). In this group, diversification rate had an early burst paralleled by an increase in body size disparity, which was then followed by a diversification slowdown. Diversification rate had a second spike in more recent times, related to an increase in beak morphology evolution as an adaptation to multiple foraging techniques (Jønsson et al., 2012).

The lack of similar studies on a larger number of Malagasy radiations, along with discrepancies on the employed methodological frameworks, hinder the comparisons among different radiations (see, for example, the methods employed in Jønsson et al., 2012; Moen et al., 2021, relative to those applied in this study), and prevent us from identifying an unambiguous common *in situ* diversification pattern for the evolution of Madagascar's vertebrate biota (if existing), although a few common trends can be mentioned. For instance, by comparing studies that applied similar methodologies (i.e., on Malagasy scincines, pseudoxyrhophiine snakes, and lemurs; Herrera, 2017, Burbrink et al., 2019), it is possible that these radiations share in their evolutionary histories a continuous increasing trend in species diversity with multiple intrinsic and extrinsic diversification drivers that were likely responsible for the diversity observed today. However, at least in the Malagasy scincines and pseudoxyrhophiine snakes it seems that none of these drivers had a predominant effect over the others. This might be due to some unique characteristics of Madagascar's natural history, amongst which a biogeographic history consisting in a long-standing isolation starting before the mass extinction at the K-T boundary that depleted Malagasy Cretaceous biota and provided plenty of opportunities for new colonisers that reached the island during the Cenozoic (Vences et al., 2009; Crottini et al., 2012). In addition, the large dimension of this continental island, the presence of a large environmental diversity, broad bioclimatic conditions and a complex and structured biota, along with the occurrence of large-scale climatic changes over the time likely played an important role in the diversification of Malagasy biota (Vences et al., 2009; Crottini et al., 2012).

CRediT authorship contribution statement

Francesco Belluardo: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **A. Jesus Muñoz-Pajares:** Conceptualization, Methodology, Software, Writing – review & editing, Resources. **Aurélien Miralles:** Conceptualization, Resources, Writing – review & editing. **Daniele Silvestro:** Conceptualization, Methodology, Validation, Writing – review & editing. **Walter Cocca:** Methodology, Resources, Writing – review & editing. **Fanomezana Mihaja Ratsoavina:** Resources, Writing – review & editing. **Andrea Villa:** Formal analysis, Resources, Writing – review & editing. **Sam Hyde Roberts:** Resources, Writing – review & editing. **Marcello Mezzasalma:** Resources, Writing – review & editing. **Alexander Zizka:** Methodology, Validation, Writing – review & editing. **Alexandre Antonelli:** Conceptualization, Resources, Writing – review & editing. **Angelica Crottini:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

Research data are available on the Mendeley Data platform (https://doi.org/10.17632/xfx2yhw949.2), which include datasets, input files and R scripts of the analyses.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2022.107635.

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