comptes rendus
palevol
2025 • 24 • 9

European origins of Squamata supported by biogeographic analysis of fossil-tip-dated phylogenies using paleocontinental plate-tectonic models

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SNAKES FROM THE CENOZOIC OF EUROPE
– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

Edited by Georgios L. GEORGALIS, Hussam ZAHER & Michel LAURIN

art. 24 (9) — Published on 26 March 2025
www.cr-palevol.fr

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

European origins of Squamata supported by biogeographic analysis of fossil-tip-dated phylogenies using paleocontinental plate-tectonic models

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Submitted on 22 August 2024 | Accepted on 20 November 2024 | Published on 26 March 2025

urn:lsid:zoobank.org:pub:258115E8-35CC-4D0A-BE72-98D1C2413F74

Wilenzik I. V. & Pyron R. A. 2025. — European origins of Squamata supported by biogeographic analysis of fossil-tip-dated phylogenies using paleocontinental plate-tectonic models, *in* Georgalis G. L., Zaher H. & Laurin M. (eds), Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis. *Comptes Rendus Palevol* 24 (9): 139-158. https://doi.org/10.5852/cr-palevol2025v24a9

ABSTRACT

A pressing issue in historical biogeography for clades with long evolutionary histories and intercontinental distributions is the ever-changing position of tectonic plates. Over time, this shifting alters the proximity between areas, a factor that very few models can easily account. In addition, the absence of fossils from most molecular phylogenies often erases biogeographic signals not retained in trees of extant taxa. Here, we adapt the paleogeographic model from Landis (2017), a potentially powerful tool for ancestral-range estimation at global scales through time. This model creates "communicating classes" of areas by assigning discrete geographic units to adjacency matrices that change across multiple time slices in the Phanerozoic to model continental drift. We apply this algorithm to three existing total-evidence datasets incorporating extinct and extant tips from the order Squamata. Our results corroborate the origin of Squamata on the Eurasian continent – specifically Europe and northeastern Asia – although phylogenies sampling more Jurassic squamate lineages showed higher support for a purely European origin. Eurasia continued to be a major source of diversification throughout the Mesozoic, with dispersals into North America in the Late Jurassic and South America in the mid-Cretaceous. For Serpentes, the ancestral ranges were unclear and inconsistent across the phylogenetic hypotheses, likely influenced by the disparate and incomplete sampling in the three phylogenies.

KEY WORDS
Biogeography,
Squamata,
snakes,
lizards,
tectonics,
paleobiogeography,
fossil.

RÉSUMÉ

Les origines européennes des Squamata soutenues par l'analyse biogéographique des phylogénies datées de pointes fossiles à l'aide de modèles de plaques tectoniques paléocontinentales.

Un enjeu majeur en biogéographie historique pour les clades ayant de longues histoires évolutives et des répartitions intercontinentales est la position changeante des plaques tectoniques. Ce mouvement modifie, au fil du temps, la proximité entre les différentes zones, un phénomène que très peu de modèles peuvent facilement prendre en compte. De plus, l'absence de fossiles dans la plupart des phylogénies moléculaires efface souvent les signaux biogéographiques qui ne sont pas conservés dans les arbres des taxons actuels. Dans cette étude, nous adaptons le modèle paléogéographique de Landis (2017), un outil potentiellement puissant pour estimer les aires ancestrales à l'échelle mondiale à travers le temps. Ce modèle crée des « classes communicantes » de zones en attribuant des unités géographiques discrètes à des matrices d'adjacence qui évoluent sur plusieurs périodes du Phanérozoïque afin de modéliser la dérive des continents. Nous appliquons cet algorithme à trois ensembles de données existants combinant des taxons fossiles et actuels de l'ordre des Squamates. Nos résultats confirment une origine des Squamates sur le continent eurasien – plus précisément en Europe et dans le nord-est de l'Asie – bien que les phylogénies échantillonnant davantage de lignées de Squamates du Jurassique apportent un soutien plus fort à une origine purement européenne. L'Eurasie est restée une source majeure de diversification tout au long du Mésozoïque, avec des dispersions vers l'Amérique du Nord à la fin du Jurassique et vers l'Amérique du Sud au milieu du Crétacé. Pour les Serpentes, les aires ancestrales restent incertaines et varient selon les hypothèses phylogénétiques, probablement en raison d'un échantillonnage disparate et incomplet dans les trois phylogénies.

MOTS CLÉS
Biogéographie,
Squamata,
serpents,
lézards,
tectonique,
paléobiogéographie,
fossile.

INTRODUCTION

Estimating the ancestral range of groups in deep time based on occurrence data (both fossil and extant), paleogeographic reconstructions, and phylogenetic inference is a major goal in systematics (Jablonski *et al.* 1985; Ree *et al.* 2005; Ronquist & Sanmartín 2011). A primary difficulty is establishing informative biogeographic areas at a global scale, given the dynamic nature of the continents throughout Earth's history (Landis 2017). The configuration of landmasses is ever changing, ranging from total conglomeration into supercontinents such as Pangaea (Rogers & Santosh 2004) to the broadly distributed orientation of today. This presents substantial challenges to establishing discrete biogeographic areas at a continental scale through time (Ree *et al.* 2005; Lomolino *et al.* 2010; Morrone 2018), especially when attempting an ancestral range estimation in taxa with an extensive evolutionary history (e.g. Wisniewski *et al.* 2022). Over hundreds of millions of years, not only have regional biotas changed drastically in both climate and floral and faunal composition, but proximity between land masses has undergone major alteration, likely influencing dispersal probabilities and the impact of vicariance (Landis *et al.* 2021). For example, while Antarctica is currently a cold desert, it was covered in temperate forests during the Cretaceous (Klages *et al.* 2020), and the Indian subcontinent was previously accreted to Antarctica before splitting off and colliding with Asia approximately 55 million years ago (Aitchison*et al.* 2007). In contrast, little to no terrestrial signature of an "Antarctic" temperate biota remains today in either Antarctica or India.

To date, these factors have not been easily quantifiable given available biogeographic models (e.g. Ree & Smith 2008; Matzke 2014), even when the phylogenies themselves contain multiple extinct lineages sampled through time. Methods that attempt to combine extant and fossil data often do so either by utilizing fossils in a non-phylogenetic framework (Pole 2001; Silvestro *et al.* 2016), as divergence calibrations in phylogenetic biogeographic analyses (Noonan & Chippindale 2006; Murienne *et al.* 2014), or as biogeographic nodal constraints (Stelbrink *et al.* 2020; Vieu *et al.* 2022; Wilenzik *et al.* 2024). Other authors have tried to account for tectonic processes using manual input of penalized biogeographic scenarios around the motion of continents through adjacency matrices (Bossuyt *et al.* 2006; Ellepola & Meegaskumbura 2023), matching tectonic events to vicariance or dispersal, either under consistent continental proximity (Heads 2010, 2023) or accounting for tectonic shifts (Lam *et al.* 2018). Many fossil-based phylogenies used for ancestral-range estimation often focus on relatively short periods of time where the effects of plate tectonics have less impact (Longrich *et al.* 2020; Griffin *et al.* 2022; Brownstein 2023; Müller *et al.* 2023).

This methodological challenge is also confounded by the typical absence of early fossil branches and their attendant occurrence records from the phylogeny of major clades, which can substantially alter hypothesis testing in historical biogeography (Crisp *et al.* 2011). Consequently deep-time ancestral-range estimates often yield broad results such as "Gondwana" or "Pangaea," based on incompletely parameterized biogeographic models from extant ranges reconstructed into the distant past without substantive historical occurrence records from fossil data (Bossuyt *et al.* 2006; Gorscak &

O'Connor 2016; Wilenzik *et al.* 2024). For clades with long and complex biogeographic histories, models based around plate tectonics across the Phanerozoic are greatly needed to estimate ancestral ranges, ideally based on fossil-tip-dated phylogenies that sample taxa through time and across areas in a way that reflects underlying processes.

A major example in terrestrial vertebrates is Squamata (Title *et al.* 2024), the *c.* 11 000 species of snakes and "lizards". Extant squamates have a near global distribution except for polar areas (Vitt & Caldwell 2014), but the early Mesozoic record of squamates is sparse, with the earliest stem squamate *Megachirella wachtleri*† Renesto & Posenato, 2003 found in the mid-Triassic of Europe (Simões *et al.* 2018). The Jurassic is better represented, with most specimens located in Europe (Hoffstetter 1964, 1967; Waldman & Savage 1972; Seiffert 1975; Estes 1983; Evans 1994a, 1998; Caldwell *et al.* 2015; Conrad 2018), as well as North America (Prothero & Estes 1980; Evans & Chure 1998b; Evans 1996; Brownstein *et al.* 2022) and Asia (Hecht & Hecht 1984; Federov & Nessov 1992; Nydam *et al.* 2013; Dong *et al.* 2019; Meyer *et al.* 2023). There is also some fragmentary Jurassic evidence of squamates in Africa (Broschinski 1999). While squamates were present in other landmasses such as South America (Bittencourt *et al.* 2020), Australia (Kear *et al.* 2005), and Antarctica (Legendre *et al.* 2020) by the Cretaceous, limited occurrences restrict our understanding of these historical dynamics during the Jurassic. By the end-Cretaceous, squamates had achieved a global distribution (see Wilenzik *et al.* 2024), including members of the marine clade Mosasauria in Antarctica (Legendre *et al.* 2020).

Despite this complexity and its importance for understanding historical diversification, few attempts have been made to analyze biogeographic patterns in Squamata in a global paleogeographic context incorporating fossil occurrences, especially within the Cenozoic of Europe (Georgalis *et al.* 2025). Our previous study (Wilenzik *et al.* 2024) estimated a broadly Pangaean origin and Eurasian regionalization during the Jurassic using a dated molecular phylogeny of extant species, area occurrences based on nine tectonic plates (Tonini *et al.* 2016) in their present-day configuration, and four Mesozoic fossil constraints. However, we were limited in our ability to incorporate paleogeographic data and the broader phylogenetic distribution of fossil squamate lineages at that time. Consequently, we hypothesize that a paleogeographic model accounting for plate tectonics across the Phanerozoic that incorporates the relatively dense fossil history of Squamata might yield more precise estimates of their ancestral range in the Mesozoic and early Cenozoic (Evans 2003; Ree & Sanmartín 2009).

Nevertheless, such a model requires a robust and well-sampled phylogenetic dataset for Squamata. Squamate phylogenies have been controversially variable from different authors, based on different underlying character matrices, taxon sampling, and inference methods (see Simões & Pyron 2021). Three major recent examples are phylogenies based on the matrices of Conrad (2008; "CON" hereafter) and Gauthier *et al.* (2012; "GAU") re-analyzed by Pyron (2017), and the new morphological matrix presented by Simões *et al.* (2018; "SIM"). Pyron (2017) and Simões *et al.* (2018) presented combined-evidence, time-calibrated, relaxed-clock Bayesian phylogenies based on the CON, GAU, and SIM matrices along with well-sampled molecular datasets (see Materials and Methods). However, these three trees vary in their sampling of characters, codings, and fossil and extant taxa, and offer differing estimates of early squamate relationships, especially with respect to Mesozoic fossil lineages. As these lineages are often found in areas not occupied by extant representatives, variable inclusion of these extinct taxa may have substantial impacts on biogeographic estimates for early Squamata.

To evaluate this, we adapt a model outlined by Landis (2017), originally introduced to jointly estimate biogeographic history and divergence dates on a known phylogeny – referred to as "biogeographic dating" – which has been used to estimate divergence times for turtles (Landis 2017), silverswords (Landis *et al.* 2018), and damselflies (Willink *et al.* 2024). Recent authors also used a version of this model for Dinosauria (Lee *et al.* 2018), establishing precedent for use on phylogenies of extinct clades in deep time. The basis of the original model centers around the idea of "communicating classes" of discrete areas which can be linked together in different arrangements through time, overcoming a limitation of other models such as DEC (see Matzke 2014). This accounts for continental drift by allowing the likelihood of dispersal between areas to vary across epochs. Specifically, the model categorizes short, medium, and long distances between 25 geographic areas that subdivide current landmasses, and estimates dispersal likelihoods based an epoch-specific Q matrix. The model then has 26 time slices across the Phanerozoic from the Ordovician to present day, which have different dispersal matrices for each time slice, approximating plate-tectonic histories of continental accretion and fragmentation.

In Landis' (2017) original formulation, divergence times and ancestral ranges were jointly estimated on a calibrated molecular phylogeny. A combined molecular and biogeographic clock thereby allowed for a temporal and spatial solution to biogeographic and evolutionary history that maximizes the probability of the present-day taxon occurrences relative to the paleogeographic history of the areas. However, there is no requirement to estimate divergence times simultaneously; well-calibrated timetrees are available for many groups, removing the need for a molecular clock if only ancestral ranges are estimated. Consequently, implementing this model on a previously dated tree potentially allows for a powerful alternative to other common approaches such as DEC+j, which cannot easily adapt to complex paleogeographic landscapes (see Ree & Smith 2008; Landis *et al.* 2013; Matzke 2014), although it has been attempted over much shorter timescales with fewer time slices and areas (Buerki *et al.* 2011).

This is likely to be important for dated trees with densely sampled fossil lineages through time, presenting occurrence series through long periods on different paleogeographic landmasses (Crisp *et al.* 2011). Evidence suggests that extant-only datasets often fail to accurately reconstruct nodes deep in geological time (Wisniewski *et al.* 2022; Faurby *et al.*

2024). Consequently, fossils often act as our only concrete evidence for the presence of groups in specific areas. This is exemplified by extralimital fossil taxa (extinct taxa located outside the range of extant members of the clade) such as the Cenozoic presence of Elapidae Boié, 1827, Teiidae Gray, 1827, Helodermatidae Gray, 1837, Varanidae Hardwicke & Gray, 1827, Boidae Gray, 1825, and Pythonidae Fitzinger, 1826 in Europe (Hoffstetter 1957; Estes 1983; Szyndlar & Rage 2003; Szyndlar *et al.* 2008; Georgalis *et al.* 2017, 2019; Ivanov *et al.* 2018; Augé & Brizuela 2020; Zaher & Smith 2020) or aniliid snakes in North America (Head 2021), with potential members of Tropidophiidae Brongersma, 1951 also occurring in Europe (Smith & Georgalis 2022).

Here, we apply the adapted model from Landis (2017) to the three richly sampled phylogenetic hypotheses (CON, GAU, and SIM) for Squamata, each containing numerous extinct branches from the Mesozoic and Cenozoic. Under our modified scenario, we hypothesize that ancestral range estimates for Squamata will be restricted to landmasses from the Laurasian paleocontinent under all three phylogenetic hypotheses, based on previous studies (Wilenzik *et al.* 2024) and the presence of the earliest known squamates on the continent of Europe (Simões *et al.* 2018). However, we anticipate that localization to more specific sub-areas within Pangaean landmasses may be facilitated by denser fossil sampling and the paleogeographic model incorporating communicating classes. Complicating this, we also expect major divergence in ancestral range estimates across the varying phylogenetic hypotheses and for many extinct clades such as Polyglyphanodontia, Paramacellodidae Estes, 1983, and Mosasauria whose placement in phylogenies remains controversial (Simões & Pyron 2021).

However, we find remarkable congruence across all three trees, supporting a European origin for Lepidosauria and crown Squamata, with subsequent movement into Asia during the Jurassic before various patterns of worldwide expansion. Late Mesozoic differences between topologies based on different sampling of phenotypic characters and fossil lineages also offer specific hypotheses to be tested by future researchers. In particular, the biogeographic origin of snakes is still unclear, and is heavily impacted by sampling of early-branching extant lineages such as scolecophidians and the inclusion and coding of various fossil snakes across stem and crown of Serpentes. Additionally, new fossil squamates continue to be discovered around the world, and recent finds might have substantial impacts on biogeographic reconstructions across phylogenetic and temporal scales. Overall, paleogeographic ancestral-range estimation using the Landis (2017) approach offers a powerful solution for densely sampled fossil phylogenies in deep time, while still sensitive to phylogenetic variability.

METHODS

PHYLOGENETIC HYPOTHESES

To address uncertainty in squamate paleosystematics (see Simões & Pyron 2021), we opted to run our model under three separate, previously published hypotheses of squamate evolution. Each phylogeny is the result of a time-calibrated, total-evidence approach, using a tip-calibrated Bayesian analysis of molecular data and a morphological matrix from one of the major morphological matrices. The first uses the matrix from Conrad (2008) in combination with the six loci molecular data from Pyron *et al.* (2013; see Pyron 2017). The CON tree has a morphological matrix of 222 species, 129 of them being extinct fossil lineages, coded for 363 characters. The second uses the matrix from Gauthier *et al.* (2012), again in combination with the six loci molecular data from Pyron *et al.* (2013; see Pyron 2017). The GAU tree has a morphological matrix consisting of 192 species, 49 of fossils, scored for 610 characters. The third tree (Simões *et al.* 2018) was based on a morphological matrix with 129 species, 25 of them fossils, and 347 characters, along with 16 genetic loci for 38 extant taxa, and combined tip and node dating. We use each tree exactly as presented by Pyron (2017) – maximum clade credibility trees – and Simões *et al.* (2018) – a majority rule consensus tree; any references made here to the topologies, their similarities, or their differences stems from the original publications.

We focus primarily on twelve extant and three extinct clades in our study that have long been foci for discussion in Squamata (Simões & Pyron 2021). For extant lineages, we examine clades that have been established in the molecular phylogenetic literature: Lepidosauria, Squamata, Dibamia, Gekkota, Scincoidea, Laterata, Unidentata (Scincoidea + Laterata + Toxicofera), Episquamata (Laterata + Toxicofera) and Toxicofera (Anguimorpha + Iguania + Serpentes) – see Burbrink *et al.* (2020) and Singhal *et al.* (2021) for definitions. These clades represent major global crown-group diversity in modern squamates that is present in each of the three phylogenies that we analyzed. There are also three major extinct clades: Mosasauria, Polyglyphanodontia, and Paramacellodidae. All three represent large squamate clades that diversified during the Mesozoic before their complete extinction by the K-Pg boundary, which extant-only biogeographic analyses cannot properly estimate (Longrich *et al.* 2012b, 2015). Their placement also influences numerous consequential hypotheses regarding squamate origins (see Conrad 2008; Gauthier *et al.* 2012; Reeder *et al.* 2015; Simões *et al.* 2018).

There are also few notable taxa missing from each phylogeny that could impact biogeographic analyses. In the SIM matrix, “scolecophidian” snakes are absent, a likely paraphyletic assemblage that contains the earliest diverging snakes (Miralles *et al.* 2018). Excluding these has potentially serious implications for the estimated history of Serpentes, as discussed later. In addition, the SIM matrix also excludes true mosasaurs, opting instead for early diverging mosasaurians. While this might not affect the ancestral range estimation for Mosasauria, it does exclude biogeographic patterns of a highly diverse and successful group of squamates, as mosasaurs are the only Mesozoic squamates found in Australia (Kear *et al.* 2005) and Antarctica (Legendre *et al.* 2020). Another extinct group of exceptional phylogenetic and biogeographic interest, Paramacellodidae, has low representation in both the SIM and GAU trees, with only one and two terminals respectively. This does not reflect the broad geographic and temporal range that this proposed family achieved during the Mesozoic (Bittencourt *et al.* 2020). Finally, an important fossil missing from the CON and GAU trees is the oldest squamate known, †*Megachirella* Renesto & Posenato, 2003, which was described after the publication of those two trees and has major implications for ancestral range estimation in Squamata. By running three fixed trees with different phylogenetic positioning and sampling, we aim to reduce the effect of these issues without changing their topologies.

It is important to remark on the incompleteness of the fossil record. A related issue specific to Squamata is the evidence of the "Lagerstätten Effect" in the Late Cretaceous, in which diversity of the clade is explained based on the presence of areas of exceptional preservation overinfluences the phylogenetic signal (Woolley *et al.* 2024). Under this paradigm, northeast Asian reconstructions are being unfairly weighted toward the Lagerstätten of Mongolia and Northern China. However, in the records of other smaller, Mesozoic tetrapods (i.e., Lissamphibia), a major portion of the limited fossil record in the Triassic and Jurassic can be explained by low diversity of the clade itself (Marjanović & Laurin 2008). If this pattern occurs in Squamata, then the patchiness in the Triassic and Jurassic could in part be explained by low diversity, which suggests presence data from early squamates could reflect their true biogeographic signals. In addition, while the model outlined here does not account directly for fossilization rates, one of the major inputs is a fixed tree. In these trees, parameters of fossilization can be accounted for when generating phylogenetic hypotheses themselves. All three phylogenies were run under relaxed clock Fossilized Birth-Death (FBD) models (Pyron 2017; Simões *et al.* 2018), and therefore broadly account for rate of fossilization. Future phylogenetic analyses could utilize the FBD model proposed by Didier & Laurin (2024), which allows for variations in cladogenetic parameters between time slices, paralleling the division of geographic events as established in the biogeographic methods we used.

Ranges and areas

The original model created by Landis (2017) included 25 regions with 26 different time slices, complete with 26 different *Q* matrices representing the communicating classes for each time slice. Most of the continents were split into smaller subunits, based on areas with substantial geological and tectonic changes across Earth's history. For example, India is treated as its own area, as it was accreted to Antarctica approximately 110-100 million years ago (Gurnis *et al.* 2012) in opposition to its current position alongside the Eurasian plate. The continents and respective regions are North America (NW, SW, SE, SW), Greenland, Europe, Asia (C, NE, E, SE), India, the Malaysian Archipelago, New Zealand, Australia (SW, NE), Antarctica (W, E) Madagascar, Africa (N, S, E, W), and South America (N, E, S).

Each taxon can be assigned to one or more of the 25 regions based on their current known distribution. Marine taxa such as mosasaurs were assigned to the areas where the fossils are located, i.e., the Moroccan mosasaur †*Tethysaurus* Bardet, Suberbiola & Jalil, 2003 is scored as Northern Africa. The model allows terminal taxa to occupy more than one area. However, it only reconstructs the ancestral ranges as occupying one area. This is useful for widely spread species and for summarizing larger groups of squamates into one terminus. We broadly consider an area supported at >80% to be "strongly" supported. Since the model only allows for the ancestral range to occupy one area, partial support for multiple areas can be interpreted in three different ways. The first covers a two-area range, when the two areas with the highest support add up to our 80% threshold, which we interpret to mean that the ancestral range potentially included both areas. The next scenario is a "majority," when one area has 50-80% support. The last scenario is "uncertain," if there is no two-area range or single majority area in the ancestral estimate. To ascertain location data for coding terminal species, we utilized the Reptile Database (Uetz *et al.* 2024) for extant species and FossilWorks through the Paleobiology Database (Behrensmeyer & Turner 2013) for extinct taxa (for analysis code and geographic states, see the online supplementary material at https://doi.org/10.5281/zenodo.13929768).

The dispersal matrices are the backbone of the paleotectonic aspects of the model. The basis for determining distance are the best estimations set out by Blakey (2008) and given in GPlates (Boyden *et al.* 2011; Gurnis *et al.* 2012). As future models of plate tectonics evolve, the *Q* matrices can be easily adapted to reflect updated understandings. For each individual time slice, two matrices are established. The first establishes all short-distance dispersals between continents (Landis 2017). The second establishes medium-distance dispersals. Long-distance dispersals are assumed for all areas without a short- or medium-distance dispersal. Additional details are given by Landis (2017); we did not alter this aspect of the model.

Finally, we implemented a few changes to the computational structure of Landis (2017). The original method generated a "biogeographic clock" conditioned on the estimated molecular clock. Instead, we opted to use a proxy based on a random, uniform distribution. This is similar to the process for estimating the biogeographic clock in the original model but is estimated independently – without reference to a molecular matrix – on a tree with fixed, pre-existing dates. We also altered the requirement that terminal taxa were all uniformly assumed to have an age of 0 (representing an extant taxon), as had been done previously for trees with only extant species. Instead, the input for fossil taxa within our updated model was the approximate age of the fossil, allowing for the extinct specimens to act as time-calibrated terminal taxa.

We implemented this modified model structure for all three phylogenies independently in RevBayes 1.2.2 (Höhna *et al.* 2016) under a Bayesian framework with 10 000 iterations and burn in period of 1 000 generations. We visualized results using the R package RevGadgets (Tribble *et al.* 2022), which reconstructed the top three highest probability ranges, with all others summarized in the "other" category. We evaluated convergence using Estimated Sample Size (ESS) values for major parameters, assuming stationarity when ESS >625 for the log-likelihood values (see Fabreti & Höhna 2022).

TABLE 1. — A breakdown of the top three ancestral range estimations of the CON matrix for each of the major nodes, along with the “other” reconstructions in the “% Other” column. Those with strongly supported reconstructions (>0.80) are **bolded**. Abbreviations: **As_C**, central Asia; **As_E**, eastern Asia; **As_NE**, northeast Asia; **Eur**, Europe.

Clade	Area #1	% Area 1	Area #2	% Area 2	Area #3	% Area 3	% Other
Lepidosauria	Eur	0.40	As_NE	0.12	As_C	0.09	0.37
Squamata	**Eur**	**0.94**	As_NE	0.04	As_C	<0.01	0
Gekkota	**As_NE**	**0.90**	As_C	0.06	As_E	0.01	0.01
Dibamia	**Eur**	**0.86**	As_NE	0.12	As_C	0.01	0
Unidentata	Eur	0.72	As_NE	0.26	As_C	0.01	0
Scincoidea	Eur	0.76	As_NE	0.22	As_C	<0.01	0
Episquamata	**As_NE**	**0.89**	Eur	0.06	As_C	0.03	<0.01
Laterata	**As_NE**	**0.90**	As_C	0.03	Eur	0.02	0.02
Toxicofera	**As_NE**	**0.95**	As_C	0.02	Eur	0.01	<0.01
Anguimorpha	**As_NE**	**0.97**	As_C	0.01	Eur	<0.01	<0.01
Iguania	**As_NE**	**0.94**	Eur	0.02	As_C	0.02	<0.01
Serpentes	As_C	0.69	As_NE	0.18	As_E	0.03	0.07
Mosasauria	**Eur**	**0.98**	As_NE	0.01	As_C	<0.01	<0.01
Polyglyphanodontia	**As_NE**	**0.99**	As_C	<0.01	As_E	<0.01	0
Paramacellodidae	**Eur**	**0.92**	As_NE	0.07	As_C	<0.01	0

All runs for each model quickly reached stationarity, with ESS well above the >625 limit for each of the three trees (>1 800 for CON and SIM and >1 600 for GAU) for all parameters, including the likelihood and dispersal rates (all code utilized here can be located in the online repository https://doi.org/10.5281/zenodo.13929768).

HYPOTHESES

Our previous analysis using extant-only trees for crown Squamata and a few Mesozoic nodal constraints reconstructed an ancestral range of Eurasia, Africa, Australia, and Sunda (Wilenzik *et al.* 2024), areas located along the coast of the paleo-ocean known as the Tethys Sea (Zhu *et al.* 2022). However, fossil-based phylogenies including early squamate lineages might shift estimates towards one or more of these localities. The CON tree is relatively well-sampled for Jurassic squamates, with the best sampling of paramacellodids including †*Becklesius* Estes, 1983 (assigned to Paramacellodidae in Evans & Chure 1998a) and †*Bavarisaurus* Hoffstetter, 1953 (assigned to Paramacellodidae in Evans 1994b), both from Europe. Also included is †*Eichstaettisaurus* Kuhn, 1958, a stem-gekkotan from Europe (Evans *et al.* 2004) and †*Ardeosaurus* Meyer, 1860, reconstructed in CON as a stem-dibamid – contrasted with recent analyses placing it within Scincoidea (Tałanda 2018) or as a Gekkotan (Simões *et al.* 2017a) – from Europe (Hoffstetter 1966). Unlike the CON tree, the GAU tree lacks many Jurassic lineages, with only the genus †*Paramacellodus* Hoffstetter, 1967 present from North America (Hoffstetter 1967; Evans & Chure 1998a), Europe (Richter 1994), and Morocco (Richter 1994). The SIM tree contains the oldest known stem-squamate †*Megachirella* from the Italian Alps (Simões *et al.* 2018), along with †*Marmoretta* Evans, 1991, another hypothesized stem-squamate (Simões *et al.* 2018; but also reconstructed as a stem-lepidosaurian, Griffiths *et al.* 2021) from Europe (Evans 1991), †*Eichstaettisaurus*, a stem-gekkotan from Europe (Evans *et al.* 2004), and †*Ardeosaurus*, reconstructed in SIM as a unidentatan of unclear affinity also from Europe (Hoffstetter 1966). Consequently, we hypothesize that all three phylogenies may shift towards estimating a European origin compared to previous extant-only results (Wilenzik *et al.* 2024), a hypothesis corroborated by the presence of early lepidosauromorphs like †*Vellbergia* Sobral Simões & Schoch, 2020 and rhynchocephalians (Sues & Schoch 2024) in Europe during the Middle Triassic.

Within Squamata, two major hypotheses regarding the placement of extinct clades based on Pyron (2017) and Simões *et al.* (2018) are: 1) Mosasauria is either sister to Serpentes or nested within Anguimorpha; and 2) Polyglyphanodontia is either paraphyletic within Laterata or monophyletic within Iguania. Our third extinct group of interest, Paramacellodidae, is consistently reconstructed as a monophyletic group sister to crown Scincoidea. In terms of biogeographic reconstructions, early mosasaurians are found mostly in Europe, such as †*Aigialosaurus* Kramberger, 1892. Consequently, the position of early mosasaurians may influence a European origin for Anguimorpha in the CON tree or for Serpentes in the GAU and SIM trees. For Polyglyphanodontia, many species are localized to northeastern Asia (Gao & Norell 2000), which could promote an estimated Asian origin for Iguania in the GAU tree or for Laterata in the CON and SIM trees. Paramacellodidae is found broadly in Laurasia (Hoffstetter 1967; Nydam 2002) and one recently discovered representative from South America, †*Neokotus* Bittencourt , Simões, Caldwell & Langer, 2020, could influence a Laurasian origin for Scincoidea. Consequently, we anticipate shifts for the Mesozoic history of Squamata based on the impact of these extinct taxa compared to the previous extant-only estimates (Wilenzik *et al.* 2024).

Finally, we note that the CON matrix is the oldest matrix of the three and lacks some key squamate taxa, i.e., †*Megachirella* (Simões *et al.* 2018) alongside potentially questionable characters and codings in some instances (e.g. Macrostomata; see Results). Nonetheless, this matrix has the highest sampling of Jurassic squamates of the three trees, including the densest sampling of Paramacellodidae and Polyglyphanodontia, which we argue make its inclusion imperative. A good instinct would be to utilize more recent, updated versions

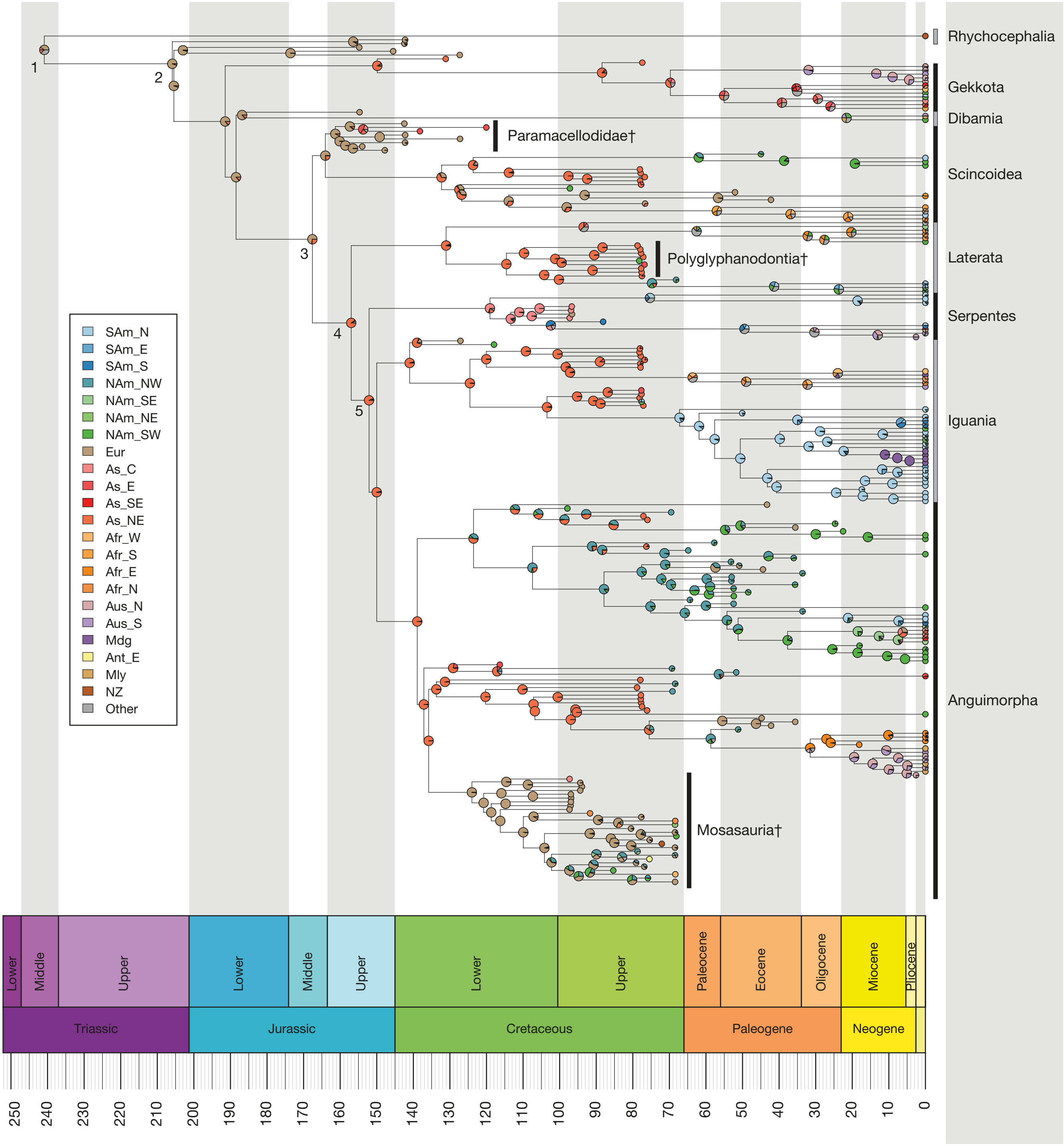

Fig. 1. — Nodal inferences of paleobiogeographic ancestral ranges using the model based on Landis (2017), based on the CON tree from Conrad (2008) reanalyzed as a total-evidence phylogeny by Pyron (2017). Important nodes are labelled: **1**, Lepidosauria; **2**, Squamata; **3**, Unidentata; **4**, Episquamata; **5**, Toxicofera. Clades labelled with † are extinct. Abbreviations for areas: **AAs_C**, Central Asia; **Afr_E**, Eastern Africa; **Afr_N**, Northern Africa; **Afr_W**, Western Africa; **Ant_E**, Eastern Antarctica; **Aus_N**, Northern Australia; **Aus_S**, Southern Australia; **As_E**, Eastern Asia; **As_NE**, Northeastern Asia; **As_SE**, Southeastern Asia; **Eur**, Europe; **fr_S**, Southern Africa; **Mdg**, Madagascar; **Mly**, Malay Archipelago; **Nam_NE**, Northeastern North America; **NAm_NW**, Northwestern North America; **NAm_SE**, Southeastern North America; **Nam_SW**, Southwestern North America; **NZ**, New Zealand; **SAm_E**, Eastern South America; **SAm_N**, Northern South America; **SAm_S**, Southern South America.

of the trees (i.e., Brownstein *et al.* 2023). However, recent literature has cautioned against iterative matrix expansions as seen in many recent squamate phylogenies (Simões *et al.* 2017b; Laurin & Piñeiro 2018). This would also necessitate full-scale re-analysis of combined-evidence phylogeny, including choosing and partitioning molecular matrices, estimating prior distributions and parameters, and evaluating entirely new topology and divergence-time estimates.

Table 2. — A breakdown of the top three ancestral range estimations of the GAU matrix for each of the major nodes, along with the “other” reconstructions in the “% Other” column. Those with strongly supported reconstructions (>0.80) are **bolded**. Abbreviations: **As_C**, central Asia; **As_E**, eastern Asia; **As_NE**, northeast Asia; **Eur**, Europe; **SAm_N**, northern South America; **SAm_S**, southern South America.

Clade	Area #1	% Area 1	Area #2	% Area 2	Area #3	% Area 3	% Other
Lepidosauria	Eur	0.55	As_NE	0.29	As_C	0.09	0.05
Squamata	As_NE	0.69	Eur	0.25	As_C	0.04	<0.01
Gekkota	Eur	0.53	As_NE	0.35	As_C	0.07	0.02
Dibamia	As_NE	0.47	As_E	0.25	As_C	0.13	0.13
Unidentata	**As_NE**	**0.89**	Eur	0.08	As_C	0.01	<0.01
Scincoidea	**As_NE**	**0.93**	As_C	0.02	Eur	0.01	0.01
Episquamata	**As_NE**	**0.92**	Eur	0.05	As_C	0.01	<0.01
Laterata	As_NE	0.75	Eur	0.06	As_C	0.06	0.11
Toxicofera	**As_NE**	**0.93**	Eur	0.05	As_C	0.01	<0.01
Anguimorpha	**As_NE**	**0.92**	As_C	0.02	As_E	0.02	0.02
Iguania	**As_NE**	**0.98**	As_C	<0.01	As_E	<0.01	<0.01
Serpentes	SAm_S	0.50	SAm_N	0.21	As_C	0.08	0.19
Mosasauria	**Eur**	**0.99**	As_NE	<0.01	As_C	<0.01	<0.01
Polyglyphanodontia	**As_NE**	**0.99**	As_C	<0.01	As_E	<0.01	0
Paramacellodidae	As_NE	0.72	Eur	0.22	As_C	0.02	0.01

Instead, we base our evaluation of the impacts of the Landis (2017) method on paleobiogeographic estimation on the three widely known, previously published estimates for ease of interpretation and comparison. In addition, our adjusted model incorporates fixed phylogenetic hypotheses and can easily be easily updated when novel phylogenetic matrices are generated in the future.

RESULTS

Conrad (2008)

For the CON tree, the lepidosaurian node is uncertain, with no majority for any of the areas (Fig. 1; Table 1; Appendix 1 for tree with terminal taxa labelled), the two highest being Europe (40%) and “other” (37%), likely driven by Sphenodon Gray, 1831 acting as the sole representative of Rhynchocephalia. Squamata is strongly reconstructed with a European origin at 94%. The first diverging squamate lineage in the CON tree is Gekkota in northeast Asia, with strong support of 90%. This reflects a likely dispersal into Asia by early gekkotans from ancestral squamate populations in Europe, while Eurasia was still a continuous part of the paleocontinent Laurasia (Seton *et al.* 2012). The next diverging group is Dibamia, with the German fossil †Ardeosaurus estimated by Pyron (2017) as a stem lineage and with strong support (86%) here for a European origin. The next node is Unidentata, with support for a two-area range consisting of Europe and northeastern Asia (72% and 26% respectively). Scincoidea has a nearly identical estimate to Unidentata, with 76% and 22% respectively for Europe and northeastern Asia. For Episquamata, there is again a contraction from a two-area range to single, strongly supported range in northeastern Asia with 89% support. This continues with Laterata (90%), Toxicofera (95%), Anguimorpha (97%), and Iguania (94%), all of which have strong support for northeastern Asia. Serpentes, the last-diverging major extant squamate clade, receives support for a two-area range of central Asia (69%) and northeastern Asia (18%), driven by the mostly Middle Eastern fossil taxa: †*Haasiophis* Tchernov, Rieppel, Zaher, Polcyn & Jacobs, 2000, †*Eupodophis* Rage & Escuillié, 2002, and †*Pachyrhachis* Haas, 1979 along with the European taxon †*Pachyophis* Nopcsa, 1923. However, a major limitation is that one of the terminal taxa in the CON matrix for Serpentes is “Macrostomata,” a polyphyletic group (see Burbrink *et al.* 2020 for more details) including most snakes (Scanferla 2016).

For fossil lineages in the CON tree, Mosasauria is monophyletic and nested within Anguimorpha. In contrast to the strongly supported northeastern origin of the anguimorph node, Mosasauria has strong support for a European origin (98%). Polyglyphanodontia is reconstructed as an extinct, paraphyletic grade within Laterata along the base of Teiidae. Similarly to Laterata, this version of Polyglyphanodontia along the lateratan stem also receives strong support for a northeastern Asian origin (99%). The CON tree also has the most Paramacellodidae taxa sampled among the three trees, which in this phylogeny is estimated as a monophyletic group at the base of Scincoidea. As opposed to Scincoidea which has a two-area estimation between Europe and northeast Asia, Paramacellodidae receives strong support for a European origin (92%). We note that †*Parmeosaurus* Goa & Norell, 2000, a proposed Mongolian paramacellodid (Gao & Norell 2000; Dong *et al.* 2018), was inferred to have a topological position outside of Paramacellodidae within Scincoidea (Conrad 2008; Pyron 2017), which could impact the estimated ancestral range.

The biogeographic origins for all examined squamate clades in the CON tree show a consistent pattern of regionalization and diversification within the supercontinent Laurasia during the Triassic and Jurassic. Even within Laurasia there is a bias towards Eurasia, with strong early support for a European origin and later expansion into Asia. In this tree, squamates do not appear in North America until the Early Cretaceous with some Anguimorpha. It was not until the later Cretaceous that they appear in Gondwana, with snakes estimated in the mid-Cretaceous and iguanians and anguimorphs towards the K-Pg boundary.

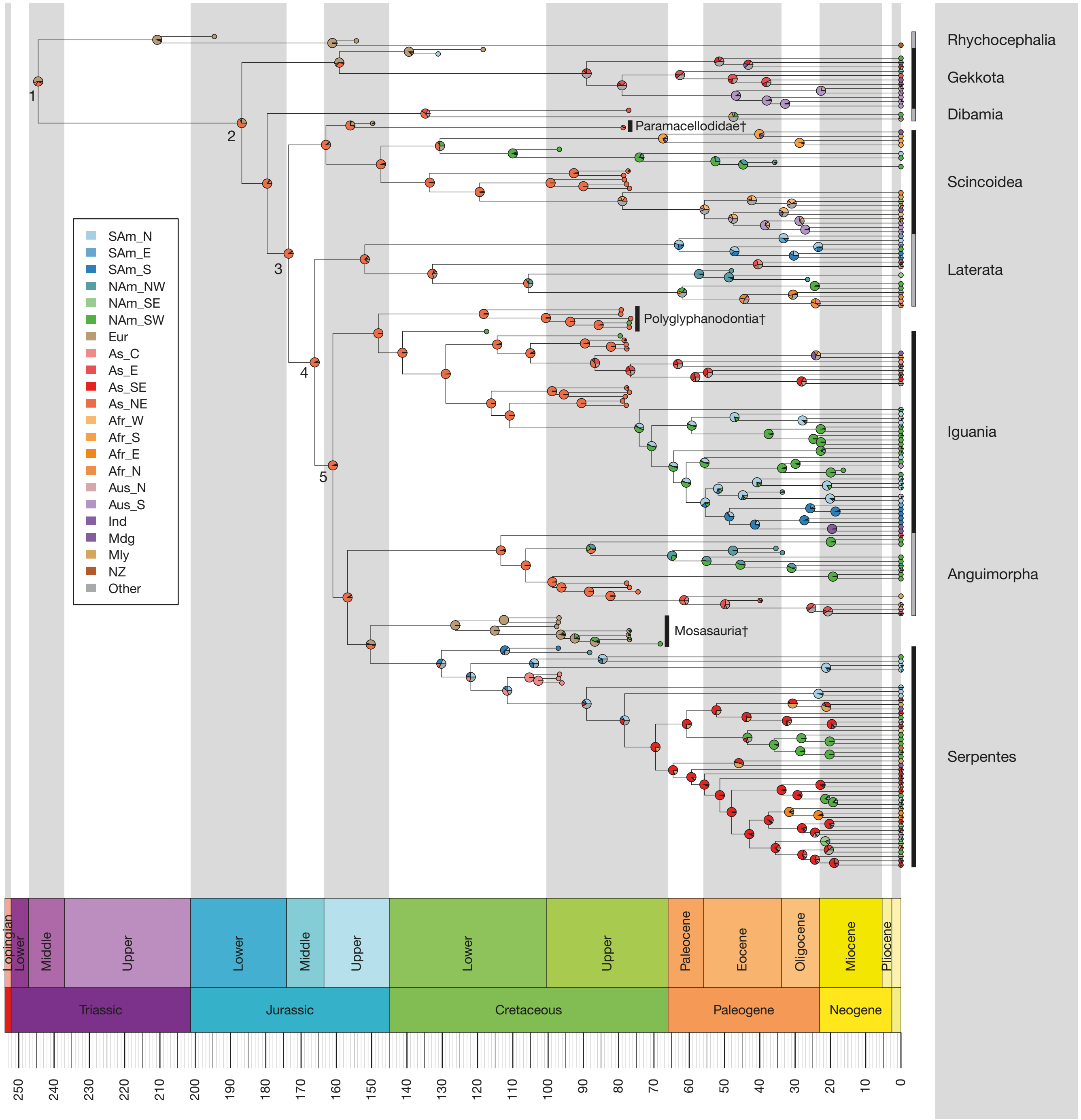

FIG. 2. — Nodal inferences of paleobiogeographic ancestral ranges using the model based on Landis (2017), based on the GAU tree from Gauthier *et al.* (2012) re-analyzed as a total-evidence phylogeny by Pyron (2017). Important nodes are labelled: **1**, Lepidosauria; **2**, Squamata; **3**, Unidentata; **4**, Episquamata; **5**, Toxicofera). Clades labelled with † are extinct. Abbreviations: **AAs_C**, Central Asia; **Afr_E**, Eastern Africa; **Afr_N**, Northern Africa; **Afr_W**, Western Africa; **Ant_E**, Eastern Antarctica; **Aus_N**, Northern Australia; **Aus_S**, Southern Australia; **As_E**, Eastern Asia; **As_NE**, Northeastern Asia; **As_SE**, Southeastern Asia; **Eur**, Europe; **fr_S**, Southern Africa; **Ind**, India; **Mdg**, Madagascar; **Mly**, Malay Archipelago; **Nam_NE**, Northeastern North America; **NAm_NW**, Northwestern North America; **NAm_SE**, Southeastern North America; **Nam_SW**, Southwestern North America; **NZ**, New Zealand; **SAm_E**, Eastern South America; **SAm_N**, Northern South America; **SAm_S**, Southern South America.

GAUTHIER *ET AL.* (2012)

The GAU tree includes three rhynchocephalians as an outgroup (Fig. 2; Appendix 2 for tree with terminal taxa labelled), including the Jurassic European fossils †*Gephyrosaurus* Evans, 1980 and †*Kallimodon* Cocude-Michel, 1963. Likely influenced by these taxa, we estimate a two-area range of Europe and northeast Asia (55% and 29% respectively; Table 2) for Lepidosauria. In contrast, the range for Squamata is northeastern Asia and Europe (69% and 25% respectively). The first diverging group in the GAU tree is Gekkota, which here is reconstructed with a two-area range of Europe (53%) and northeastern Asia (35%), similar to Lepidosauria.

TABLE 3. — A breakdown of the top three ancestral range estimations of the SIM matrix for each of the major nodes, along with the "other" reconstructions in the "% Other" column. Since only a single species represents both Dibamia and Paramacellodidae respectively in the SIM tree, a reconstruction was unable to be determined for these groups. Those with strongly supported reconstructions (>0.80) are **bolded**. Abbreviations: **As_C**, central Asia; **As_E**, eastern Asia; **As_NE**, northeast Asia; **Eur**, Europe; **Grn**, Greenland; **NAm_SE**, southeastern North America; **NAm_SW**, southwestern North America.

Clade	Area #1	% Area 1	Area #2	% Area 2	Area #3	% Area 3	% Other
Lepidosauria	**Eur**	**0.99**	Grn	<0.01	As_NE	<0.01	<0.01
Squamata	**Eur**	**0.99**	As_NE	<0.01	As_C	0	0
Gekkota	**Eur**	**0.93**	As_NE	0.045	As_C	0.01	<0.01
Dibamia	–	–	–	–	–	–	–
Unidentata	**Eur**	**0.98**	As_NE	<0.01	As_C	0	0
Scincoidea	Eur	0.28	NAm_SW	0.12	NAm_SE	0.09	0.49
Episquamata	**Eur**	**0.87**	As_NE	0.11	As_C	<0.01	0
Laterata	Eur	0.78	As_NE	0.20	As_C	0.01	0
Toxicofera	**Eur**	**0.82**	As_NE	0.14	As_C	0.02	0
Anguimorpha	NAm_SW	0.31	As_NE	0.21	Eur	0.10	0.37
Iguania	**As_NE**	**0.93**	As_C	0.03	As_E	0.02	<0.01
Serpentes	Eur	0.52	As_C	0.18	As_NE	0.14	0.15
Mosasauria	**Eur**	**0.99**	As_C	<0.01	–	0	0
Polyglyphanodontia	As_NE	0.66	Eur	0.29	As_C	0.03	<0.01
Paramacellodidae	–	–	–	–	–	–	–

The next divergence is Dibamia, which has the controversial †*Sineoamphisbaena* Wu , Brinkman, Russell, Dong, Currie, Hou & Cui, 1993 as a stem member. When first discovered in Mongolia, †*Sineoamphisbaena* was assigned as the earliest member of Amphisbaenia (hence the name; Wu *et al.* 1993), but later revisions hypothesized it to be a polyglyphanodontian (Kearney 2003). These major changes in topology are the likely reason for its designation as a rogue taxon within Squamata (Reeder *et al.* 2015). The ancestral range for Dibamia is uncertain, as none of the area reconstructions reached a majority, likely clouded by the unsettled phylogenetic position of †*Sinoamphisbaena*, a disjointed modern range of Southeast Asia and Mexico (Uetz *et al.* 2024), and a minimal fossil record consisting of one tentative dibamid from the Oligocene of Mongolia (Čerňanský 2019).

The next diverging groups, Unidentata, Scincoidea, and Episquamata all have strongly supported estimates for northeast Asia (89%, 93%, and 92% respectively). Laterata has majority support for northeastern Asia (75%), while Toxicofera, Anguimorpha, and Iguania all have strong support there (93%, 92%, and 98% respectively). Lastly, Serpentes has a majority reconstruction of southern South America at 50%, driven by the early-diverging position of †*Najash* Apesteguía & Zaher, 2006 and †*Dinilysia* Woodward, 1901. This appears to be driven by greater sampling of Mesozoic fossil snakes from widely separated areas, along with sparse sampling of fossil and extant scolecophidians. As consequence, most stem and crown nodes in the Serpentes backbone have uncertain origins, with the exception that most early afrophidian nodes (the most diverse group of alethinophidians; Burbrink *et al.* 2020) have two-area range of southeast Asia and the Malaysia Archipelago at 74% and 20%, respectively.

For the extinct clades, Mosasauria is sister to Serpentes and has a strongly supported ancestral range estimate of Europe (99%), apparently influencing the Europe + northeastern Asia estimate for the Mosasauria + Serpentes node. Polyglyphanodontia is at the base of Iguania, and shares a similar, strongly supported estimation with 99% support for northeastern Asia. Like the CON tree, Paramacellodidae is nested within Scincoidea as a stem taxon, although it is important to note that the GAU tree only has two representatives for the clade compared to eight in the CON matrix. For this group, the model reconstructs a two-area range of northeast Asian (72%) and European (21%) origin, again supporting Eurasian origins for early squamates.

Overall, the GAU tree supports a broader Eurasian origin for both Lepidosauria and Squamata, similar to our previous extant-only estimates (Wilenzik *et al.* 2024). However, this likely corresponds to the paucity of Jurassic squamates within the matrix, many of which are from Europe and are included in the CON and SIM trees. In contrast, by the Middle Jurassic, most groups were regionalized within northeastern Asia, excluding Serpentes and Mosasauria. In this tree, squamates were restricted to the Eurasian plate for a majority of the Mesozoic, most being regionalized to the northeastern Asian portion. The first dispersal into North America did not occur until the mid-Cretaceous in scincoids. Similarly, the first instances of dispersal into Gondwana occurred in the mid-Cretaceous in Serpentes and the Late Cretaceous in Iguania.

SIMÕES *ET AL.* (2018)

The SIM tree has more extensive sampling of non-lepidosaur extinct tetrapod outgroups, with less representation of extant squamates than CON or GAU (Fig. 3; Appendix 3 for tree with terminal taxa labelled). While we do not focus on the non-lepidosaur tetrapod lineages, we note that a strongly supported European origin is estimated as far back as the Carboniferous, with Lepidosauria representing a potential re-invasion of Europe from a Carboniferous African lineage when the continents were still accreted into the supercontinent Pangaea. Lepidosauria again has a strongly supported European estimate at both the stem and crown (99%; Table 3), as do most nodes in the rhynchocephalian crown group. Similarly, the squamate stem group contains several European taxa and is strongly supported with a European origin. One of these is the oldest hypothesized stem-group squamate, †*Megachirella*

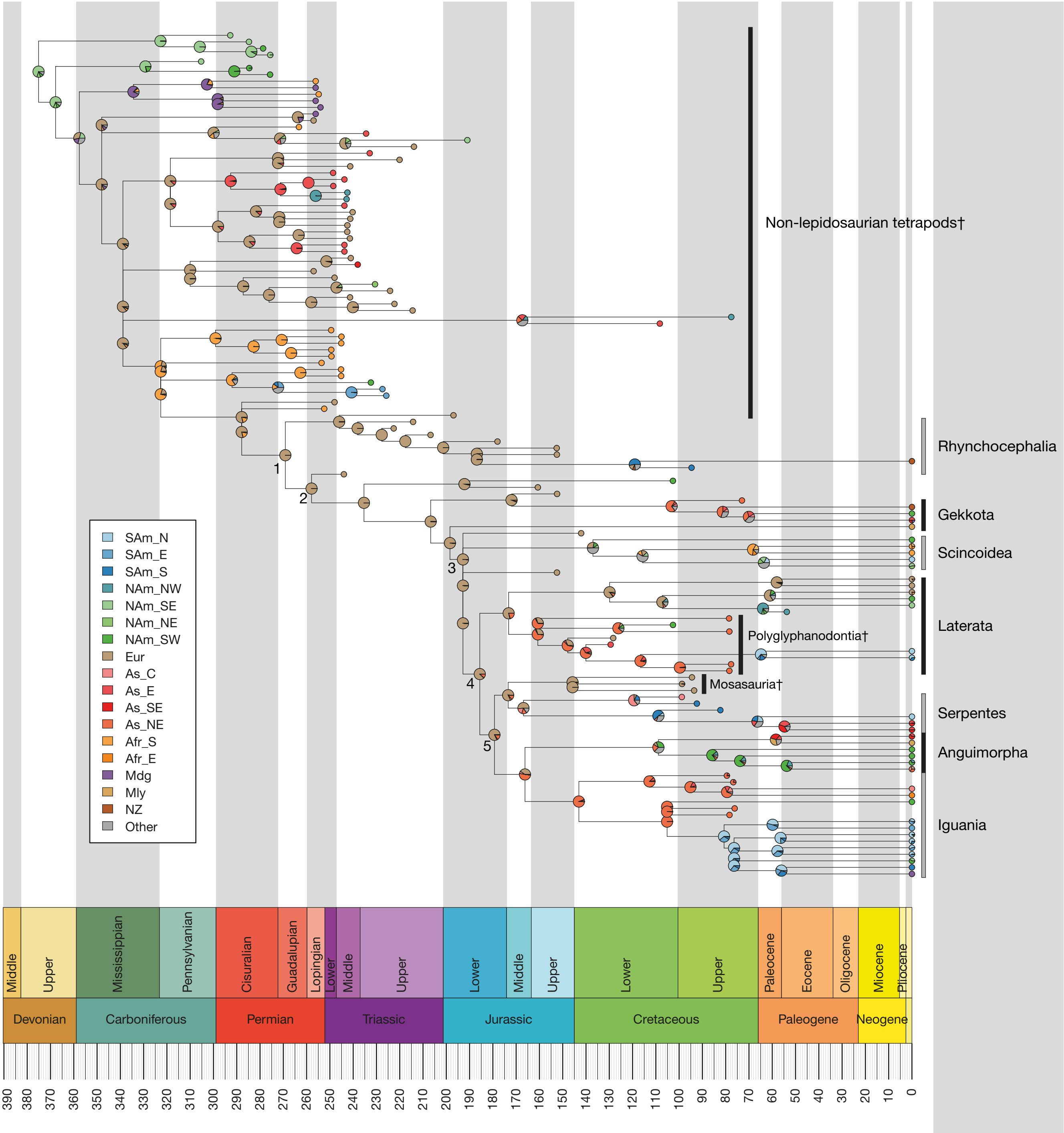

Fig. 3. — Nodal inferences of paleobiogeographic ancestral ranges using the model based on Landis (2017), based on the SIM tree from Simões *et al.* (2018). Important nodes are labelled: **1**, Lepidosauria; **2**, Squamata; **3**, Unidentata; **4**, Episquamata; **5**, Toxicofera. Clades labelled with † are extinct. Abbreviations: **AAs_C**, Central Asia; **Afr_E**, Eastern Africa; **Afr_N**, Northern Africa; **Afr_W**, Western Africa; **Ant_E**, Eastern Antarctica; **Aus_N**, Northern Australia; **Aus_S**, Southern Australia; **As_E**, Eastern Asia; **As_NE**, Northeastern Asia; **As_SE**, Southeastern Asia; **Eur**, Europe; **fr_S**, Southern Africa; **Ind**, India; **Mdg**, Madagascar; **Mly**, Malay Archipelago; **Nam_NE**, Northeastern North America; **NAm_NW**, Northwestern North America; **NAm_SE**, Southeastern North America; **Nam_SW**, Southwestern North America; **NZ**, New Zealand; **SAm_E**, Eastern South America; **SAm_N**, Northern South America; **SAm_S**, Southern South America.

from the Middle Triassic of the Italian Alps, along with †*Marmoretta* (Simões *et al.* 2018). Interestingly, the Mexican †*Huehuecuetzpalli* Reynoso, 1998 is sister to †*Marmoretta*, suggesting an expansion from Europe to North America between the early Jurassic and early Cretaceous that has little additional evidence, suggesting a cryptic biogeographic extinction.

Similarly, Squamata receives strong support (99%) for a European origin, as do Gekkota (93%), the node subtending the subsequent divergence of the sole sampled dibamian (99%), and Unidentata (98%). As there is only one dibamid in the tree, we are consequently unable to reconstruct the ancestral range of the crown group itself. The next diverging clade is Scincoidea with an uncertain ancestral range, then Episquamata with strong support (87%) for a European origin. Laterata next has a two-state range between Europe (78%) and northeast Asia (20%). Toxicofera, like most of the backbone nodes in the SIM tree, also has a strongly supported European estimate (82%). Within Toxicofera, Anguimorpha has an uncertain ancestral range, and Iguania shows a shift away from Europe, with strong support for northeast Asia (93%), corresponding to the inclusion of iguanian fossils from the Late Cretaceous of Mongolia (Magdalena & Alifanov 1991; Gao & Norell 2000). Finally, "stem" Serpentes (i.e., early snakes and Alethinophidia, without scolecophidians to determine the true stem or crown) receives majority support for a European origin.

For fossil lineages, a few biogeographic conclusions can be made, as there was only one member of Paramacellodidae sampled, from Europe and shared with the Unidentata polytomy. Within Mosasauria, the SIM tree does not include true mosasaurs and only includes early mosasaurians. Even without later-diverging mosasaurs, Mosasauria still receives strong support for an ancestral range in Europe (99%), which it shares with most of the backbone nodes and apparently influences the majority-Europe estimate for the MRCA of the sampled snake lineages. Polyglyphanodontia, which in the SIM tree is a paraphyletic grade at the base of Teiidae, has a two-area range of northeastern Asia and Europe (66% and 29% respectively) and appears to heavily influence the northeastern Asian origin of the teiid stem lineages.

Overall, for the SIM tree, the early branches of Squamata were restricted to Europe until the Middle Jurassic, corresponding with extensive fossil sampling from that period and area. Expansion into northeastern Asia did not occur until the Middle Jurassic. The first dispersal out of Eurasia into North America occurred in anguimorphs in the Late Cretaceous. Dispersal out of Laurasia into Gondwawa occurred in crown Serpentes in the mid-Cretaceous and in iguanians near the Cretaceous-Paleogene boundary. Many crown nodes in the SIM tree show low certainty, likely corresponding to limited sampling of extant lineages. For instance, in the SIM matrix for Serpentes, there are no "scolecophidian" snakes, and the three fossil snakes (†*Pachyrhachis,* †*Najash,* and †*Dinilysia*) are on the correspondingly naked stem of Alethinophidia, precluding assessment of the ancestral range of crown Serpentes.

DISCUSSION

Major biogeographic conclusions

In summary, all three analyses provide consistently strong support for a Triassic European origin of Lepidosauria and Squamata, with the GAU matrix supporting a two-area range of Eurasia, comprising Europe and northeastern Asia. Eurasia served as the major source of squamate diversification throughout the Mesozoic, with the first instance of Gondwanan dispersal in the mid-Cretaceous, well after the breakup of Pangaea into Laurasia and Gondwana (Figs 1-3). Subsequent Cenozoic radiations in Gondwana are derived from these Mesozoic patterns of dispersal and vicariance out of Eurasia. After the end-Cretaceous extinction, major Laurasian lineages such as Polyglyphanodontia and Mosasauria went extinct, eliminating most Laurasian signal from extant lineages. Limited sampling of recent lineages precludes an in-depth examination of Cenozoic patterns in most groups, particularly snakes, although the GAU tree supports a southeast Asian and Malaysian origin for most afrophidian lineages.

A previous large-scale hypothesis of squamate biogeography placed their ancestral range in the continental areas that bordered the Tethys Sea, which included the Eurasian, Australia, Africa, and Sundan plates during the Early Jurassic (Wilenzik *et al.* 2024). Our results narrow that broad estimate to the Eurasian plate during the Late Triassic, most probably Europe or northeastern Asia. The most recently updated character matrix with the most extensive fossil sampling of stem and early crown squamate lineages (Simões *et al.* 2018) shows the strongest support for a European origin of Lepidosauria and Squamata, with most lineages persisting in Europe until the Late Jurassic. All three analyses suggest Jurassic dispersals into northeastern Asia – and from there into other regions such as North and South America – by the mid-Cretaceous, from which most diverse modern radiations subsequently arose. In contrast, the K-Pg extinction erased much of the signal for Mesozoic ancestry from Europe from groups such as Mosasauria (Polcyn *et al.* 2014), and from Asia and North America for Paramacellodidae (Nydam 2002) and Polyglyphanodontia (Longrich *et al.* 2012b).

The positioning of extinct clades seems to impact biogeographic reconstructions, as their signal does not exist in extant-only datasets (Crisp *et al.* 2011). There is disagreement about the placement of Mosasauria, either as sister to Serpentes as in the GAU and SIM trees (Gauthier *et al.* 2012; Reeder *et al.* 2015; Simões *et al.* 2018) or within Anguimorpha as in the CON tree (Russell 1967; Conrad 2008). In the GAU tree, the influence of Mosasauria from Europe is unknown – the ancestral range of Serpentes is uncertain (Fig. 2) – although the Mosasauria + Serpentes node receives support for a northeastern Asian + European origin (45% and 43% respectively). In the SIM tree, Mosasauria seems to impact the ancestral range of Serpentes, with Mosasauria having a strongly supported European origin and Serpentes having a majority European origin, suggesting a common, European ancestral lineage. In the CON tree, the positioning of Mosasauria – again originating in Europe – within Anguimorpha has seemingly less impact on the strongly supported northeast Asian range of Anguimorpha (Fig. 1).

Polyglyphanodontians have two main topological hypotheses, as a monophyletic group sister to Iguania (Gauthier *et al.* 2012) or a paraphyletic grade within Laterata (Conrad 2008; Simões *et al.* 2018). When Polyglyphanodontia is sister to Iguania in the GAU tree, the ancestral range for both stem and crown Iguania and Polyglyphanodontia is strongly supported in northeastern Asia (Fig. 2). In the CON tree, both Laterata and Polyglyphanodontia have a strongly supported northeastern Asian origin (Fig. 1). In the SIM tree, Laterata and Polyglyphanodontia share a two-area range of Europe and northeastern Asia (Fig. 3). In all three phylogenies, the ancestral stem and crown range of Iguania is northeastern Asia regardless of the placement of Polyglyphanodontia. With Polyglyphanodontia as a grade inside Laterata in the CON and SIM trees (giving rise to the diverse Neotropical teiid radiation), this increases support for a crown-group radiation in northeastern Asia over the results from the GAU tree.

For Paramacellodidae, the CON and GAU trees (the phylogenies with two or more representatives) place paramacellodids as stem scincoids. With eight representatives, the CON tree strongly supports their origins in Europe, whereas the crown scincoids ancestral estimate is a two-area range of Europe and northeastern Asia. This provides evidence for a range contraction from the ancestral scincoids lineage in paramacellodids. For the GAU tree with only two representatives, the ancestral range for Paramacellodidae is a two-area range of northeastern Asia and Europe, compared to a strongly northeastern Asian origin for Scincoidea. In both instances, paramacellodids reflects a European signal present in the scincoids stem, a signal that ends in the Cretaceous when paramacellodids go extinct. The sole paramacellodid sampled in the SIM tree (from Europe) occurs on the Unidentata polytomy, and therefore shares the strongly supported European origin of most backbone nodes in that tree.

In summary, the Eurasian plate appears to act as the primary source of squamate origination and diversification during the Mesozoic, as in our previous analysis (Wilenzik *et al.* 2024), but with greater support for regionalization in Europe specifically, along with northeastern Asia. In all three trees, the early Late Cretaceous shows the first dispersal into Gondwana, as alethinophidian snakes are often reconstructed with a South American origin. This corresponds with other early Gondwanan squamates such as the paramacellodid †*Neokotus* of Early Cretaceous Brazil (Bittencourt *et al.* 2020), suggesting multiple, independent invasions of Squamata into Gondwana. The next dispersal into Gondwana is pleurodont iguanians in the Late Cretaceous, corroborated by the Brazilian iguanid †*Pristiguana* Estes & Price, 1973. Note that rhynchocephalians had apparently already arrived in South America by the Norian of the Late Triassic (Chambi-Trowell *et al.* 2021).

Both rhynchocephalians and squamates also apparently arrived in North America by the Late Jurassic (Evans & Chure 1998b; DeMar *et al.* 2022), likely from ancestral populations in Eurasia as supported here and previously (Wilenzik *et al.* 2024). These patterns of diversification in Squamata – Eurasian origin in the Triassic, spread to North America in the Jurassic, and final invasion of Gondwana in the Cretaceous – are similar to phylogenetically and temporally repeated patterns in Rhynchocephalia already seen in the fossil record as mentioned previously (Evans & Chure 1998b; DeMar *et al.* 2022). Further research may seek to elucidate the underlying processes with a more complete phylogeny of Lepidosauria, potentially cementing some of the alternative hypotheses considered here regarding the placement of extinct lineages and their impact on biogeographic estimates using methods such as ours.

UNCLEAR ESTIMATES FOR SNAKES

The phylogenetic relationships hypothesized by the three trees show substantial variation that has been addressed at length by previous authors (e.g. Reeder *et al.* 2015; Pyron 2017; Simões *et al.* 2018; Simões & Pyron 2021). We reiterated these previously established differences above to reinforce the variation they apparently induce in our models. Some of them preclude in-depth evaluation of biogeographic patterns for major groups of great interest, such as snakes. For Serpentes, the SIM tree lacks Scolecophidia (the “blind” snakes), a major clade of snakes (see Miralles *et al.* 2018). These are the earliest diverging extant snakes, as shown in both the CON and GAU trees. Given their broad global distribution, this limits inference of the early biogeographic history of snakes.

The relationships between the fossil snakes sampled in each dataset change dramatically, as well and may also be impacted by the absence of scolecophidians. In the CON tree, all fossil snake taxa are estimated within crown Serpentes. The GAU tree hypothesizes that †*Dinilysia* and †*Najash*, the two South American species (Woodward 1901; Apesteguía & Zaher 2006), form a monophyletic group sister to Serpentes, and that the three other fossil taxa (†*Haasiophis,* †*Eupodophis,* and †*Pachyrhachis*) form a monophyletic group sister to Alethinophidia. This is reflected in the majority South America ancestral range. The SIM tree has only three fossil lineages, and all are placed on the stem of Alethinophidia, but this cannot be interpreted properly in the absence of scolecophidians.

Consequently, our ancestral-range estimates for Serpentes do not offer much resolution over previous hypotheses, which have similarly broad ancestral ranges of Eurasia, Sunda, Africa, and South America (Wilenzik *et al.* 2024). The addition of more early snake taxa could help elucidate patterns that cannot be reconstructed based on the sampling found in the three phylogenies presented here. For instance, the hypothesized stem-snakes †*Coniophis* Marsh, 1892 (Longrich *et al.* 2012a) and †*Diablophis* Caldwell, Nydam, Palci & Apesteguía, 2015 from North America, †*Xiaophis* Xing, Caldwell, Chen, Nydam, Palci, Simões, McKellar, Lee, Liu, Shi, Wang & Bai, 2018 from Southeast Asia, could impact the ancestral ranges with a geographic occurrence outside of all three of the ancestral ranges estimated under the three hypotheses. In addition, Madtsoiidae, a family of snakes mostly found in Gondwana (Hoffstetter 1961), would impact biogeographic reconstructions, but said impact would be unclear with their variable placement within Serpentes (Longrich *et al.* 2012a; Zaher *et al.* 2023). Similarly, the phylogenetic positioning of the four-limbed †*Tetrapodophis* Martill, Tischlinger & Longrich, 2015 from Brazil could have major implications for early snake evolution. However, recent phylogenetic work reconstructs †*Tetrapodophis* not as a stem-snake, but rather an early-diverging mosasaurian (Caldwell *et al.* 2021). Integrating these specimens into larger scale lepidosaurian phylogenetic analysis might improve estimation of both phylogeny and ancestral range.

INCONGRUENCE, LIMITATIONS, AND FUTURE DIRECTIONS

One pattern of incongruence is a disagreement between ancestral range estimations supporting Europe specifically or Eurasia more broadly. For instance, stem Gekkota is reconstructed as originating in northeastern Asia in the CON tree, Europe in the SIM tree, and a two-area range including both Europe and northeastern Asia in the GAU tree. Similar patterns are seen in other major extant clades. For Laterata and Toxicofera, the CON and GAU trees estimate their origins in northeastern Asia while the SIM tree estimates a European origin. For Scincoidea, the CON tree estimates a European origin, the GAU tree a northeastern Asian origin, and the SIM tree is uncertain. We interpret this as stronger support for a solely European origin in the SIM tree, but a broader Eurasian origin in the CON and GAU trees, congruent with our earlier extant-only estimates of Laurasia (Wilenzik *et al.* 2024). Such variability in precision appears to be impacted heavily by the sampling and placement of fossil taxa.

Another example is the ancestral range of Toxicofera. For the CON and GAU trees, the ancestral range is strongly supported in northeastern Asia, while for the SIM tree it is in Europe. These results appear to be influenced by the placement of Mosasauria (Russell 1967; Conrad 2008; Gauthier *et al.* 2012; Reeder *et al.* 2015; Simões *et al.* 2018) and the estimated relationships of Serpentes, Iguania, and Anguimorpha (Burbrink *et al.* 2020; Singhal *et al.* 2021). Within Toxicofera, Anguimorpha also yields two distinct hypotheses. The first, supported by the CON and GAU trees, has the clade originating in northeastern Asia. The second – supported by the SIM tree – is uncertain, likely due to poor taxon sampling. The addition of fossil anguimorphs like †*Gobiderma* Borsuk-Białynicka, 1984*,* †*Estesia* Norell, McKenna & Novacek , 1992*,* and †*Aiolosaurus* Gao & Norell, 2000 and a greater sampling of extant species might increase precision. By contrast in Iguania, our results consistently support a northeastern Asian origin across all three analyses. As noted, Serpentes shows little agreement between the three datasets.

Another limitation of the model is that it does not appear robust to composites or terminal taxa that are widely distributed. In the CON tree, for instance, one of the terminals is "Macrostomata," a polyphyletic group of snakes found globally that includes a large portion of extant snake diversity (Scanferla 2016). This clade likely does not exist (see Burbrink *et al.* 2020), rendering this terminal taxon problematic for biogeographic analysis. The two reconstructed nodes preceding this terminal lineage have similarly broad ancestral range estimates, rendering them uninformative. Future studies using models such as ours will likely benefit from phylogenies that include dense sampling within key clades.

Few extant squamate clades were missing from these analyses, except for "scolecophidian" snakes in the SIM tree, while members of Dibamia were heavily under-represented in all matrices. In contrast, fossil representation varied substantially, and the CON and GAU trees are also missing the stem squamate †*Megachirella*, as it was described after those two studies were published. This appears to have a substantial impact for the estimation of a European ancestral range for Squamata. Extensive sampling of extinct taxa through time will obviously be the most important determinant of precision and accuracy in analyses such as this, reinforcing the dramatic need to expand morphological character matrices to include as many extinct lineages as possible (Mongiardino Koch *et al.* 2021; Wisniewski *et al.* 2022).

Recent fossil discoveries, such as the hypothesized stem-squamates †*Moqisaurus* Dong Wang & Evans, 2023 from the Early Cretaceous of Inner Mongolia and †*Bellairsia* Evans, 1998 from the Middle Jurassic of Scotland, may provide new hypotheses of squamate relationships and therefore new conclusions regarding biogeographic patterns. For instance, †*Moqisaurus* may support the CON and GAU result of a broader Eurasian origin, expanding an overly specific European origin from the SIM tree that is influenced heavily by †*Megachirella*, whereas †*Bellairsia* may support the narrow, European reconstruction in the SIM tree. As always, new fossil discoveries from previously unreported areas are expected to have a strong and potentially transformative effect on models such as ours, a key example being the potential for undiscovered Gondwanan invasions in the early Mesozoic.

In future, our model could be utilized for specific hypothesis to connect biogeographic changes to geological or climatological events occurring in specific areas (i.e., to analyze potential connection between Australian aridification in the Miocene (McCurry *et al.* 2022) and any potential source or sink of squamate diversity in Australia). The ability to link biogeographic events to a specific time and place opens the possibility for better hypothesis testing in biogeography. We also note that spatial patterns in fossil occurrence and abundance are potentially artifactual and exacerbated by colonialism and economic constraints placed on the Global South (Raja *et al.* 2022). Further prospecting and equity programs could greatly increase our knowledge of Mesozoic and Cenozoic squamates in the Global South.

CONCLUSION

Here, we employed a modified version of the paleogeographic model from Landis (2017) – a powerful tool to reconstruct the ancestral range of species with long evolutionary histories and broad geographic ranges – to estimate the Mesozoic history of squamate biogeography. By accounting for continental drift in the form of communicating classes, this approach can more accurately model the complexities of ancestral range estimation in ancient, widely distributed groups. Our results highlight Europe and northeast Asia as origins of squamate diversity in the Mesozoic over several recent phylogenetic hypotheses, with the strongest support for a European origin and Jurassic persistence in early Squamata from the most recent and most comprehensively sampled tree. Subsequently, many diverse extant radiations in Gekkota, Scincoidea, Laterata, Iguania, Anguimorpha, and Serpentes appear to derive from Late Jurassic or Early Cretaceous shifts into Asia, with subsequent dispersal into other areas such as North and South America. This is consistent with previous estimates of a Eurasian origin within Laurasia during the late Mesozoic. The signals from European groups such as Mosasauria and Paramacellodidae, and Asian groups such as Polyglyphanodontia were erased by the K-Pg extinction, obscuring the pattern of Eurasian origin in phylogenies of extant lineages. Major uncertainty remains regarding the biogeographic origin of snakes, and future studies should test hypotheses about how the phylogenetic relationships of fossil snakes affect ancestral range estimates for Serpentes. More complete sampling of fossil lineages will be needed to elucidate complex Cenozoic patterns of dispersal between continents. Estimates for lengthy naked stem branches such as Dibamia will likely be improved by any future fossil finds, and the inclusion of newly discovered Mesozoic taxa is also an immediate priority. Ultimately, more attention to paleogeographic processes and the temporal distribution of fossil lineages may reveal crucial insights into the spatial origin of numerous groups.

Acknowledgements

This research was supported in part by GWU Harlan fund to IVW and U.S. NSF grants DEB-0905765 and DEB-1441719 to RAP. We thank M. Landis for help with RevBayes and associated models, J. Clark for help interpreting Mesozoic fossil squamates and comments on an earlier draft along with S. Kawano, and M. Laurin, G. Georgalis, and three anonymous reviewers for their comments during the editorial process.

Supplementary material

Data available from the repository: https://doi.org/10.5281/zenodo.13929768.

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Submitted on 22 August 2024;
accepted on 20 November 2024;
published on 26 March 2025.