



RESEARCH ARTICLE

The Contemporary Distribution of Scincine Lizards Does Not Reflect Their Biogeographic Origin

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ABSTRACT

Aim: We assess the systematic relationships and historical biogeographic patterns in the subfamily Scincinae, a group of lizards that primarily inhabits the Afro-Madagascan and Saharo-Arabian regions with isolated lineages in Europe, North America, East Asia, India and Sri Lanka. The contemporary distribution of these lineages on the historical Laurasian and Gondwanan landmasses make scincines an ideal system to study the roles of vicariance and dispersal on a geologic scale of tens of millions of years.

Location: Global.

Taxon: Subfamily Scincinae (Family Scincidae).

Methods: We conducted biogeographic analyses on a reconstructed, time-calibrated species tree of scincine genera, including members of the other Scincidae subfamilies, using seven nuclear loci (~6k base pairs). We also constructed a lineage-through-time plot to assess the timing of diversification within scincines.

Results: Our analysis estimated strong support for the monophyly of Scincinae that is further comprised a strongly-supported Gondwanan clade nested within a broader Laurasian group. While most of the extant, genus-level diversity within the Gondwanan clade was accrued post-Eocene, the majority of the Laurasian lineages diverged during the Palaeocene or earlier, suggesting large-scale extinctions on continents of Laurasian origin. Counterintuitively, scincines from India and Sri Lanka have distinct biogeographical origins despite a long tectonic association between these landmasses, suggesting at least two independent, long-distance, trans-oceanic dispersal events into the subcontinent. Our biogeographic analyses suggest that scincines likely originated in East and Southeast Asia during the late Cretaceous (ca. 70 Ma), and eventually dispersed westwards to Africa and Madagascar, where their greatest current-day species richness occurs.

Main Conclusions: Our study demonstrates the concomitant roles of dispersal and extinction in shaping modern-day assemblages of ancient clades such as scincine lizards. Our range evolution analysis shows that despite the greater diversity observed in the Afro-Madagascan region, the origin of scincines can be traced back to Southeast Asia and East Asia, followed by westward dispersals. These dispersals may have been followed by significant extinctions in tropical East Asia, resulting in relatively lower diversity of scincines in these regions. Notably, our analysis reveals that Sri Lankan and Peninsular Indian scincines have distinct evolutionary origins.

1 | Introduction

Dispersalist explanations have existed since the time of Darwin (1859, 1878, 1882) to explain contemporary biotic assembly. However, with the advent and subsequent integration of cladistics and plate tectonics, vicariance biogeography gained prominence (Wiley 1988). Subsequently, dispersal was long considered merely an alternate narrative only when vicariance could be falsified (Nelson 1978; Morrone and Crisci 1995; Humphries and Parenti 1999). Biogeographers took the stance that only mechanisms of vicariance offer testable hypotheses and dispersals were largely stochastic, directionless events (see Cowie and Holland 2006). While the importance of dispersal in shaping the biota of oceanic islands was widely acknowledged (MacArthur and Wilson 1963, 2001), its role in the context of continents or continental islands had largely been reduced to ancillary and ad hoc postulation in the absence of vicariant explanations under a cladistic framework (see De Queiroz 2005 and the references therein). The re-emergence of dispersal as possibility after Darwinian times has chiefly been aided by modern methods of estimating lineage divergence times based on genetic data (Murphy and Collier 1997). Dispersal could explain taxa having more recent origins than previously supposed under models of vicariance. Recent methods of biogeographic inference recognise the significance of both dispersal and vicariance, especially in continental landmasses, and treat them as complementary, rather than competing processes that influence spatial and temporal patterns of biodiversity (Vences et al. 2004; Yu, Harris, and He 2010; Matzke 2013).

Ancient, widespread lineages such as skinks (Squamata: Scincidae) offer model groups to examine global, historical biogeographic patterns of dispersal and vicariance. Skinks are one of the oldest and most diverse lizard lineages (Brandley, Schmitz, and Reeder 2005; Brandley et al. 2011). With ~1750 species worldwide, skinks account for approximately 23% of the lizard diversity globally, and together with geckos are one of the most diverse squamate families (Uetz et al. 2023).

The classification of skinks by Greer (1970) into four different subfamilies—Acontiinae, Feyliniinae, Lygosominae and Scincinae—was based on their osteo-anatomical structure. However, most molecular phylogenetic studies have revealed Feyliniinae to be nested within Scincinae, and the former is, therefore, not considered as a valid subfamily (Whiting, Bauer, and Sites 2003; Brandley, Schmitz, and Reeder 2005). Greer (1970) considered scincines to be ‘primitive’ among all the other subfamilies within skinks which would render them paraphyletic. There have been other attempts to reclassify the subfamily Scincinae (e.g., Griffith, Ngo, and Murphy 2000; Hoser 2015); however, most recent

publications do not follow these classification schemes for a variety of reasons (see Shea 2021). For this study, we follow the skink classification scheme by Shea (2021).

Scincine lizards are known to have a disjunct, global distribution (Figure 1). The Indian subcontinent harbours six scincine genera. Two of the more cosmopolitan lineages from Northwest India (*Eurylepis* and *Ophiomorus*) have been included in a few global phylogenies (Brandley et al. 2011; Pyron, Burbrink, and Wiens 2013; Linkem, Minin, and Leaché 2016; Zheng and Wiens 2016), but the endemic peninsular Indian (*Sepsophis* and *Barkudia*) and Sri Lankan (*Nessia* and *Chalcidoseps*) lineages remain unrepresented in molecular phylogenies. While older studies rendered scincines paraphyletic with respect to lygosomines (Brandley et al. 2012; Wiens et al. 2012), more recent assessments recovered a monophyletic Scincinae, albeit with limited sampling that did not include the elusive lineages from peninsular India and Sri Lanka (Pyron, Burbrink, and Wiens 2013; Lambert, Reeder, and Wiens 2015; Linkem, Minin, and Leaché 2016). However, all studies found acontiines to be monophyletic and sister to all the other subfamilies (Whiting, Bauer, and Sites 2003; Pyron, Burbrink, and Wiens 2013; Zheng and Wiens 2016). As a result, an assessment of broad systematic relationships among scincids has been a challenge, largely because of a lack of sampling of lineages across different biogeographic regions. It is likely for this reason that the phylogeny of Scincidae is still poorly resolved, thereby limiting comparative biological analyses of this morphologically and phylogenetically diverse group.

To assess the competing hypotheses of dispersal and vicariance in the global biogeography of scincine lizards, we reconstruct a time-calibrated phylogeny of scincine genera, including lineages from India and Sri Lanka for the first time, to elucidate evolutionary relationships within this subfamily. We further conduct historical biogeographic analyses to elicit clues from the past that may explain the modern-day distributions of scincines.

2 | Materials and Methods

2.1 | Compilation of Data

We assembled a dataset consisting of 32 genera of scincids which included 27 scincines, four lygosomines (*Mochlus*, *Trachylepis*, *Emoia* and *Scincella*) and one genus as a representative of the subfamily Acontiinae (*Typhlosaurus*). We generated DNA sequences for 15 genera within Scincinae which included one or two species each of *Madascincus*, *Proscelotes*, *Scelotes*, *Scolecoseps*, *Gongylomorphus*, *Barkudia*, *Sepsophis*,

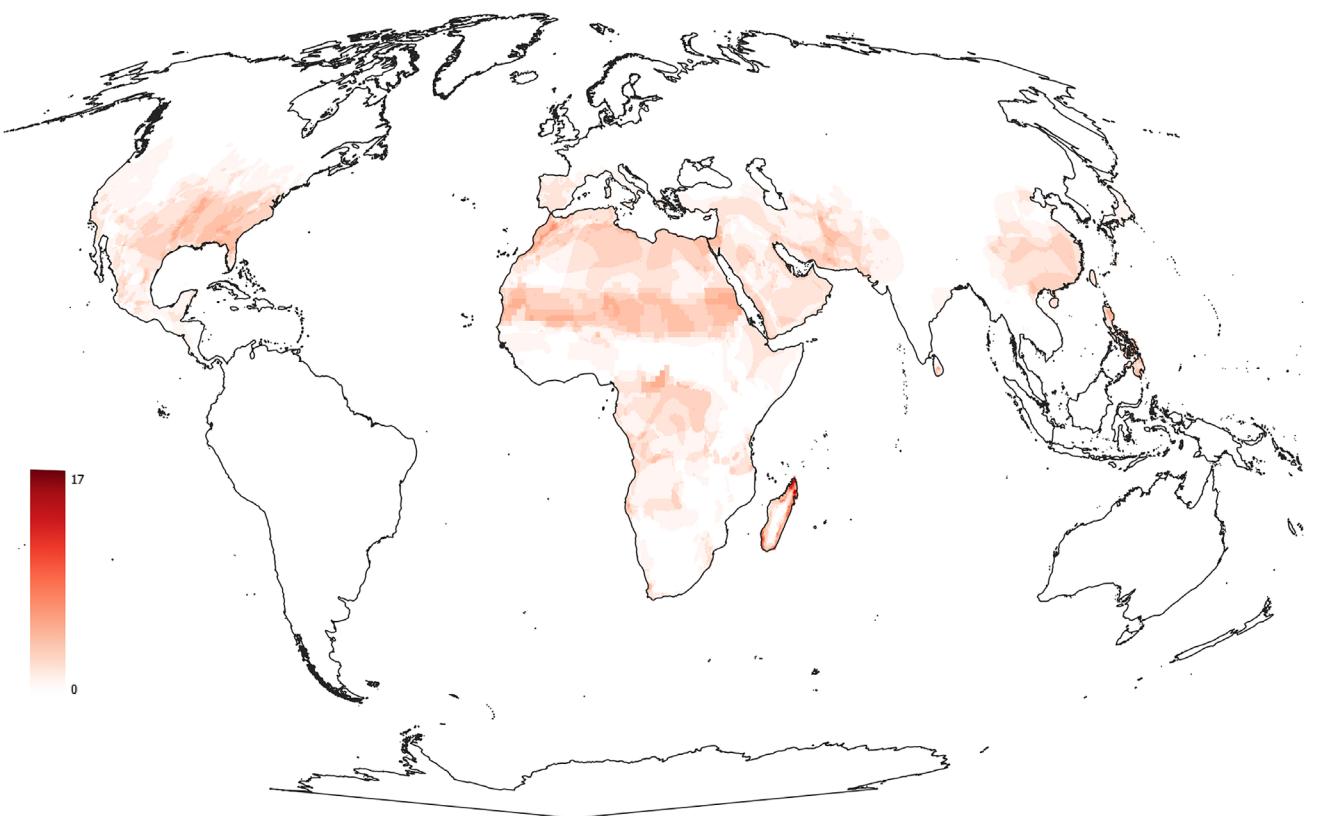


FIGURE 1 | Species richness heat map for scincines built using GARD 1.7 polygons data (Roll et al. 2017; Roll and Meiri 2022; Caetano et al. 2022). Warm colours denote high species richness. Most of the diversity persists along the northern tropics as well as the Afro-Madagascan region.

Sepsina, *Feylinia*, *Typhlacontias*, *Hakaria*, *Janetaescincus*, *Pamelaescincus*, *Nessia* and *Chalcidoseps*. Tissue samples for five of the scincine genera (*Hakaria*, *Madascincus*, *Feylinia*, *Proscelotes* and *Typhlacontias*) were acquired from the collections in the Museum of Vertebrate Zoology, Berkeley (MVZ), California Academy of Sciences, California (CAS) and South African National Wildlife Biobank. For the remaining nine genera, we used tissue samples from specimens that were freshly collected by the authors of this manuscript. The remaining scincine, lygosomine, acontiine and sequences for outgroup were available from GenBank (largely from Brandley et al. 2011). We could not include the Madagascan scincine genera *Brachyseps*, *Flexiseps*, *Pseudoacontias*, *Pygomeles* and *Voeltzkowia* from GenBank due to a lack of a sufficient number of loci that matched with our study (Belluardo et al. 2023). Omitting these genera will not heavily influence our interpretation of scincine global biogeography because all Madagascan endemic scincine genera form a well-supported monophyletic group (Belluardo et al. 2023; Miralles et al. 2015) and we have included other representative genera from that clade (*Grandidierina*, *Madascincus* and *Paracontias*) in our study. For most of the sampled genera, we did not include multiple species per genus as the scope of our study addresses only relationships among genera rather than within genus patterns of speciation. This is the most comprehensive taxonomic sampling of scincine genera to date. Representatives of other Families within Scincoidea (*Xantusia*, *Gerrhosaurus*), Iguanidae (*Basiliscus*), Lacertoidea (*Bipes*), Anniellidae (*Anniella*), Teiidae (*Aspidoscelis*) and Sphaerodactylidae (*Teratoscincus*) were included as outgroup

taxa (see Supporting Information 1 for a list of taxa included and accession numbers).

2.2 | DNA Extraction

We extracted total genomic DNA from tissue samples using a QIAGEN DNeasy blood and tissue extraction kit (Hilden, Germany) using protocols provided by the manufacturers. Upon DNA extraction we quantified the amount of DNA to determine whether the sample was required to be diluted for optimal PCR reactions. The original/diluted total genomic DNA was then used as a template for further PCR reactions. We sequenced six nuclear regions for a total of 6000 basepairs (bp) using primers from Brandley et al. (2011). The six nuclear loci were megakaryoblastic leukaemia 1 (*MKL1*, 909 bp), prolactin receptor (*PRLR*, 570 bp), prostaglandin E receptor 4 (*PTGER4*, 468 bp), RNA fingerprint protein 35 (*R35*, 682 bp), recombination activating gene 1 (*RAG-1*, 2728 bp) and synuclein alpha interacting protein (*SNCAIP*, 483 bp). The PCR products were purified using a QIAquick PCR purification kit (Qiagen, Germany) and the purified products were sequenced commercially at Medauxin Pvt. Ltd., Bangalore, India. The sequences obtained were carefully observed for any errors related to sequencing. The individual genes were aligned with sequences of other skinks (see Supporting Information 1.0) using the program MUSCLE (Edgar 2004) as incorporated in MEGA v7.0 (Tamura et al. 2011) using default parameters. We checked the translated amino acid alignments for stop

codons to confirm that we had not inadvertently sequenced any pseudogenes, and/or to ensure that there are no errors in alignments causing read-frame shifts.

2.3 | Molecular Analysis

2.3.1 | Gene Trees

We first built gene trees to estimate if individual gene alignments in our dataset could be concatenated. For each gene, the best-fit partitioning scheme and their respective DNA substitution models were obtained using the program PARTITIONFINDER v1.1.0 (Lanfear et al. 2012). For this step, we had three partitions for each individual gene (corresponding to their codon position) and let PARTITIONFINDER estimate if any of these partitions can be merged so the number of partitions is reduced. We generated maximum likelihood trees using the program RAxML GUI v1.3 (Silvestro and Michalak 2012) based on the partitions as suggested by PARTITIONFINDER. Since it is not possible to assign specific DNA substitution models in RAxML, we assigned a GTR + Γ model for all the specified partitions in the maximum likelihood analyses. The maximum likelihood tree was estimated using 20 independent ML searches, which use 20 independently generated starting trees. Branch support was estimated using 1000 bootstrap pseudoreplicates.

The Bayesian analysis was performed using MrBayes v3.1 (Ronquist and Huelsenbeck 2003). For this analysis, we specified the partitions and their respective DNA substitution models as suggested by PARTITIONFINDER v1.1.1. The individual partitions were unlinked in order to allow the model parameters for each of the partitions to be estimated independently. The program was run for four million generations utilising two runs with four chains each (1 cold, 3 hot). We sampled every 100 generations and assessed convergence using TRACER v1.6 (Rambaut et al. 2018) by confirming that all the parameters had reached an effective sample size of >200 . The first 25% of the trees were discarded as burn-in and a majority rule consensus tree was built using the remaining trees.

2.3.2 | Species Trees and Divergence Dating

As a result of the topological discordance in the individual gene trees (see Supporting Information 2), we employed a coalescent approach to assess higher level skink relationships. Besides the pronounced discordance, a multispecies coalescent approach is also recommended for deciphering higher level skink relationships according to Linkem, Minin, and Leaché (2016). To do this, we used *BEAST v2.6.6 (Drummond, Xie, and Heled 2012) for the coalescent species tree estimation as well as for divergence dating. In preparation for the species tree analysis, a single exemplar of each genus was included as previous studies have demonstrated that these genera are monophyletic (see Brandley, Schmitz, and Reeder 2005; Brandley et al. 2012; Erens et al. 2017; Miralles et al. 2015). We used an estimated relaxed lognormal clock, a population function which was linear with a constant root, in order to set the assumption that the populations for ancestral

and extant species are bound to change and are not constant. Additionally, a birth–death model was utilised for a species tree prior since it is very likely that the number of extinctions within scincines is nonnegligible.

The species tree was calibrated using two fossils. The crown age of Episquamata, represented in our alignment by *Anniella*, *Aspidoscelis*, *Bipes* and *Basiliscus*, was calibrated using the earliest stem anguimorphs, represented by *Beckelsius*, *Paramacellodus* and *Pseudosaurillus* (Conrad 2008), using similar parameters as Brandley et al. (2011), wherein the lognormal distribution of the sampled age ranged between 180 and 140 (180 mya, mean = 0, SD = 1.769). Recently, Tałanda (2018) described a near complete fossil of the oldest known member of Scincoidea *Ardeosaurus brevipes*. This fossil was unearthed from the Ettling quarry in the Solnhofen Formation, which dates between Kimmeridgian and Tithonian (Ebert, Kölbl-Ebert, and Lane 2015; Röper 2005; Schweigert 2007; Tałanda 2018) corresponding to the period 157–152 mya. We chose a lognormal distribution so that the latest possible sampled age is at a conservative 152 mya and ranges to a 97.5% quantile of 157 mya (152 mya, mean = 0, SD = 0.77). To estimate if the two calibrations were in conflict with each other, we ran the analysis twice, wherein for each run we dropped one of the calibrations. The resulting dated species trees were largely congruent allowing usage of the two calibrations together.

We conducted four initial runs for 500 million generations each to tune the operators with values as suggested by *BEAST v2.6.6 (Bouckaert et al. 2019). The final run was conducted for 1500 million generations, sampling tree space every 5000 generations. We analysed the results of the run using the program TRACER v1.6 wherein we confirmed that the effective sample sizes for all the recorded parameters were >200 . To obtain the species tree from the posterior probability distribution, we used the program TREEANNOTATOR XSEDE on the CIPRES platform (Miller, Pfeiffer, and Schwartz 2010). We discarded the first 25% of the trees as burn-in, set a posterior probability limit of zero and opted for a maximum clade credibility tree.

2.3.3 | Ancestral Range Evolution

We performed the ancestral range evolution analysis using the R package BioGeoBEARS (Matzke 2013). We demarcated a total of 10 areas/ranges for the analysis: Southeast Asia, India+Sri Lanka, East Asia, Afro-Arabia, sub-Saharan Africa, Mauritius, Socotra, Madagascar, Seychelles and Central America. We used these ranges based on the biogeographic realms provided by Holt et al. (2013) and the distribution records of scincines. The distributions for the terminal nodes were assigned based on the distribution records provided in the Reptile Database (Uetz et al. 2023), GARD 1.7 data (Roll et al. 2017; Roll and Meiri 2022; Caetano et al. 2022) and Repfocus (www.repfocus.dk). For taxa with very wide distributions, we assigned the area(s) based on their centre of origin (Matzke 2013, 2014). For instance, there are distribution records of *Chalcides* from Sri Lanka (Karunarathna et al. 2008). However, Carranza et al. (2008) suggest that the centre of origin for *Chalcides* is Morocco. Therefore, we assigned Afro-Arabia as the range for *Chalcides*. Similarly, *Plestiodon* is distributed in East Asia and North and Central America. However, Brandley et al. (2011) recover an East Asian centre of

origin for *Plestiodon* and, therefore, we assigned East Asia as the range for the genus. For the other remaining genera, we have used their current distribution as a whole.

We performed a time-stratified analysis wherein the oldest date corresponded to the root of the tree leading to scincines (~77 million years ago). We included four time periods: (a) 77–55 mya. The older time period corresponds to the root of scincines. The younger time period corresponds to the initial collision of the Indian plate with an intraoceanic island arc system close to Asia; (b) 55–35 mya, this represents the time when the Indian plate collided with the Asian plate (Aitchison, Ali, and Davis 2007) at ca. 35 mya; (c) 35–17 mya, the younger date represents the earliest possible timeframe of sub-aerial exposure of Socotra as a continental island (Ali 2018); (d) 17–8 mya, the younger date corresponds to the subaerial emergence of the volcanic island of Mauritius (Saddul 2002); (e) 8 Mya–present.

The adjacency and dispersal rates used depended on the relative distances between the regions during each specific time period mentioned above. These relative distances were extracted from the Palaeomaps dataset which is provided with the GPlates plate tectonics visualisation software. We used GPlates to conduct measurements at each of the previously mentioned time periods (77–55, 55–43, 43–8, 8–0 Mya) following Müller et al. (2018). It is worth noting that the most extensive transoceanic dispersal postulated for any skink species was performed by the genera *Leiolopisma* and *Cryptoblepharus* between Australasia and South-West Indian Ocean regions, separated by a distance of ~6000 km (Austin and Arnold 2006; Horner 2007; Chapple et al. 2023). Consequently, we assigned a low dispersal rate of 0.01 to regions separated by distances greater than 6000 km (see Supporting Information 3). Furthermore, we adopted a ‘negative linear distribution of categorical probability values,’ a methodological framework established by Biswas, Chaitanya, and Karanth (2023). This entailed assigning dispersal rates of 0.15, 0.30, 0.45, 0.60, 0.75, 0.90 and 0.95 to distance ranges falling within 6000–5000 km, 5000–4000 km, 4000–3000 km, 3000–2000 km, 2000–1000 km, 1000–500 km and distances less than 500 km respectively. We considered the possibility that the dispersal between Central America and East Asia might have occurred along North America (via Beringia; Brandley et al. 2011). However, none of the taxa in our dataset was assigned a distribution range in North America as described earlier (see the case of *Plestiodon* above).

Due to the large number of areas and the complex adjacency matrix, we were only able to run models with *j* parameters (Table 1) as they allowed for long-distance jump dispersal. Among the models we employed, DIVALIKE+j had the highest global likelihood and also showed the most probable results.

2.3.4 | Lineage Accumulation

A lineage-through-time (LTT) plot was constructed to visualise trends of lineage accumulation through time in scincines, using the package ‘Ape’ (Paradis, Claude, and Strimmer 2004) implemented in R (R Core Team 2013). We also wanted to investigate if there was higher lineage accumulation after scincines dispersed into Gondwanan landmasses. Hence, we also carried out an independent LTT plot based on the clade distributed in the landmasses

TABLE 1 | The log likelihood and AIC value comparison between different biogeographic models implemented in BioGeoBears analyses.

Models	Log Likelihood	AIC	ΔAIC
Comparison of log likelihood and AIC values of DEC+j, DIVALIKE+j and BAYAREALIKE+j models			
DIVALIKE+j	−59.41	124.82	
DEC+j	−60.02	126.03	1.21
BAYAREALIKE+j	−60.51	127.02	2.20
Models	AICwt	AICwt ratio	
Comparison of AICwt of DIVALIKE+j and DEC+j models			
DIVALIKE+j	0.65	1.83	
DEC+j	0.35	0.54	
Comparison of AICwt of DIVALIKE+j and BAYAREALIKE+j models			
DIVALIKE+j	0.75	3.0	
BAYAREALIKE+j	0.25	0.33	
Comparison of AICwt of DEC+j and BAYAREALIKE+j models			
DEC+j	0.62	1.64	
BAYAREALIKE+j	0.38	0.61	

such as India, the sub-Saharan Africa, Seychelles and Madagascar (i.e., former Gondwanan fragments). For this purpose, we pruned the tree to retain all the taxa leading to the Gondwanan clade using the package ‘Ape’ and constructed the LTT plot.

3 | Results

The gene trees for each locus that we generated in this study showed varying topologies wherein for majority of the gene trees, scincines were not monophyletic. Due to this disparity among gene trees, our preferred hypothesis of subfamilial relationships is based on the species tree reconstructed using the multispecies coalescent.

3.1 | Results From the Species Tree Analysis

Our species tree analysis shows that the family Scincidae is a monophyletic group that originated around 98 mya (CI = 84–113 mya) (Figure 2). Within Scincidae, the subfamilies Lygosominae and Scincinae represent well-supported monophyletic groups (Figure 2). Our results show that scincines were not the common ancestor for lygosomines or acontiines (Greer 1970). Rather, our phylogenetic analysis supports acontiines (represented by the genus *Typhlosaurus* in our study) as sister to the clade comprising scincines and lygosomines. A significant majority of scincines (19 out of 27 genera) form a well-supported subclade (‘Gondwanan clade’) while the rest of the scincines belong to the paraphyletic ‘Laurasian group’ (Figure 2). The Gondwanan

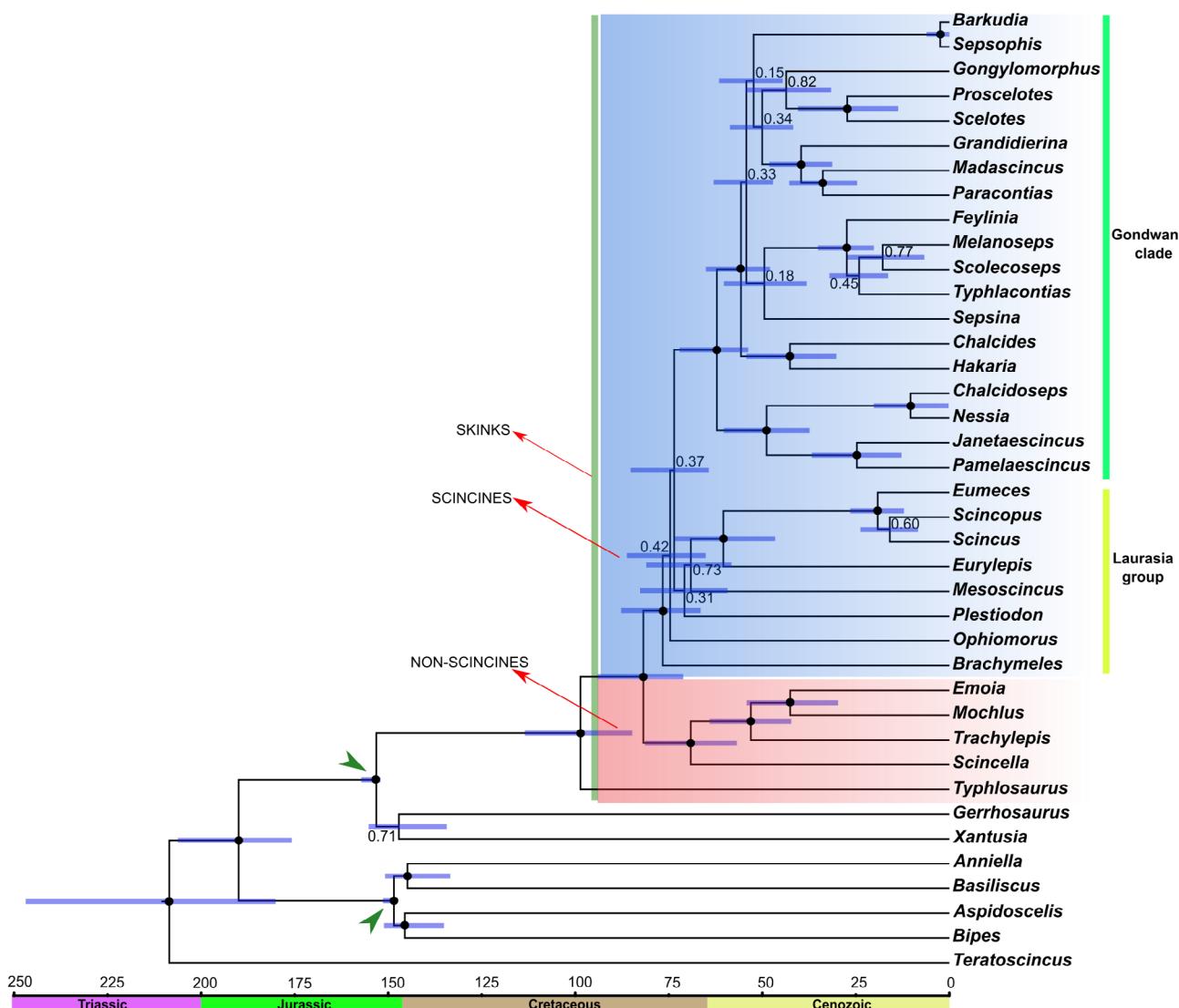


FIGURE 2 | Coalescent tree with divergence dating based on six nuclear genes and the two nodes calibrated using two fossils indicated by green arrows. The x-axis represents time in millions of years. Black dots on the nodes indicate supported nodes with posterior probability values ≥ 0.90 . Nodes with lower support show the actual posterior probability values.

clade is named as such because a large proportion of the genera within this clade have distributions in landmasses that were part of the Gondwanan supercontinent. Conversely, many of the members within the Laurasian group have contemporary distributions within landmasses with Laurasian origin.

Our phylogenetic analysis supports the genus *Brachymeles* as sister to all other scincine lineages (Figure 2). The genus *Ophiomorus*, which comprises a number of species representing a gradation in limblessness, is sister to the Gondwanan clade and a clade consisting of *Plestiodon*, *Mesoscincus*, *Eurylepis*, *Scincus*, *Scincopus* and *Eumece*, albeit with low branch support. The *Eumece* group (*Eumece*, *Scincus*, *Scincopus* and *Eurylepis*) forms a well-supported clade which is sister to *Mesoscincus*.

In the Gondwanan clade, most cladogenetic events occurred during the Eocene, and this rapid radiation may explain why support for most of the relationships within the Gondwanan clade are low (Whitfield and Lockhart 2007). The Gondwanan clade

comprises two subclades. One of the subclades comprises the Sri Lankan genera (*Nessia* & *Chalcidoseps*) and the Seychelllean (*Janetaescincus* & *Pamelaescincus*) forming a well-supported sister relationship ($PP = 1.0$). The split between these two clades corresponds to an age of about 48 mya ($CI = 37$ –60 mya). The other subclade comprises genera that are largely distributed in Africa and Madagascar. The Socotran endemic *Hakaria* and the predominantly North African genus *Chalcides* form well-supported sister lineages ($PP = 0.98$) that separated ~ 43 mya ($CI = 54$ –30 mya). The Indian sister genera *Barkudia* and *Sepsophis* are nested within a clade consisting predominantly of African scincines. The Madagascan scincines *Grandidierina*, *Madascincus* and *Paracontias* were nested within this largely African group. The Mauritian scincine *Gongylomorphus* formed a relatively well-supported ($PP = 0.82$) sister relationship with the African scincines *Scelotes* and *Proscelotes* (~ 43 mya; $CI = 54$ –31 mya). The limbless African scincines *Feylinia*, *Melanoseps*, *Scoleoseps* and *Typhlacontias* formed a well-supported clade ($PP = 1.0$), thereby corroborating the inclusion of *Feylinia* within

Scincinae rather than its recognition as a separate subfamily. This clade of limbless scincines was sister to the African scincine *Sepsina* (albeit with very low support).

3.2 | Results From the Ancestral Range Evolution Analysis

Our divergence dating analysis of the species tree revealed that the root age of scincines is approximately 77 (CI = 87–66 mya)

million years (see Supplementary Material 4 for pie chart showing likelihood of each ancestral range). The ancestral range evolution analysis revealed that the ancestral distribution for scincines initially encompassed Southeast Asia and East Asia (yellow+red coloured blocks in Figure 3). Over time, it dispersed to Afro-Arabia followed by a back-dispersal to East Asia. Notably, there were two dispersal events from East Asia to Afro-Arabia and one to Central America. Among the dispersals to Afro-Arabia, the first one occurred ca. 70 mya, while the second dispersal event occurred between 73 and 62 mya. The first

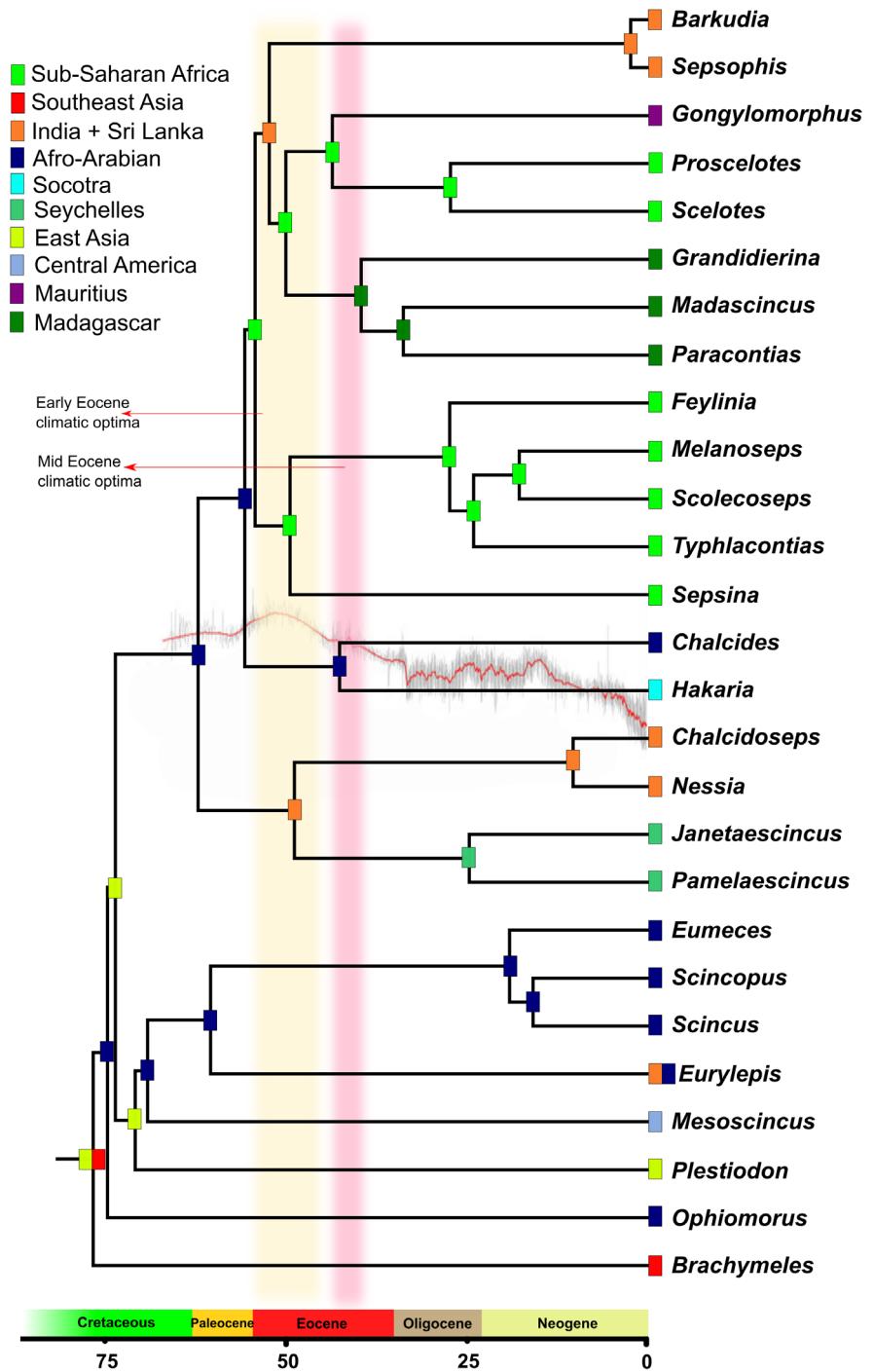


FIGURE 3 | Range evolution reconstruction for scincines, superimposed over the trend of Cenozoic global climate events (i.e., climate change over time; Figure modified from Westerhoff, Donders, and Luthi 2016) shown as a temperature profile (from Zachos et al. 2001) which uses the isotope $d^{18}O$ as a proxy for temperature. The scale on the x-axis represents time in million years.

was the dispersal of the ancestral lineage leading to *Eumeles*, *Scincopus*, *Scincus* and *Eurylepis* which is widespread across Afro-Arabia, one of which (*Eurylepis*) dispersed into India. The dispersal into Central America leading to *Mesoscincus* occurred between 81 and 58 mya. However, this relationship is retrieved with poor support in our species tree analysis. The second dispersal into Afro-Arabia constitutes the well-supported Gondwanan clade. Within this clade, the ancestral lineage that eventually gave rise to *Janetaescincus* and *Pamelaescincus* in the Seychelles dispersed from the region encompassing India and Sri Lanka 48–24 mya.

Around 55–30 mya, while one of the lineages continued in Afro-Arabia, the other lineage dispersed to sub-Saharan Africa. Interestingly, this period coincides with the early Eocene climatic optimum, which may have resulted in humid forest connections, making some of these areas contiguous (Li et al. 2022). From sub-Saharan Africa, there was one dispersal to India+ Sri Lanka (54–52 mya) which was followed by a back dispersal (52–50 mya). From sub-Saharan Africa, there were dispersals to Madagascar (58–41 mya) giving rise to the Madagascan radiation of scincines and Mauritius (54–31 mya). The ancestral lineage leading to *Hakaria* dispersed from Afro-Arabia to the island of Socotra between 54 and 30 mya. This timeframe closely coincides with the formation of the Socotra archipelago in the late Eocene (Culek 2013). However, as a disclaimer, we acknowledge that much of the relationships within the Gondwanan clade are poorly supported (see Figure 2) and our range evolution results are based on the relationships that we retrieved in this study.

3.3 | Results From the Lineages Through Time (LTT) Plot

The LTT plot of Scincinae exhibited a steady rate of lineage accumulation, except a brief period between ~55 and 45 mya. The Gondwanan clade closely mirrored the patterns observed in the whole group. This suggests that most of the cladogenetic events within Scincinae were largely driven by the lineage accumulation within the Gondwanan clade. Between ~55 and 45 mya, a slight increase in the lineage accumulation rate is observed which coincides with a period between the early Eocene and mid-Eocene climatic optima (Figure 4). Such jumps in rate are often indicative of rapid diversification (Helmstetter et al. 2022).

4 | Discussion

Phylogenetic relationships within skinks and the confusion over the monophyly of scincines have been explored using multilocus (e.g., Brandley, Schmitz, and Reeder 2005; Brandley et al., 2008; Pyron, Burbrink, and Wiens 2013; Zheng and Wiens 2016) and genomic datasets (Linkem, Minin, and Leaché 2016). However, our study includes the South Asian scincine genera (*Barkudia*, *Chalcidoseps*, *Nessia* and *Sepsophis*) and therefore better samples the breadth of ‘deep’ phylogenetic diversity in Scincinae. Brandley, Schmitz, and Reeder (2005) addressed the systematic positions of major scincid lineages; however, their dataset comprised only mitochondrial genes

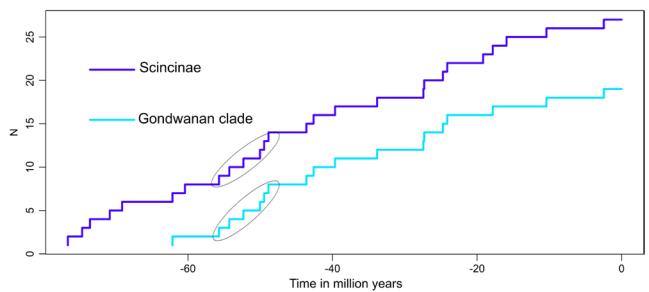


FIGURE 4 | Lineage-through-time plot for all scincines and the Gondwanan clade of scincines, with time in million years on the x-axis and number of lineages (*N*) on the y-axis. The ellipses on the plots highlights the slight increase in lineage accumulation.

which might be problematic given that there is often discordance between mitochondrial and nuclear markers with respect to higher level relationships (Brandley et al., 2008; Jana and Karanth 2019). Our study shows that even with multiple nuclear loci, the gene trees can give discordant results possibly due to rapid radiation of scincines within a short period. As suggested by other studies (Lambert, Reeder, and Wiens 2015; Linkem, Minin, and Leaché 2016), we have used a coalescent approach to assess the higher level relationships among skinks as well as to assess the systematic relationships within scincines with appropriate sampling.

In this study, we have compiled the largest molecular dataset for scincines to date, resulting in strong support for the monophyly of Scincinae. Pyron, Burbrink, and Wiens (2013) also supported the monophyly of scincines; however, their study did not include the south Asian scincine lineages and *Scoleoseps* from Africa. In our study, *Brachymeles* is sister to all the other scincines with strong support. However, Pyron, Burbrink, and Wiens (2013) estimated a sister relationship between *Brachymeles* and *Plestiodon*. Our study also does not support the sister relationship between *Mesoscincus* and *Ophiomorus* inferred by Pyron, Burbrink, and Wiens (2013). Furthermore, *Chalcides* and *Hakaria* form a well-supported relationship which differs from Pyron, Burbrink, and Wiens (2013). We estimate a relatively well supported (posterior probability of 0.82) relationship between *Gongylomorphus*, *Proscelotes* and *Scelotes* which is different from the results of Pyron, Burbrink, and Wiens (2013). Both Pyron, Burbrink, and Wiens (2013) and our study support *Sepsina* as sister to a well-supported clade of limbless African scincines *Feylinia*, *Melanoseps*, *Scoleoseps* and *Typhlacontias* as well as strong support for a single clade of Madagascan scincines. A previous assessment of lacertid lizards (Mendes et al. 2016) has already highlighted issues with the super-matrix approach used by Pyron, Burbrink, and Wiens (2013), and our estimate of the phylogeny of scincine lizards further demonstrates this.

Added value from our study is the appraisal of whether scincines are indeed ‘primitive ancestral stock’ from which the other subfamilies within skinks may have originated (see Greer 1970; Brandley, Schmitz, and Reeder 2005). Under such a scenario, nonscincine lineages would have been nested within scincines deeming scincines a paraphyletic group, a pattern not supported by our phylogenetic analyses.

4.1 | Where Did the Ancestors of Scincines Come From?

Our estimated date of 73 mya (95% CI = 64–85 mya) for the divergence of the Gondwanan clade and the Laurasian group of scincines is much younger than the tectonic breakup of Pangaea into the Gondwana and Laurasia supercontinents (≥ 200 mya; Chatterjee and Scotese 2010). In fact, the breakup into these two landmasses predates the origin of the crown group of skinks (~98 mya; CI = 113–84 mya) thereby rejecting this vicariance scenario as the best explanation for the earliest phylogenetic splits in scincines. The Gondwanan clade possesses more generic and species diversity than the Laurasian group, which would point towards a Gondwanan origin of scincines (Briggs 2000). However, our range evolution analysis clearly demonstrates that scincines originated in Asia and thereafter dispersed westwards. Many of the lineages within the Laurasian group have considerably long branches. This could suggest that there may have been a significant number of extinctions, especially in East Asia. Furthermore, Tałanda (2018) described a fossil scincoid (used as one of the calibrations in this study), *Ardeosaurus brevipes* from the Solnhofen of Germany, which displays characters that are modern skink-like and, therefore, points towards the Laurasian origin as a more plausible explanation. This fossil was unearthed from a basin that represents an age encompassing a period between 157 and 152 mya (Ebert, Kölbl-Ebert, and Lane 2015; Röper 2005; Schweigert 2007; Tałanda 2018). Furthermore, our study concurs with Wilenzik, Barger, and Pyron (2024), which suggests that early scincoids may have been regionalised in Laurasia and then subsequently dispersed to Gondwana. Our analysis reveals that the contemporary distribution of scincines were shaped by dispersals rather than by means of vicariance. Nevertheless, it must be pointed out that our biogeographic analysis is based on the tree topology recovered (Figure 2), in which some of the deeper nodes have very low support. Some of these relationships might change in the light of additional data, and therefore, the results of our biogeographic analysis must be considered a working hypothesis that requires further testing.

4.2 | Diversification Within Scincines

Our results show that a slight increase in the rate of lineage accumulation within scincines occurred between the early Eocene climatic optimum and the mid-Eocene climatic optimum and is especially evident in the Gondwanan clade. During this period, humid, suitable conditions (Li et al. 2022) may have resulted in an opportunity for the early scincines to diversify due to availability of ecological niches. It is likely due to this rapid radiation in conjunction with limited sampling of lineages that many of the previous studies have failed to retrieve a monophyletic Scincinae.

4.3 | The Curious Case of Indian and Sri Lankan Scincines

Sri Lanka and peninsular India are part of the same tectonic plate that drifted from the Southern hemisphere following the breakup of Gondwana. Contemporary peninsular India and Sri Lanka are separated by a narrow marine barrier. However, many studies have suggested that they were connected multiple times

owing to eustatic changes in sea levels (Bossuyt et al. 2004; Sudasinghe et al. 2021). This has been supported by numerous studies that suggest a corridor of dispersal between India and Sri Lanka leading to evolutionary relatedness of lineages that are endemic to these respective landmasses (Bossuyt et al. 2004; Richardson et al. 2014; Lajmi et al. 2019). Unsurprisingly, the Western Ghats of peninsular India and Sri Lanka are often together regarded as a contiguous hotspot for biodiversity. This shared biogeographic history is exemplified by studies that point towards their shared geological history (Gunawardene et al. 2007). However, our results show a novel scenario wherein the endemic Indian scincines (*Barkudia*, *Sepsophis*) and the Sri Lankan scincines (*Nessia*, *Chalcidoseps*) have deep evolutionary origins that are independent of each other.

The Sri Lankan *Nessia* and *Chalcidoseps* form a well-supported clade that is sister to the endemic Seychellean scincines *Janetaescincus* and *Pamelaescincus*. This relationship is strongly supported and forms one of the early divergences within the Gondwanan clade. Notably, the node connecting the Seychellean and Sri Lankan clade is considerably younger than the tectonic separation of the India-Seychelles plate, which occurred around 65 mya (Ali and Aitchison 2008). To account for this temporal incongruity, we propose two plausible scenarios. The first plausible scenario involves long-distance transoceanic dispersal to the Seychelles. The second plausible scenario is that a substantial number of lineages may have once bridged the gap between the Sri Lankan endemics (*Nessia* + *Chalcidoseps*) and the Seychellean clade (*Janetaescincus* + *Pamelaescincus*), but these lineages are now extinct. On the other hand, the endemic Indian scincines *Barkudia* and *Sepsophis* are nested within a predominantly African clade. The sister of the *Barkudia* + *Sepsophis* clade comprises the sub-Saharan African scincines *Proscelotes*, *Scelotes* and the Mauritian scincine *Gongylomorphus* (albeit with low branch support). This sub-Saharan+Mauritian clade is sister to the Madagascan scincines *Madascincus*, *Paracontias* and *Grandidierina*. The relationship of *Barkudia* + *Sepsophis* with the Afro-Madagascan+Mauritius scincines is also poorly supported. We think that this low support is due to the rapid radiation within the Gondwanan clade. However, given that the Sri Lankan lineages are sister to the Seychellean scincines with high support in spite of the addition of the Indian scincines, we think that this reflects their true evolutionary relationship.

A contrasting scenario has been observed in the case of the Western Ghats endemic relict frog *Nasikabatrachus* (Family Nasikabatrachidae). The closest phylogenetic relatives of Nasikabatrachidae are sooglossid frogs inhabiting the Seychelles, and that the split between these two lineages corresponded with the time that the Indian subcontinent broke away from Seychelles (~65 mya) (Biju and Bossuyt 2003; Feng et al. 2017). However, in our study, we observe that the split between the Sri Lankan *Nessia* + *Chalcidoseps* and the Seychellean *Janetaescincus* + *Pamelaescincus* is younger (48 mya; CI = 60–37 mya) than the India-Seychelles breakup (~65 mya). Even if we take the maximum bound of the time interval for this split, it corresponds to a geological setting in which the Indian plate had not yet sutured with Eurasia and was considerably distant from the Seychelles (Ali and Aitchison 2008). From our range evolution analysis, this dispersal occurred from Sri Lanka (Indian

plate) to Seychelles around 48–24 million years ago (considering the mean node age).

An intriguing result is that despite the shared geological history, there are no extant lineages related to *Nessia* + *Chalcidoseps* in peninsular India. It is likely that many of the lineages related to the Sri Lankan (SL) scincines that dispersed onto peninsular India+ SL may have become extinct in peninsular India owing to aridification and onset of seasonality (Agarwal and Ramakrishnan 2017; Deepak and Karanth 2018; Joshi and Edgecombe 2019; Sil, Aravind, and Karanth 2019). Alternatively, this might be a case of direct dispersal to Sri Lanka as seen in other taxa such as *Lyriocephalus*, *Cophotis* and *Ceratophora* agamid lizards (Grismer et al. 2016). Our study provides a unique example of an endemic lineage in the Seychelles being derived as a result of east-to-west transoceanic dispersal from the Indian plate. Our range evolution analysis also suggests that scincines attained their current distribution as a result of an east-to-west dispersal. The Laurasian group was derived from an ancestral stock which dispersed twice from East Asia to Afro-Arabian region between 74 and 69 mya. The dispersal from East Asia to Afro-Arabia eventually leading to the Gondwanan clade occurred between 73 and 62 mya. Although we have not included all members of the Madagascan scincines in our dataset, phylogenetic evidence has strongly supported the monophyly of the group (Erens et al. 2017). Therefore, we think it is unlikely that the Indian or Sri Lankan scincines would be nested within or be immediately sister to any of the Madagascan scincines.

Our ancestral range evolution results suggest that the lineage leading to *Sepsophis* and *Barkudia* dispersed from sub-Saharan Africa to the landmass comprising India and Sri Lanka around 54–52 mya. It is tempting to propose a scenario wherein the Indian plate was closer to Africa around 50 mya which may have facilitated biotic exchange of vagile lineages between the two landmasses. However, a study by Klaus et al. (2016) points out that biotic exchange between Southeast Asia and Indian subcontinent had already started gaining traction at around 50 mya. This would strongly suggest that the Indian subcontinent was relatively closer to Southeast Asia than Africa or Seychelles during this period. Therefore, this dispersal from sub-Saharan Africa to the Indian plate (followed by the subsequent back-dispersal based on our ancestral range evolution analysis) was most likely transoceanic, as the Indian plate was closer to Asia (Chatterjee and Scotese 2010; Klaus et al. 2016). Interestingly, the time of dispersal corresponds to a period encompassing the early Eocene and mid-Eocene climatic optima. Therefore, it is also possible that the lineage leading to *Barkudia* and *Sepsophis* dispersed via Afro-Arabia, which was followed by a number of extinction events. A somewhat similar scenario was reported by Barley et al. (2015), wherein the Indian radiation of sun skinks (*Eutropis*) was sister to the Philippine radiation in spite of an extremely low dispersal probability between these two regions. Barley et al. (2015) mention that this scenario can only be explained by a large number of extinctions in mainland Southeast Asia, which was the area of origin for *Eutropis*, and from which lineages dispersed both westwards (towards India) and eastwards (towards the Philippines). This was followed by extinctions in mainland Southeast Asia that resulted in the inferred sister relationship between the Indian and Philippine radiations.

4.4 | Dispersal to the Mascarene Islands From Africa

The sister relationship between the Mascarene Islands endemic *Gongylomorphus* and the African *Scelotes* and *Proscelotes* is strongly supported in our study. The Mascarene Islands are volcanic, originated no later than 8 Mya and have had no reported geological connections with any of the continental landmasses (Saddul 2002). The split between *Gongylomorphus* and *Scelotes* + *Proscelotes* is ~43 mya (CI = 54–31 mya). This is 23–46 million years before the Mascarenes emerged, so this would require cladogenesis prior to dispersal. It is plausible that the ancestor of *Gongylomorphus* colonised the Mascarene Islands via trans-oceanic dispersal from sub-Saharan Africa and subsequently became extinct on the latter. Such palaeoendemism has been demonstrated previously in the skink *Plestiodon longirostris*, given there is a ~20- to 12-million-year-old lineage endemic to the 2-million-year-old island of Bermuda (Brandley et al. 2010).

In addition to these biogeographic scenarios, there are further examples that suggest the contemporary distribution of scincines was a result of dispersal. The Socotran endemic scincine *Hakaria* is sister to *Chalcides*. The contemporary distribution of *Chalcides* also includes landmasses that were part of Laurasia. However, previous studies have shown that their Laurasian distribution may have been attained recently through multiple dispersal events from Africa and the centre of origin of *Chalcides* may have been Northern Africa (Morocco) (Carranza et al. 2008).

5 | Conclusions

Near complete sampling of scincine genera from across their distribution, in conjunction with representatives of other subfamilies, reveals that scincines form a monophyletic group. This also shows that scincines are not the ‘primitive stock’ as suggested by Greer (1970) from which other skink subfamilies have been derived. The scincines consist of two broad groups which we refer to as the Gondwanan clade and the Laurasian group owing to their predominant distribution in landmasses that once formed these supercontinents. However, the geological split of Pangaea into two supercontinents significantly predates the phylogenetic split between the Gondwanan and the Laurasian scincine groups. The members of the Gondwanan clade have more cladogenetic events and the timing of this radiation corresponds to a period between the early Eocene and mid-Eocene climatic optima. Our range evolution analysis clearly shows that in spite of the higher species richness of the Afro-Madagascan region, scincines originated in Southeast Asia+East Asia and then dispersed westwards. This dispersal may have been followed by a significant number of extinction events in tropical East Asia. Perhaps because of this reason, East Asia and Southeast Asia are depauperate in terms of generic diversity in scincines. Our results show that the contemporary distribution of scincines was primarily driven by dispersal events rather than by means of vicariance. Nevertheless, the results of our biogeographic analysis must be considered a working hypothesis given the lack of support at some of the deeper nodes. An interesting result of our analysis suggests that the Sri Lankan and the Peninsular Indian scincines belong to the

Gondwanan group but have independent evolutionary origins. Given the young divergence dates in our analysis, we hypothesise that the ancestors of the Indian and the Sri Lankan scincines were a result of independent transoceanic dispersal events. The Sri Lankan scincines may have been derived as a result of an east-to-west dispersal, while the Indian endemic scincines (*Barkudia* and *Sepsophis*) were a result of a dispersal from sub-Saharan Africa to Indian subcontinent. Both these independent transoceanic dispersals occurred in the early Eocene climatic optima. The genus *Gongylomorphus*, which is endemic to the Mascarene Islands, also arrived due to transoceanic dispersal from mainland Africa.

Author Contributions

Project was conceived by Aniruddha Datta-Roy and Matthew C. Brandley. Laboratory work was completed by Aniruddha Datta-Roy, Christopher C. Austin, Kanishka D. B. Ukuwela and Krystal A. Tolley. Analysis was conducted by Aniruddha Datta-Roy and Maitreya Sil. All authors contributed to data collection, writing and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Datadryad at https://datadryad.org/stash/share/ewYx8BydHLuVhI33v_bCChnGScISo57c4Gig5-nO_e0.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.