

Indian monsoon drove the dispersal of the *thoracica* group of *Scytodes* spitting spiders

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ABSTRACT

We examined the global biogeography of the *Scytodes thoracica* group of spitting spiders based on 23 years of sampling at the species level (61 species in the *thoracica* group and 84 species of *Scytodes*) using DNA data from six loci. Our results indicated that the *thoracica* group initially dispersed from Southeast Asia to East Africa between 46.5 and 33.0 million years ago, and dispersal events intensified between Southeast/South Asia and East/South Africa from the early to late Miocene. The timing of these events indicates that Asian-African faunal exchange of the *thoracica* group was driven by the Indian monsoon, and the pattern of dispersal suggests that colonialization took root when the Indian monsoon shifted from a North-South direction to an East-West direction from the middle Eocene.

Keywords: Geological event; Climate change; Ballooning organism; Faunal exchange; Species distribution

INTRODUCTION

The Indian monsoon constitutes an important component of the Asian meteorological system. Extensive research has indicated that it originated during the Paleocene to Eocene (~66–34 million years ago (Ma); Licht et al., 2014; Tardif et al., 2020; Wu et al., 2022; Zhang et al., 2018) and prevailed throughout the Eocene (Huber & Goldner, 2012). Uplift of the Himalayan-Xizang Plateau (HTP) has led to substantial variation in the Indian monsoon, including directional shifts and intensification events (An, 2000; An et al., 2001; Ruddiman & Kutzbach, 1990). These monsoonal changes may have facilitated long-distance dispersal of various organisms, thereby influencing diversification and faunal exchange, including those of spider populations. Here, we investigated whether the emergence and subsequent changes

of the Indian monsoon are concordant with biogeographical data pertaining to the *Scytodes thoracica* species group of spitting spiders, which are globally distributed but primarily occur in Asia.

Ballooning dispersal is a well-observed behavior in certain spider species (Morley & Robert, 2018) and is prevalent among various families such as Araneidae, Linyphiidae, Lycosidae, Oxyopidae, Philodromidae, Theridiidae, Tetragnathidae, and Scytodidae (Blandenier, 2009; Dean & Sterling, 1985; Garb & Gillespie, 2009; Greenstone, 1982; Kuntner & Agnarsson, 2011; Lee et al., 2015; Luo et al., 2020; Luo & Li, 2023; Weyman et al., 2002). For example, the golden orb spider (*Nephila*) exhibits the capacity for long-range aerial dispersal, from Africa to islands in the Indian Ocean (Kuntner & Agnarsson, 2011), which is evidently dictated by meteorological conditions, such as wind direction and intensity during monsoon periods. Consequently, this raises questions regarding the influence of monsoonal directional shifts and intensification on the patterns of faunal exchange across continents.

The globally distributed spitting spiders, belonging to the family Scytodidae, encompass four genera and 240 species, including 220 species of *Scytodes*, three species of *Scyloxes*, four species of *Dictis*, and 13 species of *Stedocys* (World Spider Catalog, 2023). The genus *Scytodes* is diverse and broadly distributed across Asia, Europe, Africa, the Americas, and Australia (World Spider Catalog, 2023). Our phylogenetic analyses have identified three distinct species groups within *Scytodes*: the *fusca* group, *thoracica* group, and Himalayas group (Luo & Li, 2022; this study, Supplementary Figure S1). Paleontological evidence suggests that the genus originated during the Paleogene (~58–33.9 Ma; Magalhaes et al., 2020; Wunderlich, 1993, 2011), with considerable diversification in the late Cenozoic (Luo & Li, 2022). Regionally, tectonic events have been important drivers for the diversification of *Stedocys* cave spiders in Southeast Asia (Luo & Li, 2018), as well as the high-elevation Himalayas group of *Scytodes* spiders around the HTP (Luo & Li, 2022). Globally, long-distance dispersal

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has played a crucial role in the expansion and diversification of the *Scytodes fusca* species complex (Luo & Li, 2023). However, the spatiotemporal distributions of the cosmopolitan *thoracica* group, as well as the mechanisms driving their distribution, remain unexplored.

In the present study, we used genetic data to generate the phylogenies of the *Scytodes* spitting spiders and dated molecular phylogenies of the *thoracica* group to investigate the composition, phylogenetic relationships, and geographic distribution patterns of the major *Scytodes* lineages over their entire distribution. We also examined global biogeographical patterns of this group and the impact of the Indian monsoon on *Scytodes thoracica* group dispersal during the Cenozoic.

MATERIALS AND METHODS

Taxon sampling and sequence analyses

Scytodes spiders were intensively sampled in Asia, Europe, the Americas, and East Africa between 2007 and 2020 (Supplementary Tables S1–S3). Taxon names, specimen vouchers, localities, longitude-latitude coordinates, and GenBank accession numbers of the *thoracica* group from Asia, Europe, Africa, and the Americas are listed in Supplementary Table S1. Samples were fixed in 95% ethanol and stored at -20°C . Based on morphological examination, we identified 76 *Scytodes* species, including 61 species belonging to the *thoracica* group. DNA was extracted using a TIANamp Genomic DNA kit (DP304-02). Polymerase chain reaction (PCR) amplification and gene sequencing were conducted following Luo & Li (2018). All primers are provided in Supplementary Table S4. Four nuclear genes (18S, 28S, *H3*, and ITS2) and two mitochondrial genes (*COI* and 16S) were sequenced. Voucher specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China. Additional sequences were obtained from GenBank.

DNA sequences were checked for quality and edited using BioEdit (Hall, 1999) and SEQUENCHER v4.1.2 (Gene Codes, USA). Protein-coding gene (*H3* and *COI*) sequences were aligned using CLUSTAL X (Jeanmougin et al., 1998) with default parameters. Alignments of the ribosomal genes (18S, 28S, 16S, and ITS2) were produced in MAFFT v7 (<http://mafft.cbrc.jp/alignment/server/>) using the E-INS-i method (Kato & Standley, 2013). DnaSP v5 (Librado & Rozas, 2009) was used to identify haplotypes. The concatenated sequences of the six genes were used for phylogenetic analyses, divergence time estimations, and biogeographical reconstructions.

Phylogenetic analysis

Initially, a molecular phylogeny of all globally sampled *Scytodes* spiders was constructed using maximum-likelihood (ML). Subsequently, molecular phylogenies of the *thoracica* group were reconstructed using both ML and Bayesian inference (BI) approaches. Outgroups were based on previous phylogenetic studies (Wheeler et al., 2017). We included the three recognized species of *Scytodes* sister genera, *Stedocys* (*S. ludiyanensis* and *S. shilinensis*) and *Scyloxes* (*S. zhaoi*) and three other species from two closely related families: Dysderidae (*Dysdera silvatica*) and Sicariidae (*Loxosceles laeta* and *L. rufescens*). The ML analyses were conducted using IQ-TREE v2.0.6 (Nguyen et al., 2015). For each gene partition or codon base, the most suitable evolutionary model across all available models (Supplementary Table S5)

(Kalyaanamoorthy et al., 2017) was identified using IQ-TREE, including the FreeRate model (+R; Soubrier et al., 2012), which relaxes the assumption of gamma-distributed rates using the MFP+MERGE function. The Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT; Guindon et al., 2010) and 1 000 ultra-fast bootstrap replicates (UFBoot; Hoang et al., 2018) were used to assess branch support. The “-bnni” command was added to improve the search for each UFBoot replicate tree. Transfer bootstrap expectation (TBE; Lemoine et al., 2018) was also conducted in IQ-TREE using the function `--tbe` following 500 standard Felsenstein bootstraps. Bayesian analysis was performed for the *thoracica* group in MrBayes v3.1.2 (Ronquist & Huelsenbeck, 2003). The best-fitting substitution model for each partition (Supplementary Table S6) was selected by jModelTest (Posada, 2008) under the Akaike information criterion. The Markov chain Monte Carlo (MCMC) simulation was run for 10 million generations with sampling every 100 generations using unlinked parameters between partitions. Tracer v1.5 (Rambaut & Drummond, 2009) was employed to verify the effective sample size (ESS) values (>200) for each parameter. A 50% majority rule consensus tree was computed after discarding the first 25% of trees as burn-in.

Divergence time estimation

Molecular dating of the *thoracica* group phylogeny was calculated using BEAST v1.6.1 (Drummond & Rambaut, 2007). First, the combined DNA sequence data were partitioned by locus and codon position. For each partition, the corresponding evolutionary model (GTR+I+G for 16S, 18S, 28S, ITS2, *COI*-1, *COI*-2, and *H3*-1; GTR+G for *COI*-3 and *H3*-3; JC for *H3*-2) was selected from jModelTest. Divergence time estimation was performed using an uncorrelated lognormal relaxed molecular clock. Analyses with a Birth-death and Yule prior were also repeated to assess the sensitivity of the results to tree prior specification. The Birth-death model outperformed the Yule model according to the marginal likelihood estimated by Stepping-stone sampling. Hence, for subsequent analyses, we focused on the chronogram resulting from the Birth-death prior. Minimum ages based on the fossils of *Scytodes weitschati* (Scytodidae, 33.9 Ma; Wunderlich, 1993, 2011), *Loxosceles defecta* (Sicariidae, 13.82 Ma; Wunderlich, 1988, 2004), *Harpactea communis* (Dysderidae, 35 Ma; Wunderlich, 2004), and *Microsegestria poinari* (Segestriidae, Dysderoidea, 125 Ma; Wunderlich & Milki, 2004) were used as calibration points (Supplementary Table S7; Donoghue & Benton, 2007; Renner, 2005). BEAST analyses were run for 50 million MCMC generations with model parameters and tree sampling every 1 000 generations. The stationarity of runs was examined using Tracer v1.6 with an ESS cutoff of >200 for all parameters. TreeAnnotator v1.6.1 (in BEAST) was used to produce a maximum clade credibility (MCC) tree after discarding 25% of the trees as burn-in.

Biogeographical reconstruction

The ancestral areas and biogeographical history of the *thoracica* group were inferred using three analytical approaches implemented in RASP v3.0 (Yu et al., 2010, 2015). Parsimony-based statistical dispersal-vicariance analysis (S-DIVA) (Yu et al., 2010), a modified form of dispersal-vicariance analysis (Ronquist, 1997), accounts for uncertainty in phylogenetic and biogeographical reconstructions (Nylander et al., 2008). The dispersal-

extinction-cladogenesis (DEC) model, which infers dispersal-mediated range expansion and extinction-mediated range contraction (Ree & Smith, 2008), allows for analytical solutions to probabilities of range transitions as a function of time, enabling free model parameters, rates of dispersal, and local extinction to be estimated by ML. The Bayesian binary MCMC (BBM) model is considered the most general and complex model in RASP (Sanmartín et al., 2001). These three analyses were conducted with the maximum area number at each node set to 2. A fossil-calibrated tree, from which the outgroups were trimmed, was employed for biogeographical reconstruction. Based on geographic divisions, climate, and current distributions of *Scytodes*, five geographical areas occupied by the *thoracica* group were delimited, namely the southern Asia/Oriental Realm, Central Asia+Europe/Palearctic, East Africa, South Africa, and the Americas.

RESULTS

Sequence characteristics

A total of 1 174 nuclear (28S: 183, 18S: 238, *H3*: 213 and ITS2: 127) and mitochondrial DNA sequences (*COI*: 223 and 16S: 190) were successfully generated from the global sampling of *Scytodes* (Supplementary Tables S1–S3), including 814 nuclear (28S: 134, 18S: 172, *H3*: 134 and ITS2: 65) and mitochondrial DNA sequences (*COI*: 153 and 16S: 156) of the *thoracica* group from Asia, Europe, the Americas, and Africa (Supplementary Table S1). The aligned sequence data of the DNA haplotypes of the *thoracica* group and outgroups were 3 363 bp long. GenBank accession numbers are provided in Supplementary Tables S1–S3.

Molecular phylogeny

The ML trees for all sampled *Scytodes* spiders are presented in Supplementary Figure S1, and the phylogenetic results are consistent with our previous study (Luo & Li, 2022). The reconstructed tree topologies of the *thoracica* group based on ML and BI analyses were largely congruent (Figure 1). Results indicated that the *thoracica* group comprised four major clades: (1) Clade I (MA), including eight species from the Malay Archipelago, South Africa, and Madagascar; (2) Clade II (EC), composed of five species from Central Asia to Europe and Canada; (3) Clade III (SC), containing eight species from the southern USA, Central America, and China; and (4) Clade IV (CI), including 33 species from China, the Indochina Peninsula, South Asia, the Malay Archipelago, and the Seychelles (Figures 1, 2). Clade IV comprised three subclades: (1) Clade IV-1, including 11 species from Southwest China to Indochina; (2) Clade IV-2, containing three species (including type species *S. thoracica*) distributed from South China eastward to the Seychelles, including Southeast Asia and South Asia; and (3) Clade IV-3, including 19 species distributed in South Asia and Southeast Asia (Figures 1, 2).

Divergence times

The time-calibrated Bayesian phylogeny is shown in Figure 3A. The initial cladogenesis within the *thoracica* group was inferred to have occurred slowly among the four major lineages between ~46.5–12.9 Ma. The diversification of Clade I started ~46.5 Ma, after the split of the most recent common ancestor (MRCA) of the group at ~54.4 Ma. Clade II originated in the early Eocene (~50.3 Ma), and the diversification of this clade occurred ~12.9 Ma across Asia, Europe, and North

America, but slowly diversified ~11.2–4.7 Ma during the late Miocene to the present. Clade II (NH, North Himalayas-Xizang) and Clades III and IV (SH, South Himalayas-Xizang) split ~50.3 Ma. The most recent speciation of Clade III occurred in China, with local species emerging ~40.2–9.5 Ma. Within Clade IV, Clade IV-1 diverged from its sister lineages Clades IV-2 and IV-3 ~42.2 Ma.

Biogeography

The current distribution of the *thoracica* group was associated with long-distance dispersal events and *in situ* allopatric speciation (Figure 4). Both the DEC (Figure 4A) and S-DIVA results (Figure 4B) were generally concordant. In the BBM analysis (Figure 4C), nodes 1, 2, 3, 6, and 15 differed from those of DEC (Figure 4A) and S-DIVA (Figure 4B).

Three possible ancestral ranges (Figure 4B) were inferred for the *thoracica* group with the same marginal probability using S-DIVA: (1) southern Asia; (2) southern Asia+Central Asia+Europe, and (3) southern Asia+East Africa+South Africa. The inference from DEC (Figure 4A) favored southern Asia+Central Asia+Europe and southern Asia+East Africa+South Africa as the most likely ancestral area of the *thoracica* group, whereas southern Asia was preferred under BBM (Figure 4C).

The inferred phylogeographic history of the *thoracica* group is shown in Figure 4. The initial burst of diversification that produced the four early-diverging lineages (Clades I–IV) was inferred to have occurred in the ancestral area during the late Paleocene and early Eocene. Long-distance dispersal and geographic isolation were the main drivers of the global distribution of the *thoracica* group. We inferred long-distance overwater dispersals from the southern Malay Peninsula and central Sumatra Island region to Madagascar and South Africa between the mid-Eocene and late Miocene, which resulted in Clade I. Certain ancestors from Southeast Asia expanded northwards to Central Asia, with subsequent geographical isolation between northern and southern Himalayas-Xizang due to the Indian-Eurasian collision and uplift of the HTP, which resulted in Clade II. The Clade II spiders expanded to Europe during the late Miocene and early Pliocene. Within Clade III, we inferred one independent overwater dispersal toward the Americas from China, starting in the mid-Eocene. The Clade IV ancestors diversified mainly in Southeast Asia from the late Eocene to present, while some Clade IV spiders expanded to South Asia and the Seychelles.

DISCUSSION

Encompassing 61 species of the *thoracica* group, this study sought to illuminate the global diversity of the group and phylogenetic relationships among its major clades. Our previous study suggested that the *Scytodes* spiders from Southeast Asia comprise three monophyletic species groups, corresponding to the Himalayas group, *fusca* group, and *thoracica* group (Luo & Li, 2022). In the current study, even after the addition of samples from Africa, Europe, the Americas, and other regions of Asia, our results reaffirmed the same lineage compositions and group-level phylogenetic relationships of *Scytodes* from Southeast Asia, thereby expanding our understanding of their phylogenetic history at a global level.

Phylogeography of *thoracica* group

This study sheds light on the phylogeography of the *thoracica*

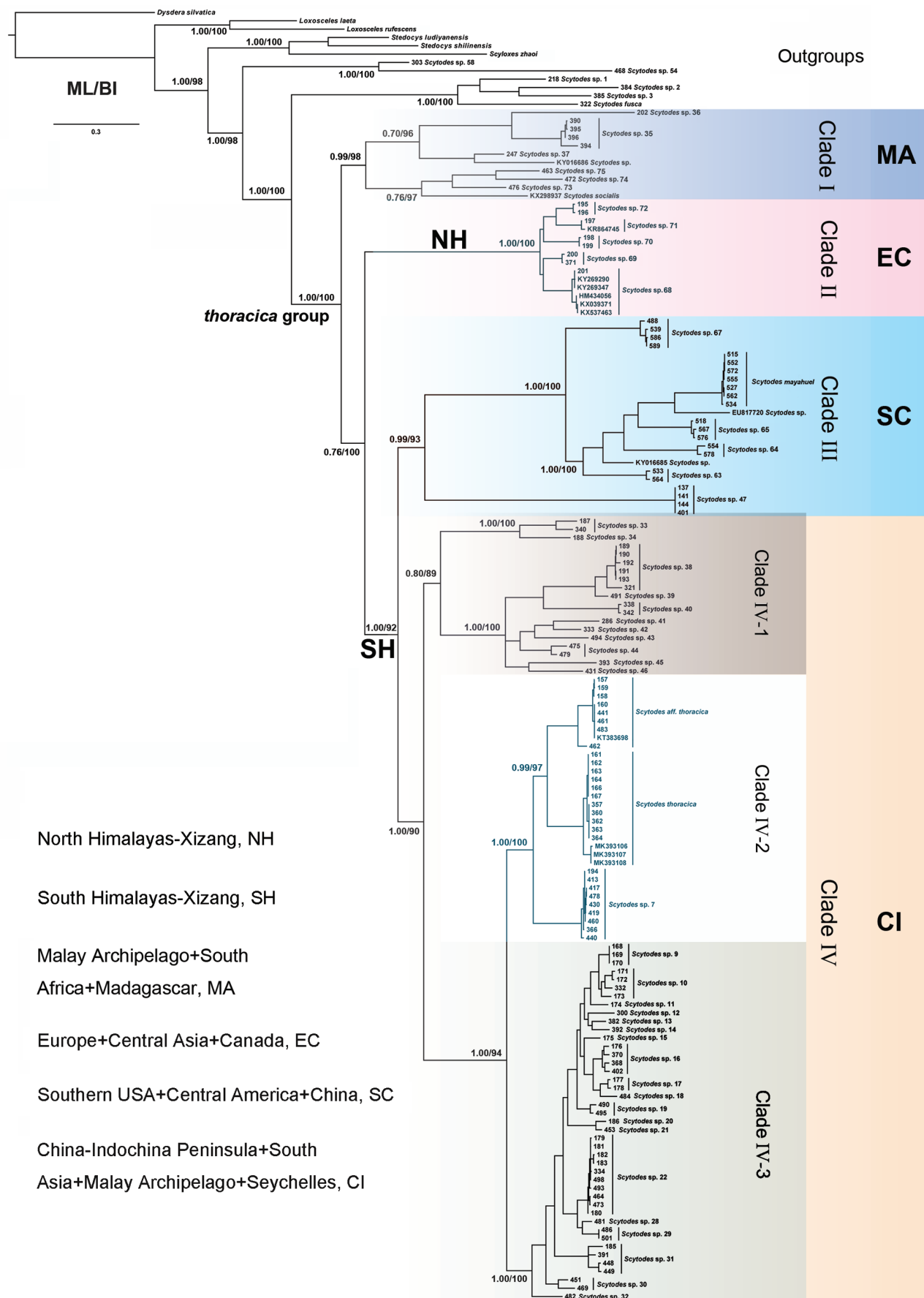


Figure 1 Summary phylogenetic tree based on ML and BI analyses of concatenated mitochondrial (*COI* and 16S) and nuclear (18S, 28S, ITS2, and *H3*) gene datasets

Numbers at nodes represent bootstrap support values/posterior probabilities from both analyses, respectively.

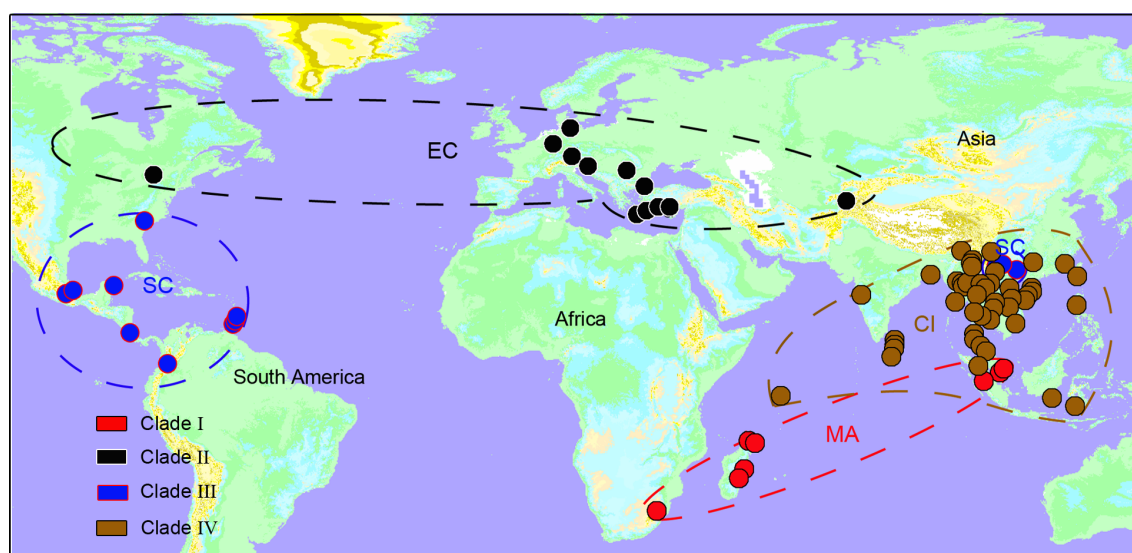


Figure 2 Sampling localities of *thoracica* group

Thoracica group included Clade I (red circles; MA, Malay Archipelago+South Africa+Madagascar), Clade II (black circles; EC, Europe+Central Asia+Canada), Clade III (blue circles; SC, southern USA+Central America+China), and Clade IV (brown circles; CI, China+Indochina peninsula+South Asia+Malay Archipelago+Seychelles) individuals. Detailed sampling information is provided in the Supplementary Materials.

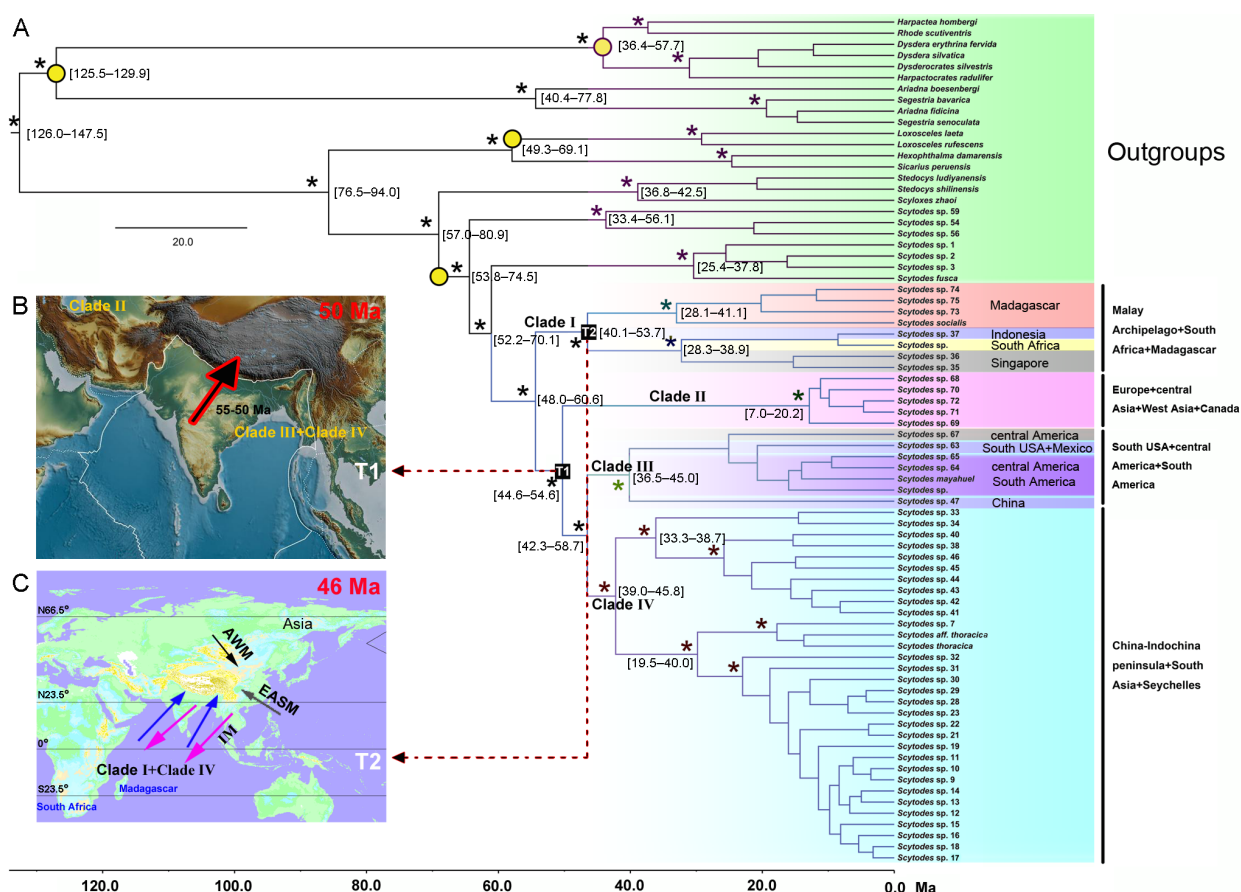


Figure 3 Evolutionary diversification of *thoracica* group with initial Indian-Asian collision and Asian monsoon

A: Time-tree of all sampled *thoracica* group species. "*" indicates stable branches with Bayesian support >0.90. Yellow circles are fossil calibration nodes. "T1" represents Clade II+Clade III+Clade IV; "T2" represents Clade I. Ma: Millions of years ago. B: Evolutionary history of *thoracica* group shown in A corresponds to tectonic hypothesis that initial Indian-Eurasian collision occurred during the early Eocene. C: Evolutionary history of *thoracica* group shown in A corresponds to climate hypothesis that Indian monsoon occurred during the middle Eocene because of the Indian-Eurasian collision. Clade I: MA, Malay Archipelago+South Africa+Madagascar; Clade II: EC, Europe+Central Asia+Canada; Clade III: SC, southern USA+Central America+China; Clade IV: CI, China+Indochina Peninsula+South Asia+Malay Archipelago+Seychelles. AWM: Asian winter monsoon; EASM: East Asian summer monsoon; IM: Indian monsoon. Numbers in "[]" at nodes indicate 95% highest posterior density interval for divergence time estimates.

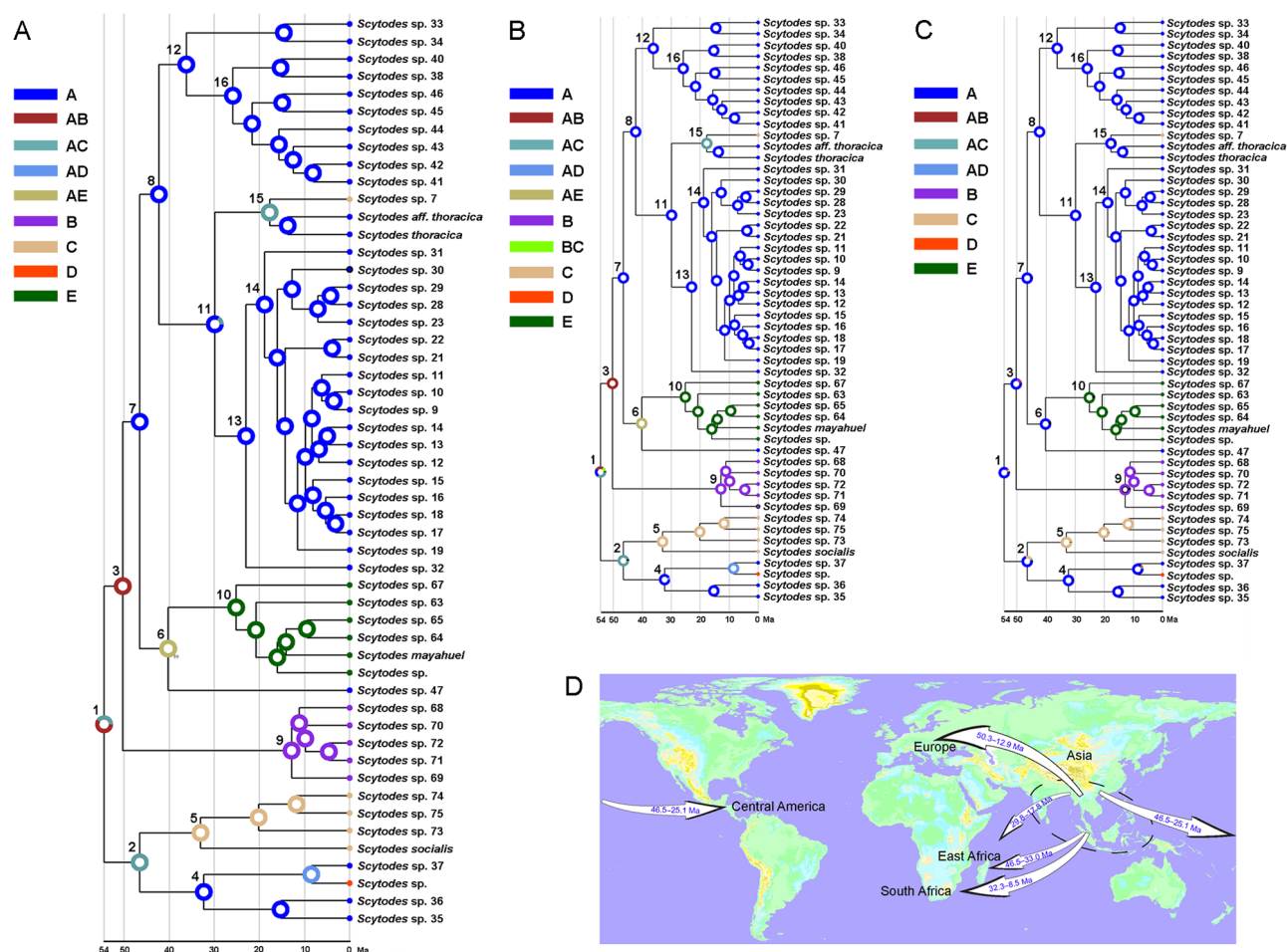


Figure 4 Biogeography of *thoracica* group and probable global dispersion routes

A–C: Reconstruction from Bayesian binary MCMC (BBM), statistical dispersal-vicariance analysis (S-DIVA), and dispersal-extinction-cladogenesis (DEC), respectively, from RASP v3.0. Colors of pie wedges at each node represent geographical areas inferred to have been occupied by ancestral taxa (A: Southern Asia/Oriental Realm; B: Central Asia+Europe/Paleartic; C: East Africa; D: South Africa; E: Americas). D: Global potential dispersion routes (arrows) of *thoracica* group.

group. Our results indicated that the group most likely originated in southern Asia around the Paleocene (~61.1 Ma) when it diverged from the *fusca* group (Figure 4). However, the initial divergence of the extant species within the *thoracica* group began at the Paleocene-Eocene boundary, when four major extant lineages diverged in succession, with rapid diversification occurring mainly in Southeast and South Asia during the Miocene (Figures 3, 4). Furthermore, our results suggested that the initial Indian-Eurasian collision and subsequent uplift of the Himalayas drove the deep lineage divergence of the *thoracica* group between the northern and southern Himalayas. The initial collision event triggered the split between Clade II and Clade III+Clade IV within the pan-Himalayas *Scytodes* group in the early Eocene (~50.3 Ma). These changes are consistent with other studies identifying the Indian-Eurasian collision as a major driving force for the phylogeography, speciation, and diversification of animals (Favre et al., 2015; Guillot & Replumaz, 2013; Licht et al., 2014; Miao et al., 2012).

Concordance of initiation time between *thoracica* group dispersal and development of Indian monsoon into South and East Africa

The phylogeographical analyses conducted in this study indicated that the Indian monsoon drove dispersal of the

thoracica group, with long-distance dispersal shaping its global distribution patterns. Our results also suggested that after the split of the MRCA of the *thoracica* group in the mid-Miocene (~54.4 Ma), Clade I dispersed by ballooning over the oceans, with the aid of the historical Indian monsoon from the Malay Archipelago to Madagascar, possibly via islands, then diverged between the two regions ~46.5 Ma (Figure 4). The timing (~46.5 Ma) of the initial dispersal of the *thoracica* group to Madagascar is concordant with that of the development of the Indian monsoon into Southeast Africa. This pattern is consistent with previous studies suggesting that the onset of the Indian monsoon during the middle Eocene acted as a significant driver of faunal exchange (Favre et al., 2015; Guillot & Replumaz, 2013; Licht et al., 2014; Miao et al., 2012). In the case of spiders, this was likely aided by ballooning dispersal, which allowed the colonization of oceanic islands and continents far from their native ranges (Kuntner & Agnarsson, 2011; Meijer, 1977; Sugg & Edwards, 1988).

Faunal exchange of the *thoracica* group between Asia and Africa correlates with the shift in Indian monsoon direction

Our results also revealed three dispersal events from Southeast Asia to Africa within the *thoracica* group (Figure 4). The timelines of these dispersals coincided with shifts in the

directionality of the Indian monsoon from North-South to East-West from the middle Eocene due to uplift of the HTP. These findings further enhance our understanding of how the complex interplay of prehistoric geological events (such as uplift of the HTP and development of the Indian monsoon) has shaped the evolution of Asian biodiversity, thus adding a new dimension to the vast body of knowledge already established (Clift & Webb, 2018; He et al., 2022; Licht et al., 2014; Prell & Kutzbach, 1992; Spicer, 2017).

DATA AVAILABILITY

All sequences generated in this study have been deposited in GenBank (accession numbers in Supplementary Tables S1, S2). All information on sampling locations is provided in Supplementary Tables S1–S3. The sequence alignment datasets of phylogeny and molecular clock analyses are publicly available on the Dryad database (online at <http://datadryad.org/>).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Y.F.L. and S.Q.L. designed the study. Y.F.L. carried out laboratory protocols and data analysis. Both authors drafted the manuscript and read and approved the final version of the manuscript.

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