

## Tropical Niche Conservatism Explains the Eocene Migration from India to Southeast Asia in Ochyroceratid Spiders

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**Abstract.**—Biological migrations between India and Southeast (SE) Asia provide an ideal system for exploring the effects of geology and climate on species ranges. Geologists have confirmed that the direct collision between India and Eurasia occurred in the Early Eocene, but most migrations occurred between the Indian subcontinent and SE Asia rather than the former and the southern margin of Eurasia. To explain this seemingly paradoxical disconnect between the routes of plate movement and biological migration, we studied the evolutionary history of the tropical spider family Ochyroceratidae based on 101 globally distributed species. We infer a robust dated phylogeny using both transcriptomic data and a data set of classical markers and relate these to biogeographic and climatic analyses. Our results indicate that the monophyly of Ochyroceratidae is strongly supported, and the divergence times suggest a Cretaceous Gondwanan origin of the family. Reconstructed biogeographic histories support a dispersal event from the Indian subcontinent to islands of SE Asia 55–38 Ma. Climatic analyses and the fossil record reveal that ochyroceratids are characterized by a high degree of tropical niche conservatism, and that the ancestor of the Indian and SE Asian clades originated in very warm, wet environments. Early Eocene tropical, perhumid climates in India, and SE Asia may have facilitated ochyroceratid migration, whereas the dry or seasonal climate extending from the eastern coast of China to Central Asia may have acted as a barrier, preventing dispersal. Our analyses suggest that climate plays a more important role than geology in biological migration from the Indian subcontinent to SE Asia, providing new insights into the Indian–Asian biogeographic link. [Biogeography; ecology; geological connections; macroevolution; paleoclimate.]

Ecology is as important as biogeographic history in determining the distribution pattern of species diversity at the global scale (Wiens and Donoghue 2004). Ecologists focus on using climatic niche conservatism and regional climate to clarify species' geographic ranges and the accumulation of species within regions (Wiens and Donoghue 2004; Pyron et al. 2015; Daru et al. 2017; Saupe et al. 2018), whereas historical biogeographers tend to use geological connections among regions (Leprieur et al. 2016). However, there is a lack of empirical studies that clarify the linkages between ecology and biogeographic history. Cenozoic biotic exchange between the Indian subcontinent and Southeast (SE) Asia is an especially useful topic for understanding the interplay between these fields, as this period has detailed geologic history and paleoclimate information.

India's northward movement and collision with Eurasia is one of the most salient geological events that Earth has experienced, and this event was followed by a massive biotic exchange between India and Asia. Paleontologic and biogeographic studies have confirmed that the number of migration events between India and SE Asia started to increase in the Early Eocene (Klaus et al. 2016). Ali and Aitchison's (2008) island arc-continent collision hypothesis was used to explain the Early Eocene biotic exchange between India and SE Asia (Klaus et al. 2010; Li et al. 2013; Grismer et al. 2016). This hypothesis proposes that the northeast corner of the Indian subcontinent made glancing contact with Sumatra (~55 Ma), and subsequently with Burma (~35 Ma). However, through the study of stratigraphy,

sedimentology, magmatism, metamorphism, structural geology, and paleomagnetism, geologists consider the island arc-continent collision model to be incorrect (Garzanti 2008; Zhang et al. 2014; Hu et al. 2016). The best explanation for all available data involves the direct collision between India and the southern margin of Eurasia in the Early Eocene (ca. 60–50 Ma) (Royden et al. 2008; Hu et al. 2016). The southern margin of Eurasia includes the Gangdese Arc trench system in the central and eastern Himalaya and the Kohistan–Ladakh island arc in the western Himalaya (Hu et al. 2016).

Direct collision should have led to biological migration between India and the southern margin of Eurasia, but the majority of organisms dispersed from India to SE Asia. The availability of land or sea corridors and the establishment of suitable climates primarily determined migration events (Klaus et al. 2010; Bacon et al. 2015). This implies that factors other than geological collision, such as climate, have shaped the distribution of biodiversity in these regions. India's drift into a warm, perhumid climate zone during the Early Eocene could have produced opportunities for migration of diverse tropical organisms into SE Asia (Morley 2018). Considering a confluence of climatic and geological factors may help elucidate the reason for the inconsistency in the actual biological migration route with the route that would be expected from the direct collision of India and Asia.

Here, we use spiders of the family Ochyroceratidae Fage, 1912, commonly known as midget ground weavers, to explore the role of climate in the Indian–Asian biological migrations. Ochyroceratidae currently contains 163 species in two subfamilies

(World Spider Catalog 2019). The subfamily Ochyroceratinae is restricted to the Neotropics, whereas the subfamily Theotiminae is more broadly distributed across the Indian subcontinent, SE Asia, tropical Africa, and the Neotropics, with most of the diversity concentrated in SE Asia (62 species, plus several described but not yet published species). These spiders prefer wet habitats and are often found in leaf litter and caves. Most species are only known from a small area and dispersal capacity is evidently low (Deeleman-Reinhold 1995). The poor dispersal capabilities and ancient origins (divergence from Scytodidae at ~150 Ma) (Fernández et al. 2018) of ochyroceratids indicate that they are an appropriate lineage for inferring Cenozoic geological and environmental history.

#### MATERIALS AND METHODS

##### *Data Set*

We used two molecular data sets: one that emphasizes genomic coverage and another that emphasizes geographic coverage (the full data sets are provided in the Supplementary Tables S1 and S2 available on Dryad at <https://doi.org/10.5061/dryad.kd2b16c>). The transcriptomic data set consisted of six novel transcriptome sequences and 119 previously available transcriptomic data (Bond et al. 2014; Fernández et al. 2014; Garrison et al. 2016; Shao and Li 2018). New transcriptomic data were generated for six species representing one ochyroceratid taxon and five psilodercid taxa (Supplementary Table S2 available on Dryad). We extracted mRNA from field collected samples using the TRIzol total RNA extraction method (Life Technologies). Purification of mRNA, library preparation, sequencing, and quality control were done by Novogene Bioinformatics Technology Co. Ltd. We used the method described in Shao and Li (2018) to generate orthologs. To minimize any negative effects of saturation, only the first and second positions of nucleotide data were used.

The newly sequenced data set using the classical markers comprised 152 taxa from six genera of the subfamilies Theotiminae and Ochyroceratinae, covering most of the known tropical geographic regions (Supplementary Fig. S1 available on Dryad). In particular, we conducted extensive dedicated Ochyroceratidae surveys in Tibet of China, Nepal, and Sri Lanka, comprising 945 person hours of sifting litter at 242 localities (Supplementary Fig. S2 available on Dryad). When possible, samples from the type localities of nominal taxa were included, and multiple samples were used to represent widespread species. Based on the phylogeny of Fernández et al. (2018), we used 13 taxa from different genera of the families Scytodidae and Sicariidae as outgroups. The complete data set totaled 165 taxa with seven classical markers, comprising five nuclear markers (*18s*, *28s*, *h3*, *wingless*, and *actin 5c*), and two mitochondrial genes (*16s* and *cox1*). DNA extraction, Polymerase Chain Reaction, and sequencing

procedures have been reported by Li and Li (2018). Primers are listed in Supplementary Table S3 available on Dryad. We aligned sequences using MAFFT 7 (<http://mafft.cbrc.jp/alignment/server/>). Alignments of the protein-coding *h3*, *wingless*, *actin 5c*, and *cox1* genes were trivial due to the lack of gaps and were produced using the L-INS-i method. Due to the highly variable nature of ribosomal genes, the E-INS-i method, which incorporates affine gap costs, was used to generate alignments of *16s*, *28s*, and *18s*. To detect and exclude ambiguously aligned regions, alignments of the ribosomal genes were processed with the program trimAl v1.3 (Capella-Gutierrez et al. 2009) using the heuristic *gappyout* method. Furthermore, this data set not only comprised 55 recognized species but also indicated a high level of cryptic diversity. To assess lineage delimitation within Ochyroceratidae, we collected *cox1* sequences from 280 individuals (*n* per taxa ranged from 1 to 5). For details on lineage delimitation, see Supplementary File S2 available on Dryad. Voucher specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS).

##### *Phylogenetic Analysis*

We used PartitionFinder 2.1.1 (Lanfear et al. 2017) to select models and partitioning schemes for the two data sets according to the Bayesian information criterion. For each data set, we inferred maximum likelihood (ML) topologies with RAxML 8.2.9 (Stamatakis 2014) based on the best partitioning strategy and the best-fit model (Supplementary Table S4 available on Dryad). For the transcriptomic data set, Bayesian inference (BI) analyses were performed under the site-heterogeneous mixture model CAT-GTR+GAMMA in PhyloBayesMPI 1.5a (Lartillot et al. 2013) using the resources available from the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway (<https://www.phylo.org/portal2>) (Miller et al. 2010). For the classical marker data set, BI analyses were performed in MrBayes 3.2.2 (Ronquist et al. 2012) using the partitioning strategy and the optimal nucleotide substitution model for each partition (Supplementary Table S4 available on Dryad).

##### *Divergence Time Estimation*

The size of our transcriptomic data set precluded the use of some computationally intensive dating methods, such as those incorporated in BEAST; instead, we used MCMCTREE in PAML 4.9 (Yang 2007) to estimate node ages which reduces computational load by using an approximate likelihood calculation. Divergence times were estimated with the uncorrelated relaxed clock and constrained by 10 conservatively selected fossil calibrations in Araneae lineages (Supplementary Fig. S3 and Table S5 available on Dryad, for details see Supplementary File S2 available on Dryad). We used the PhyloBayes topology as the reference tree. Further, we applied the most general GTR+ $\Gamma$  model permitted

by MCMCTREE and a birth–death process with species sampling for the data set. Posterior distributions of divergence times were estimated using Markov chain Monte Carlo (MCMC) sampling, with samples drawn every 500 steps over a total of two million steps after a discarded burn-in of 200,000 steps. We ran each analysis in duplicate and visually inspected the results in Tracer v1.6 (Rambaut et al. 2014) ensuring that the effective sample sizes (ESS) of all parameters were above 200.

In the data set of classical markers, each species was represented by one specimen to avoid both coalescent and zero-length branches. A likelihood ratio test in Paup 4.10b (Wilgenbusch and Swofford 2003) suggested that the molecular clock hypothesis was rejected ( $P < 0.0001$ ) for each gene. Therefore, we estimated divergence times using Bayesian relaxed clock methods in BEAST 1.8.4 (Drummond et al. 2012). We used secondary calibrations derived from the transcriptomic chronogram and fossils to calibrate the clock (Supplementary Fig. S3 and Table S6 available on Dryad; Supplementary File S2 available on Dryad). The tree obtained from the transcriptomic data set sparsely sampled ochyroceratids but included nodes shared with our tree from the data set of classical markers, such as the split between Ochyroceratidae and its sister lineage Scytodidae, and the split between Theotiminae and its sister lineage Ochyroceratinae (Fig. 1 and Supplementary Fig. S3 available on Dryad); we used the above secondary calibrations for the same nodes in our classical data set (Supplementary Table S6 available on Dryad; Supplementary File S2 available on Dryad). The extant Hispaniolan spiders of Ochyroceratinae are morphologically very similar to *Arachnolithulus longipes* described from Dominican amber from the Miocene (~15 Ma) (Wunderlich 2004). Thus, we set a minimum age of 15 Ma for this clade. We also included *Scytodes* (Wunderlich 2011) from Baltic amber (58–34 Ma) as fossil calibration points. Fossils were assigned to the stem of their most closely related lineages. Further, we ran analyses using a birth–death incomplete sampling prior that considers that we sampled a fraction of all ochyroceratid diversity (Supplementary File S2 available on Dryad). We sampled a tree every 1000 generations in each of the three independent MCMC runs with 80 million generations. The stationarity of runs was examined using Tracer v1.6 with the ESS >200 for all parameters after combining all runs. To compare the robustness of calibrations, divergence time estimation was obtained using MCMCTREE. Divergence times were estimated using the independent rates model in MCMCTREE and a birth–death process with species sampling. For MCMCTREE, constraints were the same as those used in BEAST, except that lognormal priors are not available in MCMCTREE.

#### Biogeographic and Habitat Analyses

Biogeographic areas were assigned as traits for each species in the dated phylogeny. Based on climate, geographic divisions, and the current distribution of

Ochyroceratidae, we delimited 12 areas (Fig. 2): A, South America; B, Central America (including the Caribbean); C, Africa; D, Madagascar; E, the Indian subcontinent; F, South China; G, Indo-Burma; H, Sumatra (including Malayan Peninsula and Java); I, Borneo; J, Archipelago (including Philippines and China, Taiwan Island); K, Sulawesi; and L, Fiji. Spiders were assigned to areas according to their distributional data (Supplementary Table S1 available on Dryad). As “+J” is conceptually flawed (Ree and Sanmartin 2018), biogeographic inferences were obtained using a dispersal-extinction-cladogenesis (DEC) model (Ree et al. 2005; Ree and Smith 2008) and a likelihood version of dispersal-vicariance (DIVALIKE) model (Ronquist 1997) in BioGeoBEARS (Matzke 2013). The maximum number of ancestral states at each node was set to two areas. Outgroups, *Speocera stellafera*, *Theotima minutissimus*, and *Roche roche* were excluded. This is because the widespread species *S. stellafera*, *T. minutissimus*, and *R. roche* are probably transported as cargo stowaways, like many invasive insects; thus, their dispersal potential is defined by human activities (Edwards and Edwards 2003). We used four time slices (110–90 Ma, 90–60 Ma, 60–30 Ma, and 30–0 Ma) to reflect the changing connectivity of biogeographic areas caused by plate tectonics (Supplementary Table S7 available on Dryad). The connectivity of areas in each analysis was modeled with four dispersal probabilities (1, 0.5, 0.1, and 0.01).

The ancestral reconstruction of habitat focused on the subfamily Theotiminae. Using ecological data from the literature and abundant preserved material in our own sampled collections, we delimited two states: epigeal habitats, mostly representing the litter under trees and shrubs, such as dead curled leaves, bamboo stems, and debris, and hypogean habitats, referring mainly to caves (for details see Supplementary Table S1 available on Dryad). Habitat inferences and the time of adaptation to caves were obtained under two different approaches: BI and ML. The Bayesian binary MCMC (BBM) analysis (Ronquist and Huelsenbeck 2003) in RASP v3.1 (Yu et al. 2015) was used for BI analysis. The BBM analysis was performed with 10 million cycles, sampling every 1000 cycles, and the JC69 substitution model. ML analysis was performed with the RAYDISC command in the package corHMM (Beaulieu et al. 2013) in R (Team 2013) under the equal rates, symmetrical, and all rates different. Finally, we use Akaike Information Criterion in selecting among these varying models of character evolution (Supplementary Table S8 available on Dryad).

#### Diversification Analysis

We reconstructed the dynamics of species diversification using BAMM that estimate speciation and extinction rates through time and among clades (Rabosky et al. 2013). BAMM can detect and quantify rate shifts across the phylogeny that explain the diversification dynamics of a clade without *a priori*

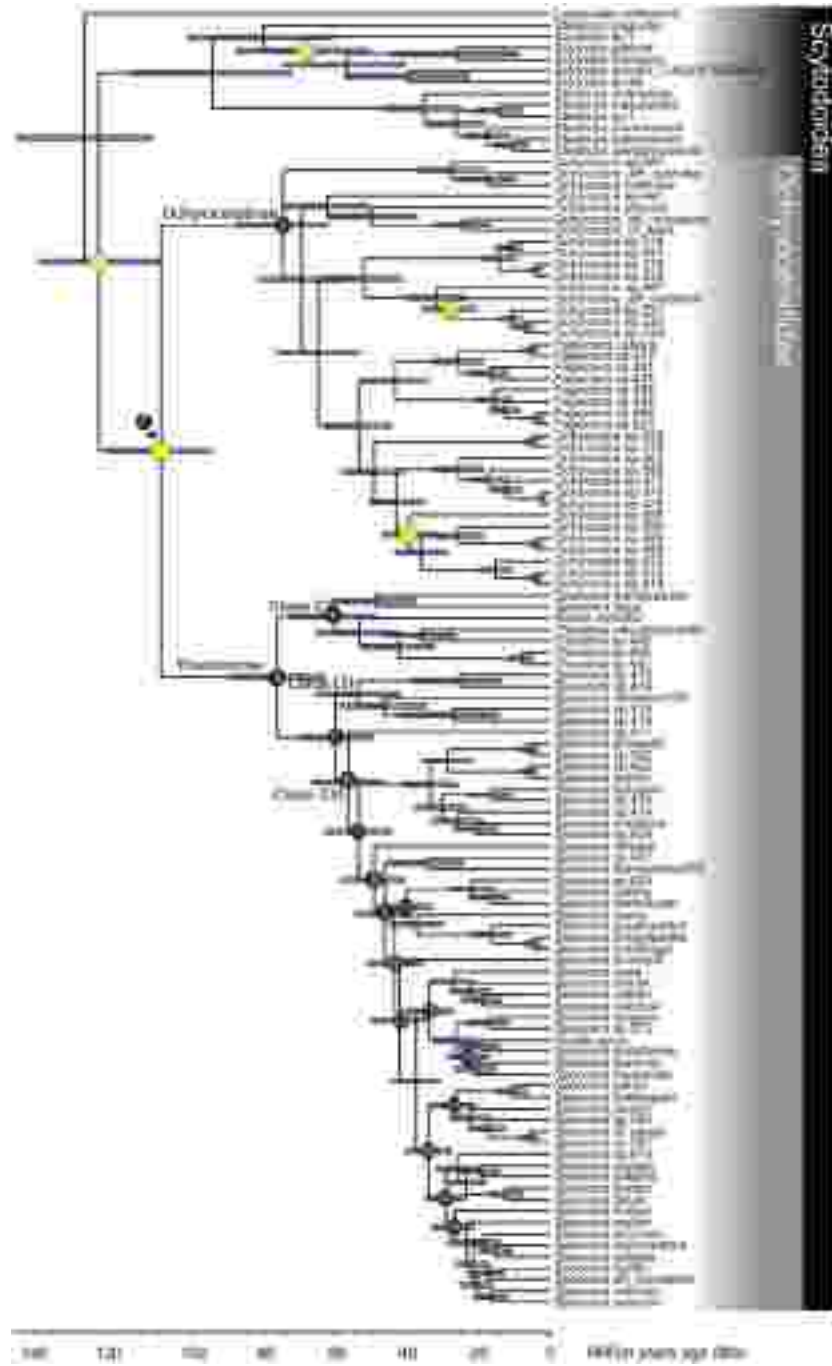


FIGURE 1. Time-calibrated phylogenetic tree for Ochyroceratidae inferred from a BEAST analysis. Chronogram based on the data set of classical markers. Circles represent calibration points. Black hexagons represent nodes in [Supplementary Figure S16](#) available on Dryad (see descriptions in [Supplementary Table S10](#) available on Dryad). Bars represent the 95% credibility interval of divergence time estimates. The star marked the endemic species of Fiji.

hypotheses on where these shifts might occur ([Rabosky 2014](#)). BMM can account statistically for incomplete taxon sampling, so we assigned sampling fractions at the geographic distribution based on the number of species following the World Spider Catalog. We used different values of a Poisson process prior (0.1, 1.0, 5.0, and 10.0) to test the sensitivity to the prior as it can affect BMM

results ([Moore et al. 2016](#)). Poisson process prior refers to `PoissonRatePrior`, which is  $\frac{1}{\text{Expected number of shifts}}$ . The BMM analysis was run for 20 million generations and sampled every 2000 generations. Convergence of the run was assessed by the log-likelihood trace and ESS of the log-likelihood. Evolutionary rate dynamics

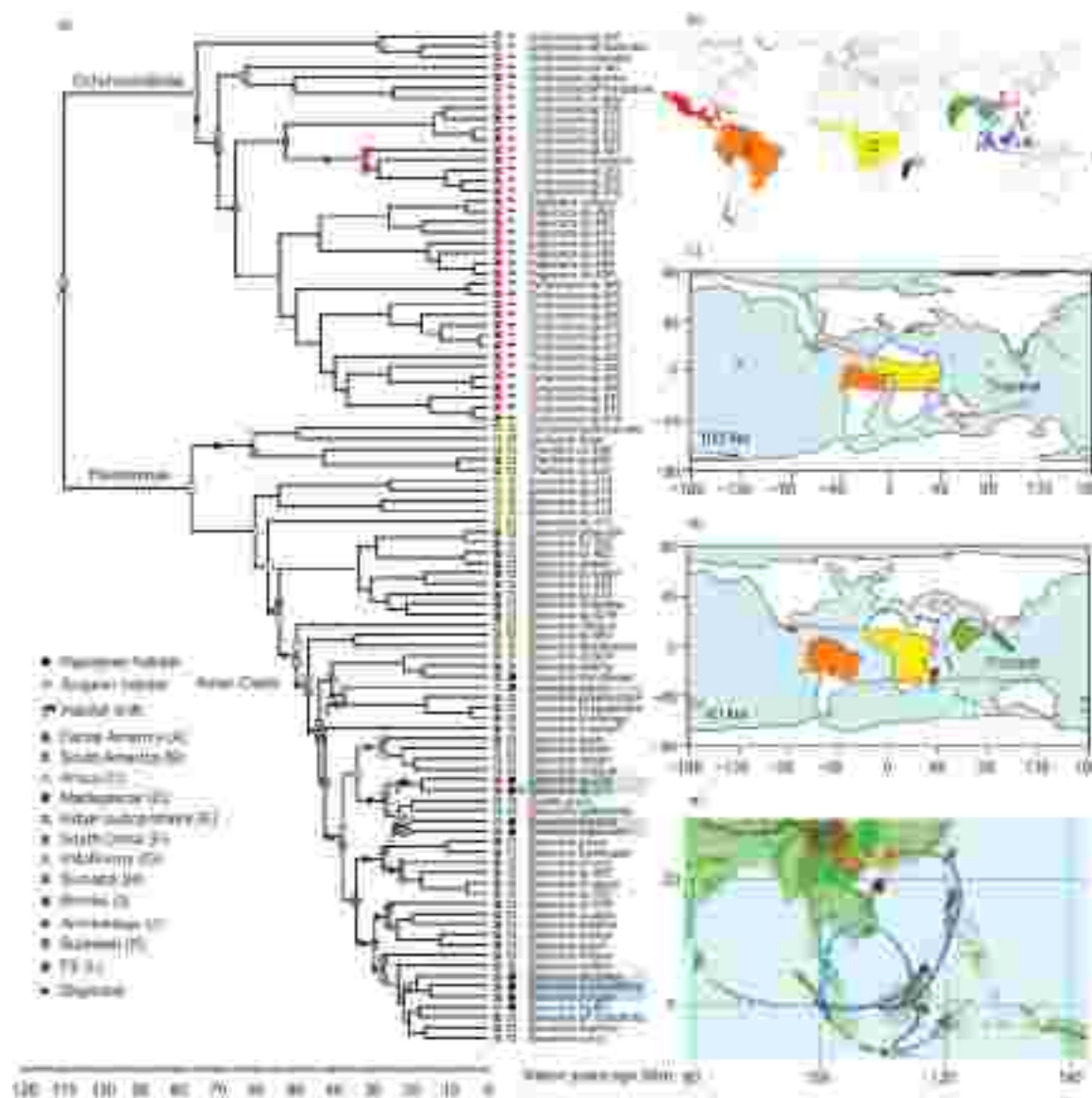


FIGURE 2. Ancestral area reconstructions (AARs) and ancestral habitat reconstructions for Ochyroceratidae and paleogeology (modified from Leprieur et al. 2016). a) Squares at tips indicate current distributions; AARs are shown using the DIVALIKE model in BioGeoBEARS; dots at tips indicate current habitats; boxes include cave-dwelling species. b) Areas defined for ancestral area analyses. c and d) On the right are maps of the distribution of land and sea at 100 Ma and 40 Ma; areas surrounded by a dashed line are the tropics. e) The sketch shows the most likely ancestral area and dispersal routes of the Asian clade.

were analyzed and visualized using BAMMtools. We also used RPANDA to infer diversity dynamics from phylogenies using a birth–death model of cladogenesis (Morlon et al. 2011). This method has the advantage of assuming extinction rates varying as a function of time (unlike BAMM, Rabosky et al. 2013). We designed six nested diversification models as follows: i) a Yule model, where speciation is constant and extinction is null; ii) a constant birth–death model, where speciation and extinction rates are constant; iii) a BVAR model, speciation rate varies exponentially and extinction is null; iv) a BVARDCST model, speciation rate varies exponentially and extinction rate is constant; v) a BCSTDVAR model, speciation rate is constant

and extinction rate varies exponentially; and vi) a BVARDCST model, speciation and extinction rates are both varying exponentially.

#### Climatic Factor-Based Analyses

*Geographical data assembly.*—We obtained all locality data of the 85 known theotimine species from the primary literature as well as data from 46 putative theotimine species reported here from our collection. For literature with only the administrative region, we assigned coordinates from administrative regions—the centroid of the polygon using Google Earth

(<http://www.google.com/earth/>). If the localities were too vague to get accurate coordinates, the data were omitted. In total, we obtained 217 occurrence records with locality information (Supplementary Table S9 available on Dryad). For each record, we extracted 19 climatic variables from the WorldClim database using ArcGIS 10.0 (ESRI, Redlands, CA, USA). We then calculated the species mean for each of the 19 variables.

*Phylogenetic principal component analysis.*—We explored the differences in the external climate between hypogean spiders and the others using an approach similar to a phylomorphospace (Sidlauskas 2008) on phylogenetic principal component analysis (pPCA; Revell, 2009). The principal component analysis was performed on the Asian clade, including theotimine species from the Indian subcontinent and SE Asia. pPCA1–pPCA3 explained more variation than expected based on a broken-stick distribution for a total of 91.3% and so were used in subsequent analyses. The first three pPCAs appear to describe precipitation of driest month/quarter, min temperature of coldest month/quarter, and precipitation of wettest month/quarter, respectively, based on the loadings of climatic variables.

## RESULTS

### Phylogeny

The transcriptomic data set comprised 339 orthologs from 125 species representing 54% of spider families. The data set of classical markers comprised 7 genes, 13 outgroups, and 101 ochyroceratid species, following previous taxonomic literature (Deeleman-Reinhold 1995) and our own results from the species delimitation analyses (see Supplementary File S2 available on Dryad). Putative species that are currently being described are referred to by unique species numbers. ML and BI analyses of both data sets yield well-resolved, similar topologies (Supplementary Figs. S4–S7 available on Dryad). Our study included, for the first time, the two subfamilies of Ochyroceratidae, and as such, a novel relationship is recovered. The results refute the relationship between Ochyroceratidae and Psilodercidae proposed by the extensive analysis of Wheeler et al. (2016). Psilodercidae are resolved as monophyletic and the sister group of the large lineages encompassing Sicariidae + Scytodidae + Ochyroceratidae (ML bootstrap = 100, BI posterior probability = 1.00; Supplementary Figs. S4 and S5 available on Dryad). Ochyroceratidae are corroborated as monophyletic (ML bootstrap = 100, BI posterior probability = 1.00), being the sister group of Scytodidae with strong support in all analyses (Supplementary Figs. S4–S7 available on Dryad). Topologies obtained from the data set of classical markers strongly support that Theotiminae and Ochyroceratinae are both monophyletic (ML bootstrap = 100, BI posterior

probability = 1.00). At the base of Theotiminae, there are six lineages that are endemic to Gondwanan continents including Africa, Madagascar, and the Indian subcontinent (Supplementary Figs. S6 and S7 available on Dryad). A clade of theotimines, which is widely distributed in SE Asia, is nested deeply in this subfamily. *Speocera* and *Ochyrocera* are the two largest genera of Ochyroceratidae, and each contains about 50 species. Our results suggest that they are polyphyletic (Supplementary Figs. S6 and S7 available on Dryad), indicating the need for taxonomic revisions. Specimens of *Theotima minutissimus* from Central America, the Indian subcontinent, South China, Indo-Burma, Sumatra, Borneo, Philippines, Sulawesi, and Fiji clearly cluster together, showing no genetic differences and, thus, its worldwide distribution reflects the potential evolutionary significance of being parthenogenetic (Edwards and Edwards 2003).

### Divergence Time

The node age estimates obtained using the transcriptomic data set are similar to a recent study on spider evolution (Fernández et al. 2018). The chronogram based on this data set suggests a Carboniferous origin of spiders (Araneae) at 385–300 Ma, overlapping with the range of 397–334 Ma in the recent study (Fernández et al. 2018). The origin of Synspermiata is dated to 234 Ma [95% credibility interval (CI) 267–207 Ma], narrower than the age interval of 271–189 Ma in Fernández et al. (2018). In the Synspermiata, the split between sister groups of Ochyroceratidae and Scytodidae occurred at 145 Ma (95% CI 173–121 Ma) (Supplementary Fig. S3 available on Dryad). The recalibrated chronogram suggests that BEAST and MCMCTREE tended to deliver similar estimates for most lineages of interest (Supplementary Table S10 available on Dryad). In particular, the estimated dates of speciation for the endemic species of Fiji postdate the emergence of the islands above sea level (Fig. 1). Because BEAST allows more complex nucleotide-substitution models than the other dating approach, the following analyses focus on the chronogram produced by BEAST (Fig. 1 and Supplementary Table S10 available on Dryad). Ochyroceratinae split from Theotiminae during the Early Cretaceous 124–95 Ma and began to diversify in the Late Cretaceous 88–62 Ma. Theotiminae also diversified into several major lineages during the Late Cretaceous 90–63 Ma. Within the subfamily Theotiminae, *Speocera* from the Indian subcontinent is recovered as the sister group of the SE Asian *Speocera*, separating around 55–38 Ma.

### Biogeographic and Habitat Estimates

The analyses conducted on the DIVALIKE and DEC models delivered identical results on the major clades (Fig. 2, Supplementary Figs. S8–S11). Ochyroceratidae diversified in the Early Cretaceous

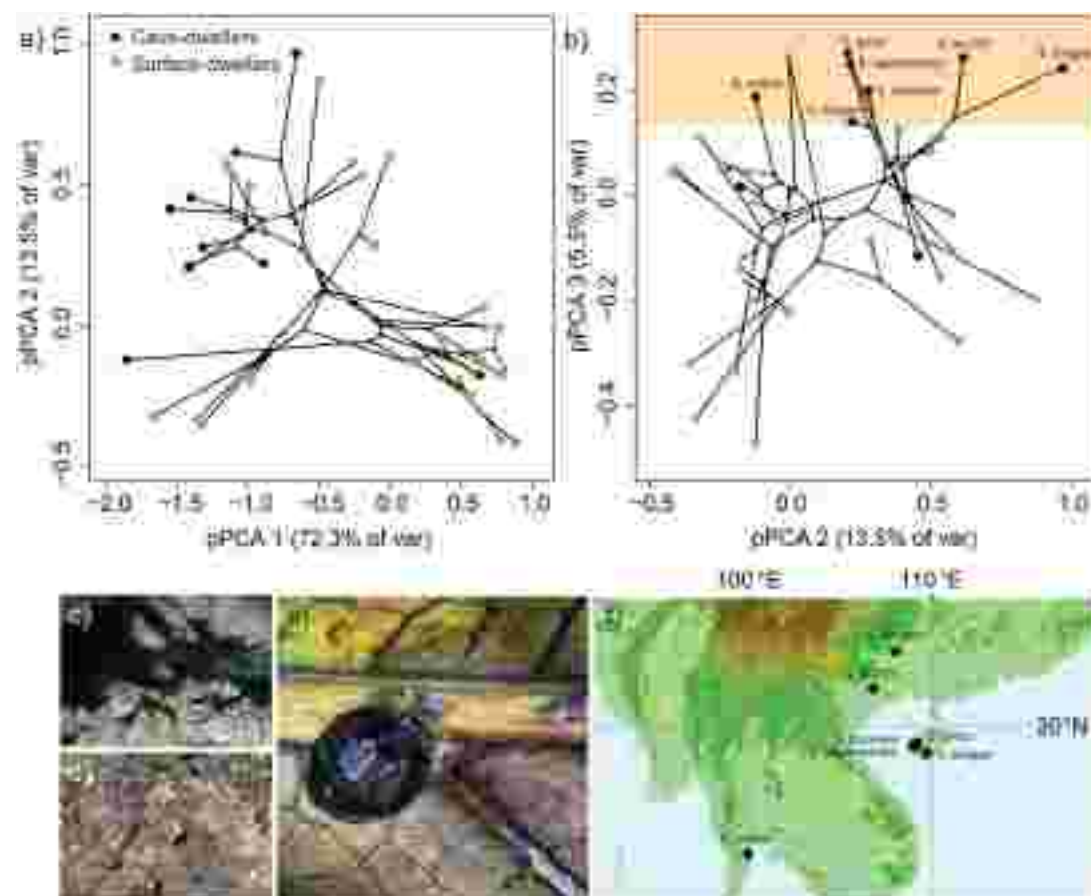


FIGURE 3. Phylomorphospace on phylogenetic principal component analysis axes and habitats of Theotiminae. a and b) Black circles indicate cave-dwelling species, and the other circles indicate surface-dwellers; axis pPCA 3 represents differences in precipitation of wettest month/quarter; the rectangular region indicates low values of precipitation; the values indicating the relative contributions of each climatic variable to the rest axes are shown in [Supplementary Table S12](#) available on Dryad. c) Epigeal habitats. d and e) Hypogean habitats. f) Black circles indicate the locations of cave-dwelling species.

within a broad geographic range including South America and Africa, followed by vicariance between the subfamilies Ochyroceratinae and Theotiminae (Fig. 2). Reconstructed biogeographic histories revealed distinct evolutionary routes of these two subfamilies. The ancestral range of ochyroceratines suggests South American origins, with dispersal from South America to Central America and trans-Pacific dispersal from Central America toward Fiji. By contrast, our ancestral reconstruction supports that theotimines originated in Africa, and then dispersed to Madagascar. Moreover, the ancestral reconstruction supports that Theotiminae dispersed from Africa to the Indian subcontinent 59–41 Ma, followed by a geographic colonization from the Indian subcontinent to Sumatra at 55–38 Ma (Fig. 2). After migration from India to SE Asia, diversity of Theotiminae arose through the combination of in situ diversification ( $n = 25$ ) and immigration ( $n = 12$ ) between six biogeographic areas of SE Asia.

For the ancestral state reconstruction, results inferred using RASP and corHMM were concordant ([Supplementary Figs. S12 and S13](#)). The ancestor of the subfamily Theotiminae is likely to have arisen from a

surface-dweller (Fig. 2, [Supplementary Figs. S12 and S13](#)). The same general habitat preference was shared with species distributed in the tropics, such as some species in subtropical regions, such as South China, developed a stronger bond with hypogean habitats. The shift to hypogean habitats is estimated to have occurred independently four or five times and follows colonization events from the tropics to marginal tropics or subtropics (Fig. 2).

#### Diversification Across Clades and Time

The exploration with pPCA revealed that the external climate of most cave-dwelling spiders diverges from that of the surface-dwellers (Fig. 3) and reflects climatic differences between different latitudes and climate zones. The climate data of different clades specialized to live in caves seems to show some component of convergence, as revealed especially by pPCA3 (Fig. 3). This PC shows the clustering of three clades and a clear distinction with respect to other members of the Asian clade. Higher values of pPCA3 were

mostly related to lower precipitation of the wettest Month/Quarter (Supplementary Table S12 available on Dryad). The relative humidity of caves is higher than that of the environment outside, and the precipitation is positively correlated with relative humidity. Thus, external unfavorable conditions (e.g., dry and seasonal climate) can render caves suitable refugia for species.

#### DISCUSSION

Biotic exchange between India and SE Asia has been widely studied. For example, Li et al. (2013) explored the correlation between the Indian–Asian faunal exchange and geological hypotheses, and Grismer et al. (2016) investigated the origin of India’s biodiversity. These studies focus on organisms that are not capable of long-distance dispersal across marine barriers. Therefore, they used the controversial geological hypothesis (i.e., island arc-continent collision) to explain the Early Eocene faunal exchange between India and SE Asia (Klaus et al. 2010; Li et al. 2013; Grismer et al. 2016). Klaus et al. (2010) supported this hypothesis, but he recognized the influence of climate on biological migrations. Biological migrations are not influenced solely by the history of geological connections but also by the history of connections among suitable climates (Klaus et al. 2010). To evaluate the role of both geological and climatic factors, we used comprehensive methods including both biogeographic and climatic analyses. Our analyses consistently support the migration of Theotiminae from the Indian subcontinent to SE Asia during the Early Eocene. Climatic data of extant Ochyroceratid species and their fossil records suggest that climatic niche is conserved across temporal scales. Their conserved climatic preferences are consistent with the Early Eocene tropical, perhumid climates in SE Asia (Friederich et al. 2016). This result suggests that the existence of tropical climate corridors might mediate biological migration from the Indian subcontinent to SE Asia, whereas unsuitable climatic conditions from the eastern coast of

China to Central Asia might act as a barrier preventing colonization (Figs. 2 and 4).

#### Evolutionary Origin of Ochyroceratidae

Our study represents the first integrative analysis of the evolutionary history of Ochyroceratidae. We found that Sicariidae + Ochyroceratidae + Scytodidae is the sister group of Psilodercidae (Supplementary Figs. S4 and S5 available on Dryad); in contrast, a previous study, with weak support, placed Psilodercidae within the Ochyroceratidae (Wheeler et al. 2016). This difference in the placement of Ochyroceratidae may result from long-branch attraction and a smaller sample of species. Ochyroceratidae originated in the Early Cretaceous ~145 Ma, when West Gondwana was still intact (Chatterjee et al. 2013). Subsequently, Ochyroceratidae diversified into two subfamilies around 109 Ma, nearly coinciding with the breakup of South America and Africa during the Early Cretaceous (Heine et al. 2013). Reconstructed biogeographic histories show that the most recent common ancestor (MRCA) of Theotiminae inhabited Africa, whereas Ochyroceratinae as a whole have a South America origin (Fig. 2). Thus, a Gondwanan vicariance scenario is regarded here as the preferred hypothesis to account for the evolutionary origin of Ochyroceratidae.

Both subfamilies originated in Gondwana but currently have different distribution patterns which are explained by the fragmentation of Gondwana and subsequent biological migrations. Theotimine species occupy pantropical regions including Madagascar, South America, the Indian subcontinent, and SE Asia, throughout tropical Africa (Fig. 4). Theotimines in Madagascar, South America, and the Indian subcontinent have post-Gondwanan (Cenozoic) origins that are best explained by dispersal rather than vicariance (Fig. 2). For example, colonization from Africa to the Indian subcontinent occurred 59–41 Ma, when the Indian subcontinent was connected to the Oman–Kohistan–Dras island arc (Fig. 4b). Such an island arc would not have been a substitute for transoceanic



FIGURE 4. Dispersal of Ochyroceratidae between areas. Paleoclimate reconstructions are modified from Morley (2018). a) India drifted into the equatorial latitudes during the Paleocene. b) India made the initial collision with Eurasia during the Early Eocene, when India and SE Asia were at the same latitude but without a land connection. c) Due to the collision between India and Eurasia, Southern Tibet reached at least an elevation of 4000 m in the Middle Eocene.



dispersal to India from Africa, but could have helped in reducing the distance to be crossed over open ocean, permitting biotic exchange with Africa (Chatterjee and Scotese 2010). After the breakup of Gondwana, the drifting Indian subcontinent underwent environmental changes induced by latitudinal migrations and the Deccan Traps (Li et al. 2013). These events resulted in massive extinctions in the Paleocene. Because South America is believed to have become isolated from all other continents 100–60 Ma, Ochyroceratinae is much more narrowly distributed than Theotiminae. Ochyroceratines have apparently dispersed only from South America to Central America, where Miocene fossils were found (Wunderlich 2004). The fossils imply a long-term tropical distribution pattern.

#### *Migration from India to SE Asia*

Recent studies have suggested that a wide variety of organisms originating in India have colonized and diversified in SE Asia (Klaus et al. 2016; Morley 2018). This evolutionary process emphasizes that migration from India to SE Asia has played an important role in SE Asian biodiversity (Li et al. 2013). Our phylogenetic analyses support the sister relationship between the Indian subcontinent clade and the SE Asian clade of Theotiminae. The MRCA of these two clades was distributed on the Indian subcontinent with a relative probability of 90% (Supplementary Fig. S11 available on Dryad). Thus, we suspect that the SE Asian theotimine spiders also originated on the Indian subcontinent. The India–Asia collision initiated 60–50 Ma (Royden et al. 2008; Hu et al. 2016), starting in the west and proceeding eastwards along the Indus–Yarlung Suture (Hu et al. 2016). Additionally, direct tectonic interaction between the Indian subcontinent and SE Asia occurred 30 million years later, in the Miocene (Khin et al. 2014). Thus, the colonization of Sumatra 55–38 Ma predates the appearance of land corridors between the Indian subcontinent and SE Asia (Fig. 2), suggesting that biological migration does not depend on geological collision. Ballooning dispersal has not been observed in these small (~1 mm body length) spiders, as they tend to have quite narrow niches that preclude convective air currents (Bell et al. 2005). However, occasionally, they can move passively on floating “vegetation-rafts” from one landmass to the next closet landmass (Brignoli 1976). In this way, just one dispersal event may have occurred from India to Sumatra prior to the establishment of a land corridor, which resulted in a monophyly of the Asian clade. Both paleontological and biogeographic data also support that minor marine barriers permitted biotic exchange between different Gondwanan landmasses (Morley 2018; Yuan et al. 2018).

After the migration from India to SE Asia, the diversity of Theotiminae was assembled by migration and in situ species diversification across SE Asia. Theotimines first diversified within Sumatra and started to colonize Borneo, followed by independent

migrations into Indo-Burma, the Philippines, and Java (Fig. 2e). Borneo, with a large area and prolonged emergent history, provides a major source–sink area for lineage migration. Subsequently, three clades from Indo-Burma and the Philippines migrated to South China independently. These migration events between the mainland and numerous islands of SE Asia are evidence for transoceanic dispersal of theotimines (Fig. 2). The geographic colonization of isolated areas lacking competitors provided opportunities for adaptive radiations. Nevertheless, Theotiminae follow a diversity-dependent pattern featuring a high initial diversification rate that decreased over time. A similar pattern has been reported in continental colonizations by murid rodents (Schenk et al. 2013). Consequently, geographic colonization does not guarantee adaptive radiations of some clades (Stroud et al. 2016).

#### *Interpreting the Effects of Climate*

The presence of climatic niche conservatism can be crucially important in shaping large-scale biogeographical patterns, because it constrains species from expanding to different climatic zones (Wiens and Donoghue 2004). Theotiminae show a high degree of niche conservatism in tropical forests (Fig. 2). Although a few species extend their distribution into margins of tropical zones, most have changed their habitats and live in caves. Our analysis indicates that habitat shifts from leaf litter to caves occurred nearly simultaneously with colonization events from the tropics to marginal tropics or subtropics (Fig. 2). Most caves have almost constant temperature and high humidity throughout the year, providing suitable shelters for theotimines in seasonally variable environments. Our pPCA approach offers additional evidence supporting niche conservatism of theotimines. Species in a wet environment can live in the litter or caves, whereas species in an environment with low precipitation are more often found in caves (Fig. 3).

Theotiminae is a tropical spider group that originated in an area of high temperature and precipitation (Fig. 2 and Supplementary File S2 available on Dryad). The MRCA of the Indian subcontinent clade and the SE Asian clade likely also lived in a very warm, wet environment, similar to the stable warm conditions in the tropics throughout the Eocene (Evans et al. 2018). During the Early Eocene, with the Indian subcontinent drifting northward across the equator (Kent and Muttoni 2008), both the Indian subcontinent and SE Asia were largely covered by tropical forests, as indicated by fossil occurrences of angiosperms (Kent and Muttoni 2008; Morley 2018; Prasad et al. 2018). Similar tropical, perhumid climates in the Early Eocene in India and SE Asia may have provided a corridor for theotimine migration (Fig. 4b and Supplementary Fig. S16 available on Dryad). In contrast to SE Asia, East Asia, including China, Japan, Korea, and Mongolia, was dominated by an arid climate with an annual precipitation less than

800 mm in the Early Eocene (Zhang et al. 2012; Liu et al. 2015). Despite no obvious geographical barrier, this dry or seasonal climate and niche conservatism acted as barriers to the colonization of East Asia by theotimines. Moreover, the southern Tibetan Plateau developed into a mountain belt with an elevation of about 4000 m in the Early Eocene, extending from roughly 10° N (± 5° N) at 90° E to 20° N (± 5° N) at 70° E (Ding et al. 2014). The rising plateau had a colder and drier climate than lower elevations, and this would have been unsuitable environment for theotimines. The India–Asia collision during the Early Eocene could not mediate biotic interchange between the Indian subcontinent and East Asia due to differences in regional climate and environmental tolerances of species. Similarly, this pattern occurs in the Great American Biotic Interchange (Marshall 1988; Sedio et al. 2013). North American mammals colonized South America via a savannah corridor and South American woody plants retained the microhabitat requirements of their North American ancestors (Klaus et al. 2016).

In conclusion, our study resolves relationships among extant ochyroceratids for the first time and provides a framework for understanding the dynamics and mechanisms of Indian–Asian biological migration. Ochyroceratids migrated from tropical forests of the Indian subcontinent into warm, wet habitats of SE Asia during the Early Eocene, a result that emphasizes the importance of climate in biogeography and helps explain the prevalence of a climatic connection as a corridor of biological migration. Our study also highlights that an integrative approach combining different sources of evidence, such as biogeography and ecology, provide more realistic reconstructions of evolutionary history. We predict that other organisms with a tropical distribution exhibit similar mechanisms of migration.

#### SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kd2b16c>.

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