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Biogeographical history of golden orbweavers: Chronology of a global conquest

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Abstract

Aim: A wholistic biogeographical reconstruction should combine a phylogeny with specifics of organismal biology, plate tectonics and consequent probabilities of historic dispersal events. Here, we demonstrate this approach by reconstructing the geographical origin and sequence of intercontinental colonization of the golden orbweaving spiders, a global clade. We test two alternative hypotheses about their ancestral range. Due to the highest contemporary species diversity in Africa, the 'Out of Africa' hypothesis predicts the Afrotropics as their most likely ancestral area. The alternative, 'Out of West Burma' hypothesis aims to explain a Burmese amber fossil as stem nephilid. Because the West Burma block probably detached from Australia, then rafted towards Laurasia, either on its own or with India, this hypothesis predicts either Australasia or Indomalaya (or both) as the ancestral area.

Location: Worldwide.

Taxon: Golden orbweaving spiders, family Nephilidae.

Methods: We construct an expanded phylogeny of nephilid spiders and apply RASP (Reconstruct Ancestral State in Phylogenies) to infer their global biogeographical history. We fit the data to six integrated biogeographical models: DEC, DIVALIKE, BAYAREALIKE and their +*j* variants. We fine-tune the analysis by evaluating varying probabilities of dispersal between geographical areas throughout the clade's evolutionary history. We use the physical distance between the areas as a proxy for dispersal probabilities, thus accounting for plate tectonics.

Results: The best supported model reconstructs both Australasia and Indomalaya as ancestral area. In several parts of the phylogeny, these areas persist for the estimated 130-million-year evolutionary history. However, numerous intercontinental shifts in nephilid biogeographical history are also inferred. Since nephilid origins are clearly Gondwanan, our study supports the interpretations that Burmese amber contains Gondwanan biota.

Main conclusions: These results are consistent with the Out of West Burma hypothesis but reject the Out of Africa hypothesis. That certain clades persist in their ancestral ranges while others may shift continents aligns well with the known nephilid biology. Our methodological approach that assesses organismal specific dispersal probabilities through concrete distances measured though time slices of the Earth's history can be applied to biogeographical reconstruction of any lineage.

KEYWORDS

ancestral areas, Burmese amber, Gondwana, jump dispersal, *Nephila*, Nephilidae, out of West Burma hypothesis, plate tectonics, spiders

1 | INTRODUCTION

A wholistic biogeographical reconstruction of a lineage should combine a robust, species-level, time-calibrated phylogeny with probabilities of historic dispersal events. Ideally, these probabilities would vary by time slices, being derived from details of biology of the studied organisms combined with accurate reconstructions of plate tectonics history, including measured distances among geographical areas. Numerous elegant biogeographical studies have combined some of these elements (e.g. Condamine, Sperling, & Kergoat, 2013; Dornburg, Moore, Beaulieu, Eytan, & Near, 2015; Dupin et al., 2017; Herrera et al., 2015; Nauheimer, Metzler, & Renner, 2012). However, to the best of our knowledge, wholistic approaches that would base the differences in dispersal probabilities through time slices on concrete measurements have not become mainstream in biogeography. Here, we outline such approach through a global biogeographical study of golden orbweaving spiders (family Nephilidae), using a well sampled and robust phylogeny (Kuntner et al., 2019), as well as estimated probabilities of their historic dispersal events.

Nephilids are renowned for their extreme phenotypes, most notably their pronounced, female-biased sexual size dimorphism (Coddington, Hormiga, & Scharff, 1997). In fact, they represent the most extreme case of sexual size dimorphism among all terrestrial animals, with females up to 500 times heavier than males (Kuntner, Zhang, Gregorič, & Li, 2012). Females, but not males, build asymmetric orb webs of sometimes exaggerated proportions (Kuntner, 2017; Kuntner et al., 2019). Nephilids are interesting also biogeographically because of their hypothesized ancient origin in the Mesozoic (Kuntner et al., 2019), their present wide distribution across most continents, and their varying dispersal propensities. Namely, some species are excellent aerial dispersers capable of long-distance, often overwater, travel, while others are not known to disperse over large distances and are distributed narrowly, such as some species of *Clitaetra*, *Nephilingis* and *Herennia* (Kuntner & Agnarsson, 2011a, 2011b). Ballooning (becoming airborne by releasing silken threads into a wind current) is a likely means of aerial dispersal in nephilids, as demonstrated in *Nephila pilipes* (Lee, Kuntner, & Li, 2015). Thus, they are also capable of sustaining gene flow across relatively large distances, for example, between islands of the Caribbean and North American mainland (Čandek, Binford, Agnarsson, & Kuntner, 2020).

Nephilid species distributions are predominantly tropical and subtropical with some species ranging into temperate regions (Figure 1; Su et al., 2011). Genera are often sympatric, with the majority of the 37 valid species (Kuntner et al., 2019, Table 1) found in the Afrotropics and Indomalaya. Specifically, *Herennia* and *Nephilengys* are co-distributed and range from India to Australia (Kuntner, 2005, 2007). *Clitaetra* inhabits tropical and subtropical Africa and some of the islands of the western Indian Ocean (Kuntner, 2006), and *Indoetra* is endemic to Sri Lanka (Kuntner, 2006; Kuntner et al., 2019). *Nephilingis* has Afrotropical species, but one extends disjunctly into South America (Kuntner, 2007; Kuntner et al., 2019). A newly reclassified *Nephila* (Kuntner et al., 2019) only contains two species: *Nephila constricta* is found in equatorial Africa (Su et al., 2011), while *N. pilipes* is widely distributed from South Asia through South-East Asia, and into Australia and the Pacific (Su, Chang, Lee, & Tso, 2007). The most species-rich nephilid genus, *Trichonephila*, has a wide distribution in tropical, subtropical and temperate regions of most continents (not Europe and Antarctica). As an exception among nephilid genera, some of the 12 extant *Trichonephila* species show temperate distributions. *Trichonephila clavata* is found from the Himalayas to Japan (Su et al., 2011), with a recent introduction to North America (Hoebeke, Huffmaster, & Freeman, 2015). *Trichonephila clavipes* is distributed from southern USA to Argentina (Kuntner, 2017), and is, along with the neotropical *Trichonephila sexpunctata*, one of the two extant nephilid species endemic to the Americas. *Trichonephila edulis* is widespread in Australia and seasonally occurs in New Zealand (Paquin, Vink, & Dupérré, 2010). The remaining *Trichonephila* species are tropical and subtropical.

Very few nephilid fossils are known (see Kuntner, Arnedo, Trontelj, Lokovšek, & Agnarsson, 2013), mostly from the Dominican (Wunderlich, 1986) and Baltic amber (Wunderlich, 2004). At least some of these fossils aged 40–16 million years have been confirmed to be nephilids, and were therefore used as phylogenetic calibration points (Kuntner et al., 2013). Most recently, Burmese amber has been hypothesized to be relevant for nephilid origins (Poinar & Buckley, 2012). Mined in the region of Myanmar that sits on the West Burma tectonic block (Cruickshank & Ko, 2003), it represents a rich source of fossilized plant and animal material. Both palaeontological—fossils aged 97–110 million years (Cruickshank & Ko, 2003)—and geological evidence (Shi et al., 2012) suggest Burmese amber to be Cretaceous. At least its insect inclusions suggest that the West Burma Block was Gondwanan in origin. How West Burma arrived at its present location, however, is unresolved. A recent hypothesis is that it may have broken off from Australia, then either rafted to its present location on its own or attached to the Indian plate (Poinar, 2018). Based on the inclusions in Burmese amber, Poinar (2018) suggests the split between the West Burma Block and Gondwana could not have occurred before Early Cretaceous. Poinar

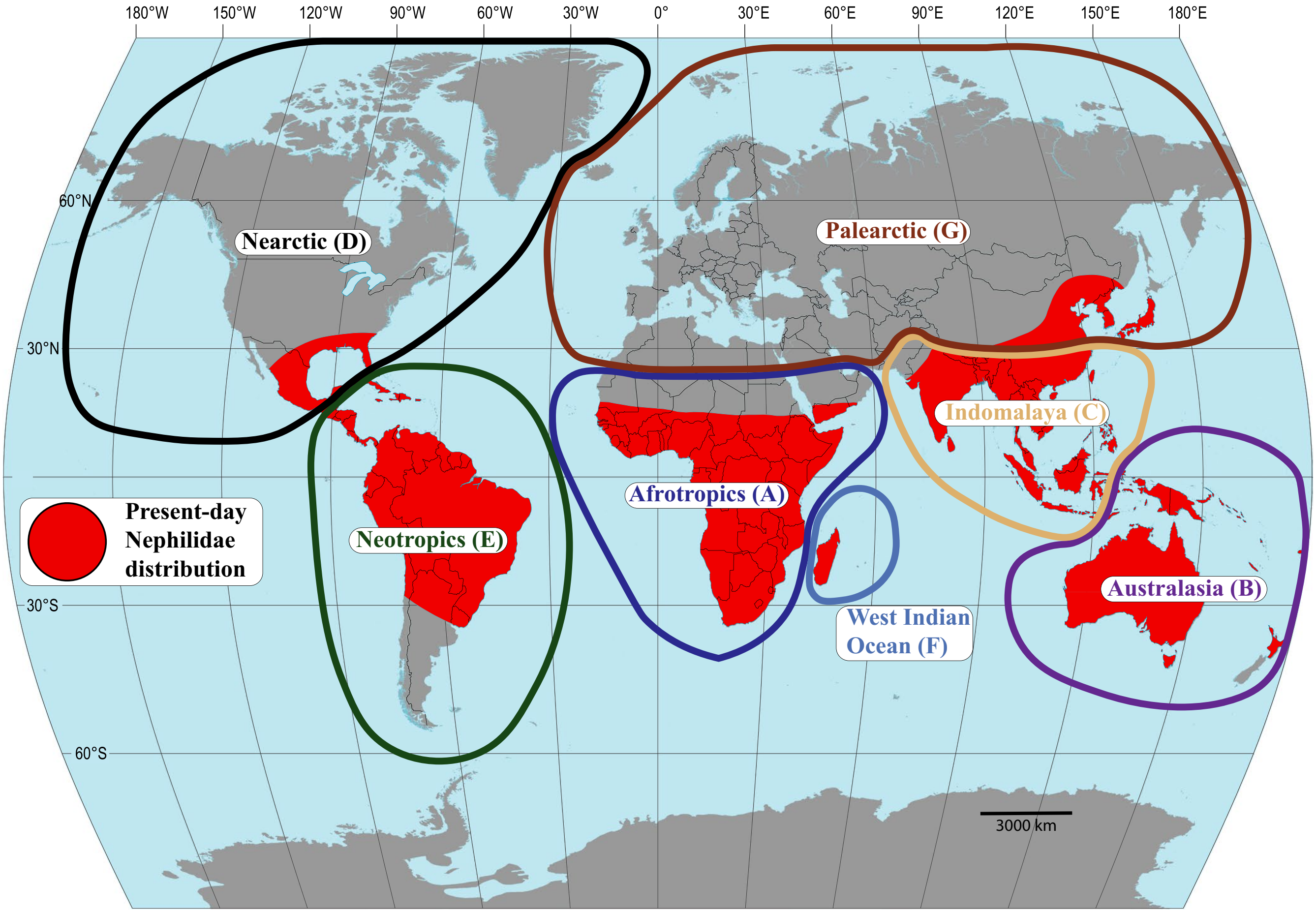

FIGURE 1 Present-day distribution of the spider family Nephilidae on a Miller global projection. Encircled are the seven biogeographical areas (A–G) used in this study [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Evaluation scores of six types of biogeographical models tested on a nephilid phylogeny using RASP. (LnL) log-likelihood; (AIC_c) Akaike information criterion corrected for small sample sizes; (AIC_c_wt) weighted AIC_c values. The asterisk indicates a statistically significant difference between the adequacy of fit of the basic and +*j* variant of each model. The model with the best overall fit is shown in bold

Model name	Ln L	AIC_c	AIC_c_wt	Δ −j/+j
DEC	−82.59	169.6	4.7e-05	*
DEC + j	−72.68	152.2	0.29	
DIVALIKE	−79.44	163.3	0.0011	*
DIVALIKE + j	**−71.81**	**150.4**	**0.68**	
BAYAREALIKE	−97.99	200.4	9.7e-12	*
BAYAREALIKE + j	−74.8	156.4	0.034	

and Buckley (2012) describe an inclusion from this amber containing one adult male and one juvenile spider, resembling modern nephilids. They name the species *Geratonephila burmanica* and suggest the presence of an adult male and a juvenile on the same web implies sociality (Poinar & Buckley, 2012). While the latter hypothesis has been rejected, *G. burmanica* has recently been interpreted as a possible stem nephilid (Kuntner et al., 2019).

The aims of the present study are to reconstruct the biogeographical history of the clade, and more precisely to test the hypothesized Gondwanan origin of Nephilidae (Kuntner, 2006). Assuming that the most recent clade age estimation at 133 Ma with a range of 97–146 Ma (Kuntner et al., 2019) is reasonably accurate, we test two alternative hypotheses about the nephilid biogeographical origin. The rationale for the first, 'Out of Africa' hypothesis, is that the continent that has retained the most taxonomic diversity from the Cretaceous to the present should correspond with the nephilid ancestral area (Lomolino, Riddle, & Whittaker, 2017). Since the Afrotropics have the most nephilid species today, the prediction of our first hypothesis is that present-day Africa should optimize as the most likely nephilid ancestral area. Assuming that *Geratonephila* from Burmese amber is indeed a stem nephilid, the second hypothesis posits that the geographical origin of nephilids was the Gondwanan fragment West Burma Block. This fragment probably got detached from Australia, then travelled to collide with SE Asia either as a distinct entity or attached to the Indian plate (Poinar, 2018). The age intervals of the fossil and the West Burma break-off partially overlap, thus we lack the resolution to precisely predict the nephilid ancestral range to either Australasia or Indomalaya. The broadly defined 'Out of West Burma' hypothesis would thus be supported if Australasia or Indomalaya (or both) optimized as the most likely nephilid ancestral area.

2 | MATERIALS AND METHODS

2.1 | Taxon selection

In order to reconstruct the biogeographical history of this lineage of spiders, a resolved species-level phylogeny is needed. Until recently, this has proven as problematic, not the least because precise familial taxonomic history has been controversial (Blackledge et al., 2009; Coddington, 1990; Dimitrov et al., 2012, 2017; Dimitrov & Hormiga, 2009; Hong-Chun, Kai-Ya, Da-Xiang, & Yang, 2004; Kallal, Dimitrov, Arnedo, Giribet, & Hormiga, 2019; Kuntner, 2006; Kuntner et al., 2013, 2019; Kuntner, Coddington, & Hormiga, 2008). In this paper, we treat nephilids at the family rank (Kuntner et al., 2019), although its rank continues to be debated (Kallal et al., 2019). The first comprehensive, global nephilid species-level phylogeny containing branch length information was constructed using three nuclear (18S rRNA, 28S rRNA, histone 3 subunit A) and five mitochondrial (COI, 12S rRNA, 16S rRNA and tRNA-leu and *nad1*) genes, additionally complemented with morphological data (Kuntner et al., 2013). The study dated nephilid origins to 40 Ma and *Nephila* origins to 16 Ma.

A recent, large-scale phylogenomic study, however, reassessed the nephilid evolutionary relationships and disputed the above hypothesized ages (Kuntner et al., 2019). This study applied Anchored Hybrid Enrichment phylogenomics to arrive at a robust, well-supported, and species-level phylogeny. The analysis targeted 585 single-copy orthologous loci, proven to reliably retrieve shallow and deep phylogenetic nodes in spiders (Hamilton, Lemmon, Lemmon, & Bond, 2016). The resulting chronogram, including 22 of 37 extant nephilid species, plus two fossils for time calibration (including *Geratonephila* from Burmese amber, see above), pushed nephilid origins back to the Early Cretaceous (133 Ma). The study also produced a phylogeny with added nephilid species without available phylogenomic data (Kuntner et al., 2019, Figure 3). Here, we further expanded this most recent phylogeny by adding undescribed *Herennia* species *H. nsp1-eva*, *H. nsp2-maj* and *H.* nsp3-tsoi to the original matrix of 31 nephilid species. This addition increased the total taxon sampling to 34 of the total 40 known (if undescribed) nephilid species (85%). To the 14 outgroup taxa from Kuntner et al. (2019) we added *Uloborus diversus*. A full matrix of aligned DNA sequences is available in Appendix S1.

2.2 | Time calibrated phylogeny

We constructed an original phylogeny based on CO1 sequences and constrained it according to the recently published phylogenomic nephilid tree (Kuntner et al., 2019). This COI matrix, building on that of Kuntner et al. (2019) with the addition of COI sequences of three previously undescribed species of *Herennia* (GenBank accession codes *H.* nsp2-maj MN855577, *H.* nsp1-eva MN855578, *H.* nsp3-tsoi MN855579), was aligned with MUSCLE (Edgar, 2004) implemented in MEGA7 (Kumar, Stecher, & Tamura, 2016). We then ran BEAST 2 (Bouckaert et al., 2014) via CIPRES (Miller, Pfeiffer, & Schwartz, 2010) on all CO1 sequences from 49 taxa. We used bModelTest (Bouckaert & Drummond, 2017) as the nucleotide substitution model and employed a relaxed log normal clock. Following Bidegaray-Batista and Arnedo (2011), the ucld.mean prior was set to have a normal distribution with a mean of 0.0199 and standard deviation of 0.001, while the ucldStdev prior was set to have an exponential distribution with a mean of 0.666. We constrained the ages of all nephilid nodes dated by Kuntner et al. (2019, Figure 2), with age estimates rounded to whole numbers and a standard deviation of 0.1. Four MCMC chains were set to run for 50 million generations.

2.3 | Ancestral area estimation

2.3.1 | Biogeographical areas

We quantified each species' geographical distribution by indicating its presence or absence in seven biogeographical areas, six of which correspond with biogeographical realms (Figure 1: A = Afrotropics, B = Australasia, C = Indomalaya, D = Nearctic, E = Neotropics and G = Palearctic). We defined an additional biogeographical area as islands of the west Indian Ocean (Figure 1: *F* = Madagascar, Réunion, Mauritius, Seychelles, Comoros) due to high level of nephilid endemism. Nephilid species ranges derived from the IUCN Red List (https://www.iucnredlist.org/).

2.3.2 | Biogeographical models

To reconstruct nephilid historical biogeography we used the software package RASP (Reconstruct Ancestral State in Phylogenies; Yu, Harris, Blair, & He, 2015) version 4.0 beta, which implements the R package BioGeoBEARS (Matzke, 2013). We fit the data to all six BioGeoBEARS models: DEC, DEC + j, DIVALIKE, DIVALIKE + j, BAYAREALIKE and BAYAREALIKE + j. These models differ in the types of cladogenetic events they allow. DEC models allow for narrow sympatry, subset sympatry and narrow vicariance, DIVALIKE models allow for narrow sympatry, narrow vicariance and widespread vicariance, and BAYAREALIKE models allow for narrow and widespread sympatry (Matzke, 2013). The '+j' variants of models account for jump dispersal, also known as founder event speciation, a common method of colonization of isolated landmasses and intercontinental dispersal. This type of model, specifically DEC + j, has recently been criticized for not modelling cladogenetic events (sympatric speciation, vicariance) as probabilistic with respect to time, unlike anagenetic events of local extinction and dispersal (Ree & Sanmartín, 2018). Consequently, the role of cladogenetic events is overestimated relative to time-dependent anagenetic range evolution. This effect is emphasized in the + *j* variant, because (a) it adds another possible cladogenetic event and (b) the probability of jump dispersal is expressed with a free

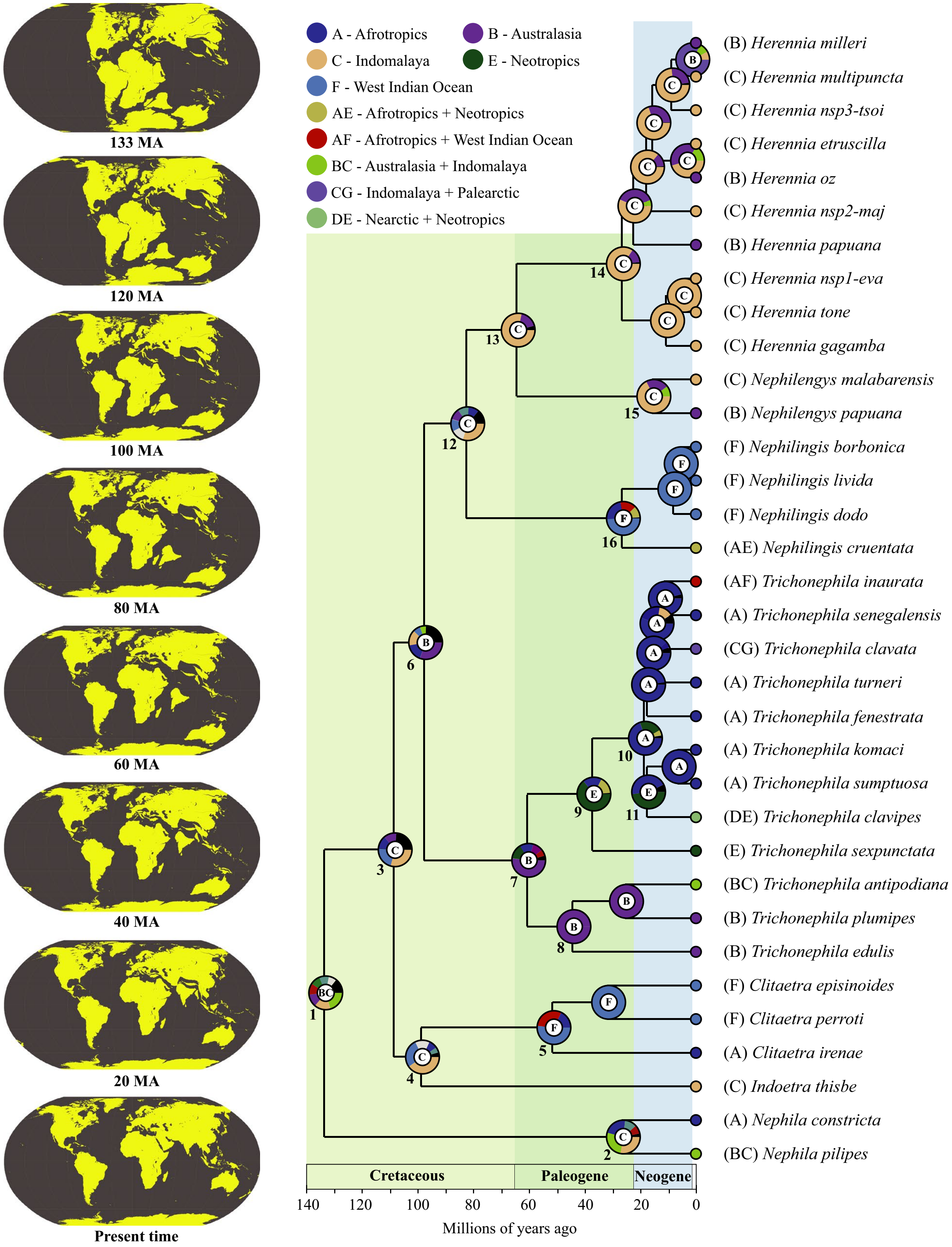

FIGURE 2 RASP global ancestral area reconstruction on a nephilid phylogeny, following the best supported model DIVALIKE + j. The letter at each node signifies the biogeographical area that received the highest support for that node. The colours of each circle reflect the relative proportion of support each biogeographical area received for that node. Letters next to extant taxa indicate their current distribution. Note that a combination of two letters indicates a distribution in both areas. The left panel shows the positions of continents from the time of nephilid origin until the present day, following Muller et al. (2019). Clade numbers match those in Table 2 and in the text [Colour figure can be viewed at wileyonlinelibrary.com]

parameter *j*, that, if maximized, makes non-jump dispersal events at deep nodes impossible (Ree & Sanmartín, 2018). However, both due to the scale investigated here and to the biology of the study organisms (orbweaving spiders are known to cross large distances via ballooning; e.g. Bell, Bohan, Shaw, & Weyman, 2005), we considered all six models.

2.3.3 | Dispersal probabilities

To fine-tune the analysis, we used time stratification to reflect the differences in probability of dispersal between geographical areas at different points in time. We used the physical distance between the closest points of the main landmasses of each pair of geographical areas as a proxy for dispersal probabilities. We measured the distances every 10 million years from 130 to 0 Ma using GPlates plate tectonics visualization software (Müller et al., 2018) on a recent tectonic reconstruction model (Müller et al., 2019), resulting in 294 measurements rounded to 10 km (see Appendices S2 and S3). We then transformed the measured distances to dispersal probabilities with low values reflecting large physical distances and vice versa. For a zero kilometre distance between areas (i.e. if areas are in physical contact), we set the highest dispersal probability to 95%, because dispersal is very likely, but not necessary. Moreover, we set the distance of 4,000 km as low (5%) dispersal probability, corresponding to the maximum distance spiders are thought to balloon. Namely, it has been inferred that Hawaii, one of the most isolated islands inhabited by spiders, have staged several colonization events from North America in the genus *Tetragnatha* alone (Gillespie, Croom, & Palumbi, 1994). The distance between Hawaii and the North American mainland is just under 4,000 km, as is the distance between another remote, spider-populated South Pacific island, Heard Island (Pugh, 2003, 2004) and Australia. We assumed a decreasing linear relationship of the remaining points between the two extremes and calculated the probabilities for all intermediate distances accordingly. All distances greater than 4,000 km were assigned an equal, 5% probability.

2.3.4 | Model evaluation

Prior to biogeographical analysis, we dropped all outgroups from the constructed phylogenetic tree, retaining only nephilid taxa. We then ran RASP, with a maximum number of areas occupied set to two. To compare the resulting model fit, RASP provides Akaike information criterion (AIC) values and Akaike weights (AIC_w). While AIC provides a common means of comparing the adequacy of the fit of alternative models to the data, small differences between AIC values are often misinterpreted and thus lead to overly confident conclusions (Wagenmakers & Farrell, 2004). To avoid this problem, AIC values can be transformed into AICw values, which, in turn, provide a straightforward measure of each model's relative probability (Wagenmakers & Farrell, 2004). Here, we report AIC_c values (AIC

TABLE 2 Three likeliest ancestral areas in 16 selected nephilid clades (labeled in Figure 2), as reconstructed by the DIVALIKE + j model in RASP. Letters correspond to the following geographical areas: A = Afrotropics, B = Australasia, C = Indomalaya, D = Nearctic, E = Neotropics, *F* = West Indian Ocean, G = Palearctic. A combination of letters signifies an ancestral distribution in both areas. All probabilities are rounded to a full number, MRCA = most recent common ancestor

Clade no.	Clade description	First (%)	Second (%)	Third (%)
1	Common nephilid ancestor	BC: 20	C: 16	B: 12
2	*Nephila* MRCA	C: 28	BC: 26	A: 23
3	All but *Nephila* MRCA	C: 30	F: 22	A: 12
4	*Clitaetra* + *Indoetra* MRCA	C: 40	F: 28	CF: 14
5	*Clitaetra* MRCA	F: 52	AF: 31	A: 18
6	*Trichonephila* + *Nephilingis* + *Nephilengys* + *Herennia* MRCA	B: 30	A: 17	C: 15
7	*Trichonephila* MRCA	B: 52	E: 15	A: 13
8	*Trichonephila antipodiana* + *Trichonephila plumipes* + *Trichonephila edulis* MRCA	B: 100	—	—
9	MRCA of all remaining *Trichonephila*	E: 64	A: 18	AE: 16
10	Clade 9 minus *T. sexpunctata*	A: 70	E: 22	AE: 5
11	*Trichonephila komaci* + *Trichonephila sumptuosa* + *Trichonephila clavipes* MRCA	E: 48	A: 45	DE: 4
12	*Nephilingis* + *Nephilengys* + *Herennia* MRCA	C: 30	CF: 13	F: 12
13	*Nephilengys* + *Herennia* MRCA	C: 78	B: 17	BC: 4
14	*Herennia* MRCA	C: 84	B: 14	BC: 2
15	*Nephilengys* MRCA	C: 68	B: 22	BC: 10
16	*Nephilingis* MRCA	F: 49	A: 23	AF: 16

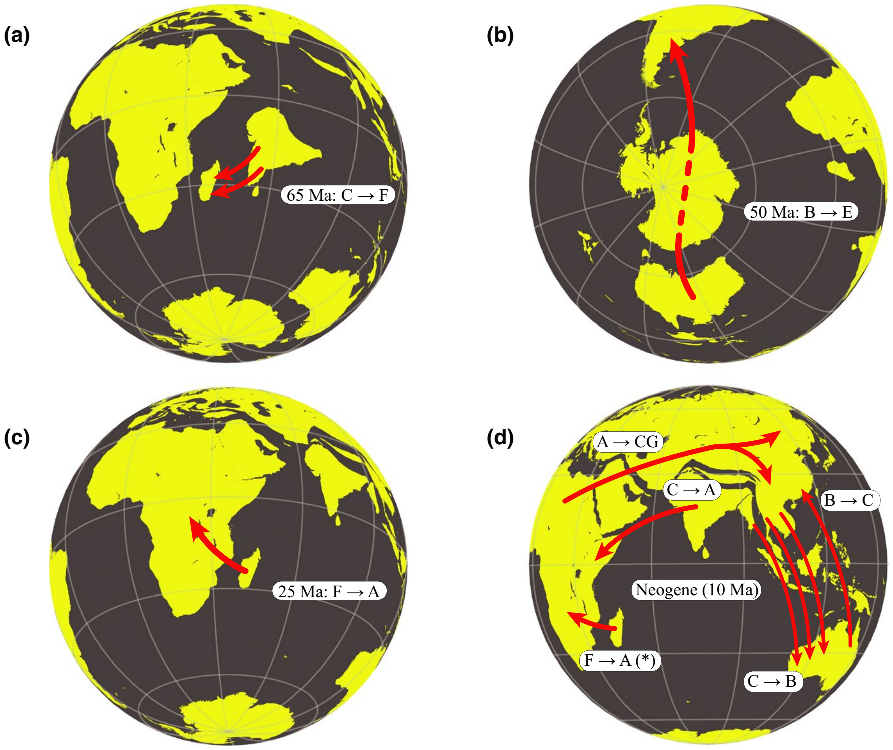

FIGURE 3 Examples of reconstructed intercontinental dispersal events in a nephilid phylogeny. The midpoint of the phylogenetic branch along which the dispersal event occurred was taken as the age of the event. Each arrow presents one independent dispersal event. (a) Dispersal from Indomalaya to West Indian Ocean islands occurred twice, by the ancestor of clade 5 and ancestor of clade 16. (b) Dispersal from Australasia to the Neotropics, presumably via Antarctica, in the ancestor of clade 9. (c) Dispersal from the West Indian Ocean islands to the Aftrotropics in the ancestor of *Clitaetra irenae*; (d) Dispersal events in the Neogene in the genera *Nephila* (C→A), *Trichonephila* (A→CG), *Nephilingis* (F→A), *Nephilengys* (C→B) and *Herennia* (B→C, 2x C→B). *The clade's (*Nephilingis cruentata*) subsequent dispersal from the Afrotropics to the Neotropics is not shown. Geographical areas: A = Afrotropics, B = Australasia, C = Indomalaya, D = Nearctic, E = Neotropics, F = West Indian Ocean, G = Palearctic [Colour figure can be viewed at wileyonlinelibrary.com]

scores corrected for small sample sizes) and their corresponding weighted values (AIC_c_wt).

3 | RESULTS

The biogeographical reconstructions are based on the chronogram from BEAST (Appendix S4) that precisely places the three undescribed *Herennia* species: *H. nsp1-eva* from Sulawesi is sister to *H. tone* from the Philippines; *H. nsp2-maj* from Vietnam is sister to a clade that contains both Indomalayan and Australasian species; *H. nsp3-tsoi* from Taiwan is sister to a clade containing *H. multipuncta* (Indomalayan) and *H. milleri* (Australasian). All other nephilid nodes are topologically constrained and thus identical to Kuntner et al. (2019).

In all three RASP model pairs, +*j* variants provide significantly different results than their basic alternatives (Table 1). DIVALIKE + j shows the lowest AIC_c and highest AICc_wt and log-likelihood (LnL) values, all indicating it as the best supported model for our data.

Table 2 summarizes the three most likely ancestral areas based on DIVALIKE + j model for 16 selected clades (for all nodes, see Figure 2). The nephilid ancestor (Clade 1; see Figure 2 and Table 2) was most likely distributed over Indomalaya and Australasia (20%). The plausible alternatives have marginally lower probabilities: Indomalaya (16%), Australasia (12%). All these results are consistent with the Out of West Burma hypothesis. An Afrotropical most recent common ancestor (MRCA) of all nephilids is much less plausible (3%), rejecting the Out of Africa hypothesis.

Several dispersal scenarios are implied (Figure 3a–d). The ancestral area of the two *Nephila* species (Clade 2) is ambiguous, with a few percent difference among the probabilities (Table 2): Indomalaya (28%), Indomalaya + Australasia (26%) and Afrotropics (23%). Within this clade, *N. constricta* likely colonized the Afrotropics (Figure 3d). The MRCA of all remaining nephilids (Clade 3) shows a likely Indomalayan distribution (30%). The ancestral area for *Clitaetra* + *Indoetra* (Clade 4) is 40% Indomalayan. The ancestor of *Clitaetra* (Clade 5) likely colonized the West Indian Ocean islands (52%; Figure 3a), with a subsequent colonization of Africa (Figure 3c); note that not all African *Clitaetra* species are included in this phylogeny. The remaining nephilids (Clade 6) had a likely Australasian ancestor (30%) whose distribution was maintained in the *Trichonephila* MRCA (Clade 7; 52%). While one of the *Trichonephila* clades (Clade 8; *T. antipodiana*, *T. plumipes* and *T. edulis*) retains this ancestral distribution (with a range expansion to Indomalaya in *T. antipodiana*), the MRCA of remaining *Trichonephila* species (Clade 9) most likely (64%) colonized the Neotropics (Figure 3b). In this clade, *T. sexpunctata* retained its Neotropical distribution, but its sister clade is reconstructed to have shifted to the Afrotropics (Clade 10; 70%). This species-rich clade shows predominantly African species distributions, with a range expansion to West Indian Ocean in *Trichonephila inaurata*, a shift to Indomalaya and Palearctics in *T. clavata* (Figure 3d), and, interestingly, another colonization of Neotropics (Clade 11). Whose ancestor achieved the latter recolonization is ambiguous (see Section 4).

The ancestor of the clade sister to *Trichonephila* (Clade 12) shows a range shift from Australasia to Indomalaya (30%). This Indomalayan range is retained in most distal splits. Thus, the origins of both *Herennia* (Clade 14; 84%) and *Nephilengys* (Clade 15; 68%), as well as their common ancestor (Clade 13; 78%) are all strongly supported as Indomalayan. However, some of *Herennia* and *Nephilengys* species (*H. milleri*, *H. oz*, *H. papuana* and *N. papuana*) shift back to Australasia in Neogene (Figure 3d). In contrast, *Nephilingis* MRCA (Clade 16) likely shifted from Indomalaya to West Indian Ocean islands (49%; Figure 3a), where most of the genus diversity remains, albeit with *N. cruentata* having shifted to the Afrotropics and Neotropics (Figure 3d).

4 | DISCUSSION

We present a historic biogeographical reconstruction of most nephilid species. We use this reconstruction to test alternative hypotheses on the precise geographical origin of this clade. The first hypothesis, Out of Africa, based on the observation that most extant species diversity lies in the Afrotropics, receives no support. Moreover, the Out of West Burma hypothesis is consistent with our results that reconstruct Indomalaya and Australasia as nephilid ancestral range. Our results suggest numerous range shifts during the roughly 130 Ma long evolution of this clade, and we discuss some of these likely events below.

4.1 | Setting dispersal probabilities using geological data

While biogeographical studies often include time stratification of dispersal probabilities between areas, the estimates are usually rough-scaled and arbitrary (e.g. Chamberland et al., 2018; Eberle, Fabrizi, Lago, & Ahrens, 2017; Weaver, Cruz, Johnson, Dupin, & Weaver, 2016). Our study adds precision to a global analysis by applying measured distances among geographical entities at geological time intervals. This level of precision was possible due to the availability of a detailed plate tectonics reconstruction model (Müller et al., 2019). We combine these data with spider dispersal biology, resulting in a credible estimation of dispersal probabilities in this lineage.

4.2 | Nephilid historic biogeography

Our results support the hypothesis that Burmese amber contains Gondwanan biota (Poinar, 2018). Regardless of the precise origin of nephilids, they are clearly Gondwanan, which means that the West Burma Block, together with its amber, is not Laurasian in origin, but indeed broke off from Gondwana in the Cretaceous and then rafted to its present location.

None of the possible ancestral areas for the nephilid MRCA receives an overwhelming support, which is unsurprising given the clade's age and present wide distribution. However, the three best supported candidates, Indomalaya, Australasia and Indomalaya + Australasia, received a combined support of 48% (Table 2). Our Out of West Burma hypothesis was defined broadly, lacking precise resolution as to the origin of nephilids. Thus, all three most plausible MRCA reconstructions would be consistent with this hypothesis. Although Kuntner et al. (2019) hypothesize that the sister clade to nephilids is a clade that contains a huge diversity of araneid genera, other authors argue that a single enigmatic Australian genus, *Paraplectanoides*, might in fact be the more appropriate outgroup to nephilids (Kallal & Hormiga, 2018; Scharff et al., 2019). If the former is true, one cannot unequivocally reconstruct the ancestral area of nephilids plus araneids. If the latter, then one would expect support for an Australasian origin of that deeper node (*Paraplectanoides* plus nephilids), perhaps adding additional resolution to the origin of nephilids that may then be more decisively Australasian. Regardless, this would corroborate Out of West Burma, and refute Out of Africa.

The frequency of dispersal events as implied by the phylogeny suggests that a few lineages, such as *Herennia*, largely persisted in their ancestral ranges for tens of millions of years, while others, such as *Trichonephila*, frequently shifted continents. This disparity aligns well with the known nephilid species biology—the species differ greatly in their dispersal propensity (Kuntner & Agnarsson, 2011b; Lee, Jiang, Su, & Tso, 2004). Interestingly, simple range expansion of a single species occurred much less frequently in the phylogeny than intercontinental jump dispersal with subsequent speciation. The reconstruction only implies four range expansion events: *N. pilipes* from Indomalaya to Indomalaya + Australasia, *T. inaurata* from the Afrotropics to the Afrotropics + West Indian Ocean, *T. antipodiana* from Australasia to Australasia + Indomalaya and, perhaps, *T. clavipes* from Neotropics to Neotropics + Nearctic (but, see below).

Moreover, the reconstruction suggests some fairly dramatic jump dispersals, especially in the *Trichonephila* clade. A surprising one is the shift of the Australasian *Trichonephila* MRCA (Clade 7) to the Neotropics (Clade 9) in mid Paleogene (Figure 3b). The distance between Australasia and Neotropics 50 Ma was approximately 6,500 km, well beyond our 4,000 km threshold for 5% dispersal probability. However, this was around the time of the Paleocene-Eocene Thermal Maximum, when the poles were ice-free (Zachos, Pagani, Sloan, Thomas, & Billups, 2001). Additionally, the Drake

Passage between South America and Antarctica had not yet opened (Livermore, Nankivell, Eagles, & Morris, 2005), providing a dispersal route between Australasia and Neotropics. Trans-Antarctic dispersal in both directions was indeed frequent in animals (Sanmartín & Ronquist, 2004), seen for example in mammals (Woodburne & Case, 1996), frogs (Duellman, Marion, & Hedges, 2016) and bees (Almeida, Pie, Brady, & Danforth, 2012).

Of the descendent species in Clade 9, only one, *T. sexpunctata*, retained a Neotropical distribution and remains the only nephilid species endemic to South America. The MRCA of all other species (Clade 10) receives high support (69%) for a transition to the Afrotropics. One of its subclades then diversified in the Afrotropics and this diversification formed the basis for our 'Out of Africa' hypothesis. The other subclade, Clade 11, is reconstructed as 48% Neotropical versus 45% Afrotropical. While the basal species in this clade, *T. clavipes*, is presently American, the remaining two species shifted back to the Afrotropics. Thus, a reconstruction of an Afrotropical Clade 11 would be more parsimonious, implying a single, not two, intercontinental dispersals. Regardless, we might assume from the diversity of fossil nephilids found in Dominican amber (Wunderlich, 1986, 1988) that they underwent a radiation once colonizing the Americas, but were subsequently affected by extinction event(s). This hypothesis could be tested by reconstructing a morphological phylogeny of fossil and extant *Trichonephila* as it is currently not known how closely the Dominican amber fossils are related to *T. clavipes*.

While Out of Africa predicted the Afrotropics as the origin of nephilids, our results instead uncover Africa among the geographical areas colonized only recently. The first MRCA reconstructed as African (Clade 10) is approximately 17 million years old (Kuntner et al., 2019). This estimated age, combined with the phylogenetic topology, would suggest that nephilids underwent a fast diversification, perhaps as a response to newly available ecological niches encountered in Africa. Concurrently, the genus *Nephilingis* (Clade 16) colonized the West Indian Ocean islands from Indomalaya (Figure 3a) and diversified there, albeit to a smaller extent. One species, *Nephilingis cruentata*, further colonized Africa and South America (Figure 3d). Judging from the areas inhabited by *N. cruentata*, we hypothesize that its colonization to Africa was natural, while that to South America, where it is confined to a few coastal areas (Kuntner, 2007), may have been recent, and anthropogenic.

Su et al. (2011) argue that diversification patterns of Asian/Australian *Nephila* (now *Trichonephila*) spiders were driven by major global climatic changes in the Neogene. Our results are consistent with this hypothesis. The dramatic decrease in global temperature, ice accumulation and lowered sea levels in the Neogene (e.g. Jansen, Sjøholm, Bleil, & Erichsen, 2012; Woodruff, 2003; Zachos et al., 2001), might have had a profound effect on ecological niche diversity, wind directions and habitat distribution. With the collision of the Turkish and Arabian plates around 20 Ma, early Neogene also saw the formation of the first land bridge between Africa and Eurasia (Rögl & Steininger, 1983). This was followed by the so-called Afro-Eurasian faunal exchange (Steininger, Rabeder, & Rögl, 1985), which slightly predates the dispersal of the ancestor of *T. clavata* out of the Afrotropics into the Palearctic region of East Asia and Indomalaya (Figure 3d). It is the only extant *Trichonephila* species to inhabit higher elevations, as well as temperate regions.

Interestingly, the basalmost nephilid genus, *Nephila*, is reconstructed to have retained the nephilid ancestral distribution, with a dispersal to the Afrotropics in the Neogene (Figure 3d), where *N. constricta* persists to date. Despite their large adult female body sizes, *Nephila* are active dispersers as tiny juveniles (Lee et al., 2015), so it is surprising that *Nephila* is not even wider spread over other continents. Knowing that *Nephila* is positioned on one of the longest phylogenetic branches in this part of the phylogeny, we hypothesize that its current snapshot of species diversity is not representative of its entire evolutionary history. Rather it may be an evolutionary leftover of a history that may have involved numerous extinctions.

5 | CONCLUSIONS

Our methodological approach adds rigor to biogeographical analysis as it includes not only a robust phylogenetic basis, but also assesses organismal specific dispersal probabilities through concrete distances measured though time slices of the Earth's history. We believe that by modifying this pipeline to fit lineage specific biologies, this methodology can be applied to biogeographical reconstruction of any organism.

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DATA AVAILABILITY STATEMENT

The new sequences are available on GenBank (MN855577-9). The alignment and the geological data are available as supplements to this paper.

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BIOSKETCH

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Author contributions: E.T. and M.K. designed the study; M.K. provided sequence and distribution data; E.T. performed geological measurements and biogeographical analyses; E.T. and K.Č. performed phylogenetic analyses; K.Č. produced the figures; E.T. led the manuscript preparation, and all authors contributed to writing.

SUPPORTING INFORMATION

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

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