

Formation of rivers and mountains drives diversification of primitively segmented spiders in continental East Asia

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Abstract

Aim: Complex topography in continental East Asia mirrors geological events such as formation of rivers and mountains, but to what extent these events drive diversification remains underexplored. We address this question by testing vicariant hypotheses using the primitively segmented spider genera *Sinothela* and *Ganthela*, focusing on diversification within *Sinothela*.

Location: Continental East Asia.

Methods: We employ a three-way test of six vicariant hypotheses derived from river and mountain formation: (a) phylogenetically, we evaluate the sister group relationships of lineages on either side of each barrier; (b) chronologically, we estimate the timing of splits in a time calibrated phylogenetic framework; (c) biogeographically, we infer whether each of these splits shows a reduction in ancestral areas.

Results: Three-way tests fully support five barrier formation events: (a) the Oligocene–Miocene origin of *Sinothela* + *Ganthela* coincides with the 23–36.5 Ma range of the Yangtze River formation; (b) the *Sinothela* split into lineages on each side of the Qinling–Dabie mountains overlaps with the estimated uplift (2.6–23 Ma); (c) the origin of lineages on each side of Taihang Mts fits its hypothesized uplift (3.6–5.3 Ma); (d) the origin of lineages on each side of mid-lower Yellow River supports the timing of its formation (1.8–3.6 Ma); (e) lineages on each side of the Yellow River eastern Ordos bend coincide with its origin (1.6 Ma). However, the Taishan Mts uplift as barrier formation is only partially supported.

Main conclusions: Our results suggest vicariant origins of *Sinothela* and provide evidence for continental-wide vicariant events that have shaped these spiders' evolutionary history in continental East Asia. Our study also highlights how dated molecular phylogenies can narrow down too widely estimated time intervals of river and mountain formation by geologists. Primitively segmented spiders thus provide an excellent model for exploring how geological events shape biodiversity.

KEYWORDS

Biogeography, Liphistiidae, mountain uplift, phylogeography, river formation, vicariance



1 | INTRODUCTION

Geological events shape biodiversity and leave genetic imprints on lineages (Cox, Moore, & Ladle, 2016; Lomolino, Riddle, Whittaker, & Brown, 2010). Emergence of physical barriers such as rivers or mountain chains drive genetic diversification and vicariant speciation by limiting dispersal and gene flow (Hoorn et al., 2010; Wang & Yan, 2014; Weir, Faccio, Pulido-Santacruz, Barrera-Guzmán, & Aleixo, 2015; Xu et al., 2016). In continental East Asia, biogeographical studies primarily focus on the Tibetan Plateau (TP), which harbours endemic plant and animal species (Favre et al., 2015; Renner, 2016). The TP uplifting is widely assumed to cause subsequent fluvial formation and orogeny in central and eastern China (Lin, Yang, Sun, & Yang, 2001; Liu et al., 2013; Zheng et al., 2013). However, how precisely these geological events have affected biotas remains poorly understood.

The high contemporary topographic complexity in central and eastern China mirrors geological events, such as the formation of rivers and mountains. In particular, links between these geological events on the one hand, and the geographical distribution of organisms on the other, have aligned both geologists' and biologists' interests (Hou, Li, & Li, 2014; Zhao & Li, 2017; Zhao, Liu, Luo, & Ji, 2011). The development of the two largest river systems in continental East Asia, the Yangtze, and Yellow Rivers (Figure 1), is believed to be closely associated with the topographic change following the collision of the Indian with the Eurasian plate, and its consequence, the TP uplifting (Yao et al., 2015, 2017). The incision of the Three Gorges (Figure 1) critically affected the evolution of the modern, eastwards flowing Yangtze River, which represents a geographical barrier (Zheng et al., 2017). However, the timing of Yangtze's incision of the Three Gorges has been controversially estimated to be as early as 40–45 Ma (Richardson, Densmore, Seward, Wipf, & Yong, 2010) or 23–36.5 Ma (Zheng et al., 2013), or as late as 12 Ma (Zhang et al., 2017), 3.2 Ma (Jia et al., 2010), or to even 0.75 Ma (Xiang et al., 2007). Similarly, as a topographic barrier between the middle and lower reaches of the Yellow River, the incision of the Sanmen Gorge is of great significance in initiating an eastward through-flow of the river (Figure 1). Yet, the timing of Yellow River's incision into the Sanmen Gorge is vague, with estimates from 1.24 to 3.63 Ma (Hu et al., 2017), 1.8 Ma (Craddock et al., 2010), 1.3–1.4 Ma (Kong, Jia, & Zheng, 2014), 0.88 Ma (Yao et al., 2017) to 0.15 Ma (Jiang, Fu, Wang, Sun, & Zhao, 2007). Furthermore, as a major feature of the course of the Yellow River, the formation of a square-shaped bend (i.e., the Ordos bend) around the Ordos block is of geographical and biogeographical importance (Figure 1). Again, age estimates of the Ordos bend formation range from 3.6 to 11.6 Ma (Lin et al., 2001) to 1.6 Ma (Li, 2009).

Mountain uplift shapes biotic diversification and distribution through rapid changes in climate, topography, and environments (e.g., Hewitt, 2004; Hoorn et al., 2010; Merckx et al., 2015; Renema et al., 2008). Again, direct biogeographical consequences of such events in central and eastern China are poorly understood. The Qinling–Dabie mountain range (Mts) started uplifting from middle Miocene, and uplifted rapidly from late Miocene to Quaternary (Dong

et al., 2011; Liu et al., 2013; Meng, 2017; Zhang, Qu, Wu, He, & Shi, 2004; Zhang et al., 1996). This range traversing west to east between the Yangtze and Yellow Rivers (Figure 1) is considered to be an important biotic barrier between southern and northern China (Meng, 2017; Zhang, 2011). The complex topography of the Qinling–Dabie Mts, its variable climates, and heterogeneous habitats, are known for exceptional biodiversity and endemism (Dong et al., 2011; Ying, 1994). These mountains have been implicated to be important in biotic vicariance since the Miocene (Fang et al., 2015; Yan, Wang, Chang, Ji, & Zhou, 2010; Zhang et al., 2014; Zhao, Zhang, & Li, 2013), but direct phylogenetic matches of diversification events with those of the mountain uplift have been hindered by geological uncertainty (Liu et al., 2013; Meng, 2017; Zhang et al., 2004).

Additional mountain ranges, including the Taishan Mts, Taihang Mts, and Lüliang Mts (listed chronologically, Figure 1) may have influenced the formation of eastern and northern Chinese biogeographical patterns. The uplift of Taishan and Mengshan Mts, despite being relatively small and low, and rarely studied, is thought to have occurred at three different phases: 16–23 Ma, 20–23 Ma, and 6.5–16 Ma (Li et al., 2013; Wang, Liu, & Zou, 2013), which may have repeatedly influenced the biotas in the area. The Taihang Mts represent a more formidable biogeographical barrier, as this large mountain range in north China runs north to south, thereby dividing the Loess Plateau to the west and the North China Plain to the east. As the uplift of the Taihang Mts is hypothesized to have occurred at three different periods, 16–23 Ma, 3.6–5.3 Ma, and 2.6 Ma (Gong, 2010), it may have had repeated biogeographical influence. To its west lies the Lüliang Mts, likewise running north–south. The uplift of this mountain range occurred 6.5–10 Ma (Li, 2009), and is thought to have importantly shaped the highly endemic local biotas (Hou et al., 2014; Wang & Yan, 2014; Zhang, Xi, & Li, 2006).

Most biogeographical studies focus on the imprints of a single regional geological event, such as a river formation (Zhao et al., 2011), or a mountain uplift on the evolution of particular organisms (Hou et al., 2014; Yan et al., 2010; Zhang et al., 2014). More studies are therefore needed to detect the effects of a mixed topographic history on regional biotas. Here, we explore how the emergence of rivers and mountains in central and eastern China has affected the biogeography of a group of ground-living spiders. The primitively segmented spiders, family Liphistiidae, form a relatively recent Cenozoic diversification within the earliest offshoot of the spider tree of life (Xu, Liu, Cheng et al., 2015). Liphistiids, as the only surviving family of the suborder Mesothelae, are recognized as “living fossils” that have retained spider plesiomorphies such as abdominal tergites and spinnerets located in the middle of the abdominal venter (Xu, Liu, Cheng et al., 2015; Xu, Liu, Chen, et al., 2015). The extant diversity of the lineage is limited to East and Southeast Asia (Xu, Liu, Chen, et al., 2015), and wherever they occur, their biogeographical imprint is predominantly vicariant (Xu, Liu, Chen, et al., 2015; Xu et al., 2016). Along with other phylogenetically old terrestrial arachnid lineages (e.g., Clouse & Giribet, 2010) and mygalomorph spiders (e.g., Hedin, Starrett, & Hayashi, 2013; Hendrixson & Bond, 2007;



FIGURE 1 Topography of continental East Asia, showing the largest rivers and mountains. Continental East Asia is divided into seven geographical areas: (A) the area between the mid Yellow River (i.e., the Ordos square bend around Ordos block) and the Weihe River; (B) the area between east Yellow River Ordos bend and Taihang Mts; (C) the area between Taihang Mts and the lower Yellow River; (D) the area between the lower Yellow River and the Taishan–Mengshan Mts; (E) the area between the Taishan–Mengshan Mts and the Qinling–Dabie Mts; (F) the area between the Qinling–Dabie Mts and the Yangtze River; and (G) the area south of the Yangtze River. The upper (U), middle (M), and lower (L) reaches of the Yellow and Yangtze Rivers are divided by white bars. The black dots show the location of Sanmen Gorge and Three Gorges [Colour figure can be viewed at wileyonlinelibrary.com]

Opatova, Bond, & Arnedo, 2016), liphistiids are excellent model organisms for understanding biogeographical events (Xu et al., 2016). Liphistiid females are sedentary and their lifestyles are confined to their burrows, although adult males are vagile. They are thus poor dispersers and have highly restricted geographical ranges (Xu, Liu, Chen, et al., 2015; Xu et al., 2016). To test biogeographical hypotheses and predictions pertaining to the main orogenic and river formation events in central and eastern China (Table 1), we combine the evidence from multilocus phylogenetic and phylogeographical analyses of *Sinothela* Haupt, 2003 (found north of the Yangtze River) and its sister group *Ganthela* Xu & Kuntner, 2015 (found south of the river), with focus on diversification within *Sinothela*.

Our six hypotheses (Table 1) all assume that geological events have formed barriers to gene flow and are thus vicariant. We tested these predictions three ways. We first used phylogenetic analysis to determine if a recovered sister group relationship at a certain phylogenetic hierarchical level between lineages on each side of a hypothesized barrier supports the vicariant scenario. Secondly, we performed divergence dating to estimate the timing of the most

recent common ancestor that gave rise to the two lineages on each side of the barrier. If that time interval fits one of the proposed geological origins of that particular barrier, this lends support to the vicariant hypothesis. Finally, we carried out biogeographical analysis to infer the ancestral and descendant area reconstruction at those nodes. Vicariant hypotheses predict an ancestral area on both sides of a barrier, and the descending areas on each side of it.

2 | MATERIALS AND METHODS

2.1 | Taxonomic and population sampling

Our taxon sample included 88 *Sinothela* specimens comprising 2 described and 8 undescribed species, collected at 16 localities in central and northern China and 14 *Ganthela* specimens representing all 7 recognized species at 6 localities as ingroups (Figure 2). We used six specimens from the other six Liphistiidae genera (*Liphistius* Schiödt, 1849, *Heptathela* Kishida, 1923, *Ryuthela* Haupt, 1983, *Qionghela* Xu & Kuntner, 2015, *Songthela* Ono, 2000 and *Vinathela*

**TABLE 1** Biogeographical hypotheses and predictions regarding the origin and diversification of *Sinothela* lineages based on the major Miocene geological events in continental East Asia

	Hypothesis	Prediction
Event 1: Incision of the mid-lower Yangtze River (downstream after Three Gorges) (Jia et al., 2010; Richardson et al., 2010; Xiang et al., 2007; Zhang et al., 2017; Zheng et al., 2013)	H₁: A sister group relationship between south of (<i>Ganthela</i>) and north of (<i>Sinothela</i>) Yangtze River lineages as a result of Event 1	Timing of split between <i>Sinothela</i> and <i>Ganthela</i> coincides with timing of Event 1 at either 45–40 Ma, or 36.5–23, or 12, or 3.2, or 0.75 Ma
Event 2: The uplift of Qinling–Dabie Mts (Liu et al., 2013; Meng, 2017; Zhang et al., 2004)	H₂: A sister group relationship between lineages south and north of Qinling–Dabie Mts as a result of Event 2	Timing of split between the two lineages coincides with timing of Event 2 at either 23–2.6, or 10–2.6 Ma
Event 3: The uplift of Taishan Mts and Mengshan Mts (Li et al., 2013; Wang et al., 2013)	H₃: A sister group relationship between lineages on each side of Taishan Mts and Mengshan Mts as a result of Event 3	Timing of split between these lineages coincides with timing of Event 3 at either 23–20, or 23–16, or 16–6.5 Ma
Event 4: The uplift of Taihang Mts (Gong, 2010)	H₄: A sister group relationship between lineages on each side of Taihang Mts as a result of Event 4	Timing of split between the two lineages coincides with timing of Event 4 at either 23–16, or 5.3–3.6, or 2.6 Ma
Event 5: The incision of mid-lower Yellow River (downstream after Sanmen Gorge) (Craddock et al., 2010; Hu et al., 2017; Jiang et al., 2007; Kong et al., 2014; Li, 2009; Lin et al., 2001; Yao et al., 2017)	H₅: A sister group relationship between lineages on each side of mid-lower Yellow River as a result of Event 5	Timing of split between the two lineages coincides with timing of Event 5 at either 3.63–1.24, or 1.8, or 1.4–1.3, or 0.88, or 0.15 Ma
Event 6: The formation of Ordos square bend of the Yellow River (Li, 2009; Lin et al., 2001)	H₆: A sister group relationship between lineages on each side of the Yellow River as a result of Event 6	Timing of split between the two lineages coincides with timing of Event 6 at either 11.6–3.6, or 1.6 Ma

Ono, 2000) as outgroups (Table S1; for sampling strategies see Appendix S1 in Supporting Information).

2.2 | Phylogeny

We targeted fragments of two mitochondrial loci (cytochrome c oxidase subunit 1 [CO1] and 16S rRNA [16S]) and three nuclear loci (28S rRNA [28S], histone 3 [H3] and internal transcribed spacer 2 [ITS2]). For primer combinations and molecular procedures, see Xu, Liu, Chen, et al., 2015. We combined and edited chromatograms, and aligned sequences using GENEIOUS 5.6.6 (Kearse et al., 2012).

We used PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) to select the best data-partitioning schemes using the greedy algorithm based on the Akaike Information Criterion (AIC), and found that GTR+I+G was the best model for all partitions. We inferred phylogenies using maximum likelihood (ML) in GARLI 2.01 (Zwickl, 2006) and Bayesian inference (BI) in MRBAYES 3.2.1 (Ronquist et al., 2012). We used the results from the full gene partition scheme for divergence time analyses (for details see Appendix S1).

2.3 | Divergence dating

As in prior analyses (Xu, Liu, Chen, et al., 2015; Xu et al., 2016), we used one Mesothelae fossil from the Middle Cretaceous of Myanmar (Wunderlich, 2017), *Cretaceothela lata* Wunderlich, 2015 by assigning a uniform prior for the liphistiid stem with a minimum bound 100 Ma, as well as mitochondrial and nuclear substitution rates as priors. We calculated the marginal likelihood values for both strict clock and relaxed clock models using the Stepping-Stone Sampling

(SS) approaches (Xie, Lewis, Fan, Kuo, & Chen, 2011) in MrBayes, then performed the likelihood ratio test (LRT) to select the relaxed molecular clock (Drummond, Ho, Phillips, & Rambaut, 2006) over the strict molecular clock model ($P < 0.01$ for SS).

Using BEAST 1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012) we evaluated three different tree prior models, Yule speciation process, Birth–Death speciation process and Birth–Death Incomplete Sampling speciation process by calculating the logarithm of marginal likelihood for each model using the Path Sampling (PS) and SS approaches with 10,000,000 generations and 100 path steps (for justification, see Baele et al., 2012). The LRT helped select the Birth–Death speciation process ($p < 0.01$, Table S2 in Appendix S1).

As above, GTR+I+G was the best substitution model. We ran BEAST analyses with two independent runs of 100 million generations sampling every 10,000 generations. We assessed convergence and sufficient burnin within each run using TRACER 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014). We removed 25% of the first generation of each run as burnin, combined the remaining log files in LOGCOMBINER (Drummond et al., 2012), then used TREEANNOTATOR (Drummond et al., 2012) to obtain consensus trees.

2.4 | Ancestral area reconstruction

We defined seven discrete biogeographical areas (Figure 1) based on plate-tectonic histories, formation of river systems, and uplifting of major mountains in central and eastern China (e.g., Craddock et al., 2010; Gong, 2010; Jia et al., 2010; Jiang et al., 2007; Lin et al., 2001; Meng, 2017; Richardson et al., 2010; Zheng et al., 2013), as well as the distribution and phylogenetic structures of *Sinothela* and *Ganthela*.

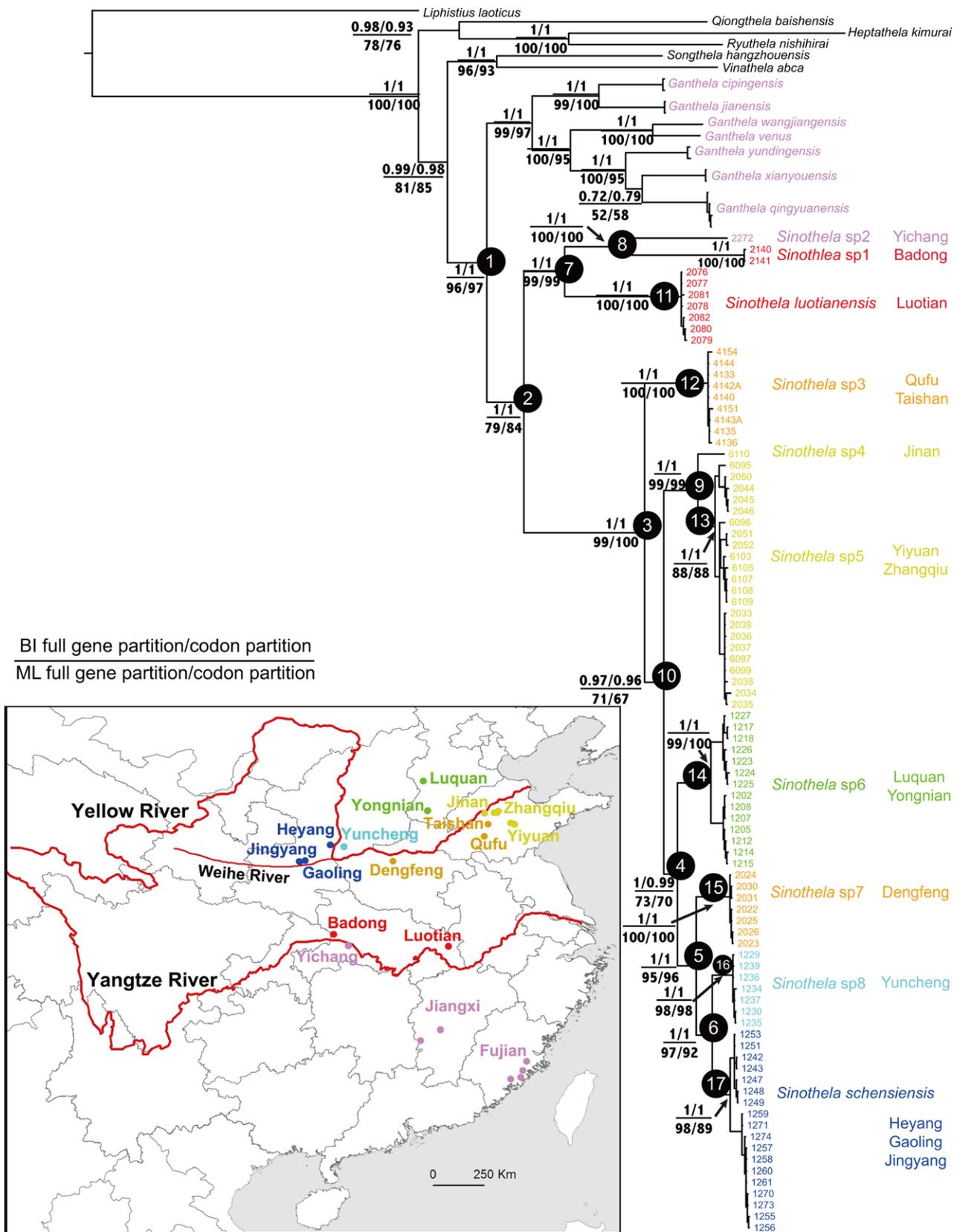


FIGURE 2 Summary phylogenetic results from Bayesian inference (BI) and maximum likelihood (ML) analyses of two different partition schemes of the primitively segmented spider genera *Sinothela* and *Ganthela*. The topology is from the Bayesian analysis of the full gene partition. Taxa and localities are colour coded in phylogenetic tree corresponding to these coloured sampling sites in the inset map, as well as according to areas defined in Figure 1. The black numbered circles represent the major clades matching those in the divergence dating and ancestral area reconstructions [Colour figure can be viewed at wileyonlinelibrary.com]



We implemented DEC, DIVALIKE, and BAYAREALIKE and each model with an additional “+J” parameter for founder events in the R 3.3.3 package ‘BioGeoBEARS’ (Matzke, 2013) to infer biogeographical events using the BEAST tree and employed Akaike Information Criterion (AIC) scores for model selection. Since Ree and Sanmartín (2018) recently identified the conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection, we only added the “+J” parameter in order to test the robustness of our results (see Supporting Information). We set the maximal number of areas to 7.

2.5 | Testing the barrier formation hypotheses

We evaluated each hypothesis (Table 1) in a phylogenetic, chronological, and biogeographical framework. Each hypothesis can be falsified by not detecting any lineage within our phylogenetic hierarchy that would show a split of sister lineage on each side of the barrier in question (phylogenetic analysis). If such lineage(s) is (are) detected, the hypothesis may be falsified if the chronology of the split, as estimated by the time calibrated phylogeny, falls outside of the hypothesized timing of the barrier formation as independently hypothesized by other studies. The final, biogeographical analysis can negate the hypothesis by failing to detect an ancestral area reconstruction consistent with an area reduction from a widespread ancestor towards descendant lineages on each side of the barrier. This progression of tests, the first being a prerequisite for the second and the third, provides a critical evaluation of each hypothetical scenario. We deem each hypothesis to be partially corroborated if it passes two tests, and fully corroborated if it passes all three.

3 | RESULTS

3.1 | Phylogeny

The full, concatenated five-gene phylogenetic matrix included 108 sequences and 2,579 sites (Table S1). BI and ML analyses with both partition schemes produced consistent topologies, confirming the monophyly of *Sinothela*, endemic to areas north of the Yangtze River, and its sister relation with *Ganthela*, endemic to areas south of the river (Figure 2). *Sinothela* (clade 2) splits into sister lineages distributed on each side of the Qinling–Dabie Mts (clade 3 to the north and clade 7 to the south; Figure 2). Within clade 7, *S. luotianensis* is sister to clade 8 that contains a species from Yichang (southern bank of the Yangtze River) and another from Badong (north of the Yangtze River). Within clade 3 we observe a sister relationship between clade 12 containing species south of the Taishan Mts, and a large clade 10. This clade then splits into clades 9 (north of the Taishan Mts) and clade 4 containing all the remaining lineages. Clade 4 splits into clades 14 (containing a species east of the Taihang Mts) and 5 that contains species to the west of these mountains (with a potential outlier, see clade 15). Clade 5 shows a sister relationship of clades 15 (just south of the Yellow River) and 6 (the westernmost *Sinothela* lineage). The latter clade shows a split

between species on each side of the eastern Ordos bend of the Yellow River (Figure 2).

3.2 | Divergence dating

The chronogram topology from BEAST matches that from the BI and ML analyses with high support values (all posterior probability = 1 for *Sinothela*), and the Birth–Death speciation model provides an estimate of divergence timing (Figure 3; Figure S1 in Appendix S2 in Supporting Information). Clade 1 (*Sinothela* + *Ganthela*) originated in Miocene (mean 19.5 Ma) although the confidence interval spans Oligocene to Miocene (12.7–30.2 Ma). Reconstructed means of clade origins suggest that the clades 2, 3, 7, 8, 10 also originated in the Miocene, and that the clades 4, 5, 6, and 9 are more recent, originating predominantly in Pliocene or Pleistocene.

3.3 | Ancestral area reconstruction

DEC was the best-fit model based on the AIC scores for models without “+J” parameter (Table 2; Figure 4; see Supporting Information for additional models). This biogeographical reconstruction suggests all seven areas (ABCDEFG), a wide area on both sides of the Yangtze River, as the most likely ancestral area for clade 1, and its separation in the descendants to G (*Ganthela*, south of the Yangtze River), and ABCDEF (*Sinothela*, north of the Yangtze River). Similarly, ABCDEF (node 2) splits into descendants ABCDE (node 3) and F (node 7) on each side of the Qinling–Dabie Mts. The chronogram predominantly shows other similar cases of area splits (e.g., originating from nodes 3, 4, 5, 6, 10) with exceptions (e.g., originating from node 9).

4 | DISCUSSION

We tested six vicariant hypotheses (Table 1) based on reconstructed historic geological events in continental East Asia that may have affected the diversification history of primitively segmented spiders. Combined evidence from our three-way evaluations (phylogenetic, chronological, biogeographical) fully supports five of the six hypotheses, and one is supported by two evaluations only. These outcomes suggest that the diversification of this spider group may have been driven by the formation of major river systems and mountain ranges. Our results also allow for additional, unknown vicariant events.

4.1 | River formation as barriers

Numerous phylogenetic lineages have been shown to be affected by river formation in the Amazon (e.g., Ferreira, Aleixo, Ribas, & Santos, 2017; references in Santorelli, Magnusson, & Deus, 2018), North America (e.g., Satler & Carstens, 2017), and Africa (e.g., Portik et al., 2017). Likewise, studies on invertebrates and vertebrates provide evidence that the Yangtze and the Yellow River formed barriers to gene flow, leading to genetic diversification and speciation (e.g. Duan

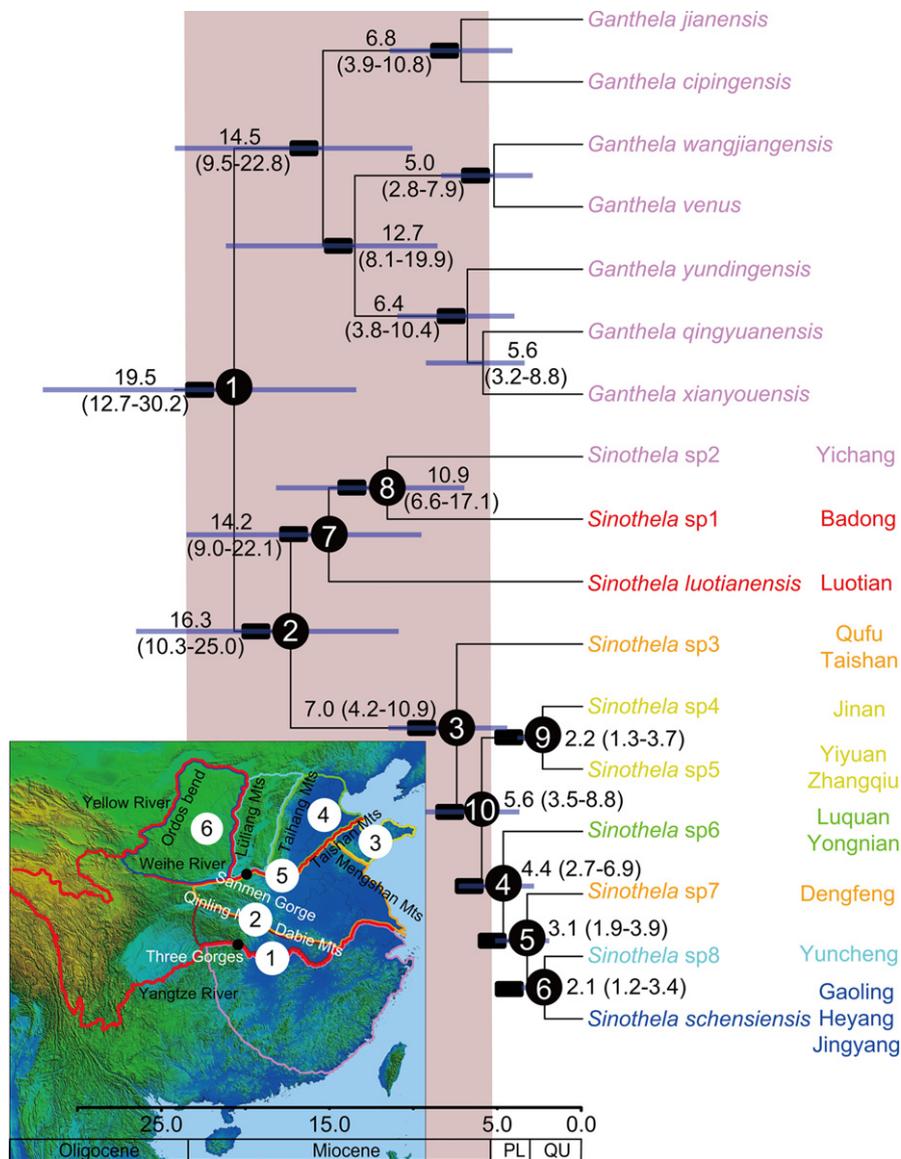


FIGURE 3 The chronogram with inferred node ages in million years (Ma) and with 95% confidence intervals (horizontal bars). Taxa are colour coded according to areas defined in Figure 1. The black numbered circles match those in the phylogenetic tree and ancestral area reconstructions. The white numbered circles in the inset map correspond to the six geological events in Table 1. The black rectangles represent BEAST support >0.95 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 BioGeoBEARS results based on *Sinothela* and *Ganthela* BEAST topology

	df	d	e	j	AIC
DEC	2	0.0016	1.00E-12	0	58.64
DIVALIKE	2	0.0041	1.00E-12	0	61.48
BAYAREALIKE	2	0.0058	0.098	0	92.24

AIC: Akaike Information Criterion.

et al., 2009; Perdices, Cunha, & Coelho, 2004; Xiao, Zhang, & Liu, 2001; Zhang et al., 2008; Zhao et al., 2011). However, the precise timing of the appearance of these two major river systems in eastern China is still debated. In the primitively segmented spiders that today inhabit this area, we found a clear phylogenetic division between

Sinothela whose species are found in areas north of Yangtze River (albeit with one exception, *Sinothela* sp2, found immediately on the southern shore of the river), and *Ganthela* whose species are to the south of the river. The split between these lineages, estimated by our divergence dating at between 13 and 30 Ma, is consistent with the growing consensus that the river formed at between 23 and 37 Ma (Zheng et al., 2013, 2017), supporting our first hypothesis (H_1 , Table 1). The biogeographical analysis also supports this vicariant event by estimating the ancestral area of this clade to be on both sides of the river, but the ancestors of *Sinothela* and *Ganthela* to be restricted to the north and south side of the river respectively. Surprisingly, phylogeographical studies on the impact of the Yangtze River formation on lineage diversification are scarce, mainly focused on fish and stream-dwelling frogs (references above), as well as

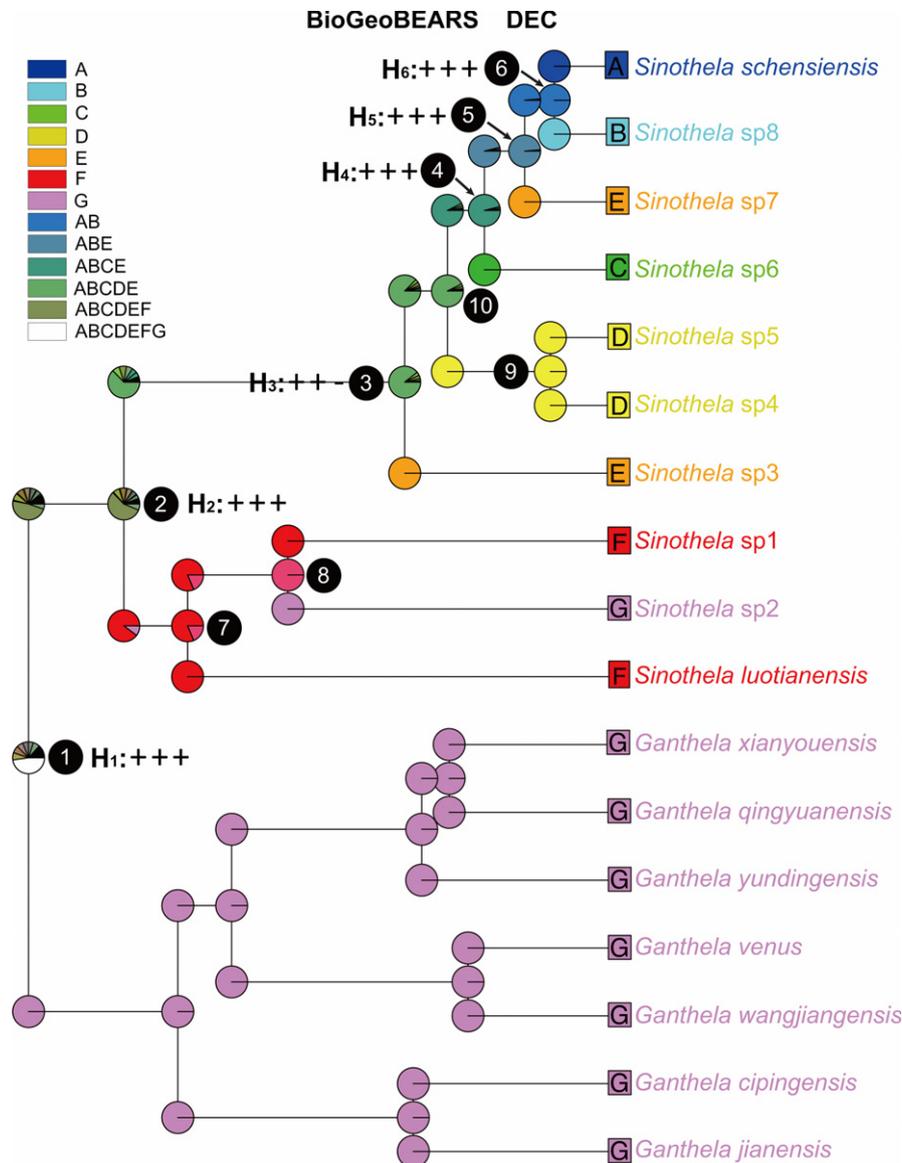


FIGURE 4 Likelihood ancestral area range estimation for the primitively segmented spider genera *Sinothela* and *Ganthela*. Geographical areas in the legend correspond to those in Figure 1. The black numbered circles match those in the phylogenetic tree and divergence dating. H with subscript numbers are the six hypotheses in Table 1, followed by information on three-way hypothesis evaluation from phylogenetic analysis, divergence dating, and biogeographical analysis, + signs indicating support, and – signs indicating rejection [Colour figure can be viewed at wileyonlinelibrary.com]

moths (Meng, Shi, & Chen, 2008), and provide very few divergence timing estimations that, when available (e.g., Yan et al., 2013), are likely gross underestimations. Ours is the first biogeographical evidence in support of a more precise scenario of Yangtze River formation timing (23–37 Ma).

The Yellow River is hypothesized to have formed the Ordos bend in the Miocene or as late as Pleistocene (event and H_6), and to have cut through eastern China in the Pliocene or even more recently (event and H_5 ; Table 1). The results from our phylogenetic analysis and divergence dating, however, suggest that event 5 in the eastern part of the river predated event 6. The lower Yellow River event 5 (H_5 , Table 1) is supported by the recovered sister group relationship between *Sinothela* sp7 (south of the Yellow River) and clade 6 north of the river at that time (although not considering its

present-day trajectory). The timing of this split, estimated at 3.1 Ma (1.9–4.9), is consistent with the prediction from H_5 . The three likely ancestral areas reconstructed at the node 5 also fit such an expected vicariant event. Similar effects of the Yellow River on lineage diversification have also been reported in other taxa (fish: Duan et al., 2009; lizards: Zhao et al., 2011). Only a few other studies exist that focus on the effects of the upper Yellow River on genetic diversification of a young species or species complex (Ma, Du, Zhang, & Wang, 2016), but these lack divergence dating estimations.

The next distal node in the phylogeny suggests that event 6, that is, the river course change to form the Ordos bend, where it flows south (Figure 1) was more recent. A phylogenetic split between *S. schensiensis* (to the west of the Ordos bend) and *Sinothela* sp8 (to its east), the estimated timing of this split to 2.1 Ma (1.2–3.4), and the

ancestral area reconstruction (both areas likely ancestral) reflect the Ordos bend formation as likely a barrier to gene flow, supporting H_6 (Table 1).

What this scenario suggests is that the older course of the middle Yellow River (i.e., along the current Weihe River to Taohuayu, Figure 1; Lin et al., 2001) affected the biotas earlier than the formation of Ordos bend. After this bend was formed, the prior existence of the more direct west–east connection was broken at its western end (Lin et al., 2001). Instead, a part of this former barrier became Weihe River that today remains only connected to the Yellow River at its eastern confluence.

4.2 | Mountain uplifting as barriers

Phylogenetic and distributional patterns across multiple taxa suggest that the emergence of mountain ranges, such as the Andes, East Africa, Mount Kinabalu in Southeast Asia, and the TP in East Asia (e.g., Favre et al., 2015; Hoorn et al., 2010; Hughes & Atchison, 2015; Merckx et al., 2015), act as biogeographical barriers. Zooming into our area of interest, studies also establish the Qinling–Dabie Mts as major geographical barriers to gene flow between northern and southern China (e.g., Yan et al., 2010; Yuan, Cheng, & Zhou, 2012; Zhang et al., 2014; but see Fang et al., 2015). The results reported here corroborate the view that the uplift of these mountain ranges must have affected the diversification history of primitively segmented spiders. The phylogeny clearly detects a sister group relationship between lineages north and south of the mountain range, and the timing of that split at 16.3 Ma (10.3–25.0) is consistent with both geological scenarios that infer this mountain uplift (Table 1). The ancestral area reconstruction at this node allows both regions north and south of the range to be equally likely, with the next distal nodes reconstructing each region. This combined evidence supports H_2 with the emergence of the Qinling–Dabie Mts as a vicariant event. Similar patterns in the same region are also commonly reported in plants and animals (references above).

The uplift of the Taishan and the Mengshan Mts, likewise, may have affected liphistiid vicariance, but the evidence for this is equivocal. The phylogenetic evidence of a sister group relationship between *Sinothela* sp3 found south of the range and the clade 10 that contains all the more distal lineages of *Sinothela* could be consistent with an isolated population to the south of the range. The timing of this split at 7.0 Ma (4.2–10.9) also overlaps with the most recent of the three uplift scenarios (Table 1), therefore consistent with H_3 . However, the ancestral area reconstruction, rather than detecting a wider ancestral area being split into areas on each side of the mountains, suggests a predominantly south of the mountain range persistence. It may be that our sampling intensity was too low in this area, or that the uplift of the Taishan and the Mengshan Mts did not present a major barrier to gene flow.

Our fourth hypothesis assumed the uplift of Taihang Mts as a barrier (Table 1). Indeed, our phylogeny detects a split between lineages on the east and west side of the mountain range, albeit with an outlying sample (*Sinothela* sp7) that could be south of the mountain range.

The timing of this split (4.4 Ma; 2.7–6.9) is also consistent with the middle of the three geologic scenarios (Table 1). Ancestral area reconstruction is also consistent with the prediction, as it detects a shift from a distribution from areas on both sides of the mountains towards areas on each side of them. A comparable vicariant event and time frame is known in *Gammarus* amphipods (Hou et al., 2014). In plants, the vicariance following the uplift of Taihang Mts was reported, but this study misinterpreted the literature (Gong, 2010) and incorrectly attributed relatively young estimates of the lineage divergence to Taihang Mts uplift (Wang & Yan, 2014).

4.3 | Unknown events and undersampling

We did not hypothesize a barrier formation that would explain the first split in clade 10. Its origin may have been affected by the uplift of the Taishan and the Mengshan Mts, although, as discussed above, this hypothesis remains equivocal. The sister group relationship between clades 4 and 9 predates the formation of the lower Yellow River (Table 1). This implies either an earlier unknown vicariant, or another diversification event. A denser sampling in the North China Plain, particularly in the areas D and E (Figure 1), is needed to determine a more precise lineage history in this area. Moreover, we have no clear explanation for the observed phylogenetic sister relationship between clades 8 and 11 that occurs between the Yangtze and Qinling–Dabie Mts. The location of *Sinothela* sp2 south of the Yangtze River cannot be explained by vicariance. Its presence on the southern bank of the river could be due to dispersal events or alternatively, the river may have changed course, suggesting the historic presence of this species north of the river.

5 | CONCLUSIONS

Previous studies have provided evidence for vicariant origins of primitively segmented spiders in the continental islands off Eastern Asia (Xu et al., 2016). This study now adds evidence for continental wide vicariant events that have also shaped these spiders' evolutionary history in continental East Asia. The formation of the Yangtze and Yellow Rivers, and the uplift of the Qinling–Dabie Mts, Taishan–Mengshan Mts, and likely the Taihang Mts, has been estimated to have taken place within extremely wide time intervals. Our study now provides evidence from dated phylogenies that further refines these estimates.

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BIOSKETCH

Xin Xu is a lecturer with research interest in spider biogeography, systematics, and evolution, focusing on primitively segmented spiders and other trap-door spiders. This work represents a component of her work, as well as of Matjaž Kuntner and Daiqin Li, on the biogeography and diversification of primitively segmented spiders in continental East Asia.

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DATA ACCESSIBILITY

These sequence data have been submitted to the GenBank database under accession number MH172680-MH173044.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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