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Spirematospermum wetzleri (Heer) Chandler (Zingiberaceae) from the Miocene of Weichang, Hebei Province, North China and the phytogeographic history of the genus

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Abstract

Spirematospermum is a well-known extinct zingiberalean taxon, characterized by trilocular capsules containing many distinctive, spirally striate and arillate seeds. It is frequently found and studied in European Neogene carpological floras, but is scarcely represented in East Asia floras. In this work we recognize a new fossil record of *Spirematospermum wetzleri* (Heer) Chandler based on the capsules and seeds from the Miocene of Weichang, Hebei Province, North China. These fossils represent the first record of the species in the Miocene of China. Fossil data indicate that *Spirematospermum* probably originated in the Late Cretaceous of North America or Central Europe. The genus still existed in the Paleocene of North America, but became extinct after that time. However, the genus successively survived in Europe from the Eocene to Pliocene, and flourished luxuriantly during the Oligocene to Miocene. As there was Turgai Strait between Europe and Asia during the Eocene, the genus did not spread to Central Asia and West Siberia until the strait closed in the late Eocene/early Oligocene, and further expanded eastwardly to eastern Siberia, Russia, northern China and central Japan during the Miocene, but became extinct in Asia after the Miocene. The genus contracted its distribution to Europe in the Pliocene, and afterwards it became extinct in the world.

Keywords: *Spirematospermum*, Zingiberaceae, Musaceae, Phytogeographic history, Neogene, Miocene, Weichang, North China

1 Introduction

Spirematospermum Chandler (Zingiberales) is an extinct genus, established for trilocular capsules containing many distinctive seeds with spirally striate testa and aril (Chandler 1925; Friedrich and Koch 1970; Fischer et al. 2009). *Spirematospermum* has long been a subject of controversy regarding its systematic affinity, since Heer (1859) first described its capsules and seeds from the Miocene of Günzburg, Germany, but he identified them as *Gardenia wetzleri* Heer (Rubiaceae). Then, Ludwig (1860) described its capsules from the Miocene of Salzhausen and other localities, Germany as *Passiflora braunii* Heer & Ludwig (Passifloraceae). Menzel (1913) suggested a possible relationship with monocotyledonous plants. Chandler (1925) studied its capsules and seeds from the late Eocene of Hordle, Hants, UK, and intensively examined many extant plants, but only in the family Zingiberaceae did they find similar peculiar seed structure, so he established a new genus, *Spirematospermum*, to accommodate these fossils and named them as *S. wetzleri* (Heer) Chandler. Friedrich and Koch (1970) further pointed out that *S. wetzleri* is quite similar to the living species *Alpinia oxymitra* K.Schum. (syn. *Cenolophon oxymitrum* (K.Schum.) Holttum) (Zingiberaceae) based on comparative study between extant Zingiberaceous materials and 70 capsules and hundreds of seeds fossils from the Miocene of Jutland, Denmark. This opinion was strengthened by their following studies (Koch and Friedrich 1971; Friedrich and Koch 1972).

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However, Manchester and Kress (1993) noticed that the unribbed fruits that taper into the basal stalk, multiple seeds per locule and the presence of a chalazal chamber in the seed suggest a close affinity to Musaceae, but *Spirematospermum* possesses a spirally striate testa that is found today in Zingiberaceae, not in Musaceae, thus displays combined characters of both Musaceae and Zingiberaceae. Rodríguez-de la Rosa and Cevallos-Ferriz (1994) interpreted *Spirematospermum* as a member of the Musaceae based on the presence of a chalazal chamber and hilar cavity in seeds. Fischer et al. (2009) made a comprehensive study of *S. wetzleri* based on an extraordinary mass occurrence of capsules and seeds, petioles, a putative pollen grain, associated rhizomes and Zingiberales-type leaves, and phytoliths of these organs from the middle Miocene of Ponholz, Germany. They placed *Spirematospermum* as sister to *Musa* L. + *Ensete* Bruce ex Horan. clade and proposed a new subfamily Parietimusoideae in the Musaceae to accommodate *Spirematospermum*, taking into account its capsule with parietal placentation and probable rhizomatous growth.

Smith et al. (2012, 2014) studied the seeds of over 50 extant species from all eight families of Zingiberales, plus the fossil *Spirematospermum* by synchrotron X-ray tomographic microscopy (SRXTM), and found that a chalazal chamber is not diagnostic of Musaceae, but also was found in Costaceae and tribe Alpiniae (Zingiberaceae), thus suggesting an affinity of *Spirematospermum* with subfamily Alpinioideae within Zingiberaceae again. The result was strengthened by the phytolith study of Zingiberales that both Zingiberaceae and *Spirematospermum* produce silica sand but Musaceae produce troughs (Chen and Smith 2013).

Spirematospermum has an exceptionally wide distribution in space and time, ranging from the Late Cretaceous of North America and Europe to the Paleogene and Neogene of Eurasia, and exists as a common element in many European Neogene carpological floras (Fischer et al. 2009; Smith et al. 2014), but it is less represented and studied in East Asia. Here we reported the capsules and seeds of *Spirematospermum* from the early Miocene of Weichang, Hebei Province, North China, which was preliminary identified to the genus by Yi et al. (2008). And in this article, we further identified them as *S. wetzleri* by comparison with all fossil species of the genus. Based on the fossil record of *Spirematospermum*, the biogeographic history and possible migration routes of the genus are discussed.

2 Materials and methods

The specimens described here were collected from an outcrop at Gaoshanjian (42°07′33″N, 117°50′28″E; 1406 ± 16 m), near Guangfayong Town, Weichang County, Chengde City, Hebei Province, North China (Fig. 1). The fossil-bearing beds are lacustrine deposits, which together with its underlying basalts belong to the Hannuoba Formation according to the 1: 200000 geological map of Qipanshan section (K-50-16) (No. 2 Regional Geological Survey Team, Hebei Bureau of Geology and Mineral Resources 1979). The beds were divided into 9 layers (Fig. 2) according to its lithological changes that include mudstone, muddy siltstone, lignite, conglomerate, and shale. *Spirematospermum* specimens were collected from the 3rd layer (Layer 3; muddy siltstone), the 8th layer (Layer 8; mud stone) and the 9th layer (Layer 9; shale) (Fig. 2). The age of Hannuoba Formation has been interpreted as

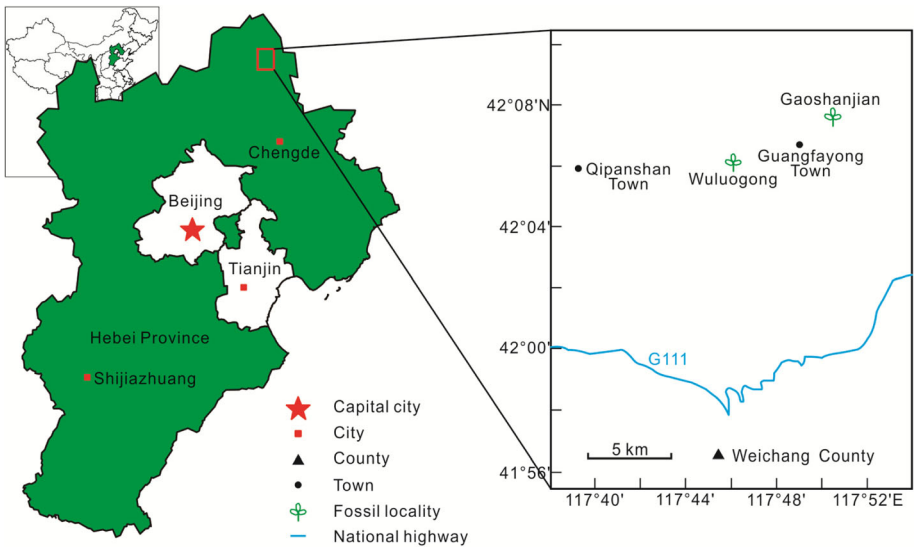

Fig. 1 Map showing fossil locality of *Spirematospermum wetzleri* at Gaoshanjian (marked as), near Guangfayong Town, Weichang County, Chengde City, Hebei Province, North China. The (insert) map of China was generated by the MapInfo data in Microsoft Office 2000

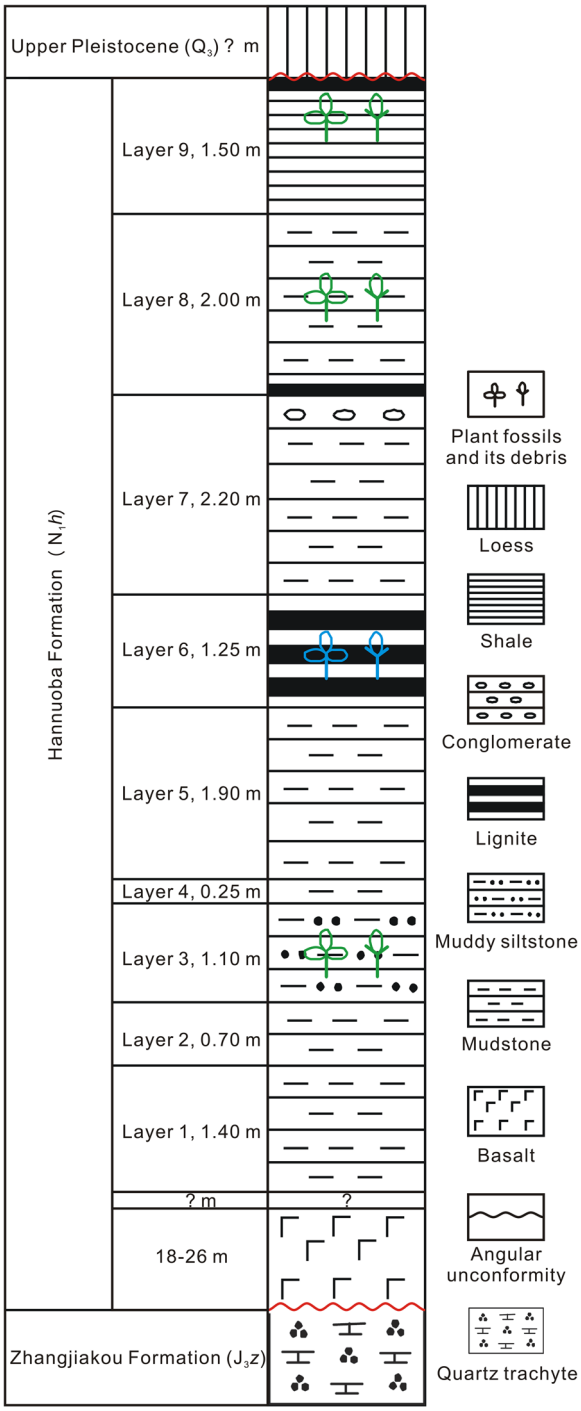

Fig. 2 Stratigraphic and lithologic column of the Gaoshanjian section (modified from Li et al. 2009), indicating where *Spirematospermum wetzleri* was found (Green leaves) and the overlying and underlying strata of Hannuoba Formation (No. 2 Regional Geological Survey Team, Hebei Bureau of Geology and Mineral Resources 1979)

early Miocene on the basis of fossil mammals *Monosaulax changpeiensis* Li and Lagomorpha gen. et sp. indet. From Wafangyingzi, Zhangbei County (Li 1962), plant fossils and sporopollen assemblages as well as the K–Ar radiometric dating of the basalt (22.1 Ma) from Wuluogong, near Guangfayong Town (No. 2 Regional Geological Survey Team, Hebei Bureau of Geology and Mineral Resources 1979).

The plant materials were collected directly from the lignite or separated from the muddy siltstone by washing in water on a 500 um sieve. The materials were successively treated with 10% HCl and 48% HF, and then rinsed with water and air dried. The *Spirematospermum* specimens with 30 capsules and 50 seeds were all deposited at the National Museum of Plant History of China, the Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences, and were allocated the inventory numbers PEPB70701–70780. The prefix PE is an international code for the Chinese National Herbarium, while the PB stands for palaeobotanical collections in the National Museum of Plant History of China.

The palaeolatitudes and palaeolongitudes of the fossil localities were converted from the present day coordinates using PointTracker v4c software (Scotese 2001). Sites were plotted on six palaeomaps (Scotese 1997; Smith et al. 2004; LePage et al. 2005) of Lambert Equal-Area Azimuthal (North Pole) projections using ArcView GIS 3.2 software, covering the following time intervals: Late Cretaceous (~ 80 Ma), Paleocene (~ 60 Ma), Eocene (~ 50 Ma), Oligocene (~ 30 Ma), Miocene (~ 20 Ma) and Pliocene (~ 5 Ma).

3 Results

Order: Zingiberales

Family: Zingiberaceae

Genus: *Spirematospermum* Chandler 1925

Species: *Spirematospermum wetzleri* (Heer 1859) Chandler 1925.

Description: Fruits are three-dimensionally preserved and compressed, and they are elongate capsules with the fragile apex being eroded away, 2.3–6.2 cm long and 0.8–2.1 cm wide (Fig. 3a, b). They are flattened (Fig. 3a) or polyhedral (Fig. 3b), and tapering into a curved stalk at the base. The surfaces of the capsules are longitudinally ribbed or not ribbed, and ornamented with several distinct longitudinal striations. The capsules are irregularly dehiscent from the apex, containing many seeds inside the locules. Seeds are either isolatedly preserved or in-situ enclosed in capsular fruits, facially compressed, 7.5–12.0 mm long and 3.0–5.0 mm wide, irregularly ellipsoidal in outline with an acute or obtuse apex and a truncate, slightly depressed base (Fig. 3c–g). Seeds usually have distinctive, spirally striate testa and a longitudinal furrow in the middle of the seed surface.

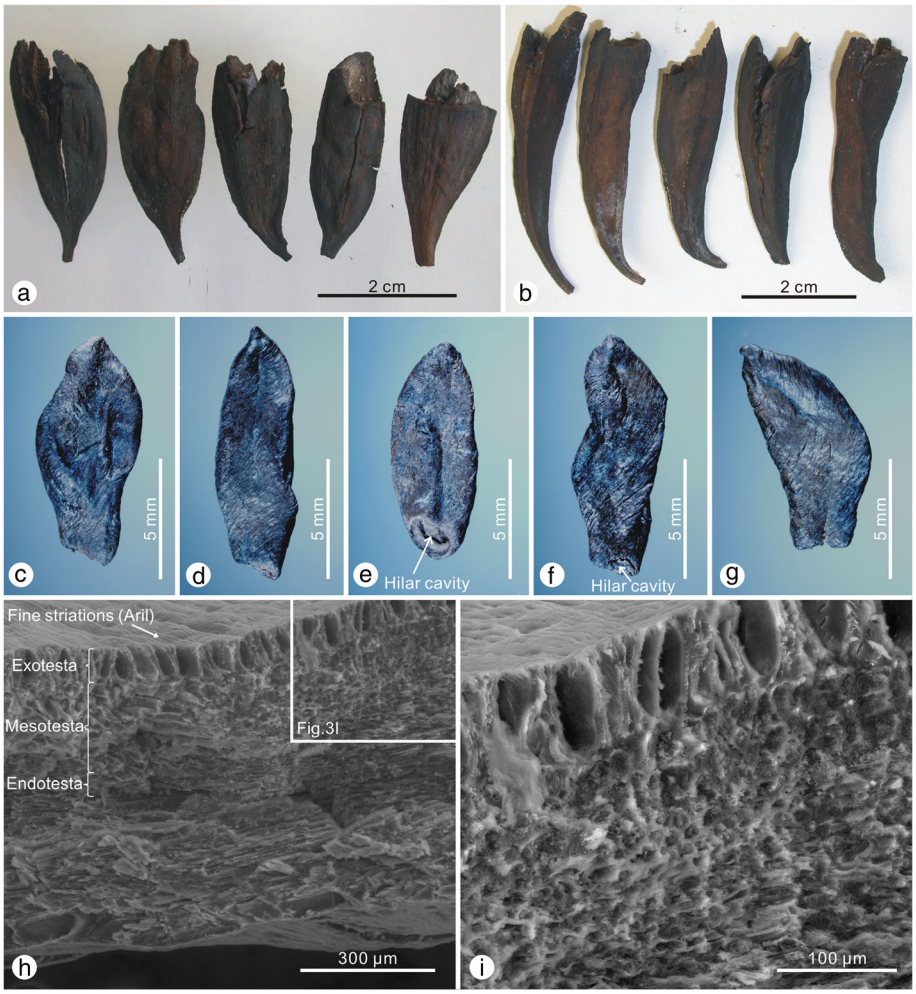

Fig. 3 Capsules and seeds of *Spirematospermum wetzleri* from the early Miocene of Weichang, Hebei Province, North China. **a** Five flattened capsules with the apex eroded away, specimen nos. PEPB70701–70705; **b** Five polyhedral capsules, tapering into a curved stalk at the base, specimen nos. PEPB70706–70710; **c**–**g** The distinctive, spirally striate and arillate seeds, specimen nos. PEPB70731–70735; **h** SEM image of the transverse section of the seed; **i** Magnification of the white rectangular part in **h**

The seed hilum is funnel-shaped with a small central aperture delimiting as hilar cavity (Fig. 3e, f). The seed coat is 0.3–0.4 mm thick, composed of three distinct layers in transverse section, viz., the exotesta consisting of a palisade layer of uniseriate, sclerified, thick-walled rectangular cells; the mesotesta being formed of isodiametric or elongate cells; and the endotesta comprising a layer of narrow, tangentially elongate sclereids (Fig. 3h, i). The tegmen is not observed in the section. The aril is present, which is indicated by the fine striations running across the outer surface of palisade sclereids (Fig. 3h).

4 Discussion

4.1 Comparisons with fossil species of *Spirematospermum*

The Weichang specimens possess the following characters, viz., the elongate capsules tapering at the base into a curved stalk, and the fruits containing many distinctively spirally striate and arillate seeds, which are all indicative of the genus *Spirematospermum* (Fig. 4). This genus includes two Cretaceous species established only by seeds, viz., *S. chandlerae* Friis from the Santonian or Campanian of North Carolina, USA (Friis 1988), and *S. friederichii* Knobloch & Mai from the Maastrichtian of Germany (Knobloch and Mai 1986). The Weichang specimens cannot be assigned to these species, mainly due to their smaller sized seeds (3.6–5.3 mm × 1.0–1.7 mm for *S. chandlerae*, and 2.0–3.5 mm × 1.0–1.5 mm for *S. friederichii*). This genus includes only one Cenozoic species, viz., *S. wetzleri* (Fig. 4), reported from the Paleogene and Neogene of Eurasia (Koch and Friedrich 1971; Fischer et al. 2009). The Weichang specimens can be assigned to this species based on their similar gross morphology and inner structure of capsules and seeds. Reexamining the seeds of *Spirematospermum* from multiple localities by synchrotron X-ray

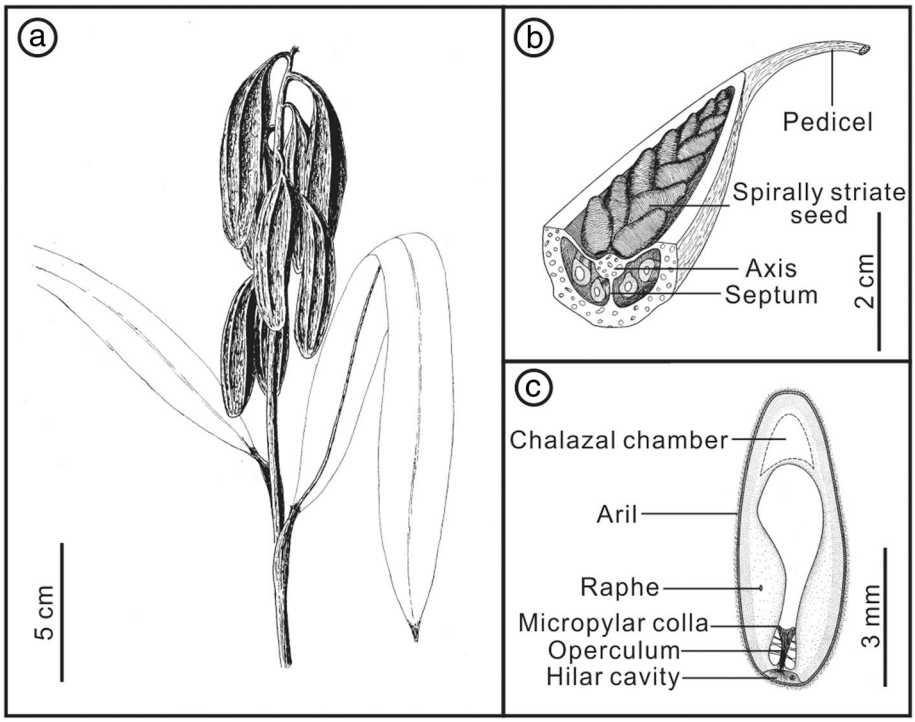

Fig. 4 Sketch drawings illustrating the morphology and anatomy of *Spirematospermum wetzleri* (Koch and Friedrich 1971). **a** The plant reconstruction; **b** Anatomical structures of a capsule; **c** Anatomical structures of a seed

tomographic microscopy (SRXTM), Smith et al. (2014) suggested that *Spirematospermum* sp. from the Cretaceous of Germany should be recognized as a fourth species, and one specimen examined from the Eocene of UK (Collinson 1983) may represent a fifth species. This suggests that *Spirematospermum* probably has greater species diversity during the geological history than we have recognized.

4.2 The phytogeographic history of *Spirematospermum*

The earliest occurrence of *Spirematospermum* is from the Santonian or Campanian of North Carolina, USA (Friis 1988), followed by the occurrences from the late Campanian to early Maastrichtian of Kössen, Austria (Goth 1986), and the Maastrichtian of Saxony-Anhalt, Germany (Knobloch and Mai 1986) (Fig. 5a). This North America-Europe distribution could be caused by the migrations via the North Atlantic Land Bridge in either direction during the Cretaceous (Fischer et al. 2009) (Fig. 6).

During the Paleocene, *Spirematospermum* is only reported from the late Paleocene of Beicegel Creek locality, McKenzie County, North Dakota, USA (Benedict et al. 2007; Fig. 5b). There are no younger occurrences of *Spirematospermum* from North America (Fig. 5c–f). *Spirematospermum* is known from the Eocene of UK and Germany (Chandler 1925; Collinson 1983; Mai and Walther 1985; Fig. 5c), and flourished luxuriantly during the Oligocene and Miocene in Europe (Koch and Friedrich 1971; Friis 1988; Fischer et al. 2009; Fig. 5d, e). *Spirematospermum* probably expanded its distribution eastward into Asia during the Oligocene after the closure of the Turgai Straits in the late Eocene/early Oligocene (Tiffney 1985; Scotese 1997; Sanmartín et al. 2001; Smith et al. 2004), and was further spread eastward into eastern Siberia, Russia, northern China and central Japan during the early Miocene (Nikitin 2007; Yi et al. 2008; Tsukagoshi and Matsuhashi 2012; Figs. 5d, e and 6). *Spirematospermum* disappeared from Asia and became less abundant in Europe during the Pliocene (Fig. 5f), and finally became extinct after Pliocene. This extinction can be related to climate deterioration during the Pliocene, as today the relatives of *Spirematospermum* are exclusively tropical and subtropical plants. Its southward migration to cope with the Pliocene/Pleistocene cooling was hampered by the East–West orientation of the Alps, the Mediterranean Sea and the Himalaya (Fischer et al. 2009).

As *Spirematospermum wetzleri* from Weichang represents the first record of the genus from China, the other two East Asian occurrences of the genus should be mentioned. Of special interest is the occurrence from the early Miocene of Omoloi River basin, Russia (Nikitin 2007), which represents the northernmost occurrence

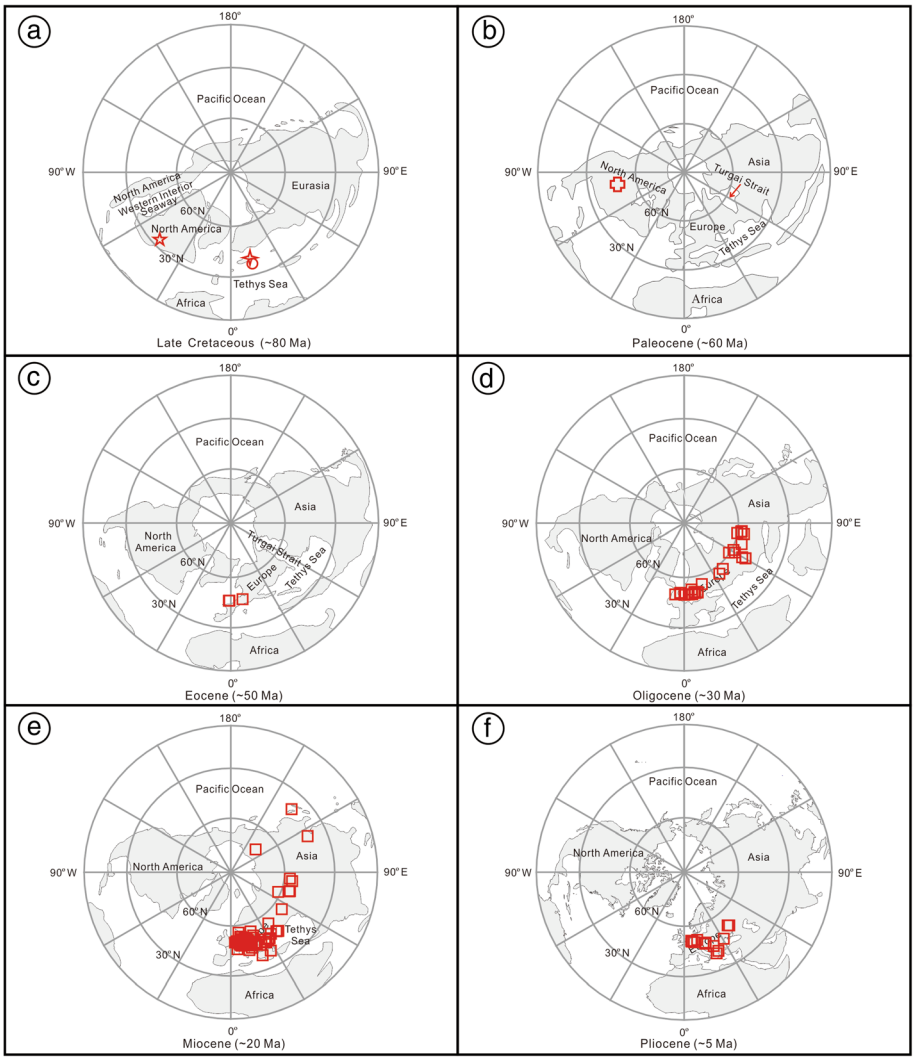

Fig. 5 Palaeogeographic maps showing the distribution of *Spirematospermum* from the Late Cretaceous to the Pliocene (**a**–**f**), based on the Cretaceous occurrences (Goth 1986; Knobloch and Mai 1986; Friis 1988) and the compilation of the Cenozoic occurrences (Fischer et al. 2009). ☆ – *S. chandlerae*; ✦ – *S. friederichii*; ○ – *S.* sp. from Austria; ✚ – *S.* sp. from USA; □ – *S. wetzleri*

(ca. 71.3°N of the palaeolatitude) of the genus for its phytogeographic history. The other occurrence is from the Lower Miocene Nakamura Formation in Kani City, central Japan, representing the first and sole record of the genus in Japan (Tsukagoshi and Matsuhashi 2012).

4.3 The accompanying flora with *Spirematospermum* at Gaoshanjian

The Miocene Gaoshanjian flora is well represented by the fossils of mosses, ferns, conifers and angiosperms (Li et al. 2009; Liang et al. 2010, 2013; Guo et al. 2013). Mosses consist of three species: *Leptodictyum riparium* (Hedw.) Warnst., *Drepanocladus subtrichophyllus* Caiqing Guo & al, *Amblystegium varium* (Hedw.) Lindb., all belonging to the family Amblystegiaceae and suggesting a wet habitat (Guo et al. 2013). Three species of angiosperms, viz., *Comptonia naumannii* (Nathorst) Huzioka, *C. tymensis* Dorofeev, *Weigela weichangensis* Ya Li & C.S.Li were discovered from this locality (Liang et al. 2010, 2013). The palynological data of the Gaoshanjian section suggest that the palaeovegetation was a mixed forest of conifers (e.g., *Pinus*, *Picea*, *Tsuga*) and broad-leaved trees (e.g., *Betula*, *Alnus*), with some subtropical elements (e.g., *Carya*), and the palaeoclimate was warm temperate to subtropical (Li et al. 2009).

The putative leaves of *Spirematospermum* (e.g., *Zingiberoideophyllum*, *Musophyllum*) have not been found at this locality. But some aquatic plants such as *Nuphar* sp. and *Potamogeton* sp. as well as the wetland plant *Epipremnites* sp. (under study) were found together with

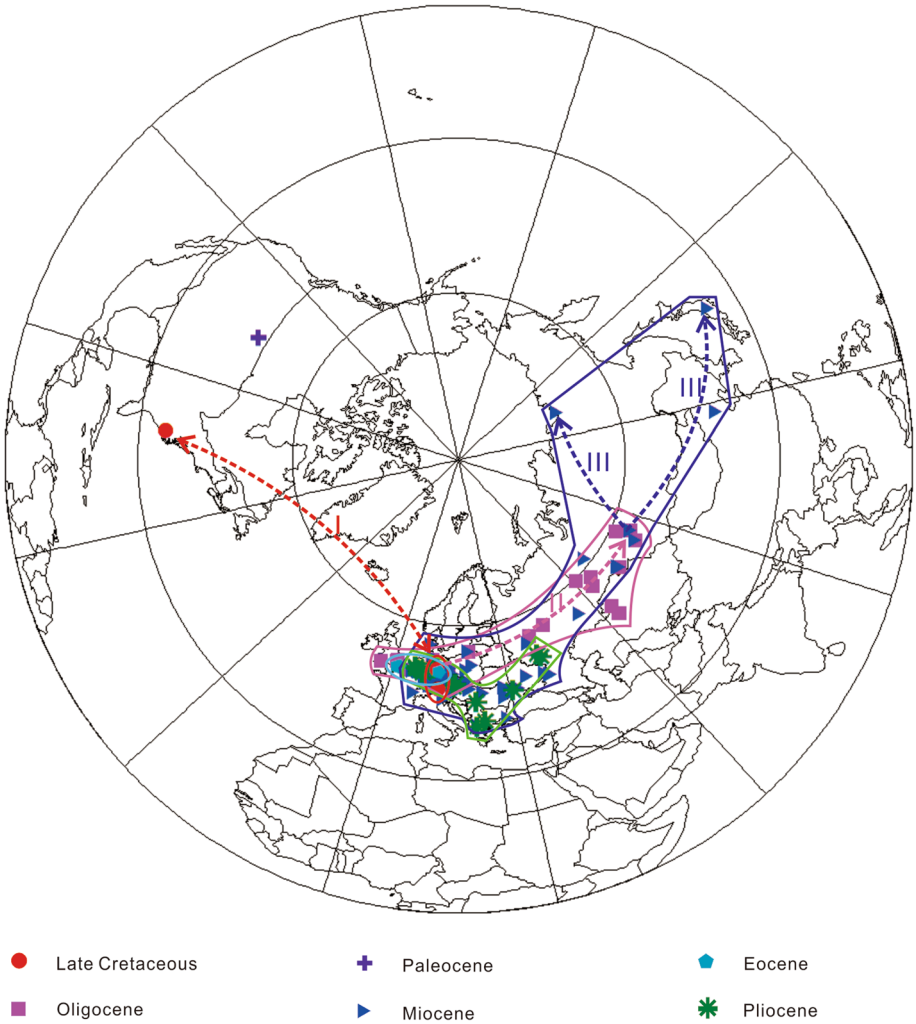

Fig. 6 Distribution and probable spreading map of *Spirematospermum* during the geological times. I – The red dashed line and arrows indicating the spreading of *Spirematospermum* via the North Atlantic Land Bridge in either direction during the Late Cretaceous; II – The purple dashed line and arrow indicating eastward expansion of *Spirematospermum* into Asia during the Oligocene; III – The blue dashed line and arrows indicating further eastward expansion of *Spirematospermum* into East Asia during the Miocene

Spirematospermum wetzleri, which supports that *S. wetzleri* was an important wetland plant with waterside or swamp habitat (Friis 1988; Fischer et al. 2009).

5 Conclusions

We reported an important fossil record of *Spirematospermum* from the early Miocene of North China. We made a detailed description of the well preserved fruits and seeds, which were assigned to *S. wetzleri* by comparing with related fossil species of the genus. Based on the occurrences of *Spirematospermum* fossils, we show the biogeographical distribution of the genus for the first time on a series of palaeogeographic maps of the Northern Hemisphere, and illustrate the probable spreading routes and directions. The accompanying flora from the Miocene of North China suggests that *S. wetzleri* lives in a waterside or swamp habitat of a warm temperate to subtropical climate.

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Authors' contributions
CSL designed the study. YL, TMY and CSL collected the materials. YL and TMY carried out the experiment and wrote the manuscript. YZL and CSL helped modify the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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