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Research paper

Involucre fossils of *Carpinus*, a northern temperate element, from the Miocene of China and the evolution of its species diversity in East Asia

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ABSTRACT

East Asia has long been recognized as a major center for temperate woody plants diversity. Although several theories have been proposed to explain how the diversity of these temperate elements accumulated in the region, the specific process remains unclear. Here we describe six species of *Carpinus*, a typical northern hemisphere temperate woody plant, from the early Miocene of the Maguan Basin, southwestern China, southern East Asia. This constitutes the southernmost, and the earliest occurrence that shows a high species diversity of the genus. Together with other *Carpinus* fossil records from East Asia, we show that the genus had achieved a high diversity in East Asia at least by the middle Miocene. Of the six species here described, three have become extinct, indicating that the genus has experienced apparent species loss during its evolutionary history in East Asia. In contrast, the remaining three species closely resemble extant species, raising the possibility that these species may have persisted in East Asia at least since the early Miocene. These findings indicate that the accumulation of species diversity of *Carpinus* in East Asia is a complex process involving extinction, persistence, and possible subsequent speciation.

1. Introduction

Species diversity of most plant groups tends to be concentrated in one or several geographic centers rather than having an even distribution within its geographic range (Jetz et al., 2012; Kiera et al., 2009; Myers et al., 2000; Pimm et al., 2014; Wu et al., 2006). Of primary interest is when and how the species diversity of plant groups accumulated in their geographic centers. For temperate woody plants of the northern hemisphere, East Asia is a major diversity center (Adair and Li, 1994; Latham and Ricklefs, 1993; Qian, 2002; Wang et al., 2011). The theoretical explanation for this phenomenon is that East Asia is an evolutionary cradle of species diversity, or a museum that accumulates lineages of both old and recent origins (Chen et al., 2018; Lu et al., 2018; Tang et al., 2018; Thorne, 1999; Tiffney, 1985). However, understanding how temperate woody plant groups has accumulated diversity requires specific tests: time-calibrated molecular phylogenetic study and paleobotanical study. In recent years, many molecular phylogenetic studies on temperate woody plants have suggested that most of them originated in the Paleogene and diversified at different times throughout the Paleogene or Neogene (Chin et al., 2014; Forest et al., 2005; Grimm and Renner, 2013; Hinsinger et al., 2013; Li et al., 2018; Naciri et al., 2019; Renner et al., 2008; Yang et al., 2019a, 2019b). Compared to molecular phylogenetic studies, paleobotanical studies provide more direct evidence of the evolutionary history of plants in East Asia; however, few paleobotanical studies have been conducted on the temperate woody plants.

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Carpinus Linnaeus in the birch family (Betulaceae Gray) is an important element of northern temperate forests (Chen, 1994a, b; Wu et al., 2006). The genus comprises about 50 species, of which 46 species are distributed in East Asia, two species in North America, and the remaining two species in Europe (Li and Skvortsov, 1999). East Asia represents a major species diversity center for the genus (Fig. 1). Earlier studies based on single or multiple gene fragment(s) show that *Carpinus* is not monophyletic due to *Ostrya* Scop. being nested within it (Chen et al., 1999; Grimm and Renner, 2013; Yang et al., 2019a; Yoo and Wen, 2002). However, a recent study based on the whole chloroplast genome indicates that the genus is monophyletic and sister to *Ostrya* (Yang et al., 2019b). Fossils of *Carpinus* are abundant in the Cenozoic of the northern hemisphere (Kim and Nam, 2017; Pigg et al., 2003). They have been extensively documented in the form of involucres, sometimes with an attached nut, and leaves, ranging from the Paleogene to the Pleistocene (Dai et al., 2013; Kim and Nam, 2017; Pigg et al., 2003; Stults et al., 2002). Despite extensive studies on *Carpinus*, few have been carried out to reveal how the diversity of the genus accumulated in East Asia.

Recently, abundant *Carpinus* involucre fossils were discovered from the early Miocene of southwestern China. In this study, we aim to (1) identify and describe these involucre fossils; (2) summarize fossil records of *Carpinus* in East Asia; and then (3) discuss the accumulation of species diversity within the genus in East Asia.

2. Material and methods

2.1. Geological setting

The involucre fossils were collected from the Maguan Basin in southeastern Yunnan province, southwestern China (23°1′N, 104°23′E, 1320 m a.s.l.; Fig. 1). The fossil-bearing layers, characterized by cyclic deposits of light-yellow or light-grey laminated mudstones and siltstones, belong to the Huazhige formation (Zhang, 1976). The Huazhige formation is also distributed in Wenshan Basin, which is 45 km from the Magaun Basin. The formation in these two basins has uncovered diverse floras, i.e. the Maguan flora and the Wenshan flora (Huang, 2017; Jia, 2018). Paleobotanical

studies show that the two flora are floristically similar except that the Maguan flora contains many extinct elements such as *Cedrelospermum* Sapota (Jia et al., 2015), *Diviacer* Manchester, and *Podocarpium* A. Braun ex Stizenberger (Jia, 2018). Therefore, the age of the Maguan assemblage is likely older than the Wenshan assemblage. Based on magnetostratigraphic study, the age of Wenshan assemblage has been assigned to the earliest Middle Miocene (15.2–16.5 Ma) (Lebreton-Anberrée et al., 2016). Beneath the Maguan assemblage, a mammal fossil from the Huangzhige formation called *Gigantamynodon* was uncovered (Qi, 1992). *Gigantamynodon* is suggested as have lived from the middle to late Oligocene (Lucas and Emry, 1996; Qi, 1992). Therefore, previous researchers have suggested that the age of the Maguan flora is likely the early Miocene (Huang, 2017; Jia, 2018; Jia et al., 2019b).

Based on preliminary study, the Maguan flora represents a subtropical evergreen broad-leafed forest that includes floristic elements such as *Burretiodendron* Rehder (Lebreton-Anberrée et al., 2015), *Pterolobium* R. Br. ex Wight et Arn. (Jia et al., 2017), *Sequoia* Endlicher. (Zhang et al., 2015), *Sladenia* Kurz (Jia et al., 2019a), and *Ulmus* L. (Zhang et al., 2018).

2.2. Examination and comparison of fossils

A total of 30 involucre fossils assigned to *Carpinus* were collected from the outcrop. These fossil specimens were first photographed using a digital camera (Nikon D700, Kanagawa, Japan), and then moved to a stereo microscope (Leica S8APO, Wetzlar, Germany) to observe fine details. Specimens from the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN) were studied for comparison purposes. Digitized specimens from the Chinese Virtual Herbarium (http://www.cvh.ac.cn/), the Global Plants on JSTOR (https://plants.jstor.org/), and the Royal Botanic Gardens, Kew (https://www.kew.org/) were also studied. Fossil records of *Carpinus* were compiled from the Cenozoic Angiosperm Database (http://www.fossil-cad.net/) (Xing et al., 2016), and published literature (Table 1). Because the leaves of *Carpinus* overlap morphologically with those of other genera in the Betulaceae, we only include involucre fossils and leaf fossils with cuticular details in the discussion. Extant occurrences of *Carpinus* were
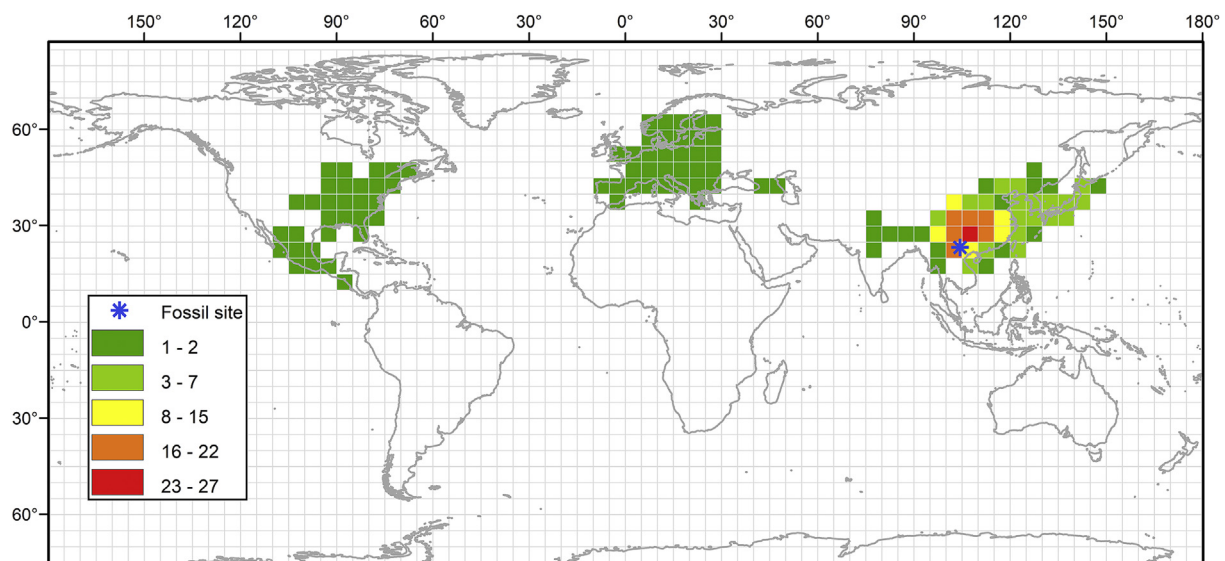

Fig. 1. Extant distribution of *Carpinus* and the position of the fossil locality in Maguan Basin, Yunnan province, China. Different colors in the map indicate the number of species in each grid. Extant occurrence data of *Carpinus* were from the Chinese Virtual Herbarium (CVH) and Global Biodiversity Information Facility (GBIF).

Table 1
Fossil records of *Carpinus* in East Asia.

	Species	Type	Age	Country	Locality	Reference
1	*C.* sp.	Involucre	Early Oligocene	China	Lvhe, Yunnan	Linnemann et al. (2017)
2	*C.* sp. cf. *C. longibracteata* Hu & Chaney	Involucre	Oligocene	Japan	Ouchiyama-kami, Yamaguchi, Honshu	Uemura et al. (1999)
3	*C.* sp.	Involucre	Oligocene	Japan	Ouchiyama-kami, Yamaguchi, Honshu	Uemura et al. (1999)
4	*C. subyedoensis* Konno	Involucre	Early Miocene	Korea	Janggi flora	Huzioka (1972)
5	*C. subcordata* Nathorst	Involucre	Early Miocene	Korea	Janggi flora, Yongdong flora	Huzioka (1972); Ablaev et al. (1993)
6	*C. subyodoensis* Kon'no	Involucre	Early Miocene	China	Weichang, Hebei	Bureau of Geology and Mineral Resources of Hebei Province (1989)
7	*C. asymmetrica* L. Xue & L.B. Jia	Involucre	Early Miocene	China	Maguan	This study
8	*C. symmetrica* L. Xue & L.B. Jia	Involucre	Early Miocene	China	Maguan	This study
9	*C.* cf. *fangiana* Hu	Involucre	Early Miocene	China	Maguan	This study
10	*C.* sp.1	Involucre	Early Miocene	China	Maguan	This study
11	*C.* sp.2	Involucre	Early Miocene	China	Maguan	This study
12	*C.* sp.3	Involucre	Early Miocene	China	Maguan	This study
13	*C. kyushinensis* Endo	Involucre	Middle Miocene	Korea	Gungsim flora	Endo (1950)
14	*C. endoi* Huzioka	Involucre	Middle Miocene	Korea	Gungsim, Gogeonwon floras	Huzioka (1972); Lim et al. (1994)
15	*C. simplicibracteata* Huzioka	Involucre	Middle Miocene	Korea	Janggi, Gogeonwon, Hamjindong floras	Huzioka (1943)
16	*C. stenophylla* Nathorst	Involucre	Middle Miocene	Japan	Kaminokuni flora	Chaney (1963)
17	*C. chaneyi* Tanai & Suzuki	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
18	*C. megabractcata* Hu & Chaney	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
19	*C. mioturczaninowii* Hu & Chaney	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
20	*C. oblongibracteata* Hu & Chaney	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
21	*C. shanwangensis* Hu & Chaney	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
22	*C. shimizui* Tanai	Involucre	Middle Miocene	China	Linju, Shandong	Sun (1999)
23	*C. subyedoensis* Kon'no	Involucre	Middle Miocene	Japan	Tsuchikumazawa	Chaney (1963)
24	*C. praejaponica* Berger	Involucre	Middle Miocene	Japan	Yamakayakusa	Chaney (1963)
25	*C. kodairae-bracteata* Huzioka	Involucre	Middle Miocene	Korea	Yeonil flora	Kim and Nam (2017)
26	*C. miofargesiana* Tanai & Onoe	Involucre	Middle Miocene	Korea	Yeonil flora	Kim and Nam (2017)
27	*C. oblongibracteata* Hu & Chaney	Involucre	Middle Miocene	Korea	Yeonil flora	Kim and Nam (2017)
28	*C. hokoensis* Endo	Involucre	Middle Miocene	Korea	Yeonil flora	Endo (1950); Lim et al. (1994)
29	*C. miofargesiana* Tanai & Onoe	Involucre	Middle Miocene	Korea	Yeonil flora	Kim and Nam (2017)
30	*C. oblongibracteata* Hu & Chaney	Involucre	Middle Miocene	Korea	Yeonil flora	Lim et al. (1994)
31	*C.* sp.	Involucre	Middle Miocene	Korea	Yeonil flora	Chun (1982)
32	*C. kodairae-bracteata* Huzioka	Involucre	Middle Miocene	Korea	Yeonil, Gogeonwon floras	Huzioka (1943); Kim and Nam (2017)
33	*C. subcordata* Nathorst	Involucre	Middle Miocene	Korea	Yeonil, Gogeonwon, Hamjindong floras	Huzioka (1972); Ablaev et al. (1993)
34	*C. stenophylla* Nathorst	Involucre	Middle Miocene	Korea	Yeonil, Janggi, Gungsim, Hamjindong floras	Huzioka (1972)
35	*C. chaneyi* Tanai & Suzuki	Involucre and leaf	Middle Miocene	Japan	Yoshioka flora	Chaney (1963)
36	*C. shimizui* Tanai	Involucre	Middle Miocene	Japan	Yoshioka flora	Chaney (1963)
37	*C. subcordata* Nathorst	Involucre and leaf	Middle Miocene	Japan	Yoshioka, Kaminokuni, Abura, Wakamatsu floras	Chaney (1963)
38	*C. subyedoensis* Kon'no	Involucre and leaf	Middle Miocene	Japan	Yoshioka, Kaminokuni, Abura, Wakamatsu floras	Chaney (1963)
39	*C. heigunensis* Huzioka	Involucre	Middle/Late Miocene	Japan	Yagii flora	Ozaki (1991)
40	*C. heigunensis* Huzioka	Involucre	Late Miocene	Japan	Seto, Itahanna, Ogawa	Ozaki (1991)
41	*C. ovatiInvolucreeata* Li & Sun	Involucre	Late Miocene	China	Shengxian, Zhejiang	Li (2010)
42	*C. orbiInvolucreeata* Li & Sun	Involucre	Late Miocene	China	Shengxian, Zhejiang	Li (2010)
43	*C. miotschonoskii* Li & Sun	Involucre	Late Miocene	China	Shengxian, Zhejiang	Li (2010)
44	*C. nipponica* Endo	Involucre	Miocene	Japan	Nishizawa	Endo (1950)
45	*C. subcordata* Nathorst	Leaf with cuticle	Miocene	China	Tengchong, Yunnan	Sun et al. (2003)
46	*C. honshuensis* Endo	Involucre	Early Pliocene (?)	Japan	Maki, Kawanishi	Endo (1950)
47	*C.* cf. *nipponica* Endo	Involucre	Pliocene	Japan	Kabutoiwa Formation	Ozaki (1991)
48	*C. tengchongensis* Dai & B.N. Sun	Leaf with cuticle	Pliocene	China	Tengchong, Yunnan	Dai et al. (2013)
49	*C. japonica* Blume	Involucre	Pleistocene	Japan	Siobara	Endo (1940)

obtained from the Chinese Virtual Herbarium and Global Biodiversity Information Facility (https://www.gbif.org/). Line drawings of the fossils were made by CorelDraw X7, and the distribution map of *Carpinus* was made by ArcGIS 10.0. As the involucre of *Carpinus* is leaf-like, the terminology used for description mainly follows Ellis et al. (2009) (Fig. 2).

3. Systematics

Family: Betulaceae.
Genus: *Carpinus* L.
Repository: Fossil specimens are stored at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).
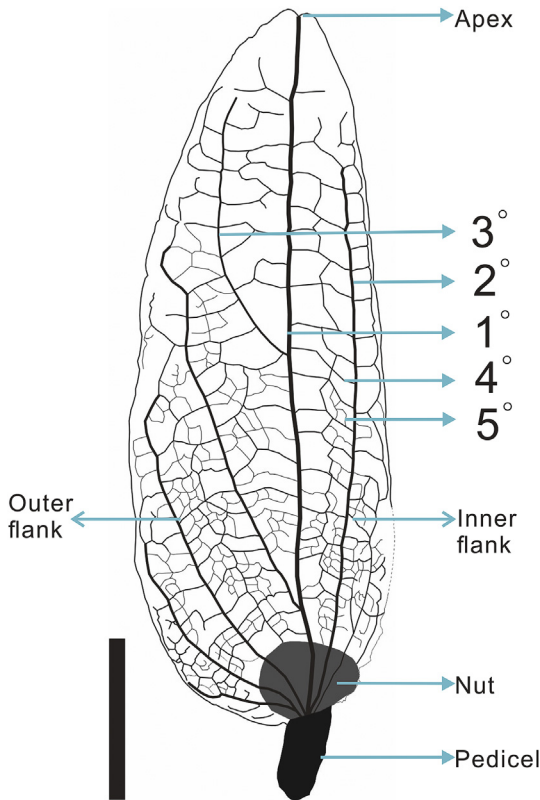
Fig. 2. Morphology of *Carpinus* involucre and corresponding terms. Scale bar = 5 mm.

Locality: Maguan Basin, southeastern Yunnan, southwestern China.

Age: early Miocene.

Section *Distegocarpus* (Sieb. et Zucc.) Sarg.

***Carpinus symmetrica* L. Xue & L.B. Jia sp. nov. (Morphotype 1).**

Holotype: MG0737 (Plate I, 1a) (designated here).

Etymology: The specific epithet "*symmetrica*" refers to the symmetry of the fossil involucre.

Specific diagnosis: Involucre oblong, symmetrical, without auricle, 19.8 mm long and 6.9 mm wide. Margin entire. Vein framework basal actinodromous with five veins.

Description: Pedicel stout, 4.9 mm long. Involucre oblong, almost symmetrical, without auricle, 19.8 mm long and 6.9 mm wide. Margin entire. Apex emarginate. Vein framework basal actinodromous with five veins. The middle vein extending straightly from the base to the apex of the bract. The left flank and the right flank populated by two to three secondary veins. Secondary and tertiary veins forming a series of loops, not reaching the margin. Quaternary vein convex.

***Carpinus* cf. *fangiana* Hu (Morphotype 2).**

Specimen: MG0743 (Plate I, 2a).

Description: Pedicel short, 0.9 mm long. Involucre ovate, symmetrical, base of the left flank enfolded, without auricle, 18.0 mm long and 7.8 mm wide. Margin with sparse teeth. Apex acute. Vein framework basal actinodromous. The middle vein located at the center of the bract, extending straightly from the base to the apex. Secondary veins extending into the teeth. Left flank, two secondary veins visible after enfolding; right flank, four secondary veins. Tertiary vein originating from the midvein and extending into the teeth or forming a chevron. Quaternary vein irregular. Quinternary vein fabric irregularly reticulate.

Section *Carpinus*.

***Carpinus* sp. 1 (Morphotype 3).**

Specimen: MG1154 (Plate I, 5a).

Description: Pedicel stout, 5.0 mm long. Involucre ovate with upper part oblique to the inner (right) flank, the margin of inner flank not well preserved, 19.9 mm long, about 12.1 mm wide, asymmetrical. Outer (left) flank, 7.0 mm wide, inner flank, about 4.9 mm wide. Vein framework basal actinodromous. Inner and outer flank populating four and six secondary veins respectively. Secondary and tertiary veins terminating into teeth. The margin of the outer flank dentate. Quaternary vein not preserved. Nut, oval.

***Carpinus asymmetrica* L. Xue & L.B. Jia sp. nov. (Morphotype 4).**

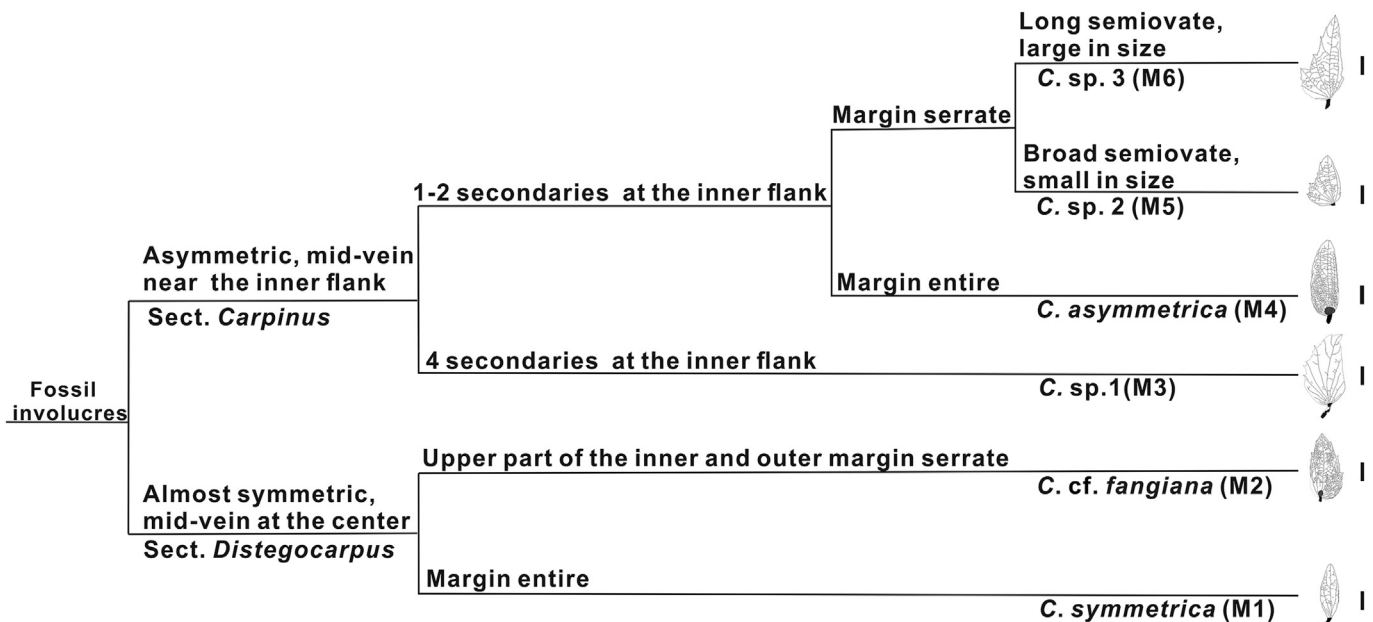**Holotype:** MG0735; MG0742 (Plate I, 3a, 4a). (designated here).

Fig. 3. Key for classifying involucre fossils of *Carpinus* from the Maguan Basin, Yunnan province, China. "M" is short for morphotype. Scale bars = 5 mm.

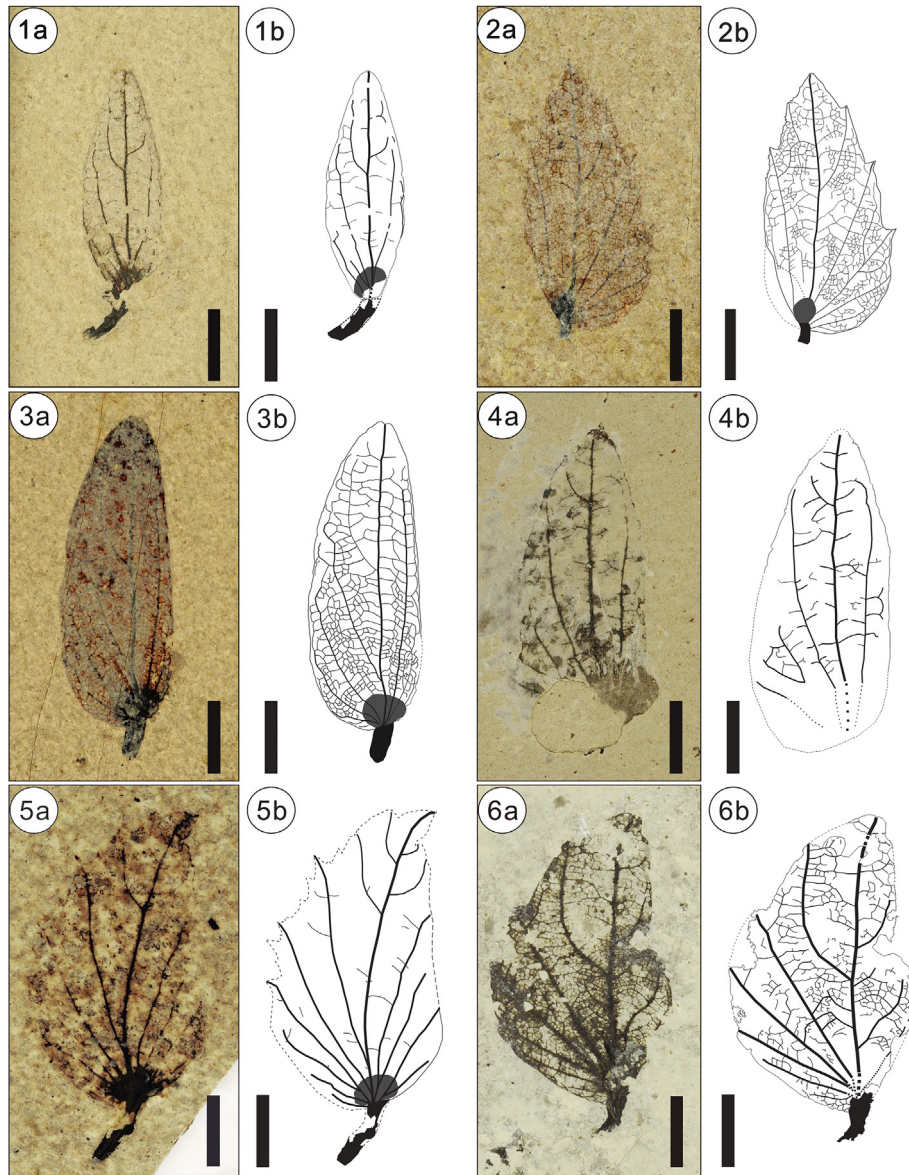**Plate I.** Fossil involucres of *Carpinus* and their line drawings. 1, *C. symmetrica* sp. nov. (morphotype 1); 2, *C.* cf. *fangiana* Hu (morphotype 2); 3, 4, *C. asymmetrica* sp. nov. (morphotype 4); 5, *C.* sp. 1 (morphotype 3); 6, *C.* sp. 2. (morphotype 5). 1, MG0737; 2, MG0743; 3, MG0735; 4, MG0742; 5, MG1154; 6, MG 2044. Scale bar = 5 mm.

Etymology: The specific epithet "*asymmetrica*" means asymmetry which is an important character of the fossil involucres.

Specific diagnosis: Involucre long elliptical, asymmetrical, without auricle, 21.9—22.7 mm long and 7.7—8.8 mm wide. Margin entire. Vein framework basal actinodromous. Inner flank two veins; outer flank four veins. Nutlet oval, about 3 mm in diameter.

Description: Pedicel stout, 2.5 mm long. Involucre long elliptical, asymmetrical, without auricle, 21.9—22.7 mm long and 7.7—8.8 mm wide. Margin entire. Inner flank, 2.7—3.6 mm wide; outer flank, 5.0—5.2 mm wide. Vein framework basal actinodromous. The middle vein situated close to the inner flank, extended from the base to the apex of the bract. Secondary veins forming a series loops with adjacent secondary veins or quaternary veins, not reaching the margin. The inner flank populated by two secondary veins and the outer flank populated by four secondary veins. Tertiary veins originating from the midvein, forming loops with secondary veins. Quaternary vein convex or forming a chevron, mixed percurrent. Quinternary vein irregularly reticulate. Nutlet small, about 3 mm in diameter.

***Carpinus* sp. 2 (Morphotype 5).**

Specimens: MG0740; MG0748; DSC1543; MG1456; MG 2047; MG 2050; MG 2051 (Plate I, 6a; Plate II).

Description: Pedicel stout, 1.2—4.7 mm long. Bract broad semiovate, asymmetrical, without auricle, 12.0—14.9 mm long, 5.8—9.9 mm wide. Inner flank, 1.9—3.9 mm wide; outer flank, 3.9—7.2 mm wide. Margin of inner flank entire or occasionally with an inconspicuous tooth. Margin of outer flank serrate. Vein framework basal actinodromous. The distal end of the midvein slightly oblique to the inner flank. The inner flank populated by one or two secondary veins; the outer flank populated by three to five secondary veins. Secondary vein losing their gauge in the course extending to the apex. Tertiary vein concave, terminating at teeth in the outer flank, forming loops or gradually lose their gauge in the inner flank. Quaternary vein convex, mixed percurrent. Quinternary vein irregular reticulate. Nut oval, 3—4 mm in diameter.
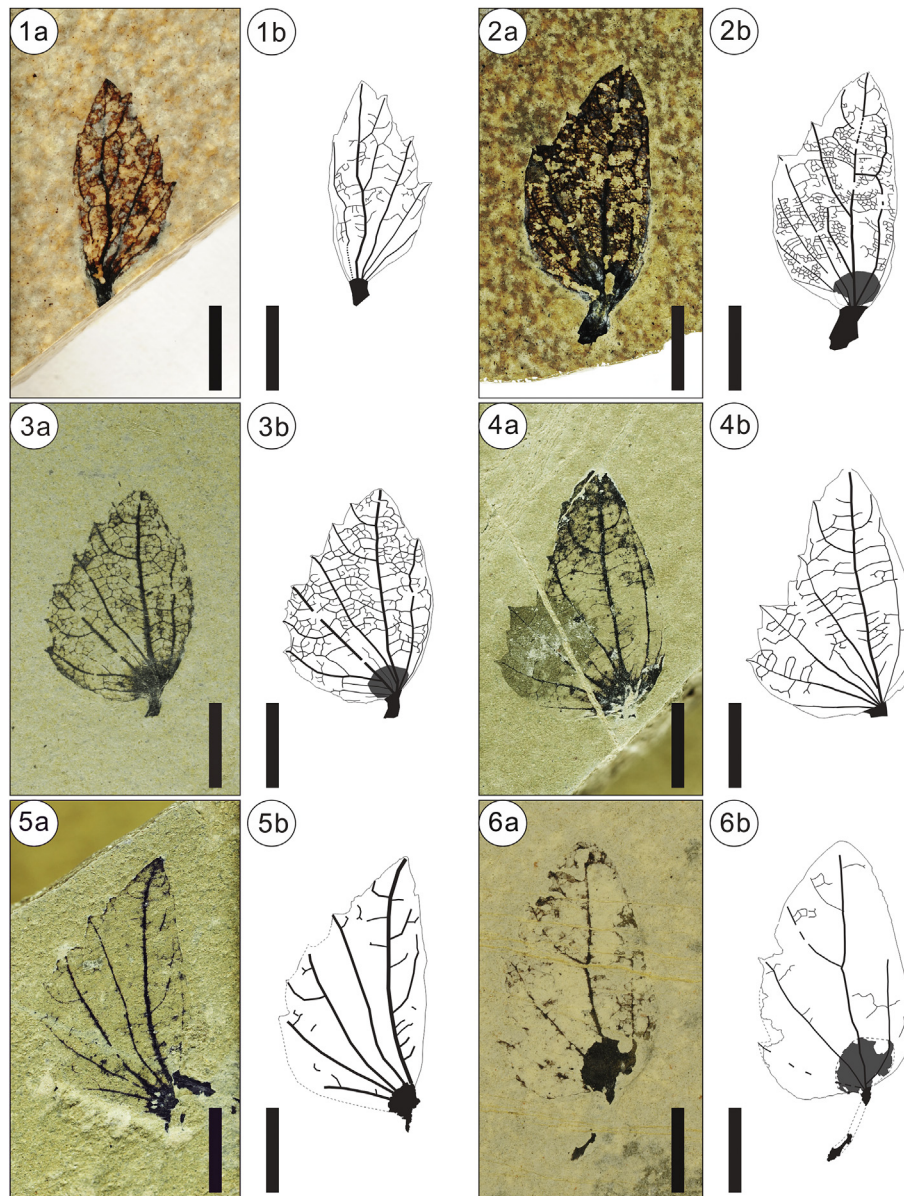
Plate II. Fossil involucres of *Carpinus* sp. 2 (morphotype 5) and their line drawings. 1, MG0748; 2, MG1456; 3, DSC1543; 4, MG2047; 5, MG2050; 6, MG0740. Scale bar = 5 mm.

Carpinus **sp. 3 (Morphotype 6).**

Specimens: MG0666; MG0735; MG0739; MG0746; MG1594; MG 2044 (Plate III).

Description: Pedicel stout, 1.2–4.1 mm long. Bract semiovate to triangular, asymmetrical, 20.0–24.7 mm long, 7.8–12.5 mm wide. Inner flank, 2.9–4.1 mm wide; outer flank, 4.8–8.4 mm wide. The margin of inner flank entire, straight or sinuous. The margin of outer flank dentate; teeth spaced irregularly, sparse; tooth prominent, lobe-like in appearance. Vein framework basal actinodromous. The middle vein extending straightly from the base to the apex or oblique to the inner flank. The inner and outer flank populated by two to three and three to four secondary veins respectively. Secondary vein terminating at teeth in the outer flank, or forming loops with adjacent tertiary vein and Quaternary vein. Tertiary vein originating from the midvein, extending into teeth or forming loops with adjacent veins. Quaternary vein straight, convex, mixed percurrent. Quinternary vein reticulate. Nutlet oval, 3.0–4.0 mm in diameter.

4. Discussion

4.1. Morphological comparisons

The studied fossils are characterized by short and stout pedicels, ovate leaf-like laminae with basal actinodromous venation, and an oval nut positioned at the base of the lamina (Plate I–III). This combination of characters is identical to involucres of *Carpinus*. Five other genera in the Betulaceae, i.e., *Corylus* L., *Cranea* Manchester & ZD Chen, *Ostrya* Scop., *Ostroyopsis* Decne., and *Paleocarpinus* Crane produce more or less similar involucres (Crane, 1981; Li and Skvortsov, 1999; Manchester and Chen, 1998). However, the involucres of *Ostrya* are saccate, and those of *Cranea*, *Corylus*, *Ostrya*, and *Ostroyopsis* are campanulate or form a tubular sheath (Li and Skvortsov, 1999; Manchester and Chen, 1998), and therefore differ from the new fossils (Plate I–III). The involucres of *Paleocarpinus* are five-lobed, enclosing two nutlets (Crane, 1981), distinguishable from those of *Carpinus*, which are one to three lobed and enclose
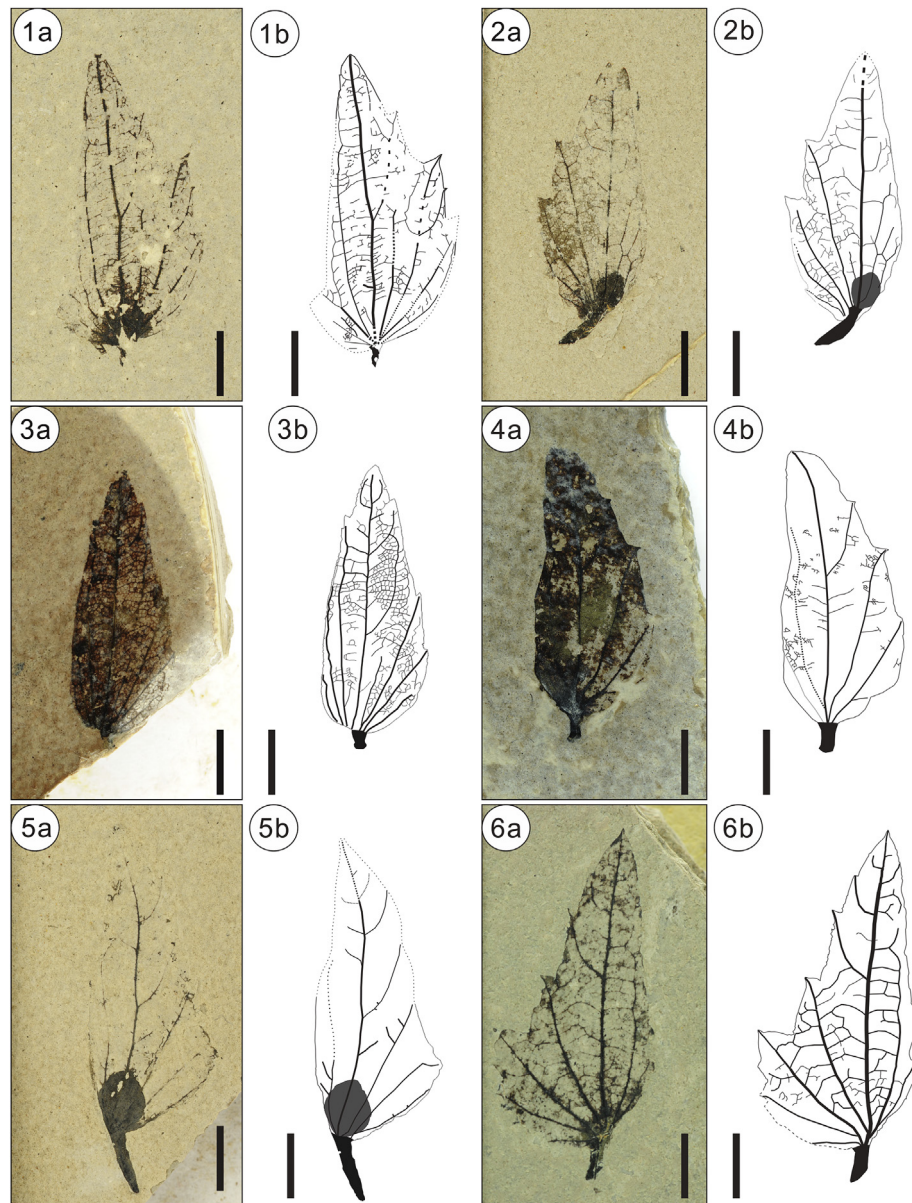
Plate III. Fossil involucres of *Carpinus* sp. 3 (morphotype 6) and their line drawings. 1, MG0735; 2, MG0739; 3, MG0666; 4, MG1594; 5, MG0746; 6, MG2044. Scale bar = 5 mm.

one nut (Plate I—III). Therefore, the new fossils can be unequivocally assigned to *Carpinus*.

Carpinus is divided into two sections, namely, section *Distegocarpus* (Sieb. et Zucc.) Sarg. and section *Carpinus* (Li and Cheng, 1979). Because the characters of the involucre are the basis for the infrageneric classification of *Carpinus* (Li and Cheng, 1979), it allows the new involucre fossils to be placed to section and even species level. In this study, we classified the new fossils by using both involucre characters of modern *Carpinus* classification systems, including the position of the midvein, presence or absence of lobes, teeth of inner and outer margins; and additional characters we regard as significant, including the numbers of veins in the inner flank and the overall shape. Based on all these characters, we recognized six morphotypes which may represent six species (Fig. 3).

Morphotypes 1 and 2 are characterized by the midvein being situated nearly in the middle of the involucre. Although the base of morphotype 2 seems asymmetric at first glance, the obvious enfolded left side indicates that it was symmetric (Plate I, 2a). This phenomenon is also observed in the extant involucres of *Carpinus*. Therefore, morphotype 1 and 2 should be assigned to the section *Distegocarpus*. Morphotype 1 has an entire margin (Plate I, 1a), apparently different from the three extant species in section *Distegocarpus* that possess sparse teeth at the apex of the involucre, i.e., *Carpinus cordata* Bl., *Carpinus fangiana* Hu, and *Carpinus rankanensis* Hayata. Thus morphotype 1 represents an extinct species within the genus. To the best of our knowledge, no fossil species have similar involucre morphology as our fossil. Therefore, we assign morphotype 1 to a new species, i.e., *C. symmetrica*. Morphotype 2 is close to *C. fangiana* Hu in size and gross morphology (Plate I, 2a; Plate IV, 1—4).

Morphotypes 3—6 are distinguished by the midvein being situated at the inner flank, and thus should be assigned to section *Carpinus*. This section is divided into subsections *Carpinus*, *Monbeigianae* (Hu). P. C. Li, and *Polyneurae* (Hu) P. C. Li (Li and Cheng, 1979). The inner and outer flanks of morphotypes 3—6 have no
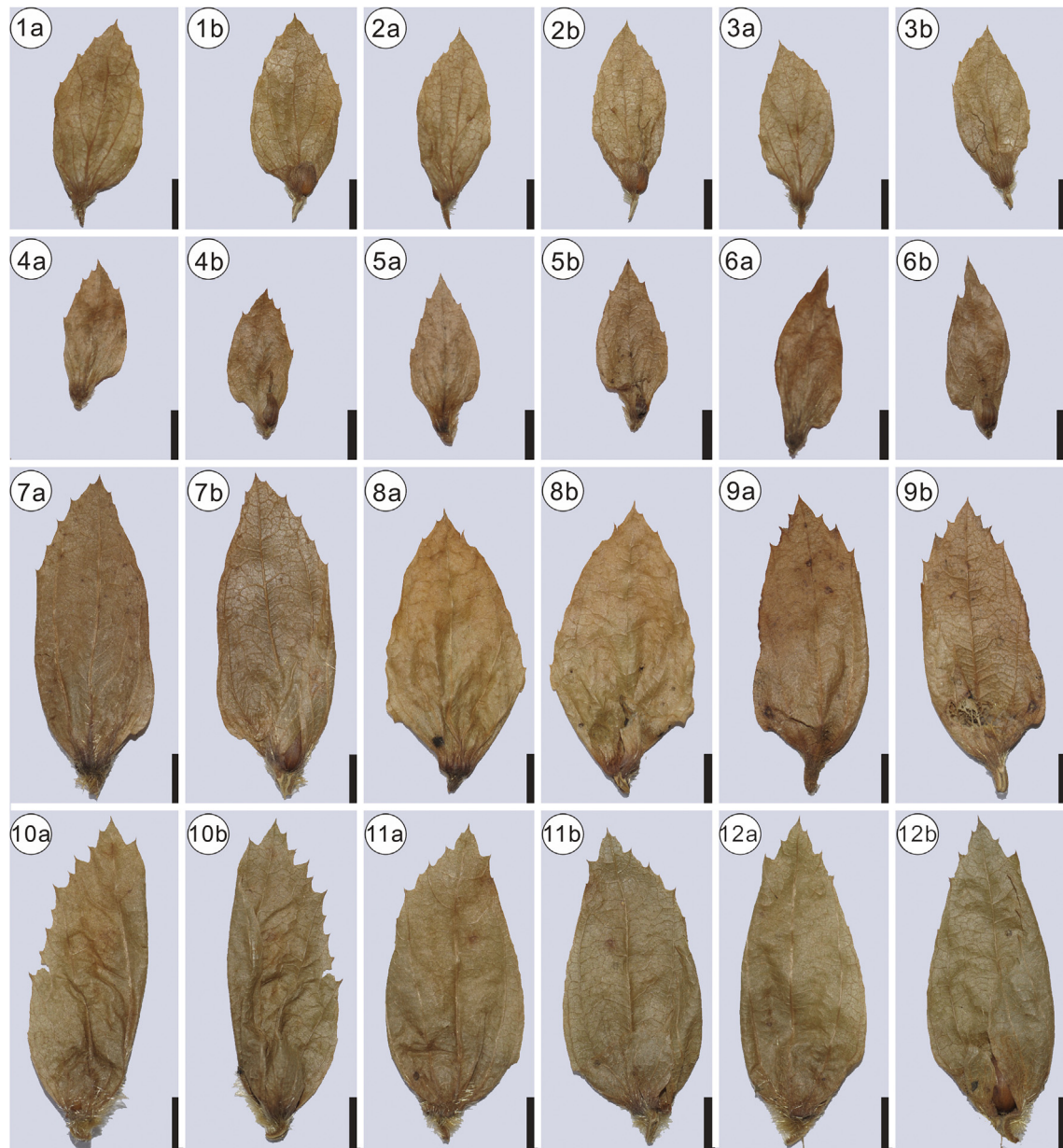
Plate IV. Involucre morphology of *Carpinus* section *Distegocapus*. 1—3, *C. fangiana* Hu; 4—6, *C. rankanensis* Hayata; 7—9, *C. cordata* Bl.; 10—12, *C. cordata* Bl. var. *chinensis* Franch. "a" indicates the reverse side of the involucre; "b" indicates the front side of the involucre. Scale bars = 5 mm.

lobes, and thus differ from subsection *Carpinus*. Therefore, they represent members of subsection *Monbeigianae* or subsection *Polyneurae*. However, it is difficult to precisely assign them to either of the two subsections. Morphotype 3 has an almost equal number of veins at the inner and outer flank of involucre (Plate I, 5a), which makes it to some extent similar to section *Distegocarpus*. However, morphotype 3 has five veins at the outer flank and an asymmetrical shape (Plate I, 5a), which justifies our placement within section *Carpinus*. Compared with other extant species in section *Carpinus*, morphotype 3 has more secondary veins originating from the inner flank of involucre. Therefore, it may represent an extinct species in the genus. However, as the inner flank of the specimen is not well preserved, we here leave the nomenclature of morphotype 3 open for discussion. Morphotype 4 is to some extent similar to *Carpinus pubescens* Burk. in having an elliptical shape and round apex (Plate I, 3a, 4a). However, the former is different from the latter in having

an entire margin. To our best knowledge, no fossil species resemble morphotype 4. Therefore, morphotype 4 likely represents another extinct species. Here we assign morphotype 4 to a new species, *C. asymmetrica*. Morphotype 5 is small and broadly semiovate (Plate I, 6a; Plate II), and thus is morphologically similar to four extant species, *Carpinus kweichowensis* Hu, *Carpinus monbeigiana* Hand.-Mazz., *Carpinus rupestris* A. Camus, and *Carpinus turczaniowii* var. *stiputale* (H. Winkl.) H. Winkl. (Plate IV—VII). Morphotype 6 is elongated semiovate (Plate III), closely resembling *Carpinus mollicoma* Hu and *Carpinus omeiensis* Hu & Fang (Plate IV—VII).

4.2. High diversity in East Asia at least since the middle Miocene

Reliable fossil records of *Carpinus* from the East Asian Paleogene are relatively scarce (Table 1). Based on our knowledge, the involucre fossil record from the early Oligocene of the Lvhe flora in

Plate V. Involucre morphology of *Carpinus* subsection *Carpinus*. 1—3, *C. viminea* Wall.; 4, *C. tientaiensis* Cheng; 5—6, *C. londoniana* H. Winkl. var. *Lanceolata* (Hand. -Mazz.) P. C. Li; 7—9, *C. londonniana* H. Winkl.; 10—12, *C. londonniana* H. Winkl. var. *xiphocteata* P. C. Li. "a" indicates the reverse side of the involucre; "b" indicates the front side of the involucre. Scale bars = 5 mm.

southwestern China represents the earliest record of the genus in East Asia (Linnemann et al., 2017). The other Paleogene record is from the Oligocene Ouchiyama-kami flora in Japan, where two species were recognized (Uemura et al., 1999) (Table 1). For the early Miocene, only three species have been reported from northern China and Korea (Ablaev et al., 1993; Bureau of Geology and Mineral Resources of Hebei Province, 1989; Huzioka, 1972) (Table 1). Our discovery of six *Carpinus* species from the Maguan flora constitutes the southernmost fossil occurrence, and also the earliest occurrence that shows a high diversity for the genus. This find demonstrates that *Carpinus* had already reached southern East Asia and achieved a relatively high species diversity there at least by the early Miocene. In total, nine *Carpinus* species are known

from the early Miocene of East Asia (Table 1), indicating that the species diversity of the genus has increased since then. Middle Miocene *Carpinus* fossils has been extensively described from northern and southern East Asia (Table 1). In all, 18 species have been reported, showing that the genus had achieved a high diversity by the middle Miocene (Table 1). Few studies have reported *Carpinus* species from the late Miocene and Pliocene. This gap in fossil may be due to under-investigation, taphonomic bias, or possible extinction event (Table 1).

A distinctive distributional feature of *Carpinus* in East Asia is that a small region commonly harbors a high diversity of *Carpinus* species. For example, in the Wenshan Nature Reserve and Mount Jinggangshan regions, 12 *Carpinus* species have been documented
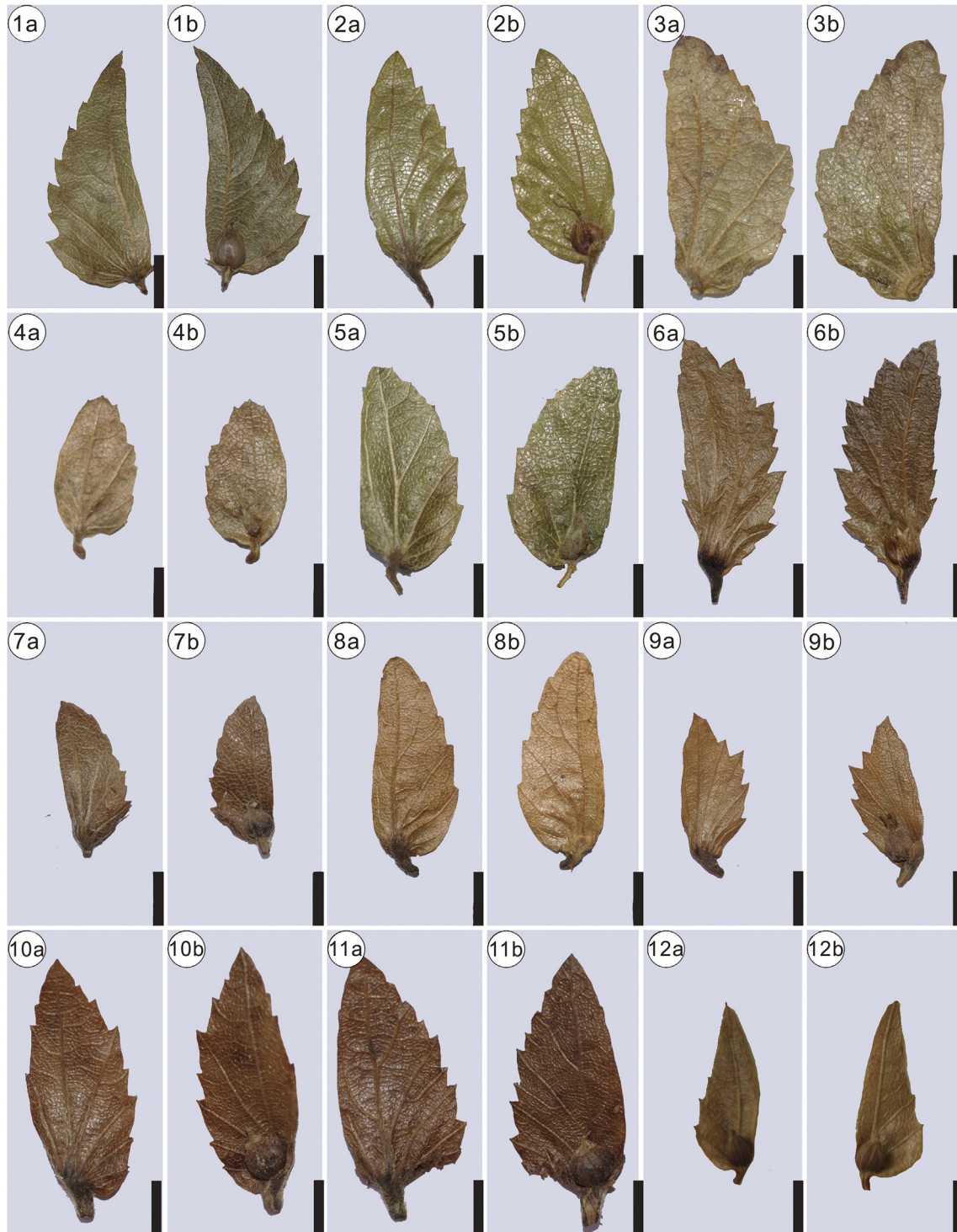
Plate VI. Involucre morphology of *Carpinus* subsection *Monbeigianae* (Hu). P. C. Li. 1—2, *C. fargesiana* H. Winkl.; 3, *C. kweichowensis* Hu; 4—5, *C. monbeigiana* Hand.-Mazz.; 6, *C. turczaniowii Hance*; 7—8, *C. pubescens* Burk.; 9, *C. turczaninowii* Hance var. *stipulata* (H. Winkl.) H. Winkl.; 10—11, *C. tsaiana* Hu; 12, *C. chuniana* Hu. "a" indicates the reverse side of the involucre; "b" indicates the front side of the involucre. Scale bars = 5 mm.

(Liao, 2014; Yang et al., 2008); and in Mount Emei, five *Carpinus* species were discovered (Li and Shi, 2007). Thus, understanding when this pattern was formed is of great interest. Because mega-fossils usually represent floristic elements of regions proximal to the site of deposition, the diversity of plant groups in paleofloras can directly reflect the level of species diversity of taxa in a region in the geological past (Huang et al., 2015). Six *Carpinus* species were discovered from the early Miocene of southeastern China, southern East Asia and, five species have been reported from the middle Miocene of Shanwang flora, China, central East Asia (Sun, 1999), while six species have been documented from the middle Miocene of Yeonil flora, Korea, northern East Asia (Kim and Nam, 2017). This
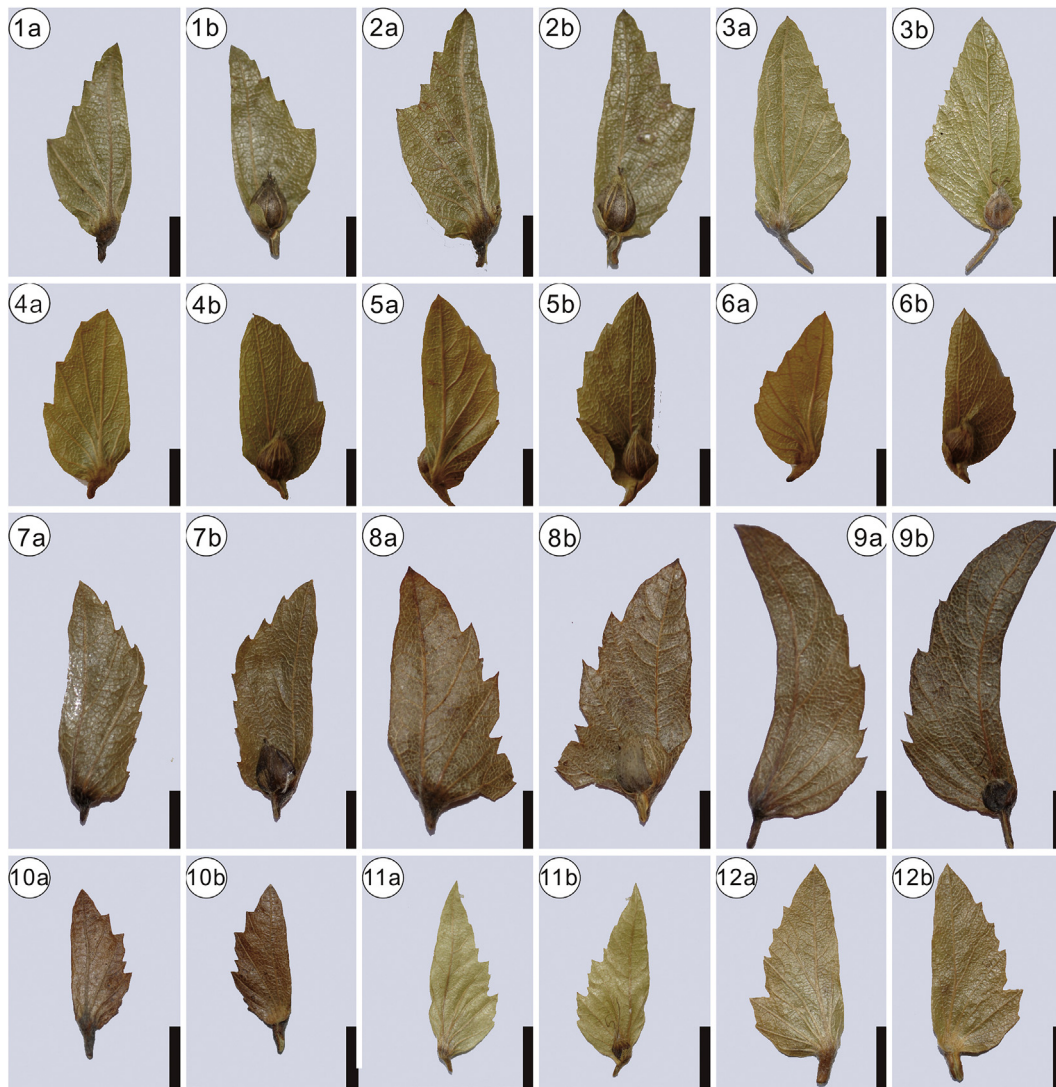
Plate VII. Involucre morphology of *Carpinus* subsection *Polyneurae*. 1–2, *C. mollicoma* Hu; 3, *C. omeiensis* Hu; 4–6, *C. rupestris* A. Camus; 7–8, *C. tschonoskii* Maxima.; 9, *C. tschonoskii* Maxim. var. *falcatibracteata* (Hu) P. C. Li; 10–12, *C. polyneura* Franch. "a" indicates the reverse side of the involucre; "b" indicates the front side of the involucre. Scale bars = 5 mm.

pattern is indicative that the phenomenon which a small region harbors a high diversity of *Carpinus* species can at least be traced back to the middle Miocene across East Asia.

4.3. Extinction and persistence in southern East Asia

Extinction events are an essential aspect of the evolution of diversity. In this study, we identified three extinct *Carpinus* species, namely *C. symmetrica*, *C. asymmetrica*, and *C.* sp. 1. The discovery of these species shows that extinction events have taken place in the evolution of *Carpinus* in East Asia. Such extinction events have been also found in other taxa such as *Cedrelospermum* Saporta, *Cedrus* Trew, and *Sequoia* Endlicher. in southwestern China (Jia et al., 2015, 2019b; Su et al., 2013; Zhang et al., 2015). These extinctions have been ascribed to the southeastern extrusion of the Tibetan Plateau and the intensification of the East Asian monsoon (Jia et al., 2015; Su et al., 2013). The three *Carpinus* species described in this study might have experienced a similar fate, although the exact reason for the extinction could not yet be determined.

Although *C.* cf. *fangiana*, *C.* 2, and *C.* 3 closely resemble several extant *Carpinus* species in morphology, they could not be unequivocally assigned to a specific extant species. These extant species now have a wide a distribution range in southwestern China. The resemblance of these fossils to extant species raises the possibility that the wide climatic tolerance species of these species has allowed their sustained presence in southwestern China since the early Miocene.

To conclude, our findings indicate that the accumulation of *Carpinus* species diversity in East Asia was a complex process, involving extinction, persistence, and possible subsequent speciation because the species diversity of the genus known in fossil records is much lower than its modern diversity in East Asia.

Author contributions

LJ and SZ conceived and designed the research. LX, LJ, GN, YH, SZ, YW, ZZ and YC performed research and analyzed data. LX and LJ wrote the paper.

Declaration of Competing Interest

None.

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