Quaternary International 392 (2016) 224–232

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Continuous existence of *Zanthoxylum* (Rutaceae) in Southwest China since the Miocene

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ARTICLE INFO

Article history:
Available online 2 July 2015

Keywords:
Zanthoxylum
Fossil seed
Miocene
Pliocene
Pleistocene
Southwest China

ABSTRACT

Fossil seeds of *Zanthoxylum* L. (Rutaceae) were studied from three fossil floras in Yunnan Province, Southwest China, the late Miocene Shuitangba, late Pliocene Fudong, and early Pleistocene Nanbanbang. Based on seed morphological characters, the Shuitangba seeds were assigned to a new fossil species, *Zanthoxylum trachyspermum* sp. nov. H. Zhu et Z.K. Zhou, the Fudong seeds were determined only at the generic level, and the Nanbanbang seeds were designated to a modern species, *Zanthoxylum avicennae* (Lam.) DC. These three new fossil records, together with *Z. tertiarium* (Heer) Gregor et Hantke from the early to middle Miocene Mangdan flora and modern distributions of *Zanthoxylum* in Southwest China, imply that *Zanthoxylum* has continuously existed in this region at least since the early to middle Miocene. Quaternary glaciations have not caused the disappearance of *Zanthoxylum* from Southwest China, differing from the situation in Europe where the genus was well represented prior to the Pleistocene but became extinct thereafter. The severe post-Miocene environmental changes caused by the continuous uplift of the Qinghai-Tibet Plateau and adjacent areas might have promoted the establishment of its modern high diversity in Southwest China through enlarging environmental heterogeneity.

1. Introduction

Zanthoxylum L. is a species-rich genus in the rue family (Rutaceae), consisting of about 230 species of evergreen and deciduous trees, shrubs, or woody climbers (Zhang et al., 2008; Kubitzki et al., 2011). It is native primarily to tropical and subtropical regions worldwide, and approximately 15 species extend into the temperate zones in eastern Asia and North America (Porter, 1976; Beurton, 1994; Zhang et al., 2008; Kubitzki et al., 2011). Southwest China is home to 36 of the total 41 Chinese *Zanthoxylum* species (Huang, 1997; Zhang et al., 2008), representing one of the modern diversity centres of the genus (Tiffney, 1980).

In eastern Asian countries, *Zanthoxylum* has long attracted people's interest for its extensive applications of their fruits as spices (Huang, 1997; Rakić et al., 2009), mainly owing to the tingling oral sensation created by a chemical constituent called alkylamides (Bryant and Mezine, 1999; Yang, 2008). This is particularly famous in Southwest Chinese provinces, such as Yunnan and Sichuan, where fruits of several *Zanthoxylum* speices, e.g., *Z. armatum*, *Z. bungeanum*, and *Z. schinifolium* are commonly used in “Chinese cuisines” to improve the dishes' taste (Huang, 1997; Yang, 2008; Lu et al., 2011). Fruits of the genus therefore are also called Chinese pepper or Sichuan pepper by the local people.

In contrast to its sound fascination as a seasoning source in Southwest China, historical occurrences of *Zanthoxylum* have attracted little attention. Although *Zanthoxylum* has an excellent fossil record in European and North American countries (e.g., Chandler, 1964; Gregor, 1977, 1978, 1989; Mai and Walther, 1978; Tiffney, 1980, 1994; Gregor and Hantke, 1983; Łańcucka-Środoniowa, 1984; Van der Burgh, 1987; Martinetto et al., 1997, 2014), and Japan (e.g., Miki, 1937, 1941), it has scarce fossils reported from China. To date, only two fossil occurrences of *Zanthoxylum* have been documented in this country. They are a leaf of *Z. prunifolium* Hu et Chaney from the middle Miocene Shanwang flora in East China (Sun, 1999), and seeds of *Z.*

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http://dx.doi.org/10.1016/j.quaint.2015.05.020
1040-6182/

tertiarium (Heer) Gregor et Hantke from the early to middle Miocene Mangdan flora in Southwest China (Zhao et al., 2004). The Mangdan seeds indicate that *Zanthoxylum* already grew in Southwest China no later than the early to middle Miocene. However, in the absence of post middle Miocene fossils, its historical occurrences from the middle Miocene to present day in this region are still unknown.

In this study, we report three fossil occurrences of *Zanthoxylum* from Southwest China, on the basis of seed remains (sclerotesta) which extend from the early Pleistocene into the late Miocene. The fossil seeds were studied morphologically and taxonomically. The biogeographic and evolutionary implications of these new findings discussed.

2. Material and methods

2.1. Fossil sites

The studied fossil seeds were collected from three fossil floras in Yunnan Province, Southwest China, Shuitangba, Fudong, and Nanbanbang (Fig. 1).

The Shuitangba flora is within an open-pit coal mine in the Zhaotong Basin, northeastern Yunnan (27°20′, 103°44′; 1918 m a.s.l.). The geological setting of the fossil site was described by Ji et al. (2013). Fossil remains of seeds, together with those of juvenile hominoid cranium, rodent and large mammals, were deposited within several peaty clay layers (Ji et al., 2013; Jablonski et al., 2014). The geological age of the fossiliferous peaty clay layers is 6.5–6.0 Ma (late Miocene), based on the biochronological and geochronological investigations (Zhu et al., 2008), and paleomagnetical analysis (Ji et al., 2013).

The Fudong flora is located at the northern terminal part of the Lanping Basin, northwestern Yunnan (26°28′ N, 99°26′ E; 2470 m a.s.l.). The geological setting of the fossil site was described repeatedly (WGRSY, 1978; Tao, 1986; Huang et al., 2012). Sediments of the fossil site belong to the Sanying Formation, which was determined to be late Pliocene based on various evidence including regional stratigraphic correlations (WGRSY, 1978; BGMRYP, 1990; Ge and Li, 1999), floristic comparison (Tao and Kong, 1973; Tao, 1986; Ge and Li, 1999), mammalian fossils (Su et al., 2011), and magneto-stratigraphic analysis (Li et al., 2013).

The Nanbanbang flora is situated in the Heqing Basin, northwestern Yunnan (26°31′ N, 100°10′ E, 2200 m a.s.l.). Lithological investigations indicate that the basal layer of the sediments in the basin is ca. 2.78 Ma (Xiao et al., 2006; Shen et al., 2007). The sedimentary layers of the basin were lithologically described, and their ages were estimated according to stratigraphic and lithological correlations (Xiao et al., 2006). Our fossil seeds were collected from the horizontally laminated carbonaceous layers which were dated to 2.46–2.02 Ma (early Pleistocene; Xiao et al., 2006).

2.2. Specimen examinations

Fossil seeds of *Zanthoxylum* from the Shuitangba and Nanbanbang floras were collected for the first time, and those from the Fudong flora were obtained directly from the existing fossil collection kept in the Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences. In total, 27, 7, and 19 fossil seeds were obtained respectively from the Shuitangba, Fudong, and Nanbanbang floras. Among them, seeds from the Shuitangba and Nanbanbang floras are relatively well-preserved, while those from the Fudong

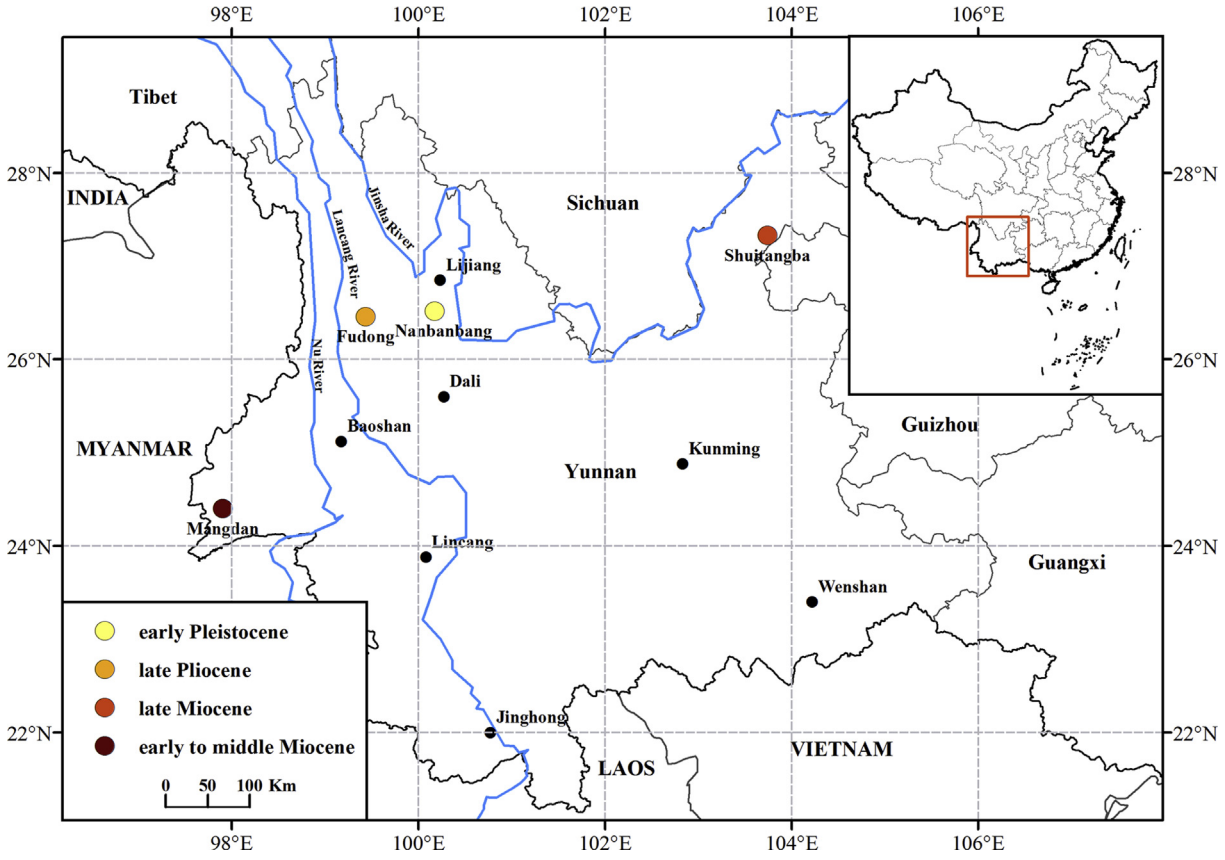

Fig. 1. Map showing the locations of the three fossil floras, Shuitangba, Fudong and Nanbanbang where the present fossil seeds were collected, and the early to middle Miocene Mangdan flora.

flora are fragmentary. Seed specimens from the three floras were cleaned separately with an ultrasonic cleaner (UC, KO-50M) at a frequency of 40 KHz for 5–10 s to remove the clay particles adhering to the surface. Air dried, the fossils were observed under a binocular microscope (Leica, S8AP0), and pictures were taken using a Leica camera (DFC295) mounted on the binocular microscope. Two specimens from each flora were chosen for further examinations under a scanning electron microscope (SEM, Zeiss EVO LS10). To compare with modern species, seed morphology of extant *Zanthoxylum* was studied from herbarium specimens housed at the Herbarium of Kunming Institute of Botany (KUN), using the same procedures as for the fossils. The morphological terminology used is after Tiffney (1980), and Collinson and Gregor (1988). All fossil specimens are numbered and deposited at the Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences.

3. Systematics

Family: Rutaceae Jussieu, 1789

Genus: Zanthoxylum L., 1753

Generic diagnosis: Seeds elliptic, ovate or nearly rounded from the lateral view; two lateral faces convex; dorsal margin convex, and ventral margin convex or slightly straight; surface smooth, rugose, reticulate, bumpy or tuberculate, underlain by a finer pattern of very small pits; hilar scar (elongate-) triangular, elliptic or (elongate-) linear.

3.1. Late Miocene Shuitangba seeds

Species: Zanthoxylum trachyspermum sp. nov. H. Zhu et Z.K. Zhou.

Holotype: STB 003 (Fig. 2 $_4$; Fig. 3 $_2$) here designated.

Paratypes: STB 001 (Fig. 2 $_2$), STB 002 (Fig. 2 $_3$), STB 004 (Fig. 2 $_5$), STB 005 (Fig. 2 $_6$; Fig. 3 $_{1, 4}$), STB 006 (Fig. 2 $_{7, 11}$), STB 007 (Fig. 2 $_8$), STB 008 (Fig. 2 $_9$), STB 009 (Fig. 2 $_{10}$)

Etymology: The specific epithet "*trachyspermum*" consists of two Greek words, *trachys* and *sperma*, meaning coarse and seed, respectively, in reference to the bumpy surface of the fossil seeds.

Description: Seeds are hollow, inflated, and ellipsoid or spherical in shape (Fig. 2). They are 3.1–4.3 mm long and 2.7–3.4 mm wide, with a length–width ratio of 1.1–1.5. Both dorsal and ventral sides are convex (Fig. 2 $_{2–11}$). Basal end is rounded (Fig. 2 $_{2–5, 7–11}$) or occasionally pointed (Fig. 2 $_6$; Fig. 3 $_1$), and apical end is pointed (Fig. 2 $_{2–6, 9–10}$) to weakly rounded (Fig. 2 $_{8, 11}$). The hilar scar is triangular (Fig. 3 $_2$), occupying 1/3–1/2 of the length of the ventral face (Fig. 2 $_{2–4, 7}$; Fig. 3 $_2$) with the raphal entrance on the end (Fig. 2 $_7$; Fig. 3 $_2$). The raphal crest, overlying on the raphal path, is bulgy

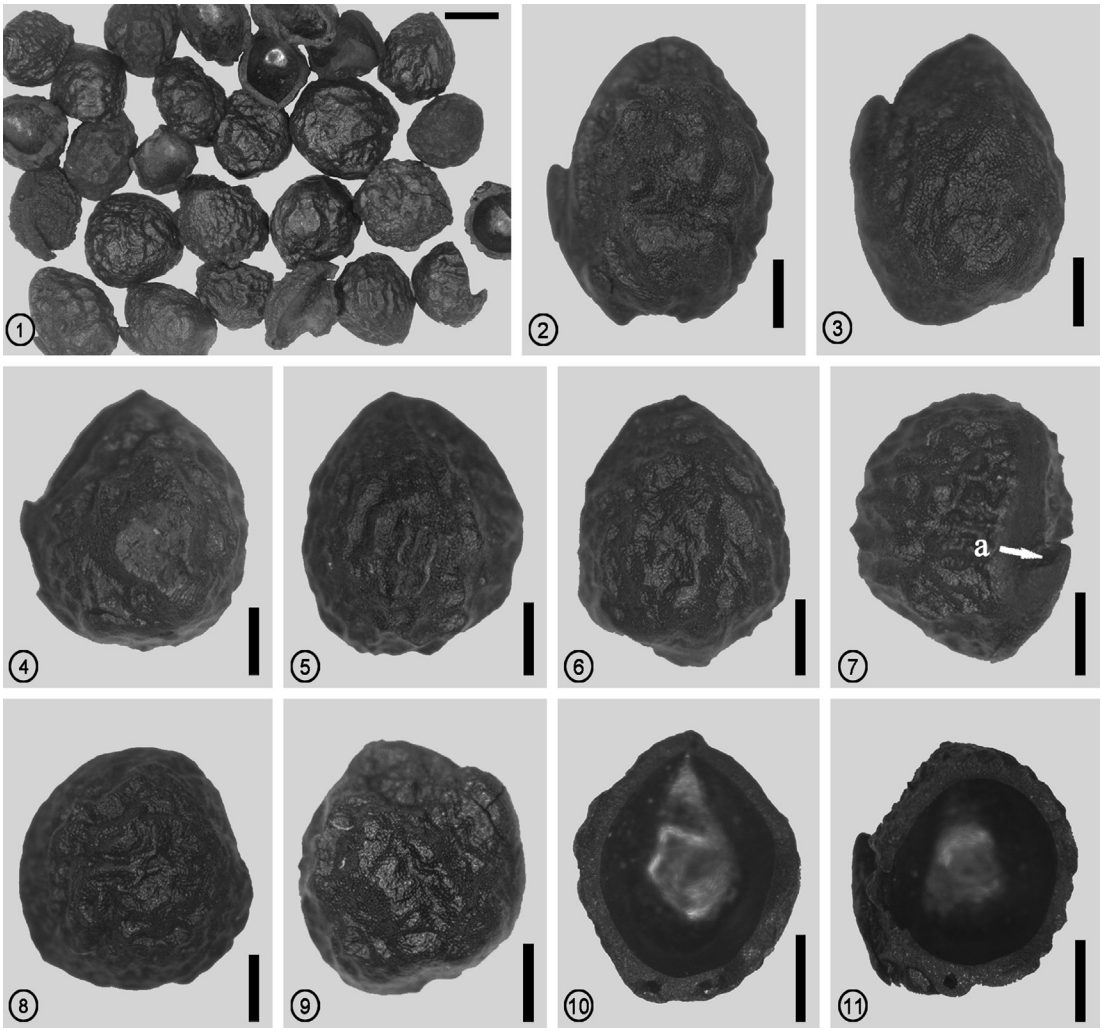

Fig. 2. Seeds of *Zanthoxylum trachyspermum* sp. nov. from the Shuitangba flora under the binocular microscope: scale bar = 2 mm for 1, and 1 mm for the other images; a – raphal entrance.

and prominent (Fig. 2 2–4, 7; Fig. 3 2), occupying the rest of the ventral face. The surface of the sclerotesta is bumpy and tuberculate (Fig. 2; Fig. 3 1, 2), and is finely pitted (Fig. 3 4).

Comments: The Shuitangba seeds appear similar to those of *Z. alpinum*, a modern species living in Southwest China, by sharing an elliptic general morphology, convex ventral and dorsal sides, similar length–width ratio, and a bumpy to tuberculate surface with finer small pits (Fig. 3). Characters such as seed size and hilum scar, however, are slightly different between them. The fossil seeds (3.1–4.3 × 2.7–3.4 mm) are smaller than *Z. alpinum* seeds (~5.2 × 4.0 mm); the hilum scar of the fossils is triangular in shape, which is different from the linear one of *Z. alpinum* seeds. Moreover, the bumpy sculptures seen on the fossils are less prominent than those of *Z. alpinum* seeds.

3.2. Late Pliocene Fudong fragmentary seeds

Species: Zanthoxylum sp.

Studied materials: Seven seed fragments (FD 015 (Fig. 4 3), FD 016, FD 017, FD 091 (Fig. 4 4, 5), FD 092 (Fig. 4 1, 2), FD 093 (Fig. 4 6), FD 094 (Fig. 4 7, 8))

Description: Seed fragments are slightly convex (Fig. 4 1–6). Hilar scars are only weakly observable on the upper part of the ventral face (Fig. 4 1, 6). The exterior surface of the sclerotesta is rugose, forming shallow-basin-like structures (Fig. 4 7), and underlain by a finer pattern of small pits (Fig. 4 8).

Comments: Despite their fragmentary preservation, the Fudong seeds have well-preserved surface ornamentation which still allows for a reliable generic determination. The surface of these fragments is rugose, irregularly bearing shallow-basin-like structures, and is obviously finely pitted under the SEM (Fig. 4 7–8). This is thought one of the key diagnostic characters of *Zanthoxylum* seeds (Tiffney, 1980). However, other seed characters such as seed shape, size, and the shape and length of hilar scar, which are instructive in species identification, are missing. In this regard, we have left the species delimitation of the Fudong seeds unresolved.

3.3. Early Pleistocene Nanbanbang seeds

Species: Zanthoxylum avicennae (Lam.) DC. 1824.

Studied materials: Nineteen fossil seeds (NBB 001 (Fig. 5 1,11,12), NBB 002 (Fig. 5 2; Fig. 6 1), NBB 003 (Fig. 5 3), NBB 004 (Fig. 5 4), NBB 005 (Fig. 5 5), NBB 006 (Fig. 5 6), NBB 007 (Fig. 5 7), NBB 008 (Fig. 5 8; Fig. 6 2, 5, 6), NBB 009 (Fig. 5 9; Fig. 6 3), NBB 010 (Fig. 5 10), NBB 011, NBB 012, NBB 013, NBB 014, NBB 015, NBB 016, NBB 017, NBB 018, NBB 019)

Description: Seeds are inflated, and ellipsoidal to ovate in shape (Fig. 5). They are 3.8–4.6 mm long and 2.7–3.2 mm wide, with a length–width ratio of 1.2–1.6. Both dorsal and ventral sides are generally convex (Fig. 5 1–8). Basal end is rounded (Fig. 5 2–8) or truncate rounded (Fig. 5 1), and apical end is pointed (Fig. 5 1, 4, 6–8) or rounded (Fig. 5 2, 3, 5). The hilar scar is triangular (Fig. 5 10) to elliptic (Fig. 5 9; Fig. 6 3), close to the apex and occupying 1/3–2/3 of the length of the ventral face. The raphal path is marked by the overlain prominent raphal crest (Fig. 5 9, 10; Fig. 6 3), with the raphal entrance on the basal part of the hilar scar (Fig. 5 9, 10; Fig. 6 3) and stretching throughout the rest of the ventral face to the basal elliptic or nearly circular chalaza (Fig. 5 12). The surface is rugose and reticulate, displaying basin-like structures (Fig. 6 1, 2, 5), and is thoroughly ornamented by finer small pits (Fig. 6 6).

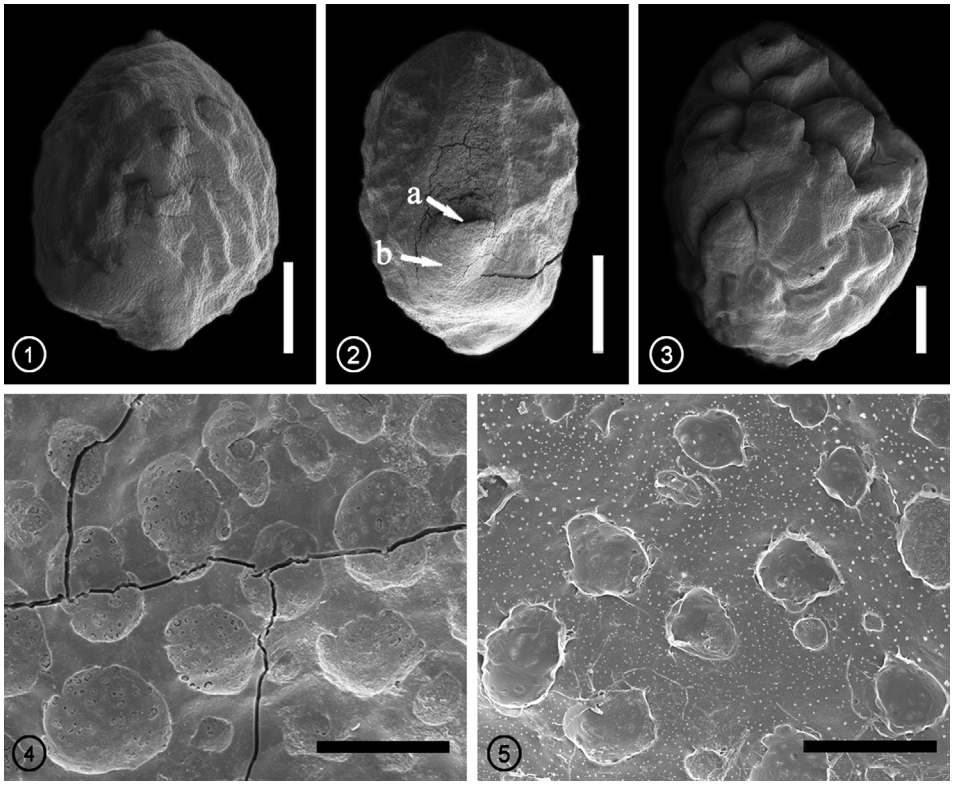

Fig. 3. Seeds of *Zanthoxylum trachyspermum* sp. nov., and an extant seed of *Z. alpinum* under the SEM: scale bars = 1 mm for 1–3, and 0.05 mm for 4, 5; 1 – seed general view of *Z. trachyspermum*; 2 – seed side view of *Z. trachyspermum*; 3 – seed general view of *Z. alpinum*; 4 – seed surface of *Z. trachyspermum*; 5 – seed surface of *Z. alpinum*; a – raphal entrance; b – raphal crest.

Comments: Fossil seeds from the Nanbanbang flora show similarities to four living members of *Zanthoxylum*, i.e., *Z. acanthopodium* var. *timber*, *Z. armatum*, *Z. alatum*, and *Z. avicennae*, by sharing features such as an elliptic to ovate outline, convex ventral and dorsal sides, a rounded basal end and a rounded to pointed apical end, a triangular hilum scar, and a rugose to reticulate surface sculptured by finer small pits. The fossil seeds appear to particularly resemble the seeds of *Z. avicennae* by having similar length–width ratio and hilum length. Assuming that the evolution process from the early Pleistocene to today can be minute, we have designated the Nanbanbang seeds to this living species, viz., *Z. avicennae*.

4. Discussion

The fossil seeds from the Mangdan flora (Zhao et al., 2004) indicate the existence of *Zanthoxylum* in Southwest China at least since the early to middle Miocene. The present fossil seeds yielded by three strata with different ages indicate the existence of the genus in this region during the late Miocene, late Pliocene and early Pleistocene, respectively. Today, *Zanthoxylum* is still living naturally in Southwest China where 36 species occur (Huang, 1997; Zhang et al., 2008). Based on the fossil and modern occurrences (Table 1), it can be hypothesized that *Zanthoxylum* most likely has continuously existed in Southwest China since its first emergence. This pattern may be different from situations in other territories. In Europe, fossil records show that *Zanthoxylum* persisted from the Eocene to early Pleistocene, but subsequently disappeared (Table 1). The post early-Pleistocene disappearance of *Zanthoxylum* from Europe can be attributable to the drastic glaciations, a hypothesis which has also been proposed to explain the extinction of other plant groups in the continent (e.g., *Zelkova*, Follieri et al., 1986). Southwest China, however, is located in a comparatively low latitude and has been affected moderately by Quaternary glaciers (Li et al., 2004), with only some mountain peaks once being covered by ice sheets (Zheng and Rutter, 1998; Shi, 2002; Owen, 2009). The relatively warm conditions there probably have provided suitable habitats for the successful survival of *Zanthoxylum* throughout the Quaternary in Southwest China.

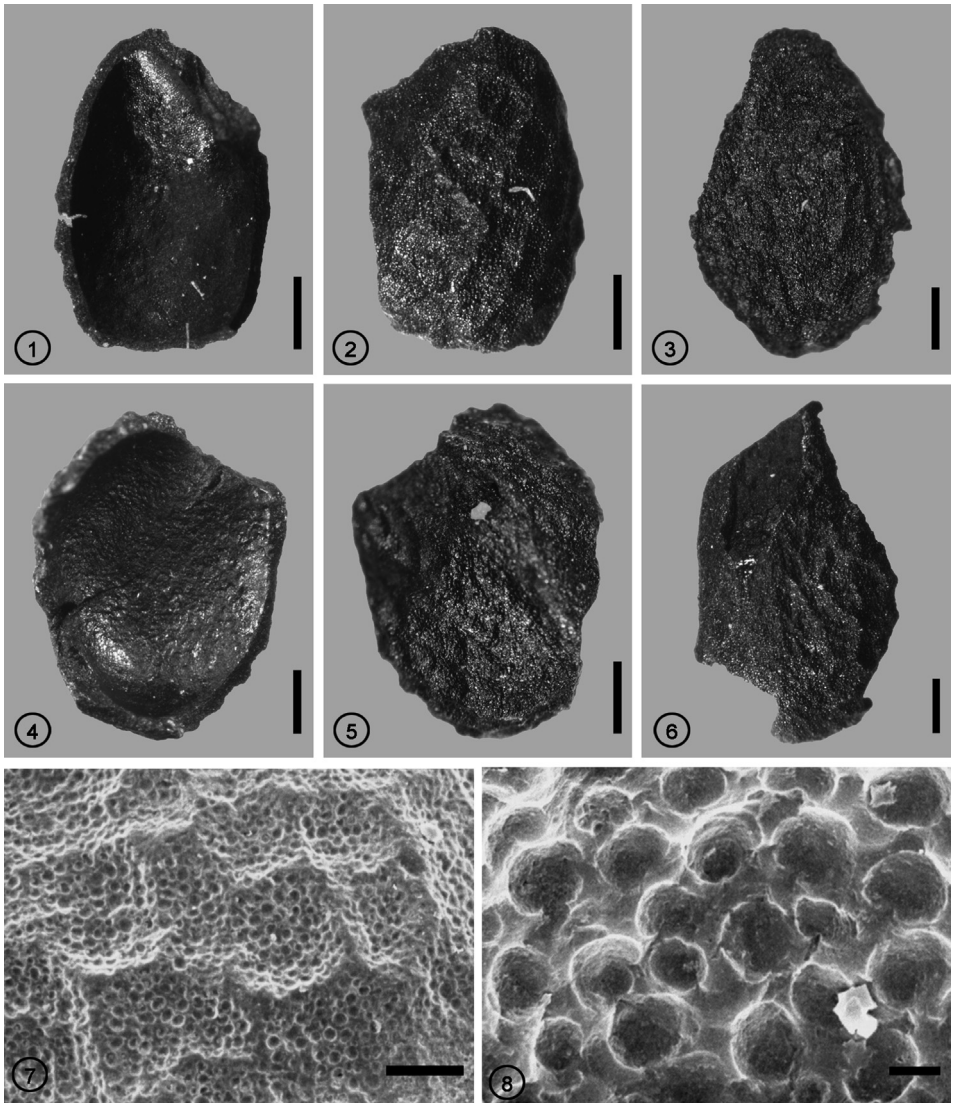

Fig. 4. Seed fragments of *Zanthoxylum* sp. from the Fudong flora: scale bars = 0.5 mm for 1–6, 0.2 mm for 7, and 0.02 mm for 8; 1–6 – general view; 7, 8 – surface details.

In Southwest China, profound environmental changes had taken place during the Neogene and Quaternary, largely caused by the continuous uplift of the Qinghai-Tibet Plateau and adjacent mountainous areas (Kutzbach et al., 1993; Ge and Li, 1999; Schoenbohm et al., 2006; Westaway, 2009; Zhang et al., 2012). The land surface in this region uplifted more rapidly in its northern portion (Jacques et al., 2014), resulting in significant spatial differentiations of altitude. Moreover, temperature declined in response to altitude increase plus the overall global cooling trend (Kou et al., 2006; Sun et al., 2011; Su et al., 2013a); the Asian monsoon climate intensified associated with the continuously uplifting Qinghai-Tibet Plateau (Sun and Wang, 2005; Xia et al., 2009; Jacques et al., 2011; Xing et al., 2012; Su et al., 2013a); and the winter became increasingly dry (Su et al., 2013a; Zhang et al., 2015). Topographic and climatic changes had potentially impacted the evolution and distribution of plants. They might either have promoted the diversification of some plant groups presumably by enlarging environmental heterogeneity (e.g., *Nannoglottis* Maxim., Liu et al., 2002; Nie et al., 2005; *Caragana* Fabr., Zhang and Fritsch, 2010; *Incarvillea* Juss., Chen et al., 2012), or have caused the contraction or even regional extinction of some other plant lineages. For example, the post-Pliocene intensification of the Asian winter monsoon was thought to have caused the disappearance of *Cedrus* Trew (Su et al., 2013b) and *Sequoia* Endlicher (Zhang et al., 2015) from Southwest China. For *Zanthoxylum*, the inferred continuous existence since the early to middle Miocene implies that those environmental changes did not lead to any disappearance of the genus from Southwest China. By contrast, the genus appears to have undergone a diversification process, eventually leading to the acquirement of its modern high diversity in this region.

Today, *Zanthoxylum* is distributed in tropical, subtropical to temperate zones (Zhang et al., 2008; Kubitzki et al., 2011), with a wide habitat preference ranging from wet to arid conditions (Tiffney, 1980; Appelhans et al., 2014). The genus is capable of adapting to various sorts of climatic conditions or niches. In Southwest China, there are seven climatic zones home to different vegetation types (WGVY, 1987; Wang, 2006), providing various living conditions in which *Zanthoxylum* plants can survive and populate. This wide environmental heterogeneity may have promoted the diversification of the genus and resulted in the high species diversity of *Zanthoxylum* in Southwest China at present. Correlation between high species diversity and wide environmental heterogeneity has also been observed in several other plant

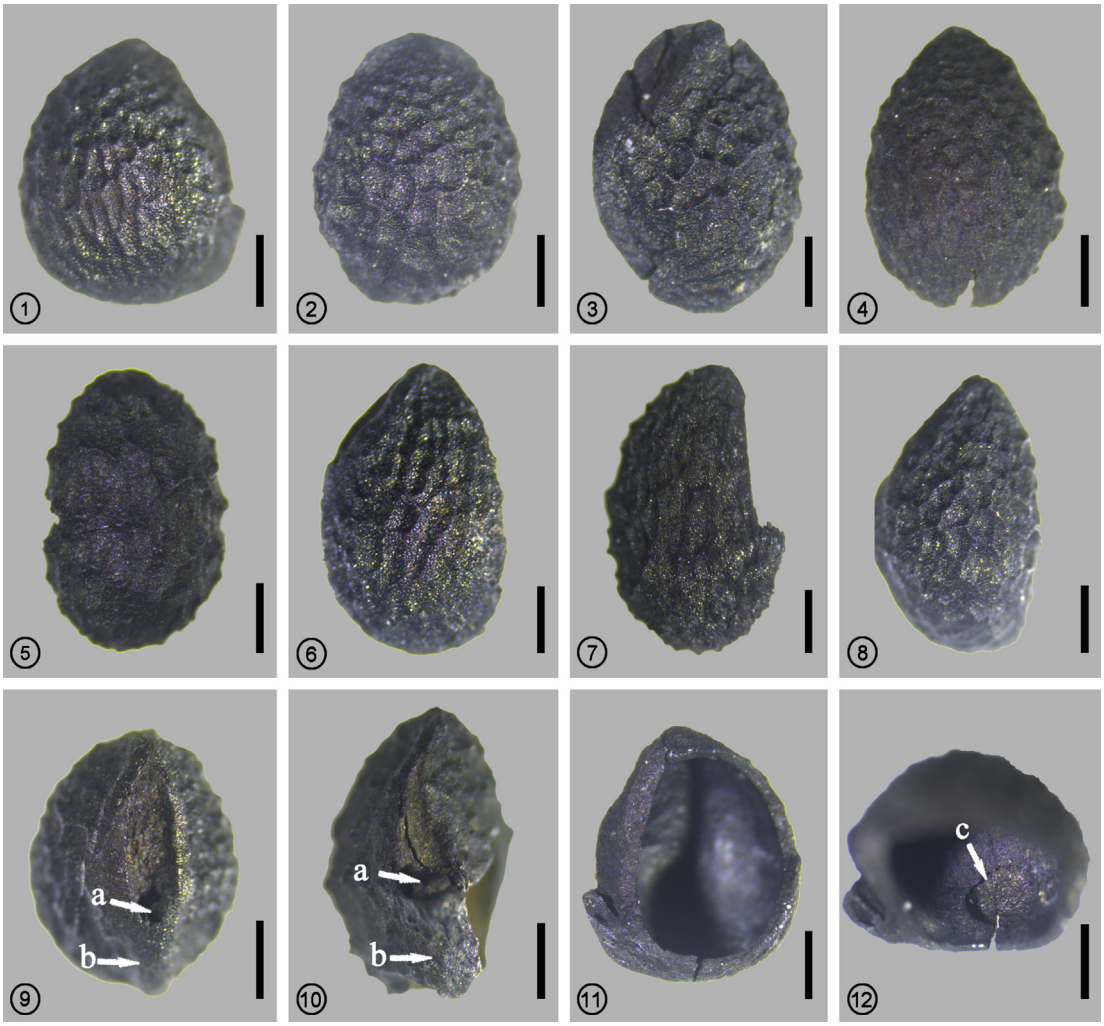

Fig. 5. Seeds of *Zanthoxylum aviceennae* from the Nanbanbang flora under the binocular microscope: scale bars = 1 mm for all images; a – raphal entrance; b – raphal crest; c – chalaza.

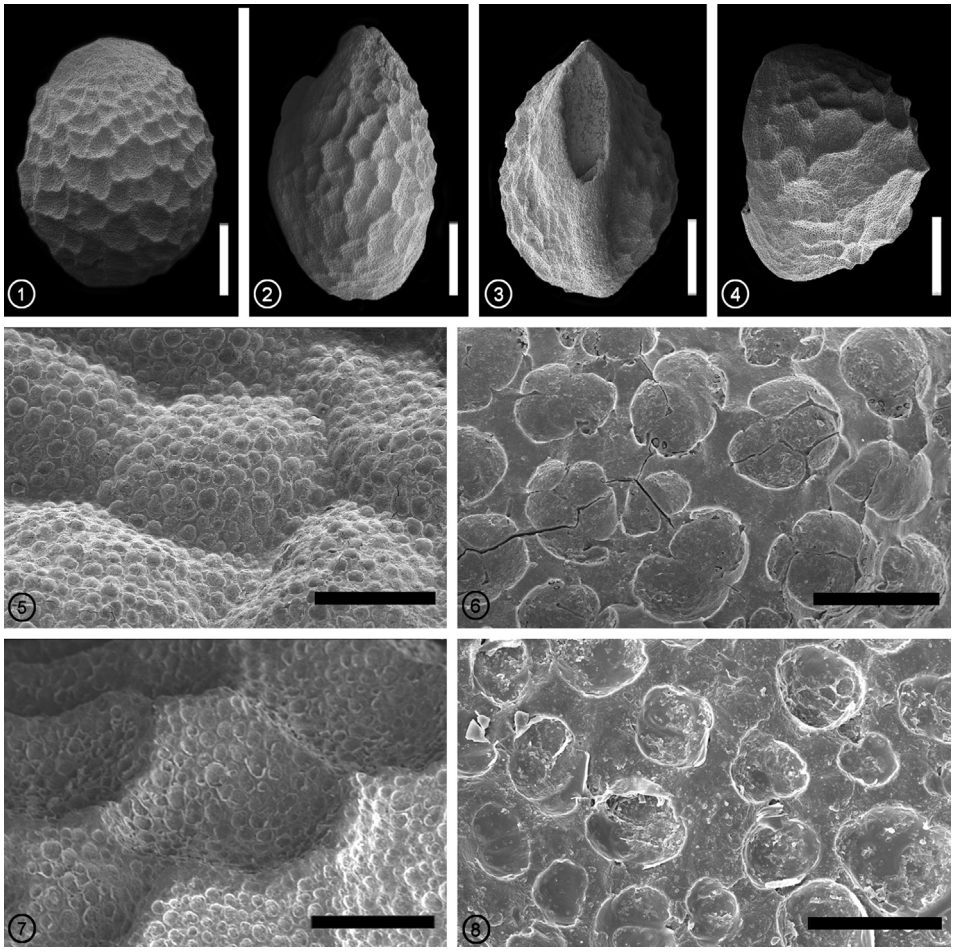

Fig. 6. Fossil and extant seeds of *Zanthoxylum avicennae* under the SEM: scale bars = 1 mm for 1–4, 0.25 mm for 5, 7, and 0.05 mm for 6, 8; 1, 2 – general view of the fossil seed; 3 – side view of the fossil seed; 4 – general view of the extant seed; 5, 6 – surface details of the fossil seed; 7, 8 – surface details of the extant seed.

Table 1
Comparisons of fossil and modern occurrences of *Zanthoxylum* between Europe and Southwest China.

Age	Europe		Southwest China	
	Existence	References	Existence	References
Modern	No	Porter, 1976; Kubitzki et al., 2011	Yes	Huang, 1997; Zhang et al., 2008
Pleistocene	Yes	Martinetto et al., 2014	Yes	This paper
Pliocene	Yes	Martinetto et al., 1997	Yes	This paper
Miocene	Yes	Łańcucka-Środoniowa, 1984; Van der Burgh, 1987	Yes	Zhao et al., 2004; This paper
Oligocene	Yes	Mai and Walther, 1978	Unknown	/
Eocene	Yes	Chandler, 1964	Unknown	/

lineages in this region, e.g., *Nannoglottis* (Liu et al., 2002), *Rheum* L. (Wang et al., 2005), *Buddleja* L. (Chen et al., 2007), *Dipentodon* Dunn (Yuan et al., 2008), *Caragana* (Zhang and Fritsch, 2010).

Acknowledgements

We thank Dr. F.M.B. Jacques, Dr. Y.W. Xing, and J. Huang from Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, L.B. Jia from Kunming Institute of Botany, Chinese Academy of Sciences, and members from Yunnan Institute of Cultural Relics and Archaeology, Zhaotong Institute of Cultural Relics, and Zhaoyang Museum for help with fossil collections; Dr. Z. Zhou from Kunming Institute of Botany, Chinese Academy of Sciences, for help with the etymology; Dr. L. Wang from the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, for technical assistance with the SEM; Professor E. Martinetto for improving the paper; the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences, for providing modern seed materials; and the Central Lab of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, for the SEM. This study was supported by the National Natural Science Foundation of China (No. 31300187, No. 41030212), the Yunnan Natural Science Foundation (No. 2010CC010), and the Foundation of the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (No. 123107).

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