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New fossil seeds of *Eurya* (Theaceae) from East Asia and their paleobiogeographic implications

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A R T I C L E I N F O

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A B S T R A C T

Eurya has an excellent fossil record in Europe, but it has only a few fossil occurrences in East Asia though this vast area houses the highest modern diversity of the genus. In this study, three-dimensionally preserved fossil seeds of *Eurya stigmosa* (Ludwig) Mai from the late Pliocene of northwestern Yunnan, southwestern China are described. The seeds are compressed and flattened, slightly campylotropous, and nearly circular to slightly angular in shape. The surface of the seeds is sculptured by a distinctive foveolate pattern, consisting of funnel-shaped and finely pitted cells. Each seed valve contains a reniform or horseshoe-shaped embryo cavity, a characteristic condyle structure and an internal raphe. These fossil seeds represent one of the few fossil records of *Eurya* in East Asia. This new finding therefore largely extends the distributional ranges of *Eurya* during Neogene. Fossil records summarized here show that *Eurya* persisted in Europe until the early Pleistocene, but disappeared thereafter. The genus might have first appeared in East Asia no later than the late Oligocene, and dispersed widely in regions such as Japan, Nepal, and southwestern China.

1. Introduction

Eurya Thunb. is a large genus of the tea family Theaceae, comprising approximately 130 species (Min and Bartholomew, 2007). Its extant species are mainly distributed in tropical to subtropical Asia, and in the western and southern Pacific Islands (Min and Bartholomew, 2007), with a few species in tropical regions of the New World (Łańcucka-Środoniowa, 1966). They are evergreen shrubs, small trees, and rarely large trees, commonly found as dominant understory elements in tropical to subtropical broad-leaved evergreen forests (WGVY, 1987; Min and Bartholomew, 2007).

Although *Eurya* is not distributed in Europe now, its fossil record is especially rich in this continent, where at least 12 extinct species from the Late Cretaceous to early Pleistocene have been documented (Mai, 1960, 1971; Knobloch, 1977; Łańcucka-Środoniowa, 1981; Friis, 1985; Knobloch and Mai, 1986; van der Burgh, 1987; Friis et al., 2011; Martinetto et al., 2015). Unlike Europe, the fossil occurrences of *Eurya* in East Asia are rather scarce (Tanai and Uemura, 1991; Momohara, 1992; Momohara and Saito, 2001; Yamakawa et al., 2015), even though this region shows the highest species richness of the genus today. Although molecular data can explain the emergence and diversification of *Eurya* (Wu et al., 2007), the lack of fossil evidence limits further understanding of the evolution and establishment of its high modern species diversity in East Asia.

In this study, we report a new fossil record of *Eurya* based on three-dimensionally preserved seeds from the late Pliocene of northwestern Yunnan, southwestern China. We perform detailed morphological and anatomical examinations of these fossil seeds,

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and discuss the paleobiogeographic implications of this new fossil finding.

2. Materials and methods

2.1. Fossil site and geological horizon

The present fossil seeds were collected from deposits at Nanbanbang Village, Heqing Basin, northwestern Yunnan Province (26°31′ N, 100°10′ E; 2200 m a.s.l.; Fig. 1). The Heqing Basin is located at the southeastern fringe of the Qinghai-Tibet Plateau within the renowned Hengduan Mountains. It is a tectonic default basin surrounded by mountains with a distinguishable vertical vegetation belt spectrum (Shen et al., 2007). The local climate is primarily influenced by the Indian Monsoon, which is characterized by warm, wet summers and cool, dry winters (Xiao et al., 2010; An et al., 2011). The section studied is unconformably overlain by Quaternary deposits and is composed of horizontally laminated carbonaceous layers imbedded by fine gray sandstones. These carbonaceous layers contain abundant plant remains, mainly fruits and seeds. The age of the carbonaceous layers was previously assigned to the early Pleistocene (Zhu et al., 2016). The latest geological survey shows that the underlying sedimentary layers beneath these carbonaceous layers contain abundant leaf fossils dominated by evergreen sclerophyllous oaks (*Quercus* sect. *Heterobalanus*). In northwestern Yunnan, the dominance of evergreen sclerophyllous oaks in a fossil flora is a common indicator of the Sanying Formation (Tao, 1986), which has been determined to be the late Pliocene based on stratigraphic correlations, palynological information, mammal fossils, and paleomagnetic data (Tao and Kong, 1973; Tao, 1986; Ge and Li, 1999; Su et al., 2011; Li et al., 2013). Therefore, the age of the present fossil seeds and fruits is assigned to the late Pliocene.

2.2. Fossil materials and examination

More than 1000 specimens of charcoalified fruits and seeds were collected from the fossil site. Among them, more than 80 seeds and seed fragments of *Eurya* were identified through observations under a binocular microscope (Leica, S8AP0). The fossil seeds were cleaned by an ultrasonic cleaner at 40 kHz (KO-50M) for 5–10 s. Air dried, they were then observed under a 3D Super Depth Digital Microscope (ZEISS Smartzoom 5) and images were taken. Five seed specimens were further studied under a scanning electron microscope (SEM, Zeiss EVO LS10) both morphologically and anatomically. For comparative analysis, extant seeds of *Eurya* obtained from herbarium specimens housed at the Herbarium of Kunming Institute of Botany (KUN) were also examined using the same procedure as the fossils. The descriptive terminology mainly follows Friis (1985). All studied fossil specimens are numbered and kept at the KUN.

3. Systematics

Family: Theaceae Mirb., 1816

Genus: *Eurya* Thunb., 1783

Species: *Eurya stigmosa* (Ludwig) Mai, 1960

Fossil specimens: NBB 020 (Plate I, 1), NBB 021 (Plate I, 2), NBB 022 (Plate I, 3), NBB 023 (Plate I, 4), NBB 024 (Plate I, 5), NBB 025 (Plate I, 6), NBB 026 (Plate I, 7), NBB 027 (Plate I, 8), NBB 028 (Plate I, 9), NBB 029 (Plate I, 10), NBB 030 (Plate I, 11), NBB 031 (Plate I, 12), NBB 032 (Plate II, 1, 8), NBB 033 (Plate II, 2), NBB 034 (Plate II, 3), NBB 035 (Plate II, 4, 6, 7), NBB 036 (Plate II, 5, 9, 10, 11, 12), and NBB 037–072.

Fossil locality: Nanbanbang Village, Heqing County, northwest Yunnan Province, southwest China (26°31′ N, 100°10′ E; 2200 m a.s.l.)

Stratigraphic horizon: The upper Pliocene Sanying Formation

Description: Seeds are slightly campylotropous, laterally flattened, and subcircular to slightly angular in outline (Plate I). They are 1.07–2.02 mm in length and 1.03–1.96 mm in width, with a length–width ratio of 0.82–1.32. The seed surface is foveolate with funnel-shaped cells (Plate II, 1–4, 6), which are concentrically arranged around the condyle-raphe region in 8–12 rows parallel to the seed margin (Plate II, 1–4, 6–8). The cells are 0.03–0.15 mm (0.08 mm on average) in diameter, with thickened and finely pitted inner periclinal and anticlinal walls (Plate II, 7), and with cell lumens that gradually narrow towards the base with

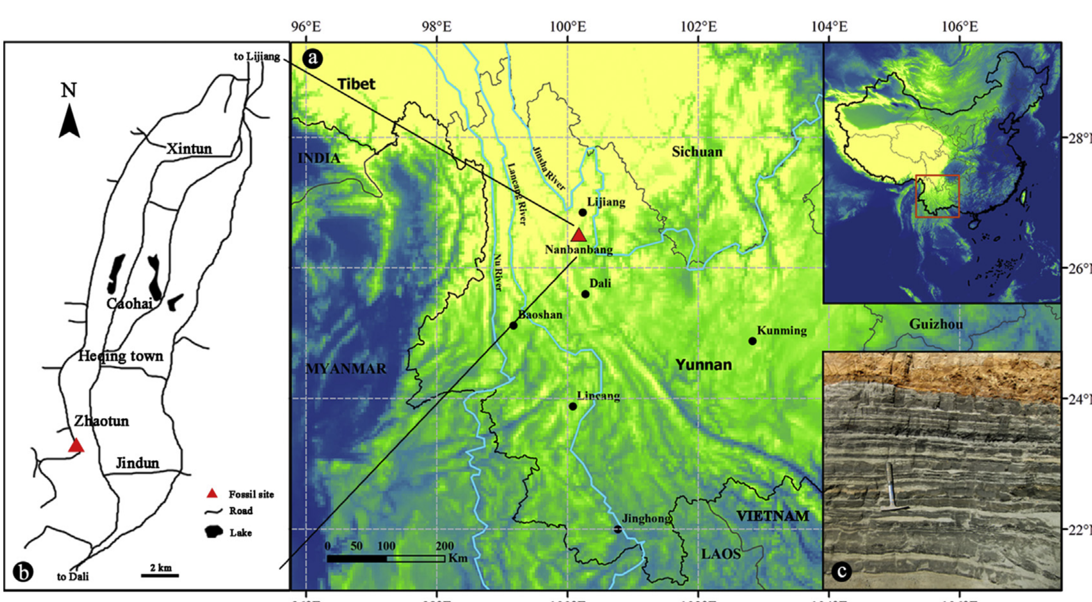


Fig. 1. Map showing the fossil site (a, b) and outcrops (c) from which the present fossil seeds were collected.

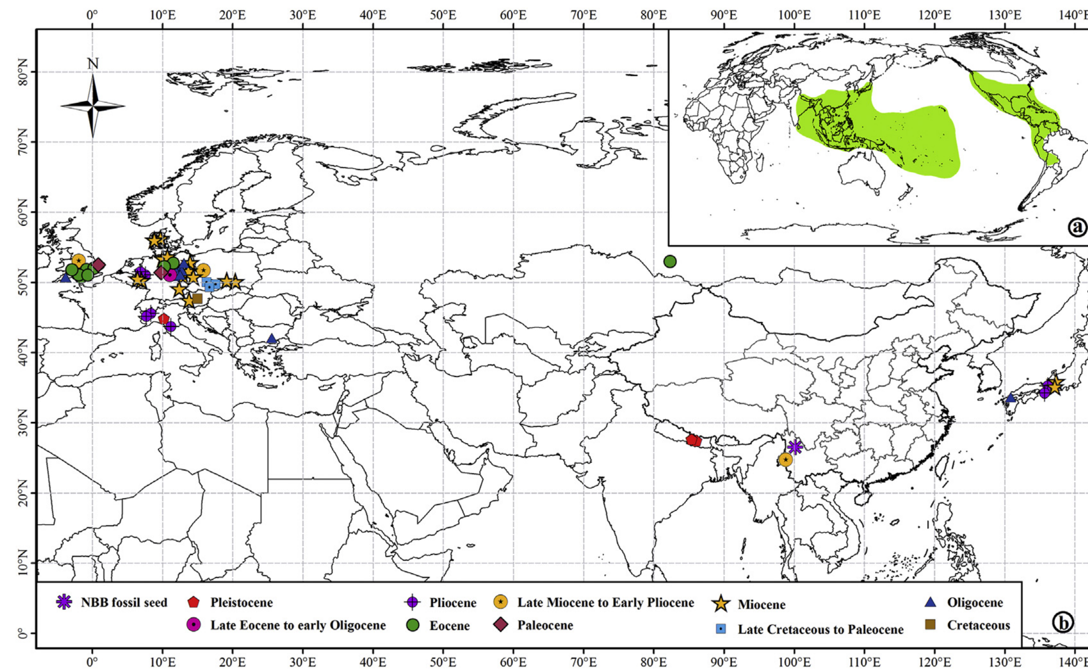


Fig. 2. Spatial distribution of modern (a) and fossil (b) species of *Eurya*.

polygonal facets (Plate II, 6–7). The cavity of each seed valve is subdivided by a characteristic reversed and slightly curved V-shaped condyle into a reniform or horseshoe-shaped embryo cavity and raphe (Plate II, 10). The condyle consists of two limbs with equal length but unequal width, which extend from the seed base to almost half of the seed width (Plate II, 10). The raphe is

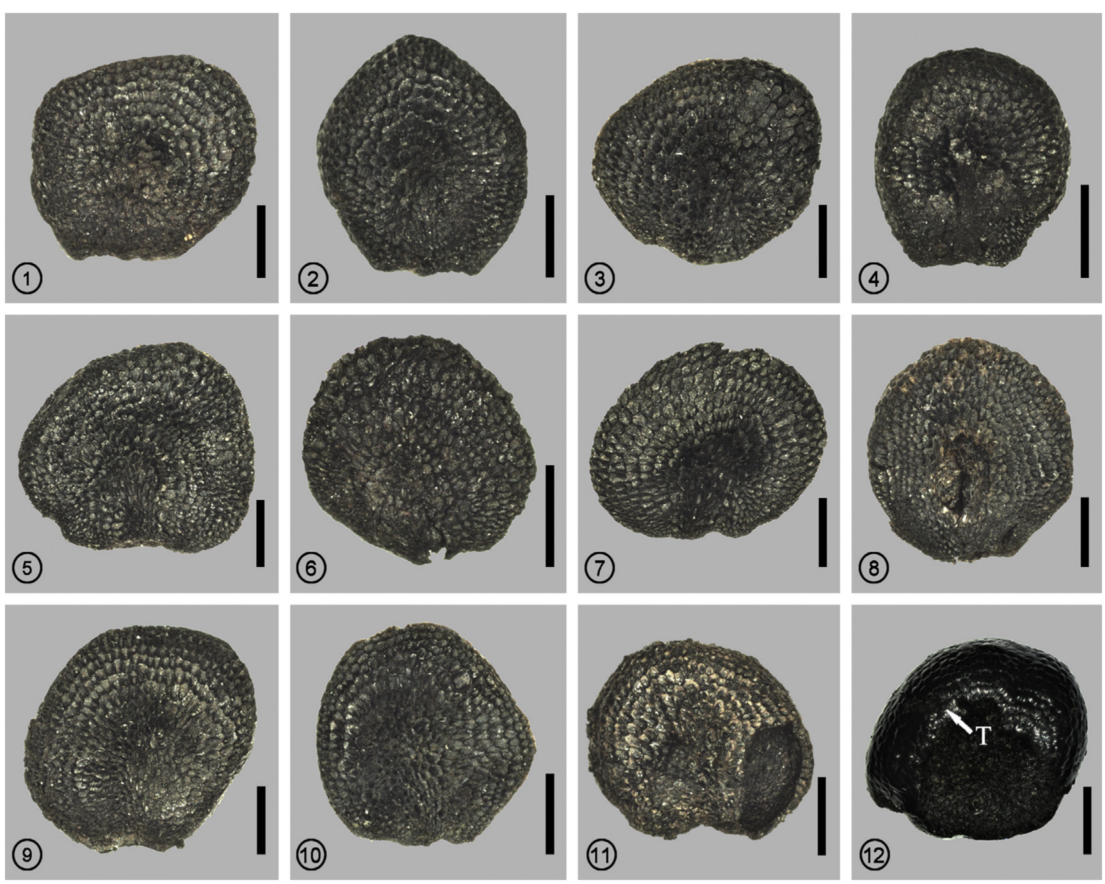


Plate I. Fossil seeds of *Eurya stigmosa* from Nanbanbang under the 3D Super Depth Digital Microscope. Scale bars = 0.5 mm for all images. T = tegmen.

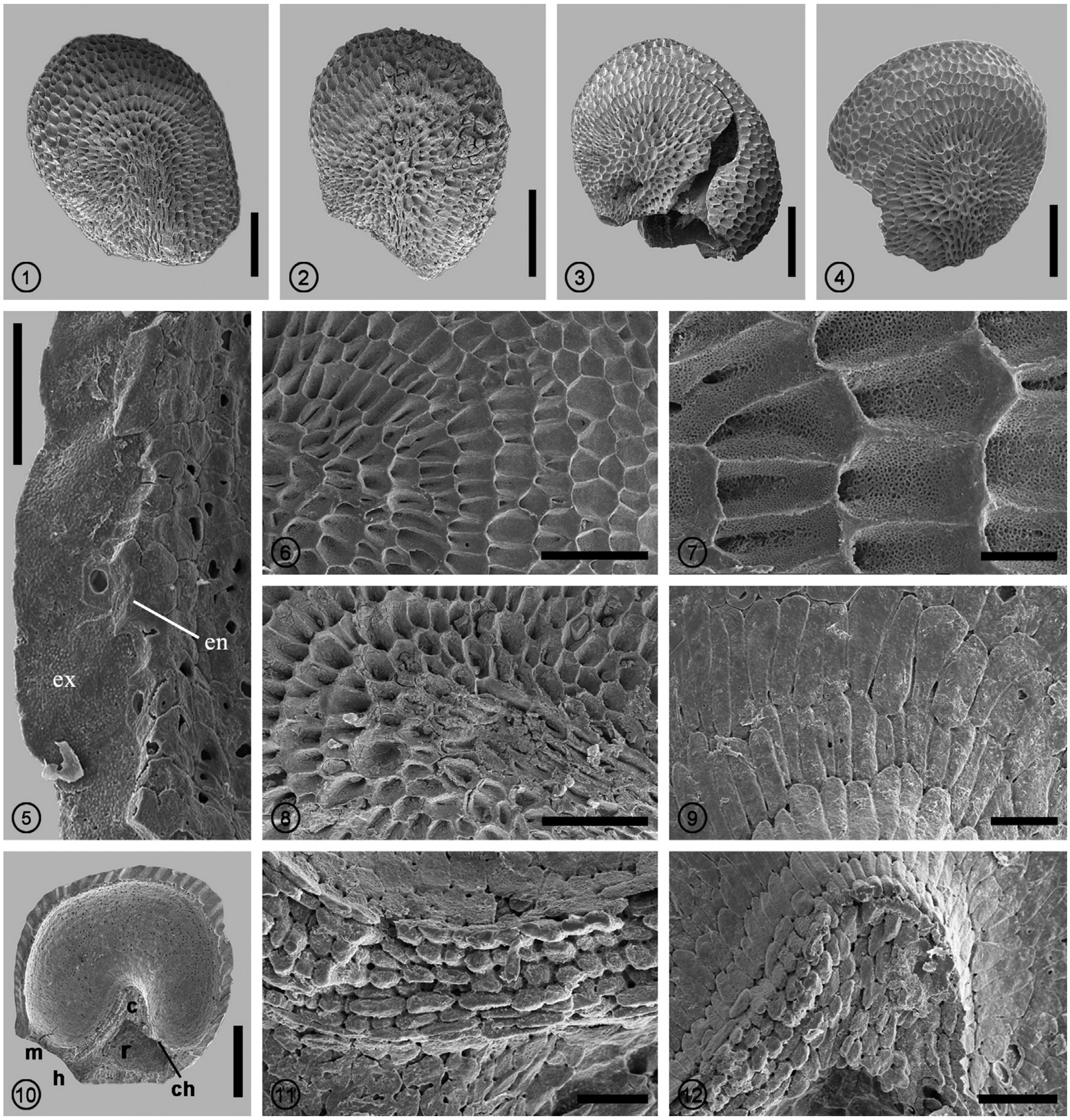
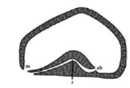
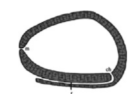


Plate II. Fossil seeds of *Eurya stigmosa* from Nanbanbang under the SEM. Scale bars = 0.25 mm for 6 and 8; 0.05 mm for 7, 9, and 12; 0.1 mm for 5 and 11; and 0.5 mm for 1–4, and 10. 1–4. General shape of the fossil seeds. 5. Longitudinal section of the seed wall showing the two distinct layers consisting of large cells of the exotesta and small cells of the endotesta. 6. External surface of the seed showing the concentrically arranged cells. 7. Details of the cells on the seed external surface, showing the funnel-shaped and strongly thickened cells of the testa with finely pitted walls. 8. Cells on the center part of the seed external surface, showing the compact, less visible cell lumens and thicker walls. 9. Internal surface of the seed showing elongated elliptic and slightly thickened cells, which are concentrically arranged around the condyle. 10. Internal view of the seed showing the reniform or horseshoe-shaped embryo cavity, reversed and slightly curved V-shaped condyle, subtriangular raphe cavity, micropyle, hilum, and chalaza. 11, 12. Details of the condyle showing the clavate cells. ex = exotesta, en = endotesta, c = condyle, ch = chalaza, h = hilum, m = micropyle, r = raphe.

marked by a subtriangular cavity, and is formed by the encompassment of the condyle and seed basal margin. The hilar scar is oblong and located between the raphe and micropyle. The seed internal surface is covered by elongated elliptic and slightly thickened cells, which are concentrically arranged around the condyle in rows parallel to the seed margin (Plate II, 9–10). The seed wall is 0.06–0.16 mm thick, sclerotic, composed of a thick exotesta, with large cells, and a thin endotesta, with small cells (Plate II, 5). The thin, membranous remains of the tegmen can be observed attached to the external surface of testa in several seeds (Plate I, 12).

Morphological comparisons: Although seeds of *Eurya* are seemingly similar to those of its relatives, such as *Adinandra* W. Jack, *Cleyera* Thunberg, and *Freziera* Willd, they can be reliably distinguished from these genera by key structural details (Friis, 1985; Table 1). Generally, *Eurya* seeds are characterized by a reticulum of funnel-shaped cells with polygonal facets on the external seed surface (Friis, 1985). This diagnostic feature is consistent with our fossil seeds, which differs from the other three genera. Moreover, our fossils also share some other important anatomical features with extant *Eurya* seeds, such as the reniform or horseshoe-shaped embryo cavity, the prominent condyle in the seed valve, and the position of raphe and hilum (Friis, 1985). All of these traits suggest that our fossil seeds can be ascribed to *Eurya*. Among the examined modern seeds of *Eurya*, *Eurya yunnanensis*, a species presently found mainly in western and southeastern Yunnan, shows the greatest resemblance to the fossil seeds under study. However, the fossil seeds are distinct from this species by

Table 1
Morphological comparisons of modern seeds of *Eurya* and three related genera in Theaceae after Friis (1985).

Genus	Seed general shape	Exotesta		Endotesta		Seed draft
		Cell shape	Cell wall	Layers of crystal cells	Cell wall	
Adinandra	Slightly campylotropous	Not funnel-shaped	Equally thick	One to several layers	Often thick	
Cleyera	Strongly campylotropous, usually larger than those of the other three genera	Not funnel-shaped	Equally thick	Usually one layer	–	
Eurya	Slightly campylotropous, or more rarely anatropous	Funnel-shaped	Strongly thickened	One or two layers	Rather thin	
Freziera	Usually anatropous or slightly campylotropous	Not funnel-shaped	Equally thick	Several layers	Strongly thickened	

their slightly larger size, finely pitted cells on the seed external surface, and the difference in cell types on the condyle and seed internal surface (Plates II and III).

Fossil seeds of *Eurya* that have previously been described are largely from Europe (Chandler, 1963; Mai, 1971; Knobloch, 1977; Łańcucka-Środoniowa, 1981; Friis, 1985; Knobloch and Mai, 1986;

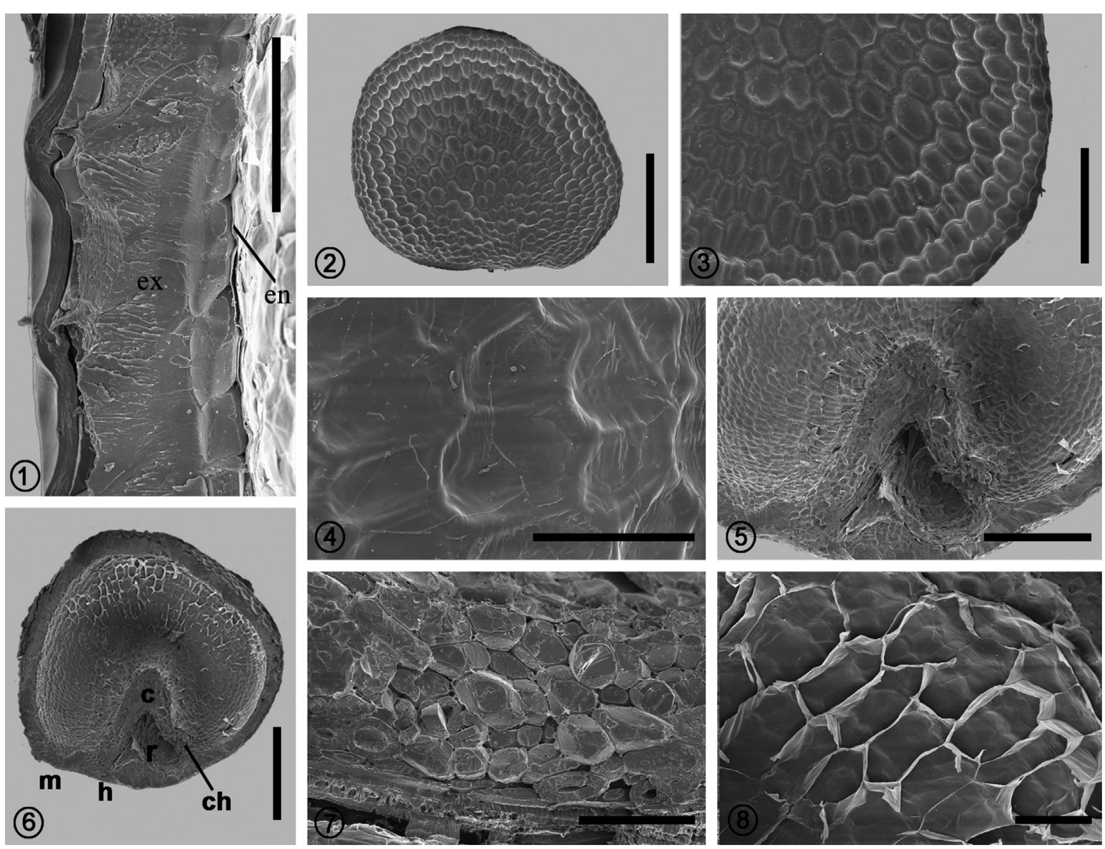


Plate III. Extant seeds of *Eurya yunnanensis* under the SEM. Scale bars = 0.25 mm for 3 and 5; 0.05 mm for 1, 4, 7, and 8; and 0.5 mm for 2 and 6. 1. Longitudinal section of the seed wall, showing the two distinct layers consisting of large cells of the exotesta and small cells of the endotesta. 2. General shape of the seed and the cells concentrically arranged on the external surface. 3, 4. Details of the cells on the seed external surface, showing the funnel-shaped cells of the testa with smooth surface. 5. The condyle structure and the elongated polygonal cells on the internal surface of the seed which are concentrically arranged around the condyle. 6. Internal view of the seed showing the reniform or horseshoe-shaped embryo cavity, reversed and slightly curved V-shaped condyle, subtriangular raphe cavity, micropyle, hilum, and chalaza. 7. Details of the condyle showing the elliptic or subcircular cells. 8. Details of the cells on the internal surface of the seed, showing the thin and raised cell wall. ex = exotesta, en = endotesta, c = condyle, ch = chalaza, h = hilum, m = micropyle, r = raphe.

Table 2
Carpological comparisons of fossil seeds between *Eurya stigmosa* from Nanbanbang village, Heqing county and other fossil species of the genus.

Taxa	Cells on the external surface	Seed size	Shape	Testa	References
E. stigmosa (Ludwig) Mai	Large, 0.03–0.15 (0.08 on average) mm in diameter	Medium, 1.07–2.02 × 1.03 –1.96 (1.47 × 1.45 on average) mm	Subcircular, campylotropous, laterally flattened	Thick, 0.06–0.16 mm	This study
E. mudensis Chandler	Large, 0.05–0.2 (0.1 on average) mm in diameter	Small, 1.0–1.5 mm in diameter	More rounded	Thick, brittle	Mai (1971)
E. stigmosa (Ludwig) Mai	Large cavites, 0.05–0.2 (0.1 on average) mm in diameter	Medium, 1.0–2.5 (rarely 3) mm in diameter	Great variable (reniform, broadly oval, sub-triangular, angular to almost circular)	Thick, brittle, 0.05–0.15 mm	Mai (1971) and Friis (1985)
E. poolensis (Chandler) Mai	Large, 0.05–0.2 (0.1 on average) mm in diameter	Medium, 1.9–2.3 mm in diameter	Very oblique oval	Thick, brittle	Mai (1971)
E. lusatica Mai	Large cavites, 0.05–0.2 (0.1 on average) mm in diameter	Large, 2.0–3.2 mm in diameter	Subcircular to obliquely oval	Thick, brittle	Mai (1971)
E. becktonensis Chandler	Large, 0.05–0.2 (0.1 on average) mm in diameter	Large, 1.8–4.2 mm in diameter	Elongated oval to obliquely triangular, somewhat angular	Thick, brittle	Mai (1971)
E. maii Knobloch	Large, 0.06–0.13 mm in diameter, eccentric, large (sometimes heptagonal) polygons	Medium, 1.22–2.02 × 0.97 –2.0 (1.62 × 1.38 on average) mm	Roundish-lenticular to oval, more or less compressed	Excessively thick, 0.13 –0.22 mm	Knobloch (1977)
E. boveyana (Chandler) Mai	Fine, 0.02–0.08 (0.05 on average) mm in diameter	Medium, 1.0–2.0 mm in diameter	Subcircular to oval, more or less rounded, always compressed	Thin, elastic	Mai (1971)
E. obliqua (Chandler) Mai	Fine, 0.02–0.08 (0.05 on average) mm in diameter	Small, 1.25–1.7 mm in diameter	Rounded triangular to irregular, always somewhat angular	Thick, brittle, strongly thickened in the central area	Mai (1971)
E. dubia (Chandler) Mai	Fine, 0.02–0.08 (0.05 on average) mm in diameter	Medium, 1.25–2.0 mm in diameter	Rounded triangular to irregular, always somewhat angular	Thick, brittle, strongly thickened in the central area	Mai (1971)
E. lentiformis (Chandler) Mai	Fine, 0.02–0.08 (0.05 on average) mm in diameter	Large, about 2.5 mm in diameter	Rounded triangular to irregular, always somewhat angular	Thick, brittle, strongly thickened in the central area	Mai (1971)
E. crassitesta Knobloch	Fine, about 0.05 mm in diameter, concentric, equal, rounded and annular thickened polygons	Small, 0.8–1.4 × 0.7 –1.8 mm	Rounded	Thick, 0.08–0.8 mm	Knobloch (1977)
E. holyi Knobloch	Fine, eccentric, equally sized polygons	Small, 0.75–1.33 × 0.55 –0.97 (1.02 × 0.8 on average) mm	Semicircular, spherical, broadly elliptic, rarely rounded	Thick, 0.08–0.11 mm	Knobloch (1977)

van der Burgh, 1987; Martinetto et al., 2015), and to a limited extent from Japan in East Asia (Momohara, 1992; Momohara and Saito, 2001; Yamakawa et al., 2015) and Nepal in South Asia (Bhandari et al., 2009, 2010). They are assigned to 12 fossil species and one modern species (Table 3). We compared our fossil seeds with these 12 fossil species using four key characteristics: size of the cells on the seed external surface, seed size, seed shape, and testa thickness (Table 2). Our fossil seeds most resemble the seeds of *E. stigmosa* (Ludwig) Mai reported from Paleocene to early Pleistocene of Europe (Table 3), that have similarly large cells on the seed external surface. Our fossils also have similar seed size (1.07–2.02 × 1.03–1.96 mm) and testa thickness (0.06–0.16 mm) with those of *E. stigmosa*. Other important seed characteristics, such as the subcircular to slightly angular seed shape, are also shared by our fossils and this species. We have therefore treated our fossils as belonging to *E. stigmosa*.

4. Paleobiogeographic implications

Eurya has a rich fossil record, represented primarily by seed remains and a few leaf impressions (Tao and Du, 1982; Ozaki, 1991; Tanai and Uemura, 1991; Bozukov et al., 2008). The oldest known records of the genus are seed remains from the middle to Late Cretaceous in Austria (Knobloch and Mai, 1986, 1991) and from the Late Cretaceous to Paleocene in the Czech Republic, central Europe (Knobloch, 1977). This may imply a central European origin. Fossil record also indicates that Europe, where about 12 known fossil species of the genus have been reported, may have been a center for *Eurya* evolution and diversification in the past (Chandler, 1963; Mai, 1971; Knobloch, 1977; Łańcucka-Środoniowa, 1981; Gregor, 1982; Friis, 1985; Knobloch and Mai, 1986; van der Burgh, 1987; Martinetto et al., 2015) (Table 3; Fig. 2). This hypothesis may be consistent with the warm and humid climate throughout the European Cenozoic (Mosbrugger et al., 2005). Based on the lack of fossil occurrences in the continent after the early Pleistocene, the genus likely disappeared from Europe by that time (Martinetto et al., 2015). This may be largely attributed to the more severe effect of the Quaternary glaciations on Europe compared with relatively low latitude regions (Ehlers et al., 2011).

In contrast to Europe, East Asia has revealed a much lower diversity of *Eurya* in its geological past. Despite flourishing in the modern era, there are only six documented fossil occurrences of *Eurya* in East Asia (Tao and Du, 1982; Ozaki, 1991; Tanai and Uemura, 1991; Momohara, 1992; Momohara and Saito, 2001; Yamakawa et al., 2015). The oldest known fossil record is dated to the late Oligocene (Tanai and Uemura, 1991), implying that *Eurya* probably first appeared in East Asia no later than the late Oligocene. The newly described fossil occurrence represents the first seed fossil record of *Eurya* in China, and one of the few fossil records of the genus in East Asia. As *E. stigmosa* has been frequently documented from the Paleocene to early Pleistocene of Europe (Mai, 1971; Łańcucka-Środoniowa, 1981; Gregor, 1982; Friis, 1985; van der Burgh, 1987; Teodoridis and Kvaček, 2006; Martinetto et al., 2015), it may indicate a close affinity between East Asian and European species of the genus. It may suggest the ancient species of East Asian *Eurya* originated in Europe. The genus may have further dispersed to other regions of Asia, as some other fossil occurrences of *Eurya* are also reported from the continent, e.g., the late Miocene and late Pliocene of Japan (Ozaki, 1991; Yamakawa et al., 2015), and the late Pleistocene of Nepal (Bhandari et al., 2009, 2010). These

Table 3
Detailed information on macrofossil records of *Eurya*.

Taxa	Age	Fossil type	Locality	References
E. sp.	Late Pleistocene	Seed	Central Nepal	Bhandari et al. (2009, 2010)
E. stigmosa (Ludwig) Mai	Late Pliocene	Seed	NW Yunnan, SW China	This study
E. japonica Thunberg	Late Pliocene	Seed	Central Japan	Yamakawa et al. (2015)
E. sp.	Late Pliocene	Seed	SW Japan	Momohara (1992)
E. stigmosa (Ludwig) Mai	Early Pliocene–Early Pleistocene	Seed	N Italy	Martinetto et al. (2015)
E. stigmosa (Ludwig) Mai	Middle Pliocene	Seed	Central Italy	Martinetto (2001)
E. stigmosa (Ludwig) Mai	Middle Pliocene	Seed	NW Italy	Basilici et al. (1997)
E. stigmosa (Ludwig) Mai	Early Pliocene	Seed	NW Italy	Martinetto et al. (1997)
E. stigmosa (Ludwig) Mai	Pliocene	Seed	Germany	van der Burgh (1978, 1983)
E. sp.	Late Miocene to Early Pliocene	Seed	England	Boulter (1971)
E. ciliata Merrill	Late Miocene to Early Pliocene	Leaf	SW Yunnan, SW China	Tao and Du (1982)
E. stigmosa (Ludwig) Mai	Late Miocene to Early Pliocene	Seed	SW Poland	Dyjor et al. (1992)
E. sp.	Late Miocene	Leaf	Japan	Ozaki (1991)
E. lusatica Mai	Late Miocene	Seed	Eschweiler, Germany	van der Burgh (1987)
E. japonica Thunberg	Late Miocene	Seed	Central Japan	Momohara and Saito (2001)
E. stigmosa (Ludwig) Mai	Late Miocene	Seed	Eschweiler, Germany	van der Burgh (1987)
E. stigmosa (Ludwig) Mai	Middle Miocene	Seed	Denmark	Friis (1979, 1985)
E. stigmosa (Ludwig) Mai	Early Miocene	Seed	Czech	Teodoridis and Kvaček (2006)
E. stigmosa (Ludwig) Mai	Early Miocene	Seed	Austria	Meller (1998) and Meller et al. (1999)
E. stigmosa (Ludwig) Mai	Miocene	Seed	South Poland	Lańcucka-Środoniowa (1966, 1981, 1984)
E. stigmosa (Ludwig) Mai	Miocene	Seed	Germany	Gregor (1982)
E. stigmosa (Ludwig) Mai	Miocene	Seed	Germany	Mai (1960)
E. lusatica Mai	Miocene	Seed	Puschwitz, Germany	Mai (1971)
E. aff. *acuminatissima* Merr. & Chun	Late Oligocene	Leaf	SE Bulgaria	Bozukov and Palamarev (1995) and Bozukov et al. (2008)
E. sp.	Late Oligocene	Leaf	Japan	Tanai and Uemura (1991)
E. dubia (Chandler) Mai	Middle Oligocene	Seed	Devonshire, England	Mai (1971)
E. dubia (Chandler) Mai	Middle Oligocene	Seed	Nerchau, Germany	Mai (1971)
E. mudensis Chandler	Middle Oligocene	Seed	Germany	Mai (1971)
E. stigmosa (Ludwig) *Mai*	Middle Oligocene	Seed	Devonshire, England	Mai (1971)
E. boveyana (Chandler) *Mai*	Middle Oligocene	Seed	Devonshire, England	Mai (1971)
E. boveyana (Chandler) Mai	Oligocene	Seed	Germany	Mai and Walther (1978)
E. boveyana (Chandler) Mai	Late Eocene to early Oligocene	Seed	Germany	Mai (1971)
E. sp.	Late Eocene	Seed	Russia	Nikitin (2006)
E. lentiformis (Chandler) Mai	Late Eocene	Seed	Wight, England	Mai (1971)
E. becktonensis Chandler	Late Eocene	Seed	Hants, England	Mai (1971)
E. mudensis Chandler	Late Eocene	Seed	England	Chandler (1963) and Mai (1971)
E. obliqua (Chandler) Mai	Middle Eocene	Seed	Egeln, Germany	Mai (1971)
E. poolensis (Chandler) Mai	Middle Eocene	Seed	Bournemouth, England	Mai (1971)
E. stigmosa (Ludwig) *Mai*	Middle Eocene	Seed	Bournemouth, England	Mai (1971)
E. obliqua (Chandler) Mai	Early Eocene	Seed	Dorset, England	Mai (1971)
E. stigmosa (Ludwig) *Mai*	Early Eocene	Seed	Oscherslebener Mulde, Germany	Mai (1971)
E. stigmosa (Ludwig) *Mai*	Paleocene	Seed	Reading Beds, England	Mai (1971)
E. mudensis Chandler	Paleocene	Seed	Germany	Mai (1971)
E. crassitesta Knobloch	Late Cretaceous to Paleocene	Seed	Moravian Carpathian, Czech Republic	Knobloch (1977)
E. maii Knobloch	Late Cretaceous to Paleocene	Seed	Moravian Carpathian, Czech Republic	Knobloch (1977)
E. holyi Knobloch	Late Cretaceous to Paleocene	Seed	Moravian Carpathian, Czech Republic	Knobloch (1977)
E. crassitesta Knobloch	Middle–Late Cretaceous	Seed	Austria	Knobloch and Mai (1986, 1991)

fossils may represent partial histories of the ancient lineages of modern *Eurya* in Asia.

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