Review article

Early Oligocene *Itea* (Iteaceae) leaves from East Asia and their biogeographic implications

Yi-Min Tian [a], Jian Huang [b, **], Tao Su [b, c], Shi-Tao Zhang [a, *]

[a] *Kunming University of Science and Technology, Kunming, Yunnan, 650500, China*
[b] *Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, 666303, China*
[c] *University of the Chinese Academy of Sciences, Beijing, 100049, China*

A B S T R A C T

Compressed materials of fossil foliage described here as *Itea polyneura* sp. nov. (Iteaceae) were collected from the Oligocene of Wenshan, Yunnan Province, southwestern China. The identification is based on the following characters: eucamptodromous secondary veins, strict scalariform tertiary veins, irregular tooth with setaceous apex. The leaf morphology of all modern and fossil species was compared with the new species from Wenshan and show that *I. polyneura* is most similar to the extant East Asian species *Itea omeiensis*, which inhabits subtropical forests of southern China. This discovery represents the first unambiguous leaf fossil record of *Itea* in East Asia. Together with other species in the Wenshan flora and evidence from several other flora in southern China, these findings demonstrate that *Itea* from East Asia arose with the Paleogene modernization.

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1. Introduction

In the early Cenozoic, the Northern Hemisphere may have been covered by vast subtropical broad-leaved evergreen forests (Wolfe, 1985; Milne and Abbott, 2002). A large number of fossil species (e.g., Fagaceae Dumort., Lauraceae Juss., Theaceae Mirb., Magnoliaceae Juss.) found in North America and Europe, ranging from the Paleocene to Miocene, are almost morphologically identical to extant taxa in southern China (Mai, 1995; Manchester, 1999). Because few Paleogene fossil localities have been reported in East Asia, the biogeographical histories of these taxa have mostly been interpreted on the basis of materials from North America and Europe. Researchers have speculated that East Asia is a 'refugium' rather than the source of the Northern Hemisphere's biodiversity (Axelrod et al., 1998; Tiffney and Manchester, 2001). In recent years, many fossil floras from the Paleogene have been discovered in southern China (Quan et al., 2016). They show a high degree of similarity to the extant East Asian evergreen broad-leaved forests, which offers an excellent opportunity to understand the origin and evolution of modern flora in East Asia.

Itea L. are small trees, shrubs or sometimes scramble plants that grow in forests and thickets (Jin and Ohba, 2001; Kubitzki, 2007). *Itea* belongs to Iteaceae J. Agardh, Saxifragales Bercht. & J. Presl, although it was formerly included in Escalloniaceae R. Br. ex Dumort., Grossulariaceae DC. or Saxifragaceae. Molecular analyses place it as an independent family into the Core Saxifragales sister to *Pterostemon* S. Schauer (Savolainen et al., 2000; Fishbein et al., 2001). There are 21 species in the genus, and most of them are evergreen and distributed in the subtropical to tropical regions of East Asia (Guo and Ricklefs, 2000; Kubitzki, 2007). Thus, the subtropical evergreen broad-leaved forest region in southern China is *Itea*'s modern biodiversity center (Guo and Ricklefs, 2000). The distribution of *Itea* displays an East Asian-eastern North American-southeastern African disjunction (Fig. 1), which is unusual among genera with a North American-East Asian disjunction pattern (Wen, 1999). Although the genus is primarily subtropical, two species of deciduous trees inhabit the temperate forests of Japan and eastern North America (Kubitzki, 2007). Thus, the distribution pattern of

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* Corresponding author. Faculty of Land Resource Engineering, Kunming University of Science and Technology, Kunming, Yunnan 650093, China. Fax: +86 0871 65177163.
** Corresponding author. Fax: +86 0691 8713226.
E-mail addresses: huangjian@xtbg.ac.cn (J. Huang), taogezhang@hotmail.com (S.-T. Zhang).
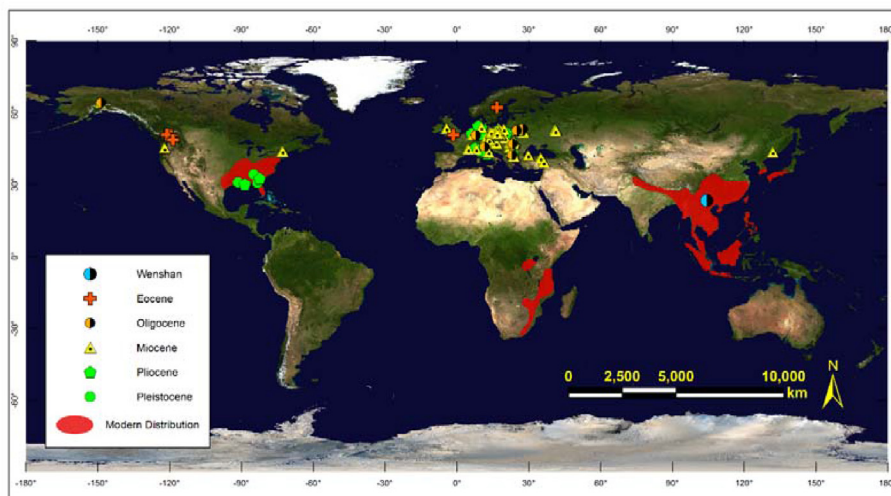
Fig. 1. Map showing the modern distribution of *Itea* and the locations from which *Itea* fossils were recovered.

Itea provides an opportunity to study the origin and differentiation of Northern Hemisphere temperate forests (Folk et al., 2019).

Itea pollen grain can easily be distinguished by its unique bilaterally symmetrical and diporate morphology, and fossil records of iteoide pollen grains are common in the Cenozoic of Europe and North America (Hermsen, 2013). In addition, its distinctive infructescence structure is highly recognizable for its identification, and fossil fruits of *Itea europaea* are also widely reported in Europe from the Eocene to Pliocene (Mai, 2001; Hermsen, 2013). However, confirmed leaf fossils of *Itea* are rare and only known from western North America (Wolfe and Wehr, 1987; Hermsen, Personal communication). Nevertheless, leaves of *Itea* species can be easily identified because of their unique characteristics (e.g., eucamptodromous secondary veins, strict scalariform tertiary veins, irregular teeth).

In this paper, we identified fossil leaves of *Itea* from the early Oligocene of Wenshan Basin, Yunnan, southwestern China, which constitutes the first reliable leaf fossil record of the genus from East Asia and Eurasia. This study establishes a new species of *Itea* to accommodate these new fossils with distinct and diagnostic leaf architecture, and compares it with all extant and fossil species of the genus. Furthermore, this study discusses the implications this finding has for our understanding of the histories of the 'Tertiary relic flora' (Milne and Abbott, 2002) and East Asian-North American disjunct distributions.

2. Materials and methods

2.1. Fossil materials

Compressed leaf fossils studied here were collected from the Wenshan Basin, Yunnan Province, southwestern China (23°20′N; 104°17′E, 1271 m a.s.l.) (Fig. 2). Wenshan is a fault basin in a group of the Wenshan-Funing fold that belongs to the southeast Yunnan fold belt of the China Caledonian Fold System; the Wenshan Basin is divided into the Yangtze platform by geotectonic characteristics.

Leaf fossils were found in a grey, light grey, and greyish yellow mudstone and marlstone. The environment of deposition is interpreted to be lacustrine facies. The fossil-bearing stratum belongs to the Huazhige Formation. This outcrop was previously assigned to different periods of the Miocene by biostratigraphic correlation and magnetostratigraphic study (Lebreton-Anberrée et al., 2016). However, a recent U—Pb dating of zircon from *in*

Fig. 2. Location of the fossil site (leaf symbol).

situ volcanic ash reveals a much earlier geological time, the early Oligocene (~30/32 Ma), not the Miocene as previously suggested (Tian et al., unpublished).

2.2. Extant materials and morphological observation

Herbarium specimens of extant *Itea* species used for comparison were accessed from online data sources such as JSTOR Global Plants (http://plants.jstor.org/) and the Chinese Virtual Herbarium (http://www.cvh.org.cn/). Cleared leaf materials of extant species were collected from the Xishuangbanna Tropical Botanical Garden (XTBG). These leaves were cleared following the protocol developed by Li (1987). Several photographs of cleared leaves of extant *Itea* species were downloaded from the Smithsonian Cleared Leaf Collection, and their contrasts were adjusted using Adobe Photoshop. All fossil and modern specimens were photographed using a digital camera (Nikon D700). Further, the details of the fossils were photographed using a stereomicroscope (Leica

S8APO). In addition, line-drawings and plates were created using CorelDRAW X7. Digital photographs of extant and fossil specimens were measured using ImageJ 1.45s software. The leaf architecture terminology followed Ellis et al. (2009).

3. Results

3.1. Systematic palaeobotany

Family: Iteaceae J. Agardh 1858
Genus: *Itea* L. 1753.
Species: *Itea polyneura* J. Huang et Y.M. Tian sp. nov.
Etymology: The species epithet *polyneura* refers to its leaves with more secondary veins (~7−8 pairs) than other species of the genus.
Holotype: DMS-1846 (designated here) (Plate Ia, b).
**Paratypes:** DMS-1647 (designated here) (Plate Ic).

Repository: Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.
**Type locality:** Dashidong Village, Wenshan, Yunnan, China.
Stratigraphy: Oligocene, Huazhige Formation.
Diagnosis: Leaf oblong, size ~4.5−~8.0 cm long × 2.5−3.4 cm wide; secondary veins eucamptodromous, ~7−8 pairs; inter-secondaries absent; tertiary veins densely scalariform; margin with crenate to serrate teeth, spacing irregular, tooth apex simple or setaceous (Fig. 3).
Description: Isolated leaves, simple, petiolate. Petiole marginally attached to the blade, terete (Plate Ib). Lamina symmetric, oblong to obovate, mesophyll, physical size = 2.7−7 cm long × 2.5−3.3 cm wide, assuming size = ~4.5−~8 cm long × 2.5−3.4 cm wide, assuming length to width ratio (L: W) = (~2.0−2.5). Lamina apex not preserved (Plate Ia−c), base insertion asymmetrical, slightly decurrent (Plate Ib), acute (~80°), shape concave to truncate (Plate Ib, c). Lamina vernation pinnate. Midvein distinctly raised abaxially, impressed adaxially. Secondary veins eucamptodromous, arcuate
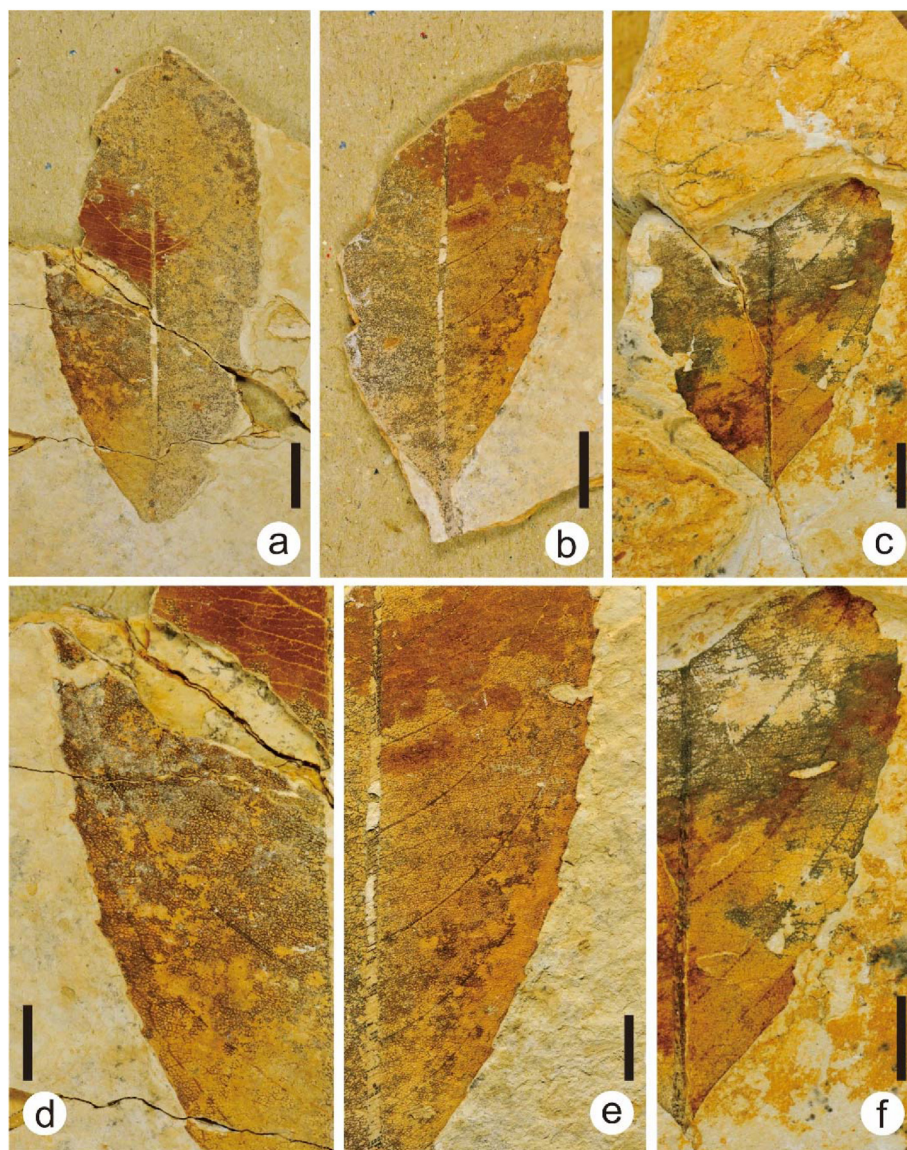
Plate I. *Itea polyneura* from the Oligocene of Wenshan flora, Yunnan, China. (**a**) DMS-1846A (holotype); (**b**) DMS-1846B (counterpart of DMS-1846A); (**c**) DMS-1647 (paratype); (**d**) Detailed venation of DMS-1846A, showing irregular tooth arrangement and scalariform tertiary veins. (**e**) Detailed leaf margin of DMS-1846B, showing eucamptodromous secondary veins and irregular tooth arrangement. (**f**) Detailed venation of DMS-1647, showing eucamptodromous secondary veins and scalariform tertiary veins. Scale bar = 1 cm in (**a−c**); Scale bar = 0.5 cm in (**d−f**).
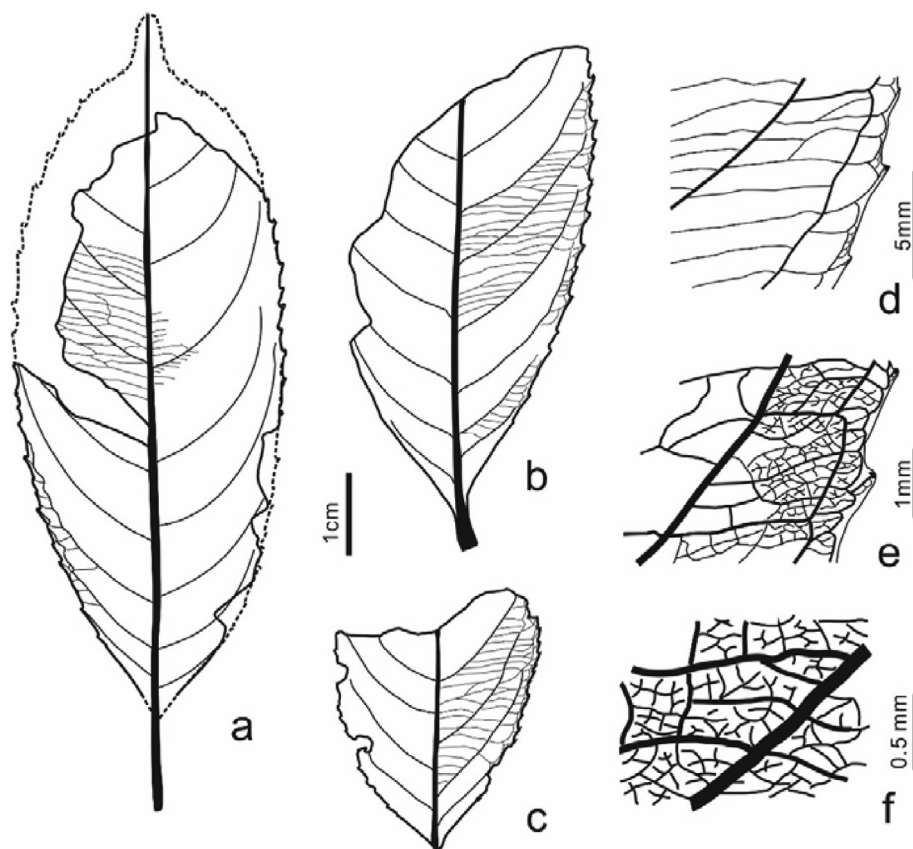
Fig. 3. Line drawing of *Itea polyneura* sp. nov. (**a**) DMS-1846A; (**b**) DMS-1846B; (**c**) DMS-1647. (**d**) Detailed leaf margin veins of DMS-1846B, showing the tertiary vein and exterior tertiary pattern. (**e**) Detailed leaf margin veins of DMS-1846B, showing higher order and marginal vein pattern. (**f**) Detailed higher order veins of DMS-1846A, showing veinlets. Scale bar = 1 cm in (**a**—**c**); 5 mm in (**d**); 1 mm in (**e**); 0.5 mm in (**f**).

curved upward, ~7—8 pairs, spacing decreasing proximally, attachment alternate (Plate Ia—c), decurrent (Plate IId). Inter-secondaries absent; tertiary veins scalariform, straight opposite percurrent (rarely mixed percurrent), perpendicular (or slightly acute) to midvein, vein angle consistent (Plate Id—f). Exterior tertiary course looped. Quaternary veins irregular reticulate. Areolation with moderate development (Plate IIe); freely ending veinlets mostly two-branched with simple termination. Marginal ultimate venation looped (Fig. 3).

Margin crenate to serrate. Tooth spacing irregular, one order, with rounded sinus. Tooth shapes concave/flexuous (cc/fl); principal vein present, terminates at the apex of a tooth; accessory veins only occur on the proximal flank, convex, looped (Plate IIc); tooth apex simple or setaceous (sometimes with a deciduous seta) (Plate IIIa—b).

3.2. Generic determination

Three typical venations are characteristics of the fossil specimens described below.

(a) Eucamptodromous venation is a special venation pattern in dicotyledonous leaves (Plate Ia, c), with the major secondaries connecting to superjacent secondaries via tertiaries without forming margin loops of secondary gauge (Ellis et al., 2009). These secondaries curve gradually, and their angles to the midrib are reduced correspondingly. Most of the plant taxa with eucamptodromous secondaries have margins over the entire leaves (e.g., *Cornus* L., Dipterocarpaceae Blume, Rhamnaceae Juss., Rubiaceae Juss.).

(b) Scalariform tertiary veins (straight opposite percurrent tertiaries perpendicular to midvein forming a ladder-like pattern) (Plate IIa, c). The tertiary venation frameworks of eucamptodromous leaves are not fixed, but percurrent tertiaries (tertiaries cross between adjacent secondaries) are common and may be physiologically more efficient. The scalariform shape is a unique pattern of percurrent tertiaries, with an easily varied set of courses and angles. Moreover, scalariform tertiary veins can be classified as 'strict' or 'not strict'. In the strict form, the tertiary vein angles are consistent and always perpendicular to the midvein. Therefore, the angle between tertiaries and secondaries changes with the arching of secondaries. In the form that is not strict, the connections often have corresponding angle adjustments, and the tertiaries are often vertically connected to secondaries. This results in 'basally concentric tertiaries'.

(c) Tooth spacing is irregular, and the tooth shapes are also irregular (crenate to serrate) (Plate Id, f). Teeth are almost non-specific, but sometimes deciduous seta on apex can be observed (Plate IIIa, b). These tooth morphological features may indicate a transitional subtropical habitat.

To our knowledge, only a few extant taxa share this combination of traits with the fossils we have described (summarized in Table 1). However, our fossil finding and members of the genus *Itea* share similar characteristics, including the venation framework, teeth structure and the form of the teeth exfoliation (Table 1). Therefore, these fossils from Wenshan are likely to belong to the genus *Itea*.
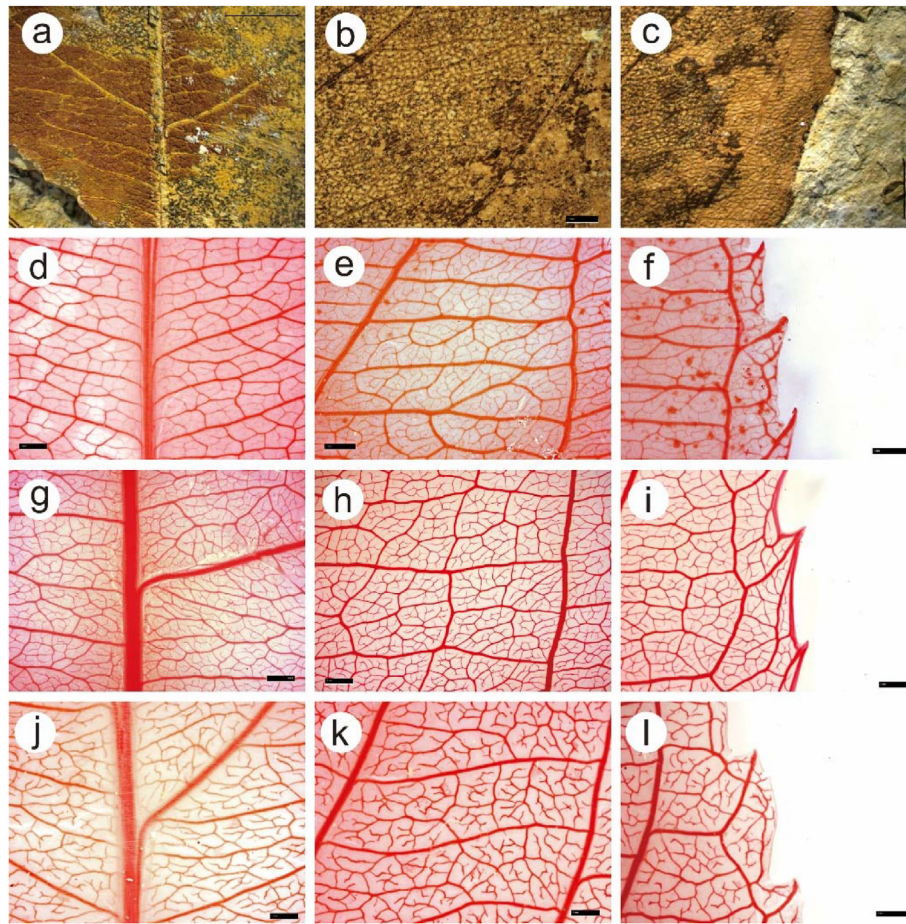
Plate II. Comparison of higher order venation in *Itea polyneura* and extant taxa. (**a**–**c**) *Itea polyneura* (DMS-1846AB); (**d**–**f**) *Itea chinensis* (PRGCL-F127-001); (**g**–**i**) *Turpinia pomifera* (PRGCL-F226-001); (**j**–**l**) *Viburnum brachybotryum* (PRGCL-F408-001); (**a,d,g,j**) secondary and tertiary veins attached to midvein patterns; (**c,e,h,k**) Tertiary, higher order veins and areoles patterns; (**c,f,i,l**) Teeth structure patterns. Scale bar = 1 mm. All the leaves are preserved in Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

These combinations of leaf architecture features not only place our fossil in genus *Itea* but also exclude some of species formerly included in *Itea*. For instance, *Itea javanica* Blume is a synonym of *Pittosporum ferrugineum* W.T. Aiton (Pittosporaceae); *Itea fragrans* Wall. is a synonym of *Polyosma fragrans* (Wall.) Benn. (Escalloniaceae), and *Itea caroliniana* Lam., *Itea cyrilla* Sw. and *Itea floribunda* Salisb. are all synonyms of *Cyrilla racemiflora* L. (Cyrillaceae). In addition, these taxa are toothless, and their secondary veins are not eucamptodromous. Their exclusion from *Itea* reflects the structural stability of *Itea* leaf architecture.

3.3. Morphological comparison with fossils and extant Itea species

There are 21 accepted modern species in the genus *Itea* (International Plant Names Index, https://www.ipni.org/) (Table 1). Most of them (19 spp.) are evergreen (SE Asian & African species) and only one species from Japan (*Itea japonica* Oliv.) and one species from North America (*Itea virginica* L.) are deciduous. Moreover, Engler (1890, 1928) subdivided the extant *Itea* species into two sections based on their life forms: Sect. *Deciduae* Engler and Sect. *Sempervirentes* Engler.

Sect. *Deciduae* comprised two deciduous species with ovoid seeds (*Itea virginica* and *I. japonica*), while Sect. *Sempervirentes*

comprised the evergreen Asian species with fusiform seeds. This division was consistent until African *Choristylis rhamnoides* Harv. was transferred into *Itea* (Kubitzki, 2007). *Itea rhamnoides* (Harv.) Kubitzki has more or less ovoid seeds but is evergreen. These evergreen and deciduous *Itea* can be distinguished by their leaf architecture. All Sect. *Sempervirentes* have scalariform tertiary veins and crenate to serrate teeth, which are stable traits associated with plants residing in a moist subtropical habitat (Plate IVa–g). In contrast, Sect. *Deciduae* tertiary veins are more reticulate (alternate percurrent, more intersecondaries) (Plate IVh, i) and the teeth are usually serrate. However, *I. rhamnoides* is much more similar to the deciduous *I. japonica* of Sect. *Deciduae* in having acute, serrate, sometimes compound teeth. Its evergreen habitat may be due to its climatic conditions. Morphologically, the fossil leaves from Wenshan clearly belong to Sect. *Sempervirentes*.

The leaf shapes of *Itea* are most commonly oblong to elliptical. This is particularly true for subtropical species at its southern China diversity center. Other leaf shapes are relatively rare and exhibit high ecological correlations. For instance, ovate leaves appear in the temperate *I. japonica* of Sect. *Deciduae* and its close African sister *I. rhamnoides*; obolanceolate and lanceolate leaves only appear in *Itea riparia* Coll. et Hemsl., *Itea tenuinervia* S. Y. Liu and *Itea amoena* Chun, which grow on riverside rocks (Table 1; Plate IV).

Table 1
Comparison of leaf architecture in the Wenshan fossil and possible extant genera.

Taxa	Secondaries	Tertiaries	Higher order veins	Areole development	Teeth density	Teeth regularity	Margin shape and tooth type	Note
Wenshan fossil	simple eucamptodromous	strict scalariform	irregular reticulate	moderate	medium	irregular	crenate to serrate, theoid and rosoid	Plate II 1-3
Casearia Jacq.,*Xylosma* G. Forst. (Salicaceae Mirb.)	simple eucamptodromous	not strict scalariform, distal course perpendicular to secondaries	mixed percurrent to irregular reticulate	moderate	medium, high	mostly irregular	round to crenate, salicoid	–
Celastrus L., *Tontelea* Miers, *Hippocratea* L., *Hylenaea* Miers, *Wimmeria* Schltdl & Cham. (Celastraceae)	Often with prominent inter-secondaries	often mixed percurrent	mixed percurrent to irregular reticulate	moderate	medium, high	regular	crenate to serrate, theoid	–
Deutzia, Dichroa, Hydrangea (Hydrangeaceae R. Br.)	Often with prominent inter-secondaries	percurrent to reticulate	reticulate	good to paxillate	medium, high	regular, irregular	(shallow) serrate, rosoid	–
Itea (Iteaceae)	simple eucamptodromous	strict scalariform	irregular reticulate	moderate	medium, high	irregular, regular	crenate to serrate, theoid or rosoid	Plate II 4-6
Leea D. Royen ex L. (Vitaceae Juss.)	dense (more than 13 pairs), often opposite	sinous percurrent, distal course often perpendicular to secondaries	mixed percurrent	moderate, good	high	irregular, often compound	round, dentate to serrate, theoid	Leaflet of pinnate compound leaf
Rhamnus L., *Rhamnella* Miq., *Ventilago* Gaertn. (Rhamnaceae Juss.)	simple eucamptodromous	sinous percurrent, strict scalariform	alternate percurrent or regular reticulate	moderate, good	high	regular, irregular	crenate, rounded (without spinose trend), cunuoid	–
Rubus L. (Rosaceae Juss.)	Basal-most secondaries with minor secondaries	often mixed percurrent	mixed percurrent	good	high	irregular, often compound	serrate, rosoid	Simple leaf or leaflet
Turpinia Vent. (Staphyleaceae Martinov)	often nearly opposite	inconsistent, trend to reticulate	alternate percurrent to irregular reticulate	moderate	high	mostly regular	crenate to serrate, theoid	Leaflet of pinnate compound leaf, Plate II 7-9
Viburnum L. (Adoxaceae E.Mey.)	often with side branches	often mixed percurrent	often absent	poor	variable	mostly irregular	variable, rosid	Plate II 10-12
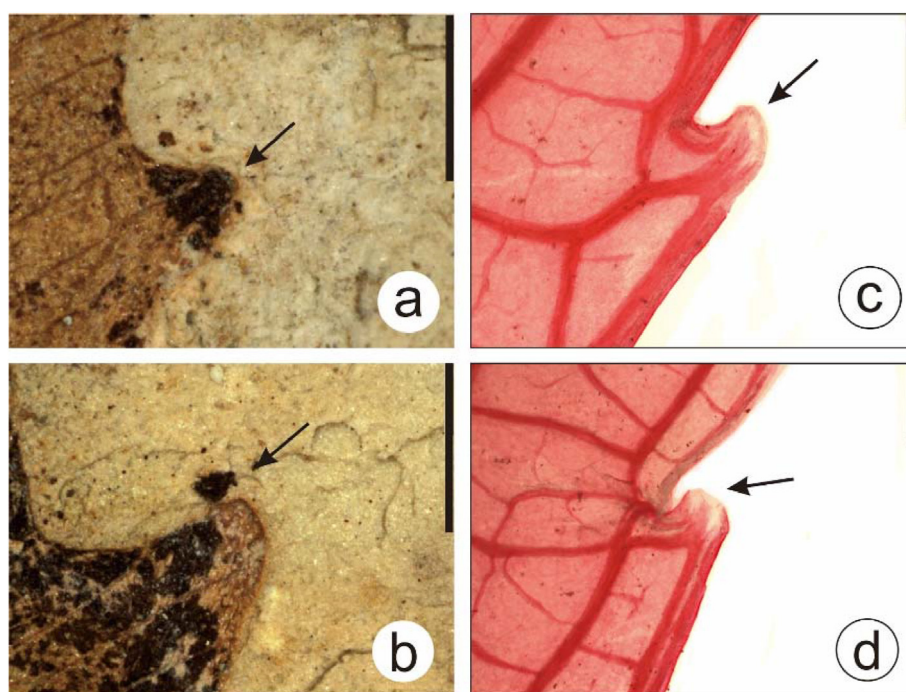
Plate III. Deciduous tooth seta of *Itea*. (**a**−**b**) Fossil *I. polyneura* (DMS-1846B). (**c**−**d**) Extant *I. chinensis* (PRGCL-F127-001). (**a, c**) Tooth apex with seta. (**b, d**) Tooth apex without seta. (**b**) State of the seta when falling off. Scale bar = 0.5 mm.

Table 2
Comparison of the leaf morphology in extant and fossil *Itea* species. The value of the length, width and L:W ratio is expressed as "minimum−maximum (average)"; The number of secondary veins is expressed as "minimum−maximum (median)".

Taxa	Distribution	Leaf Length (cm)	Leaf Width (cm)	L: W	Secondary Pairs	Leaf Shape	Tooth Density, Regularity & Shape
Itea polyneura J. Huang et Y.M. Tian	SW China	4.5—8	2.5—3.4	2—2.4	6—8	Oblong	Medium, Irregular, Crenate to Serrate
Iteaphyllum wehrii Hermsen	NW United States	0.9—13.6 (6.6)	0.8—6.7 (3.5)	1.1—2.9 (1.9)	4—7 (5)	Ovate	Dense, Regular, Crenate
Itea amoena Chun	S China	7.8—13.1 (9.8)	1.2—1.8 (1.5)	5.5—8.1 (6.8)	5—7 (6)	Lanceolate	Sparse, Irregular, Crenate
I. chinensis Hook. et Arn.	S China	4.6—12 (8.7)	2.8—4.9 (3.8)	1.6—2.5 (2.2)	4—5 (5)	Oblong	Medium, Irregular, Crenate to Serrate
I. coriacea Y. C. Wu	S China	4.8—11.3 (8)	1.9—4.3 (3.3)	2—2.9 (2.4)	5—6 (6)	Oblong	Sparse, Irregular, Crenate
I. glutinosa Hand.-Mazz.	S China	5.6—12.2 (9.4)	3.1—6.1 (4.6)	1.8—2.4 (4)	4—6 (5)	Oblong	Dense, Irregular, Serrate
I. ilicifolia Oliv.	SW China	3.3—8.1 (6.4)	2—5.5 (3.8)	1.3—2.4 (1.7)	3—7 (5)	Round, Obovate	Sparse, Irregular, Spinose
I. indochinensis Merr.	S China & Indochina	7.4—21.5 (12.5)	3.2—11.1 (6)	1.9—2.3 (2.1)	5—9 (6)	Oblong	Dense, Irregular, Crenate
I. japonica Oliv.	S Japan	5.3—10.2 (7.5)	1.9—5.4 (3.4)	1.8—3.2 (2.3)	5—7 (7)	Ovate	Dense, Regular, Serrate
I. kiukiangensis C. C. Huang et S. C. Huang	SW China	3.4—13.6 (9.8)	1.9—6.9 (5)	1.3—2.3 (1.9)	4—7 (6)	Oblong	Medium, Irregular, Crenate
I. kwangsiensis H. T. Chang	S China	7.9—18.9 (14.5)	3.4—8.6 (6.3)	1.7—2.8 (2.3)	5—9 (8)	Oblong	Medium, Irregular, Crenate
I. macrophylla Wall. ex Roxb.	Trop. Asia	7.9—15.9 (12.4)	4.1—8.8 (6.3)	1.8—2.5 (2)	5—7 (6)	Oblong	Medium, Irregular, Crenate
I. nutans Royle	NW Himalayas	3.8—16.3 (9.2)	2.3—6.8 (4.4)	1.6—2.5 (2)	4—7 (5)	Oblong	Medium, Irregular, Spinose
I. oldhamii Schneid.	Taiwan & Ryukyu	4.4—7.3 (6.6)	2.7—3.2 (2.9)	1.6—2.6 (2.3)	3—5 (4)	Obovate	Sparse, Irregular, Spinose
I. omeiensis C. K. Schneid.	S China	5.3—12.3 (9.1)	2.6—4.9 (3.6)	2—2.8 (2.5)	5—7 (6)	Oblong	Medium, Irregular, Crenate to Serrate
I. parviflora Hemsl.	Taiwan	5.4—11.1 (8)	1.7—4.7 (3.6)	1.5—3.2 (2.3)	4—5 (5)	Oblong	Medium, Irregular, Crenate
I. rhamnoides (Harv.) Kubitzki	SE Africa	5.7—8.2 (7.2)	3.4—4.5 (4.1)	1.6—2.2 (1.8)	6—7 (7)	Ovate	Dense, Regular, Serrate
I. riparia Coll. et Hemsl.	S China & Indochina	2.8—8.3 (5.4)	0.7—2.9 (1.7)	2.1—5.1 (3.3)	5—6 (5)	Obolanceolate	Medium, Irregular, Crenate
I. tenuinervia S. Y. Liu	S China	2.8—6.3 (5.1)	1.1—2 (1.7)	2.5—3.5 (2.9)	5—6 (5)	Obolanceolate	Medium, Irregular, Crenate
I. virginica L.	SE United States	2.4—9.4 (5.6)	1.8—3.7 (2.7)	1.3—2.5 (2)	4—6 (5)	Oblong	Medium, Irregular, Serrate
I. yangchunensis S.Y. Jin	S China	5.5—10 (7.6)	2.1—3.2 (2.5)	2.4—3.5 (3.1)	3—5 (4)	Oblong	Sparse, Irregular, Crenate
I. yunnanensis Franch.	SW China & E Himalays	3.9—9.2 (7)	2.4—4.4 (3.3)	1.4—2.9 (2.2)	4—6 (5)	Oblong	Sparse, Irregular, Spinose

The leaf size of *Itea* also varies to a certain degree, and the leaves of tropical species are larger (e.g., *Itea indochinensis* Merr., *Itea kwangsiensis* H. T. Chang and *Itea macrophylla* Wall. ex Roxb.). Subtropical taxa generally have medium-sized leaves that are 5—15 cm long. Leaves of different sizes, particularly smaller ones, often appear on the same plant (Table 1).

The curved eucamptodromous secondary veins, with a larger single cover area, are often relatively small in number. Most species of extant *Itea* have an average of only 4—6 pairs of secondary veins, whereas only *I. japonica* and *I. rhamnoides* have an average of 7 pairs (Table 1). When leaves have higher numbers of secondary veins, the angles between these veins and the middle veins are smaller (Plate IV).

Most of the evergreen *Itea* species are irregularly crenate to serrate toothed. In limestone hills, species such as *Itea yunnanensis* Franch. and *Itea ilicifolia* Oliv. have teeth that are specialized into spinose. In the temperate deciduous taxa *I. japonica* and *I. virginica*, the teeth become serrate. These characteristics of plants might be an evolution indicator for adapting the environment change (drought/cold) (Table 2; Plate IV).

The Wenshan fossil leaves have a smaller size, oblong shape and irregular crenate to serrate teeth with medium density. Comparative morphological analysis of the Wenshan fossils showed that their leaf size, shape and architecture are most similar to the extant *Itea omeiensis*. The main difference between the Wenshan fossils and *I. omeiensis* is that the Wenshan fossils have significantly more secondary vein pairs. Therefore, it is treated as a new species

(*I. polyneura*). *I. omeiensis* is a widely distributed species in the subtropical evergreen broad-leaved forest region in southern China (Fang et al., 2011). In addition, its area of distribution differs slightly from the equally common *Itea chinensis* Hook. et Aru. Moreover, *I. omeiensis* is less distributed in the Yunnan plateau region than is *I. chinensis*, which is characterized by the Sino-Japan floristic region (Table 2).

4. Discussion

4.1. General fossil history

Hermsen (2013) summarized the fossil records of iteoide plants (*Itea* and its affinities) (Fig. 1). The fossil *Divisestylus* from the late Cretaceous (~90 Ma) was not *Itea* but a stem-group *Itea* (Hermsen et al., 2003). The earliest occurrence of confirmed *Itea* is pollen from the early Eocene Okanogan Highlands floras of western North America (Moss et al., 2005). Leaves have been found in Oligocene Republic flora of western North America (Wolfe and Wehr, 1987). In Europe, the earliest report of iteoide plants is a flower called *Adenanthemum iteoides* Hermsen from the late Eocene Baltic Amber (Conwentz, 1886). Pollen (*Iteapollis* Ziemb. -Tworz. & *Itea*) and fruit (*I. europaea* Mai) fossils from the Oligocene have since been widely reported in Europe (Mai, 1995). The distinctive pollen of *Itea* has also been found in Alaska, North America (Wahrhaftig et al., 1969). Iteoide fossils from the early Miocene have been found all over the North Hemisphere, including west and east North America, as well
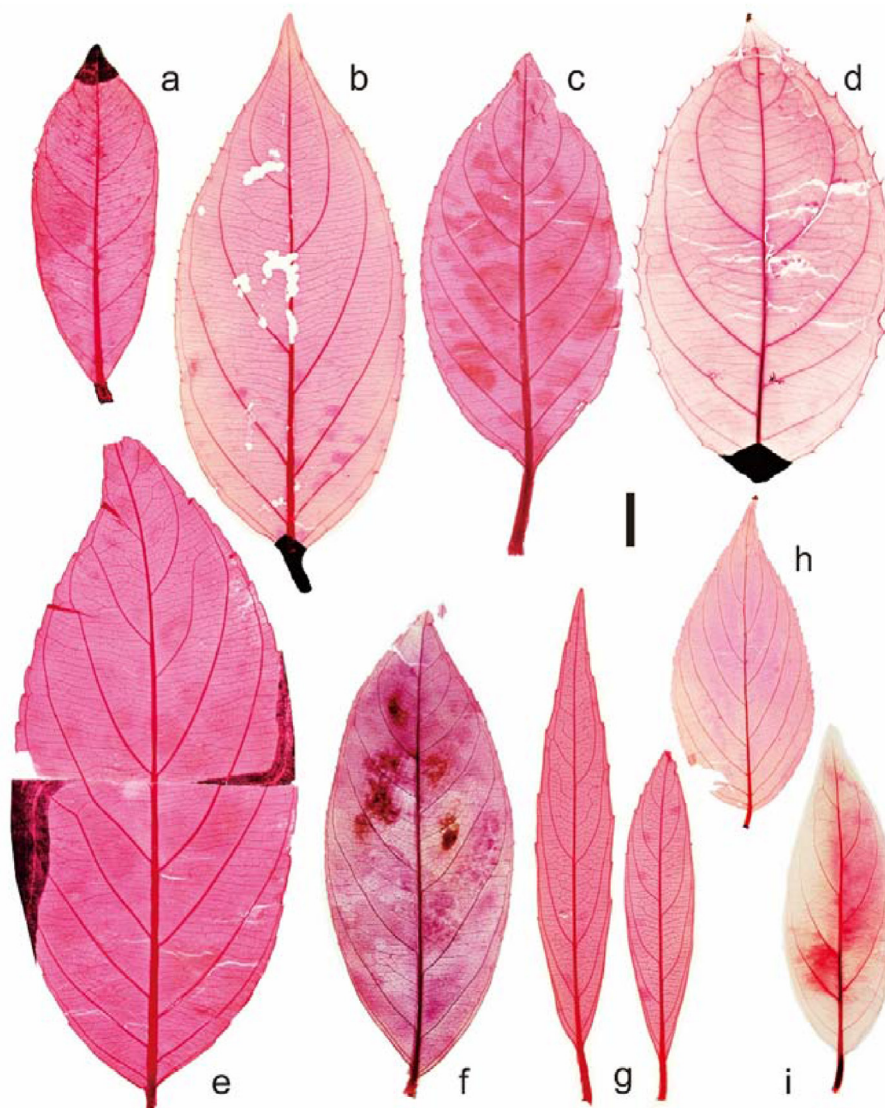
Plate IV. Leaf architecture diversity of extant *Itea* species. (**a**) *I. oldhamii* (NCLC-W-8918); (**b**) *I. nutans* (NCLC-W-8920); (**c**) *I. maesaefolia* (NCLC-W-8921); (**d**) *I. yunnanensis* (NCLC-W-1133b); (**e**) *I. macrophylla* (NCLC-W-8919); (**f**) *I. chinensis* (NCLC-3199); (**g**) *I. amoena* (NCLC-W-8913b); (**h**) *I. japonica* (NCLC-W-8917); (**i**) *I. virginica* (NCLC-3198). Scale bar = 1 cm. All the leaves are preserved in Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

as the Far East of Russia (Pavlyutkin and Petrenko, 2010). Iteoide fossils from the late Miocene to Pleistocene are well documented in the southeastern United States and Europe. North American pollen records have sometimes been assigned to the extant species *I. virginica*. The latest European record of iteoide fossils dates to the Pliocene (Hermsen, 2013).

4.2. Evergreen origins and deciduous adaptations

All iteoide fossils preserved in Europe are pollen and fruit. Pollen fossils are mostly of Sect. *Sempervirentes*, whereas, the fruit *I. europaea* may belong to Sect. *Deciduae* (close to *I. virginica*). Evidence of pollen spans the entire Cenozoic, whereas *I. europaea* is only found after the Miocene. This record indicates that Sect. *Sempervirentes* appeared earlier in the geological record of Europe and remained present for a long period. Evidence of pollen spans the entire Cenozoic, whereas *I. europaea* is only found after the Miocene. This record indicates that Sect. *Sempervirentes* appeared
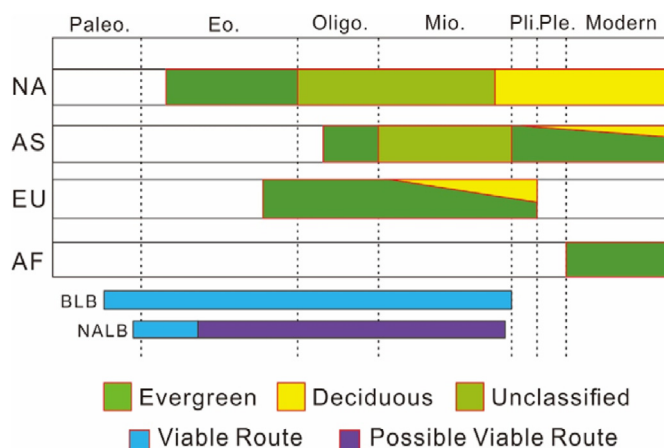
Fig. 4. Distribution of *Itea* over geological time. NA, North America; AS, East Asia; EU, Europe; AF, Africa.

earlier in the geological record of Europe and remained present for a long period (Fig. 4).

In North America, Eocene leaves with distinct scalariform tertiary veins are probably Sect. *Semperiventes* (Wolfe and Wehr, 1987). North American records from the Oligocene to Pleistocene records are all pollen. Most of the records after the late Miocene were considered similar to deciduous *I. virginica* (Hermsen, 2013). However, it has been difficult to determine whether other records from the Oligocene to Miocene are evergreen or deciduous (Fig. 4).

In East Asia, iteoide fossil records are rare. This study proposes that Oligocene *Itea polyneura* is an evergreen species. It has not yet been possible to identify the subdivision of Miocene Far East Russian *Itea* pollen. Evergreen *Itea* pollen has been reported in southern China from the Quaternary (Tang et al., 2016) (Fig. 4).

Based on the fossil records of Europe, North America, and East Asia (Fig. 4), Sect. *Deciduae* is more likely to be a group that divided later. This differentiation may be related to global cooling after the Oligocene (Zachos et al., 2001; Liu et al., 2009), but its place of origin is still unknown. It could have originated from Europe or from North America and migrated via the North Atlantic Land Bridge (NALB) (Fig. 4). *Itea virginica* and *I. japonica*, two extant deciduous species of *Itea*, follow the typical East Asia-eastern North America disjunction pattern. They may have crossed the continents over the Bering Land Bridge (BLB) in the northern Pacific (Milne, 2006) (Fig. 4). However, the direction of migration is not certain either.

The distribution of *Itea rhamnoides*, which is distributed in southern Africa, is indeed somewhat peculiar. Because it is a transition between the evergreen and deciduous groups, it may belong to a unique clade adapted to the seasonal dry environment of the savannas in tropical Africa. Hermsen (2013) also suggested that the extinct *I. europaea* could possibly be the precursor to *I. rhamnoides*.

4.3. Implications from Wenshan fossils

The *Itea* leaf fossils from the Oligocene Wenshan flora in this study are the oldest occurrence of the genus in East Asia. These are the second confirmed leaf fossils of the genus. The *Itea* leaf fossils are morphologically similar to extant *I. omeiensis* of the Sect. *Sempervirentes*. This fossil record shows that at least in the Oligocene the evergreen *Itea* was present in southwestern China, which is the center of diversity of the genus today. Moreover, there are many other extant taxa in the Oligocene Wenshan flora that also have the center of diversity in the South East Asia today, such as Fagaceae, Lauraceae, *Calocedrus* Kurz (Zhang et al., 2015), *Exbucklandia* R.W. Br (Huang et al., 2017), *Ficus* L. (Huang et al., 2018a), *Mahonia* Nutt (Huang et al., 2016a), *Burretiodendron* Rehder (Lebreton-Anberrée et al., 2015), and the evergreen *Ulmus* L. (Zhang et al., 2018). Thus, this flora may indicate at least an Oligocene origin for the East Asian flora.

The possible Oligocene origin for the East Asian flora, of which our fossil finding is an example, supports the 'Tertiary North Hemisphere broad-leaved evergreen forest' hypothesis (Milne and Abbott, 2002). However, the timing of the development of this biome on different continents may be problematic. According to previous research, some angiosperm taxa endemic to or present in eastern Asia today have a more ancient record in Europe and North America. Manchester (1999), Tiffney and Manchester (2001), Manchester et al. (2009) suggested that East Asia may be a refugium for some formerly more widespread genera rather than a center of origin. Hermsen (2013) also expressed similar views, namely that *Itea* fits this pattern and should have appeared much later in eastern Asia than in North America or Europe.

However, many fossil flora from the Eocene to Oligocene in southern China (including Wenshan) that have been found and studied in recent years have similar chronological appearances and taxa composition (Shi et al., 2014; Spicer et al., 2014; Quan et al., 2016; Herman et al., 2017; Jin et al., 2017; Linnemann et al., 2018), such as the evergreen Fagaceae (Huang et al., 2018b; Liu et al., 2019), *Liquidambar* L. (Kodrul et al., 2018), and *Camellia* L. (Huang et al., 2016b). The geological record of forest flora in East Asia may be much older than previously thought (Linnemann et al., 2018). Therefore, many Tertiary relict taxa have been found in Eocene North America and Europe may not necessarily reflect the origin area.

Although the phylogeny of genus *Itea* has not been updated, the presence in East Asia of all the different types of groups of the genus (terminal/axillary inflorescence, half-superior/inferior ovary) suggest that East Asia is probably a center of paleoendemism. The origin of the genus may have been in the paleotropics, which were widely spread throughout the Northern Hemisphere during the Paleogene, possibly by the 'Malpighiaceae route' (Davis et al., 2002; Jia et al., 2019).

The ecological breadth of *Itea* is quite extensive. It grows well not only in the understories of tropical rain forests, evergreen broad-leaved forests, and even temperate deciduous forests (Jin and Ohba, 2001), but it is often the dominant species in the shady small tree layer. Moreover, it is also very competitive in open habitats, and often becomes the dominant species in rocky areas in southeastern Africa (e.g., *I. rhamnoides*) (Van Wyk and Van Wyk, 2013) and in karst areas of southwestern China (e.g., *Itea yangchunensis* S. Y. Jin and *I. yunnanensis*) (Fang et al., 2011). Trait variations in *Itea* may have given these plants the ability to adapt the change of environment in East Asia, Africa and North America.

5. Conclusion

This study describes a new fossil species, *Itea polyneura* J. Huang et Y.M. Tian sp. nov. The genus has a worldwide disjunct distribution with the center of diversity in eastern Asia. *I. polyneura* bears a close morphological resemblance to the extant species *I. omeiensis*, which is distributed in southeastern China. The fossil is the first determinate leaf fossil and the oldest record of *Itea* in East Asia and Eurasia. It provides evidence that *Itea* appeared in the East Asian subtropical forests by the early Oligocene. As an example, it shows that the East Asian flora may have an older origin and could be a center of paleoendemism.

Author Contributions

YMT and JH conceived and designed the study, performed the analysis, made the visualization and wrote the manuscript. All authors conducted the field surveys, collected the samples, reviewed and approved the manuscript.

Declaration of competing interest

There is no possibility of a potential conflict of interest.

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