



FRAXINUS L. (OLEACEAE) FRUITS FROM THE EARLY OLIGOCENE OF SOUTHWEST CHINA AND THEIR BIOGEOGRAPHIC IMPLICATIONS

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Wu, M.-X., Huang, J., Su, T., Zhou, Z.-K., Xing, Y.-W. (2022): *Fraxinus* L. (Oleaceae) fruits from the early Oligocene of Southwest China and their biogeographic implications. – *Fossil Imprint*, 77(2): 287–298, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Two new fossil taxa of the ash tree, namely *F. zlatkoi* MENG-XIAOWU et J.HUANG sp. nov. and *Fraxinus* cf. *honshuensis* TANAI et ONOE were reported from the early Oligocene of the Lühe flora, Yunnan Province, Southwest China. The fruit traits were used to assign the proposed species to the genus *Fraxinus*. These traits were a flattened and symmetrical shape, a single seed located in the base of the fruit and veins parallel to the long axis of each fruit. The new species have low length to width ratio and an obovate seed. Our fossils represent the oldest records of *Fraxinus* in the low latitude region of the Northern Hemisphere. These fossils provide evidence that Section *Dipetalae* and Section *Ornus* had appeared in Southwest China by the early Oligocene.

Key words: *Fraxinus*, fruit, Oligocene, Yunnan, plant diversity, ash tree, biogeography

Received: April 28, 2021 | Accepted: October 11, 2021 | Issued: February 18, 2022

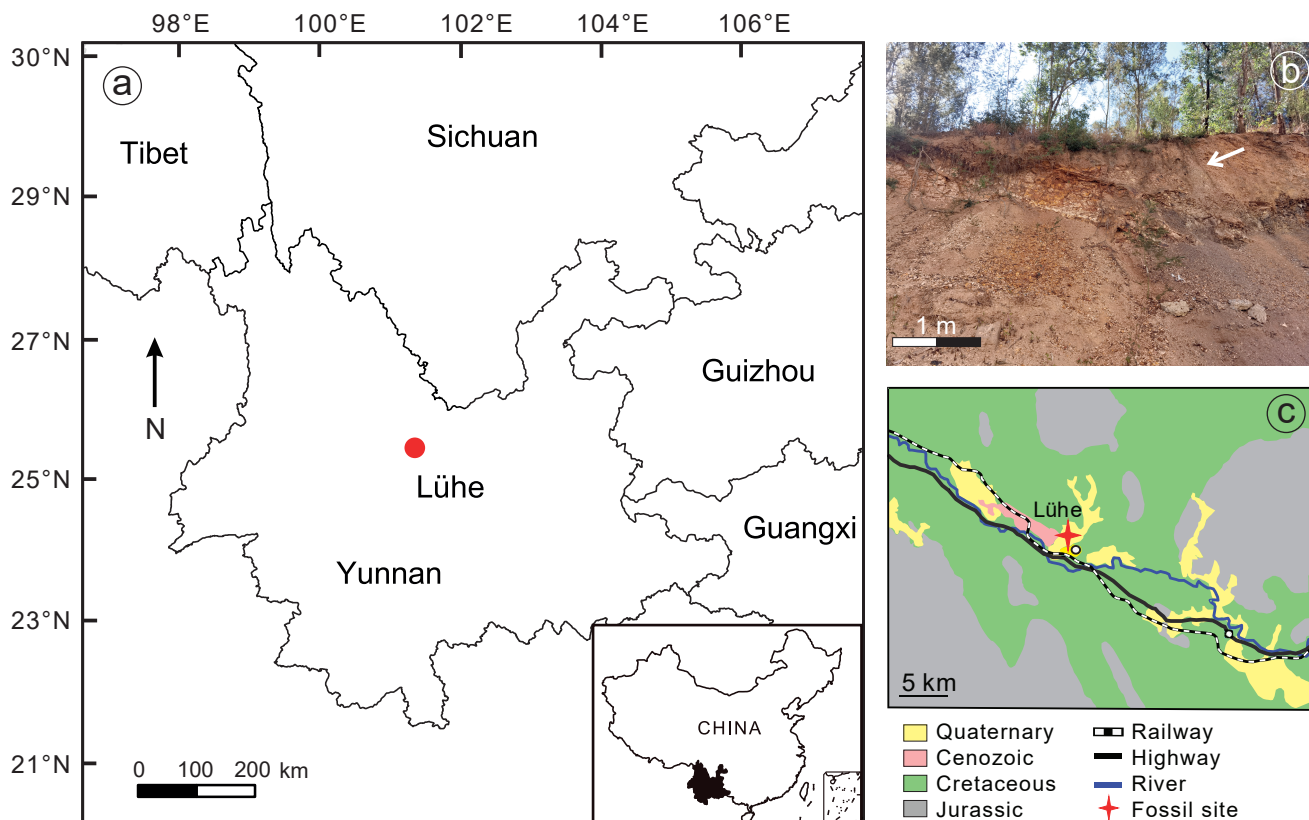
Introduction

The ash tree, *Fraxinus* L. (Family: Oleaceae) is widely distributed in the North Hemisphere. Most of the species occur in the temperate and subtropical middle latitudes, but a few are present in the lower latitudes of tropical regions, such as the tropics of Cuba, Central America, the Philippines and Java (Besnard et al. 2009, Hinsinger et al. 2013). The species *F. griffithii* C.B. CLARKE even extends into the South Hemisphere (Backer and Backhuizen 1965). *Fraxinus* are deciduous, rarely evergreen trees or shrubs, which grow in a range of habitats, from sea level to subalpine elevations (Hinsinger et al. 2013). Species of *Fraxinus* possess complete (with two or four petals), incomplete (no corolla, stamen or pistil), or naked flowers (Hinsinger et al. 2013). Taxonomists have described 40 to 65 living species (The plant list (<http://www.theplantlist.org/>), Sun 1985, Jeandroz et al. 1997). The living species have been assigned to six sections on the basis of phylogenetic studies (Jeandroz et al. 1997, Wallander 2008, Hinsinger et al. 2013). Consensus has not been obtained on the names of each section and the phylogenetic position of several species. In the recent phylogeny of Hinsinger et al. (2013), 43 species were assigned to six sections, i.e., the sections *Dipetalae*,

Pauciflorae, *Ornus*, *Sciadhanthus*, *Melioides* and *Fraxinus*. In this study, we follow this system.

Based on phylogenetic analyses, *Fraxinus* originated in North America, during the Eocene (Jeandroz et al. 1997, Wallander 2008, Hinsinger et al. 2013). The species of Sect. *Melioides* and Sect. *Ornus* were assumed to have migrated from North America to Asia via the Pacific track (Hinsinger et al. 2013). However, fossil records reflect a more complex biogeographic history and more extensive historical distribution regions (Leroy and Roiron 1996, Kvaček and Walther 1998, Grímsson et al. 2007). Fossils of Sect. *Ornus* appeared in North America and Asia at the same time, namely in the early Oligocene epoch (Axelrod 1998, this study). These records challenged the dispersal history inferred in phylogenetic studies. Due to vicariance and extinction events, it would be difficult to rely solely on phylogenetic analyses of extant species to explain the biogeography of *Fraxinus*.

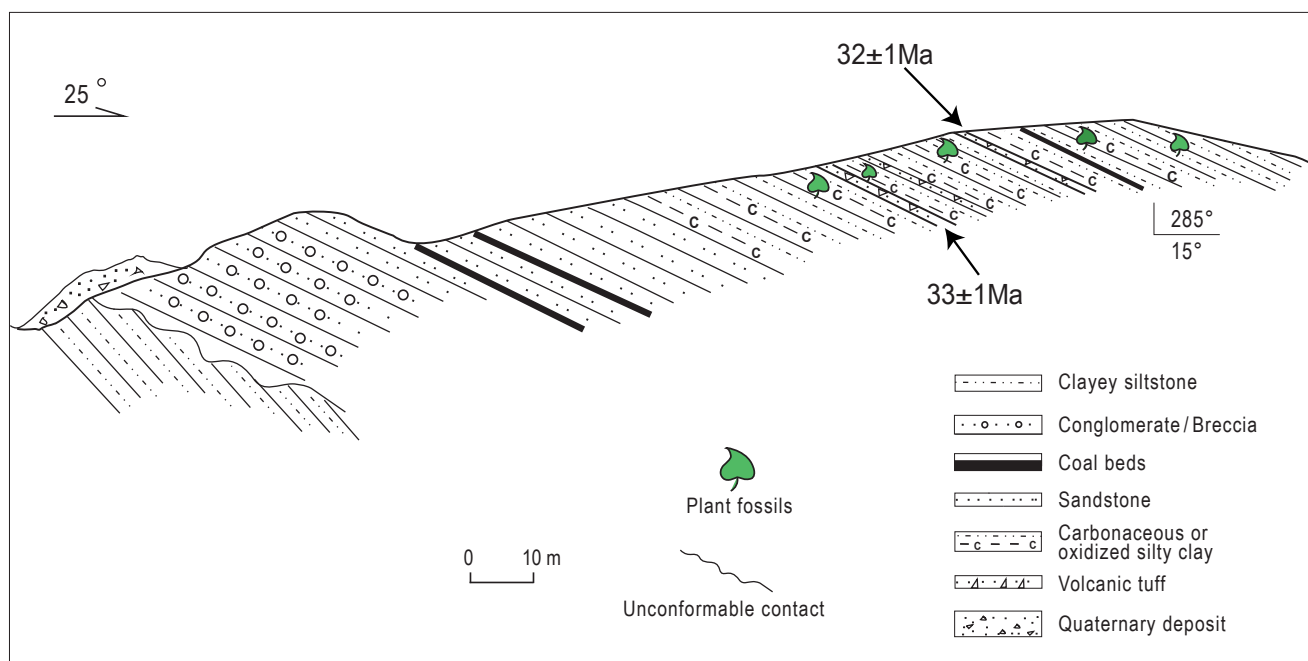
Fraxinus leaves are highly variable in terms of leaf organization, size and shape. In contrast, fruits show more structural consistency, are easily recognized and hence more reliably determined to the generic level in the fossil record. *Fraxinus* fruits are flattened and symmetrical with a single ellipsoidal seed located at the base of a prominent elongate wing, with veins extending parallel to the long axis of the



Text-fig. 1. Location of the study site. a: the location of Lühe Town, Yunnan, SW China; b: fossil bearing section, white arrow indicates the fossil collection stratum; c: geological map of fossil site.

wing. This structure of *Fraxinus* fruits appears to slow their speed of descent and increase the likelihood of dispersal by wind (Green 1980). This process would ultimately facilitate the dispersal of the species over large distances, given sufficient time and a suitable environment (Augsburger 1986). The oldest macrofossils of *Fraxinus* were fruits reported from

the early Eocene strata in California, USA (MacGinitie 1941). Fossil fruits have also been discovered in middle Eocene strata in North America, while leaves have been discovered in strata in East Asia (WGPC 1978). Numerous leaves and fruits have also been reported from Neogene strata at a number of localities in the North Hemisphere (Wang et al. 2012).



Text-fig. 2. Geological cross section of the outcrop in Lühe Town, Yunnan, SW China.

Fraxinus fossils are abundant in sediments from localities at middle latitudes, which coincides with the distribution of most living species. Records from low latitude localities are rare (Wang et al. 2012). *Fraxinus* cf. *honshuensis* from the late Miocene of Lincang, Yunnan, Southwest China is the only reliable published record of *Fraxinus* from a low latitude, outside the core area referred to above (Wang et al. 2012). The lack of pre-Miocene fossil material in the lower latitudes has limited our understanding of the biogeography, diversification and evolutionary history of this genus.

Description of fruit impressions of two *Fraxinus* species, including one new species, from the early Oligocene Lühe flora, Yunnan Province, Southwest China, has been presented in this paper. They represent the oldest fossil records of *Fraxinus* from a lower latitude and shed new insights on the radiation and diversification of *Fraxinus*.

Materials and methods

Geological setting

The new species described herein are from a fossil site is located in Lühe Town (25°08.5' N, 101°22.5' E, 1,890 m a.m.s.l.), Chuxiong Autonomous Prefecture, Yunnan Province, Southwest China (Text-fig. 1a). The lacustrine sediments there are characterized by laminated yellow and dark grey silty mudstone, with several layers of coal and volcanic ash (Text-fig. 1b, c). The intercalated thin coal beds are lithostratigraphically correlated with the nearby open cast coal mine (Chuxiong Lühe Coal Industry Co., Ltd.). *Sequoia* branchlets, Taxodiaceae wood and rhizomes have been found at the coal mine (Ma et al. 2000, Yi et al. 2005, Zhang et al. 2007, Linnemann et al. 2017). The U-Pb zircon ages for the volcanic ash beds range from 33 ± 1 to 32 ± 1 Ma (Linnemann et al. 2017; Text-fig. 2). This age has been corroborated by $^{40}\text{Ar}/^{39}\text{Ar}$ dating of stratigraphically comparable volcanic ashes exposed in the nearby open cast coal mine (Li et al. 2020). More than 3,000 plant fossil specimens were collected at Lühe Town by the Palaeoecology Research Group, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences from 2016 to 2020. Fossil materials included four *Fraxinus* fruit specimens used as the basis for the present study. Several species in the flora have already been published such as *Cryptomeria*, *Tsuga*, *Dipteronia* and *Ostrya* (Ding et al. 2018a, b, Wang et al. 2019, Wu et al. 2019).

Morphological investigation

A Nikon D850 digital camera was used to take photos of the fossils and living specimens. Detailed structures of these specimens were observed and photographed with a Zeiss Smartzoom 5, a Leica S8APO stereo microscope and Zeiss Xradia 410 versa X-ray microscope. The fossil morphology was described following Call and Dilcher (1992). Fruit fossil records with clear figures or descriptions were compiled for comparison. Fossils were compared with extant specimens in the herbarium at the Kunming Institute of Botany (KUN), U. S. Forest Service Herbarium (USFS), Royal Botanic Garden Kew (K), Rancho Santa Ana Botanic Garden (RSA). Based on morphological similarity with fossils and the number of specimens available in the herbarium, two species were

selected for each section. Five to ten fruits of each species have been measured by ImageJ software (Version 1.52a; Wayne Rasband, National Institutes of Health, USA). In most *Fraxinus* species, seed shape observed by digital camera and X-ray Microscopy are similar to each other (Text-fig. 5b, c). In some species, the fruit twists and there is an air sac above the seed so the in the digital camera pictures we measured the seed length plus the air sac length (Text-fig. 5a). Since the fossils were preserved only as impressions, and were not investigated by X-ray, our estimates of seed length might include also the air sac length.

New name of plant fossil is registered in the Plant Fossil Names Registry, which is hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP), each with a unique PFN number.

Systematic palaeobotany

Order Lamiales BROMHEAD, 1838

Family Oleaceae HOFFMANNS. et LINK, 1809 nom. cons.

Genus *Fraxinus* L., 1753

Fraxinus zlatkoi MENG-XIAO WU et J.HUANG sp. nov.

Text-fig. 3a–e, l, m

H o l o t y p e . XTBGPC-LH3-0341 (Text-fig. 3a, b).

P a r a t y p e . XTBGPC-LH3-1138 (Text-fig. 3d).

P l a n t F o s s i l N a m e s R e g i s t r y N u m b e r . PFN002614.

R e p o s i t o r y . Fossils are deposited in Palaeoecology Collections, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences, Menglung, China.

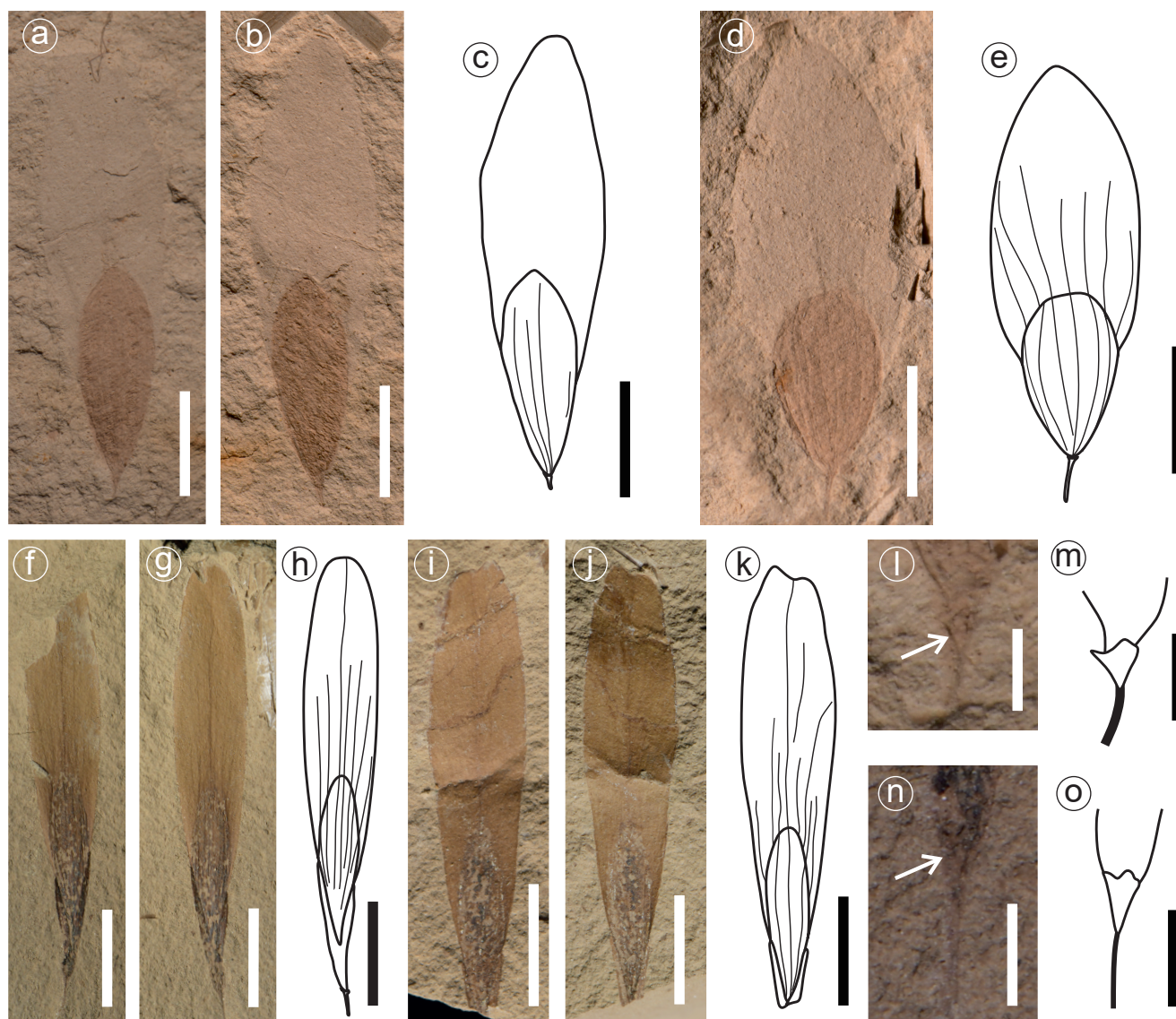
E t y m o l o g y . The specific epithet “*zlatkoi*” refers to the palaeobotanist Prof. Zlatko Kvaček recognizing his significant contributions to long-term research on the floras of the Cenozoic.

T y p e l o c a l i t y . Lühe Town, Chuxiong, Yunnan Province, China (25°08.5' N, 101°22.5' E).

A g e . 33 ± 1 to 32 ± 1 Ma (Rupelian stage, Oligocene).

D i a g n o s i s . Fruit a samara, flattened, symmetrical, one seed located in the base, veins parallel to the long axis, length to width ratio of fruit 2.5–3.4 : 1; seed obovate, symmetric.

D e s c r i p t i o n . Fruits samaras elliptic, symmetric, 16–19 mm long, 5–6 mm wide at the broadest point (Text-fig. 3a–e), length to width ratio 2.5–3.4 : 1. Pedicel short, 1.0 mm long, 0.1 mm wide. Calyx hypogynous, persistent, campanulate, cupping fruit base (Text-fig. 3l, m). Two calyx teeth visible, fused at base, apices acute, 0.4–0.6 mm long and 0.8 mm wide. Fruit body flattened in the plane of the wing. Wing decurrent, flattened, entire margin, attached to the apex of fruit body and clasping its lateral margins nearly to middle, the widest part in the middle of fruit. Two carpel ventral sutures united to form midvein, stigmas or stylar remnant not visible. Wing apex symmetric, rounded with eight veins visible parallel to the long axis of the fruit, extending from the base of the fruit to its apex (Text-fig. 3d).



Text-fig. 3. Fossil fruits of *Fraxinus*: photos and drawings. a–e: *F. zlatkoi* MENG-XIAO WU et J. HUANG sp. nov., a–c – the holotype image and its line drawing (XTBG-PC-LH3-0341), d, e – paratype image and its line drawing (XTBGPC-LH3-1138); f–k: *Fraxinus* cf. *honshuensis* TANAI et ONOE, f–h – XTBG-PC-LH2-0111, i–k – XTBG-PC-LH1-0578; l, m: enlargement of (b) and its line drawing; n, o: enlargement of (g) and its line drawing. Arrows in (i) and (n) refer to the calyxes. Scale bars = 5 mm for a–k, scale bars = 1 mm for i–o.

One seed located in the base of fruit, obovate, symmetric (Text-fig. 3a–e), 6–9 mm long, 3–4 mm wide. Fruit length 2.1–2.5 times longer than the seed. seed base cuneate, apex rounded or obtusely rounded with pointed apex; long axis parallel to the long axis of fruit.

***Fraxinus* cf. *honshuensis* TANAI et ONOE, 1961**

Text-fig. 3f–k, n, o

Specimens checked. XTBGPC-LH2-0111 (Text-fig. 3f, g), XTBGPC-LH1-0578 (Text-fig. 3i, j).

Description. Fruits samaras, long obovate, symmetric, 21 mm long and 3–4 mm wide at the broadest point (Text-fig. 3f–k), length to width ratio 6:1. Pedicel short and 1.0 mm long. Calyx hypogynous, persistent, campanulate, cupping base of fruit body. Two calyx teeth fused at base, apices acute, 1.0 mm long and 0.5 mm wide (Text-fig. 3n, o). Fruit body flattened in the plane of the

wing. Wing decurrent, flattened, entire margin, attached to the apex of fruit body and clasping its lateral margin nearly to base, widest at the apical half of fruit. Wing apex symmetric or extension asymmetric, emarginate or rounded (Text-fig. 3f–k). Stigmas or styler remnant not visible, 9–11 veins visible parallel to the long axis of the fruit, central vein thick (Text-fig. 3h, k), extending from the fruit base to its apex. One seed located in the base of fruit, spindle, symmetric, 7–8 mm long and 2 mm wide, the ratio of fruit length to seed length 2.6, base and apex acuminate; long axis parallel to long axis of fruit (Text-fig. 3h, k).

Discussion

Systematics of the fossil species

The morphology of the fossil material described in this study is similar to symmetric single-winged fruits of four



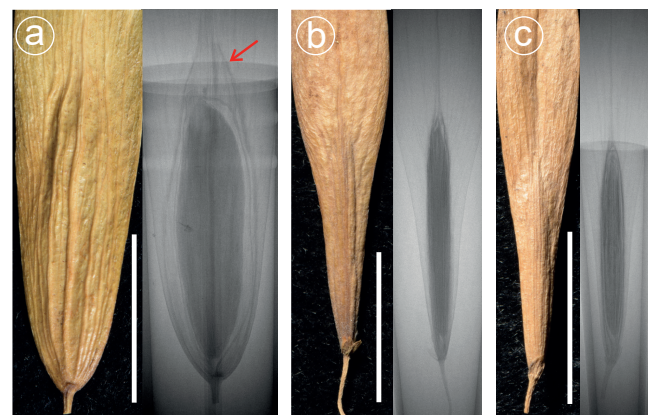
Text-fig. 4. Extant *Fraxinus* fruits and other groups with similar fruits. a: *Ventilago leiocarpa* BENTH. (KUN 06190258); b: *Liriodendron chinense* (HEMSL.) SARG. (KUN 0040571); c: *Plenckia populnea* REISSEK (K 000537359); d: *Fraxinus nigra* MARSHALL (KUN 0937878); e: *F. anomala* TORR. ex S.WATSON (RSA 0064862); f: *F. gooddingii* LITTLE (USFS 0030124); g: *F. platypoda* OLIV. (KUN 0027753); h: *F. malacophylla* HEMSL. (K 000901679); i: *F. chinensis* ROXB. (KUN 0027530). Scale bar = 1 cm.

extant genera, namely *Ventilago* GAERTN. (Rhamnaceae), *Liriodendron* L. (Magnoliaceae), *Plenckia* REISSEK (Celastraceae) and *Fraxinus* (Oleaceae) (Text-fig. 4a–d). The seed of *Ventilago* (Text-fig. 4a) is globose with 1/3–1/2 of the base surrounded by a persistent calyx tube and hence different to the Lühe fossils. The fruit of *Liriodendron* does not possess a persistent pistil, nor pedicel, and its seed is thin, elliptical and relatively small, with the seed length accounting for less than 1/5 of the whole length of the fruit (Text-fig. 4b). *Plenckia* is similar to the Lühe fossils in fruit type and seed shape, yet the veins of *Plenckia* fruit are not parallel to the central vein (Text-fig. 4c), in contrast to the parallel veins of *Fraxinus* fruit. In addition, the calyx lobes of *Plenckia* are reflexed, whereas those of *Fraxinus* clasp the base of the fruit (Call and Dilcher 1992). Our fossils are characterized by symmetric fruits, obovate, or spindle seed shapes, with veins parallel to the midvein.

Within *Fraxinus*, the flowers of species in the Sect. *Fraxinus* have no calyx except *F. nigra* MARSHALL (Text-fig. 4d), while species in the other five sections have persistent calyx (Hingsinger et al. 2013). Two North American sections (viz. Sect. *Dipetalae* and Sect. *Pauciflorae*; Text-fig. 4e, f) have relatively smaller and wider fruits (Tab. 2). Fruits are relatively short (length to width ratio lower), in these two sections, compared to the fruits of other sections. There is morphological character overlap in Sect. *Ornus*, Sect. *Melioides* and Sect. *Sciadanthus*. The seeds of these three sections are elliptical, with the fruits ovate, obovate, or elliptical. The fruit length to width ratio and fruit length to seed length ratio of Sect. *Sciadanthus* are close to Sect. *Ornus*, but the fruits of Sect. *Sciadanthus* are usually 10–

20 mm bigger than those of Sect. *Ornus* (Tab. 2). Fruit size of Sect. *Melioides* and Sect. *Sciadanthus* are close to each other, but their fruit length to width ratio is different. Sect. *Melioides* has the highest fruit length to width ratio in *Fraxinus* and the ratio is 0.63–1.96 more than that of Sect. *Sciadanthus* (Tab. 2). We used these features to assign our fossils, and some of those previously described in the literature, to extant sections.

The two species from Lühe town can easily be distinguished by fruit width and seed shape. *F. zlatkoi* possesses relatively wider fruit among fossils, with



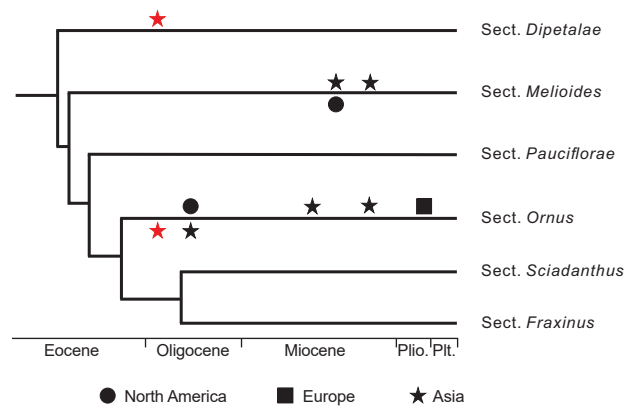
Text-fig. 5. Extant *Fraxinus* fruits photographed by digital camera and X-ray microscopy. a: *F. excelsior* L. (Sect. *Fraxinus*); b: *F. xanthoxyloides* WALL. (Sect. *Sciadanthus*); c: *F. malacophylla* HEMSL. (Sect. *Ornus*). Red arrow refers to the air sac above seed, scale bars = 1 cm.

Table 1. Selected fossil records of *Fraxinus* fruits with localities and ages.

Age	Locality	Taxa	NLR(s)	Section	Fruit size (length × width; mm)	Seed size (length × width; mm)	Fruit length/ seed length	Reference
Early Eocene	Quilchena locality, British Columbia, Canada	<i>Fraxinus eomarginata</i> MATHEWES, S.B.-ARCHIBALD et A.-LUNDGREN	not certain	not certain	(12.0–29.5) × (3.1–6.8)	5.6–17.1	1.7–2.1	Mathewes et al. 2021
Middle Eocene	western Tennessee, USA	<i>F. wilcoxiana</i> E.W.BERRY	not certain	not certain	(18.0–31.0) × (3.5–9.0)	(11.0–15.0) × (3.0–4.8)	1.6–2.1	Call and Dilcher 1992
Early Oligocene	Lühe, Yunnan, China	<i>F. zlatkoi</i> MENG-XIAO WU et J.HUANG sp. nov.	<i>F. anomala</i> TORR. ex S.WASTON	<i>Dipetalae</i>	(16.2–21.6) × (5.8–6.2)	(6.4–10.6) × (3.7–3.9)	2.1–2.5	This study
Early Oligocene	Lühe, Yunnan, China	<i>Fraxinus</i> cf. <i>honsuensis</i> TANAI et ONOE	<i>F. malacophylla</i> HEMSLE.	<i>Ornus</i>	(19.2–22.5) × (4.0–4.2)	(6.7–8.1) × (2.0–2.2)	2.6	This study
Early Oligocene	Kundratice, North Bohemia, the Czech Republic	<i>Fraxinus</i> sp.	not certain	not certain	35.0 × 5.0	14.1 × 3.3	2.5	Kvaček and Walther 1998
Early Oligocene	Bridge Creek, Oregon, USA	<i>Fraxinus</i> sp.	not certain	not certain	(23.0–25.0) × 6.0	(12.0–15.0) × (3.5–4.0)	1.7–2.0	Meyer and Manchester 1997
Middle Oligocene	Haynes Creek, Idaho, USA	<i>F. stenocarpa</i> AXELROD	<i>F. chinensis</i> ROXB.	<i>Ornus</i>	25 × 3.0	8.8 × 2.1	2.8	Axelrod 1998
Late Oligocene	Beaverhead, Montana, USA	<i>F. brevitata</i> H.F.BECKER	not certain	not certain	15.0 × 3.3	8.5 × 1.3	1.8	Becker 1969
Late Oligocene	Beaverhead, Montana, USA	<i>F. rupinarum</i> H.F.BECKER	not certain	not certain	14.5 length	not certain	not certain	Becker 1969
Oligocene	Mormon, Montana, USA	<i>F. yubaensis</i> MACGINTIE	not certain	not certain	20.0 × (3.5–4.5)	6.0 × 2.0	3.3	Becker 1960
Oligocene	Longjing, Jilin, China	<i>F. honsuensis</i> TANAI et ONOE	<i>F. chinensis</i> subsp. <i>rhyngo-phylla</i> (HANCE) A.E.MURRAY	<i>Ornus</i>	20.0 × 4.0	8.0 × 2.0	2.5	Guo and Zhang 2002
Early Miocene	Maguan, Yunnan, China	<i>Fraxinus</i> sp.	not certain	not certain	(22.3–27.8) × (3.8–6.3)	(8.0–11.0) × (3.8–6.3)	2.5–2.8	Jia 2017
Early Miocene	Güvem, Anatolia, Turkey	<i>Fraxinus</i> sp.	not certain	not certain	23.0 × 5.0	not certain	not certain	Denk et al. 2017
Middle Miocene	Shanwang, Shandong, China	<i>F. dayana</i> R.W.CHANEY et AXELROD	<i>F. platypoda</i> OLIV.	<i>Meloides</i>	(45.0–60.0) × (9.0–11.0)	13–16 length	3.5–3.8	WGCP 1978; Yang and Yang 1994
Middle Miocene	Shanwang, Shandong, China	<i>F. microcarpa</i> GENG	not certain	not certain	(30.0–35.0) × 5.0	10–11 length	3.0–3.2	WGCP 1978; Yang and Yang 1994
Middle Miocene	Samakesaroma, Hokkaido, Japan	<i>F. honsuensis</i> TANAI et ONOE	<i>F. longicauspis</i> SEEBOLD et ZUCC.	<i>Ornus</i>	(21.0–22.0) × (4.0–7.0)	11.0 × 0.3	2.0	Tanai and Suzuki 1965
Middle Miocene	Pohang, South Korea	<i>F. oishii</i> HUZIOKA	not certain	not certain	(20.0–22.0) × (5.0–6.0)	12.0 × (4.0–5.0)	1.7	Huzioka 1972
Middle Miocene	Pohang, South Korea	<i>F. oishii</i> HUZIOKA	not certain	not certain	(27.0–36.0) × (7.0–10.0)	(12.0–20.0) × (5.0–7.0)	1.8–2.3	Jung and Lee 2009
Middle Miocene	Pohang, South Korea	<i>Fraxinus</i> sp.	not certain	not certain	33.0 × 5.0	9.0 × 3.0	3.7	Jung and Lee 2009
Middle Miocene	Tafla, Ketilsyri, Iceland	<i>Fraxinus</i> sp.	not certain	not certain	20.0 × 3.5	3.4 × 9.0	5.9	Grimsson et al. 2007
Middle Miocene	Middlegate Basin, Nevada, USA	<i>F. coulteri</i> DORF	not certain	not certain	not certain	8.0 × 2.2	not certain	Axelrod 1985
Late Miocene	Lincang, Yunnan, China	<i>F.</i> cf. <i>honsuensis</i> TANAI et ONOE	<i>F. chinensis</i> subsp. <i>rhyngo-phylla</i> (HANCE) A.E.MURRAY	<i>Ornus</i>	(19.8–20.7) × (3.7–4.3)	(8.1–9.2) × (1.1–1.9)	2.3–2.4	Wang et al. 2012

Table 1. continued.

Age	Locality	Taxa	NLR(s)	Section	Fruit size (length × width; mm)	Seed size (length × width; mm)	Fruit length/ seed length	Reference
Late Miocene	Shanabuchi, Hokkaido, Japan	<i>F. k-yamadai</i> TANAI et N.SUZUKI	<i>F. americana</i> L.	<i>Melioides</i>	43.0 × 9.0	28.0 × 4.0	1.5	Tanai and Suzuki 1965
Late Miocene	Southwest Honshu, Japan	<i>F. k-yamadai</i> TANAI et N.SUZUKI	<i>F. platypoda</i> OLIV. <i>F. latifolia</i> BENTH.	<i>Melioides</i>	49.7 × 17.2	not certain	not certain	Ozaki 1980
Late Miocene	Owyhee, Idaho, USA	<i>F. coulteri</i> DORF	not certain	not certain	30.0 × (4.0–5.0)	not certain	not certain	Buechler et al. 2007
Late Miocene	Owyhee, Idaho, USA	<i>F. dayana</i> R.W.CHANEY et AXELROD	not certain	not certain	36.0 × 8.0	not certain	not certain	Buechler et al. 2007
Miocene	Thorn Creek, Idaho, USA	<i>F. leptocarya</i> H.V.SM.	not certain	not certain	(16.0–19.0) × (3.0–4.5)	not certain	not certain	Smith 1941
Miocene	Potlatch Creek, Idaho, USA	<i>Fraxinus idahoensis</i> R.W.BR.	<i>F. platypoda</i> OLIV.	<i>Melioides</i>	39.0 × 8.0	18.0 × 6.0	2.2	Brown 1935
Miocene	Kudo, Hokkaido, Japan	<i>F. wakataniensis</i> TANAI et N.SUZUKI	not certain	not certain	not certain	6.6 × 2.0	not certain	Tanai and Suzuki 1972
Miocene	Noroshi, Noto peninsula, Japan	<i>F. honshuensis</i> TANAI et ONOE	<i>F. chinensis</i> subsp. <i>rhynchophylla</i> (HANCE) A.E.MURRAY	<i>Ornus</i>	(21.0–26.0) × (4.0–5.5)	(8.0–14.0) × (2.0–2.5)	1.9–2.6	Ishida 1970
Late Pliocene	Bernasso, France	<i>F. ornus</i> L.	<i>F. ornus</i> L.	<i>Ornus</i>	20.0 × 4.5	not certain	not certain	Leroy and Roiron 1996



Text-fig. 6. Stratigraphic and phylogenetic placement inferred for fossil *Fraxinus* fruits. Only *Fraxinus* fossil fruits identified on the section level are included. The black color represents selected fossil fruits from published literature (excluding some Eocene North American occurrences not assigned to section), the red color represents the fossil fruits from the Lühe flora, Yunnan, Southwest China. The phylogenetic relationships are based on Hinsinger et al. (2013).

a width close to that of *F. oishii* HUZIOKA, from the Middle Miocene of South Korea. However, the fruit length to seed length ratio of *F. oishii* is lower. In addition, the *F. zlatkoi* seed is obovate while *F. oishii* seed is rhombic or ellipsoidal.

The fruit and seed size, the ratio of fruit length to seed length of the second species described above, coincides closely with *Fraxinus honshuensis*. This fossil species is common in the Oligocene to late Miocene fossil records of East Asia. *F. japonica* BLUME ex KOCH (synonym of *Fraxinus chinensis* subsp. *rhynchophylla* (HANCE) A.E.MURRAY; Text-fig. 4i) has been widely accepted as the nearest living relative of *F. honshuensis* (Ishida 1970, Guo and Zhang 2002, Wang et al. 2012). However, *F. chinensis* ROXB. has the longest calyx of the genus (2–3 mm) (Flora of China, <http://www.iplant.cn/frps>), which is much longer than the fossil species (1 mm). *F. chinensis* also has bigger fruit and seed than the fossil species. In terms of extant species, we found that *F. malacophylla* HEMSL. (Text-fig. 4h) is the most similar to *F. cf. honshuensis* from Lühe, in terms of fruit size, fruit shape, fruit length to width ratio, fruit length to seed length ratio and calyx length (Tab. 2).

Fraxinus cf. honshuensis from Lühe is similar to previously published records of *F. honshuensis* in fruit and seed shape (including length to width ratio), but it is smaller than *F. honshuensis* from the Oligocene of Longjing, Jilin, China, Miocene of Noto Peninsula, Japan and Miocene of Hokkaido, Japan (Ishida 1970, Tanai and Suzuki 1972, Guo and Zhang 2002). It resembles *F. cf. honshuensis* from the middle Miocene of Lincang, Southwestern China (Wang et al. 2012; Tab. 1).

According to the special characters of the new fossil species, the nearest living relatives (NLR) were inferred. The length to width ratio of *F. zlatkoi* fruit is 2.5–3.4 : 1, which is different from most living species (viz. 3.3–7.9 : 1; Tab. 2), but close to *F. anomala* TORR. ex S.WASTON (Text-fig. 4e). This species possesses obovate seeds similar to our fossils, but the fruit of *F. anomala* is smaller than that of the *F. zlatkoi*.

Table 2. Measurements of selected living species (mm). Abbreviations: FL/FW = fruit length/fruit width; SL/SW = seed length/seed width; FL/SL = fruit length/seed length.

Section	Species	Number of specimens	Fruit length	Fruit width	FL/FW	Seed length	Seed width	SL/SW	FL/SL
<i>Dipetalae</i>	<i>F. anomala</i>	10	16.0–25.8	6.4–7.2	2.3–3.6	9.1–17.1	3.6–5.1	2.0–3.3	1.4–1.8
	<i>F. dipetala</i>	5	21.0–27.1	5.0–7.1	3.6–4.3	11.0–16.9	4.2–5.0	2.6–3.5	1.5–1.9
<i>Melioides</i>	<i>F. americana</i>	6	28.2–42.5	3.7–5.4	6.0–7.9	10.0–13.7	1.9–3.7	3.7–7.2	2.1–3.1
	<i>F. platypoda</i>	5	54.0–60.5	8.3–11.3	5.1–6.5	23.9–29.2	6.0–7.5	3.4–4.3	2.0–2.4
<i>Pauciflorae</i>	<i>F. purpusii</i>	10	19.3–24.3	4.6–5.8	3.3–4.5	6.9–12.0	2.6–3.8	2.6–4.0	1.9–2.8
	<i>F. goodingii</i>	6	15.0–17.7	3.1–3.9	4.2–4.8	5.9–7.6	1.2–2.1	3.1–6.2	2.2–2.5
<i>Sciadanthus</i>	<i>F. hubeiensis</i>	5	39.1–45.3	8.3–9.5	4.5–4.8	14.3–16.3	3.9–4.2	3.6–4.2	2.5–2.9
	<i>F. xanthoxyloides</i>	5	28.2–31.4	5.0–6.5	4.8–5.6	12.5–16.0	1.9–2.0	6.0–8.4	1.8–2.6
<i>Fraxinus</i>	<i>F. excelsior</i>	7	25.5–32.0	6.7–7.7	3.4–4.5	14.3–19.5	4.1–6.2	2.7–4.8	1.5–2.1
	<i>F. mandshurica</i>	5	29.4–35.5	7.0–8.3	3.5–4.3	15.2–16.9	4.9–6.2	2.6–3.3	1.8–2.2
<i>Ornus</i>	<i>F. chinensis</i>	5	30.7–34.9	5.5–6.3	4.9–5.8	11.5–13.7	1.6–2.7	5.1–7.8	2.4–2.8
	<i>F. malacophylla</i>	9	19.6–27.0	3.4–5.2	4.3–5.8	6.9–10.6	1.3–2.3	3.8–5.4	2.7–2.9

The *Fraxinus* fruit fossil species and other fossil records with clear figures and/or descriptions were compiled in Table 1. Both species in this study are smaller than contemporary fruits from North America and Europe, where fruits are typically more than 25 mm in length (Axelrod 1998, Kvaček and Walther 1998). *F. yubaensis* MACGINITIE and *Fraxinus* spp. from the Oligocene of Montana and Oregon, USA, are different from our two species in fruit length to seed length ratio (Becker 1960, Meyer and Manchester 1997).

The fruits of two Oligocene species from North America, namely *F. breviaolata* H.F.BECKER and *F. rupinarum* H.F.BECKER have lengths less than 16 mm (Becker 1969). The morphology of fruits from the Miocene is highly variable. *F. k-yamadai* TANAI et N.SUZUKI, *F. dayana* R.W.CHANEY et AXELROD and *F. idahoensis* R.W.BR. possess bigger fruits than those from the Paleogene (Tab. 1). *Fraxinus* sp. from Tafla, Ketilseyri and Iceland show the highest fruit length to seed length ratio of nearly 6 : 1 (Grimsson et al. 2007). *Fraxinus* sp. from Pohang, South Korea, *F. wakamatsuensis* TANAI et N.SUZUKI and *F. microcarpa* GENG also show a ratio greater than 3 : 1 (Tanai and Suzuki 1972, WGCP 1978).

Palaeobiogeographical implications

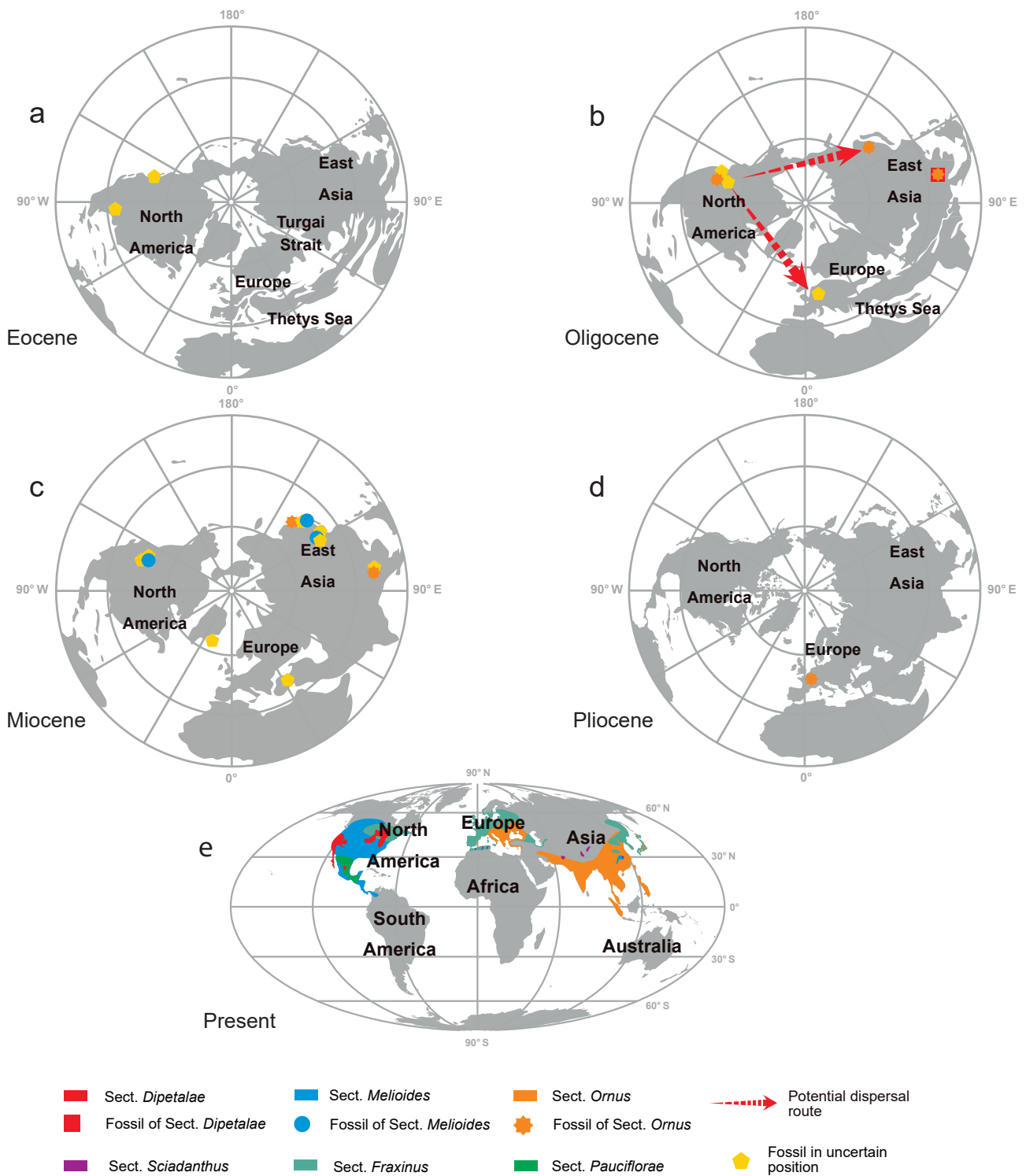
The earliest unequivocal fossil records for *Fraxinus* were reported from the early Eocene of North America (Mathewes et al. 2021). The North America origin of *Fraxinus* was supported by palaeobotanical evidence and biogeographical analysis (Call and Dilcher 1992, Wallander 2008, Hingsinger et al. 2013). This implies that six extant sections had diverged before the Miocene (Call and Dilcher 1992, Hingsinger et al. 2013). Due to the morphological overlap of the sections, the taxonomic affinities of some fossil fruits to NLRs were not designated to species level, there were only a few records with NLR affinities inferred (Tab. 1). The NLRs determined here were inferred mainly by the ratio of fruit to seed length and the ratio of fruit length to width. The fruit characters such as fruit length and width, the ratio of fruit length to seed length denote potential synapomorphy of each section (Tab. 2), making it possible to decide the section of fossil fruit by NLRs. For example, *F. k-yamadai* is 43 × 9 in fruit size

and 28 × 4 in seed size (Tanai and Suzuki 1965); only fruit of Sect. *Melioides* has similar size, thus *F. k-yamadai* was attributed to Sect. *Melioides*.

Leaves and fruits of *Fraxinus* have been reported from North America in the Eocene while reliable fossil records of the genus have not been published in Europe and East Asia until the early Oligocene (Kvaček and Walther 1998, Guo and Zhang 2002). The dispersal of *Fraxinus* fruits is governed by physics instead of the variable and unpredictable movement by animal dispersers, under suitable conditions they can spread about 200 m from the parent tree (Augsperger et al. 2017). Geographic dispersal into Europe and Asia probably involved two main migration routes, namely the Beringia (for Asia) and North Atlantic (for Europe) land bridges (Tiffney 1985, Manchester et al. 2009, Wen et al. 2016). The dispersal of *Fraxinus* into Europe and Asia may have involved both pathways, as the earliest reported occurrence of *Fraxinus* on both continents is Paleogene (Text-fig. 7).

In Europe, Sect. *Fraxinus* (*F. excelsior* L. and *F. angustifolia* VAHL.) is widely distributed, growing throughout the European temperate zone, in contrast to Sect. *Ornus* (*F. ornus* L.). Sect. *Ornus* has a more limited distribution in Mediterranean area in Europe (Hingsinger et al. 2013, San-Miguel-Ayanz 2016). Fossils of Sect. *Ornus* have been reported from the Pliocene of France (Leroy and Roiron 1996). The current narrower distribution of Sect. *Ornus* could be attributed to global cooling in Pleistocene (Zachos et al. 2001, Pérez-Díaz and López-Sáez 2021). The fruit from the Oligocene of Iceland also supported that *Fraxinus* had a wider historical distribution range (Grimsson et al. 2007).

Sect. *Dipetalae* is inferred based on molecular investigations to be the oldest lineage of *Fraxinus* and contains three living species restricted to North America (Hingsinger et al. 2013). *F. zlatkoi* represents the earliest fossil record of the section, which indicates that the section may have migrated to East Asia by the early Oligocene. Sect. *Dipetalae* produces more obovate seeds, which is different from the other sections bearing elliptic seeds. The fruit length to width ratio of Sect. *Dipetalae* is lower than in other sections (Tab. 2). At the same length, the narrower fruits



Text-fig. 7. Distribution maps and potential dispersal routes of *Fraxinus* during the Cenozoic. The maps cover five intervals, namely the Eocene (ca. 40 Ma), Oligocene (ca. 30 Ma) and Miocene (ca. 20 Ma) based on Deep Time Maps (<https://deeptimemaps.com/>) and the Pliocene (ca. 3 Ma) based on the current world map.

are lighter and hence have the potential to spread further (Augspurger 1986, 1988). Compared with obovate seed, elliptic seed falls more slowly, which facilitates dispersal by wind (Augspurger 1986, Wang et al. 2012). The species of Sect. *Dipetalae* therefore possess fruit traits similar to *F. zlatkoi*, but with a distribution restricted to North America. Sect. *Ornus* includes the southernmost species of *Fraxinus*. This section is widely distributed in Asia, North Africa and

the Mediterranean. This section represents the most diverse lineage in Southwest China and Southeast Asia. The section is also the one best represented in terms of the amount of material in the fossil record (Text-fig. 6). *Fraxinus* cf. *honshuensis* discovered from Lühe is the earliest record of this section, which may indicate that Sect. *Ornus* appeared in the Southeast China before the early Oligocene and subsequently spread to the lower latitude region.

Conclusion

Well-preserved fossil fruits of *Fraxinus* were found in the early Oligocene of Lühe, Yunnan Province, Southwest China and two species were identified. *F. zlatkoi* resembles basal species which are distributed in the North America only. While *Fraxinus* cf. *honsuensis* resembles Sect. *Ornus* which is the most widespread lineage of Asia. This finding represents the oldest records of *Fraxinus* in low latitude region of the North Hemisphere, indicating a long persistence of *Fraxinus* in Southwest China since the late Paleogene and southward to the lower latitude region, gradually forming present distribution. The Lühe flora is evergreen deciduous broad leaved mixed forest which is similar to other Paleogene floras in Southwest China. Various wind-dispersed diaspores such as *Acer*, *Cryptomeria*, *Ailanthus*, *Dipteronia*, *Carpinus* and *Ostrya* have been found, reflecting an open environment in the seed ripening season.

Acknowledgements

The authors are grateful to members of the Palaeoecology Research Group at the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences for their assistance with the collection of fossil materials. Staff members at the Public Technology Service Center in XTBG are thanked for their help with the microscopic photography. We are indebted to Prof. Steven R. Manchester for his advice with regard to the identification of fossil materials and the recommendation of references to be consulted. This work is supported by National Natural Science Foundation of China (Nos. 42072024, 41922010, 41772026, 31800183); Chinese Academy of Sciences ‘Light of the West China’ Program; Yunnan Basic Research Projects (No. 2019FB026); the Strategic Priority Research Program, CAS (Nos. XDA 20070301, XDB26000000); and the NSFC project Basic Science Center for Tibetan Plateau Earth System (BCTES, No. 41988101).

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