Article

First fruit record of *Pterocarya* (Juglandaceae) from the upper Eocene of the central Qinghai-Tibetan Plateau, China

XIANG-BO SONG[1, 2], ZI-XI WANG[1, *], TAO SU[3], CHONG DONG[1] & DI-YING HUANG[1]

[1]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China*
[2]*University of Chinese Academy of Sciences, Beijing 100049, China*
[3]*State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation & Institute of Sedimentary Geology, Chengdu University of Technology, Chengdu 610059, China*
✉ *xbsong@nigpas.ac.cn;* ⓘ *https://orcid.org/0009-0009-7153-1005*
✉ *zxwang@nigpas.ac.cn;* ⓘ *https://orcid.org/0000-0002-3914-148X*
✉ *sutao@xtbg.org.cn;* ⓘ *https://orcid.org/0000-0002-9148-6127*
✉ *cdong@nigpas.ac.cn;* ⓘ *https://orcid.org/0000-0001-9983-4352*
✉ *dyhuang@nigpas.ac.cn;* ⓘ *https://orcid.org/0000-0002-5637-4867*
*Corresponding author

Abstract

The Juglandaceae family experienced significant diversification during the early Tertiary, as evidenced by fossil records showing a broad expansion of both extant and extinct taxa. The genus *Pterocarya* is characterized by its distinctive fruit with butterfly-shaped wings and a small nutlet. Macrofossil records suggest that this genus was distributed widely in the Northern Hemisphere. However, the fossil record of *Pterocarya* in China is limited. In this study, we describe a well-preserved *Pterocarya* fossil winged fruit from the middle-upper member of the Niubao Formation (the upper Eocene) of the central Qinghai-Tibetan Plateau, China. The winged fruit is identified as *Pterocarya liae* **sp. nov.** based on detailed morphological comparison, representing the earliest known record of *Pterocarya* winged fruit in Asia. The new finding extends the paleobiogeographic distribution of *Pterocarya* during the Eocene and provides new insights into the early stage of the diversification of this genus.

Keywords: *Pterocarya*, fossil winged fruit, Eocene, Tibet

Introduction

The fossil records of Juglandaceae de Candolle & Perleb in the Northern Hemisphere are extensive, containing fruits, flowers, pollen, leaves, and wood from both extant and extinct genera (Manos *et al*., 2007). The genus *Pterocarya* Kunth with six extant species, primarily inhabits deciduous broadleaf forest and is currently distributed disjunctively in East Asia and the Caucasus region (Lu *et al*., 1999; Kozlowski *et al*., 2018; Song *et al*., 2020). This genus is characterized by its distinctive winged fruits, the bi-winged nutlet with bifurcating subparallel wing venation, four sepals arise near the apex of the nut that surround the two styles, and the nutlet is oblique to the plane of the wings (Manning, 1940; Manchester & Dilcher, 1982, 1997). *Pterocarya* is a sister group to *Juglans* Linnaeus and likely originated from the extinct part of *Engelhardia* Leschenault & Blume or shares a common ancestor with it (Lu, 1982; Stanford *et al*., 2000). However, the taxonomic treatment of *Pterocarya* is controversial. Phylogenetic and morphological evidence suggests that *Pterocarya* can be divided into two sections. Section *Pterocarya* (naked buds) includes *P. fraxinifolia*, *P. hupehensis*, *P. stenoptera*, and *P. tonkinensis* and section *Platyptera* (scaled buds) includes *P. delavayi*, *P. insignis*, *P. macroptera*, and *P. rhoifolia* (Lu, 1982; Song *et al*., 2020). The recent phylogenetic study divided *Pterocarya* into another two clades. Clade I, which includes *P. stenoptera*, *P. tonkinensis*, *P. hupehensis*, and *P. rhoifolia*, and Clade II, comprising *P. fraxinifolia*, *P. macroptera*, *P. delavayi*, and *P. insignis*. And their research shows that the stem and crown age of *Pterocarya* were estimated at 53.28 Ma and 40.46 Ma, respectively (Yan *et al*., 2024).

Some fossil wood, leaves, and pollen grains assigned to *Pterocarya* could actually be *Cyclocarya* Iljinskaya, *Juglans*, or other extinct genera. For example, *P. macginitii* was initially classified as a member of

Pterocarya but was later reassigned to the extinct genus *Hooleya* Reid & Chandler (Manchester, 1987 & 1991). Similarly, *Cyclocarya paliurus* (Batalin) Iljinskaya was also mistakenly attributed to *Pterocarya* in earlier fossil records (Miki, 1955). Fruits are considered the most reliable organs for distinguishing genera within the Juglandaceae (Manchester & Dilcher, 1982), because fruits have significantly morphological differences compared to other organs. Fossil winged fruits identified as *Pterocarya* are known from many Cenozoic deposits in the Northern Hemisphere, including localities in North America, Europe, and Asia (*e.g.*, Buechler *et al.*, 2007; Worobiec *et al.*, 2012; Narita *et al.*, 2020), while extant species are limited in East Asia and the Caucasus region.

Here, a new species of winged fruit, *Pterocarya liae* **sp. nov.**, from the Eocene of the central Qinghai-Tibetan Plateau (QTP), China is reported, representing the earliest record of *Pterocarya* winged fruit in Asia. The new discovery contributes important information to the historical biogeography and increases the known diversity of *Pterocarya* during the Eocene.

Geological setting

The Nima Basin is a Cenozoic continental basin located in the central QTP, the west of the adjacent Lunpola Basin (Kapp *et al.*, 2007), and trends east-west along the Bangong-Nujiang suture zone (Kapp *et al.*, 2005; DeCelles *et al.*, 2007; Kapp *et al.*, 2007). The Niubao Formation is characterized by reddish clastic deposits, primarily composed of mudstones, sandstones, and gravels, representing a fluvial to marginal lacustrine environment (Rowley & Currie, 2006; Deng & Ding,

2015; Wu *et al.*, 2016; Liu *et al.*, 2019; Tang *et al.*, 2019). The middle member of the Niubao Formation yields abundant and well-preserved fossil plants, including *Illigera eocenica* Manchester & O'Leary, *Ailanthus maximus* Liu, Su & Zhou, *Lagokarpos tibetensis* Tang, Su & Zhou, *Asclepiadospermum marginatum* Del Rio, Su & Zhou, *Equisetum* cf. *oppositum* Ma, Su & Zhang, and some plant spines (Yang *et al.*, 2016; Liu *et al.*, 2019; Tang *et al.*, 2019; Del Rio *et al.*, 2020; Wang *et al.*, 2021; Zhang *et al.*, 2022a). The holotype (PB205514) with part and counterpart preserved in a yellowish-brown mudstone bed, collected from the middle-upper member of the Niubao Formation of Nima Basin, at the Jiangnongtangga, Nima County, Naqu City, Xizang Autonomous Region, China (31°79′ N, 87°76′ E, 4700 m *a.s.l.*; Fig. 1). The fossil-bearing layer contains abundant ostracods.

Radiometric dating indicates that the geological ages of the Dawei and Dayu sections in the middle-upper member of the Niubao Formation in the Lunpola Basin are 38.2 ± 1.2 Ma and approximately 38.5 ± 0.2 Ma, respectively (Xiong *et al.*, 2022). The heteropteran insect *Aquarius lunpolaensis* (Lin) Anderson is well represented in both the Dayu section of the Lunpola Basin and Jiangnongtaga section of the Nima Basin, indicating a stratigraphic correlation (Cai *et al.*, 2019). Consequently, we suggest that the age of the new fossil from Jiangnongtangga is most likely the late Bartonian.

Material and methods

The studied fossil specimen and modern materials for comparison were photographed using a Nikon D810 digital camera equipped with a 90 mm Nikkor macrolens under oblique illumination in the laboratory. The fossil
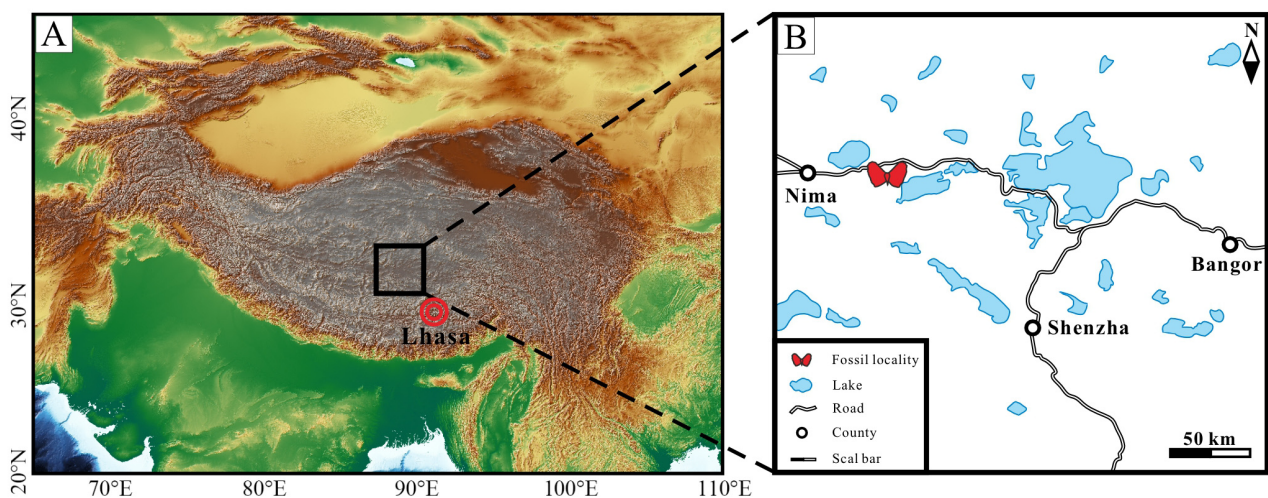

FIGURE 1. The locality of fossil site. **A**, Map showing the fossil locality in central Tibet Autonomous Region. **B**, Detailed view of the outlined area, with the locality of *Pterocarya liae* **sp. nov.** indicated by red marker.
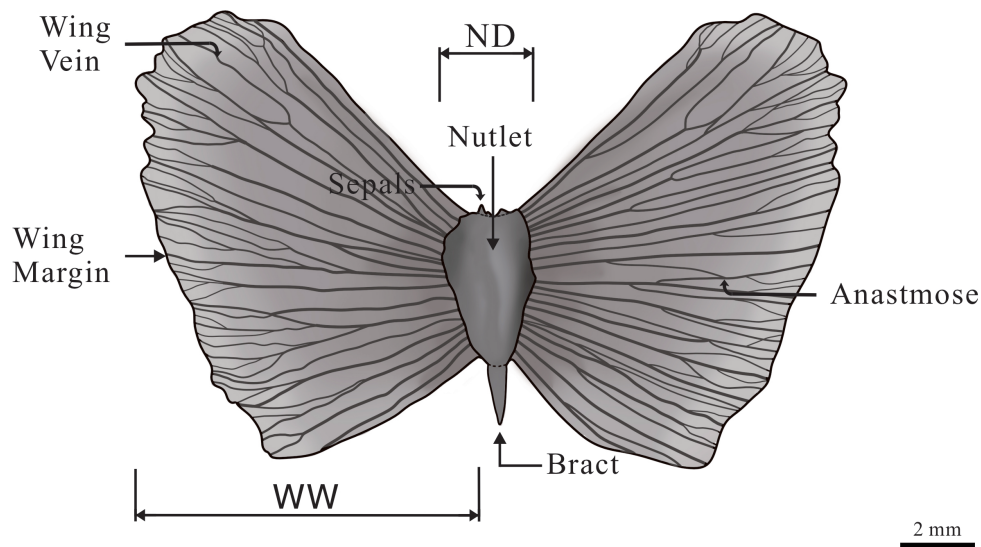
FIGURE 2. Line drawings of winged fruit and general characters for measurement of *Pterocarya*, showing terms used in description of fossil material. ND = total diameter of nutlets; WW = total width of each wing. Scale bars = 2 mm.

details were observed and photographed with a Leica M205A stereo microscope equipped with a Axiocam 512 colour digital camera. The extant materials for comparison are collected from the Institute of Botany, Jiangsu Province, the Nanjing Botanical Garden Memorial Sun Yat-Sen, and the Kunming Botanical Garden, Chinses Academy of Sciences, and the online databases of China digital library CVH (www.cvh.ac.cn). The studied fossil specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (PB205514). The terms used here to describe the fossil fruits (Fig. 2) are based on the terminology in Manning (1940), Manchester (1987), and Lu *et al*. (1999).

Systematic palaeontology

Order Fagales Engler, 1892
Family Juglandaceae de Candolle & Perleb, 1818
Genus *Pterocarya* Kunth, 1824

***Pterocarya liae* Song & Wang sp. nov.**
(Figs 3, 4A)

Holotype. PB205514, housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology. The specific epithet honours of the late Dr Juan Li for her contributions to the research of sedimentology in QTP, China.

Diagnosis. Winged fruit with an obovate nutlet and two laterally wings. Wing subfan-shaped and wing margins undulated. Wing venation radiated from nutlet in subparallel pattern, bifurcate and occasional anastomoses extending to margin. Nutlet with acuminate base and conical apex. Bract preserved as a tiny appendage at point of union of two wings.

Type locality and horizon. Jiangnongtangga (31°79′ N, 87°76′ E), Nima County, Naqu City of Xizang Autonomous Region, China. Middle-upper sections of the Niubao Formation.

Description. Fruit includes a small nutlet and two laterally adjoining wings; wing subfan-shaped, gradually becoming narrower from top to bottom with broader at top and taper towards bottom. Total diameter of the fruit, from wing tip to wing tip, *ca.* 12 mm long and 20 mm wide (Fig. 3A, B). Each wing *ca.* 12 mm long and 9 mm wide, with undulate margins (Fig. 3A–E); wings extended outward in a plane, oblique at about 70° angle to the central axis of the nutlet (Fig. 3A, C). Wing venation apparent and veins taper from the nutlet wing margin; wing venations radial, with each adjacent venation in subparallel from nutlet to wing margin, with bifurcations and rarely anastomosing along a course to the wing margin (Fig. 3E). Nutlet obovate, with acuminate base and conical apex, *ca.* 4 mm long and 2.2 mm wide, with a length/width ratio of about 2:1; the orientation of nutlet very oblique and nearly parallel to wing planes (Fig. 3F). Nutlet surface invisible. Bract preserved as a tiny appendage at the jointing point of the two wings,
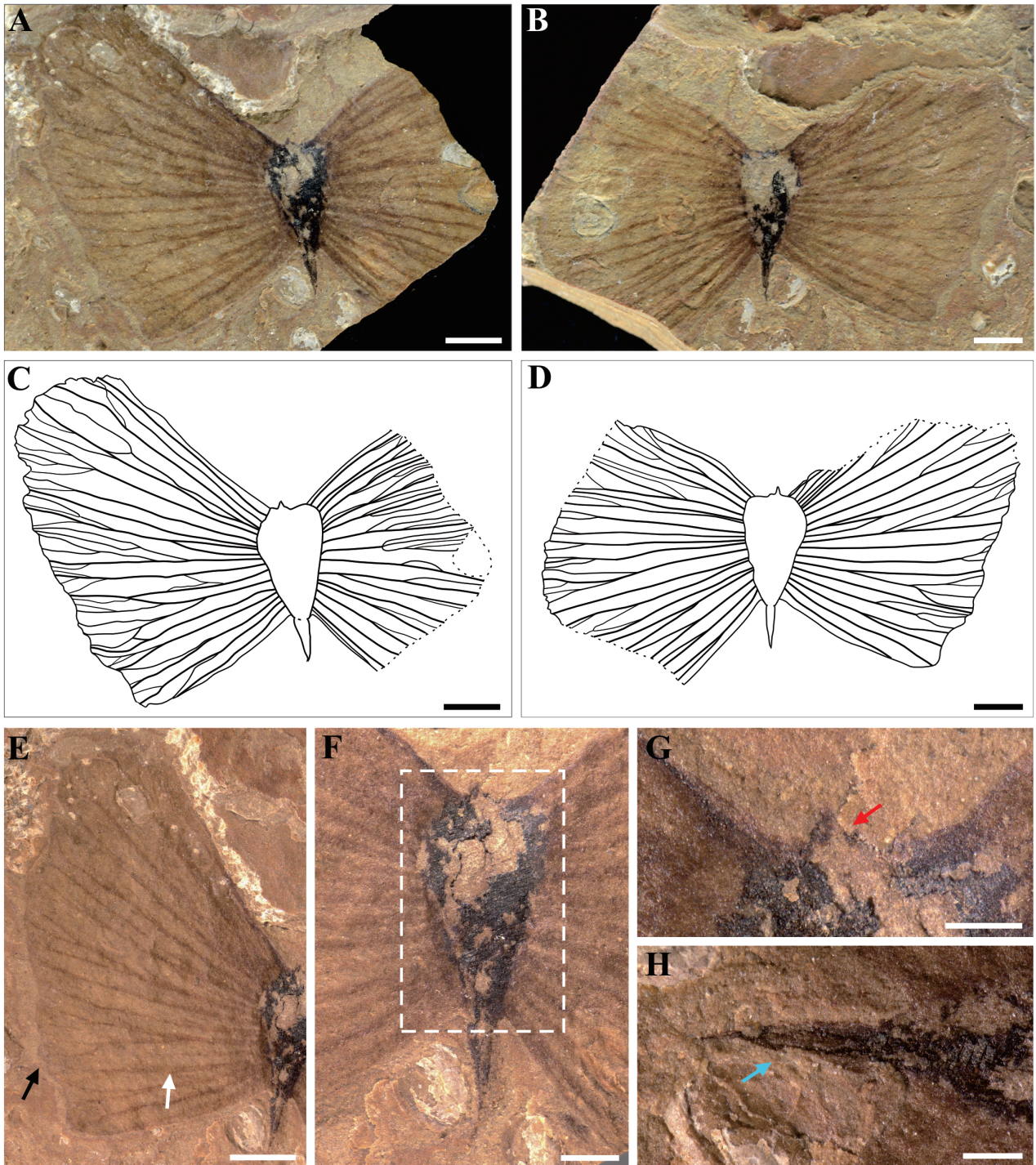
FIGURE 3. Fossil fruits of *Pterocarya liae* **sp. nov. A**, Well-preserved fruit from Niubao Formation (specimen No. PB 205514a). **B**, Counterpart of **A** showing basal surface of fruit (specimen No. PB 205514b). **C**, Line drawings of **A**. **D**, Line drawings of **B**. **E**, Showing Wing morphology of the winged fruit, undulatory wing margin marked with black arrow and wing vein anastomose marked with white arrow. **F**, Showing Morphology nutlet of the winged fruits, outlined in white. **G**, Styles arising near the apex of the nutlet, marked with red arrow. **H**, Persistent bract as a tiny appendage at the point of union of the two wings, marked with a blue arrow. Scale bars = 2 mm in **A**, **B**, **C**, **D**, **E**; 1mm in **F**; 500 μm in **G**, **H**.

ca. 1.5 mm long and 0.4 mm wide (Fig. 3H). Sepals partly preserved, apex of nutlet visible (Fig. 3G). Styles invisible.

Discussion

Morphological comparison
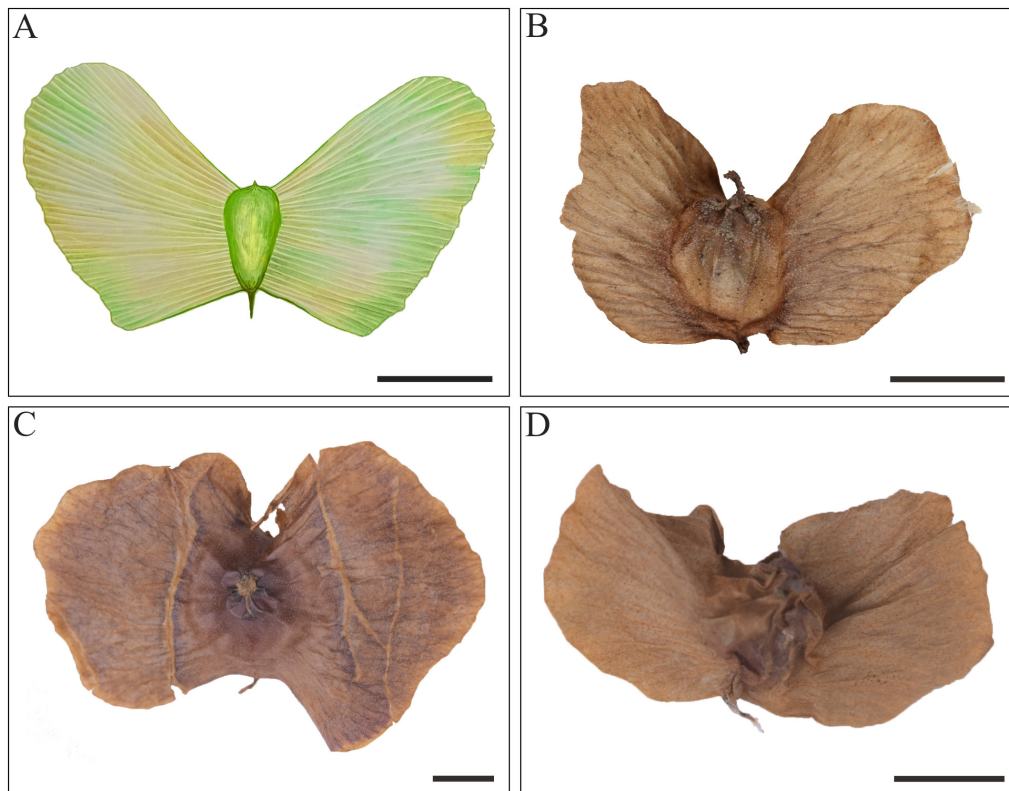The present fossil displays two laterally adjoining

FIGURE 4. Reconstructions of *P. liae* **sp. nov.** and related extant representatives in *Pterocarya*. **A**, Reconstructions of *P. liae* **sp. nov. B**, Showing living specimen of *P. hupehensis* Skan. Specimen registered number: No. 940. **C**, Showing living specimen of *P. macroptera* Batalin. Specimen registered number: No.10689. **D**, Showing living specimen of *P. rhoifolia* Siebold & Zucc. Specimen registered number: No. 2070634. Scale bars = 5 mm.

obovate wings, with symmetric sinuses between the wing lobes that reach the nutlet, resembling the overall shape of butterfly wings accompanied by a small nutlet (Manchester & Dilcher, 1997; Tan *et al*., 2018). The combination of characteristic is similar to some groups within the Malpighiaceae known from the North America and Africa (*e.g.*, *Aenigmatanthera* Anderson; *Hiraea* Jacquin; *Amorimia* Anderson) and some genera of Asterceae Berchtold & Presl, Oleaceae Hoffmannsegg & Link, Combretaceae Brown, Sapindaceae Jussieu and Juglandaceae (Tan *et al*., 2018). However, the wing venation of the new fossil radiates outward from the nutlet in a subparallel pattern, with occasional dichotomies and anastomosing toward the margin, which are typical of pterocaryoid venation and suggest its placement within the Juglandaceae. The extant genera *Platycarya* Siebold & Zucc and *Pterocarya*, as well as the extinct genus *Hooleya* and *Palaeoplatycarya* Manchester (Manchester, 1987), are similar with the present fossil. Furthermore, the bracts of *Hooleya* and *Palaeoplatycarya* persist on the axis of the infructescence and are not dispersed with the fruit, and *Hooleya* has a slightly concave nutlet base. Additionally, *Platycarya* lacks sepals, and its small wings feature few or no veins (Manchester, 1987; Kozlowski *et al*., 2018). Therefore, the fossil specimen described here can be confidently assigned to the *Pterocarya*.

Wing characteristics, such as size, shape, venation pattern, and wing position, are important diagnostic features for identifying winged fruit fossils (Manchester & O'Leary, 2010). Among extant species of *Pterocarya*, *P. fraxinifolia* (Poiret) Spach, *P. hupehensis* Skan (Fig. 4B), *P. macroptera* Batalin (Fig. 4C) and *P. rhoifolia* Siebold & Zuccarini (Fig. 4D) have fruits with two laterally adjoining broad wings (Kozlowski *et al*., 2018), which are morphologically similar to the new species described here. Nevertheless, *P. fraxinifolia* and *P. rhoifolia* differ from the present fossil specimen primarily in having elliptical wings with shorter lengths compared to their widths and round nutlets. Additionally, *P. rhoifolia* features a round nutlet base and a broadly conical nutlet apex. *Pterocarya hupehensis* possesses broadly elliptical-ovate wings that join to form a seam at the nutlet base, whereas the wings of the new fossil connect at the base of nutlets. The orientation of the nutlet in the new fossil is nearly parallel to the wing planes, while in *P. macroptera*, the nutlet is oriented almost perpendicular to the wing planes. Therefore, the fossil cannot be assigned to any extant species.
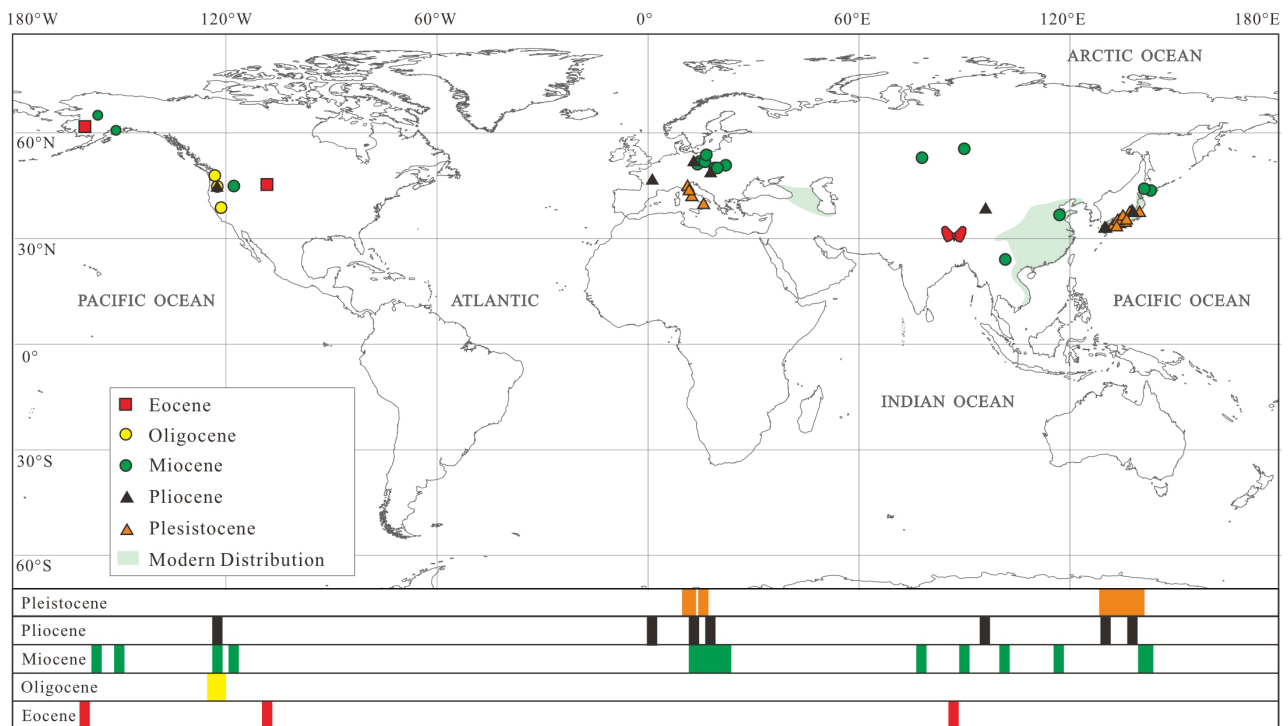
FIGURE 5. Map showing the distributions of modern and macrofossils of *Pterocarya*. Extant distribution is in light green, the symbols indicate the fossil localities of *Pterocarya* from different ages. Base map comes from http://www.geodata.cn.

Numerous *Pterocarya* fossil fruits have been reported, but some, such as *P. crassa* Dorofeev (Dorofeev, 1963), *P. kireevskiana* Dorofeev (Dorofeev, 1963) and *Pterocarya* sp. from the Miocene, are preserved only as nutlets (Manchester, 1987), which hinders morphological comparison with the new fossil. *Pterocarya protostenptera* Tanai (Tanai, 1965; Yabe, 2009) has strap-shaped wings that diverge in a V-shaped pattern, which is easily to be distinguished from our fossil specimen. *Pterocarya occidentalis* Manchester from the Oligocene (Manchester, 1987), as well as *P. smileyi* Manchester (Manchester, 1987*)*, *Pterocarya eomacroptera* Manchester (Manchester, 1987), and *P. asymmetrosa* Konno (Tanai & Suzuki, 1972) from the Miocene, are similar to the studied fossil in having two laterally adjoining butterfly-shaped wings (Table 1). The wing shape in the new fossil is subfan-shaped, with ratio (L:W) of wing about 1.2:1. However, *P. occidentalis* possesses oval to almost circular wings with smooth or slightly undulate margin, the wing venation flaring downward in the basal one-fourth, and larger, round nutlets. The wing shape of *P. asymmetrosa* is reniform in outline and nutlet axis perpendicular to the wing planes. *Pterocarya eomacroptera* from Idaho has elliptical wings and also preserves a bract at the base of nutlet; however, its wings join to form a seam at the nutlet junction, and the wing length is shorter than its width. The wings of *P. smileyi* also join to form a seam at the nutlet junction; additionally, the wing length is twice the

width. Compared to all known fossil records and extant *Pterocarya* species, the studied fossil exhibits much more elongated nutlets with a notably higher ratio (L:W) of about 2:1. Thus, here we treat it as a new species, *P. liae* **sp. nov.**

Review of the macrofossil records of Pterocarya
Macrofossils of *Pterocarya*, including leaves, wood, and fruits, have been widely found across the Northern Hemisphere during the Cenozoic (Fig. 5; Manchester, 1987, 1989). However, some of these identifications are not reliable. For example, *P. macginitii* Manchester & Dilcher was originally considered the earliest fossil winged fruit of *Pterocarya* (Manchester, 1987) but was later reclassified into the extinct genus *Hooleya* (Manchester, 1991). *Pterocarya* has it highest diversity from the Miocene to the Pliocene. During the Pleistocene, *Pterocarya* is mainly known from Eurasia (*e.g.*, Miki, 1955; Martinetto, 2001).

In North America, the earliest reliable evidence of *Pterocarya* includes the wood of *P. knowltoni* Wheeler, Scott & Barghoorn from the middle Eocene of Yellowstone National Park (Wheeler *et al*., 1978) and the leaves of *P. pugetensis* Wolfe from the Pacific Northwest and Alaska (Wolfe, 1977). Additional leaves and fruits of this genus have also been reported from the Oligocene to Pliocene deposits in the USA (*e.g.*, Manchester, 1987; Meyer, 1973; Chaney *et al*., 1944; Meyer, 1973;

TABLE 1. Morphological comparison of winged fruits among simliar fossil species of *Pterocarya*.

Species	Locality	Age	Morphological characters										Reference
			Fruit size	Wing shape	Wing margin	Wing seam at nutlet base	Nutlet shape	Nutlet (diameter)	Nutlet axis relative to wing plane	Nutlet surface	Bract		
Pterocarya occidentalis Manchester	California, Oregon, Washington (USA)	Oligocene	9-10 mm × 18–25 mm	oval to almost circular	smooth or slightly undulatory	unknown	round	3–5 mm	unknown	8-10 longitudinal exterior ribs	unknown		Manchester, 1987
P. smileyi Manchester	Idaho, Oregon (USA)	Miocene	9–12 mm × 14 mm	small and rounded	unknown	yes	round	4 mm	slightly oblique	longitudinal ribs	preserved		Manchester, 1987
P. eomacroptera Manchester	Idaho (USA)	Miocene	10–12 mm × 33 mm	large and rounded	unknown	yes	round	8 mm	oblique	unknown	1.5 mm × 1.2 mm		Manchester, 1987
P. asymmetrosa Konno	Hokkaido (Japan)	Miocene	15–20 mm × 32–35 mm	reniform	unknown	no	round	6–7 mm	perpendicular	8 sharp ridges and 8 deep grooves	unknown		Tanai, 1965
The current fossil	Tibet Autonomous Region (China)	Late Eocene	12 mm × 20 mm	subfan-shaped	undulatory	no	obovate	2.2 mm × 4 mm	near parallel	unknown	1.5 mm × 0.5 mm		This paper

Manchester, 1987). *Pterocarya* occurred in North America from the Eocene and flourished until the Pliocene. The known fossil records of *Pterocarya* from North America gradually decreased and eventually disappeared in the Pleistocene.

In Europe, the most ancient fossils of *Pterocarya* are fruits and leaves from the Miocene of Germany, Poland, and Russia (*e.g.*, Dorofeev, 1963; Gregor, 1978; Worobiec *et al*., 2008, 2012). *Pterocarya rhoifolia*, *P. insignis* and *P. stenoptera* have been found near Bogatynia in Poland (Czeczott & Skirgiełło, 1961), and *P. fraxinifolia* is reported from the Pleistocene in Italy (Follieri *et al*., 1986) and has survived to the present. *Pterocarya limburgensis* C. Reid & E. Reid is very common during the Pleistocene, with endocarps of *P. limburgensis* even were found (Martinetto, 2001; Denk *et al*., 2022).

In Asia, the new described winged fruit of *P. liae* **sp. nov.** from upper middle Eocene of QTP, China is the earliest fossil record of *Pterocarya*. Some Miocene leaves and wood have been found in Shandong and Yunnan provinces of China and in Japan (*e.g.*, Hu & Chaney, 1938; Xia *et al*., 2009; Cheng *et al*., 2014; Narita *et al*., 2020). *Pterocarya stenoptera* was also found in the Pliocene strata of Xinjiang, Northwest China (Liu *et al*., 1996). Abundant fossil leaves and fruits of *P. rhoifolia* are reported from the Pleistocene in Japan (Miki, 1955), where the species has survived to the present.

Fossil records indicate that *Pterocarya* was distributed in the Northern Hemisphere during the Eocene, with a possible origin in East Asia or North America, though further fossil records are needed to confirm this hypothesis. Additionally, Yan *et al*. (2024) suggests that the most recent common ancestor of *Pterocarya* diverged in East Asia in the late Eocene. During the Miocene, fossil records of *Pterocarya* became particularly abundant as global temperatures increased. To date, more than half of the known *Pterocarya* fossils are widely recorded from the Northern Hemisphere during the Miocene (Yan *et al*., 2024), with frequently occurring in high-altitude areas of the Northern Hemisphere (*e.g.*, Dorofeev, 1963; Wolfe, 1966). The absence of fossil record of *Pterocarya* in South America is likely a result of the Central American seaway, which remained a barrier between North and South America. However, the distribution of the genus in North America began to decline in the late Pliocene. The beginning of the Quaternary glaciation introduced significant climatic changes to the high-latitude regions of the Northern Hemisphere, leading to increasingly unfavourable conditions for the survival of *Pterocarya* (Zhang *et al*., 2022b; Yan *et al*., 2024). By the early Pleistocene, the genus had become extinct in the mid- to high-latitude regions of the Eurasian continent. Fossil evidence from this period is limited to certain parts of Europe and East Asia, corresponding to the current distribution of *Pterocarya* habitats. Meanwhile, the modern distribution of *Pterocarya* is attributed to historical connectivity among continents at high latitudes (Yan *et al*., 2024).

In summary, the new species *Pterocarya liae* **sp. nov.** described herein represents the earliest fossil fruit record of this genus. Our finding provides additional evidence of its early biogeographic history. Our discovery of *Pterocarya* from the central QTP demonstrates that this genus was not only distributed in North America but also inhabited Asia during the Eocene. In contrast to its modern distribution, the geographical range of *Pterocarya* was much wider before the Quaternary.

References

Buechler, W.K., Dunn, M.T. & Rember, W.C. (2007) Late Miocene Pickett Creek flora of Owyhee County, Idaho. *Contrib Mus Paleontol Univ Michigan*, 31 (12), 305–362.

Cai, C.Y., Huang, D.Y., Wu, F.X., Zhao, M. & Wang, N. (2019) Tertiary water striders (Hemiptera, Gerromorpha, Gerridae) from the central Tibetan Plateau and their palaeobiogeographic implications. *Journal of Asian Earth Sciences*, 175, 121–127.
https://doi.org/10.1016/j.jseaes.2017.12.014

Chaney, R.W., Condit, C. & Axebrod, D. (1944) Pliocene floras of California and Oregon. Carnegie Institution.
https://doi.org/10.1086/395459

Cheng, Y.M., Wang, Y.F., Li, C.S. & Wang, Y. (2014) Late Miocene wood flora associated with the Yuanmou hominoid fauna from Yunnan, southwestern China and its palaeoenvironmental implication. *Journal of Palaeogeography*, 3 (3), 323–330.
https://doi.org/10.3724/SP.J.1261.2014.00059

Czeczott, H. & Skirgiełło, A. (1961) Dicotyledones-Juglandaceae, Lorantaceae, Aceraceae. In: H. Czeczott (Ed.), *Flora kopalna Turowa koło Bogatyni [The fossil flora of Turów near Bogatynia]*. Wydawnictwa Geologiczne, pp.51–81.

DeCelles, P.G., Kapp, P.A., Ding, L. & Gehrels, G.E. (2007) Late Cretaceous to middle Tertiary basin evolution in the central Tibetan Plateau: Changing environments in response to tectonic partitioning, aridification, and regional elevation gain. *Geological Society of America Bulletin*, 119, 654–680.
https://doi.org/10.1130/B26074.1

Del Rio, C., Wang, T.X., Liu, J., Liang, S.Q., Spicer, R.A., Wu, F.X., Zhou, Z.K. & Su, T. (2020) *Asclepiadospermum* gen. nov., the earliest fossil record of Asclepiadoideae (Apocynaceae) from the early Eocene of central Qinghai-Tibetan Plateau, and its biogeographic implications. *American Journal of Botany*, 107 (1), 126–138.
https://doi.org/10.1002/ajb2.1418

Deng, T. & Ding, L. (2015) Paleoaltimetry reconstructions of the Tibetan Plateau: progress and contradictions. *National Science Review*, 2 (4), 417–437.
https://doi.org/10.1093/nsr/nwv062

Denk, T., Sami, M., Teodoridis, V. & Martinetto, E. (2022) The late early Pleistocene flora of Oriolo, Faenza (Italy): assembly of the modern forest biome. *Fossil Imprint*, 78, 217–262.
https://doi.org/10.37520/fi.2022.009

Dorofeev, P.I. (1963) *Tretichnye flory zapadnoi Sibiri.* Izvestiya Akademii Nauk Moscow, 345 pp.

Follieri, M., Magri, D. & Sadori, L. (1986) Late Pleistocene Zelkova Extinction in Central Italy. *New Phytologist*, 103 (1), 269–273.
https://doi.org/10.1111/j.1469-8137.1986.tb00613.x

Gregor, H.J. (1978) Die miozänen Frucht-und Samen-Floren der Oberpfälzer Braunkohle. I. Funde aus den sandigen Zwischenmitteln. *Palaeontographica Abteilung B*, 167, 8–103.

Hu, H.H. & Chaney, R.W. (1938) *A Miocene flora from Shantung province, China (No. 507)*. Carnegie Institution of Washington. pp. 1–82.
https://doi.org/10.1086/625047

Kapp, P., DeCelles, P.G., Gehrels, G.E., Heizler, M. & Ding, L. (2007) Geological records of the Lhasa-Qiangtang and Indo-Asian collisions in the Nima area of central Tibet. *Geological Society of America Bulletin*, 119 (7-8), 917–933.
https://doi.org/10.1130/b26033.1

Kapp, P., Yin, A., Harrison, T.M. & Ding, L. (2005) Cretaceous-Tertiary shortening, basin development, and volcanism in central Tibet. *Geological Society of America Bulletin*, 117 (7-8), 865–878.
https://doi.org/10.1130/B25595.1

Kozlowski, G., Bétrisey, S., Song, Y.G. & Alvarado, E.V. (2018) *Wingnuts (Pterocarya) & walnut family: relict trees: linking the past, present and future.* Natural History Museum Fribourg, Switzerland, 127 pp.

Liu, J., Su, T., Spicer, R.A., Tang, H., Deng, W.Y.D., Wu, F.X., Srivastava, G., Spicer, T., Do, T.V., Deng, T. & Zhou, Z.K. (2019) Biotic interchange through lowlands of Tibetan Plateau suture zones during Paleogene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 524, 33–40.
https://doi.org/10.1016/j.palaeo.2019.02.022

Liu, Y.S., Guo, S. & Ferguson, D.K. (1996) Catalogue of Cenozoic megafossil plants in China. *Palaeontographica Abteilung B*, 238, 141–179.

Lu, A., Stone, D. & Grauke, L. (1999) Juglandaceae. *Flora of China*, 4, 277–285.

Lu, A.M. (1982) On the geographical distribution of the Juglandaceae. *Journal of Systematics and Evolution,* 20 (3), 257.

Manchester, S.R. (1987) *The fossil history of the Juglandaceae.* Missouri Botanical Garden, 137 pp.
https://doi.org/10.5962/bhl.title.154222

Manchester, S.R. (1989) Early history of the Juglandaceae. *Plant Systematics and Evolution*, 162, 231–250.
https://doi.org/10.1007/BF00936919

Manchester, S.R. (1991) *Cruciptera*, a New Juglandaceous Winged fruit from the Eocene and Oligocene of western North America. *Systematic Botany*, 715–725.
https://doi.org/10.2307/2418873

Manchester, S.R. & Dilcher, D.L. (1982) Pterocaryoid fruits (Juglandaceae) in the Paleogene of North America and their evolutionary and biogeographic significance. *American Journal of Botany*, 69 (2), 275–286.
https://doi.org/10.1002/j.1537-2197.1982.tb13258.x

Manchester, S.R. & Dilcher, D.L. (1997) Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana. *American Journal of Botany*, 84 (5), 649–663.
https://doi.org/10.2307/2445902

Manchester, S.R. & O'Leary, E.L. (2010) Phylogenetic Distribution and Identification of Fin-winged Fruits. *The Botanical Review*, 76 (1), 1–82.
https://doi.org/10.1007/s12229-010-9041-0

Manning, W.E. (1940) The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruit. *American Journal of Botany*, 839–852.
https://doi.org/10.1002/j.1537-2197.1940.tb13945.x

Manos, P.S., Soltis, P.S., Soltis, D.E., Manchester, S.R., Oh, S.H., Bell, C.D., Dilcher D.L. & Stone, D.E. (2007) Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. *Systematic Biology*, 56 (3), 412–430.
https://doi.org/10.1080/10635150701408523

Martinetto, E. (2001) Studies on some exotic elements of the Pliocene floras of Italy. *Palaeontographica Abteilung B Paläophytologie*, 259, 149–166.
https://doi.org/10.1127/palb/259/2001/149

Meyer, H. (1973) The Oligocene Lyons flora of northwestern Oregon. *Oregon Department of Geology and Mineral Resources, Oregon Bin*, 35, 37–51.

Miki, S. (1955) Nut remains of Juglandaceae in Japan. *Journal of the Institute of Polytechnics, Osaka City University, Series D*, 6, 131–144.

Narita, A., Yabe, A., Uemura, K. & Matsumoto, M. (2020) Late middle Miocene Konan flora from northern Hokkaido, Japan. *Acta Palaeobotanica*, 60 (2), 259–295. https://doi.org/10.35535/acpa-2020-0012

Rowley, D.B. & Currie, B.S. (2006) Palaeo-altimetry of the late Eocene to Miocene Lunpola basin, central Tibet. *Nature*, 439 (7077), 677–681. https://doi.org/10.1038/nature04506

Song, Y.G., Li, Y., Meng, H.H., Fragnière, Y., Ge, B.J., Sakio, H., Yousefzadeh, H., Bétrisey, S. & Kozlowski, G. (2020) Phylogeny, Taxonomy, and Biogeography of *Pterocarya* (Juglandaceae). *Plants*, 9 (11), 1524. https://doi.org/10.3390/plants9111524

Stanford, A.M., Harden, R. & Parks, C.R. (2000) Phylogeny and biogeography of *Juglans* (Juglandaceae) based on matK and ITS sequence data. *American Journal of Botany*, 87 (6), 872–882. https://doi.org/10.2307/2656895

Tanai, T. (1965) Late Tertiary floras from northeastern Hokkaido, Japan. *Palaeontological Society of Japan, Special Papers*, 10, 1–117.

Tanai, T. & Suzuki, N. (1972) Additions to the Miocene floras of southwestern Hokkaido, Japan. *Journal of the Faculty of Science*, 15 (1–2), 281–359.

Tan, K., Dong, S.P., Lu, T., Zhang, Y.J, Xu, T.T. & Ren, M.X. (2018) Diversity and evolution of samara in angiosperm. *Chinese Journal of Plant Ecology*, 42 (8), 806–817. https://doi.org/10.17521/cjpe.2018.0053

Tang, H., Liu, J., Wu, F.X., Spicer, T., Spicer, R.A., Deng, W.Y.D., Xu, C.L., Zhao, F., Huang, J. & Li, S.F. (2019) Extinct genus *Lagokarpos* reveals a biogeographic connection between Tibet and other regions in the Northern Hemisphere during the Paleogene. *Journal of Systematics and Evolution*, 57 (6), 670–677. https://doi.org/10.1111/jse.12505

Wang, T.X., Del Rio, C., Manchester, S.R., Liu, J., Wu, F.X., Deng, W.Y.D., Su, T. & Zhou, Z.K. (2021) Fossil fruits of *Illigera* (Hernandiaceae) from the Eocene of central Tibetan Plateau. *Journal of Systematics and Evolution*, 59 (6), 1276–1286. https://doi.org/10.1111/jse.12687

Wheeler, E.F., Scott, R.A. & Barghoorn, E.S. (1978) Fossil dicotyledonous woods from Yellowstone National Park, II. *Journal of the Arnold Arboretum*, 59 (1), 1–31. https://doi.org/10.5962/p.185868

Wolfe J.A. (1966) Tertiary plants from the Cook Inlet region, Alaska. *US Geological Survey Professional Paper*, 398-B, 1–32.

Wolfe, J.A. (1977) Paleogene floras from the Gulf of Alaska region, *U.S. Geological Survey*, 997, 1–107. https://doi.org/10.3133/PP997

Worobiec, G., Worobiec, E. & Kasiński, J. (2008) Plant assemblages of the drill cores from the Neogene Ruja lignite deposit near Legnica (Lower Silesia, Poland). *Acta Palaeobotanica*, 48 (2), 191–275.

Worobiec, G., Worobiec, E. & Szynkiewicz, A. (2012) Plant assemblage from the Upper Miocene deposits of the Bełchatów Lignite Mine (Central Poland). *Acta Palaeobotanica*, 52 (2), 369–413.

Wu, Z., Zhang, Q., Wu, Y. & Ye, P. (2016) Response of sedimentary depression to crustal thickening in the Silin Co Basin and its adjacent areas, Tibet. *Acta Geologica Sinica*, 90 (9), 2181–2191.

Xia, K., Su, T., Liu, Y.S., Xing, Y.W., Jacques, F.M.B. & Zhou, Z.K. (2009) Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 276 (1-4), 80–86. https://doi.org/10.1016/j.palaeo.2009.02.024

Xiong, Z., Liu, X., Ding, L., Farnsworth, A., Spicer, R.A., Xu, Q., Valdes, P., He, S., Zeng, D. & Wang, C. (2022) The rise and demise of the Paleogene Central Tibetan Valley. *Science Advances*, 8 (6), eabj0944. https://doi.org/10.1126/sciadv.abj0944

Yabe, A. (2009) Early Miocene terrestrial climate inferred from plant megafossil assemblages of the Joban and Soma areas, Northeast Honshu, Japan. *Bulletin of the Geological Survey of Japan*, 59 (7-8), 397–413.

Yan, H., Zhou, P., Wang, W., Ye, J.F., Tan, S.L., Guo, C.C., Zhang, W.G., Zhu, Z.W., Liu, Y.Z. & Xiang, X.G. (2024) Biogeographic history of *Pterocarya* (Juglandaceae) inferred from phylogenomic and fossil data. *Journal of Systematics and Evolution*. https://doi.org/10.1111/jse.13055

Yang, G.L., Wang, Z.X., Chen, J.W., Yan, D.F. & Sun, B.N. (2016) *Equisetum* cf. *oppositum* (Equisetaceae) from the Paleocene-Eocene of Tibet in southwestern China and its paleoenvironmental implications. *Arabian Journal of Geosciences*, 9, 1–10. https://doi.org/10.1007/s12517-016-2777-z

Zhang, X., Gélin, U., Spicer, R.A., Wu, F., Farnsworth, A., Chen, P., Del Rio, C., Li, S., Liu, J. & Huang, J. (2022a) Rapid Eocene diversification of spiny plants in subtropical woodlands of central Tibet. *Nature Communications*, 13 (1), 3787. https://doi.org/10.1038/s41467-022-31512-z

Zhang, Q., Ree, R.H., Salamin, N., Xing, Y., Silvestro, D. & López-Fernández, H. (2022b) Fossil-Informed Models Reveal a Boreotropical Origin and Divergent Evolutionary Trajectories in the Walnut Family (Juglandaceae). *Systematic Biology*, 71 (1), 242–258. https://doi.org/10.1093/sysbio/syab030