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Fruits of *Firmiana* and *Craigia* (Malvaceae) from the Eocene of the Central Tibetan Plateau with emphasis on biogeographic history

Running title: Malvaceae from the Eocene of the Tibetan Plateau

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The fossil record evidences an old origin and diversification of Malvaceae in the Northern Hemisphere. The central Tibetan Plateau was at a low elevation with a monsoon influence during the Eocene, allowing the development of a subtropical flora containing Malvaceae. The taxonomic study of fossils from the Eocene of what is now the Tibetan Plateau is still ongoing. Malvaceae fossils from the Eocene Jianglang flora, are attributed to sub-families Tilioideae and Sterculioideae, and are compared with modern species. A new specimen of *Firmiana* is described based on a fruit valve with a pinnate venation, the secondary veins starting at the ventral suture and reaching the midvein, and the seeds attached at the proximal part of the ventral suture. This specimen represents the earliest known occurrence of the genus. A new occurrence of *Craigia* is also reported based on detached membranous valves of a fruit capsule with a prominent fusiform locular area and radiating venation. Based on the fossil record of *Firmiana* and its modern distribution, we infer that the genus may have originated in East Asia and subsequently diversified in South China and Southeast Asia. The new occurrence of *Craigia* indicates that the genus was distributed in humid areas in South, Southwest and North China during the Eocene. Both fossil records evidence the important role that the Tibetan region played in the diversification of plants in East and Southeast Asia.

KEY WORDS Plant diversity; Biogeography; China; Malvaceae; Paleobotany; Paleogene.

1.Introduction

Malvaceae Juss. is a widely dispersed family occurring today in warm regions of all vegetated continents (Bayer and Kubitzki, 2003). This family exhibits diverse growth forms, including trees, shrubs and herbs, and in rare cases, climbers (Bayer and Kubitzki, 2003). The concept of Malvaceae currently includes several formerly recognized families, namely Sterculiaceae Vent., Tiliaceae Juss., Bombacaceae Kunth, Byttneriaceae R. Br., and Malvaceae s.s. based on plastid *atpB* and *rbcL* sequences (Alverson et al., 1998, 1999; Baum et al., 1998; Bayer et al., 1999), as well as morphological, anatomical, palynological and phytochemical characters (Judd and Manchester, 1997). The synapomorphies of the family include hairs on the sepals acting as densely packed nectaries, palmate venation, cymose inflorescences, calyces that are valvate, and stellate hairs (Judd and Manchester, 1997; Bayer and Kubitzki, 2003; Cvetković et al., 2021). Malvaceae, as recently defined, contains about 4200 species in 249 genera (Christenhusz and Byng, 2016, Plants of the World Online; POWO, 2019) and nine sub-families: namely Bombacoideae, Brownlowioideae, Byttnerioideae, Dombeyoideae, Grewioideae, Helicteroideae, Malvoideae, Sterculioideae and Tilioideae (Bayer et al., 1999). The origin age of the Malvaceae has been inferred to have been in the Late Cretaceous (98 Ma), with the sub-families originating during the Late Cretaceous to the Paleogene based on fossil records and a secondary calibration of a Malvales phylogeny (Hernández-Gutiérrez and Magallón, 2019). Although a recent study suggested a Late Jurassic (152 Ma) origin, with the sub-families arising during the Cretaceous-Paleogene (Cvetković et al., 2021), this would predate the oldest unequivocal angiosperm fossils (Herendeen et al. 2017). This discrepancy arises from differences in the methodology (the later study did not use secondary calibration) rather than the fossil constraints (Cvetković et al., 2021).

Malvaceae was already radiating during the Late Cretaceous based on fossil woods, pollen and leaves from North America and Antarctica (Wheeler et al., 1987; Dutra and Batten, 2000;

Wheeler and Lehman, 2000; Estrada-Ruiz et al., 2007). Fossil records show this family was abundant during the Paleogene (e.g., Manchester, 1994; Kvaček et al., 2005; Hernández-Gutiérrez and Magallón, 2019). In particular, the subfamilies Tilioideae and Sterculioideae have numerous Cenozoic fossil records and there have been several attempts to reconstruct their biogeographic history in the Northern Hemisphere (Prakash, 1973; Manchester, 1979, 1980, 1994; Terada and Suzuki, 1998; Sun, 1999; Mehrotra, 2000; Kvaček et al., 2005; Jeong et al., 2009; Srivastava and Mehrotra, 2013; Xie et al., 2014). Here, we report fossil records of *Craigia* W.W. Sm. & W.E. Evans in Tilioideae and *Firmiana* Marsili in Sterculioideae from the middle Eocene of central Tibet, marking their first fossil occurrences in this region.

Firmiana, in Sterculioideae, contains 17 species distributed across East Asia, India, Southeast Asia, and Oceania (POWO, 2019). *Firmiana* could not be differentiated from the genus *Hildegardia* Schott et Endl. using molecular data, which might be because of frequent hybridization (Wilkie et al., 2006; Abdullah et al., 2019). However, *Firmiana* is distinguishable from other genera based on its distinctive open fruit follicles with at least two marginal seeds. In the fossil record, foliaceous valves corresponding to *Firmiana* are found in Neogene deposits in China and South Korea, and leaves apparently representing the genus occur in the Oligocene of India (Sun, 1999; Srivastava and Mehrotra, 2013; Xie et al., 2014; Jia et al., 2021).

Craigia in Tilioideae, contains only two species today distributed in south China, north Vietnam and north Myanmar (Kvaček et al., 2005, Ding et al. 2019). *Craigia* is recovered as a sister group of *Tilia* L. based on phylogenetic studies using morphological and molecular data (e.g., Judd and Manchester, 1997; Alverson et al., 1999; Wariss et al., 2019). The genus is mainly distinguishable from other genera based on its five-winged capsules, petaloid staminodes and a lack of petals (Shu, 2007). The fruit remains of the fossil genus *Pteleacarpum* Weyland, at one time interpreted as valves of extinct Sapindaceae, have been referred to extant *Craigia* (Kvaček et al., 1991). These fruits comprise capsules with fusiform locules and

radiating venation, co-occur with leaves, and are well represented in the Cenozoic of the Northern Hemisphere (Kvaček et al., 2005). *Craigia* appears in the fossil record in North Asia during the Paleocene and became more abundant in North America and East Asia during the Eocene (Kvaček et al., 2005; Manchester et al., 2005; Jin et al., 2009; Liu et al., 2012). During the Oligocene, it persisted in North America and Asia and became abundant in Europe. The genus became extinct by the Miocene in North America, during the Pliocene in Europe and persisted to the present day in eastern Asia (Kvaček et al., 2005; Wang et al., 2021a).

Despite these previous findings of *Firmiana* and *Craigia* fossils, especially in East Asia (Xie et al., 2014; Jia et al., 2021; Wang et al., 2021a), no occurrence has been reported from what is now the Tibetan Plateau. The Tibetan Plateau, also called the 'Third Pole' of the world (Qiu, 2008), is the highest plateau worldwide. Increasing paleontological and geological evidence shows that the Paleogene topographic development of the Tibetan region was complex (Spicer et al., 2020a, 2020b). During the Eocene, the modern central Tibetan Plateau was at low elevation with a subtropical climate, as shown by the occurrence of many fossils from the upper Eocene part of the Dayu section in the Lunpola Basin (revised age of Fang et al., 2020). These fossils include a frond of the coryphoid palm *Sabalites* Sap. (Su et al., 2019), fruits of Sapindaceae (*Koelreuteria*; Jiang et al., 2019), Ulmaceae (*Cedrelospermum*; Jia et al., 2019), and leaves of Araceae (*Limnobiophyllum*; Low et al., 2020) and fishes including the climbing perch of the family Anabantidae (Eonabas; Wu et al., 2017), as well as water strider (*Aquarius*, Cai et al., 2017). However, the fossil site with the richest plant species found so far in this region is that of the middle Eocene (~47 Ma) Jianglang outcrop in the Bangor Basin (Su et al., 2020). This site has yielded more than 70 morphotypes of fruits, seeds, and leaves, and leaf physiognomy points to a low elevation subtropical valley ecosystem under a monsoonal climate (Su et al., 2020).

Our aims in this paper are to describe and compare in detail fossil remains attributed to Malvaceae from this middle Eocene Jianglang flora, and to evaluate the biogeographic significance of these recent findings.

2. Geological setting

The fossil site is near Jianglang village, Bangor Basin, central Tibetan Plateau (31°37.5'N, 90°1.5'E, 4850 m a.m.s.l.), located along the Bangong-Nujiang suture. The fossiliferous sections are in the middle part of the Niubao Formation, and represent an ancient fluvial to lacustrine environment. Fossils of plants, insects and vertebrates were recovered from five gray mudstone horizons (Su et al., 2020). The stratigraphy has been described in previous articles (Tang et al., 2019; Su et al., 2020). The age of the site is considered as middle Eocene based on combined paleontological and stratigraphic studies (Xia, 1982; Wu et al., 2016; Tang et al., 2019; Su et al., 2020) with the oldest depositional age of the site estimated at 47.5 ± 0.7 Ma, based on U-Pb radiometric dating of detrital zircons (Su et al., 2020). Nearly 3000 fossils have been excavated by the Paleoecology Research Group from Xishuangbanna Tropical Botanical Garden, CAS, during four fieldwork seasons (2016-2018 and 2020). The plant fossils represent different organs such as leaves (64.1%), fruits and seeds (19.5%), stems (12.7%), tubers (3.5%) and flowers (0.3%). A preliminary biodiversity analysis shows that these fossils represent at least 70 morphotypes indicative of a subtropical environment (Su et al., 2020). The quantitative environmental analysis based on leaf form is supported by detailed taxonomic works on species growing in modern, or reconstructed, subtropical floras such as the fossil genus *Lagokarpos* McMurrin et Manchester (Tang et al., 2019), *Ailanthus* Desf. (Liu et al., 2019), *Stephania* Lour. (Del Rio et al., 2021a), *Ventilago* Gaertn. (Del Rio et al., 2021b) and *Illigera* Blume (Wang et al., 2021b).

3. Materials and methods

All three fruit fossils studied here, numbered XZBGJL1-0319, XZBGJL1-0510 and XZBGJL1-0014 (from the section 1, Su et al., 2020) in the collection, are compressed specimens from the Jianglang site (Su et al., 2020). These fruits, as well as all the paleobotanical collection from the Jianglang site, are housed in the Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, China. The specimens were observed using a stereomicroscope (Leica S8APO, Germany) and for detailed information on the venation photographed using a smart digital microscope (Zeiss Smart Zoom 5, Germany) and, for a general view, a Nikon D850. Measurements were made from the photographs using ImageJ software (Rasband, 2016).

Because the specimens studied here are fin-winged fruits, we follow the venation terminology developed previously for leaves (Ellis, 2009), as well as terminology in prior relevant literature relating to these types of fruit (Manchester and O’Leary, 2010; Jia et al., 2021; Wang et al., 2021a). Initial comparisons were made with existing literature describing fin-winged fruits (Manchester and O’Leary, 2010) and herbarium sheets consulted online (Appendix 1), including the Queensland Department of Environment and Science (2020), the New York Botanical Garden (NYBG), the National Herbarium of the Netherland (NHN), the Muséum National d’Histoire Naturelle, Herbier National (P), the Harvard University Herbaria (HUH), the Kew Herbarium (K), the Guangxi Institute of Botany (IBK) and the Chinese National Herbarium (PE). Photographs of modern specimens figured in this paper were taken from the online digital databases of these herbaria (See vouchers in appendix 1). The map reconstruction (Fig. 4) was made using the software QGIS 3.18 and the base map is from the Natural Earth Website (<https://www.natureearthdata.com>).

4. Systematics

Family – Malvaceae Juss.

Sub-family – Sterculioideae Burnett

Genus – *Firmiana* Marsili

Species – *Firmiana* sp.

Exemplary specimen – XZBGJL1-0510

Repository – Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, China.

Stratigraphy – Niubao Formation, Bangor Basin, middle Eocene.

Locality – Jianglang village, Bangor County, central Tibetan Plateau, China.

Description – Fruit valve foliaceous (Fig. 1), elliptical, dehiscent, which is opened in the distal and proximal part and attached in the seeds area in our specimen (Fig. 1A), oblong, or ovate if fully opened, length min. 50 mm, width ca. 17 mm (ca. 31 mm fully opened). Proximal end not preserved, distal end constricted and acute (Fig. 1A). Ventral suture corresponding to the margin of the valve (dehiscence zone) thick. Dorsal suture (or midvein) straight and thick. Venation pinnate, secondary veins starting at the ventral suture, ramifying in the course and reaching the dorsal suture (Fig. 1BD), tertiary veins percurrent, straight or sinuous (Fig. 1D). Quaternary veins not preserved. Seed scars positioned on each side of the ventral suture in the proximal thickened part of the valve margin (Fig 1ABC), two per side as revealed by the attachment scar zones (Fig. 1AB).

Systematic affinity – The fruit presented here corresponds to a dehiscent foliaceous valve, with pinnate venation, and seeds positioned on each side of the ventral suture. These characters point to an affinity to the sub-family Sterculioideae in the family Malvaceae (Bayer and Kubitzki, 2003) and exclude its affinity to other angiosperm families. The morphological variation of fruits in the Sterculioideae is wide, and has been investigated previously using an optimization of fruit characters phylogeny (Wilkie et al., 2006).

Among Sterculioideae, only few genera possess fruits with a papery texture (sensu Wilkie et al., 2006) showing clear venation such as in our fossils, namely, *Hildegardia* Schott & Endl., *Firmiana*, *Pterocymbium* R. Br., and *Scaphium* Schott & Endl (Wilkie et al., 2006). These genera form a clade within “the Colas clade” whose fruit texture is the synapomorphy (Wilkie et al. 2006). *Hildegardia* has an indehiscent follicle (Fig. 2A) (Wilkie et al., 2006) and *Pterocymbium* and *Scaphium* have basal seeds, contrary to what is seen in our specimen (figs. 2B, 2C). Only *Firmiana* exhibits all characters that can be observed from our fossil material (Fig. 2D). Despite the fact that the number of ovules per locule is more than one and the marginal position of the seeds seen in our fossil is plesiomorphic within the Colas clade (Wilkie et al., 2006), the venation pattern is identical to that seen in modern fruits of *Firmiana* and can be apomorphic to the genus (Fig. 1D, Fig. 2G). The shape of the seed-scar is also identical (Fig. 2F). The secondary veins starting at the ventral suture and then ramifying and reaching the dorsal suture is a unique feature already noted (Xie et al. 2014; figs. 1D, 2G). The fossil specimen is open in the distal part as well as in the proximal part, and attached in the medium part of the fruit (Fig. 1A). The fruit of *Firmiana* is completely open at full maturity (Fig. 2D), but we can find examples of fruits having a similar structure due to immaturity of the fruits and/or compressions in collections of modern species (Fig. 2E). Therefore, the characters of the fossil specimen from Jianglang are consistent with it being a compression of a fruit of *Firmiana*.

However, the genus *Firmiana* seems paraphyletic, and the generic delimitation between *Hildegardia* and *Firmiana* was not resolvable based on sequence data from a single chloroplast region (Wilkie et al. 2006). This result might be due to frequent hybridization that can lead to poor resolution in the phylogenetic analysis (Wilkie et al., 2006; Abdullah et al., 2019); however, results from a broader sampling of genes including from the nuclear genome are not yet available. The molecular data available thus might fail to differentiate both closely related genera rather than point out a paraphyletic issue, as previously suggested (Xie et al. 2014). The

traditional delimitation of these genera was made using fruit characters (dehiscence vs indehiscence), a delimitation that we use here to define *Firmiana*.

There are only a few leaf fossil records of *Firmiana* and they are reported from the late Oligocene of India, and the Miocene of China and South Korea (Wolfe, 1977; Srivastava and Mehrotra, 2013; Xie et al., 2014; Jia et al., 2021). Fossil folicles are represented by only two species, *Firmiana sinomiocenica* Hu et Chaney and *F. yunnanensis* Xie et Manchester from the Neogene in Asia (Table 1). *Firmiana yunnanensis* is characterized by a weak, zigzag midvein that contrasts with the strong and nearly straight midvein of our specimen (Fig. 1, Table 2). *Firmiana sinomiocenica* has a similar venation pattern to our specimens, but its round apex and weak marginal vein are different from the specimen described here (Fig. 1A, Table 2). However, we have only one specimen, which prevents any interpretation of intra-specific variation and so leads us away from describing at species level based on these few differences.

There are 17 modern species of *Firmiana* (POWO, 2019) ranging from East Africa to East Asia and Malesia, and the diversity center today is in East Asia (Appendix 2). The fruit is highly conservative among modern species with only few differences in the size, general shape, apex shape, and the midvein course (Tang, 2007; Xie et al., 2014; Jia et al., 2021). However, Xia et al. (2014) show that these differences are often overlapping due to natural intraspecific variation of living species in China (Tang, 2007; Huang et al., 2011). Here we further confirm that many characters overlap among modern species of the genus (Table 2). Among all species of *Firmiana*, only two have a thick marginal vein, both occur in South China, namely *Firmiana calcarea* C.F.Liang & S.L.Mo ex Y.S.Huang and *Firmiana hainanensis* Kosterm (Table 2). These two species are similar to our fossil and may indicate an affinity of our fossil with these modern South China species.

Sub-family – Tilioideae Arnott

Genus – *Craigia* W.W. Sm. & W.E. Evans

Species – *Craigia* sp.

Repository – Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, China.

Stratigraphy – Niubao Formation, Bangor Basin, middle Eocene.

Locality – Jianglang village, Bangor County, central Tibetan Plateau, China.

Specimens checked– XZBGJL1-0014, XZBGJL1-0319.

Description –Detached membranous valves of fruit capsule (Fig. 3), elliptical and symmetric, with a distinct median suture line. Apex slightly emarginate (Fig. 3A), base round (inferred from the preserved left part, Fig. 3B, 3C), margin entire, length 14.2 mm, width min. 10 mm. Prominent fusiform locular area present in the middle part of the capsule (figs. 3A, 3B, 3C), length 8–10 mm, width 3.5–4.0 mm, crossed by the median suture. Venation straight (at least 22 veins extending left and right) radiating outward from the locule and reaching the margin of the wings (figs. 3A, 3B). Detail of the secondary venation in wing, cuticle and seeds not preserved.

Systematic affinity – Only two specimens of this morphotype were recorded from Jianglang figs. 3A, 3B). Although the fossil record of *Craigia* is well represented in the Northern Hemisphere, many fossil sites only bear a single specimen, or just a few as in our site (Kvaček et al., 2005), which might indicate that *Craigia* was not dominant in the ancient forest, or it was not close to the lakeshore or riverside. The specimen presented here is characterized by a membranous elliptical valve with a prominent fusiform locule area, and venation starting at the locule and radiating outward. These kinds of fruits are found in both Sapindaceae and Malvaceae (Manchester and O’Leary, 2010). However, the characteristic radiating venation with a fusiform locule is diagnostic for the genus *Craigia* (Fig. 3D) in Malvaceae (Wang et al., 2021a). Malvaceae capsules from other genera share several characters with our fossils, but can

be distinguished as follows: *Burretiodendron* Rehder fruits are very similar to those of *Craigia*, but the veins of *Burretiodendron* are much more densely arranged (e.g., Xu et al., 2020); the capsule of *Abroma* Jacq. has an obovate shape with ascending venation that is very different to our fossils; the capsule of *Kleinhovia* L. has an obcordate shape with a reticulate venation (Wang et al. 2021a).

Several fossil species of *Craigia* have been described previously based on overall shape and seed characters (Table 1). The specimens of *Craigia* described here differ from *Craigia hainanensis* in their general shape and size (ca. 11 mm length for *C. hainanensis*, ca. 14 mm length for the specimens here) and the rounded base (Jin et al., 2009). The specimens from Jianglang are very similar to other fossil species described from Eurasia and North America, namely *Craigia lincangensis*, *C. bronni*, and *C. oregonensis* (Kvaček et al., 2005; Wang et al., 2021a). These species are distinguished by the number and shape of their seeds, and in part their size and base morphology (Wang et al., 2021a). However, seeds and the basal part of the fruits are not preserved in our specimens. The size of our specimens also matches those of all three fossil species (Wang et al., 2021a).

There are only two modern species of *Craigia*, namely *Craigia kwangsiensis* H.H.Hsue and *Craigia yunnanensis* W.W.Sm. & W.E.Evans (POWO, 2019). *Craigia* is a tree present in nothophyllous evergreen forests to paratropical evergreen rainforests in Yunnan, south of Guangxi, Guizhou and Tibet, as well as in north Vietnam and Myanmar (Kvaček et al., 2005, Ding et al. 2019). These species are described based on differences in leaf characters, but the fruits of both species are not distinguishable and differ from the fossils, including from the specimens presented here by having a larger size (ca. 2.5-3.5 cm in length) (Shu, 2007). In this study, we describe these specimens only as *Craigia* sp. Specimens with more morphological characters are needed to identify our fossil material to species level.

5. Discussion

The *Firmiana* fossil record is sparse with all unambiguous (fruits) record only found in Asia (Table 1, Fig. 4A). The fruit presented here is the first definitive report of *Firmiana* during the Eocene, and consistent with a prior estimation of the age of origin of *Firmiana* as being during the Eocene, which was based on the fossil record of Malvaceae and molecular data (Cvetković et al., 2021). Some leaf fragments assigned to *Firmiana* have been described from the Eocene of Liaoning Province, but remain ambiguous without co-occurrences of the fruits (Hu and Chaney, 1940; WGCPC, 1978; Xie et al., 2014). Pollen grains have been reported from the Eocene Shahejie Formation, China and may be morphologically close to *Firmiana simplex* (Song et al., 2004). Allegedly Oligocene leaves have been reported from Liaoning Province, but without any descriptions or illustrations (Jin and Shang, 1998). Leaves from the Oligocene of Assam, India, have also been reported (Srivastava and Mehrotra, 2013), and named *Firmiana oligocenica* Srivastava and Mehrotra, a species which has a close resemblance with those of *Firmiana* and considered here as a reliable record despite the lack of co-occurring fruits. Wolfe (1977) mentioned *Firmiana alaskana* (Newb.) Wolfe in a list of leaf species from the Oligocene Alaska. This combination is not formal due to the lack of any morphological description. The basionym corresponds to *Ficus alaskana* Newb. (Newberry, 1898). The leaf is trilobate, wide ovate in shape, actinodromously veined, and has a cordate base without evident dentation on its margin (images presented in appendix 3). This morphology indeed resembles those found in modern *Firmiana* species, e.g., *Firmiana kwangsiensis* (H.H. Hsue) H.H. Sue, but is also indistinguishable from the morphotaxon, i.e., *Dombeyopsis lobata* Unger, which is considered to be the foliage corresponding to fruits of *Craigia brownii* due to their consistent association at European fossil sites (Kvaček et al., 2005). Consequently, we consider this record of Alaskan record of *Firmiana* as uncertain and do not take it into account unless its affinity is confirmed by further examination.

Several Miocene fruit species have been recorded in East Asia, namely *Firmiana sinamiocenica* Hu and Chaney from Shangdong, China and North Gyeongsang, South Korea, as well as *Firmiana yunnanensis* Xie and Manchester from Yunnan and Shangdong, China (WGCP, 1978; Xie et al., 2014; Wang, Shi, et al., 2020; Jia et al., 2021). Based on the fossil record of *Firmiana*, we infer that the genus probably originated in Asia, and especially in East Asia as shown by the earliest fossil record described here, as well as the summary of the fossil record (Table 1), and its modern distribution (Fig. 4A, Appendix 2). The group may have dispersed into India during the late Eocene-Oligocene and to Southeast Asia and Oceania during the Neogene (Fig. 4A). Until now, it is too early to develop the origin region and spreading routes due to very scarce fossil record of *Firmiana*.

The fossil record of *Craigia* encompasses several species (Table 1), but contains many occurrences based on fruits and leaves (Kvaček et al., 2005; Wang et al., 2021a). An exhaustive overview of the occurrences has been summarized before (Kvaček et al., 2005; Wang et al., 2021a), so here we give only a brief review of the fossil record and biogeographic history of *Craigia* to emphasize the importance of this new occurrence.

The earliest occurrence of fruits of *Craigia* is from the Paleogene of northwestern Kamchatka and South Sakhalin (North Asia, Fig 4B). During the Eocene, *Craigia* migrated to East Asia and North America (Fig. 4B), and during the Oligocene, it became a common element in the forests of Europe, as well as being present in North America and Asia (Table 1). This period probably represented the largest distribution range of *Craigia* in the Northern Hemisphere. During the Neogene, *Craigia* disappeared in North America, and gradually declined in Europe where it persisted until the end of the Pliocene. In Asia, the fossil record indicates that *Craigia* inhabited northern part of the region until the Miocene (Fig. 4B), but a new fruit specimen from Lincang, Southwest Yunnan, indicates that *Craigia* already occupied its modern distribution area in the late Miocene (Wang et al., 2021a). The new occurrence

presented here, together with previous records show that *Craigia* was already widespread in East Asia during the Eocene in terms of longitude (Fig. 4B). Tectonically, the Jianglang site was about 9 degrees southward of its present position during the Eocene (Su et al., 2020).

In the middle Eocene, the Jianglang site was at a relatively low elevation of $\sim 1.5 \text{ km} \pm 0.9 \text{ km}$ and experienced a subtropical monsoonal climate (Su et al., 2020). This climate was similar to that experienced by contemporaneous locations in South China where *Craigia* is also known to have existed, such as Hainan Island (Jin et al., 2009) where temperature and precipitation estimates are identical to those of Jianglang within uncertainty (Spicer et al., 2014; 2016, 2017). However, while South China experienced a summer-wet regime similar to that of the present day, the Central Tibetan Valley hosting the Jianglang flora appears to have been winter wet (Xiong et al., In Press). These occurrences show that *Craigia* occupied a wide latitudinal range in East Asia during the Eocene (Fig. 4B), when a humid climate spanned both south and north China in the Eocene (Sun and Wang, 2005). When in the year most of the precipitation occurred does not appear to have been important to *Craigia's* presence. The persistence of a warm and wet climate in south China during the Oligocene and Neogene (e.g., Linnemann et al., 2018) perhaps suggests why this genus survived in this part of Asia where is now threatened with extinction (International Union for Conservation of Nature, IUCN, 1998a; b).

Together, the new fossil records described here of *Firmiana* and *Craigia* attest to the occurrence of arborescent Malvaceae in the Tibetan region during the middle Eocene. It is becoming increasingly apparent that the Tibetan region played a key role in the diversification of *Firmiana* in East Asia, and provided a suitable environment for the survival of *Craigia* at a low latitude. The Eocene Tibetan region appears to be an important area to understand the modern diversity and biogeographic pattern of plants in Asia and across the North Hemisphere today (Deng et al., 2020).

6. Conclusion

The family Malvaceae is represented by two arborescent genera found in the middle Eocene Jianglang site, namely *Firmiana* and *Craigia*. The *Firmiana* specimen represents the earliest occurrence of the genus so far and is consistent with a prior estimation of the age of origin of *Firmiana* as being during the Eocene, which was based on a combination of the fossil record of Malvaceae and molecular data. From the fossil record of *Firmiana* and its modern distribution, we infer that the genus may have originated in East Asia and subsequently diversified in South China and Southeast Asia. The new occurrence of *Craigia* confirms that the genus was already widely distributed in Asia during the Eocene

We conclude that the Tibetan region played a key role in the diversification of *Firmiana* in East Asia, and provided a suitable environment for the survival of *Craigia* at a low latitude. The Tibetan region in the Eocene, long overlooked from a paleobotanical perspective, appears to be an important area to understand the modern diversity and biogeographic pattern of plants in Asia and across the Northern Hemisphere today.

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TABLE 1. Fossil record of *Craigia* W.W. Sm. & W.E. Evans and *Firmiana* Marsili.

Taxon	Organs	Area	Age	Reference
<i>Craigia brononii</i> (Unger)	Fruit		Late Eocene	Kvaček et al.
Kvaček, Bůžek & Manchester	& leaf	Europe*	to Late Pliocene	2005, Wang et al. 2021
<i>Craigia hainanensis</i> J. H. Jin et T. M. Kodrul	Fruit	Hainan, China	Early-Late Eocene	Jin et al. 2009
<i>Craigia lincangensis</i> Wang and Xie	Fruit	Yunnan, China	Late Miocene	Wang et al. 2021
<i>Craigia oregonensis</i> (Arnold) Kvaček, Bůžek & Manchester	Fruit & leaf	East and Central Asia*, North America*	Paleocene to Late Miocene	Kvaček et al. 2005, Wang et al. 2021
<i>Firmiana oligocenica</i> Srivastava and Mehrotra	Leaf	Assam, India	Oligocene	Srivastava and Mehrotra 2013
<i>Firmiana sinamiocenica</i> Hu and Chaney	Fruit & leaf	Shangdong, China and North Gyeongsang, South Korea	Early-Middle Miocene	Hu and Chaney 1940, Jia et al. 2021
<i>Firmiana yunnanensis</i> Xie and Manchester	Fruit	Yunnan and Shangdong, China	Early-Late Miocene	Xie et al. 2014, Wang et al. 2020

*note: for details of the areas please refer to the references cited.

TABLE 2. Morphological comparison of *Firmiana* Marsili modified from Xie et al. 2014 with additions of species outside of China. In bold: fossil species. See appendix 1 for full herbaria reference.

Species	Length (cm)	Width (cm)	Length/Width ratio	Seed number	Shape	Marginal vein thickness	Apex shape	Midvein course	References/voucher
<i>Firmiana</i> sp.	min. 5	ca. 3.1	NA	4	Oblong-ovate	Thick	Acute	Straight	This study
<i>Firmiana yunnanensis</i> Xie et Manchester	4.7-8.5	2.7-3.8	1.7-2.2	2-4	Oblong-ovate	Thick	Retuse	Zigzag	Xie et al. 2014
<i>Firmiana sinamiocenic</i> Hu et Chaney	7.5-10.5	2.4-4.2	2.4-2.5	2-4	Oblong-ovate	Weak	Rounded	Straight	Wang et al. 2020, Jia et al. 2021
<i>Firmiana bracteata</i> DC.	10-10.6	3.2-3.3	3.1-3.2	2	Oblong-elliptical	Weak	Rounded	Straight	Balansa 3743
<i>Firmiana calcarea</i> C.F.Liang & S.L.Mo ex Y.S.Huang	5-7	2-3	2.3-2.5	2-4	Ovoid	Thick	Retuse	Straight	Huang et al. 2011, Xie et al. 2014
<i>Firmiana colorata</i> (Roxb.) R.Br.	7.2-9.9	2.8-3.2	2.6-3.3	2-4	Tongue-shaped	Weak	Rounded	Straight	Tang et al. 2007, Xie et al. 2014
<i>Firmiana danxiaensis</i> H.H.Hsue & H.S.Kiu	8-10	2.5-3	3.2-3.3	2-3	Oblong-lanceolate	Weak	Rounded	Straight	Tang et al. 2007, Xie et al. 2014
<i>Firmiana diversifolia</i> A.Gray	6-7	1.9-2.8	2.4-3	1-2	Oblong-lanceolate	Weak	Acute	Straight	A.C. Smith 7059, 7307
<i>Firmiana fulgens</i> (Wall. ex Mast.) K.Schum.	6	2.3	2.6	1-2	Oblong-ovate	Weak	Rounded	Straight	Karm Singh Kaloce 28

<i>Firmiana hainanensis</i> Kosterm.	7	3	2.3	3-5	Ovoid Oblong-lanceolate	Thick	Wedge	Acute	Strongly straight	Tang et al. 2007, Xie et al. 2014
<i>Firmiana kerrii</i> (Craib) Kosterm.	4-7.5	1.1-2.5	2.9-3.2	1-2	Ovoid Oblong-lanceolate	Weak	Rounded	Acute	Strongly straight	J.F. Maxwell 197-299, 06-271
<i>Firmiana major</i> (W.W.Sm.) Hand.-Mazz.	7	4.5	1.6	NA	Ovate Oblong	Weak	Rounded	Acute	Strongly straight	Tang et al. 2007, Xie et al. 2014
<i>Firmiana malayana</i> Kosterm.	6.9-10.6	2-3	2.5-3.6	2	Ovate Oblong-lanceolate	Weak	Rounded	Acute	Strongly straight	V. Balgooy 2567, FRI 4670
<i>Firmiana papuana</i> Mildbr.	5.5-7.3	2.4-3.1	2.1-2.6	1-5	Ovate Oblong	Weak	Rounded	Acute	Strongly straight	A.G. Floyd 5255, P.I. Forster 28747
<i>Firmiana simplex</i> (L.) W.Wight	6-11	1.5-2.5	4-4.4	2-4	Ovate Oblong	Weak	Rounded	Acute	Strongly straight	Tang et al. 2007, Xie et al. 2014
<i>Firmiana subglabra</i> (V.Abraham & Dutt) Kosterm.	ca. 5	ca. 3	NA	2-4?	Ovate Oblong-lanceolate	Weak	Rounded	Acute	Strongly straight	A.K. Dutt 139
<i>Firmiana sumbawaensis</i> Kosterm.	6.8-7.5	2.3-2.7	2.5-3	2-4	Ovate Oblong	Weak	Rounded	Acute	Strongly straight	Kostermans 19110

note: *Firmiana kwangsiensis* H.H.Hsue, *Firmiana minahassae* (Koord.) Kosterm. and *Firmiana pulcherrima* H.H.Hsue have no data for the fruit.

Figures

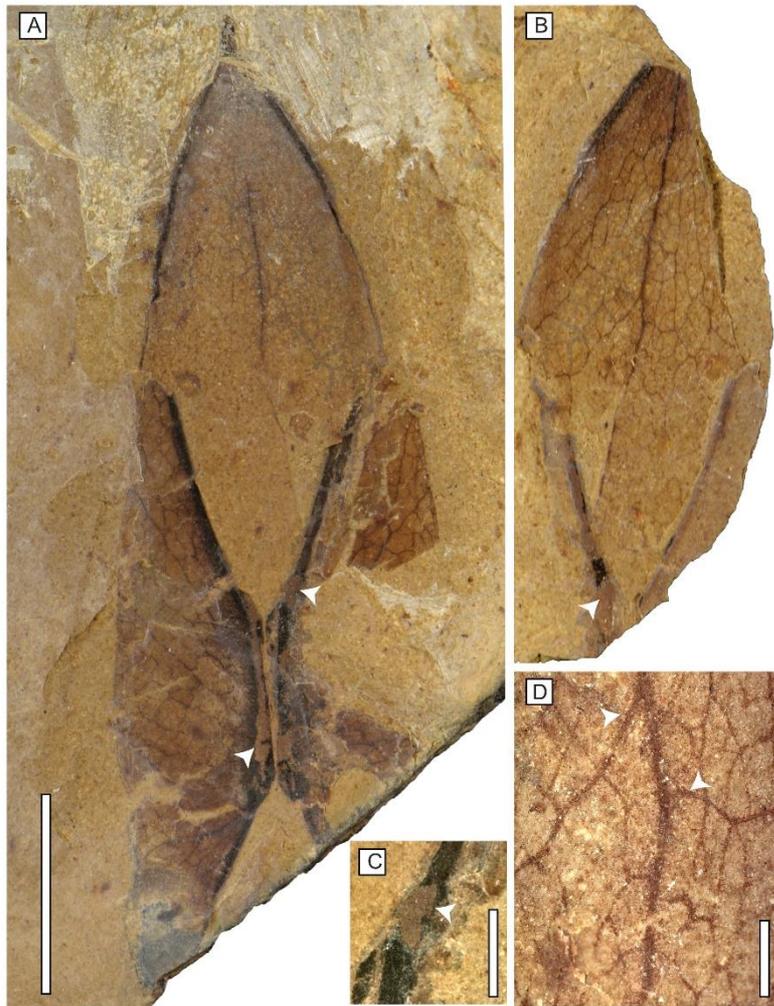


Figure 1 *Firmiana* from Jianglang, central Tibetan Plateau. A, Specimen XZBGJL1-0510. Arrows = seed scars at the margin of the fruit. B, Counterpart of the specimen. Arrows = another seed scar at the margin of the fruit. C, Detail of a seed scar. D, Detail of the venation from the counterpart. Arrows = secondary veins reaching the dorsal suture. Scale bars A, B, D = 10 mm; C = 2mm.

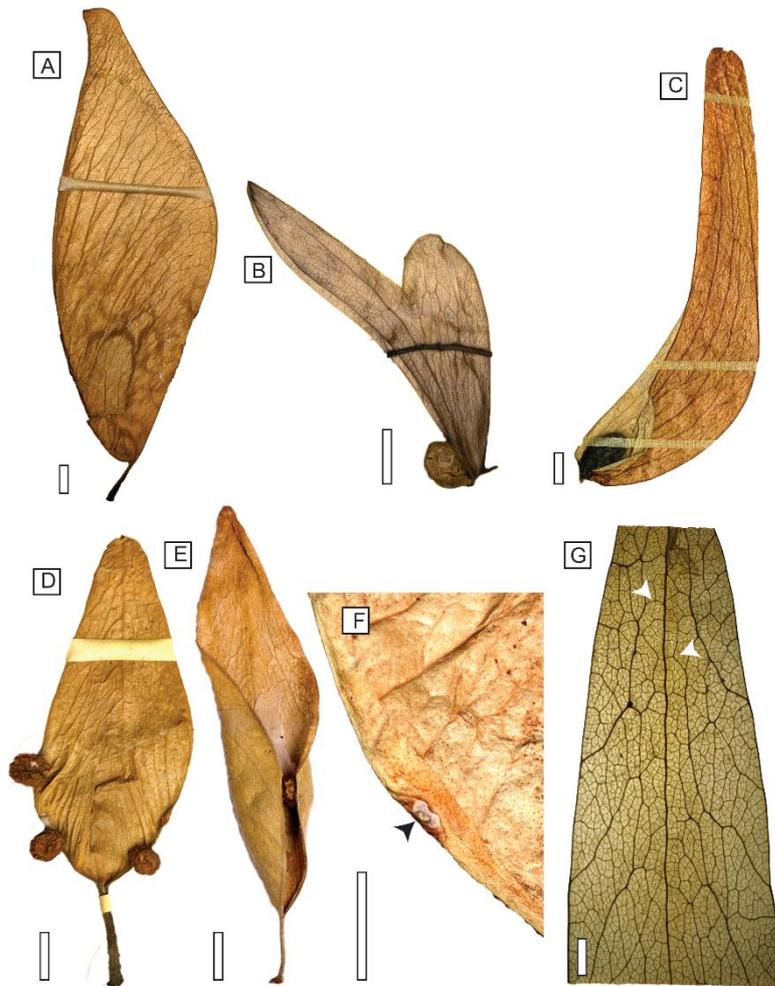


Figure 2 Modern fruit specimens of Sterculioideae Burnett sharing a similar papery character as inferred for the fossil material. A, *Hildegardia perrieri* (Hochr.) Arènes (Voucher = 8585-SF). B, *Pterocymbium* sp. (Voucher = Sangkhachang 109). C, *Scaphium macropodum* (Miq.) Beumée ex K.Heyne (Voucher = Elmer 21759). D, *Firmiana hainanensis* Kosterm. (Voucher = Lau 1932). E, *Firmiana papuana* mildbr (Voucher = S. McKenna SM88). F, Detail of the seed scar at the margin of the fruit of *Firmiana simplex* (L.) W.Wight, (Voucher = Anonymous 230). G, Detail of the venation of the fruit of *Firmiana colorata* (Roxb.) R.Br. (XTBG living collection, collected in January 2021, CDR). Arrow = secondary veins reaching the dorsal suture. Scale bars = 10 mm.

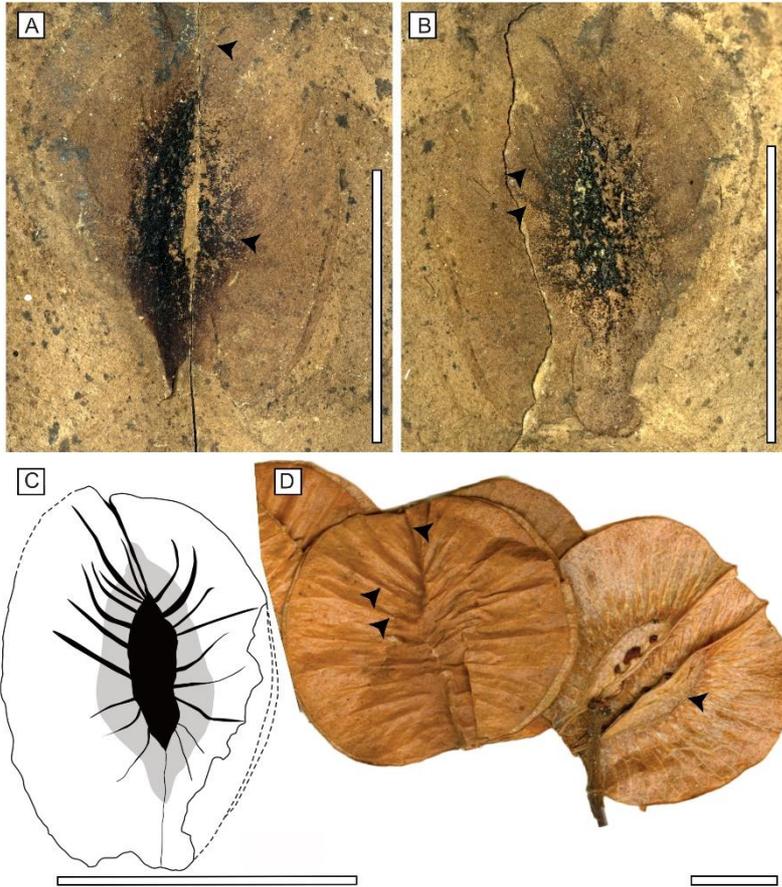


Figure 3 *Craigia* sp. from Jianglang central Tibetan Plateau and modern species *Craigia yunnanensis* W.W.Sm. & W.E.Evans A, Specimen XZBGJL1-0014. Upper arrow = median suture line, right arrow= locule impression. B, Specimen XZBGJL1-0319. Arrows = radiating venation. C, Diagrammatic view of the specimen XZBGJL1-0319. D, Modern fruits of *C. yunnanensis* (Voucher: A. Henry 11442). Upper arrow = median suture line, left arrows = radiating venation, right arrows = locule impression. Scale bars = 10 mm.

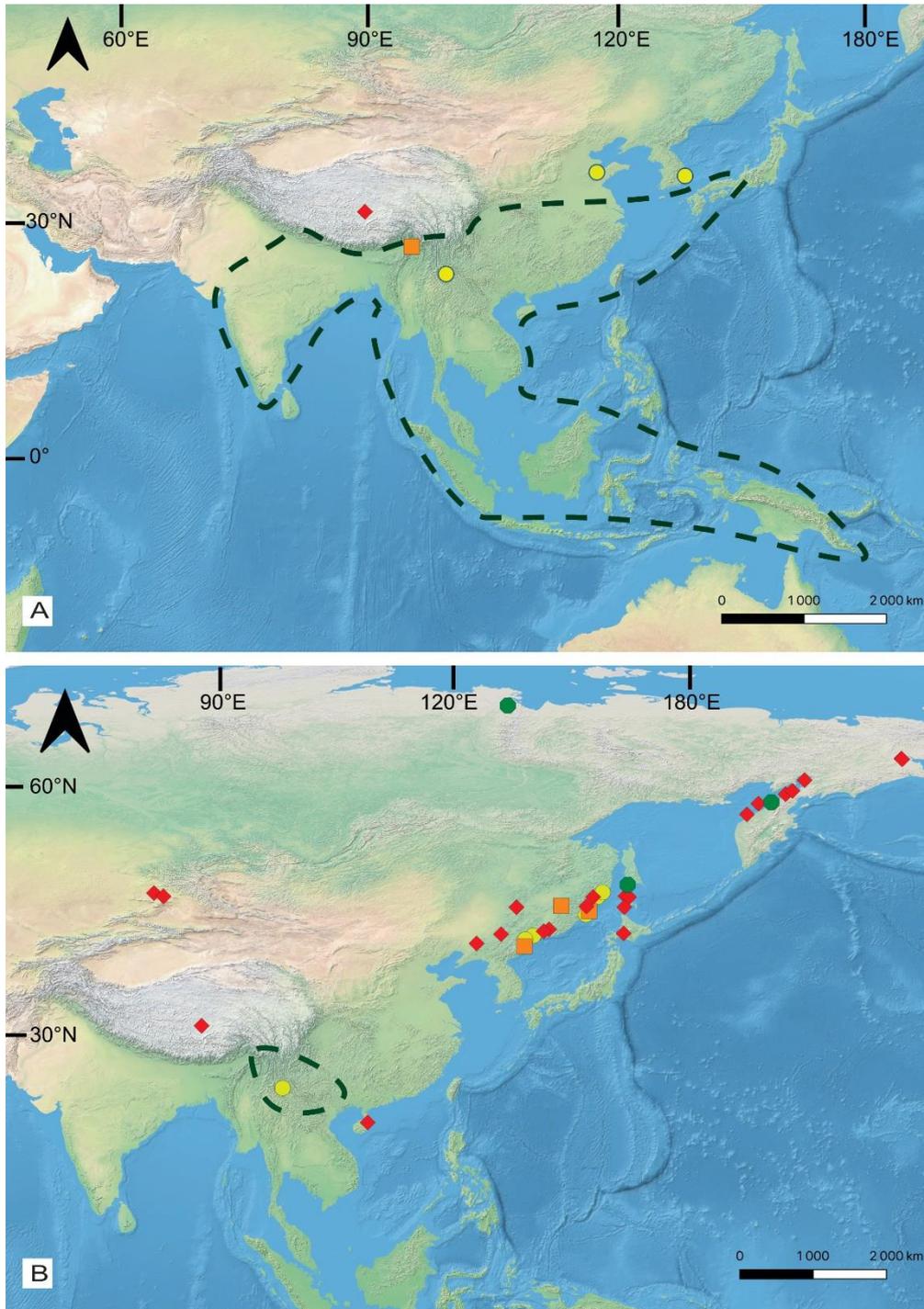


Figure 4 A, Map showing fossil macrofossil record of *Firmiana*, and part of its modern distribution (excluding Africa). B, Map showing fossil *Craigia* during the Cenozoic in Asia and modern distribution. Paleocene: green polygon, Eocene: red rhombus, Oligocene: orange square, Miocene: yellow circle. Modern distribution: dotted line (data from POWO 2019, Appendix 2). Base map is from the Natural Earth website <https://www.naturalearthdata.com>.