Original article

Ayano Ito[1], Arata Momohara[2*] and Zhekun Zhou[3]:
Pleistocene fossil leaflets of *Albizia kalkora* (Roxb.) Prain (Leguminosae subfamily Mimosoideae) from central Honshu, Japan, and its implications for historical biogeography

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オオバネムノキ *Albizia kalkora* (Roxb.) Prain（マメ科ネムノキ亜科）の
本州中部更新統産小葉化石と，その歴史生物地理学的意味

Abstract *Albizia kalkora* (Leguminosae subfam. Mimosoideae) is a deciduous tree distributed in Japan, China, Korea, and other countries from Southeast Asia to India. In Japan, its distribution is restricted to the evergreen broadleaved forest zone in southern Kyushu, whereas it is widely distributed in the deciduous broadleaved forest zone in China. Fossil records of *A. kalkora* from the Plio-Pleistocene have been limited in Kyushu, although *A. miokalkora*, a closely related fossil taxon, from the Miocene has been found in China, Korea, and Japan. We describe herein *A. kalkora* leaflet fossils from the Lower Pleistocene Sayama Formation and Middle Pleistocene Shoudai Formation in central Japan. We compared the leaflets with those of modern species in China with similar morphology and identified them as those of *A. kalkora* based on their size (2–3 cm long), the medial and base asymmetry, and the presence of 2–3 slender secondary veins diverging at the base. Their association with evergreen broadleaved trees in fossil assemblages indicates that *A. kalkora* expanded its distribution to central Japan during stages with warm winter temperatures. Its distribution was limited to southern Kyushu during the Late Quaternary in Japan, whereas in China it expanded widely into the deciduous broadleaved forest zone, possibly by adapting to cold winter conditions during glacial stages.
Key words: *Albizia kalkora*, biogeography, China, evergreen broadleaved forest, Pleistocene

要　旨　オオバネムノキ *Albitzia kalkora* (Roxb.) Prain（マメ科ネムノキ亜科）は，日本，中国，韓国，東南アジアからインドにかけて分布する落葉高木である。日本では九州南部の常緑広葉樹林域に分布が限られているが，中国大陸では落葉広葉樹林域にまで広く分布している。これまで日本，中国，韓国の中新統から近縁の化石種 *Albizia miokalkora* Hu et Chaney の化石が見つかっているが，鮮新・更新統の化石記録は九州に限られていた。今回，中部日本の下部更新統狭山層および中部更新統招提層から見つかった小葉の *A. kalkora* の化石を記載する。中国大陸に分布する類似の小葉形態の種と比較し，2〜3 cm のサイズで，小葉の中部・基部が非対照，基部から 2，3 本の 2 次脈を分枝するという特徴で，オオバネムノキと他の種を区別した。これまでの化石記録と同様にオオバネムノキには常緑広葉樹が随伴することから，冬季の気温が温暖な時代に中部日本に分布拡大したと考えられる。日本では第四紀後半には南九州に分布が限定されるようになったが，おそらく氷期の寒冷な冬季の気候に適応した結果，中国大陸では落葉広葉樹林帯に分布拡大するようになったと考えられる。
キーワード：オオバネムノキ，生物地理学，中国，常緑広葉樹林，更新世

Introduction

Albizia kalkora (Roxb.) Prain (Leguminosae subfam. Mimosoideae) is a deciduous tree distributed in subtropical and temperate zones of Japan, China, Korea, and other countries from Southeast and South Asia to India. In China, it is distributed widely from Yunnan and Hainan Provinces to Hebei Province (Li et al., 1998), whereas their distribution in Japan and Korea is very limited (Fig. 1). It occurs in maritime areas between Nobeoka and Hyuga in the Miyazaki Pre-

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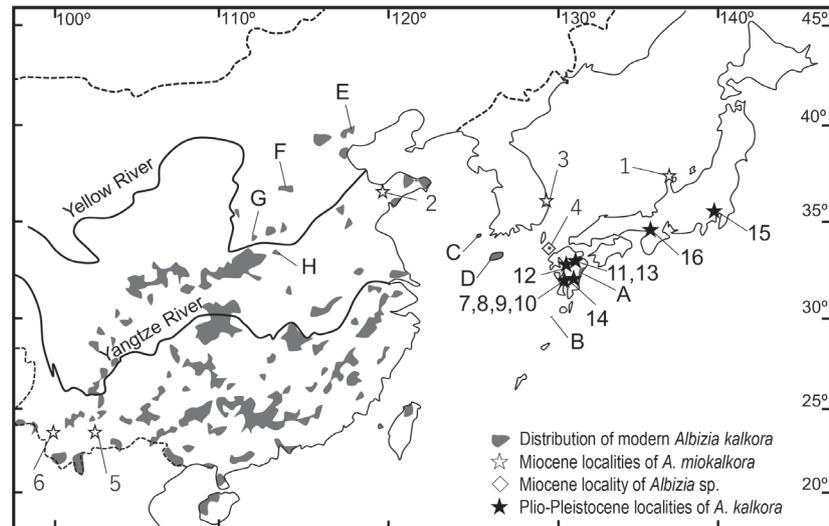
Fig. 1 Distribution of modern *Albizia kalkora* (dark gray areas, Li et al., 1998) and fossil localities from the Miocene (open stars for *A. miokalkora* and open diamond for *Albizia* sp.) and Plio-Pleistocene (closed stars) in China, Korea, and Japan. Numbers for fossil localities are shown in Table 1. Localities discussed in this paper: A, Miyazaki Prefecture; B, Nakanoshima Island; C, Hukusan Island; D, Jeju Island; E, Beijing; F, Taihang Mountains; G, Zhongtiao Mountains; H, Mt. Songshan.

fecture (Hirata, 1984) and on Nakanoshima Island in the Tokara Islands (Hatusima, 2004) in Japan and on Jeju and Huksan Islands in southwestern Korea (Oh & Pak, 2001). The population of this species in Japan is decreasing because of land development, and the species is listed as endangered (EN) in the Red Data Book of Japan (Yahara & Nagata, 2003).

Albizia miokalkora Hu et Chaney, a fossil taxon closely related to *A. kalkora*, has been described from the Miocene deposits in southern and eastern China, southeastern Korea, and western and central Japan (Table 1). The species was established by Hu & Chaney (1940) based on a leaflet found from the Shanwang Formation in Shandong Province (locality 2 in Fig. 1), which was dated to ca. 17 Ma near the end of the Early Miocene (He et al., 2011). Subsequently, legumes attributed to this species were described from the same locality (WGCPC, 1978). *Albizia kalkora* fossils from the Plio-Pleistocene have been found in Kyushu in Japan (Table 1), whereas they have not been found elsewhere in Japan.

We found leaflets of *A. kalkora* from Early and Middle Pleistocene sediment in central Japan. One was from the Lower Pleistocene Sayama Formation (locality 15 in Fig. 1) in the Kanto District, and the other was from the Middle Pleistocene Shoudai Formation in the Osaka Group (locality 16 in Fig. 1) in the Kinki District. This provides evidence of the wide distribution of *A. kalkora* during the Early and Middle Pleistocene.

In this paper, we describe the morphology of fossil leaflets from these two formations. Based on the species composition of the fossil assemblages including *A. kalkora*, we discuss the paleoenvironment of the habitat and distribution history of *A. kalkora*. The Neogene and early Quaternary floras in Japan are known to be related to the modern flora in China (Momohara, 2005), but the morphology of Chinese species relative to fossils from Japan has not been fully studied. Based on herbarium work in China and Japan, we compared the fossil leaflets with those of extant species in China, which have morphology similar to that of *A. kalkora*.

Material and methods
1. Geological settings of the fossil materials
Fossil leaflets of *A. kalkora* were included in the leaf fossil assemblages in the Lower Pleistocene Sayama Formation in the Sayama Hills in western Tokyo and the Middle Pleistocene Shoudai Formation in the Osaka Group in the Keihanna Hills in southwestern Kyoto. The locality of the Sayama Formation is a portion of riverbed of the Osawa River (35°46′33″N, 139°22′43″E, 130 m a.s.l.) in the Sayama Hills in western Tokyo. The Sayama Formation is composed of alternating sand and silt beds that are approximately 50 m thick with intercalated gravel layers (Saitama Res. Group & Kanto Quat. Res. Group, 1970; Nirei & Takegoshi, 2007). Leaf fossils were in 3 m thick fluvial silt that was conformably overlain by 7 m of marine sediment. Based on the geological structure, dipping 2° eastward with the strike of N7°W around the fossil

Table 1 Fossil records of *Albizia* during the Neogene and Quaternary in East Asia (Locality number (No.) as in Fig. 1)

No.	Species	Organs	Epoch	Locality	Formation	Age	Reference
1	*A. miokalkora*	leaflet	Early Miocene	Noto Peninsula, C. Japan	Yanagida	ca. 20 Ma, F.T. and K-Ar ages (Kano et al., 2002)	Ishida, 1969
2	*A. miokalkora*	leaflet, fruit	Early Miocene	Linqu, Shandong Prov., E. China	Shanwang	ca. 17 Ma, ^{40}Ar/^{39}Ar ages (He et al., 2011)	Hu & Chaney, 1940; WGCPC, 1978
3	*A. miokalkora*	fruit	Middle Miocene	Pohang, Gyeongsangbug-do, E. Korea	Duho	ca. 14–12 Ma (Lee et al. 1999)	Kim, 2005
4	*A.* sp.[1]	leaflet	Middle Miocene	Iki Is., Nagasaki Pref., W. Japan	Chojabaru	ca. 15 Ma (Takeshita et al. 1987)	Hayashi, 1975
5	*A. miokalkora*	leaflet	early Late Miocene	Kaiyuan, Yunnan Prov., SW. China	Xiaolong-tan	ca. 11 Ma, magnetostratigraphy (Li et al., 2015)	Tao et al., 2000
	A. bracteata	leaflet	ditto	ditto	ditto	ditto	WGCPC, 1978; Tao et al., 2000
	Albizia, Pithecellobium, Archidendron, sp. 1	leaflet	ditto	ditto	ditto	ditto	Guo & Zhou, 1992
	Albizia, Pithecellobium, Archidendron, sp. 2	leaflet	ditto	ditto	ditto	ditto	ditto
6	*A. miokalkora*	leaflet	Late Miocene	Lincang, Yunnan Prov., SW. China	Bangmai	older than 3.8 Ma, K-Ar age and floral composition (Jacques et al., 2011)	Tao & Cheng, 1983
	A. julibrissin	leaflet	ditto	ditto	ditto	ditto	ditto
7	*A. kalkora*[2]	leaflet	Late Pliocene	Daiwa, Kagoshima Pref., S. Japan	Daiwa	between 2.6 ± 0.2 Ma, F.T. age and 2.1 ± 0.5 Ma, K-Ar age (Hase & Hatanaka, 1984; Hase & Danbara, 1985)	Hase, 1988
8	*A. kalkora*[2]	?	Early Pleistocene	Nagano and Arakawauchi, Kagoshima Pref., S. Japan	Nagano	between 2.4 ± 0.3 Ma, F.T. age and 2.3 ± 0.4 Ma, K-Ar age (Hase & Hatanaka, 1984; Hase & Danbara, 1985)	ditto
9	*A. kalkora*[2]	leaflet	Early Pleistocene	Yamanokuchi, Kagoshima Pref., S. Japan	Yamano-kuchi	ca. 1.2 Ma, F.T. age (Nishimura & Miyachi, 1976; Hase & Hatanaka, 1984)	ditto
10	*A. kalkora*[2]	?	Early Pleistocene	Kagoshima Bay, Kagoshima Pref., S. Japan	Kajiki	0.96 ± 0.17 Ma, F.T. age (Hase & Hatanaka, 1984; Hase & Danbara, 1985)	ditto
11	*A. kalkora*[2]	?	Early Pleistocene	Hosenji, Oita Pref., S. Japan	Hosenji	older than 0.7 ± 0.3 Ma and 0.8 ± 0.3Ma, K-Ar ages (Kamata & Muraoka, 1982)	Iwauchi & Hase, 1987
12	*A. kalkora*[2]	leaflet	Middle Pleistocene	Yoshino, Kumamoto Pref., S. Japan	Yoshino	older than 0.37 ± 0.04 Ma, F.T. age (Iwauchi & Hase,1992)	Iwauchi & Hase, 1992
13	*A. kalkora*[2]	?	Middle Pleistocene	Shimohara to Okunameshi, Oita Pref., S. Japan	Nogami	older than 0.36 ± 0.12 Ma, F.T. age (Iwauchi & Hase, 1987)	Iwauchi & Hase, 1987
14	*A. kalkora*[3]	leaflet	Late Pleistocene	Ikemure, Miyazaki Pref., S. Japan	Ikemure	based on stratigraphic relationships (Hase, 1988)	Onoe, 1971
15	*A. kalkora*	leaflet	Early Pleistocene	Sayama Hills, Tokyo, C. Japan	Sayama	between 1.64 ± 0.1 Ma, F.T. age and 1.81 ± 0.1 Ma, F.T. age (Muramatsu, 2008)	this paper
16	*A. kalkora*	leaflet	Middle Pleistocene	Keihanna Hills, Kyoto Pref., C. Japan	Shoudai	ca. 0.5 Ma, astronomically tuned age (Lisiecki & Raymo, 2007)	this paper

[1] Described under the name of *A. miokalkora* in Hayashi (1975), but identifiable as *A. julibrissin* and related species (see text).
[2] Lacking morphological descriptions and images.
[3] Described under the name of *A.* sp. in Onoe (1971), but identifiable as *A. kalkora* (see text).

site (Ueki & Sakai, 2007), the horizon of fossil assemblage was 13 m below the Sayama-gomashio tephra bed (SGO) dated to 1.64 ± 0.1 Ma by the fission track (FT) method (Muramatsu, 2008) and 16 m above the Sayama-garasushitu tephra bed (SYG) dated to 1.81 ± 0.1 Ma by the FT method (Muramatsu, 2008). The SYG tephra bed was correlated with the Tsuike tephra bed in the Uonuma Group, deposited approximately 1.7 Ma (Sakai & Kurokawa, 2002; Suzuki et al., 2011). Therefore, the age of this fossil assemblage was estimated to be 1.64–1.7 Ma.

The locality of the Osaka Group is site No. 110 in Mitamura (1992), situated in Minoyama (34°50′13″N, 135°43′24″E, 45 m a.s.l.), Yawata City, Kyoto Prefecture. The sediments including the leaf fossil assemblage belonged to the Shoudai Formation in the upper part of the Osaka Group (Mitamura, 1992). The leaf fossil assemblage was in fluvial silt 2.5 m below the Kasuri tephra bed, dated to 0.42 ± 0.08 Ma by the FT method (Suzuki, 1988). The Ma 8 marine clay bed situated just at or several meters above the Kasuri tephra bed in this area (Mitamura, 1992) was correlated with MIS 13 (Yoshikawa & Mitamura, 1999), which was astronomically tuned to ca. 0.5 Ma (Lisiecki & Raymo, 2007).

2. Preparation of fossil leaf materials

We collected several sediment blocks that included leaf fossils from outcrops and brought them to the laboratory. The sediment blocks were placed on a stainless steel net and macerated by freezing or chemicals. The blocks from the Sayama Formation were macerated by freezing, followed by melting in a heater three times.

The sediment blocks from the Shoudai Formation were placed in 1% KOH solution for 3 days, neutralized in acetic acid, and then placed in 0.1% hydrogen peroxide (H_2O_2) solution for approximately 10 minutes. After maceration, we soaked the blocks on a net in a water tub and sprayed water from a syringe to remove silt on leaves. We removed leaf fossils from the sediment blocks using a paintbrush and tweezers. To remove inorganic materials, leaves were placed into a solution of 20% hydrogen fluoride (HF) for approximately one week and neutralized in a solution of sodium hydrogen carbonate ($NaHCO_3$). We stored the leaves with 70% ethanol between two sheets of plastic film for preservation and observation. The specimen from the Shoudai Formation was cleared in 3% KOH solution and chloral hydrate, stained in a safranin solution, dehydrated using an ethanol–xylene series, and mounted into biolite (Okenshoji Co., Ltd.) to prepare a glass slide.

For identification of fossil leaves, we compared them with modern specimens stored in the herbarium of the Faculty of Horticulture, Chiba University (MTDO) and cleared leaf specimens made from the herbarium specimens.

3. Herbarium works

To select taxa with leaflet morphology similar to that of *A. kalkora*, we reviewed floras of China (Chen ed., 1988; Cui ed., 1998; Fu ed., 1993; Lee ed., 1995; Wei ed., 1994; Wu & Nielsen, 2010) and images of herbarium specimens in the Chinese Virtual Herbarium (CVH) (IBCAS, 2013). We chose 10 genera, including species with leaflet morphology similar to that of *A. kalkora*, that is, bilaterally asymmetrical leaflets approximately 3 cm in longitudinal length. Those were *Adenanthera*, *Albizia*, and *Entada* in Leguminosae subfamily Mimosoideae, and *Caesalpinia*, *Cassia*, *Gleditsia*, *Gymnocladus, Peltophorum, Pterolobium*, and *Tamarindus* in Leguminosae subfamily Caesalpinaceae (Table 2). Tribe Ingeae of the subfamily Mimosoideae native to China and Japan includes *Albizia*, *Archidendron*, and *Pithecellobium* (Wu & Nielsen, 2010), but the latter two genera have large (more than 4 cm in length) and bilaterally symmetrical leaflets.

The genus *Albizia* native in China, Korea, and Japan includes 17 species (Chen ed., 1988; Wu & Nielsen, 2010). Among them, *A. attopeuensis* (Pierre) Nielsen and *A. lucidior* (Steud.) Nielsen have larger leaves, 5–10 cm in length, and six other species such as *A. chinensis* (Osbeck) Merr., *A. garrettii* Nielsen, *A. julibrissin* Durazz., *A. mollis* (Wall.) Boiv., *A. sherriffii* Baker, and *A. simeonis* Harms have leaves smaller than 1.8 cm. We excluded these eight species from the comparison with the fossil leaflets.

We conducted herbarium work in the Xishuangbanna Tropical Botanical Garden (HITBC) and Kunming Institute of Botany (KUN), which has a vast collection of subtropical and temperate legumes, in China, and the University Museum, University of Tokyo (TI), and Faculty of Horticulture, Chiba University (MTDO) for *Albizia* distributed in Japan. We observed herbarium specimens of taxa belonging to the selected genera, and took their photos and made sketches of their leaflets.

Results

1. Description of fossil *Albizia kalkola*

Materials studied: Two leaflets (AI0001, AI0002) from the Sayama Formation. One leaflet (AM335-1) from the Shoudai Formation of the Osaka Group (Fig. 2).

Description: Leaflet (Fig. 2) coriaceous, ovate, asymmetrical (narrower upper side), length 2.8–3.5 cm, width 1.2–1.3 cm, asymmetrical (rounded upper side and truncate lower side) at the base, obtuse at the apex, entire margin; primary vein moderate, strait or weakly curved, positioned about one third close to upper margin, penetrate to apex; secondary veins slender, eucamptodromous, looped several times near the margin; a clear secondary vein diverging at angles of about 30° from base and extending to upper half of leaflet; one or two subordinate secondary veins diverging at angles of about 50° to 70° from the base of leaflet; four or five secondary veins diverging at angles of about 40° from middle and upper part of primary vein; two or three interior secondary veins parallel to secondary veins; epidermal and intercostal tertiary veins reticulate; exterior tertiary veins branching from the secondary veins and looping to adjacent exterior tertiary veins near the margin (Fig. 3); quaternary and quinternary veins reticulate, forming areoles of 0.1–0.2 mm size; freely ending veinlets branched two or more times, ending with idioblasts (Fig. 4); petiole length 1 mm, with inflated, transversely wrinkled pulvinus.

2. Morphology of modern leaflets of *Albizia kalkora* and related species

Based on herbarium work on taxa distributed in Japan and/or China, we selected 25 species with leaflets of 2–3 cm in length and asymmetrical bases, similar to *A. kalkora*. They were classified into five morphological types (Types A–E) based on the number of secondary veins diverging at the base, the medial symmetry, and the shape of the leaflet base (Table 2, Figs. 5, 6). Type A had one secondary vein diverging at the base and included 21 species: *Adenanthera pavonina, Albizia bracteata, A. crassiramea, A. duclouxii, A. procera,*
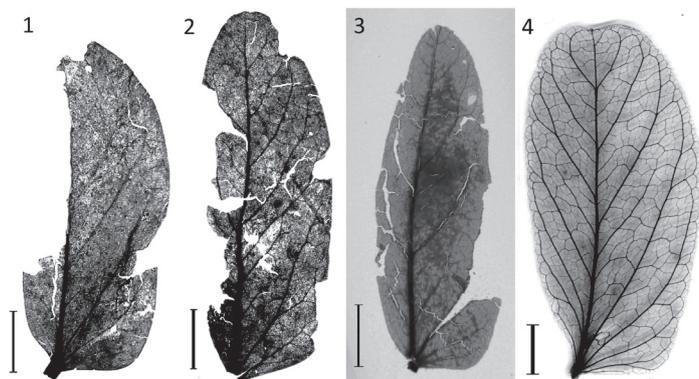
Fig. 2 Leaflets of fossil and modern *Albizia kalkora* (Scale bar: 5 mm). 1, 2: fossils from the Sayama Formation (1, AI0001; 2, AI0002); 3: fossil from the Shoudai Formation (AM335-1); 4: modern (MTDO10001-1).
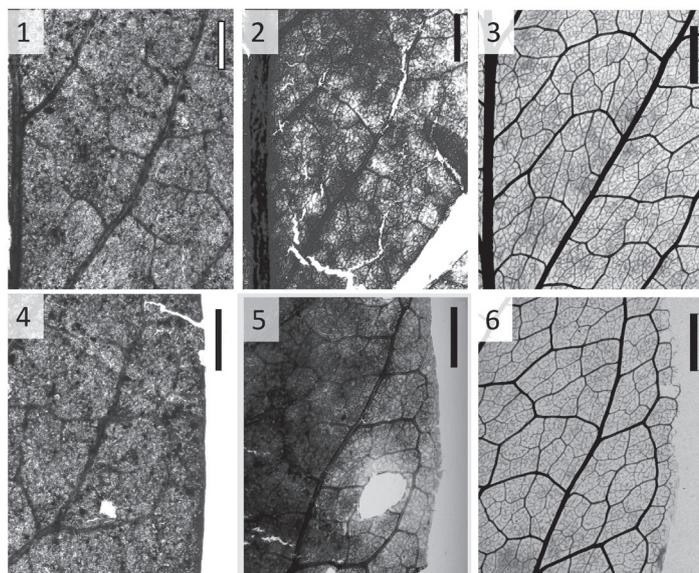
Fig. 3 Tertiary veins of fossil and modern *Albizia kalkora* leaflets (Scale bar: 1 mm). 1–3: epidermal and intercostal tertiary veins; 4–6: exterior tertiary veins. 1, 4: fossils from the Sayama Formation (AI0002); 2, 5: fossils from the Shoudai Formation (AM335-1); 3, 6: modern (MTDO10001-1).
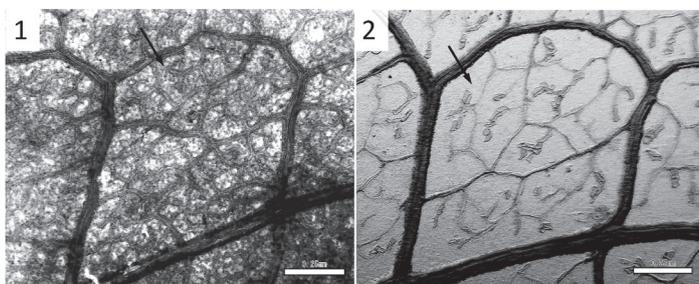
Fig. 4 Areoles of the *Albizia kalkora* leaflet (Scale bar: 0.25 mm). 1: fossil from the Shoudai Formation (AM335-1); 2: modern (MTDO10001-1). Arrow indicates typical areole.

and *Entada phaseoloides* in subfamily Mimosoideae and *Caesalpinia bondac*, *C. crista*, *C. cucullata*, *C. decapetala*, *C. enneaphylla*, *C. hymenocarpa*, *C. minax*, *Cassia bicapsularis*, *Gleditsia australis*, *G. fera*, *G. japonica*, *G. microphylla*, *G. sinensis*, *Gymnocladus chinensis*, and *Peltophorum tonkinense* in subfamily Caesalpinaceae. Type B consisted of species having leaflets with two or three secondary veins diverging at the base and medial symmetrical leaflets, i.e., the midrib was at the center of the leaflet, and included *Albizia corniculata* and *A. retusa* of subfamily Mimosoideae and *Pterolobium macropterum* of subfamily Caesal-

pinaceae. Types C–E consisted of species having medial asymmetrical leaflets, i.e., the midrib was not at the center of the leaflet, and included three *Albizia* species. Medial asymmetrical type leaflets were further classified into three types based on the shape of the lower side of the base: rounded (Type C, *A. calcarea*), lobate (widely projected) (Type D, *A. odratissima*), and truncate (slightly projected) (Type E, *A. kalkora*).

Leaflet fossils described in this paper were classified as Type E, with characters in common with modern *A. kalkora*, including two or three secondary veins diverging at the lower side of the base, midrib close to the
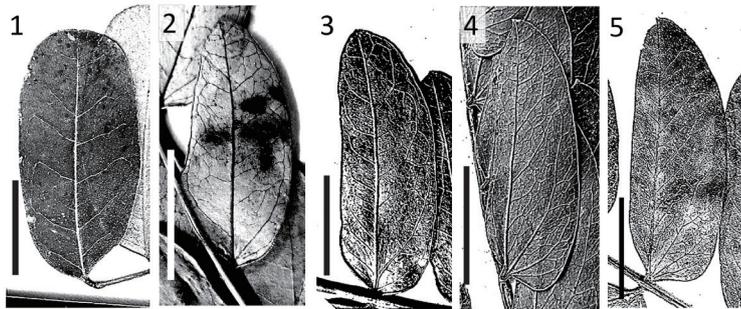
Fig. 5 Modern leaflet of selected taxa similar to *Albizia kalkora* (scale bar: 1 cm); 1, Type A, *Adenanthera pavonina*; 2, Type B, *Albizia retusa*; 3, Type C, *Albizia calcarea*; 4, Type D, *Albizia odratissima*; 5, Type E, *Albizia kalkora*.
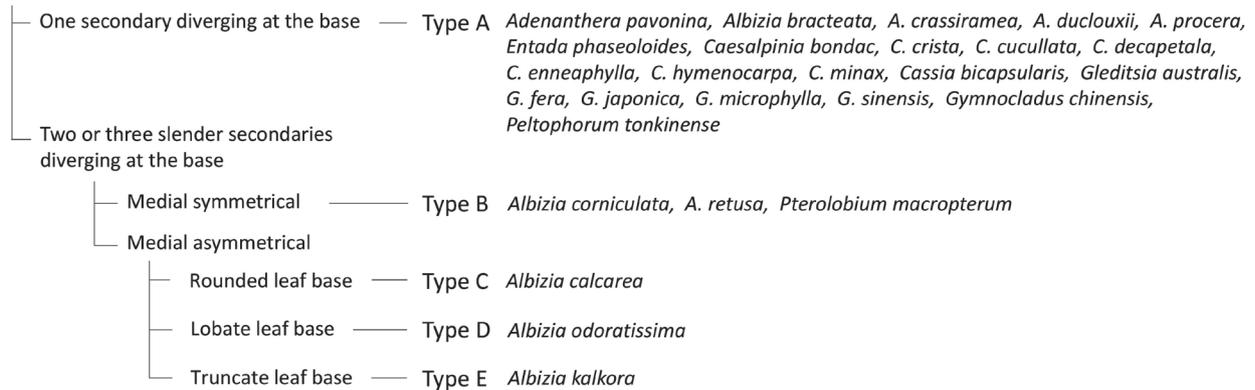
Fig. 6 Classification chart of leaflet morphology of selected taxa similar to *Albizia kalkora*.

Table 2 Leaflet types and herbarium specimen numbers of selected taxa having leaflets similar to those of *Albizia kalkora*

Taxa	Leaflet type[1]	Herbarium[2]	Specimen Number
MIMOSOIDEAE			
Adenanthera pavonina L.	A	HTIBC	105160, 127395
Albizia bracteata Dunn	A	HTIBC	017901, 017903
A. calcarea Y. H. Huang	C	KUN	0598747
A. corniculata (Lour.) Druce	B	HTIBC	017923, 145262, 145923, 147706
A. crassiramea Lace	A	HTIBC	017946, 017950, 018026, 058436, 058439, 120318, 124468, 132723
A. duclouxii Gagnep.	A	HTIBC	017925
A. kalkora (Roxb.) Prain	E	HTIBC	112354, 113797, 114642, 115546, 116255, 117080, 145968, 017927, 017928, 017929, 017376, 017926
		MTDO	10001
A. odoratissima (L. f.) Benth.	D	HTIBC	017995
A. procera (Roxb.) Benth.	A	HTIBC	017380, 018012, 018015, 018018
A. retusa Benth.	B	TI	S. Noshiro & M. Suzuki, 5046[3]; H. Ohashi & Y. Tateishi, 968[3]
Entada phaseoloides (Li.) Merr.	A	HTIBC	018051
CAESALPINOIDEAE			
Caesalpinia bonduc (L.) Roxb.	A	TI	T. Yamazaki & H. Usui, 2086[3]
C. crista L.	A	HTIBC	017560
C. cucullata Roxb.	A	HTIBC	126944
C. decapetala (Roth) Alston	A	HTIBC	017512
C. enneaphylla Roxb.	A	HTIBC	017525
C. hymenocarpa (Prain) Hattink	A	HTIBC	017520, 120240
C. minax Hance	A	HTIBC	057193
Cassia bicapsularis L.	A	HTIBC	105132
Gleditsia australis Hemsl.	A	HTIBC	144505
G. fera (Lour.) Merr.	A	HTIBC	017695, 017696, 017697, 017698, 146428
G. japonica Miq.	A	KUN	0126889, 0126895, 0126896, 0126901
G. microphylla Gordon ex Y. T. Lee	A	HTIBC	126451
G. sinensis Lam.	A	HTIBC	103020, 103189, 017700, 129596, 017700, 129596
Gymnocladus chinensis Baill.	A	KUN	0127020
Peltophorum tonkinense (Pierre) Gagnep.	A	HTIBC	057975
Pterolobium macropterum Kurz	B	HTIBC	017581, 017582

1) Leaflet type as in Fig. 6.
2) Abbreviation of herbarium (herbarium code); HTIBC, Xishuangbanna Tropical Botanical Garden; KUN, Kunming Institute of Botany; MTDO, Faculty of Horticulture, Chiba University; TI, University of Tokyo.
3) Collection number allotted by collectors.

upper margin, and a truncate lower base. The framework of higher-order venations than the quaternary vein in one of the fossil materials (AM335-1) from the Shoudai Formation was almost the same as that of modern *A. kalkora*, whereas those of the other two materials could not be observed. Fossil leaflets had better developed reticulation of quinternary veins and smaller (0.1–0.2 mm) areoles than modern ones (0.2–0.4 mm size) (Fig. 4). Freely ending veinlets were more finely branched in the fossil leaflets than in the modern ones.

3. Composition of leaf fossil assemblages including *Albizia kalkora*

Sayama Formation

The leaf assemblage in the Sayama Formation consisted of at least 42 species belonging to 19 families and 31 genera, including 1 pteridophyte, 2 gymnosperms, and 39 angiosperms composed of 3 evergreen and 35 deciduous broadleaved trees and 1 herb (Table 3). Six taxa including *Ginkgo biloba*, *Cunninghamia lanceolata* var. *konishii*, *Fagus stuxbergi*, *Liquidambar formosana*, *Cercis chinensis*, and *Lagerstroemia indica* are extinct from Japan, but they or their relatives remain in China. *Fagus crenata* leaves were the most dominant in number. Cool-temperate trees such as *Betula glossa*, *Fagus crenata*, *Cercidiphyllum japonicum*, *Acer diabolicum*, and *Aesculus turbinata* were included, whereas warm-temperate trees were abundant, including conifers such as *Ginkgo biloba* and *Cunninghamia lanceolata* var. *konishii*, evergreen broadleaved trees such as *Quercus gilva*, *Cinnamomum yabunikkei*, and *Cinnamomum camphora*, and deciduous broadleaved trees such as *Quercus acutissima*, *Celtis sinensis*, *Albizia kalkora*, *Cercis chinensis*, *Liquidambar formosana*, and *Lagerstroemia indica*.

Shoudai Formation

The leaf assemblage in the Shoudai Formation consisted of at least 16 species belonging to 11 families and 13 genera, including 1 conifer and 4 evergreen and 11 deciduous broadleaved trees (Table 4). Three taxa, *Fagus microcarpa*, *Ilex cornuta*, and *Paliurus nipponicus,* are now extinct from Japan, but they or their relatives remain in China. *Zelkova* sp. was similar to *Z. ungeri* (Ettingshausen) Kovats, but differed in having smaller (ca. 20 mm long) and elliptical leaves. *Fagus microcarpa* was the most dominant in number. Warm-temperate trees were numerous, including evergreen broadleaved trees such as *Quercus salicina*, *Q. myrsinifolia*, *Ilex cornuta*, and *Ficus pumila* and deciduous broadleaved trees such as *Paliurus nipponicus* and

Table 3 Leaf fossil assemblage from the Lower Pleistocene Sayama Formation in western Tokyo, central Japan

Pteridophyta	
Pteridaceae	*Pteris* cf. *cretica* L.
Spermatophyta	
Gymnospermae	
Ginkgoaceae	*Ginkgo biloba* L.
Taxodiaceae	*Cunninghamia lanceolata* (Lamb.) Hook. var. *konishii* (Hayata) Fujita
Angiospermae	
Salicaceae	*Salix gilgiana* Seemen
	S. sieboldiana Blume
	S. subfragilis Andersson
Betulaceae	*Alnus* cf. *japonica* (Thunb.) Steud.
	Betula grossa Siebold et Zucc.
	Carpinus laxiflora (Siebold et Zucc.) Blume
	C. tschonoskii Maxim.
	Ostrya cf. *japonica* Sarg.
Fagaceae	*Fagus crenata* Blume
	F. japonica Maxim.
	F. stuxbergi (Nathorst) Tanai
	Quercus acutissima Carruth.
	Q. serrata Murray
	Q. sect. *Prinus* sp.
	Q. gilva Blume
	Q. subgen. *Cyclobalanopsis* sp.
Ulmaceae	*Celtis sinensis* Pers.
	Ulmus davidiana Planch. var. *japonica* (Rehder) Nakai
	Zelkova serrata (Thunb.) Makino
Lauraceae	*Cinnamomum camphora* (L.) J.Presl
	C. tenuifolium (Makino) Sugim. ex H. Hara
	Lindera umbellata Thunb.
Cercidiphyllaceae	*Cercidiphyllum* cf. *japonicum* Siebold et Zucc. ex Hoffm. et Schult.
Hamamelidaceae	*Liquidambar formosana* Hance
Rosaceae	*Sorbus* cf. *commixta* Hedl.
	Rosa cf. *multiflora* Thunb.
Leguminosae	*Albizia kalkora* (Roxb.) Prain
	Cercis chinensis Bunge
	Lespedeza cyrtobotrya Miq.
	Wisteria floribunda (Willd.) DC.
	Leguminosae (Fabaceae) spp.
Aceraceae	*Acer diabolicum* Blume ex K.Koch
	A. palmatum Thunb.
	A. pictum Thunb.
Hippocastanaceae	*Aesculus turbinata* Blume
Tiliaceae	*Tilia* sp.
Lythraceae	*Lagerstroemia indica* L.
Ericaceae	Ericaceae sp.
Oleaceae	*Fraxinus japonica* Blume ex K. Koch
Liliaceae	*Smilax china* L.

Table 4 Leaf fossil assemblage from the Middle Pleistocene Shoudai Formation in southern Kyoto, central Japan

Gymnospermae	
Pinaceae	*Abies firma* Siebold et Zucc.
Angiospermae	
Fagaceae	*Fagus japonica* Maxim.
	F. microcarpa Miki
	Quercus myrsinifolia Blume
	Q. salicina Blume
	Q. serrata Murray
Betulaceae	*Carpinus tschonoskii* Maxim.
Ulmaceae	*Zelkova* sp.
Moraceae	*Ficus pumila* L.
Lauraceae	*Lindera praecox* (Siebold et Zucc.) Blume
Leguminosae	*Albizia kalkora* (Roxb.) Prain
	Wisteria floribunda (Willd.) DC.
Aceraceae	*Acer amoenum* Carrière
Aquifoliaceae	*Ilex cornuta* Lindl. & Paxton
Rhamnaceae	*Paliurus nipponicus* Miki
Oleaceae	*Fraxinus* sp.

Albizia kalkora, whereas cool-temperate trees were not detected.

Discussion

1. Identification of fossil *Albizia kalkora*

Species with leaflets similar to those of *A. kalkora* belong to a wide range of genera in two subfamilies. The character of two or three secondary veins diverging at the base was found in another subfamily. This indicated the importance of references, not only for Japanese taxa, but also for a wide range of taxa distributed throughout China for identification of Leguminosae fossil leaflets. The morphology of higher-order venation was different between modern and fossil *A. kalkora*. However, it is necessary to check a range of modern materials because the difference in higher-order structures might be related to intraspecific variation.

Albizia miokalkora leaflets described from the Early Miocene in the Noto Peninsula had characteristics in common with modern *A. kalkora* (Ishida, 1969). However, fossil leaflets described under the name of *A. miokalkora* from the Chojabaru Formation (Plate 15-9, 10 in Hayashi, 1975; specimens NSM PP11082 and NSM PP11083 stored in the National Science Museum) differed from *A. kalkora* in smaller leaf size (4–9 mm in length) and mid-veins extremely close to upper margins (Fig. 7). It was identifiable as *A. julibrissin* and its relatives distributed in China. The record from Pohang in southeastern Korea was based on legumes (Kim, 2005), whereas the records from Kaiyun (Tao et al., 2000) and Lincang (Tao & Cheng, 1983) in Yunnan Province in southwestern China were based on leaflets of medially asymmetrical shape (Table 1).

Pliocene and Pleistocene fossil records from Kyushu are abundant (Hase, 1988; Iwauchi & Hase, 1987, 1992), but lack morphological descriptions and images. The only record that has a description and images of fossil leaflets is "*Albizia* sp." from the upper Pleistocene Ikemure Formation (Onoe, 1971). The images of leaflets in Figs. 13–15 in Plate VI in Onoe (1971) exhibit two or three secondary veins diverging at the lower side of the base, the midrib close to the upper margin, and the leaf base truncate on the lower side. They are thus identifiable as *A. kalkora*.

Fossil records of *Albizia* and relative taxa from China were reviewed by Guo and Zhou (1992). They listed fossil records of *A. bracteata* from Kaiyuan, Yunnan (WGCPC, 1978), *A. julibrissin* from Lincang, Yunnan (Tao & Cheng, 1983), and *A. miokalkora* from Linqu, Shandong (Hu & Chaney, 1940; WGCPC, 1978) (Table 1). In addition to these, they described
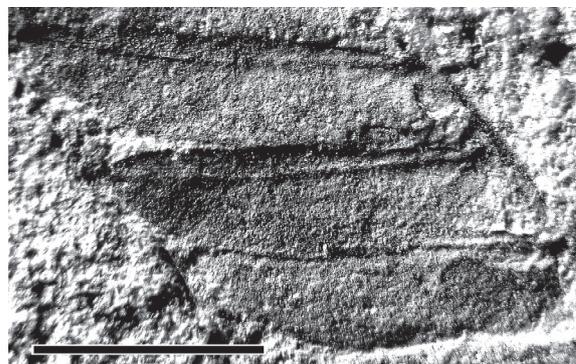
Fig. 7 *Albizia kalkora* fossil from the Chojabaru Formation (NSM PP11082, scale bar: 5 mm).

two fossil morphotypes under the name of "cf. *Albizia*, *Pithecellobium*, *Archidendron*, spp. 1 and 2" from the Xiaolongtan Formation in Kaiyuan, Yunnan. They mentioned that "sp. 1" was similar to *A. bracteata* and "sp. 2" was similar to *A. procera*. Both morphotypes belonged to type A in this paper.

2. Distribution history of *Albizia kalkora* in the Neogene and Quaternary

Assemblages in both the Sayama and Shoudai Formations included evergreen broadleaved trees such as *Cinnamomum* and *Quercus* subgen. *Cyclobalanopsis* as well as numerous warm-temperate trees. Deciduous broadleaved trees generally dominated with temperate conifers in the Plio-Pleistocene macrofossil assemblages in sediment during the warm stages in central Honshu (Momohara, 2016). Warm-stage assemblages with abundant evergreen broadleaved tree taxa are very limited and include those of the early Late Pliocene and interglacial stages MIS 11 and 13 in the Middle Pleistocene (Momohara, 1997; Momohara, 2016). The fossil assemblage in the Shoudai Formation belongs to the interglacial stage, MIS 13, in which evergreen broadleaved tree taxa are often found in the Ma 8 marine clay bed in the Osaka Group (Momohara, 2016). The leaf assemblages were in the fluvial silt 2.5 m below the Kasuri tephra bed distributed just at or several meters below the Ma 8 marine clay bed. Similarly, the leaf assemblages in the Sayama Formation were in fluvial silt overlain conformably by marine sediments. These stratigraphic positions represent the deposition of leaf fossils in a fluvial system near the coast just before a marine transgression. In those stages having winter temperatures sufficiently high for evergreen *Quercus* to have grown, *A. kalkora* was a member of the paleovegetation near the coast that included evergreen broadleaved trees, whereas *Fagus* species were dominant in

deciduous broadleaved forests in hills and mountains behind the coastal plain.

In contrast with the scarcity of evergreen broadleaved trees in central Honshu, the Plio-Pleistocene plant assemblages found in Kyushu include common and rich evergreen broadleaved tree taxa (Hase, 1988; Iwauchi, 1994), whose occurrence was possibly influenced by a warmer climate than that of central Honshu (Momohara, 2016). In the Plio-Pleistocene fossil leaf assemblages in southern and central Kyushu, *A. kalkora* occurs commonly and is always accompanied by evergreen broadleaved tree taxa (Onoe, 1971; Hase, 1988; Iwauchi & Hase, 1987, 1992) according to their identification. The percentage of evergreen broadleaved trees in the total broadleaved tree taxa in each assemblage including *A. kalkora* is between 2.8% (Daiwa Formation; Hase, 1988) and 28.1% (Ikemure Formation; Onoe, 1971) in southern Kyushu and lower in central Kyushu at 1.0% in the Yoshino Formation (Iwauchi & Hase, 1992)(Table 1). Thus, *A. kalkora* was a component of vegetation including evergreen broadleaved trees in southern Japan since the Late Pliocene to Middle Pleistocene. This indicates that *A. kalkora* was mainly distributed in southern Japan where evergreen broadleaved trees were common in the forest and expanded its distribution to central Japan during the interglacial stages under warm winter conditions.

The pre-Pleistocene fossil leaflets similar to those of modern *A. kalkora* were identified as the fossil species *A. miokalkora*. The fossil records of *A. miokalkora* from eastern China, southeastern Korea, and central Japan are from sediments of the late Early and Middle Miocene (ca. 20–12 Ma). Fossil leaf assemblages during this stage in Honshu are characterized by numerous evergreen broadleaved tree taxa and are called "Daijima type flora" (Tanai, 1961). The percentage of evergreen taxa in the total broadleaved tree taxa is 15% in the Yanagida Formation (ca. 20 Ma) in Noto Peninsula (Ishida, 1969) and 33% in the Duho Formation (14–12 Ma) in southeastern Korea (Lim et al., 2010). Fossil assemblages in the Shanwang Formation (ca. 17 Ma) includes evergreen Fagaceae (*Castanopsis* sp.) and Lauraceae (*Cinnamomum* spp. and *Litsea* sp.).

A temperature decrease was recorded in the marine oxygen isotope curve beginning at ca. 15 Ma in the early Middle Miocene (Zachos et al., 2001). It influenced compositional changes of fossil floras in central Japan, which became dominated by temperate deciduous broadleaved trees in the Late Miocene (Tanai, 1961). In contrast, Late Miocene leaf assemblages including *A. miokalkora* in Kaiyuan (ca. 11 Ma) and

Lincang (older than 3.8 Ma) in Yunnan Province includes rich subtropical and evergreen broadleaved tree taxa. The temporal and spatial distribution of *A. miokalkora* indicated that the fossil species expanded their distribution to higher latitudes (36°–37°N) with the evergreen broadleaved tree taxa approximately during the mid-Miocene climate optimum and contracted their distribution to lower latitudes, around 24°N, in the Late Miocene (Fig. 1).

The modern distribution of *A. kalkora* is much limited to the southern part of Japan and Korea, where evergreen broadleaved forests are distributed under warm winter conditions. The coldest month mean temperature in the habitat of *A. kalkora* in Nobeoka, northern Miyazaki Prefecture is 6.6 °C, and the coldness index is 0 °C·month (Hirata, 1984). Distribution in Korea is limited to Jeju (Loc. D in Fig. 1) and Huksan (Loc. C in Fig. 1) Islands in the southwestern sea off the Korean Peninsula (Oh & Pak, 2001), which are influenced by the Tsushima Warm Current.

In contrast with the present limited distribution in Japan and Korea, the distribution in China extends widely from subtropical areas in Yunnan Province to Beijing and Hebei Province (Chen ed., 1988). The areas in Hebei and Beijing are farther north and/or inland than the distributional limit of the evergreen broadleaved forests (Fang & Yoda, 1990). Based on the data in JMA (2016), the warmth index in Beijing (Loc. E in Fig. 1) is 114 °C·month and the coldness index is -19 °C·month. The areas are in the warm temperate zone, but cold winter temperatures prevent the growth of evergreen broadleaved trees (Kira, 1948). In the Taihang Mountains (Loc. F in Fig. 1; Song & Qu, 1996) in eastern Shanxi Province, the Zhongtiao Mountains (Loc. G in Fig. 1; Li. 1995) in southwestern Shanxi Province, and Mt. Songshan (Loc. H in Fig. 1; Ye & Wu, 1993) in north Henan Province, *A. kalkora* is distributed in deciduous broadleaved forest. Climate conditions for populations in northern China are quite different from those reconstructed from fossil assemblages including *A. kalkora* and *A. miokalkora*.

Albizia kalkora populations in China likely evolved cold tolerance and expanded their distribution, whereas the distribution became limited in Japan during the late Quaternary. Although it is not possible to discern the history of *A. kalkora* since the Pliocene in China, because of poor preservation of Pleistocene plant macrofossils throughout China (Li et al., 1995), its present distribution indicates that glacial refugia expanded more widely in China than in Japan. Its larger population size with higher intraspecific diversity possibly enhanced adaptivity to cold and dry climates that pre-

vailed in China in the Quaternary glacial stages.

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