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THE REVISION OF THE SO-CALLED “CERCIDIPHYLLUM” LEAVES FROM THE PALEogene OF NORTH JAPAN*

by

Toshimasa Tanai

(with 4 text-figures, 1 table and 12 plates)

Abstract

Leaves superficially similar to Cercidiphyllum have been commonly reported from the Paleogene of the Northern Hemisphere. These leaves include various shapes with acrodromous veins, and with crenate to nearly entire margin. My recent investigation of the fine venation character reveals that Paleogene leaves referred once to Cercidiphyllum from Japan contain various genera such as Cocculus, Disanthus, Populus and Tetracentron. Leaves of Cocculus and Disanthus with no marginal glands are easily excluded from Cercidiphyllum-like fossils. On the other hand, leaves of three genera, Populus, Tetracentron and Cercidiphyllum, are liable to confuse each other. Populus leaves are usually small in areolation intruded by thick veinlets with asterate branching, while leaves of Cercidiphyllum and Tetracentron are mostly large in areolation intruded by thin, irregularly branching veinlets. There are, however, some marked differences in the secondary looping and venation within the teeth area between the typical leaves of Cercidiphyllum and Tetracentron, but their features contain many exceptions. The nature of marginal glands is a most note-worthy distinction between these two genera. The combination of the above-noted characters can lead to accurate generic assignment of “Cercidiphyllum” leaves in the Paleogene.

Introduction

The genus Cercidiphyllum is composed of only two extant species and one variety, all of whose species are confined to East Asia in their distribution. C. japonicum Sieb. et Zucc. and C. magnificum (Nakai) Nakai are living in cool-temperate forest of Japan, while C. japonicum var. sinense Rehd. et Wils. is in the Mesophytic Forest of Central China. On the other hand, leaves once referred to this genus have been widely reported from the Tertiary of the Northern Hemisphere; Cercidiphyllum have been considered to represent one of the most common member in the Tertiary temperate forest. The recent cautious reinvestigations of fossil leaves by some workers have revealed that Paleogene leaves of “Cercidiphyllum arcticum” from North America are of diverse taxonomic origin (Wolfe, 1966, 1977; Hickey, 1977). However, their investigations of Cercidiphyllum have been not yet completed.

Leaves referred or similar to Cercidiphyllum are abundant in the Tertiary of East Asia, especially in the Paleogene of North Japan. I have engaged in study of Paleogene floras of this region during these several years. I can reach a conclusion that the so-called “Cercidiphyllum” leaves from the East Asian Paleogene also contain various genera, although there are still leaves doubtlessly referable to Cercidiphyllum. This paper is aimed at the taxonomical revision of these leaves.

* Contribution from the Department of Geology and Mineralogy, Faculty of Science, Hokkaido University, No. 1695.
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Recent Investigations of Fossil Cercidiphyllum

Leaves superficially similar to "Cercidiphyllum" have been widely reported from the Tertiary of the Northern Hemisphere, especially common from the Paleogene. These leaves include various shapes with acrodromous veins, and also with crenate or remotely serrate to entire margin. By various authors these leaves were once referred to the genera such as Cercis, Cissus, Dombeyopsis, Ficus, Grewia, Hedera, Paliurus, Piper, Populus, Smilax, Zizyphus and others, based only on their superficial resemblance.

Through his extensive investigation of North American fossil leaves, Brown (1939) assigned most of Late Cretaceous-Paleogene tri-plinerved leaves to the genus Cercidiphyllum, and he distinguished the following four species mainly by foliar shape, venation and margin: *C. ellipticum* (Newb.) Brown of the Upper Cretaceous and the Paleocene, *C. arcticum* (Heer) Brown of the Paleocene to the middle Eocene, *C. elongatum* Brown of the middle Eocene to the lower Miocene and *C. crenatum* (Heer) Brown of the Oligocene to the Miocene. Many Paleogene leaves named under various genera were included in the above-noted three species excepting the last by him. Since then, most workers have followed Brown's definition, and thus Cercidiphyllum was believed to have had a wide distribution with abundant occurrence in the Northern Hemisphere during Paleogene time. Thus, until the recent time when some workers started to reinvestigate, Paleogene Cercidiphyllum have been considered to include acrodromous leaves with various shapes and other characters (for instance, entire to toothed margin, long to medium petiole). It was partly supported by the fact that the "locule" like fossils referred to Cercidiphyllum by Brown (1939) are commonly known in the Paleogene, associated with "Cercidiphyllum-like" leaves.

Chandler (1961) reinvestigated leaves referred to Cercidiphyllum from the Paleocene Reading Formation of southern England. She called in question about the generic assignment for leaves regarded by Brown (1939) as characteristic of Cercidiphyllum. The leaves from the Reading Formation were considered to ascribe to the Hamamelidaceae by her. Furthermore, she demonstrated that "locule" fossils regarded as Cercidiphyllum by Brown are not related to this genus.

Based on the detailed investigation of Alaskan Paleogene specimens, especially giving attention to the fine veinlets, venation order and tooth architecture of leaves, Wolfe (1966, 1977) revealed that most leaves referred to Cercidiphyllum arcticum by Brown (1936) belong to other genera, and that leaves definitely assignable to Cercidiphyllum were rather few in the Paleogene of North America. Wolfe's result was followed by Hickey (1977) who described in detail the Paleocene-Eocene floras of Dakota. A key note for the taxonomical classification of the so-called "C. arcticum complex" was presented by him; it is useful for
the identification of *Cercidiphyllum* leaves, because we can eliminate other genera from *C. arcticum* which has been abused until that time.

On the other hand, Chandrasekharam (1974) investigated foliar morphology of the modern *Cercidiphyllum* (*C. japonicum* and *C. magnificum*) on the basis of statistical treatment of leaf shape and venation characters. Applying these results to the fossil leaves, he described two new species of *Cercidiphyllum* from the Paleocene of Alberta, Canada. Although his work is mostly persuasible for the characters of the modern leaves of *Cercidiphyllum*, the fossil leaves referred to this genus by him do not always show sufficient characters to be separated from other genera which have similar leaves.

![Text-fig. 1 The Distribution of Paleogene Coal Fields in Northern Japan.](image)

**Investigation of the so-called *Cercidiphyllum* in the Paleogene of Japan**

The Paleogene coal-bearing deposits are distributed principally in North Kyushu and Hokkaido, and partly in north-eastern Honshu, western Honshu and central Shikoku island. From these deposits a number of plants occur, and they were sometimes described up to the present by some workers. Nagai (1957) reported two ill-preserved leaves as *Cercidiphyllum*
Endo from the Upper Eocene Kuma Group of Shikoku. Matsuo (196b) reported a fragmentary leaf with acrodromous veins as *C. takashimensis* Matsuo from the Eocene Takashima flora of North Kyushu. However, these specimens from western Japan are too ill-preserved to be assignable to this genus.

Endo (1968) who studied a Paleogene flora from the Ikushunbetsu Formation of the southern Ishikari coal field, Hokkaido, described four species and one variety of *Cercidiphyllum*, including one new species. However, he failed to show a definite generic criterion for this genus; leaves assigned to *Cercidiphyllum* by him are composed of several taxonomic origins. When I (Tanai, 1970) described the Oligocene floras from the Kushiro coal field of eastern Hokkaido, *Cercidiphyllum*-like leaves were classified into two species, *C. eoaponicum* Endo and *Cocculus ezoensis* Tanai by venation and marginal characters. Furthermore, Paleogene leaves of the so-called "*Cercidiphyllum*" described by several authors until that time were discussed in their generic status, although his revision was incomplete.

During these several years I have investigated Paleogene floras of Northern Japan, especially of central Hokkaido, where the Eocene to Oligocene plant-bearing deposits are typically developed (Text-fig. 1). From these deposits there are commonly found ovate to oval leaves with acrodromous venation, which show close resemblance to leaves of *Cercidiphyllum* in general appearance. Most of these specimens are represented by leaf impressions with no carbonized films; they are unsuitable for the cuticular analysis, but they are, in most cases, excellently preserved in the fine venation to ascertain generic comparison. As discussed by Wolfe (1964), the marginal and venation characters are effective to distinguish *Cercidiphyllum* leaves from other genera having similar leaves. Therefore, I have investigated all the specimens superficially similar to *Cercidiphyllum*, which were collected from the Paleogene of northern Japan, along with the type specimens reported by several authors.

As usually well-known, leaves of the extant *Cercidiphyllum* are glandular in marginal crenation; we can readily exclude non-glandular margined leaves from "*Cercidiphyllum*-like fossils", although similar in foliar shape and marginal crenation. Most of these non-glandular leaves are referable to such genera as *Cocculus*, *Cercis* or *Disanthus* by marginal looping, areoles and veinlets, as described later in the systematic discussion.

Fossil leaves with glandular teeth are classified into two groups by the venation characters such as the areolation and veinlets. In the first group, the areolation is usually small (0.3 to 0.7mm in size), and is intruded by thick veinlets with asterate branching. The marginal glands are larger and irregular in shape. On the one hand, the areolation in the second group is usually large (0.7 to 1.5mm in size), and is intruded by thin veinlets with 2 or 3 times, irregularly branching. Leaves of the first group belong to the genus *Populus*; their venation and marginal glands are consistent with those of the extant cottonwood leaves, although the basal pair of lateral primary veins is more highly arising up near the apex, comparing with those of the extant leaves. Leaves of the second group are similar to those of *Cercidiphyllum* and *Tetracentron* in their venation, but leaves of these two genera are rather difficult to distinguish by size and shape of areoles and veinlets.
There are some marked differences in the venation within the tooth region between the leaves of *Cercidiphyllum* and *Tetracentron*. As described by Wolfe (1977), "most significant is that in *Tetracentron* the veins connect the glandular region of the tooth to the adjacent sinuses, but in *Cercidiphyllum* such veins are absent". Actually, these differences are
generally accepted in the typical extant leaves as shown in Text-fig. 2; however, these features involves some exceptions, especially in the case of *Cercidiphyllum* leaves with conspicuous crenate margin. As seen in the extant *C. magnificum*, a pair of veins from the adjacent sinuses converges in the marginal glands, although they are sometimes brochidodromously looping. Therefore, in the case of fossils such vein character within the tooth region may be not always clear for the identification of *Cercidiphyllum*.
PALEOGENE CERCIDIPHYLLUM LEAVES

A most noteworthy difference between leaves of *Cercidiphyllum* and *Tetracentron* is in the feature of marginal glands: those of *Cercidiphyllum* are globular in shape, and sometimes project out of marginal teeth, while glands of *Tetracentron* are capped by undetached setae, and veins entering teeth tip look like gradual thickening toward the tooth apex. Such difference of glandular character is usually observed among the fossil leaves. If the fine venation and marginal glands are observable, the combination of the above-noted characters can lead to accurate assignment for *Cercidiphyllum* leaves in the Paleogene. Thus, a key for the identification of “Cercidiphyllum-like leaves” from the Paleogene of Japan is presented as shown in Table 1. Through my reinvestigation, *Cercidiphyllum* leaves were confirmed to be not always abundant during the Older Tertiary in Japan as formerly reported or expected.

Table 1 A Key for the Identification of several Acrodromous Leaves from the Paleogene of North Japan.

1. Serrate, crenate or dentate margin with glandular teeth.
   (1) Areolation large (0.7-1.5 mm), intruded by thin veinlets with 2 or 3 times branching.
   (A) Marginal glands small, globular, projecting beyond tooth apex; a vein from the sinus bottom mostly lacking, or not reaching tooth apex .......................... *Cercidiphyllum palaeojaponicum*
   (B) Marginal glands large, gradually thickening toward tooth apex; a pair of prominent veins converging toward tooth apex .......................... *Tetracentron piperoides*
   (2) Areolation small (0.3-0.7 mm), intruded by thick veinlets with aterate branching; marginal glands large but irregular in shape .......................... *Populus yubariensis*

2. Entire, sinuate or lobed margin without glands.
   (1) Areolation large (0.8-1 mm), sided by thin, third- to fourth-order veins; veinlets thin, branching more than two times .......................... *Disanthus kujianus*
   (2) Areolation small (0.3-0.7 mm), sided by thick, third- to fifth-order veins.
      (A) Secondary loops enclosed by third-order arches.
         (a) Leaf base ducurrent along the petiole; veinlets none or single .......................... *Cocculus ezoeensis*
         (b) Leaf base cordate; veinlets single or once branching .......................... *Menispermites ishikarakensis*
      (B) Secondary loops enclosed by third- to fifth-order arches; veinlets single or once branching .......................... *Cercis nipponica*

In the Paleogene of East Asian region adjacent to Japan, leaves resembling *Cercidiphyllum* have been also commonly reported by many authors. Most of these leaves from Russian Asia Region (Kryshtofovich, 1958; Baikovskaya, 1959) were named as *Trochodendroides smilacifolia* (Newb.) Kryshtofovich, which belongs to a form-genus. I cannot now determine only by the illustrations whether or not these Russian specimens belong to *Cercidiphyllum*. Beside them, leaves of *Cercidiphyllum* were reported from the Oligocene Fushun flora (Acad. Sinica, 1978), an Eocene flora of Zeya-Breya Plain (Baikovskaya, 1950) and an Oligocene flora of Saghaline (Borsuk, 1956). All of these specimens are doubtful to be referable to *Cercidiphyllum* as far as judged from their illustrations.

At the last, I have to refer to the fruits which have been referred frequently to *Cercidiphyllum* by many authors. These fruits are mostly found as detached, elongate-elliptic follicles with a short stalk. These follicles apparently form a raceme as shown in
Text-fig. 4 The Fine venation and Marginal Characters of the Extant and Fossil Cercis, Disanthus and Menispermaceae.

a. Cocculus trilobus Dc. H.U.P.B. slide no. 404. x 12.5
c. Disanthus cercidifolius Maxim. H.U.P.B. Slide no. 30. x 12.5
d. Cercis canadensis Linn. H.U.P.B. slide no. 170 x 12.5
e, f. Menispermites ishikariensis Tanai. H.U.M.P. holotype no 26868 (Pl.4, fig.6). e: x 5, f: x 12.5
g, h. Disanthus kujianus Tanai. H.U.M.P. holotype no. 26166 (Pl.6, fig.6). g: x 3, j: x 12.5
k, l. Cercis nipponica (Tanai) Tanai. H.U.M.P. hypotype no. (pl.8, fig.9). k: x 3, l: x 12.5

Figs. 2 and 3 of Plate 9; they attached alternately and singly on the peduncle. The inflorescence type of these fossils is quite different from that of the extant Cercidiphyllum which shows unbel's. Swamy and Bailey (1949) interpreted the inflorescence of the extant Cercidiphyllum as a pseudoantherium resulting from the reduction of a receme. However,
the fossil follicles are further different from those of the extant species in many morphological feature, and they are also found in the Upper Cretaceous (Tanai, 1979), in which no definite leaves of *Cercidiphyllum* are found. Thus, I prefer now to place the fossil follicles in a form-genus, *Carpolithes*.

**Systematic Descriptions**

In the following systematic descriptions, the specimen type numbers refer those in the Museum of Paleontology, Hokkaido University at Sapporo (abbreviation: H.U.M.P.) and in the National Science Museum at Tokyo (abbreviation: NSM). The localities shown by numbers and the plant-bearing formations are explained in the appendix. Terminology in description of leaves follows Hickey (1973). Fossil species are arranged in the Takhtajan’s system of dicotyledon classification.

**Family Menispermaceae**
**Genus Cocculus De Candolle**

*Cocculus ezoensis* Tanai

(Pl. 7, figs. 1-7; pl. 8, figs. 1-7; text-fig. 4, i, j)


*Type:* Holotype H.U.M.P. no. 25906b, paratype no. 25964. Okotsu coal mine, Harutori, Kushiro City, Hokkaido (Harutori formation, Early Oligocene).

*Supplementary description:* Leaves highly variable in shape and size, commonest forms being oblate to wide ovate or very wide obovate, occasionally orbiculate; length/width ratio of leaves 3.8 to 8.6 (average 0.78 for 25 specimens); length 3 to 6.7 cm and width 3.7 to 6.8 cm; apex rounded, occasionally retuse to emarginate, the termination of medial primary vein mucronate, but generally not well preserved; base cuneate or obtuse to broadly rounded and nearly truncate, with slightly decurrent part near the petiole; margin variable from nearly entire to irregularly undulate with broadly rounded crenations or shallow irregular lobes; petiole thick, medium to long, 1.5 to 2.7 cm in length; texture chartaceous to subcoriaceous. Venation perfect basal acrodromous with three strong primaries and a pair of secondaries, all of them originating from the top of petiole; medial primary vein thick but abruptly slender toward the apex, somewhat flexuous in the upper part of blade, giving off two or three pairs of camptodromous secondary veins; lateral primaries branching three or four times toward the margin to form the sets of progressively smaller loops of higher order veins; tertiary veins between primaries and secondaries or among intersecondary spaces thin, irregularly percurrent, forked or sinuous in course; highest order of venation fifth or sixth; higher order venation thin and irregular in course; areoles small to moderate in size (0.3 to 0.7 mm), four- to five-sided; freely-ending veinlets none or single, very rarely once branching.

*Discussion:* The previous reference of the Oligocene Kushiro specimens to the genus *Cocculus* have been proved to be valid by the following characters: generally entire margin with no glands, mucronate apex, mostly orthogonal areoles arranged in ranks and files, and
secondary loops enclosed by distinct arches of the third-order veins. These Paleogene leaves are easily distinguishable from *Cercidiphyllum*, *Populus* and *Tetracentron* by the entire margin; although sometimes irregularly and shallowly lobate, the margin is usually non-glandular.

*C. ezoensis* is, as stated already by me (Tanai, 1970), closely similar to *C. flabella* (Newb.) Wolfe from the Paleocene of Alaska (Wolfe, 1966) in foliar shape, margin and venation characters, excepting for the ultimate veinlets: the freely-ending veinlets are none or single (very rarely once branching) in *C. ezoensis*, while none in *C. flabella*. According to Wolfe (1964), the Alaskan specimens are unfortunately ill-preserved to define validly the veinlet character of *C. flabella*. The areolations of the above two species are similar in shape and size, along with other foliar characters. A further investigation of fine veinlets on North American better-preserved specimens may ascertain that the both species are conspecific. *C. ezoensis* is very variable in foliar shape and marginal feature; leaves of some type are closely similar to *Dicotylophyllum mercerensis* Hickey from the Paleogene of Dakota (Hickey, 1977), but they are different in size of areoles and freely-ending veinlets.

*C. ezoensis* is commonly found through the Paleogene of North Japan, especially abundant from the Urahoro Group and the Ishikari Group in Hokkaido. The species listed in the above synonymy are included in *C. ezoensis*.

**Occurrence:** Ishikari coal field Ic-1, Ic-2, Ic-3, Ic-4, Ic-6, Ic-7, Ic-8, Ic-9, Ic-10, Ic-11, Bc-1, Bc-2, Yc-2, Yc-3, Nc-1, Nc-2, Nc-3; Kushiro coal field Kh-1, Ky-2; Kuji coal field Kj-1, Kj-2, Kj-3, Kj-4.

**Collections:** Holotype H.U.M.P. no. 26906b; paratype no. 26964; hypotypes nos. 26966, 26141-26150; NSM no. 10522, 10523, 10526A, 10526B, 10527, 10533, 10560, 10567.

**Genus Menispermites** Lesquereux

*Menispermites ishikariensis* Tanai, sp. nov.  
(Pl. 4, fig. 6; text-fig. 4, e, f)

**Type:** Holotype H.U.M.P. no. 26868. Higure-zawa, Ikushunbetsu, Mikasa City (Early Oligocene).

**Description:** Leaf very wide ovate in shape, 7.3 cm long and 6.3 cm wide; apex acute with mucronate remain; base cordate; margin entire but slightly undulate, apparently non-glandular; texture subcoriaceous; petiole missing. Venation perfect basal acrodromous with three strong primaries; medial primary thick, slightly flexuous toward apex, giving off three pairs of the secondaries at the upper part of blade, which are brochidodromous; lateral primaries gently curving up, connecting with the secondaries emerginating from midvein; the
PALEOGENE CERCIDIPHYLUM LEAVES

Plate 1
secondaries from lateral primaries and their branches forming large loops near the margin, further enclosing small loops of tertiary veins along the margin; tertiary veins distinct but thin, sinuous in course or random reticulate; rank of highest order vein sixth; areolation small, 0.4 to 0.6 mm in size, four-sided by third- to fifth-order veins, intruded by single or once branching veinlets.

Discussion: The affinity of this leaf to the Menispermaceae is based on the mucro remain of leaf apex and marginal looping features of tertiary veins. This single leaf is closely similar to Cocculus ezoensis in foliar morphology and even venation character excepting for cordate base and freely-ending veinlets. A number of leaves of C. ezoensis are found from the Paleogene of northern Japan; all the specimens are usually ducurrent to cuneate at the base, and are generally none or single in veinlets. Cercis niponica resembles also Menispermites ishikariensis, but is distinguishable in marginal looping features.

This single leaf is somewhat similar to non-lobed leaves of the extant Sinomenium acutum (Thunb.) Rehd. et Wils. of southern Japan, but differs in freely-ending veinlets.

Occurrence: Ishikari coal field Ic-4.


Family Tetracentraceae

Genus Tetracentron Oliver

_Tetracentron piperoides_ (Lesquereux) Wolfe

_(Pl. 2, figs. 7, 8; pl. 4, fig. 3; pl. 6 figs. 2, 7; text-fig. 3, i, j)_

_Tetracentron piperoides_ (Lesquereux) Wolfe. 1977. U.S. Geol. Survey Prof. Paper (997); 61. pl. 5. f. 4; pl. 22. f. 3; pl. 28. f. 7. (see synonymy).


_Discussion:_ Leaves of _Cercidiphyllum_ and _Tetracentron_ are closely similar each other in size and shape of the areolation, and also in the freely-ending veinlets. It is therefore difficult to distinguish fossil leaves of these two genera in venation, although _Tetracentron_ leaves have a tendency to show the flexuous looping of the secondary veins against smooth looping in _Cercidiphyllum_ leaves. As stated by Wolfe (1977), in _Tetracentron_ veins connect the glandular region of the tooth to the adjacent sinuses, but in _Cercidiphyllum_ such veins are absent.

In actual, the differences of the venation features in secondary looping and within the teeth region are generally observed in the typical leaves of these two genera, excepting for some exceptions. A most noteworthy difference between _Cercidiphyllum_ and _Tetracentron_
is in the nature of marginal glands as stated in earlier page. Based on these characters, our Pedogene leaves of northern Japan are doubtlessly referable to the genus *Tetracentron*, though somewhat incomplete in preservation. *T. ibei* described from the Upper Miocene of northern Kwanto region of Japan (K. Suzuki, 1967) is more akin to the extant *T. sinense* Oliver of China in foliar shape, venation and margin. Our Pedogene leaves are variable in shape and marginal teeth, and are referred to *T. piperoides* recently emended by Wolfe (1977) from the Pedogene of North America.

**Occurrence:** Ishikari coal field Ic-6, Ic-11; Kuji coal field Kj-1, Kj-3.

**Collection:** Hypotypes H.U.M.P. nos. 26154-26157.

**Family Cercidiphyllaceae**

**Genus Cercidiphyllum Sieb. & Zucc.**

*Cercidiphyllum palaeojaponicum* Endo, n. emend.

(Pl. 1, figs. 1-6; pl. 2, figs. 1-3, 6; pl. 9, fig. 8, pl. 10, figs. 3, 4; text-fig. 2, g-1; text-fig. 3, h)


**Type:** Holotype NSM no. 10506, Dam site, Shimizusawa, Yubari City. Hokkaido. (Ikushunbetsu Formation, Early Oligocene).

**Supplementary description:** Leaves variable in shape, generally wide ovate to very wide ovate, rarely wide elliptic; length/width ratio of leaves 0.86 to 1.41 (average 1.04); length 2.6 to 9.6 cm and width 2.1 to 9.7 cm; apex obtuse, occasionally acute; base rounded to slightly cordate, sometimes deeply cordate; margin evenly serrate, occasionally crenate and glandular; teeth marked by rounded or acute sinuses, having a small gland on each tooth tip in which a vein from marginal loop end; the lower side of the teeth usually convex, while the upper side generally convex, very rarely slightly concave; leaf texture chartaceous to subcoriaceous; petiole incomplete, more than 2 cm long. Venation perfect basal acrodromous with three to five primary veins originating from the base; primary veins generally three, nearly equal in thickness, and rarely five; outmost secondaries flanked by a pair of secondaries originating from the top of the petiole; secondaries diverging at acute angles from the medial primary, nearly parallel, forming large loops; outer secondaries comptodromous to form large marginal looping; secondary loops giving off a branch to run to the teeth.

**Explanation of Plate 3**

(all natural size unless otherwise stated)

Figs. 1, 4 *Populus yubariensis* Tanai, H.U.M.P. hypotype no. 26173, 26174 (Loc. Ic-10).

Fig. 2 *Populus yubariensis* Tanai. H.U.M.P. hypotype no. 26175 (Loc. Ic-2).

Fig. 3 *Populus yubariensis* Tanai. NSM hypotype no. 10529 (Loc. Ic-12).

Fig. 5 *Populus yubariensis* Tanai. H.U.M.P. holotype no. 26170 (Loc. Ic-11).

Fig. 6 Showing the venation and glandular margin of fig.3. x 6
tip or to form smaller looping; tertiary veins thin but distinct, irregularly percurrent, and simple to forked in course; higher order venation thin and irregular in course; highest order of venation fifth or sixth; areoles moderate to large (0.7 to 1.5 mm), irregular in size and shape; ultimate veinlets slender, three or four times branching, being generally of equal thickness throughout their course.

Discussion: It is sometimes difficult to distinguish fossil leaves of *Populus, Cercidiphyllum, Tetracentron* and some genera only by superficial features, though many paleobotanists have been elaborated to distinguish. The assignment of our Paleogene leaves to *Cercidiphyllum* is proved by the following characters: the globular glands on the marginal teeth, and medium to large areoles intruded by irregularly branching veinlets which are nearly equal-sized in thickness throughout their course.

Recently Chandrasekharam (1974) and Hickey (1977) established some new species or new combination of *Cercidiphyllum* independently from the Paleocene of Canada and the Eocene of the United States. These North American species designated by them include many leaves being very different from those of the extant *Cercidiphyllum* in shape including apex and base, though they seem to have marginal glands and ultimate veinlets similar to the extant species. On the other hand, our Paleogene leaves from North Japan are generally close to those of the extant *C. japonicum* S. et Z. and *C. magnificum* (Nakai) Nakai in general shape, excepting for the fact that the fossil leaves are mostly with large teeth. Two extant species are indistinguishable in foliar characters including the venation, because their leaves are very variable in shape. Generally, leaves of *C. magnificum* are of more deeply-cordate base and large-toothed than those of *C. japonicum*, although these differences include many exceptions. Our Japanese Paleogene fossils may be close to *C. magnificum* in the marginal crenation, but their leaves are rounded to shallowly or deeply cordate base excepting small immature leaves (pl.2, figs.1, 6).

I once referred the Oligocene *Cercidiphyllum* leaves of Hokkaido (Tanai, 1970) to *C. eojaponicum* Endo, which was reported from the Fushun coal field, Manchuria by Endo (1942). But this species is unfortunately a nomen nudum, because it was unaccompanied by any scientific description. The valid epithet referable to our specimens is “*palaeojaponicum*”, which was given for the Paleogene specimens of Hokkaido by Endo (1968). All the specimens listed in the synonymy are included in *C. palaeojaponicum* redesignated here.

*C. palaeojaponicum* is distinguishable from *C. generatrix* (Hewb.) Hickey from the Golden Valley Formation of the United States (Hickey, 1977), whose leaves are commonly cuneate

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**Explanation of Plate 4**
(all natural size unless otherwise stated)

**Fig. 1** *Populus yubariensis* Tanai. H.U.M.P. hypotype no. 26176 (Loc. Ic-5).

**Fig. 2** *Populus yubariensis* Tanai. H.U.M.P. paratype no. 26171 (Loc. Ic-9).

**Fig. 3** *Tetracentron piperoides* (Lesq.) Wolf e. H.U.M.P. hypotype no. 26155 (Loc. Ic-10).

**Figs. 4, 5** *Populus yubariensis* Tanai. H.U.M.P. hypotypes nos. 26177 (Loc. Ic-12), 26178 (Loc. Ic-6).

**Fig. 5:** x 1.5

**Fig. 6** *Menispermites ishikariensis* Tanai. H.U.M.P. holotype no. 26868 (Loc. Ic-4).
at the base and acuminate at the apex. Among three species from Genesee, Alberta (Chandrasekharam, 1974), C. flexuosum (Hollick) Chandrasekharum is most similar to C. palaeojaponicum in foliar shape and margin. However, judging from the vein islet number described by him, the areoles of this Genesee species are far smaller with 0.28-0.77 mm (in diameter) than those of C. palaeojaponicum.

Occurrence: Ishikari coal field Ic-3, Ic-7, Ic-9, Ic-10, Ic-11, Ic-12; Kushiro coal field Kh-1, Ky-2, Ky-3.

Collections: Holotype NSM no. 10506; paratype NSM no. 10478A; hypotypes NSM nos. 10475, 10482, 10530, 10564; Hypotypes, H.U.M.P. nos. 26955-26958, 26158-26165.

Family Hamamelidaceae
Genus Disanthus Maxim.

Disanthus kujianus Tanai, sp. nov.

Type: Holotype, H.U.M.P. no. 26166; coastal cliff near Minato, Kuji City, Iwate Prefecture (Minato Formation, Early Oligocene).

Description: Leaves wide ovate in shape; length/width ratio of leaves 0.94 to 1.18; length 4.6 to 6.8 cm and width 4 to 7.2 cm; apex obtuse or slightly acute; base broadly rounded to broadly cordate; margin entire, somewhat revolute; leaf texture chartaceous; petiole missing. Venation perfect basal acrodromous with three primary veins originating from the base and a slender pair of the secondaries outside them; medial primary vein nearly straight at the lower and then slightly flexuous toward the apex, giving off two or three pairs of secondaries which are brochidodromous with lateral primaries, four or five secondaries emerging toward both outer sides of the lateral primaries at acute angles, forming large loops with branches emerging from superadjacent secondaries; secondary loops enclosing the smaller tertiary and quaternary arches along the margin, which are mostly pentagonal in shape; tertiaries among the intersecondary spaces slender, and weakly percurrent, simple to forked in course; rank of highest order venation sixth; areoles composed of third to fifth-order veins, moderately in size (0.8 to 1 mm), irregular in shape; ultimate veinlets very thin, irregularly and more than two times branching.

Discussion: The large areoles (0.8 to 1 mm in size) intruded by irregularly and more than twice branching veinlets, pentagonal features of tertiary looping and thin veins of higher orders, indicate that these entire-margined leaves are not referable to the genus Cercis but to the genus Disanthus. The modern leaves of these two genera are difficult to distinguish only by superficial features; however, they are different in the areolation, marginal looping and freely-ending veinlets. The above-noted venation characters eliminate leaves of Cocculus ezoensis which show also entire margin. Other family examined because of their superficial

Explanation of Plate 5
(all natural size)
Fig. 1 Populus yuboriensis Tanai. H.U.M.P. hypotype no. 26179 (Loc. Ic-10).
Fig. 2 Populus yuboriensis Tanai. NSM hypotype no. 10486B (Loc. Ic-11).
Figs. 3-5 Populus yuboriensis Tanai. H.U.M.P. hypotypes nos. 26180, 26181, 26182 (Loc. Ic-9).
PALEOGENE CERCIDYPHYLLUM LEAVES

Plate 5
similarities is Piperaceae; but leaves of Piper are quite different in the ultimate veinlets. Because leaves described as Disanthus from Hokkaido (Tanai, 1967) are transferred to Cercis as discussed later, no fossil leaves of Disanthus are found in the Paleogene of Hokkaido.

**Occurrence:** Kuji coal field Kj-I, Kj-2.

**Collection:** Holotype, H.U.M.P. no. 26166, Paratype no. 26167, Hypotypes nos. 26168.

**Family Salicaceae**

**Genus Populus** Linn.

*Populus yubariensis* Tanai, sp. nov.

(Pl.2, figs.4, 5; pl.3, figs.1-6; pl.4, figs.1, 2, 4, 5; pl.5, figs.1-5; pl.6, figs.1, 4; pl.9, figs.1, 6, 7; pl.10, figs.1, 2; text-fig. 3, a-g)


**Type:** Holotype, H.U.M.P. no. 26170, Shimizusawa, Yubari City, Hokkaido (Ikushunbetsu Formation, Early Oligocene); paratypes, H.U.M.P. no. 26171, Reisui-yama, Yubari City (Ikushunbetsu Formation).

**Description:** Leaves highly variable in shape and size, commonest forms being narrow-ovate to wide ovate, followed by ovate and very wide ovate; length/width ratio of leaves 0.9 to 1.6 (average 1.2); length 4 to 11 cm and width 4 to 10.8 cm; apex mostly acute, or sometimes slightly acuminate; base commonly obtuse to rounded, rarely truncate, and sometimes abruptly cuneate near the petiole; margin unevenly crenate and glandular; crenate teeth considerably adapical and marked by rounded sinuses; marginal glands large, marked by setae and located on the upper side of crenation where a vein terminate; leaf texture chartaceous to subcoriaceous; petiole long, 3 to 5.2 cm in length; several parallel grooves running on the petiole. Venation perfect acrodromous (mostly basal but occasionally suprabasal) with three stout primaries flanked by a pair of secondaries originating at the top of the petiole; medial primary somewhat thicker than the laterals, giving 4 or 5 pairs of camptodromous secondaries; outer secondaries diverging at acute angles from lateral primaries, five or six in number on each side; secondaries and their branches looping near the margin; tertiary veins rather strong, convexly percurrent or nearly straight between the primaries or the secondaries; a vein branching from the marginal loops entering glandular teeth on whose outer side two or three order series of smaller loops are enclosed; higher order veins thin but distinct; highest order of venation sixth or seventh; areoles small to medium (0.3 to 0.7 mm), irregular in size, mostly four-sided; ultimate veinlets thick and then gradually thinner, with three- or four-times branched to asterate freely endings.

**Explanation of Plate 6**

(all natural size unless otherwise stated)

**Fig. 1** *Populus yubariensis* Tanai. H.U.M.P. hypotype no. 26183 (Loc. Ie-9)

**Figs. 2, 7** *Tetracentron piperoides* (Lesq.) Wolfe. H.U.M.P. hypotypes nos. 26157 (Loc. Kj-1). fig. 2: x 2

**Fig. 3** *Disanthus kujianus* Tanai. H.U.M.P. paratype no. 26167 (Loc. Kj-1).

**Fig. 4** *Populus yubariensis* Tanai. H.U.M.P. hypotype no. 26184 (Loc. Ic-2).

**Fig. 5** *Disanthus kujianus* Tanai. H.U.M.P. hypotype no. 26168 (Loc. Kj-1).

**Fig. 6** *Disanthus kujianus* Tanai. H.U.M.P. holotype no. 26166 (Loc. Kj-1).
PALEOGENE *CERCIDIPHYLUM* LEAVES

Plate 6
Discussion: The considerably adpalical crenate margin with large glands located on the upper side (occasionally concave) of the teeth, small to medium areoles (generally 0.3 to 0.5 mm in diameter) intruded by freely-ending asterate veinlets, and long petiole (generally longer than leaf length) indicate that these fossils are members of the genus *Populus*, although the acropetiolar or basilaminar glands were not fully confirmed in these Paleogene specimens. It is also a base for referring these leaves to *Populus* that the marginal crenation consists alternatively of large and small teeth as frequently observed in some species of the extant *Populus*. Most of the extant popular leaves are characterized by acropetiolar glands, but these glands are occasionally lacking in some species or even in leaves of same species (Eckenwalder, 1977).

These Paleogene leaves described above are superficially similar to leaves of *Cercidiphyllum* and *Tetracentron*, especially to the former, but they are easily distinguishable from these two genera by smaller areoles, thicker freely-ending veinlets, larger marginal glands with pointed-tipped setae, and thicker tertiary veins. In the extant leaves of *Cercidiphyllum* with very broadly-crenated crenation the marginal glands are located occasionally on the upper side of teeth or even near the sinus-bottom as in our fossil leaves; however, marginal glands of *Cercidiphyllum* are usually globular in shape, quite different from those of our fossils.

Considering the marginal characters of leaves, *Populus yubariensis* designated here, belongs probably to the section Aigeiros*, and actually resembles leaves of *Populus fremontii* S. Watson and *P. deltoides* Bart. ex Marsh. living in the United States, as shown in Plates 11 and 12. Our fossil leaves are very variable in shape as in leaves of these two North American cottonwoods. However, the extant leaves are usually imperfect acrodromous in principal venation; the lateral primary veins are running up less than a half distance to the apex.

Leaves included in *Populus yubariensis*, as shown in plates 3-5, are highly variable in foliar shape and marginal serration, and they may be separated into several species only by superficial characters. They seem, however, proper now to be included in one species, because their morphological differences of each leaf are too overlapped to distinguish as the independent species. Furthermore, all the specimens are consistent in the characters of marginal glands, areolation size and veinlets.

It is confirmed that *Populus* leaves are abundant through the Paleogene of northern Japan. Based on my reinvestigation, *Antholithes cruciatus* Tanai from the Oligocene of eastern Hokkaido (Tanai, 1970) closely resembles the woody pericarp of capsule of the genus *Populus*, and is probably to represent the capsule of *P. yubariensis*.

Occurrence: Ishikari coal field Ic-1, Ic-3, Ic-5, Ic-6, Ic-7, Ic-8, Ic-9, Ic-10, Ic-11, Ic-12, Yc-2, Nc-1, Nc-2; Kabato and Uryu coal fields Ka-1, Ka-2, Ow-1, Ur-1; Kushiro coal field Kh-1.

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Explanation of Plate 7
(all natural size unless otherwise stated)
Fig. 6. *Cocculus ezoensis* Tanai. H.U.M.P. hypotype no. 26148A (Loc. Ic-9). x 1.5

* *Populus mexicana* Wesmela is excluded from the Section Aigeiros by Eckenwalder (1977).
Ky-3, Ks-1; Kuji coal field Kj-1, Kj-2.

Collections: Holotype H.U.M.P. no. 26170, paratype no. 26171, hypotypes nos. 26172-26186; hypotypes NSM nos. 10486B, 10508, 10513, 10529, 10532.

Family Leguminosae
Genus Cercis Linn.

Cercis nipponica (Tanai) Tanai, comb. nov.

(Pl.8, figs.8-10; text-fig.4, k, 1)


Type: Holotype H.U.M.P. no. 26862, Higure-zawa, Ikushunbetsu, Mikasa City, Hokkaido (Ikushunbetsu Formation, Early Oligocene).

Discussion: These depressed-ovate leaves with imperfectly acrodromous veins are referred to the genus Cercis by the following venation characters: the venation is composed of six-orders, the areoles composed of thick fourth- and fifth-order veins are small (0.3-0.4 mm) and are intruded by single or once-branching veinlets, and the secondary loops are enclosed by the smaller arches of the tertiary and quaternary veins. The reinvestigation of the type specimens described as Disanthus nipponicus from the Paleogene of Hokkaido (Tanaï, 1967) reveals that these specimens are transferred to Cercis, showing quite similar characters of the above-noted venation.

Leaves of Disanthus are distinguishable from Cercis by larger areolation, irregularly and more than twice branching veinlets, and pentagonal tertiary loops of the margin, as shown in Plate 12. The entire-margined leaves of Cocculus ezoensis described in earlier pages show a close resemblance to Cercis nipponica in general appearance, but they are easily distinguishable in larger areoles and marginal looping characters.

Occurrence: Ishikari coal field Ic-4, Ic-6, Ic-9, Ic-10; Kushiro coal field Kh-1.


Insertae Sedis
Genus Carpolithes Brongniart

Carpolithes arcticus (Heer) Hickey


Nyssa arctica Heer. 1969. Flora fossilis arctica. 4(4); 477. pl43. f.12c; pl50. f.5-7.


Cercidiphyllyum arcticum (Heer) auct. non Endo. 1968[part]. ibid. pl20. f.5.

Explanation of Plate 8
(all natural size)

Figs. 2, 4. Cocculus ezoensis Tanai. NSM hypotypes nos. 10523, 10526A (Loc. Ic-10).
Rejected Citation of Cercidiphyllum in the Paleogene of East Asia

The following specimens were reported as *Cercidiphyllum* from the Paleogene of East Asia by several authors. However, no definite characters to be referable to the genus *Cercidiphyllum* are not found in these specimens.


This species was established on an incomplete leaf from the Fushun coal field of northeastern China by Endo (1942), and its epithet has been used for Paleogene leaves of *Cercidiphyllum* by some authors including me. However, Endo (1942) failed to give any scientific description and designation of the type. He described only superficial features that this specimen was closely similar to leaves of young shoot of the extant *Cercidiphyllum japonicum*. Thus, the epithet, "*eoajapanicum*" is nomen nudum. Even if this epithet is valid in publication, we should further reinvestigate whether or not its original specimen is referable to *Cercidiphyllum*.


As judged from its illustration, the irregularly lobed margin and cuneate base indicate that this specimen from Zeya-Bureya Plain is probably referable to *Coccus ezoensis*.


This specimen reported from Brodyazhenskaya valley of North Saghaline is superficially similar to leaves of *Cercidiphyllum*, but it seems referable to *Populus yubariensis* by the marginal serration with incurved teeth. A further investigation of fine vanation is necessary.

Explanation of Plate 9
(all natural size unless otherwise stated)


Fig. 7. *Populus yubariensis* Tanai. Showing the venation and marginal glands of paratype (pl.4, fig.2). × 6

Fig. 8. *Cercidiphyllum palaeojaponicum* Endo. Showing the venation and marginal glands of a specimen (pl.1, fig. 2) × 6
for its accurate generic assignment.

2(4): 76. text-f.2 = genus and species indetermined.

Two specimens described as *Cercidiphyllum* from the Eocene Kuma Group of Shikoku are rejected from *Cercidiphyllum* by their entire margin and venation. Huzioka and Takahashi (1970) who described the Eocene Ube flora of West Honshu, transferred these Kuma specimens to *Paliurus ubensis* Huzioka et Takahashi, but these specimens need to be reinvestigated in venation character.


This specimen from the Eocene Hashima Formation of Kyushu is too fragmentary to make its generic assignment. The long petiole may exclude this species from *Cercidiphyllum*.

433. pl.10 f.3 = *Alangium basiobliquum* (Oishi et Huzioka) Tanai.

The strongly oblique base of blade, well-developed secondary veins from the midvein and entire margin exclude this specimen from *Cercidiphyllum*. This specimen is referable to *Alangium basiobliquum* which is a common member of the Paleogene floras of Japan.


f.4 = genus and species indetermined.

These two specimens from Yubari of Hokkaido are two ill-preserved to make their generic assignment.


These specimens from the Fushun coal field are too ill-illustrated to determine their generic status. However, the nearly entire to undulate margin and long petiole suggest that these Fushun specimens seem referable to *Cocculus ezoensis* Tanai.

**Explanation of Plate 10**

Figs. 1, 2. *Populus yubariensis* Tanai. holotype (pl.3, fig.5). Showing the marginal glands and fine venation. fig.1: x 6, fig.2: x 10

Figs. 3, 4. *Cercidiphyllum palaeojaponicum* Endo. holotype (pl.1, fig.6). fig.3: x 3, fig.4: x 6
References


Tanai, T., 1979. Late Cretaceous floras from the Kuji district, northeastern Honshu, Japan. *J. Fac. Sci.,

Explanation of Plante 11

Showing the venation and glandular margin of the extant leaves for comparison of the fossils. x 10

Fig. 1. *Cercidiphyllum japonicum* Sieb. et Zucc. H.U.P.B. slide no. 1298.

Fig. 2. *Cercidiphyllum magnificum* (Nakai) Nakai. H.U.P.B. slide no. 1331.

Fig. 3. *Populus deltoides* Bert. ex Marsh. H.U.P.B. slide no. 187.

Fig. 4. *Tetracentron sinense* Oliver. H.U.P.B. slide no. 1819.
Appendix. Localities and formations in which fossils occur.

Excepting in the case of surface exposures, all the plant fossils were collected from the waste rocks of coal mines which had been working.

**Ishikari Coal Field, Central Hokkaido**

**Noborikawa Formation (Lower Eocene)**
- Nc-1: the Mitsubishi-Bibai coal mine (closed now), Sanno-sawa, Bibai City.
- Nc-2: the Kamoi coal mine, Kamoi, Utashinai City.
- Nc-3: Road cliff, Honcho, Yubari City.

**Yubari Formation (Middle Eocene)**
- Ye-1: the Naie coal mine (closed now), Naie-cho.
- Ye-2: the Shimizusawa coal mine (closed now), Shimizusawa, Yubari City.
- Ye-3: the Oyubari coal mine (closed now), Kashima, Yubari City.

**Bibai Formation (Upper Eocene)**
- Be-1: the Chashinai coal mine (closed now), Chashinai, Bibai City.
- Be-2: the Mitsubishi-Bibai coal mine (closed now), Tokiwadai, Bibai City.

**Ikushunbetsu Formation (Lower Oligocene)**
- Ic-1: road cliff south of the Sunagawa coal mine, Kami-sunagawa-cho.
- Ic-2: cliff along the Naie River, Naie-cho.
- Ic-3: cliff along Banno-sawa, Bannosawa, Bibai City.
- Ic-4: cliff along Higure-zawa, Ikushunbetsu, Mikasa City.
- Ic-5: the Miruto coal mine (closed now), Miruto, Kurisawa-cho.
- Ic-6: cliff along the river, south of the Kakuta coal mine (closed now), Hinode, Kuriyama-cho.
- Ic-7: road cliff, Shakonosawa, Yubari City.
- Ic-8: cliff along the river, Teimi, Yubari City.
- Ic-9: cliff near the top of Reisui-yama, Yubari City.
- Ic-10: road cliff, Shimizu-no-sawa, Heiwa, Yubari City.
- Ic-11: cliff near the dam-site, Shimizusawa, Yubari City.
- Ic-12: cliff along the Enhoro River, Enhoro, Yubari City.

**Uryu and Kabato Coal fields, Central Hokkaido**

**Ury coal-bearing Formation (Upper Eocene)**
- Ur-1: the Furukawa-Uryu Coal mine (closed now), Horoshin, Numata-cho.

**Owada coal-bearing Formation (Lower Oligocene)**
- Ow-1: the Owada coal mine (closed now), Rumoe City.

**Kabato coal-bearing Formation (Lower Oligocene)**
- Ka-1: Tsukigata coal mine (closed now), at the end of the Subetsu River, Tsukigata-cho.
- Ka-2: cliff along Sattekainai-zawa, Satteki, Urausu-cho.

**Explanation of Plate 12**

Showing the venation and marginal looping or glands for comparison of the fossils. x 10
- Fig. 1. *Cocculus trilobus* Dc. H.U.P.B. slide no. 404.
- Fig. 2. *Cercis chinensis* Bge. H.U.P.B. slide no. 792.
- Fig. 3. *Disanthus cercidifolius* Maxim. H.U.P.B. slide no. 30.
- Fig. 4. *Populus fremontii* S. Watson. H.U.P.B. slide no. 1064.
Kushiro coal Field, eastern Hokkaido

Harutori Formation (Lower Oligocene)
   Kh-1: Harutori and Okotsu pits, Taiheiyo coal mine, Harutori, Kushiro City.

Yubetsu Formation (Middle Oligocene)
   Ky-1: the Shakubetsu coal mine (closed now), Shakubetsu, Onbetsu-cho.
   Ky-2: Nakanosawa near the Yubetsu coal mine (closed now), Yubetsu, Akan-cho.
   Ky-3: the Ponki coal mine (closed now), Shoro, Shiranuka-cho.

Shakubetsu Formation (Middle Oligocene)
   Ks-1: cliff along the Shitakara River, Yubetsu, Akan-cho.
   Ks-2: the Shin-Shiranuka coal mine (closed now), Shiranuka-cho.
   Ks-3: cliff along Chinomi-sawa, Shoro, Shiranuka-cho.
   Ks-4: the Onbetsu coal mine (closed now), Kami-onbetsu, Onbetsu-cho.

Kuji Coal Field, Iwate Prefecture, Honshu

Minato Formation (Lower Oligocene)
   Kj-1: coastal cliff, Minato, Kuji City.
   Kj-2: Matsukurazawa, Natsui, Kuji City.
   Kj-3: the Ube coal mine (closed now), Ube, Kuji City

Kuki Formation (Lower Oligocene)
   Kj-4: road cliff along the sea, Kuki, Kuji City.