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FOSSIL LEAVES OF THE NYSSACEAE FROM
THE MIOCENE OF JAPAN

by

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(with 2 text-figures and 3 plates)

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Abstract

The genus *Nyssa* has been widely recorded in the Tertiary of the Northern Hemisphere, based on leaves, fruits, woods and pollen. However, few fossil leaves seem to be doubtlessly referable by conspicuous identifying characters of this genus. Several leaves showing close affinity to the extant *Nyssa aquatica* L. were recently found from the Miocene of western Honshu. Investigating these fossils together with the nyssaceous leaves described from the Miocene of south-western Hokkaido (Tanai & N. Suzuki, 1963), the latter were transferred to the genus *Camptotheca*.

Introduction

The family Nyssaceae is composed of two genera, *Nyssa* Linn. and *Camptotheca* Decne., and their extant species are confined in geographical distribution. On the one hand, the fossil records of the genus *Nyssa* have been widely known in the Northern Hemisphere, and this genus represents one of the marked relict genera in angiosperms. A number of fossil *Nyssa* species have been described from the Tertiary, partly even from the Pleistocene, based on leaves, fruits, woods and pollen. These fossil records until 1938 were catalogued by Kirchheimer (1938), and the subsequent ones were listed with the critical reinvestigation by Eyde and Barghoorn (1963).

Eyde and Barghoorn (1963) cautiously reinvestigated the fossils reported as *Nyssa*, mainly based on the fruits, because leaves of the genus *Nyssa* are frequently difficult to distinguish from those of other genera. Actually, as already pointed out by Kirchheimer, the *Nyssa* leaves with entire margin are sometimes similar in general appearance to leaves of some genera of the Magnoliaceae, Fagaceae, Annonaceae and Apocynaceae.

According to Eyde and Barghoorn (1963), the definite occurrence of the genus *Nyssa* can trace back to the Paleocene on the basis of fossil fruits, woods or pollen, while most of Cretaceous nyssoid fossils seem to be doubtful. In Japan the genus *Nyssa* has been widely known from the Upper Tertiary mainly

by the fruits (Miki, 1956). Nyssoïd woods described as *Nyssonoxylon* were known from the Eocene or the Oligocene of Hokkaido (Mädel, 1959; M. Suzuki, 1975), and a wood of the genus *Camptotheca* was recently described from the Oligocene of Kyushu (M. Suzuki, 1975).

Though a number of *Nyssa* leaves have been recorded from the Upper Cretaceous to the Pliocene in the Northern Hemisphere, few fossil leaves seem to be definitely referable to this genus by marked identifiable characters. Recently I could find several nyssoïd leaves among the Miocene plants from the Kobe Group of western Honshu, which were entrusted me to identify from Mr. A. Yokoyama. These nyssoïd leaves are doubtlessly referable to the genus *Nyssa* in all characters, though they do not well preserve the fine venation. In 1963 I reported several leaves as *Nyssa japonica* from the Miocene Yoshioka flora of southwestern Hokkaido (Tanai & N. Suzuki, 1963). I reinvestigate these specimens together with the Kobe specimens, and could conclude that the Yoshioka specimens should be changed to the genus *Camptotheca*. In this paper the leaves of these two genera shall be discussed taxonomically.

I wish to express my gratitude to Mr. Akira Yokoyama of Kobe Noda High School, offered me a part of his collection to do the final identification. Thanks are also to Dr. Herman F. Becker of the New York Botanical Garden, who kindly sent me several modern leaves of *Nyssa* for comparison.

Modern Species of the Nyssaceae and their Distribution

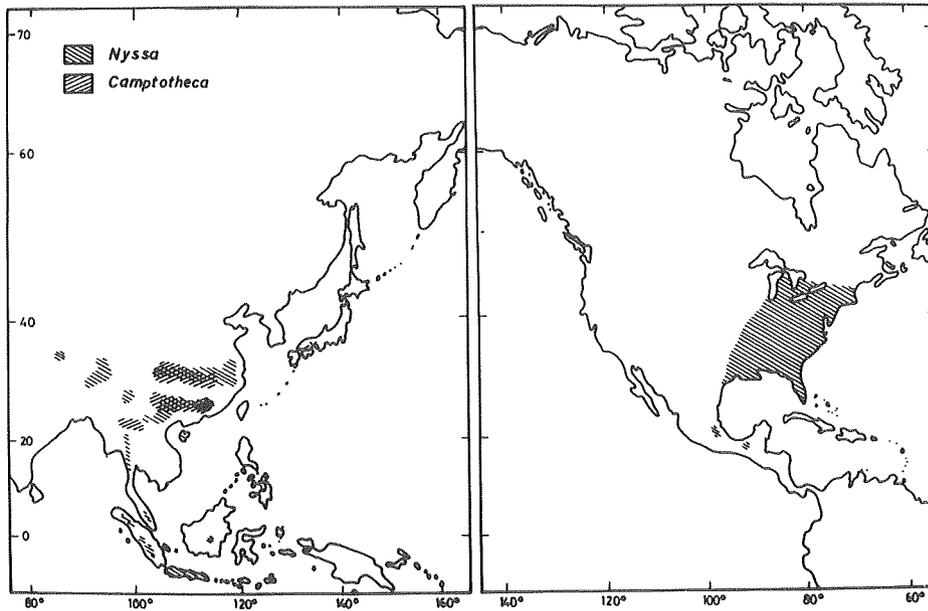
The family Nyssaceae is now limited in geographic distribution. The living species of the genus *Nyssa* L. are disjunctively distributed in eastern North America, East Asia and partly in Central America: four species in eastern North America, two species in east Asia and one species in Mexico. Excluding these species, some taxonomists may add some species or varieties to the genus *Nyssa* in North America. On the one hand, the monotypic genus *Camptotheca* Decne. is confined to East Asia: only one species, *C. acuminata* Decne. is distributed in central and southern China, extending into Tibet.

Prior to the investigation of fossil remains, Eyde (1963) precisely surveyed all the living species of the Nyssaceae, regarding morphological characters and geographical distribution. Text-figure 1 was briefly compiled principally on the basis of some detailed distributional maps (Eyde, 1963; Little, 1971). According his survey, the genus *Nyssa* is composed of six living species as follows:

Nyssa aquatica Linnaeus: the southeastern United States

Nyssa biflora Walter: the southeastern United States

Nyssa javanica (Bl.) Wangerin: Malaysia, Java, Sumatra, Burma, Assam and



Text-fig. 1 The modern distribution of the family Nyssaceae.

others

Nyssa ogeche Marshall: the southeastern United States

Nyssa sinensis Oliver: central and southern China

Nyssa sylvatica Marshall: the eastern United States and Mexico

Of these six species *N. sylvatica*, *N. biflora* and *N. sinensis* show a close similarity in morphological characters, even in habitat condition; Eyde (1963) grouped them as the *Nyssa sylvatica* complex. The other three species are different in many morphological features from the *N. sylvatica* complex. The similarity and difference of characters among these six extant species are well documented by Eyde.

Descriptions of the Species

Family Nyssaceae Genus *Nyssa* Linnaeus

Nyssa a-yokoyamai Tanai, sp. nov.

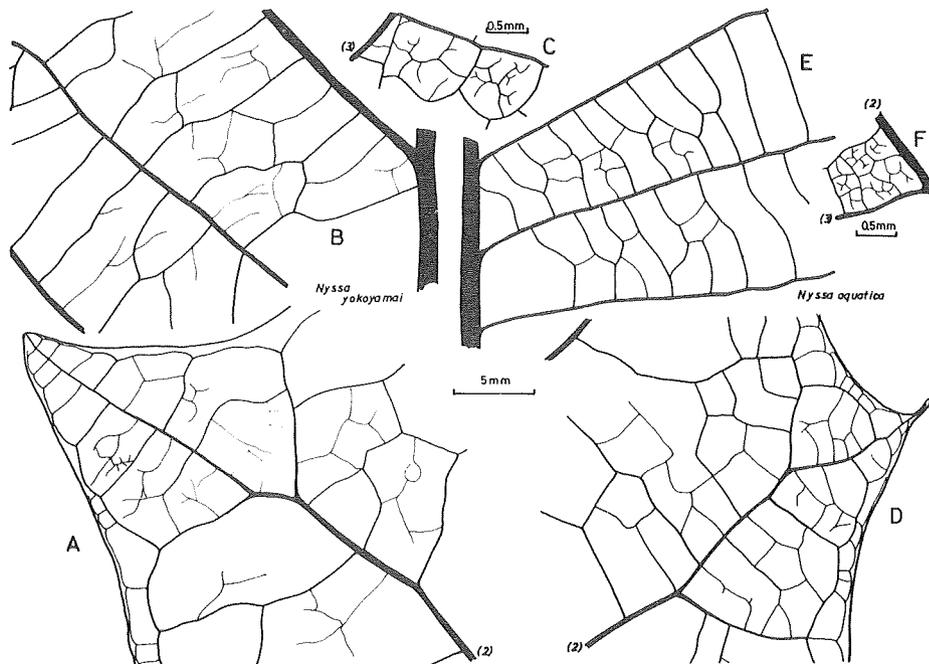
(Pl. 1, fig. 1; pl. 2, figs. 1, 4; pl. 3, figs. 5, 6; text-fig. 2, A-C)

Magnolia miocenica Hu et Chaney, Hori. On the study of the Kobe group, Rokko highlands. p. 111, pl. 20, fig. 78; pl. 21, fig. 78; photo-pl. 9, fig. 4, 1976.

Magnolia sp. A, Hori. *ibid.*, p. 111, pl. 20, fig. 79; pl. 22, fig. 79; pl. 23, fig. 79.

Description: Leaves incomplete, somewhat variable in shape, ovate to ovate-

oblong in general outline, 10 (estimated) to 22 cm long and 8 to 12.4 cm wide; apex acuminate or slightly attenuate; base variable in shape, acute to rounded, sometimes slightly cordate; midvein thick, straight; secondary veins moderate, 13 to 15 subopposite pairs, irregularly spaced, diverging from the midvein at various angles with 50° to nearly 90° , gently curving up and slightly sinuous, or sometimes forking on the half or the two-third way to the margin, abruptly arising up near the margin and joining the superadjacent secondaries at acute angles to form large marginal loops, outside of which tertiary and quaternary veins forming small loops along the margin; intersecondary veins sometimes present; a pair of slender subsecondary veins from near base extending up along the margin (pl. 2, fig. 1); intercostal tertiaries transverse, rather regularly percurrent, simple or sometimes forking; the quaternary veins forming large, quadrangular or pentagonal networks with the tertiaries, enclosing fine reticulation composed of fifth-order veins; ultimate veinlets not well preserved, but probably branched (text-fig. 2C); margin nearly entire with irregular undulation or irregularly dentate with large deltoid teeth (text-fig. 2, A); where teeth present, a thick tertiary branch emerginating from brochidromous



Text-fig. 2 The comparison of the venation characters between *Nyssa a-yokoyamai* Tanai (A-C) and *Nyssa aquatica* Linnaeus (D-F).

A, D: dentate teeth (\times ca 2.1). B, E: tertiary venation (\times ca 2.1). C, F: areoles and ultimate veinlets (\times ca 11).

secondary arch, reaching apex of dents; petiole thick, but nearly missing.

Discussion: These leaves from the Kobe Group are suggested to be referable to the genus *Nyssa* by the above-noted characters. Especially, they show a close affinity with the extant *N. aquatica* in the unusual features: the brochidromous secondary veins are irregularly spaced and sinuous, margin is irregularly undulate or dentate with large teeth, and a pair of slender subsecondary veins extend up along the basal margin. According to Eyde's description, the leaves of *N. sylvatica* are almost always entire in margin, but some leaves are rarely with a few coarse teeth. In general, *N. aquatica* and *N. sylvatica* are different in foliar shape and average size. Furthermore, these two species are distinguishable in tertiary venation: the transverse tertiary veins in the former species are more densely (nearly twice) percurrent than in the latter, in comparison of the same sized leaves (pl. 3, figs. 1, 2). Our fossil leaves closely resemble those of the extant *N. aquatica* in such tertiary venation characters as shown in text-fig. 2.

A number of *Nyssa* species have been reported from the Tertiary of Europe, North America and East Asia. In these reports their occurrences were partly supported by associated nysoid pollen or fruits, along with well-preserved leaf specimens. However all of Tertiary leaves described as *Nyssa* seem not always to provide sufficiently any definite characters of this genus.

There are many toothed leaves of *Nyssa* from the Tertiary of Europe and western North America, which are comparable to our specimens. European fossils similar to *N. a-yokoyamai* are *N. europaea* Unger (Berger, 1952; Kolakovsky, 1959), *N. hungaricum* Andreanszky (Andreanszky, 1959) and *Nyssa* sp. (Hantke, 1965), all of which specimens were included in *N. meriami* (Heer) Knobloch (Knobloch, 1969). These European leaves resemble our new species in the sense of having irregularly spaced secondary veins and dentate margin, but are not sufficiently comparable in venation characters of tertiary and quaternary orders. North American fossil leaves with teeth were reported as *N. hesperia* Berry (Chaney & Axelrod, 1959) and *N. knowltoni* Berry (Brown, 1937); these leaves show close similarity in venation to our specimens, but are somewhat different in marginal teeth, even though considering a wide range of variation. Two leaves were illustrated as *N. knowltoni* from the Oligocene Weaverville flora of California (MacGinitie, 1937); one specimen with toothed margin (Pl. 12, fig. 3) has the tertiary veins obliquely crossed with the secondaries, and seems to be different from those of *N. aquatica*. But another specimens (Pl. 14, fig. 3) is closely similar in venation character to our new species, although it is of entire margin.

Four leaves described as *Magnolia miocenica* Hu et Chaney and *Magnolia* sp. A from the Kobe Group (Hori, 1976) are included in *N. a-yokoyamai* by all characters. Although leaves of *Magnolia* are sometimes similar to those of *Nyssa*

in foliar shape and marginal looping, they are quite different in tertiary and quaternary veins as shown in the figures 1 and 2 of plate 3.

The tupelo gum, *Nyssa aquatica*, which is most allied to *N. a-yokoyamai*, is one of the representative semi-aquatic trees in the swampy regions along the Mississippi River and the Coastal Plain of the southeastern United States. The modern forests in these wet regions and adjacent slopes contain many relict trees, most of which show the East Asian-North American relationships in phytogeography. These relict genera and their ancestral analogues are found in the Miocene Kobe Group (Hori, 1976). A deeply lobed oak, *Quercus kobatakei*, recently described from the Group (Tanai & Yokoyama, 1975) represents one of these analogues.

Occurrence: Shirakawa-toge and Husehata, Suma-ku, Kobe City, Hyogo Prefecture. Shirakawa Formation (Middle Miocene).

Collection: Holotype U.H.M.P. no. 25972; paratypes nos. 25973, 25974; no. 25975.

Genus *Camptotheca* Decne.

Camptotheca japonica (Tanai & N. Suzuki) Tanai, comb. nov.

(pl. 1, figs. 2, 3)

Nyssa japonica Tanai et N. Suzuki. Tertiary Floras of Japan, Miocene Floras. p. 146, pl. 24, figs. 1, 2, 5, 1963.

Discussion: These leaves from the Miocene Yoshioka flora of Hokkaido were once considered to be allied to *Nyssa aquatica*. The precise reinvestigation revealed that these leaves are different in venation characters from the above-described *N. a-yokoyamai*, although similar in some characters such as brochidromous secondary veins and undulate margin. In *N. a-yokoyamai* the lower sets of the secondaries are emarginating generally with wider angles; especially, this character is conspicuous in the case of round-based leaves (pl. 2, fig. 4) as similar as in the leaves of the extant *N. aquatica*.

On the one hand, in the Yoshioka specimens the secondary veins are nearly

Explanation of plate 1

(natural size unless otherwise stated)

Fig. 1 *Nyssa a-yokoyamai* Tanai. Shirakawa-toge, Kobe City (Shirakawa Formation). x 0.85 Holotype, U.H.M.P. no. 25972.

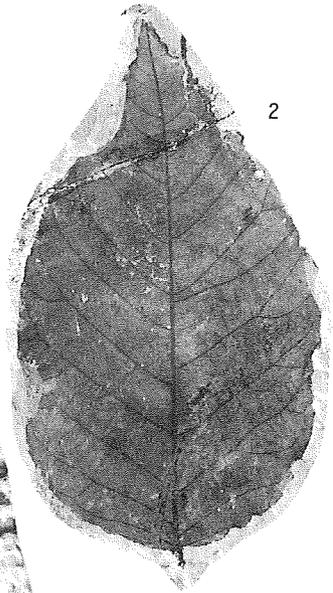
Figs. 2, 3 *Camptotheca japonica* (Tanai et N. Suzuki) Tanai. Yoshioka, Fukushima-cho, Hokkaido (Yoshioka Formation). U.H.M.P. paratype no. 25412, holotype no. 25414.

FOSSIL LEAVES OF NYSSACEAE

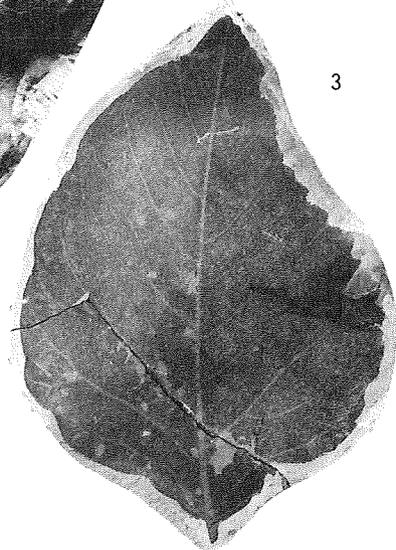
Plate 1



1



2



3

parallel each other, and are extending more upward. The tertiary veins are transversely precurrent as in *N. a-yokoyamai*, but usually emit a subtertiary veins perpendicularly at the middle as seen in modern leaves of the *Camptotheca*. Considering these venation characters in addition of the original description, the Yoshioka nysoid leaves are referable to the genus *Camptotheca*, and is closely related to *C. acuminata* Decne. living in China and Tibet. Based on Alaskan Miocene specimens, Wolfe (1966) transferred the original specimens of Hokkaido to the genus *Cladrastis*, and compared to *C. lutea* (Michx.) K. Koch. However, the Yoshioka specimens are distinguishable from *C. lutea* by more than two series of marginal tertiary loops and by rather regular precurrent intercostal tertiaries.

The fossil wood of *Camptotheca* was recently reported from the Oligocene of North Kyushu (M. Suzuki, 1975). Thus, it is supported that the genus *Camptotheca* was once living in Japanese islands during middle Tertiary time. Several fossil fruits were once described as *Camptotheca* from the Pliocene of Europe (Reid & Reid, 1915), but were later transferred to the genus *Halesia* Ellis. by Kirchheimer (1943, 1957). Accordingly, as far as known at present, the fossil record of the genus *Camptotheca* is confined in East Asia.

Occurrence: Yoshioka, Fukushima-cho, Matsumae-gun, Hokkaido. Yoshioka Formation (Middle Miocene).

Collection: Holotype U.H.M.P. no. 25414, paratype no. 25412, hypotype no. 25413.

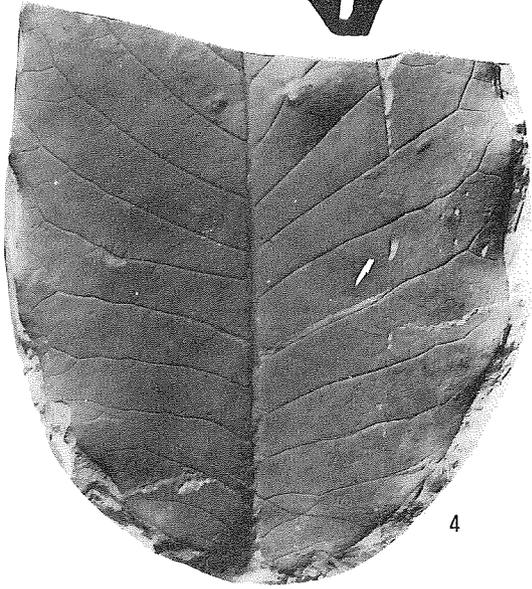
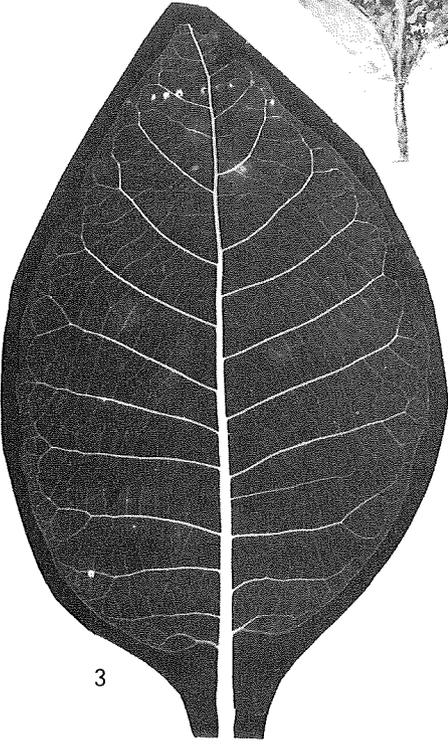
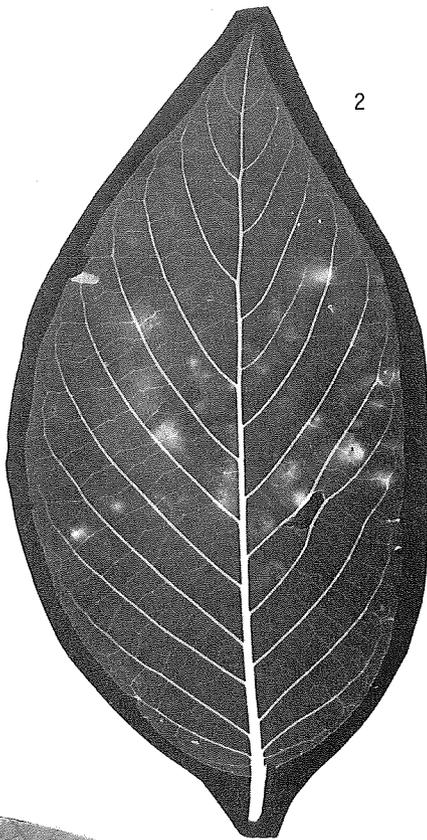
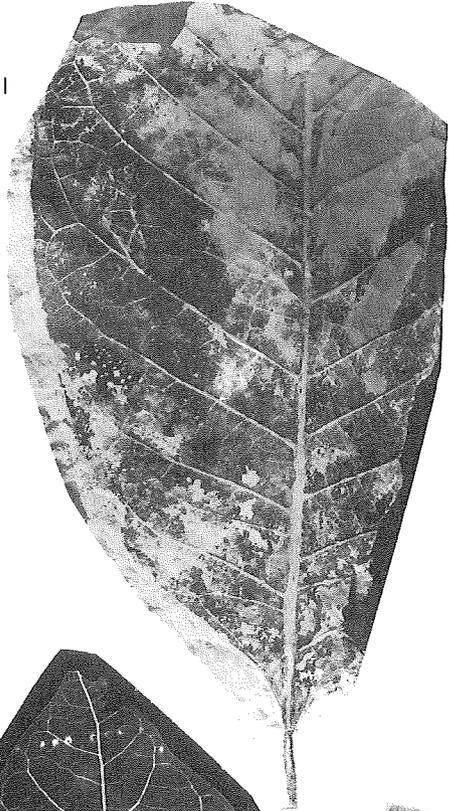
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Explanation of Plate 2

(all natural size)

- Fig. 1 *Nyssa a-yokoyamai* Tanai. Shirakawa-toge, Kobe City (Shirakawa Formation). Paratype, U.H.M.P. no. 25973.
- Fig. 2 *Camptotheca acuminata* Decne. U.H.P.B. slide no. 95. (cultivated in the Asakawa Experimental Forest, Forest Experimental Station, Tokyo)
- Fig. 3 *Nyssa aquatica* Linn. U.H.P.B. slide no. 94 (The New York Botanical Garden, U.S.A.).
- Fig. 4 *Nyssa a-yokoyamai* Tanai. Shirakawa-toge, Kobe City (Shirakawa Formation). Paratype, U.H.M.P. no. 25974.



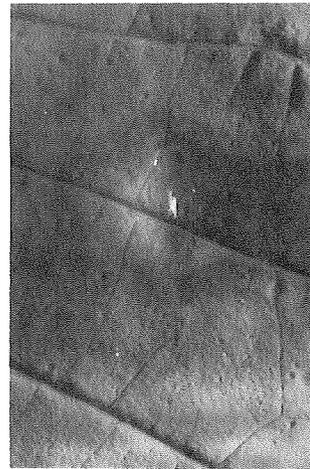
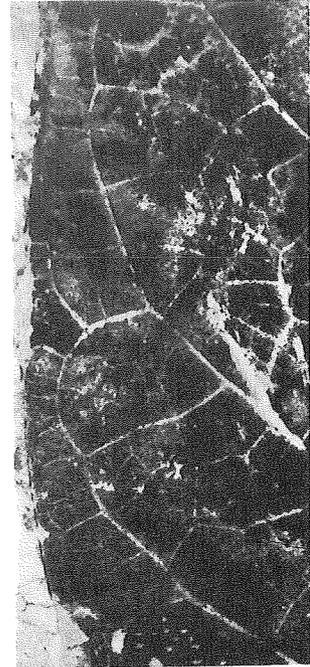
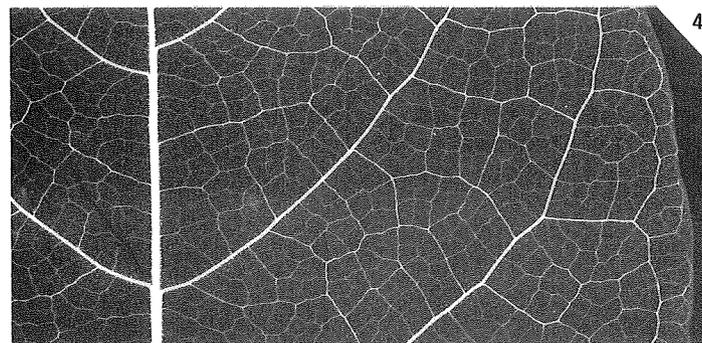
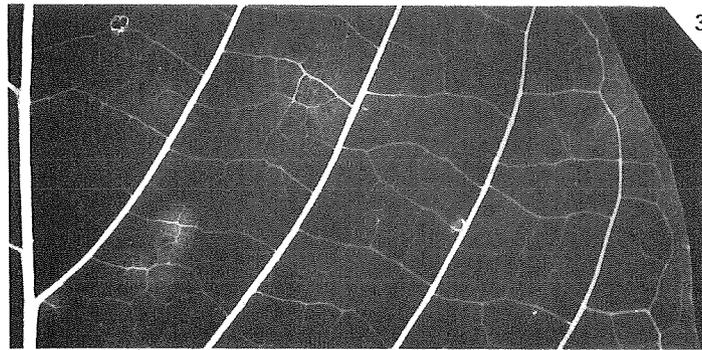
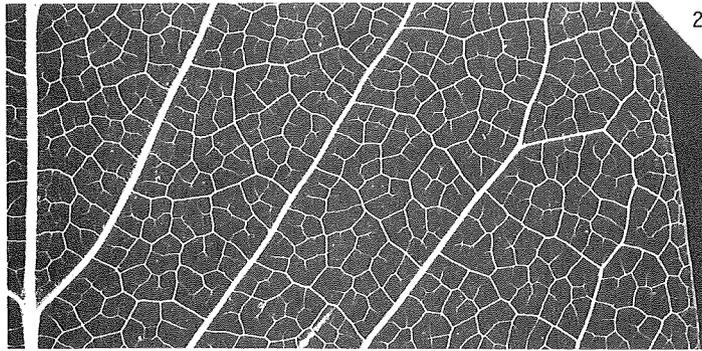
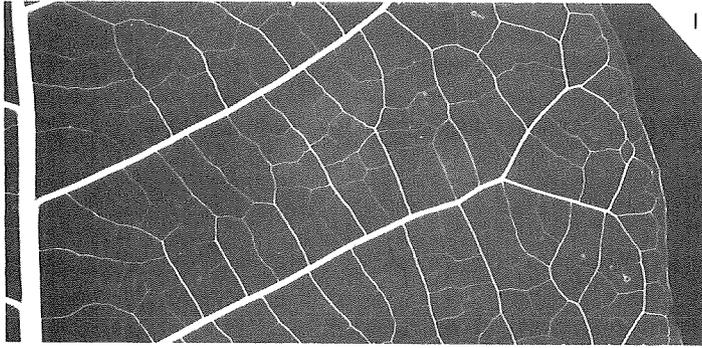
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Explanation of Plate 3

- Fig. 1 *Nyssa aquatica* Linn. × 5 U.H.P.B. slide no. 94.
- Fig. 2 *Magnolia kobus* Dc. × 5 U.H.P.B. slide no. 276 (Mt. Osore-san, Aomori Prefecture)
- Fig. 3 *Camptotheca acuminata* Decne. × 5 U.H.P.B. slide no. 95.
- Fig. 4 *Nyssa sylvatica* Marsh. × 5 U.H.P.B. slide no. 93 (Harkers Ferry, West Virginia, U.S.A.).
- Fig. 5 *Nyssa a-yokoyamai* Tanai. × ca 3 Showing the marginal looping of the paratype (U.H.M.P. no. 25973).
- Fig. 6 *Nyssa a-yokoyamai* Tanai. × ca 3.5 Showing the tertiary venation of the paratype (U.H.M.P. no. 25974).

FOSSIL LEAVES OF NYSSACEAE

Plate 3



5

6

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