The Revision of the so-called "Alangium" Leaves from the Paleogene of Hokkaido, Japan

By

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Abstract Fossil leaves referred to the genus Alangium have been widely recorded from the Tertiary of East Asia, especially common from the Eocene to the Miocene. Based on a large collection, analysis of the venation features indicates that Paleogene Alangium or Alangium-like leaves of Hokkaido are of diverse taxonomic origin. Most of these leaves are referred to the genus Mallotus (Euphorbiaceae), 3 genera of Byttneria, Kleinhovia and Pterygota (Sterculiaceae) and 2 extinct genera of Actinovena and Plafkeria (Tiliaceae). Only a few leaves are referable to Alangium. New taxa and combinations proposed are: Actinovena ishikariensis, n. gen. and n. sp.; Alangium columbioides, n. comb.; Byttneria iizimae, n. sp.; Kleinhovia basitruncata, n. comb.; Plafkeria basiobliqua, n. comb.; Pterygota ezona, n. sp.

Introduction

Fossil leaves referred to the genus *Alangium* have been widely recorded through the Tertiary of East Asia by various authors (e.g. OISHI, 1950; TANAI, 1961; HUZIOKA, 1964; Acad. Sinica, 1978; BAIKOVSKAYA, 1974), Especially, Miocene leaves have been described mostly as *Alangium aequalifolium*; this species is one of the representative plants in the Lower to lower-Middle Miocene of East Asia. *Alangium aequalifolium* characterized by leaves having markedly asymmetric base is closely similar or nearly identical to "*Ficus*" *tiliaefolia* (Al. Br.) Heer, which has been commonly known in the Miocene of Central Europe.

Taxonomy of "Ficus" tiliaefolia has been disputed by various authors during more than one hundred years, referred to various genera such as Alangium, Byttneria, Dombeya (Dombeyopsis), Pterospermites and others. Based on leaf anatomy of Pliocene materials from Czechoslovakia, Knobloch and Kvacek (1965 a) concluded to ascribe "Ficus" tiliaefolia to the Sterculiaceae, adopting the form-genus Byttnerio-phyllum which was originally proposed with no valid diagnosis by Givulescu (1959). However, taxomic controversy on Byttneriophyllum-Alangium has continued up to the recent (Czeczott, 1967; Iljinskaya, 1968; Eyde et al., 1969; Givulescu, 1970; Jähnichen, 1984).

KNOBLOCH & KVACEK (1965b) synonymized all the leaves of *Alangium aequalifolium* of the East Asian Miocene to *Byttneriophyllum tiliaefolium* which was emended by them. But my recent provisional reinvestigation indicates that "A. aequalifolium" from the Miocene of East Asia is of several taxonomic origin: based on venation

characters, most of the specimens are referable to the Sterculiaceae or Tiliaceae, while some leaves from Honshu and Korea are doubtlessly referred to the genus *Alangium*. In actual, *Alangium mikii* from the Miocene of Alaska (Wolfe & Tanai, 1980) is closely similar to "Ficus" tiliaefolia in gross features such as markedly asymmetric base and principal venations, although quite different in the fine venation and trichome. Accordingly, the so-called "Ficus" tiliaefolia appears to be not represented by a single taxon, and it may be a leaf type complex of several taxonomic origin.

Compared with extensive records of "Alangium" in the Neogene, Paleogne records have been not always common in East Asia, except those of Hokkaido (OISHI, 1950, TANAI, 1970) and western Honshu (HUZIOKA & TAKAHASHI, 1970). It is mainly due to the fact that Paleogene floras have not been fully investigated in East Asia up to the present. However, leaves that are similar to Alangium in gross features, are abundant in the Eocene and Oligocene of Japan, especially from Hokkaido. These leaves are closely related to Miocene "Ficus tiliaefolia complex" in general features such as leaf shape and venation, and some Miocene species appear to be contained in certain Paleogene phylads. I have investigated all the Paleogene leaves which were once referred to Alangium or closely similar to it. I can reach a conclusion that these Paleogene leaves are of diverse taxonomic origin.

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Material and the Plant-bearing Formations

The material on which this study is principally based was collected from many localities from the Ishikari Group and its correlatives in Hokkaido by me during many years. Additional specimens were examined in the Museum of Paleontology, Hokkaido University (HUMP), Sapporo and National Science Museum (NSM), Tokyo. All the fossils are represented by leaf impressions, most of which shows the finer details of venation.

Paleogene plants are included in the coal-bearing formations of the Ishikari, Rumoi and Kabato coal fields in central Hokkaido, and of the Kushiro and Rikubetsu-Kitami coal fields in eastern Hokkaido (Fig. 1). The coal-bearing deposits of

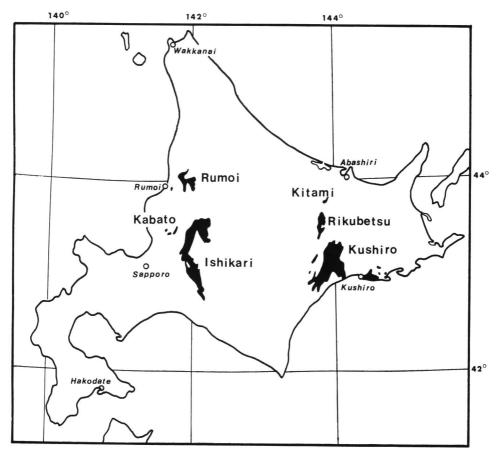


Fig. 1. The Distribution of Paleogene Coal Fields in Hokkaido.

these fields, sometimes intercalated by marine formations, are usually covered by Paleogene marine thick argillaceous formations. Paleogene formations of these fields are similar in lithology, and even in fossil assmblages of both plants and animals. The Paleogene sequence is most well-developed in the Ishikari field, represented by the coal-bearing Ishikari Group and the covering marine Poronai Group. In other fields the sequence is incomplete, represented only by a part of the Ishikari sequence. The geological investigations by various authors revealed the stratigraphic correlation of the Paleogene in these fields. Based on the stratigraphic relationships and the floristic composition, the Paleogene plant-bearing formations of Hokkaido are divided into six horizons in ascending orders as shown in Table 1. Fossil localities are shown in appendix.

The Paleogene of Hokkaido has been considered to range from Eocene to Oligocene in age by many authors. Despite of many recent paleontologic contribu-

Table 1. Stratigraphic relationships of Paleogene plant-bearing formations in Hokkaido.

- Horizon 1. Noborikawa Formation (Is*)
- Horizon 2. Yubari Formation (Is)
- Horizon 3. Bibai Formation (Is), Uryu Formation (Rm).
- Horizon 4. Ikushunbetsu Formation (Is), Kabato Formation (Kb) Owada and Tachibestsu Formations (Rm), Harutori and Yubetsu Formations (Ks), Rikubetsu Formation (Rk-Ki).
- Horizon 5. Ashibetsu Formation (Is), Shakubetsu Formation (Ks).
- Horizon 6. Wakamatsuzawa Formation (Rk-Ki).
- * Letters in parenthesis show the coal field. Is: Ishikari. Kb: Kabato. Ks: Kushiro. Kb: Kabato. Rk-Ki: Rikubetsu-Kitami. Rm: Rumoe.

tions by various authors, the precise ages of the Ishikari Group and its correlatives have been debated up to the present. It is due to the fact that the Groups contains few marine planktonic microfossils definitely applicable for the correlation of international scale. Based on a few planktonic foraminifers from the Poronai Formation which covers the Ishikari Group with disconformity, Kaiho (1984) asserted that the Poronai Formation is largely of Middle to Late Eocene age, except its upper part ranging up to the Lower Oligocene. However, his age assignments provide no parallel to the radiometric ages of the volcanic ash partings which are contained in coals of the Ishikari Group; the Wakkanabe and Yubari Formations are 41.5±3.5 and 44.1±3.1 Ma in age respectively (TANAI, 1984). Paleogene land floral sequence of Hokkaido indicates that a considerable climatic deterioration occurred between horizons 3 and 4. This shows probably the "Terminal Ecoene Event" proposed by WOLFE (1978). Considering the floristic sequence together with available radiometric ages, the Paleogene plant-bearing formation of Hokkaido are considered to be from Middle to Late Eocene in age: horizons 1-3 are Middle Eocene, horizons 4-5 are Late Eocene, and horizon 6 is late-Early Oligocene in age respectively.

"Alangium"-like Leaves in the Paleogene of Hokkaido

Alangium leaves from the Paleogene of Japan were first described as Marlea by Oishi (1950); he distinguished two species by leaf shape, M. basiobliqua Oishi & Huzioka and M. basitruncata Oishi & Huzioka from the Ikushunbetsu Formation of the Ishikari coal field, Hokkaido. Later, along with additional occurrence from the Kushiro coal field and others, these two species were emended to Alangium by Tanai (1961, 1970), because Marlea is a section name of the genus Alangium. A. basiobliquum is represented by considerably inequilateral ovate leaves with markedly oblique base, while A. basitruncatum is represented by wide ovate or pentagonal leaves with truncate base. These both leaves are usually entire on margin, but A. basitruncatum has sometimes two small lobes on the upper margin. On the one hand, ignored these descriptions, Endo (1968) referred "Alangium"-like leaves of the

Ikushunbetsu Formation to the genus Ficus without any valid discussion.

A number of *Alangium* or *Alangium*-like leaves are contained in my extensive collection. These specimens include leaves doubtlessly referable to *A. basiobliquum* and *A. basitruncatum*. But there are also many leaves doubtful to be included in these two species of *Alangium*, although closely similar in general features. These leaves show an intergradation of gross characters which may sometimes render separation extremely difficult unless the finer details of venation are examined.

The extant leaves of *Alangium* (*Marlea*) are characterized by veinlets profusely branching within areoles (Fig. 2-A) different from most leaves of the Sterculiaceae whose veinlets are lacking or single. Investigated the collections including type specimens, all the Paleogene *Alangium* or *Alangium*-like leaves are confirmed to be lacking or single in the freely ending veinlets, except for several specimens. As far as I reinvetigated, the Paleogene true *Alangium* is represented only by a leaf which was described as *Ficus columbioides* by ENDO (1968).

Leaves of "Alangium basiobliquum" with markedly oblique base, although very variable in shape, show that the veinlets are lacking or single in four-sided areoles (0.25–0.43 mm across), and that the secondary veins form loops just within the margin. These features indicate that A. basiobliquum is referable to the form-genus Plafkeria which was proposed as an extinct genus of the Tiliaceae by Wolfe (1977). P. basiobliquum is one of the most common species in the Paleogene of Hokkaido, with wide stratigraphic and areal distribution. Plafkeria was widely known with 4 species during the Eocene and Oligocene of Alaska, Washington and Oregon (Wolfe, 1968, 1977; Manchester, 1987). This extinct genus may be one of the evidences which show the phytogeographic connection between East Asia and western North America during the late Paleogene.

Leaves of "Alangium basitruncatum" having also single veinlet in minute four-sided areoles (0.15 mm across) are characterized by thin tertiary veins and quaternary veins that are arranged perpendicular to the tertiaries with a close distance. Considering these venation characters together with other features, A. basitruncatum is referred to the genus Kleinhovia of the Sterculiaceae. Kleinhovia is monotypic; the extant K. hospita L. is distributed in tropical lowlands of Southeast Asia. It is noteworthy for paleoclimatic consideration that K. basitruncatum is widely known in Hokkaido during the Eocene.

Beside the abundant occurrence of the above two plants, more equilateral ovate leaves are commonly found in my collection. Although these leaves are sometimes similar to less inequilateral leaves of *Plafkeria* in gross features, they are distinguishable in the venation characters such as the quaternary veins, areole size and veinlets. These equilateral leaves are grouped into two types: the one is cordate or deeply cordate at the base, and the other is rounded or obtuse.

The leaves with cordate base are lacking or single in the veinlet, and are separated further to two taxa by the extension of an apical pair of the lateral primary veins, feature of the quaternaries and areole size. Leaves having larger areoles (0.35 mm

Table 2. A Key for the Identification of the so-called "Alangium" leaves from the Paleogene of Hokkaido.

1. Leaf considerably inequilateral

- 1. Leaf nearly equilateral or slightly inequilateral.
 - 2. Base cordate.

 - 3. An apical pair of lateral primary veins extending about 2/3 the distance to apex.

 - 4. Quaternary veins thick, forming 4 or 5 sided large meshes; areoles large, 0.5-1 mm across; veinlets profusely branching.......Alangium columbioides
 - 2. Base non-cordate.
 - Base truncate, leaf usually wide-ovate.
 Quaternary veins thin, perpendicular to tertiaries with 0.4-1 mm distance, straight or forking; areoles minute, 0.15 mm across; veinlets lacking or single.
 - Base rounded; leaf usually narrow ovate.
 Quaternary veins thick, forming irregular small polygonal meshes; areoles minute,
 0.15-0.25 mm across; veinlets lacking or single.........Actinovena ishikariensis

across) is referred to the genus *Pterygota*, while leaves with smaller areoles (0.15–0.25 mm across) are referable to the genus *Byttneria*. Especially, the latter leaves are well characterized by the subtertiary or quaternary branches, which sometimes emerges perpendicularly at the half way of intercostal tertiary vein and then curves abruptly parallel to it. Such subtertiary veins in the intercostal area are usually found in the extant leaves of *Byttneria*, as already pointed out by WOLFE (1977).

Of the equilateral leaf specimens, leaves with obtuse base are referred to the genus *Mallotus* by large areoles (0.5–1 mm across), profusely branching veinlets, marginal protuberance and gland scattered on the undersurface. On the one hand, leaves with rounded base are distinguishable from above-noted genera of the Sterculiaceae, although the veinlets are lacking or single in minute areoles (0.15–0.25 mm across). These leaves are now considered to be an extinct genus *Actinovena* of the Tiliaceae, as proposed later.

Through the investigation of Alangium or Alangium-like leaves from the Paleogene of Hokkaido, seven taxa of four families are confirmed: Alangiaceae (Alangium), Euphorbiaceae (Mallotus), Sterculiaceae (Byttneria, Kleinhovia, Pterygota), and

Tiliaceae (Actinovena, Plafkeria). It is noticeable that leaves doubtlessly identified to Alangium are rather rare in the Paleogene of Hokkaido. A key for the identification of "Alangium" leaves from the Paleogene of Hokkaido is presented in Table 2.

Beside Hokkaido, Alangium basiobliquum was described from the Eocene Ube Group, western Honshu (Huzioka & Takahashi, E., 1970). My provisional examination of the original specimens indicates that they are not Alangium because of single veinlet. Leaves of "Ficus tiliaefolia" were described from the Ecoene Kuma Group (Nagai, 1957) and the Eocene Oyake Formation of North Kyushu (Takahashi, K. & Obata, 1962). It is difficult to do their revision, only based on the published illustrations. However, NSM collection from the Kuma Group (by Tanai and Uemura) contains many leaves similar to "Ficus tiliaefolia" in gross features; these leaves are inequilaterally cordate at the base, and are lacking or single in veinlet within four sided areoles. These Kuma leaf specimens are associated with several large winged seeds, which are similar to "Banisteriaecarpum giganteum (Goeppert) Kräusel. It is noteworthy that such co-occurrence of leaves and winged seeds are similar to the case of European "Ficus tiliaefolia", as pointed out by Czeczott (1967). The Kuma leaf specimens are different from any species of Hokkaido, and their taxonomic discussion shall appear in later paper.

Systematic Descriptions

Family Alangiaceae

Genus Alangium Lam.

Alangium columbioides (ENDO) TANAI comb. nov.

(Pl. 1, fig. 1; Fig. 2-C, D)

Ficus columbioides Endo. Bull. Natn. Sci. Mus., 11(4): 428, pl. 11, f. 3, 4.

Type: Holotype NSM 10484; Dam-site, Shimizusawa, Yubari, Hokkaido; Ikushubetsu Formation (Late Eocene).

Emended Description: Leaves equilateral, somewhat variable in shape from narrow ovate to ovate, 9.5 to 9.7 cm long and 4.9 to 5 cm wide; apex acuminate with somewhat long tip; base slightly cordate; margin entire; petiole missing. Venation basal actinodromous with 3 primary veins; mid-primary thick, straight; lateral primaries thick, making angles of 25° to 30° with the midvein, extending about two-thirds the distance to apex, nearly straight, curving abruptly to form a series of loops with tertiary branches of basal secondary; 6 or 8 pairs of the secondaries parallel to lateral primary but at obtuse angles on the apex part; exmedial secondaries from lateral primary 7 or 8 in number, diverging at acute angles, nearly straight, giving off abaxially 5 to 7 camptodromous tertiaries all the secondaries curving sharply near the margin to form prominent loops enclosing tertiary arches; intercostal tertiaries percurrent, straight or slightly convex, sometimes forking, irregularly spaced with the distance of 2 to 4 mm; quaternary veins rather thick, typically perpendicular and

sometimes parallel to the tertiaries, forming irregular 4 or 5 sided, large meshes; the higher order veins very thin; the highest order venation sixth; areoles irregularly sized, usually large, 0.5 to 1 mm across; veinlets profusely branching.

Discussion: The reinvestigation of the holotype specimen of Ficus columbioides revealed that it is referable not to Ficus but to Alangium by the following features: the irregularly spaced tertiary veins sometimes forking; the quaternaries typically perpendicular to the tertiary forming large meshes; markedly thin quinternary veins; irregularly sized and large areoles intruded by profusely branching veinlets. Because Alangium columbioides is usually very thin in the quinternary and higher order venation, the ill-preserved leaves are sometimes difficult to be distinguished from other similar leaves only by gross features.

A. columbioides is closely related to the extant A. chinense (LOUR.) HARMS. and A. bandelii SCHNARF. of tropical East Asia; the fossil is, however, different from the former in having the narrow averaged distance of tertiary veins and acuminate apex, and from the latter in having nearly equilateral base.

Occurrence: Ishikari coal field Ic-3, Ic-11.

Collection: Holotype NSM 10484; NSM PP 10340.

Family Euphorbiaceae

Genus Mallotus Lour.

Mallotus hokkaidoensis TANAI

(Pl. 1, figs. 2, 3; Fig. 2-G, H)

Mallotus hokkaidoensis Tanai. J. Fac. Sci., Hokkaido Univ. [4], 14(4): 487. pl. 13. f. 8, 1970.

Discussion: The palmate venation with three prominent primary veins, distinct percurrent tertiaries, thin quaternary veins forming 4 or 5 sided large meshes, large areoles formed by quinternary veins, and profusely branching veinlets indicate that these incomplete leaves are doubtlessly referable to the genus Mallotus. Furthermore, this identification of these fossils is confirmed by the glandular spots scattered on the undersurface of blade and the glandular proturberance existing on the margin in which branches from tertiary loops end.

The fossil leaves of the Ishikari coal field are referable to *Mallotus hokkaidoensis* of the Kushiro field in shape, feutures of the lower order venation, although the holotype specimen does not preserve the higher order veins than the quinternary. *M. hokkaidoensis* is closely related to the extant *M. japonicus* MUELL.-ARG. and *M. philippensis* MUEL.-ARG., especially to the former in having thin quarternary veins. However, leaves of *M. japonicus* are variable in shape from narrow-ovate or ovate to trilobed; *M. hokkaidoensis* is closely similar to narrow ovate leaves of the extant species.

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

Collections: Holotype HUMP no. 26979; hypotypes NSM PP 10289, 10319.

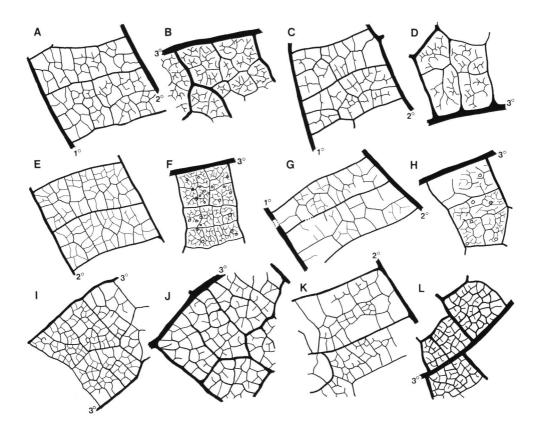


Fig. 2. The Venation of Costal Area and Areole of the Fossil and Extant *Alangium*, *Mallotus* and *Pterygota*.

 $(A, C, E, G, I, K \times 3; B, D, F, H, J, L \times 11.5)$

- A, B. Alangium premnifolium OHWI. NSM Paleob. Ref. Coll. no. T-251.
- C, D. Alangium columbioides (ENDO) TANAI. NSM 10484 (pl. 1, fig. 1).
- E, F. Mallotus japonicus MUELL.-ARG. NSM Paleob. Ref. Coll. no. T-372.
- G, H. Mallotus hokkaidoensis TANAI. NSM PP 10289 (pl. 1, fig. 2).
- I, J. Pterygota alata (ROXB.) R. BR. NSM Paleobot. Ref. Coll. no. T-2491.
- K, L. Pterygota ezoana TANAI. NSM PP 10301 (pl. 6, fig. 4).

Family Sterculiaceae

Genus Byttneria Loefl.

Byttneria iizimae TANAI sp. nov.

(Pl. 1, figs. 4, 5; pl. 2, figs. 1, 5; pl. 3, figs. 1, 2, 4; pl. 9, figs. 1, 2; fig. 3-E, F)

Ficus tennesseensis auct. non Berry. Endo. Bull. Natn. Sci. Mus. 11(4): 431. pl. 13. f. 3, 4 1968.

Type: Holotype NSM PP 10290; Reisuizan, Yubari, Hokkaido; Ikushunbetsu Formation (Late Eocene).

Description: Leaves ovate to widely ovate, slightly inequilateral in general outline, 5.8 to 20.5 cm long and 4.3 to 13.5 cm wide, length/width ratio 1.27 to 1.57; base slightly asymmetric, broadly to deeply cordate; apex abruptly acute or slightly acuminate with pointed tip; margin entire; petiole long and thick, typically more than a half of leaf length, somewhat swollen at its top attaching the lamina. Venation basal actinodromous with 5 to 7 primary veins; midvein thicker than other lateral primaries, straight; an apical pair of lateral primaries thick, diverging at angles of 30° to 40°, nearly straight, extending two-thirds the distance to the apex, giving off abaxially 5 to 7 secondaries; a pair of second lateral primaries making angles of 60° to 90° with midvein, somewhat thinner than apical ones, giving off basally 5 to 6 secondaries; one more basal pair of lateral primaries sometimes present, thin, extending down basally; 6 to 7 secondary veins from midvein parallel to apical primaries; all the lateral primaries and secondaries curving up near the margin, forming distinct large loops which enclose tertiary and quaternary arches; intercostal tertiary veins distinct, straight or slightly convex percurrent, typically with distance of 3 to 4 mm, at the half way sometimes branching off a subtertiary vein perpendicularly which curves abruptly parallel to the tertiaries; quaternaries typically perpendicular to tertiaries or forking; quinternary and the higher order veins forming 4 or 5 sided areoles which are 0.15 to 0.25 mm across; the highest order venation seventh; ultimate veinlets typically lacking, but rarely single.

Discussion: These leaves are characterized especially by the following venation characters: marginal loops developing distinctly 2 or 3 series; the subtertiary veins sometimes emerge perpendicularly at the half way of the tertiary, and then abruptly curve to parallel to the tertiaries; the areoles are usually very small, and are intruded rarely by single freely ending veinlets. These characters indicate that the fossil leaves are referable to the genus Byttneria. As in the extant leaves of this genus, the fossil leaves usually shallowly to deeply cordate at the base, although the extant leaves have usually symmetrical base. Among the extant species, B. aspera COLEBR. and B. integrifolia LACE living from South China to India have leaves most similar in many characters to the fossils.

Less asymmetrical leaves of *Plafkeria basiobliqua* are somewhat similar to *Byttneria iizimae* in general appearance, but they are easily distinguishable in having the oblique base, inframarginal loops closer to the margin, the rectangular quaternary veins and larger areoles sided by thin veins. A leaf described as *Ficus tennesseensis* by ENDO (1968) is included in *B. iizimae*, as the reinvestigation of these specimens reveals to match well in the venation characters.

Reinvestigating "Ficus tiliaefolia" which is a common Miocene species of Europe, KNOBLOCH and KVACEK (1965a, b) revealed that leaves of this species are most similar to Byttneria, especially to the extant Byttneria aspera in features of trichome, stomata and epidermis structures. They proposed to treat this species as the form genus

Byttneriophyllum, considering these anatomical result together with paleoecology and composition of the "Ficus tiliaefolia" bearing flora. However, such nomenclature has to be further disputed, because the taxonomy should not include other factors such as assemblage and climate under which the taxon inhabits (CZECZOTT, 1967). In any way, Byttneria iizimae is distinguishable from Byttneriophyllum in nearly equilateral base of blade and wider distance of the tertiary veins.

This species is named for Professor Azuma IIZIMA of University of Tokyo, who kindly helped me to collect these specimens in the Ishikari coal field.

Occurrence: Ishikari coal field Ic-9, Ic-10; Rumoi coal field Ow-1.

Collection: Holotype NSM PP 10290; hypotypes 10291–10295; 10320–10324, 10337.

Genus Kleinhovia Linne

Kleinhovia basitruncata (OISHI et HUZIOKA) TANAI com. nov.

(Pl. 4, figs. 2-4; pl. 5, figs. 1, 4; pl. 8, figs. 3, 4; Fig. 3-C, D)

Marlea basitruncata Oishi et Huzioka. in Oishi. 1950. Illust. Cat. East Asiatic Fossil Plants. p. 170, pl. 49, f. 7.

Alangium basitruncatum (Oishi et Huzioka) Tanai. 1970. J. Fac. Sci. Hokkaido Univ. [4], 14(4): 497. pl. 17. f. 1.

Type: Holotype. Oishi, 1950. pl. 49, fig. 7; Mitsubishi Bibai coal mine (closed now), Bibai, Hokkaido; Ikushunbetsu Formation (Late Eocene).

Emended Description: Leaves slightly inequilateral, wide ovate to pentagonal in shape, sometimes shallowly trilobed with small lobes, 6 to 14.5 cm long and 5 to 10.5 cm wide, length/width ratio 1.05 to 1.38 (mostly 1.1 to 1.2); apex acuminate with drip point, and also lobe apex acuminate when lateral lobes exist; base truncate to broadly rounded; petiole thick and long, more than a half of leaf length, somewhat swollen at its top attaching the leaf lamina. Venation basal actinodrmous with 5 primary veins; midvein thick, straight; an apical pair of lateral primaries thick, diverging at angles of 25° to 30°, nearly straight or broadly curving up to form large loops, or entering lobe apex; a second pair of lateral primaries, diverging at 60° to 65°, nearly straight, camptodromous; 5 or 6 pairs of secondaries diverging from the midvein, parallel to lateral primaries, giving off abaxially 1 or 2 branches near the margin typically in the lower secondaries, forming conspicuously marginal loops which enclose tertiary and quaternary arches; the basal lateral primaries also giving off abaxially 6 to 8 secondaries which form regular loops within the margin; intercostal tertiary veins distinct, straight-percurrent with distance of 1.5 to 3 mm; quaternary veins transversing perpendicularly to the tertiaries, arranged with 0.4 to 1 mm distance, straight or forking; the higher order veins forming small four-sided areoles which are mostly 0.15 mm across; the highest order veins sixth; the freely ending veinlets lacking or single.

Discussion: These leaves are not Alangium (Marlea) in small areoles and veinlet,

because leaves of Alangium have large, irregularly shaped areoles intruded by profusely branching veinlets. The following features indicate that these leaves are referable to the genus Kleinhovia: the regular loops along the margin, the quaternary veins which perpendicularly and densely cross with the narrowly distanced tertiaries, minute four-sided areoles intruded by single freely ending veinlet. The genus Kleinhovia is monotypic, and is now distributed in the tropics of East Asia. Leaves of the extant K. hospita L. are typically entire on the margin and cordate at base, but they have sometimes small lobes on the upper margin. The entire margined leaves of the extant Mallotus japonicus Muell.-Arg. resemble K. basitruncata in a general apperance, especially in having small lobes on upper margin and the quaternary veins crossing perpendicularly with the tertiaries, but they are different from Kleinhovia in having usually larger areoles, profusely branching veinlets and proturberance on the margin.

Occurrence: Ishikari coal field Yc-2, Ic-3, Ic-5, Ic-7, Ic-11; Kabato coal field Ow-1; Kushiro coal field Kh-1, Ky-2, Ky-3, Ks-1, Ks-3.

Collections: Hypotype HUMP no. 27004; no. 27005. Hypotypes NSM PP 10296–10300.

Genus Pterygota SCHOTT. et ENDL.

Pterygota ezoana TANAI sp. nov.

(Pl. 2, fig. 4; pl. 3, fig. 5; pl. 6, figs. 1, 4; pl. 8, figs. 1, 2; Fig. 2-K, L)

Type: Holotype NSM PP 10301; Reisuizan, Yubari, Hokkaido; Ikushunbetsu Formation (Late Eocene).

Description: Leaves ovate to narrow ovate, nearly equilateral in general outline, 5.3 to 14 (estimated) cm long and 4 to 9.3 (estimated) cm wide, length/width ratio 1.52 to 1.76; apex gradually narrowed with somewhat long attenuate tip; base broadly rounded to broadly cordate; margin entire; petiole thick, with more than one-thirds of leaf length. Venation basal actinodromous with 3 primary veins; central primary stout, nearly straight or slightly arcuate; lateral primaries somewhat thinner than the central; lateral primaries diverging at angles of 25° to 40°, nearly straight or gently curving, along the margin to form loops with tertiary branches of basal secondary vein, extending about half the distance to the apex; 5 or 6 secondaries diverging abaxially from lateral primary, nearly perpendicular to midvein, forming large loops along the basal margin; 6 pairs of secondaries from the midvein parallel to the lateral primary, curving up to form a series of prominent loops with 2 or 3 abaxial branches of superadjacent secondaries; marginal loops of lateral primaries and secondaries enclosing tertiary arches within the margin; intercostal tertiary veins rather thin, irregularly percurrent with various distance of 3 to 7 mm, frequently sinuous or forking; quaternary veins mostly perpendicular to the tertiaries, sometimes forking, forming large four- or five-sided meshes; the highest order veins sixth; quinternary and higher order veins forming five-sided areoles which are 0.35 mm across; freely

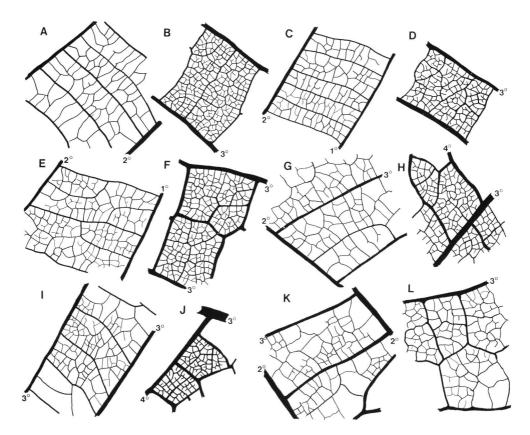


Fig. 3. The Venation of Costal Area and Areoles of the Fossil or extant *Kleinhovia*, *Byttneria*, *Actinovena* and *Plafkeria*.

- (A, C, E, G, I, K \times 3; B, D, F, H, J, L \times 11.5)
- A, B. Kleinhovia hospita LINN. NSM Paleob. Ref. Coll. no. T-2213.
- C, D. Kleinhovia basitruncata (OISHI & HUZIOKA) TANAI. NSM PP 10297 (pl. 4, fig. 3).
- E, F. Byttneria aspera Colebr. NSM Paleobot. Paleobot. Ref. Coll. no. T-264.
- G, H. Byttneria iizimae Tanai. G. NSM PP 10290 (pl. 2, fig. 1); H: NSM PP 10295 (pl. 3, fig. 4).
- I, J. Actinovena ishikariensis TANAI. NSM PP 10308a (pl. 7, fig. 5).
- K, L. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. NSM PP 10313 (pl. 4, fig. 1).

ending veinlets single or lacking.

Discussion: The leaf shape, 3 palmate venation, irregularly percurrent tertiaries, small areoles intruded by single veinlet are characteristics of certain genera of the Sterculiaceae. Of the extant leaves of this family having similar gross features the fossil leaves are closely similar to those of *Pterocymbium* and *Pterygota*, and are referable to the latter genus in orthogonal or pentagonal meshes of the quaternary vein, size of areoles, and petiole length. *Pterygota ezoana* is closely related to the

extant *P. alata* (RoxB.) R. Br. of Southeast Asia, but the extant leaves have usually broadly cordate base and wider distance of the tertiary veins.

P. ezoana resembles non-lobed leaves of Kleinhovia basitruncata in a general appearance, because the lateral primaries give off abaxially the secondary veins to appear 5 palmate veined at the base. P. ezoana is, however, distinguishable from K. basitruncata in having more much secondaries, quaternary veins of large orthogonal or pentagonal meshes, larger areoles and shorter petiole.

Occeurrnce: Ishikari coal field, Nc-1, Ic-9.

Collection: Holotype NSM PP 10301; hypotypes 10302-10304; 10327, 10328.

Family Tiliaceae

Genus Actinovena Tanai gen. nov.

Type species: Actinovena ishikariensis TANAI.

Description: Leaves nearly equilateral, narrow ovate, entire in margin, slightly acuminate at apex, broadly rounded at base; venation palmate with 3 primary veins; lateral primaries extending more than half the distance to the apex; secondaries nearly straight, looping angularly just within the margin; abmedial tertiaries forming a series of submarginal loops; intercostal tertiaries distinct, convex percurrent, somewhat irregularly spaced, sometimes forking; intercostal quaternaries thick, forming small polygonal meshes with thick quinternary veins; marginal quaternaries irregularly looping outside of tertiary loops, sometimes joining marginal thickening; areoles small; veinlets lacking or single.

Discussion: The equilateral shape, palmate venation, prominent secondary loops, marginal tertiaries or their branches joining the marginal thickening, minute areoles intruded sometimes by single veinlet are characteristics of certain genera of the Tiliaceae, such as Burretiodendron, Schoutenia, Microcos and Pentace. Leaves of these extant genera have usually fewer secondary veins than the fossil leaves. Especially the fossil leaves resemble leaves of some species of the Pentace living in Southeast Asia, although being more secondaries in fossils. Leaves of the genus Hainania of south China are also similar to the fossil leaves in the venation features, excepting for craspedodromous secondary veins. The fossil leaves of the Ishikari coal field are assigned to a new genus of the Tiliaceae now considered to be extinct.

The generic name was derived from the word actinodromous (primary veins radiating from a single point) and vena (vein in Latin).

Actinovena ishikariensis TANAI sp. nov.

(Pl. 7, figs. 1-3, 5; pl. 8, figs. 7, 8; Fig. 3-I, J)

Type: Holotype NSM PP 10305; Road cliff of Shimizu-no-sawa, Heiwa, Yubari, Hokkaido; Ikushunbetsu Formation (Late Eocene).

Description: Leaves nearly equilateral, narrow ovate, 6.8 to 9.8 cm long and

4 to 5.9 cm wide, length/width ratio 1.61 to 1.72; apex acuminate with somewhat long tip; base broadly rounded; margin entire, thickened; petiole thick, swollen at both the ends, about one-fourths of the leaf length. Venation basal actinodromous, with 3 prominent primary veins; medial primary thick, straight; lateral primaries diverging at 25° to 30°, extending about two-thirds the distance to the apex, abruptly curving near the margin to loop with a few tertiary branches of basal secondary vein, giving off abaxially 6 to 8 secondaries which form regular loops along the margin; a pair of basal secondaries diverging from the base, giving off basally 5 or 6 camptodromous tertiaries; 6 to 8 pairs of secondary veins parallel to the lateral primary, forming angular loops within the margin; intercostal tertiaries convex percurrent, sometimes forking, irregularly spaced with the distance of 1.5 to 3 mm; sometimes branching from the tertiary, parallel or oblique to the tertiary; marginal tertiary loops or their branches frequently joining the marginal thickening; quaternary thick, forming small, irregularly polygonal meshes with quinternaries; the highest order venation 7th; areoles minute, 4 or 5 sided, 0.15 to 0.25 mm across; veinlets lacking or single.

Discussion: These leaves are characterized by the symmetrically narrow ovate shape, prominent 3 primary veins, small meshes sided by thick 4 and 5 ordered veins and minute areoles. These characters distinguish Actinovena ishikariensis from leaves of the Sterculiaceae described in the preceding pages, which are similar in gross features. A. ishikariensis is similar to Pterygota ezoana in general appearance, but differs in having much secondary veins, more upward extending lateral primary veins, features of the higher order venation. Some leaves of A. ishikariensis appear hairy on the undersurface, because the fine venation is somewhat obscure on impression, despite of well-preserved specimens. The above-described Alangium columbioides shows a close resemblance to Actinovena ishikariensis in foliar shape and gross feutures of venation, but is different in large areoles and profusely branching veinlets.

Occurrence: Ishikari coal field Nc-2, Ic-9, Ic-10.

Collection: Holotype NSM PP 10305; hypotypes 10306–10308; 10325, 10326.

Genus Plafkeria Wolfe

Plafkeria basiobliqua (OISHI et HUZIOKA) TANAI comb. nov.

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(Pl. 2, figs. 2, 3; pl. 3, fig. 3; pl. 4, fig. 1; pl. 5, figs. 2, 3; pl. 6, figs. 2, 3; pl. 7, figs. 4, 6; pl. 8, figs. 5, 6; Fig. 3–K, L)
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Marlea basioblqua Oishi et Huzioka, in Oishi. 1950. Illust. Catalog. East Asiatic Plants. p. 117 pl. 171, f. 8.

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Alangium basiobliquum (OISHI et HUZIOKA) TANAI. 1961. J. Fac. Sci. Hokkaido Univ., [4]. 11(2): 372, pl. 30, f. 11. TANAI, 1970. Ditto. 14(4): 372, pl. 18, f. 4, 5; pl. f. 1.
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Ficus ezoensis Endo. 1968. Bull. Natn. Sci. Mus. 11(4): 429. pl. 9. f. 3.

Ficus planicosta ENDO. 1968. Ditto. 11(4): 429. pl. 9. f. 3.

Ficus platanifolioides ENDO. 1968. Ditto. 11(4): 430, pl. 12. f. 4.

Ficus tiliaefolia (Braun) auct. non Heer, Endo. 1968. Ditto. 11(4): 432, pl. 15, f. 1, 2. Ficus yubariensis Endo (part). 1968. Ditto. 11(4): 432, pl. 14, f. 2.

Type: Holotype, Oishi (1950) pl. 49, fig. 8; Yubari coal mine (closed now), Yubari, Hokkaido; Ikushunbetsu Formation (Late Eocene).

Emended Description: Leaves, markedly inequilateral, typically ovate but variable in shape from narrow ovate to very wide ovate, 2.7 to 11.0 cm long and 2 to 10.0 cm wide, length/width ratio 1.10 to 1.93 (mostly 1.4 to 1.6); base considerably asymmetric, rounded on broad side and cuneate or obliquely straight on narrow side; apex acuminate with drip tip; margin entire, somewhat revolute. Venation palmate; medial primary vein stout, straight; an apical pair of lateral primaries thick, diverging at angles of 25° to 35°, gently curving, extending half to two-thirds the distance to the apex; a basal pair of lateral primaries weak, making 30° to 50° with midvein on cuneate side and 60° to 90° on rounded side; secondary veins from the medial primary 4 or 6 pairs, curving up, then forking at wide angles near the margin to form distinct loop just within the margin; lateral abmedial secondaries from the lateral primaries 5 or 6 at broad side of blade and 3 or 4 at narrow side, looping conspicuously within basal margin; intercostal tertiaries percurrent, nearly straight, rarely forking, with 1.5 to 3 mm distance in small and medium-sized leaves and with 3.5 to 5 mm distance in large leaves; quaternary veins perpendicular and parallel to intercostal tertiaries, forming large four-sided meshes; the highest order venation sixth; higher order veins forming typically small four-sided areoles (0.25 to 0.43 mm across); ultimate veinlets mostly lacking but rarely single. Petiole thick, about half to two-thirds of leaf length, somewhat swollen at its top attaching the leaf blade.

Discussion: All the fossil leaves illustrated here are identical to Alangium basiobliquum, which was originally assigned to Marlea by Oishi and Huzioka (in Oishi, 1950). These leaves are, however, distinguishable from the genus Alangium (Marlea) in the higher order venation. As already pointed out by Govindarajala (1961) and Wolfe (1977), leaves of Alangium (especially, section Marlea) have the following venation characters: the areolation is larger, and the freely-ending veinlets are profusely branching. The features of leaves from the Paleogene of Hokkaido indicate that they are referable to the extinct genus Plafkeria: markedly asymmetric leaf blade, conspicuous loops of the lateral primary and secondary veins just within the margin, comparatively regular and four-sided areoles, and typically lacking or rarely single freely-ending veinlets. These leaves are somewhat variable in palmate venation: the second basal primary veins are sometimes weak, although two pairs of the basal primaries are distinctly observed in most specimens.

All the leaves described as *Alangium* or *Ficus* from the Paleogene of Hokkaido (Tanai, 1961, 1970; Endo, 1968) are included in *Plafkeria basiobliqua* by their asymmetric base and venation feuture, although some of them were invalidly illustrated by Endo (1968). Of three species known from the Paleogene of North America, *P. basiobliqua* closely resembles *P. obliquifolia* (Chaney) Wolfe from the Early Oligocene of Oregon (Wolfe, 1977), but it is distinguishable in having more widely

spaced intercostal tertiary veins and larger areoles. In such venation characters *P. basiobliqua* shows a close similarity to an incomplete leaf of *Plafkeria* sp. from the Eocene Kushutaka Formation of Alaska (Wolfe, 1977). A further detailed comparison of these specimens may reveal that the Alaskan specimen is included in *P. basiobliqua*. The extinct genus *Plafkeria* was originally described in the name of *Willisia*, based on the specimens of the Upper Eocene of Washington (Wolfe, 1968). However, the name *Plafkeria* was later proposed (Wolfe, 1977), because the name *Willisia* is already preoccupied by a genus of the Podostemaceae. *Plafkeria* was assigned to belong to the family Tiliaceae in the original description (Wolfe, 1968), because leaves of the genotype having the highly asymmetric base and four-sided areoles intruded by single veinlet show close similarity to leaves of some genera of the Tiliaceae such as *Grewia*, *Luhea* and *Microcos* excepting for the marginal characters. It is noticeable that such similar characters of leaves are also found in leaves of some genera of the Sterculiaceae such as *Pterocymbium* and *Pterospermum*.

Occurrence: Ishikari coal field Nc-2, Yc-2, Yc-3, Ic-2, Ic-5, Ic-6, Ic-7, Ic-8, Ic-9, Ic-10, Ic-11, Ic-13; Kabato coal field Ow-1, Ka-1; Kushiro coal Field Kh-1, Ky-2, Ky-3, Ks-1, Ks-3, Ks-4.

Collections: Hypotypes HUMP nos. 27001–27003; hypotypes NSM PP 10309–10318; 10329–10333a, 10338, 10339.

Appendix. The localities and formations in which fossils were collected. Excepting in the case of surface exposures, all the fossils were from the waste rocks of coal mines which had been working.

Ishikari coal field, central Hokkaido

Noborikawa Formation (Middle Eocene)

Nc-1: the Mitsubishi-Bibai coal mine (closed now), Sannosawa, Bibai City.

Nc-2: the Kamoi coal mine (closed now), Kamoi, Utashinai City.

Yubari Formation (Middle Eocene)

Yc-1: the Shimizusawa coal mine (closed now), Shimizusawa, Yubari City.

Yc-3: the Oyubari coal mine (closed now), Kashima, Yubari City.

Ikushunbetsu Formation (early-Late Eocene)

Ic-2: cliff along the Naie River, Naie-cho.

Ic-3: cliff along Takino-sawa, Bannosawa, Bibai 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 Yubari River, Teimi, Yubari City.

Ic-9: cliff near the top of Reisui-zan, Yubari City.

Ic-10: road cliff, Shimizuno-sawa, Heiwa, Yubari City.

Ic-11: cliff near the dam-site, Shimizusawa, Yubari City.

Ic-13: the Chashinai coal mine (closed now), Chashinai, Bibai City.

Uryu and Kabato coal field, central Hokkaido

Owada coal-bearing Formation (early-Late Eocene)

Ow-1: the Owada coal mine (closed now), Rumoi City.

Kabato coal-bearing Formation (early-Late Eocene)

Ka-1: the Tsukigata coal mine (closed now) at the end of the Subetsu River, Tsukigata-cho.

Kushiro coal field, eastern Hokkaido

Harutori Formation (early-Late Eocene)

Kh-1: Harutori and Okotsu pits, Taiheiyo coal mine, Harutori, Kushiro City.

Yubetsu Formation (early-Late Eocene)

Ky-2: cliff along Nakanosawa, Yubetsu, Akan-cho.

Ky-3: the Ponki coal mine (closed now), Shoro, Shiranuka-cho.

Shakubetsu Formation (Late Eocene)

Ks-1: cliff along the Shitakara River, Yubetsu, Akan-cho.

Ks-4: the Onbetsu coal mine (closed now), Kami-onbetsu, Onbetsu-cho.

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Explanation of Plates

(All figures in natural size unless otherwise stated)

Plate 1

- Fig. 1. Alangium columbioides (Endo) TANAI. Holotype NSM 10484 (Ic-11).
- Figs. 2, 3. Mallotus hokkaidoensis Tanal. Hypotypes NSM PP 10289 (Ic-9), 10319 (Ic-10).
- Fig. 4. Byttneria iizimae TANAI. Hypotype NSM PP 10291 (Ic-9).
- Fig. 5. Byttneria iizimae TANAI. Hypotype NSM PP 10309 (Ic-9).

Plate 2

- Fig. 1. Byttneria iizimae Tanai. Holotype NSM PP 10290 (Ic-9).
- Figs. 2, 3. *Plafkeria basiobliqua* (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10310b (Ic-9), 10311 (Ic-9).
- Fig. 4. Pterygota ezoana TANAI. Hypotype NSM PP 10302 (Ic-9).
- Fig. 5. Byttneria iizimae TANAI. Hypotype NSM PP 10292 (Ic-9).

Plate 3

- Figs. 1, 2. Byttneria iizimae Tanai. Hypotypes NSM PP 10293 (Ic-10), 10294 (Ic-9).
- Fig. 3. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. Hypotype NSM PP 10312 (Ic-9).
- Fig. 4. Byttneria iizimae Tanai. Hypotype NSM PP 10295 (Ic-9).
- Fig. 5. Pterygota ezoana TANAI. Hypotype NSM PP 10303 (Ic-9).

Plate 4

Fig. 1. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. Hypotype NSM PP 10313 (Ic-9).

Fig. 2-4. Kleinhovia basituncata (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10296 (Ic-9), 10297 (Ic-9), 10298 (Ic-9).

Plate 5

- Figs. 1, 4. Kleinhovia basitruncata (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10299 (Ic-9), 10300 (Ow-1).
- Figs. 2, 3a, b. *Plafkeria basiobliqua* (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10314 (Ic-9), 10315a, b (Ic-10).

Plate 6

- Fig. 1. Pterygota ezoana TANAI. Hypotype NSM PP 10304 (Ic-9).
- Figs. 2, 3. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10316 (Ic-9), 10310a (Ic-9).
- Fig. 4. Pterygota ezoana TANAI. Holotype NSM PP 10301 (Ic-9).

Plate 7

- Fig. 1. Actinovena ishikariensis TANAI. Holotype NSM PP 10305 (Ic-9).
- Figs. 2, 3. Actinovena ishikariensis Tanai. Hypotypes NSM PP 10306 (Nc-2), 10307 (Ic-9).
- Figs. 4, 6. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. Hypotypes NSM PP 10317 (Ic-9), 10318 (Ic-2).
- Fig. 5. Actinovena ishikariensis Tanai. Hypotype NSM PP 10308a (Ic-9).

Plate 8

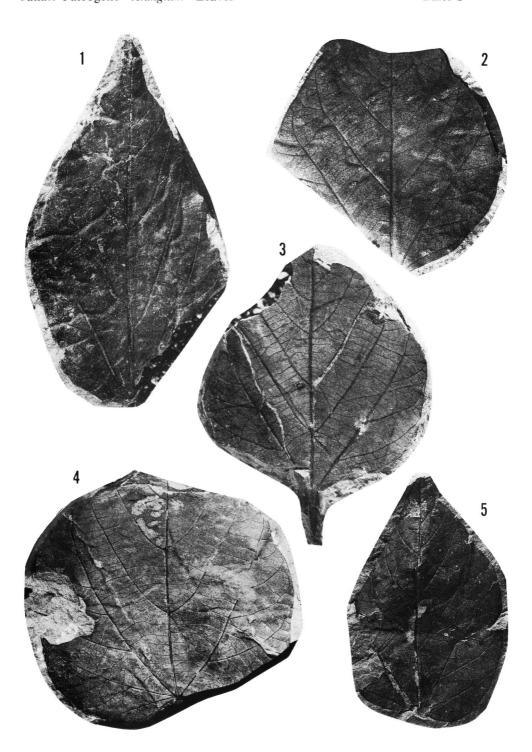
(figs. 1, 3, 5, 7×9 ; figs. 2, 4, 6, 8×35)

- Figs. 1, 2. Pterygota ezoana TANAI. NSM PP 10304 (pl. 6, fig. 1).
- Figs. 3, 4. Kleinhovia basitruncata (OISHI & HUZIOKA) TANAI. NSM PP 10297 (pl. 4, fig. 3).
- Figs. 5, 6. Plafkeria basiobliqua (OISHI & HUZIOKA) TANAI. NSM PP 10311 (pl. 2, fig. 3).
- Figs. 7, 8. Actinovena ishikariensis TANAI. NSM PP 10305 (pl. 7, fig. 1).

Plate 9

(figs. 1, 3, 5, 7×9 ; figs. 2, 4, 6, 8×35)

- Figs. 1, 2. Byttneria iizimae Tanai. NSM PP 10295 (pl. 3, fig. 4).
- Figs. 3, 4. Byttneria aspera Colebr. NSM Paleobot. Ref. Coll. no. T-264.
- Figs. 5, 6. Kleinhovia hospita Linn. NSM Paleobot. Ref. Coll. no. T-2213.
- Figs. 7, 8. Pterygota alata (ROXB.) R. BR. NSM Paleobot. Ref. Coll. no. T-2491.



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