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TAXONOMICAL INVESTIGATION OF THE LIVING SPECIES OF THE GENUS *ACER* L., BASED ON VEIN ARCHITECTURE OF LEAVES

by

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(with 9 text-figures and 9 plates)

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Abstract

The genus *Acer* is commonly known in the Tertiary of the Northern Hemisphere, represented by leaves (or leaflets) and winged seeds. However, these fossil leaves have been frequently difficult to determine their modern relationships only by gross features. In order to compare accurately the fossils with the extant species, the vein system of 117 living species of the genus *Acer* have been examined by the cleared leaf method. Based on areolation and minor venation characters, all the species in the world are classified into two groups. In the first group the ultimate veinlets ramify more than twice within the areoles, while in the second group the freely-ending veinlets are mostly lacking or single, and rarely once branching. The taxonomic system of the genus *Acer* has been proposed by various authors, since Pax (1885–1886) first published the detailed systematics. Compared with these systems, the above-noted classification by the venation characters are well consistent with the system described by Ogata (1967), excepting a few species. Following to Ogata's system, the venation characters of the genus *Acer* are briefly described with the illustrations.

Introduction

The genus *Acer* L. is widely distributed in the Northern Hemisphere during the past and the present. The evolutionary trends of this genus provide a good indicator to clarify the phytogeographical changes of the temperate forests since the Tertiary in the Northern Hemisphere. I once discussed on general Tertiary history of the genus *Acer* in East Asia and western North America (Tanai, 1974, 1977), though based on insufficient knowledges. Most of the fossil *Acer* are largely represented by leaves or leaflets, and also commonly by winged seeds. Both of the living and fossil leaves are too variable in their shapes to distinguish sufficiently their specific status only by gross features such as shape and marginal serration and even by cuticle characters. Thus a number of the fossil species of the genus *Acer* have been established on the basis of gross features of leaves in the Tertiary of the Northern Hemisphere. These fossil

species are doubtlessly partly akin to the living species, while some of them are very doubtful whether or not they are referable to the genus *Acer*.

Tertiary leaf-paleobotany has recently considerably progressed by two different methods fit for the specimens: the carbonized materials are examined by cuticle and epidermis characters, while the impressed materials with no carbonized film are by the scheme of fine venation. The former method has been used mainly by the European paleobotanists, and the latter has been recently elaborated by the North American workers. The reason why the investigating methods are different to apply, is due to the preservation of fossil leaves which are largely found in the both continents respectively. Such methods for the identification of angiosperm leaf remains were critically reviewed by Dilcher (1974).

A large proportion of Tertiary remains of angiosperms in East Asia are of leaf impression, and few remains are preserved with carbonized materials. For the purpose of identifying more exactly leaf impressions, I have investigated the living species of the genus *Acer*, especially on their fine venation characters of leaves by preparation of cleared leaf slides suggested by Dr. Wolfe. Through these investigation I found an interesting fact of the venation characters of the genus *Acer*. This paper is aimed to describe the general features of fine venation, and also to discuss critically on the taxonomical systems of the genus *Acer*, which have been proposed by various authors.

Acknowledgements

I wish to express my great appreciation to Dr. Jack A. Wolfe, U.S. Geological Survey at Menlo Park, California, who extended me his kindness to use all his collection of the cleared leaf slides, and furthermore to give many suggestions on the vein scheme of angiosperm leaves. Acknowledgements are also due to the following scholars to send me some of the extant leaves: Dr. Richard A. Howard of the Arnold Arboretum of Harvard University at Jamaica Plain, Massachusetts, the late Dr. Hans Tralau of Swedish Museum of Natural History at Stockholm, and Dr. Herman F. Becker and Mr. Thomas J. Delendick of New York Botanical Garden at New York. The following institutions kindly permitted to collect the leaves for my investigation: the Botanical Garden of Hokkaido University at Sapporo, the Botanical Garden of University of Tokyo at Tokyo, the Arboretum of the Government Forest Experiment Station at Asakawa, the Arboretum of Kyoto University at Kyoto, the Botanical Garden of Osaka City University at Osaka, and the Arboretum of Kagoshima University at Kagoshima.

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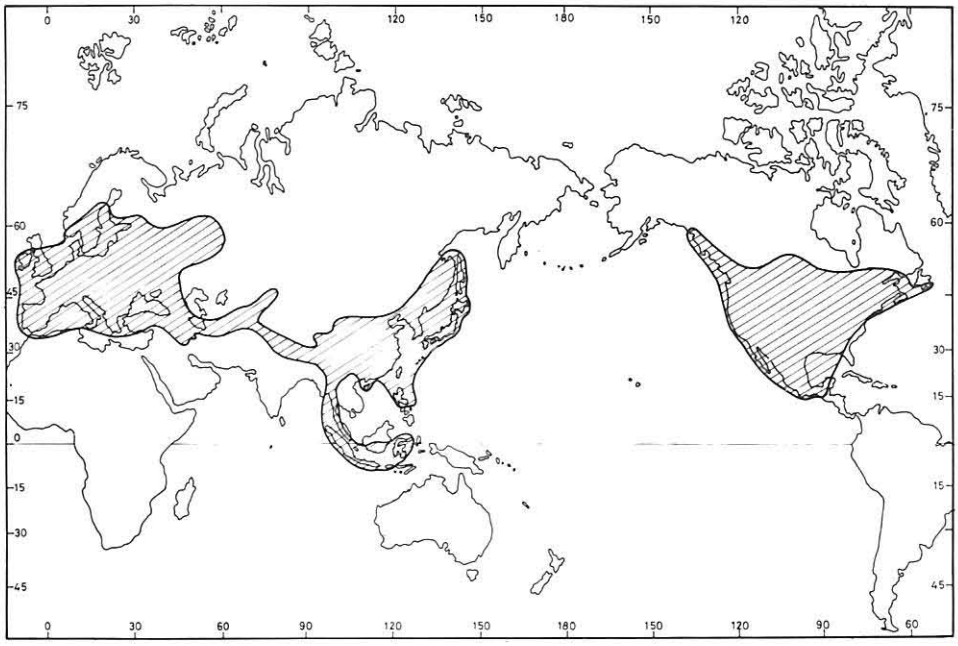
A Brief History on Taxonomy of the Genus *Acer*

The family Aceraceae belonging to the order Sapindales, is composed of two genera, *Acer* L. and *Dipteronia* Oliver. The latter genus is confined to central China in its modern distribution, and the fossil records have been known only from the Oligocene of North America (Brown, 1936; Becker, 1961; others). On the contrary, the genus *Acer* is widely distributed in the temperate regions of the Northern Hemisphere, a few extending into the subarctic in Europe (up to 63°N. Lat. in Sweden) and North America (up to 59°N. Lat. in Alaska), as well as into the tropics in central America (Mexico and Guatemala) and in Southeast Asia (in the mountains of Malaysia, Java, Sumatra, Boreneo, Celebes, Mindanao and others), as shown in text-figure 1. The extant species of the genus *Acer* are more than 150 species in the world, and are centered in East Asia where about two-thirds of all the species occur. The fossil records of *Acer* have been widely known in the Northern Hemisphere since Early Tertiary time, and this genus represents one of the most common angiosperm fossils.



Text-fig. 1 Map showing the modern distribution of the genus *Acer* Linn.

Since the end of last century the genus *Acer* has been investigated in detail by various workers, but its taxonomy has been not always settled up to the present. Various systems were proposed by many authors, due to the difference of the principal morphological characters selected. All of these important researches done until the recent time have been critically reviewed by Ogata (1967). Only the comprehensive studies including phylogeny are here summarized as follows.

The systematics of the genus *Acer* was first established by Pax (1885–1886), with the descriptive morphology, geographical distribution, fossil evidences and phylogenetical discussion. Revising his system several year later, he (Pax, 1902) classified 114 species of the world into 13 sections. Considering the relationships between disc shape and stamen as a most important character, he suggested the primitive type was represented by ill-developed disc and stamens attaching around the ovule base. His systems based on flower elements have been followed by many later authors. Rehder (1905) added a new section (Arguta) to Pax's system, and furthermore he (1911, 1922, 1927) revised Pax's system, especially re-arranging the species of the sections Macrantha, Lithocarpa and Indivisa. Later, Rehder (1949) divided the genus *Acer* into two sections, Acer and Negundo; the former is further subdivided into 13 series. The Pax-Rehder system has been adopted fundamentally by most later workers, although several revisions were done later.

Based mainly on inflorescence, sexuality, number of sepals and relationship between disc and stamen, Koidzumi (1911a) classified Japanese species into two large groups (Intrastaminalia and Extrastaminalia) and further into 19 sections. Furthermore, he (Koidzumi, 1911b) discussed the phylogenetic relationships of each section, but his system is essentially not different from Pax-Rehder's.

Reinvestigating critically all the systems proposed, Pojarkova (1933) divided all the species into 17 sections and 32 series. Considering together with fossil materials, she discussed the phylogenetic and distributional history of the genus *Acer,* and concluded that the primitive types of this genus may be centered in East Asia. By her excellent works Pax-Rehder's system was much revised. By means of the turbidometric totration Momotani (1961–1962) revealed that seed protein components of *Acer* are related with taxonomical affinity of each species, showing diagramatically the degree of their affinity. Combined protein affinity with morphological characters, he divided 128 species of the world into three subgenus (Acer, Negundo, Carpinifolia) and 19 sections. Momotani's system seems to be a modification of the Pojarkova's.

In Chinese Mainland the extant species of *Acer* occupy nearly two-thirds of all the species living in the world. Fang (1939, 1966) investigated their

characters and distribution, and classified them into two subgenus and 19 sections. Fang's system is generally followed to the Pax-Rehder's, although many new species and several new sections were established. Beside the above-noted comprehensive works, there were a number of investigations on taxonomy or phylogeny of the genus *Acer*; especially, it is noteworthy for our taxonomical consideration that Watari (1936) described a detailed anatomy of the petiole on 42 species living in Japan and Taiwan, and also that Warsow (1903) gave a detailed anatomy of leaves on 110 species. Since the taxonomical system was first founded by Pax during 1885–1903, it has been much revised by many taxonomists such as Rehder, Pojarkova, Koidzumi, Momotani and others, especially on the classifications of the sections or series. These taxonomical investigations were based mainly on flower structure or elements, additionally combined with other morphological characters.

Based on the reinvestigation of all the exomorphic characters including wood anatomy, Ogata (1965, 1967) divided 140 species of the world into 26 sections as shown in Table 1, and also discussed the phylogenetic relationships of each section. His taxonomic system including six new sections is based synthetically on all the characters such as winter bud, inflorescence, sexuality, flower, fruit, embryo, leaf, and wood, and seems to be further revised than the previous systems.

Table 1 Systematics of the Genus *Acer*

After Ogata (1967)

Sect. 1. Macrantha Pax

A. davidii Franch., *A. laxiflorum* Pax, *A. grosseri* Pax, *A. wardii* W.W. Smith, *A. metcalfii* Rehd.*, *A. chienii* Hu et Cheng*, *A. kawakamii* Koidz., *A. insulare* Makino, *A. crataegifolium* S. et Z., *A. hookeri* Miq., *A. pectinatum* Wall., *A. tegmentosum* Maxim., *A. pennsylvanicum* L., *A. sikkimense* Miq., *A. rubescens* Hayata, *A. morifolium* Koidz., *A. capillipes* Maxim., *A. rufinerve* S. et Z., *A. maximowiczii* Pax. *A. tschonoskii* Maxim., *A. micranthum* S. et Z.

Sect. 2. Distyla Ogata

A. distylum S. et Z.

Sect. 3. Parviflora Koidz.

A. nipponicum Hara

Sect. 4. Spicata Pax

A. caudatum Wall., *A. ukurunduense* Trautv. et Mey., *A. spicatum* Lam.

Sect. 5. Palmata Pax

A. sinense Pax, *A. campbellii* Hook f. et Thoms., *A. erianthum* Schw., *A. flabellatum* Rehd., *A. tutcheri* Duthie, *A. wilsonii* Rehd., *A. robustum* Pax, *A. pseudosieboldianum* Komar., *A. takeshimense* Nakai, *A. ishidoyanum* Nakai*, *A. nudicarpum* Nakai, *A. sieboldianum* Miq., *A. japonicum* Thunb., *A. tenuifolium* Koidz., *A. shirasawanum* Koidz., *A. palmatum* Thunb., *A. amoenum* Carr., *A. circinatum* Pursh, *A. serrulatum* Hayata, *A. oliverianum* Pax, *A. schneiderianum* Pax et K. Hoffm., *A. heptalobum* Diels, *A. pubipalmatum* Fang, *A. pauciflorum* Fang, *A. ceriferum* Rehd., *A. chingii* Hu*, *A. confertifolium* Merr. et Metcalf*, *A. johnedwardianum* Metcalf, *A. laevigatum* Wall., *A. fabri* Hance, *A. reticulatum* Champ.*, *A. dimorphifolium* Metcalf*, *A. cordatum* Pax

Sect. 6. Glabra Pax

A. glabrum Torr.

Sect. 7. Arguta Rehd.
A. tetramerum Pax, *A. stachyophyllum* Hiern, *A. acuminatum* Wall., *A. barbinerve* Maxim., *A. argutum* Maxim.
Sect. 8. Negundo (Boehm.) Maxim.
A. negundo L.
Sect. 9. Cissifolia Koidz.
A. henryi Pax, *A. cissifolium* (S. et Z.) K. Koch.
Sect. 10. Trilobata Pojark.
A. tataricum L., *A. semenovii* Regel et Herder, *A. ginnala* Maxim., *A. aidzuense* (Franch.) Nakai
Sect. 11. Rubra Pax
A. rubrum L., *A. pycnathum* K. Koch., *A. saccharinum* L.
Sect. 12. Platanoidea Pax
A. longipes Franch., *A. amplum* Rehd., *A. tenellum* Pax, *A. catalpifolium* Rehd., *A. fulvescens* Rehd., *A. acutum* Fang*, *A. chunii* Fang*, *A. tibetense* Fang*, *A. cappadocicum* Gleditsch, *A. turkestanicum* Pax, *A. mono* Maxim., *A. okamotoanum* Nakai, *A. truncatum* Bunge, *A. lobelii* Tenore*, *A. platanoides* L.
Sect. 13. Campestria Pax
A. miaotaiense Tsoong*, *A. miyabei* Maxim., *A. campestre* L.
Sect. 14. Pubescentia (Pojark.) Ogata
A. pubescens Franch., *A. regelii* Pax*, *A. stenolobum* Rehd.*
Sect. 15. Acer
A. pseudoplatanus L., *A. velutinum* Boiss., *A. caesium* Wall., *A. trauvetterii* Medw., *A. heldreichii* Orph.
Sect. 16. Goniocarpa Pojark.
A. opalus Mill., *A. hispanicum* Pour.*, *A. obtusatum* Wald. et Kitaib., *A. tauricolum* Boiss. et Bal., *A. hyrcanum* Fisch. et Mey., *A. stevenii* Pojark.*, *A. monspessulanum* L., *A. cinerascens* Boiss., *A. assyriacum* Pojark.*, *A. turkomanicum* Pojark.
Sect. 17. Saccharina Pax
A. grandidentatum Nutt., *A. saccharum* Marsh., *A. barbatum* Michx., *A. nigrum* Michx., *A. leucoderme* Small
Sect. 18. Integrifolia Pax
A. oblongum Wall,, *A. buergerianum* Miq., *A. paxii* Franch.
Sect. 19. Syriaca Ogata
A. syriacum Boiss. et Gaill., *A. orientale* L., *A. persicum* Pojark.*, *A. pentaponicum* Stew.*
Sect. 20. Trifoliata Pax
A. sutchuense Franch., *A. manchuricum* Maxim., *A. griseum* (Franch.) Pax, *A. triflorum* Komar., *A. nikoense* Maxim.
Sect. 21. Lithocarpa Pax
A. thomsonii Miq.*, *A. villosum* Wall., *A. franchetii* Pax, *A. schoenermarkiae* Pax*, *A. sinopurpurascens* Cheng*, *A. diabolicum* Blume
Sect. 22. Macrophylla (Pojark.) Ogata
A. macrophyllum Franch.
Sect. 23. Laurina Ogata
A. laurinum Hassk.
Sect. 24. Decandra Ogata
A. decandrum Merr.
Sect. 25. Indivisa Pax
A. carpinifolium S. et Z.
Sect. 26. Pentaphylla Hu et Cheng
A. pentaphyllum Hu et Chang

The species with asterik were not yet investigated by the author, because their leaves could not be obtained.

Investigation of Venation System by Cleared Leaves

Leaves of the genus *Acer* are highly various in form, single to compound or palmate; furthermore single-form leaves are undivided to lobed in shape. Leaf shape seems generally characteristic for respective species, and it is, of course, useful for identification in specific level. In the classification of the section Pax (1885) seems to use leaf shape in some case such as the sections of Palmata, Integrifolia and Trifoliata. However, leaf shape or form are frequently variable even within one species as well known, and are not always reliable for a criterion of the section. Actually in the fossil materials of East Asia, five-lobed leaves with a few dents on margin are frequently difficult to distinguish each other; it is further difficult to determine to which section they belong among the sections Campestria, Macrophylla and Lithocarpa.

In order to compare the fossils with the extant leaves in venation system, I have prepared to have the cleared leaf specimens of all the species of the genus *Acer*. Based mainly on fine venation characters, I have investigated various taxonomical systems proposed by many authors.

Preparation of the cleared leaves

Leaf specimens were collected from all trees sufficiently grown in the fields or the botanical gardens at various localities. In each of the species were chosen which would at maturity have been close to the mean leaf size and standard shape. However, a few specimens sent from abroad include immature leaves. There are many methods for clearing modern leaves as listed by Lersten (1967); each technique is respectively useful for leaves of various kinds such as differences of texture and chemical reaction.

The procedure for clearing leaves suggested by Dr. Wolfe (personal communication), is somewhat modified as follows:

(1) Place the dried leaf in a petri dish in a solution of 10% sodium hydroxide (NaOH) for 48 to 72 hours changing the solution once.
(2) Wash in water, followed by a rinse in acetic acid.
(3) Add commercial bleach; when leaf is bleached (this can be from a few minutes), wash 2 or 3 times in water.
(4) Place in 250% chloral hydrate [$CCl_3CH(OH)_2$] for 12 or 16 hours; wash 2 or 3 times in water.
(5) Put the leaf through ethanol series (50%–75%–100%) to dehydrate. During dehydration by ethanol (50%–75%) stain with suffranin "O".
(6) If the leaf does not well pick up the stain, add stain solution (100% ethanol plus suffranin "O"); then pour in toluene.
(7) Mount the leaf in Eukitt (O. Kindler Co., Germany) between 2 glass slides (usually 8 x 12.5 cm and 12.5 x 16 cm).

(8) These slides are dried at about 40°C either on warming tables or in a oven.

The leaves of the genus *Acer* treated until today are 75 species in my laboratory and 92 species in the Paleobotany Laboratory of the U.S. Geological Survey, although many of them are common in species. Of 140 species listed in Ogata's system (1967), 117 species has been examined. Through investigation of the vein system, the minor venation including veinlets is occasionally somewhat different between the central and marginal areas of the blade in a leaf. Furthermore, the freely-ending veinlets are also sometimes different in ramification in the areas near or apart from the secondary veins. Thus, the fine venation representing each species, are taken from the center of central part in a single leaf (leaflet) and central lobe of palmate leaf.

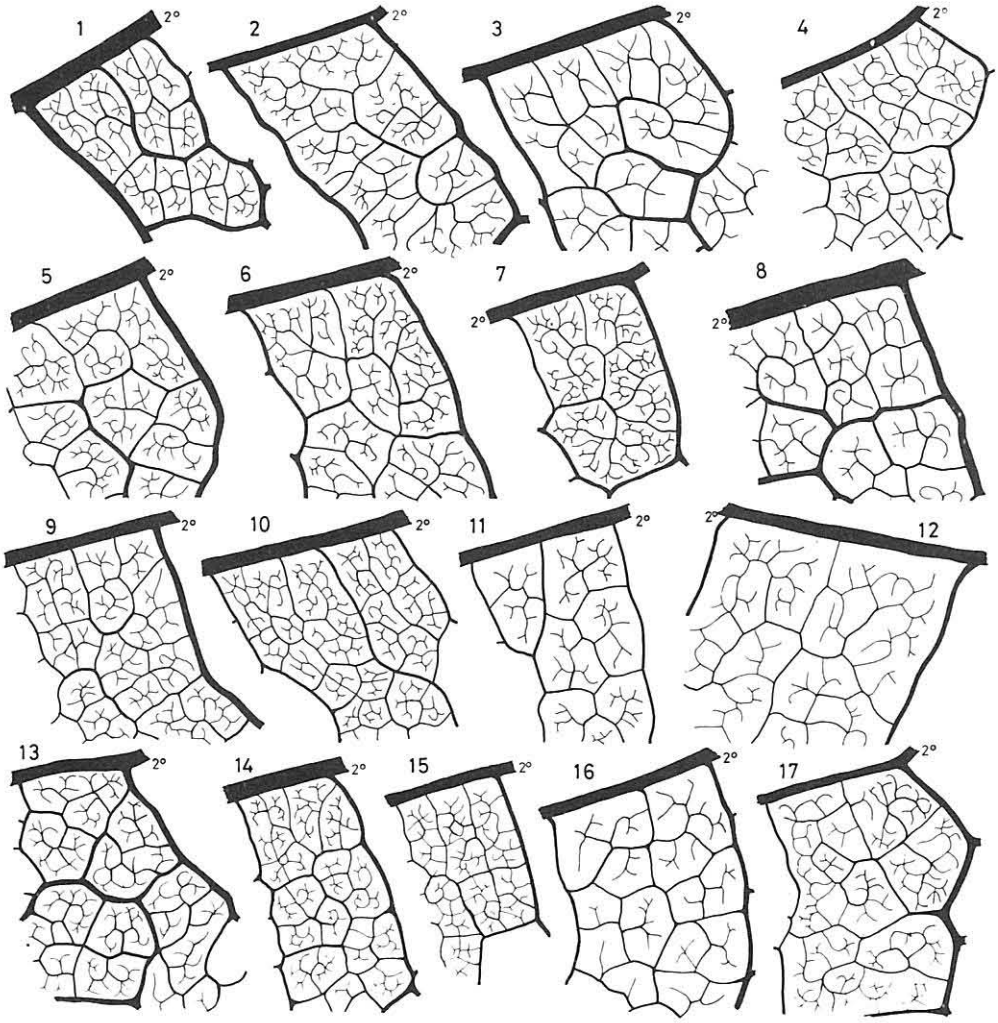
Fine venation characters of Leaves

Through investigating 117 extant species of the world, I could confirm that the polygonal areoles and the freely-ending veinlets show a certain characters peculiar to each species, and also that these characters are nearly similar among the species of each section. The genus *Acer* is divided into two groups by the minor venation characters: in the first group the ultimate veinlets ramify more than twice within the areoles, and show sometimes a complex system with many tips; on the other hand, the ultimate veinlets are mostly lacking or single, and rarely once branching in the second group.

Compared with the taxnomic systems proposed by many authors, the above-noted venation characters are well consistent with Ogata's system excepting for a few species: the species of each section in his system are common in veinlets characters. However, the species belonging to the first and second groups are coexistent within a section in other systems excluding Ogata's. Accordingly, following to Ogata's system, the venation characters of the genus *Acer* are briefly described below.

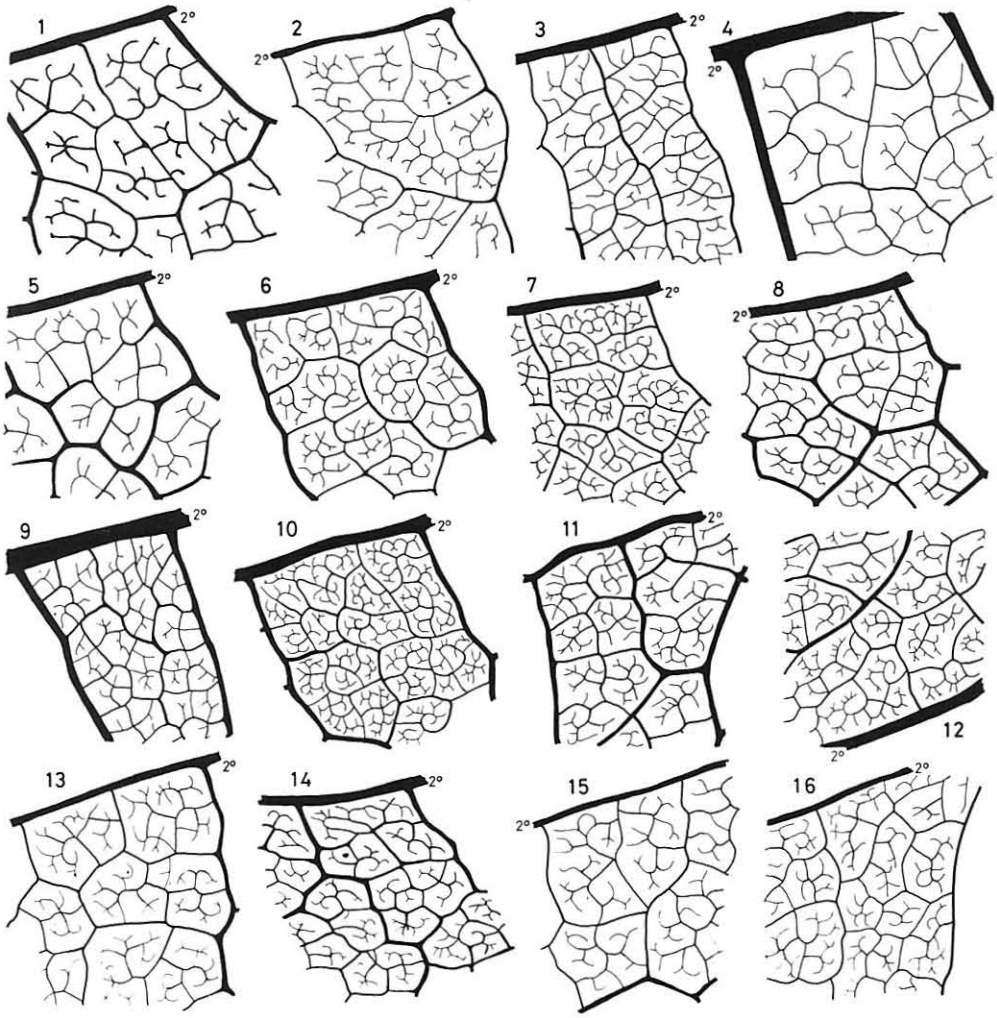
The First Group

The species belonging to the first group are generally characterized by complicated veinlets, which ramify usually more than twice but rarely with once branching. These species belong to 11 sections of Ogata's system such as Macrantha, Spicata, Palmata, Glabra, Arguta, Negundo, Cissifolia, Trilobata, Pubescentia, Macrophylla and Indivisa. The veinlets in each section are somewhat different in detailed characters respectively.



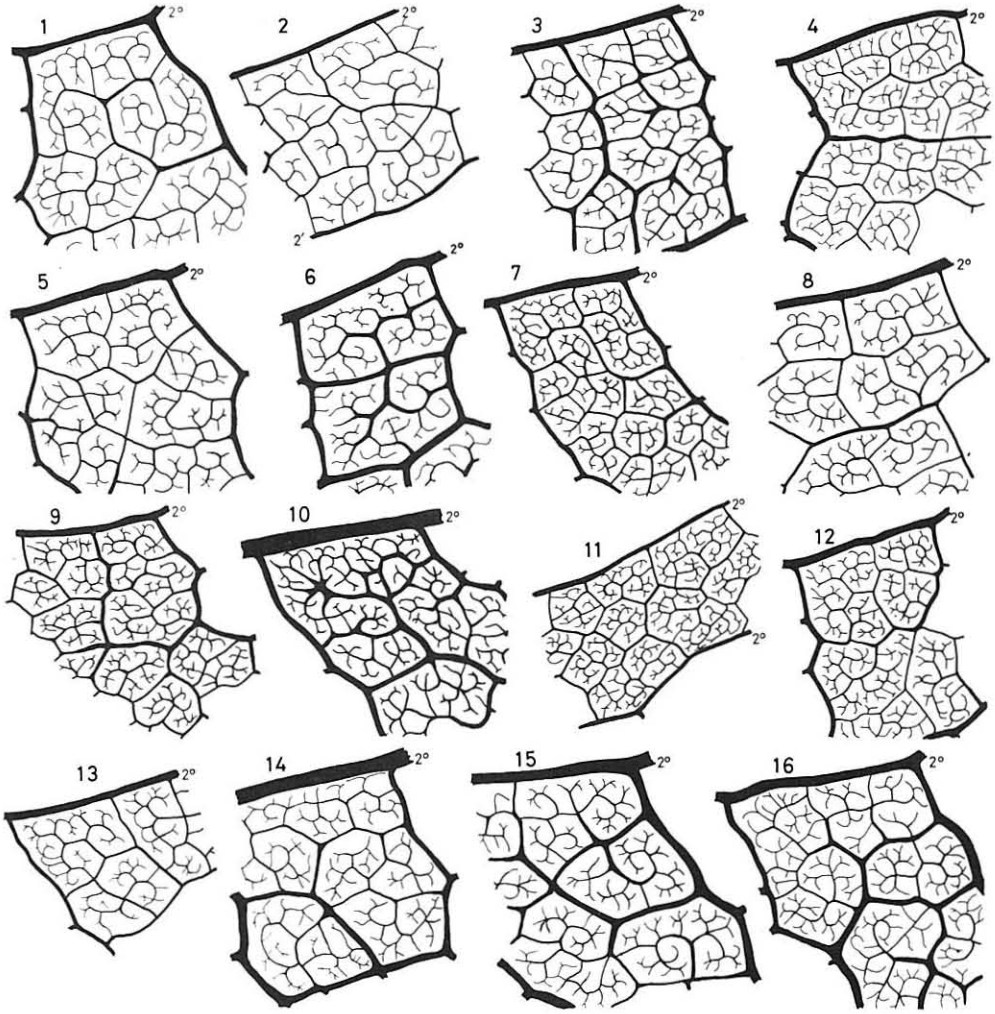
Text-fig. 2 Diagram illustrating the minor venation in the leaves of the section Macrantha. (all figures X12)

1. *Acer davidii* Franch. (U.S.G.S. slide no. 1185b) 2. *Acer wardii* W.W. Smith. (U.S.G.S. slide no. 2626a) 3. *Acer laxiflorum* Pax. (U.S.G.S. slide no. 7630) 4. *Acer grosseri* Pax. (U.S.G.S. slide no. 8595a) 5. *Acer kawakamii* Koidzumi. (U.S.G.S. slide no. 8610a) 6. *Acer insulare* Makino. (H.U.P.B. slide no. 180) 7. *Acer crataegifolium* Sieb. et Zucc. (H.U.P.B. slide no. 229) 8. *Acer hookeri* Miq. (U.S.G.S. slide no. 8599) 9. *Acer tegmentosum* Maxim. (U.S.G.S. slide no. 8622a) 10. *Acer pectinatum* Wall. (H.U.P.B. slide no. 885) 11. *Acer pennsylvanicum* Linn. (U.S.G.S. slide no. 1176b) 12. *Acer sikkimense* Miq. (U.S.G.S. slide no. 1135b) 13. *Acer rebescens* Hayata. (U.S.G.S. slide no. 8610) 14. *Acer morifolium* Koidzumi. (H.U.P.B. slide no. 179) 15. *Acer capillipes* Maxim. (U.S.G.S. slide no. 8582) 16. *Acer rufinerve* Sieb. et Zucc. (H.U.P.B. slide no. 237) 17. *Acer maximowiczii* Pax. (U.S.G.S. slide no. 8606a)



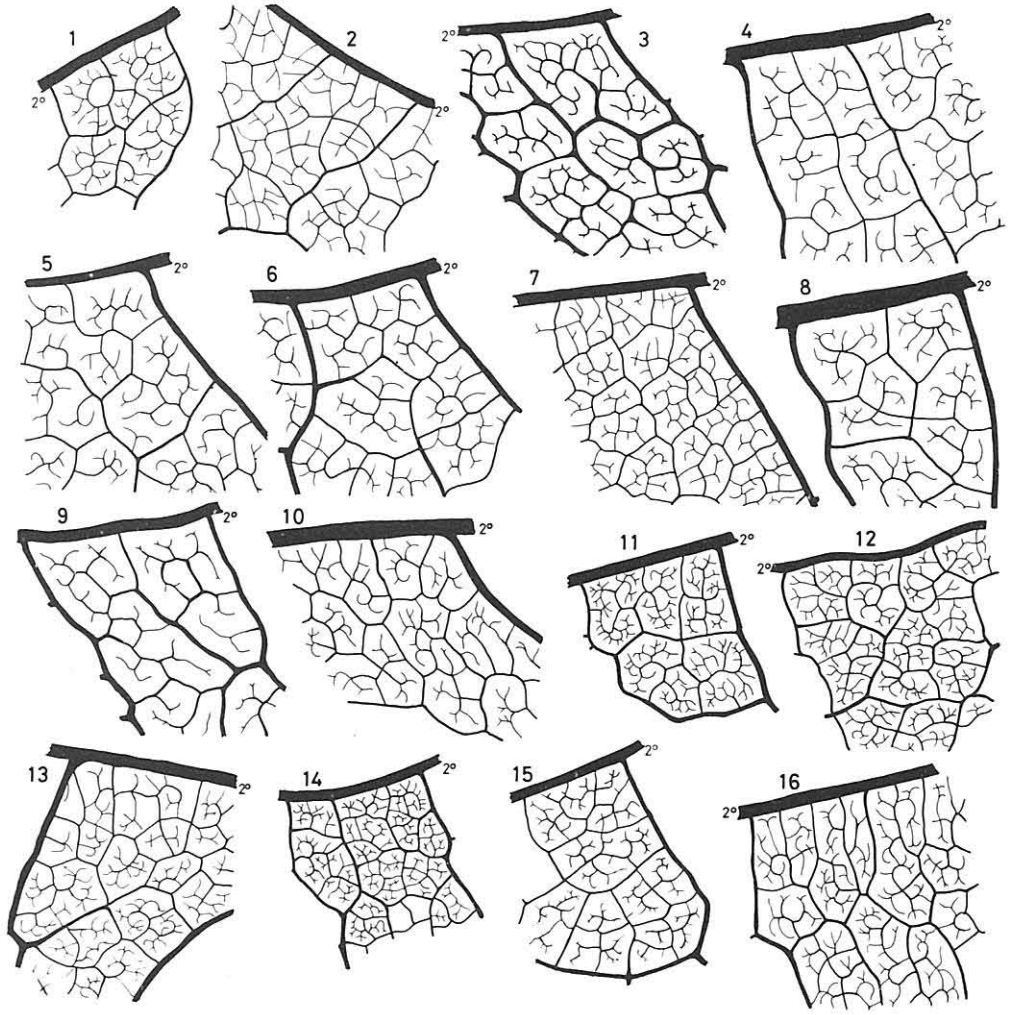
Text-fig. 3 Diagram illustrating the minor venation in the leaves of the sections Macrantha (continued), Spicata and Palmata. (all figures X12)

1. *Acer tchonoskii* Maxim. (H.U.P.B. slide no. 876) 2. *Acer micranthum* Sieb. et Zucc. (H.U.P.B. slide no. 244) 3. *Acer caudatum* Wall. (U.S.G.S. slide no. 8583a) 4. *Acer spicatum* Lam. (U.S.G.S. slide no. 1182) 5. *Acer ukurunduense* Trautv. et Mey. (U.S.G.S. slide no. 9613) 6. *Acer sinense* Pax. (U.S.G.S. slide no. 7622) 7. *Acer campbellii* Hook. f. et Thoms. (U.S.G.S. slide no. 8531) 8. *Acer erianthum* Schw. (U.S.G.S. slide no. 7626a) 9. *Acer flabellatum* Rehd. (U.S.G.S. slide no. 7627) 10. *Acer tutcheri* Duthie. (U.S.G.S. slide no. 8625) 11. *Acer robustum* Pax. (U.S.G.S. slide no. 8620b) 12. *Acer wilsonii* Rehd. (U.S.G.S. slide no. 8627b) 13. *Acer peudosieboldianum* Komarov. (U.S.G.S. slide no. 8618) 14. *Acer takeshimense* Nakai. (H.U.P.B. slide no. 827) 15. *Acer sieboldianum* Miq. (U.S.G.S. slide no. 1220b) 16. *Acer nudicarpum* Nakai. (U.S.G.S. slide no. 8613)



Text-fig. 4 Diagram illustrating the minor venation in the leaves of the sections Palmata (continued). (all figures X12)

1. *Acer japonicum* Thunb. (U.S.G.S. slide no. 8600) 2. *Acer tenuifolium* Koidzumi. (H.U.P.B. slide no. 737) 3. *Acer shirasawanum* Koidzumi. (H.U.P.B. slide no. 182) 4. *Acer palmatum* Thunb. (U.S.G.S. slide no. 8616a) 5. *Acer circinatum* Pursh. (U.S.G.S. slide no. 594) 6. *Acer serrulatum* Hayata. (H.U.P.B. slide no. 341) 7. *Acer schneiderianum* Pax et K. Hoffm. (H.U.P.B. slide no. 883) 8. *Acer oliverianum* Pax. (U.S.G.S. slide no. 8615a) 9. *Acer pauciflorum* Fang. (H.U.P.B. slide no. 882) 10. *Acer heptalobum* Diels. (H.U.P.B. slide no. 888) 11. *Acer pubipalmatum* Fang. (H.U.P.B. slide no. 880) 12. *Acer ceriferum* Rehd. (U.S.G.S. slide no. 8584a) 13. *Acer johnedwardianum* Metcalf. (U.S.G.S. slide no. 8598) 14. *Acer laevigatum* Wall. (U.S.G.S. slide no. 7629) 15. *Acer fabri* Hance. (U.S.G.S. slide no. 8591) 16. *Acer cordatum* Pax. (U.S.G.S. slide no. 8588a)



Text-fig. 5 Diagram illustrating the minor venation in the leaves of the sections Glabra, Arguta, Negundo, Cissifolia, Trilobata, Pubescentia, Macrophylla and Indivisa. (all figures X12)

1. *Acer glabrum* Torr. (U.S.G.S. slide no. 315) 2. *Acer tetramerum* Pax. (U.S.G.S. slide no. 7635) 3. *Acer acuminatum* Wall. (H.U.P.B. slide no. 164) 4. *Acer stachyophyllum* Hiern. (H.U.P.B. slide no. 996) 5. *Acer barbinerve* Maxim. (U.S.G.S. slide no. 8579) 6. *Acer argutum* Maxim. (U.S.G.S. slide no. 8578) 7. *Acer negundo* Linn. (U.S.G.S. slide no. 935c) 8. *Acer henryi* Pax. (U.S.G.S. slide no. 8597) 9. *Acer cissifolium* (S. et Z.) K. Koch. (H.U.P.B. slide no. 231) 10. *Acer tataricum* Linn. (U.S.G.S. slide no. 6781) 11. *Acer ginnala* Maxim. (U.S.G.S. slide no. 7) 12. *Acer semenovii* Regel et Herder. (U.S.G.S. slide no. 9627) 13. *Acer aidzuense* (Franch.) Nakai. (U.S.G.S. slide no. 8576b) 14. *Acer pubescens* Franch. (H.U.P.B. slide no. 828) 15. *Acer macrophyllum* Pursh. (U.S.G.S. slide no. 306b) 16. *Acer carpinifolium* Sieb. et Zucc. (U.S.G.S. slide no. 6780)

(1) Sect. Macrantha Pax

(Text-fig.2, 1-16; text-fig.3, 1-2; pl.1, figs.1-8; pl.2, figs.1, 2)

The section Macrantha is composed of 21 species, all of which are now confined to East Asia, excepting for *A. pennsylvanicum* living in eastern North America. All the species of this section excluding *A. metcalfii* and *A. chienii* not yet examined, are ramified more than three times in veinlets, though somewhat irregularly branching. In the most of the species the areoles are imperfect, especially in *A. hookeri, A. micranthum, A. maximowiczii* and *A. sikkimense.* This section is subdivided into three series, Macrantha, Rufinervia and Micrantha, but the venation characters are difficult to distinguish among these series. It is interesting that all leaves belonging to this section are ill-stained by the ordinary treatment, campared with leaves of other sections.

(2) Sect. Spicata Pax

(Text-fig.3, 3-5; pl.2, figs.3, 4)

Three species belonging to the section Spicata are disjunctively distributed in eastern North America and East Asia including Himalaya. Leaves of these species are three- to five-lobed with coarsely serrate margin. Their veinlets are somewhat irregularly branching but ramified more than three times, with gradually thinning tips. The minor venation characters of this section are closely similar to those of the above section Macrantha.

(3) Sect. Palmata Pax

(Text-fig.3, 6-16; text-fig.4, 1-16; pl.2, figs.5-7; pl.3, figs.1-6, 8)

The section Palmata including 33 species, seems to be most diversified in the genus *Acer.* All of these species are now distributed in East Asia, excepting for *A. circinatum* living in western North America. This section is subdivided into three series such as Sinensia, Palmata and Laevigata, but no conspicuous difference is found among them. Leaves of Sinensia and Palmata are mainly from 5- to 11-lobed and are serrate to doubly-serrate in margin, while leaves of Laevigata are mostly oblong to ovate in shape and entire in margin. In all the species of this section excluding one, the veinlets show complicated pattern with regularly, several times branching; they terminate with gradually thinning tips within the areoles. In an exceptional species, *A. flabellatum* (the series Sinensia), the veinlets are composed mixedly of once and twice ramifying within the areoles, and are somewhat simpler than those of other species.

Five species* of the series Laevigata had been included in the section Indivisa by many authors (Pax, 1902; Rehder, 1949; Momotani, 1962) because of their foliar shape. The veinlet characters of these species are indistinguishable from those of the series Sinensia and Palmata, although the third- and fourth-order veins are somewhat thicker.

(4) Sect. Glabra Pax
(Text-fig.5, 1; pl.3, fig.7)

The section Glabra is represented by only one species, *A. glabrum* living in western North America. Leaves of this species are usually three- to five-lobed, and doubly serrate in margin. The veinlets are irregular in ramification, and are once to several times branching with thick, truncate tips.

(5) Sect. Arguta Rehder
(Text-fig.5, 2-6; pl.4, figs.1, 2, 4)

The section Acer is composed of five species, which are common in their leaves are three- to seven-lobed with doubly-serrate margin, excepting one species with undivided leaves (*A. tetramerum*). The veinlets are somewhat irregular in ramification, once to three times branching with rather thick tips within the areoles. This section, as established by Rehder (1905), seems to form a natural group characterized well by inflorescence, bud-scale, flower elements and fruit.

(6) Sect. Negundo (Boehm.) Maxim. and Sect. Cissifolia Koidz.
(Text-fig.5, 7-9; pl.4, figs.3, 5)

The section Negundo represented by only one North American species, *A. negundo,* which leaves are mostly three- to seven-foliate with pinnate leaflets. The section Cissifolia composed of two East Asiatic species, *A. henryi* and *A. cissifolium,* which leaves are trifoliate. These two sections have been variously discussed on their taxonomy: some authors considered the Negundo as an independent genus of the Aceraceae (Plowman, 1915; Hall, 1951) or a subgenus of *Acer* (Momotani, 1962), while many authors treated two species of the Cissifolia to be included in the Negundo. In actual, these two sections are closely similar in sexuality, inflorescence, fruits and foliate leaves. However, Ogata (1967) divided them into the independent section respectively, because they are distinguishable in number of bud-scales, flower and ray of wood.

* Of five species *A. dimorpholium* and *A. reticulatum* are not yet examined.

Leaves of these two sections seem to be distinguishable in venation characters, although their leaflets are similar in gross feature. The veinlets of *A. negundo* are composed mixedly of once to twice branching with thick termination within the small areoles. On the other hand, the veinlets of the Cissifolia are of irrugular ramification, with twice to several times branching within large areoles. However, *A. cissifolium* and *A. henryi* are somewhat different in the venation: the former is twice larger in the areole than the latter; and the former veinlets terminate with thick tips, while the latter's are gradually thinning.

(7) Sect. Trilobata Pojarkova
(Text-fig.5, 10-13; pl.4, figs.6-8)

Four species belonging to the section Trilobata are distributed from eastern Europe to East Asia through Central Asia. They are undivided or three-lobed in leaves, and are common in many characters such as flower elements, inflorescence, fruits and others. The venation characters are also closely similar in these four species; the veinlets ramify several times within comparatively small areoles. The ramified pattern of this section is more complicated than that of the section Palmata, though somewhat irregular.

(8) Sect. Pubescentia (Pojark.) Ogata
(Text-fig.5, 14; pl.5, fig.2)

The section Pubescentia contains three species now distributed in Kazakhstane region (Turkestan) and central China, but only one species, *A. pubescens,* is examined. The venation is characteristic: rather small areoles are formed by thick fourth- and fifth-order veins, and the veinlets are irregularly twice or thrice ramified with thick tips. The species belonging to this section have been once included in the section Campestria (Pax. 1902) or in the Platanoidea (Rehder, 1922), but are quite different from them in the veinlet characters.

(9) Sect. Macrophylla (Pojark.) Ogata
(Text-fig.5, 15; pl.5, fig.1)

The section Macrophylla is represented only by one species, *A. macrophyllum* now living in the Pacific coastal slope of western North America. Leaves of this species are usually three- to five-lobed with a few, large dents on

margin. The veinlets are very slender and three or five times ramified within small areoles, thinning gradually toward the tips. *A. macrophyllum* was once included in the section Spicata (Pax, 1885; Rehder, 1940) or in the section Lithocarpa (Pojarkova, 1933). This species is more regular and more complicated in ramification of the veinlets than the species of the Spicata, although it is common in some characters such as sexuality, inflorescense, flower elements and folding manners of cotyledons. As already pointed out by Ogata (1967), *A. macrophyllum* is very apart from the Lithocarpa in many morphologic characters, and actually is also quite different in minor venation.

(10) Sect. Indivisa Pax
(Text-fig.5, 16; pl.5, fig.3)

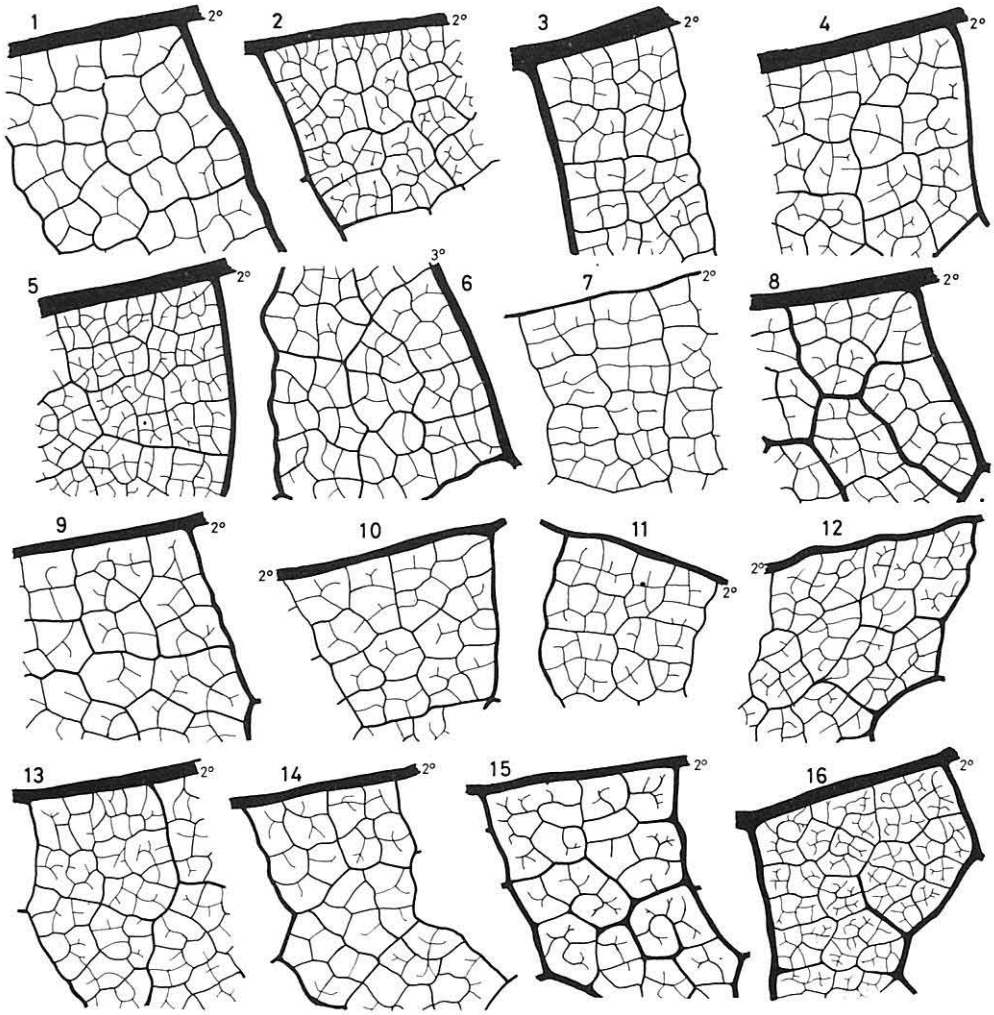
The section Indivisa is represented only by *A. carpinifolium,* endemic to Japan, which leaves are characterized by ovate shape and pinnate veins, showing a superficial resemblance to leaves of the genus *Carpinus* (Family Betulaceae). *A. carpinifolium* was first included in the Indivisa along with other 8 species by Pax (1902), which were transferred to other sections by later authors. Considering protein components of seeds, Momotani (1962) established a subgenus Indivisa on the basis of *A. carpinifolium,* while Ogata (1967) pointed out this species is considerably larger in ray of wood than any other species of the genus *Acer.* The venation character of leaves is also remarkably different from all other species of *Acer*: the veinlets are highly irregular in ramification, and are twice to several times branching with gradually thinning tips within oblong-quadrangular areoles.

The Second Group

In the species belonging to the second group the freely-ending veinlets are mostly single or nearly lacking, and very rarely once ramified within the areoles. When the veinlets exist, they are usually with thick, truncate tips. These species showing such veinlet characters are included in 15 sections of Ogata's system such as Distyla, Parviflora, Rubra, Platanoidea, Campestria, Acer, Goniocarpa, Saccharina, Integrifolia, Syriaca, Trifoliata, Lithocarpa, Laurina, Decandra and Pentaphylla.

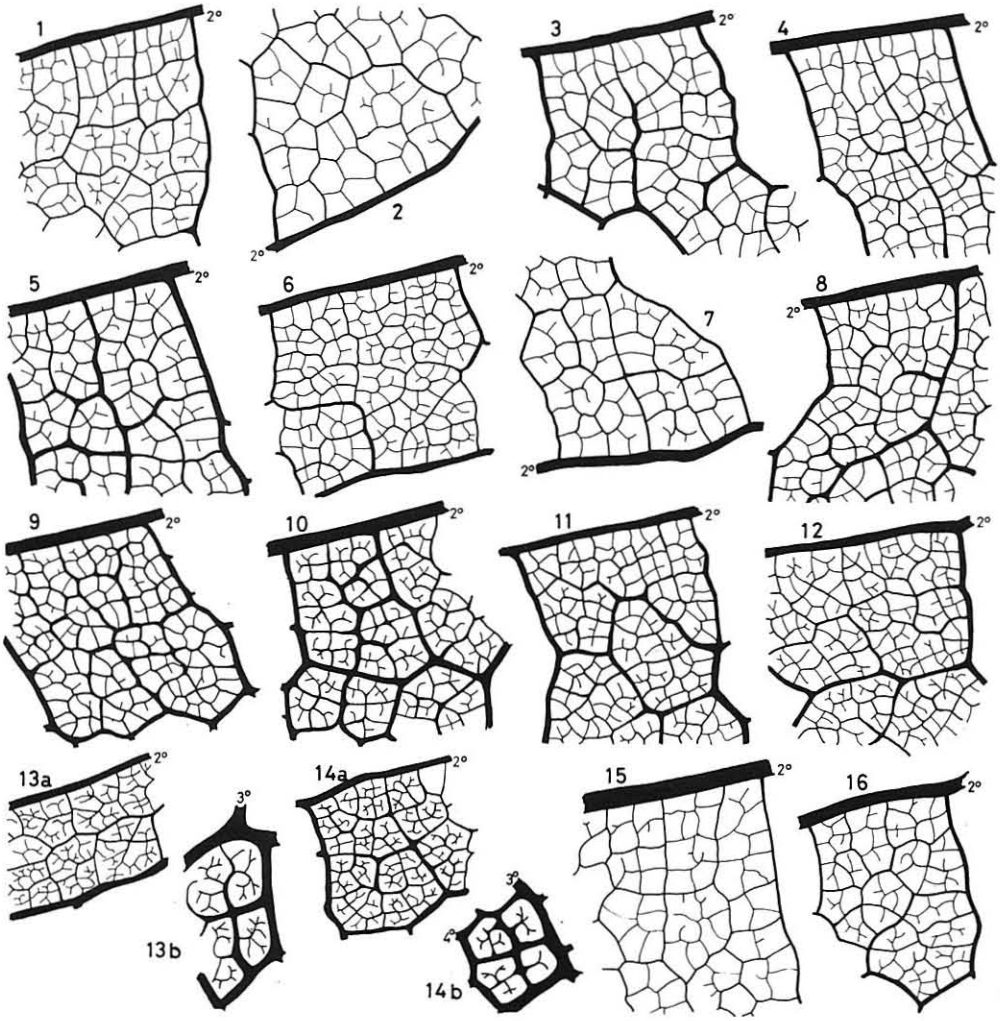
(1) Sect. Distyla Ogata
(Text-fig.6, 1; pl.5, fig.4)

The section Distyla represented only by *A. distylum,* endemic to Japan,



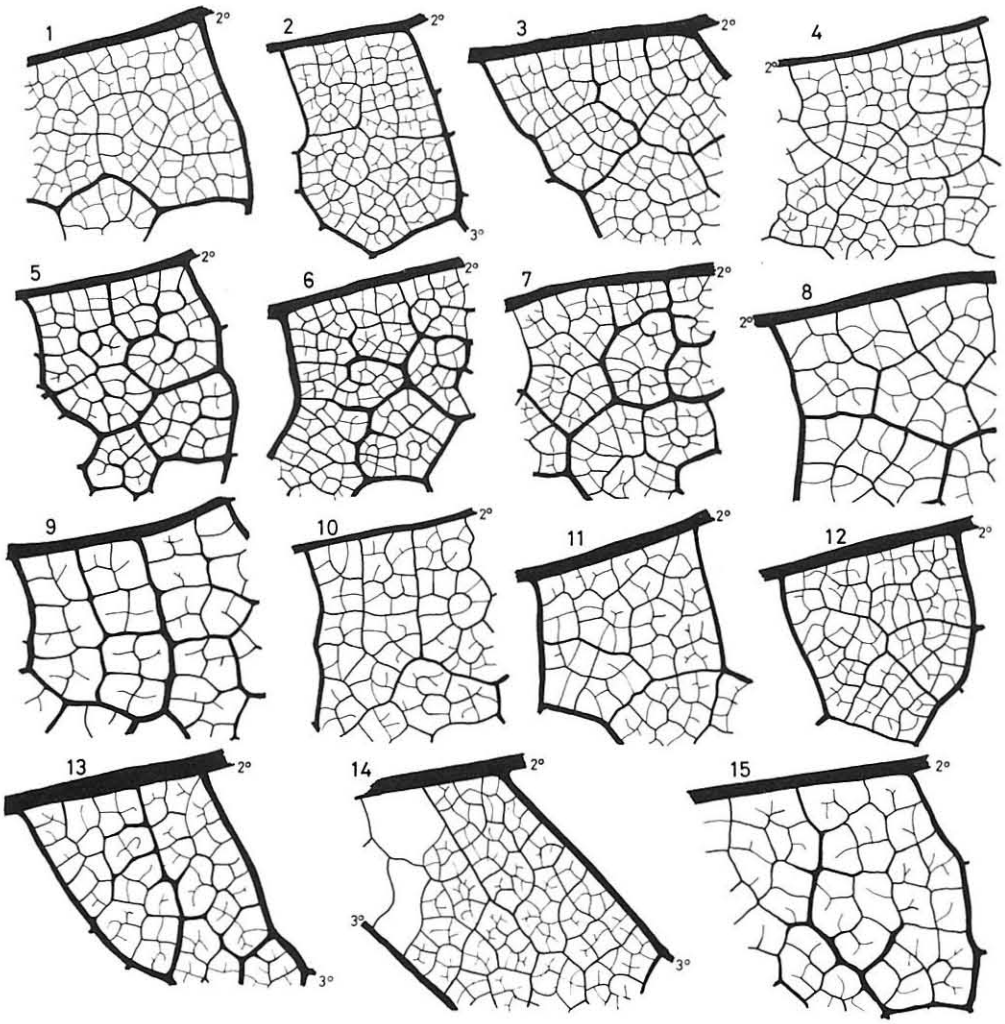
Text-fig. 6 Diagram illustrating the minor venation in the leaves of the sections Distyla, Parviflora, Rubra and Platanoidea. (all figures X12)

1. *Acer distylum* Sieb. et Zucc. (U.S.G.S. slide no. 8589b) 2. *Acer nipponicum* Hara (U.S.G.S. slide no. 8612) 3. *Acer rubrum* Linn. (U.S.G.S. slide no. 1181c) 4. *Acer pycnanthum* K. Koch. (U.S.G.S. slide no. 8619b) 5. *Acer saccharinum* Linn. (U.S.G.S. slide no. 819) 6. *Acer amplum* Rehd. (U.S.G.S. slide no. 7620) 7. *Acer tenellum* Pax. (H.U.P.B. slide no. 879) 8. *Acer catalpifolium* Rehd. (U.S.G.S. slide no. 7624) 9. *Acer fulvescens* Rehd. (U.S.G.S. slide no. 8593b) 10. *Acer cappadocicum* Gleditsch. (U.S.G.S. slide no. 7623b) 11. *Acer mono* Maxim. (U.S.G.S. slide no. 8609) 12. *Acer okamotoanum* Nakai. (U.S.G.S. slide no. 8614b) 13. *Acer platanoides* Linn. (U.S.G.S. slide no. 9625b) 15. *Acer longipes* Franch. (U.S.G.S. slide no. 8603) 16. *Acer turkestanicum* Pax. (U.S.G.S. slide no. 9630)



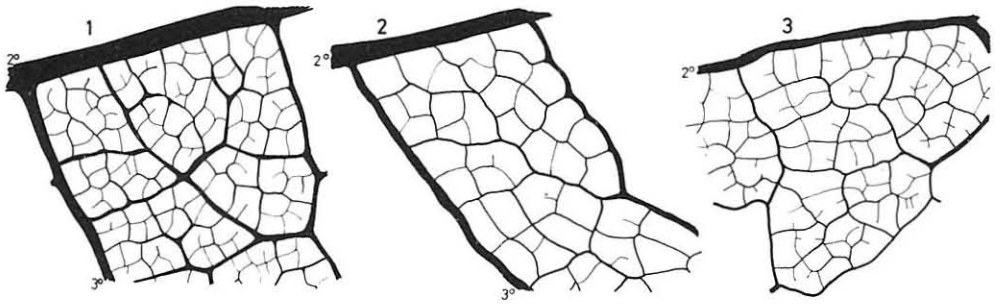
Text-fig. 7 Diagram illustrating the minor venation in the leaves of the sections Campestria, Acer, Goniocarpa and Saccharina. (all figures X12 unless otherwise stated)

1. *Acer campestre* Linn. (U.S.G.S. slide no. 1186) 2. *Acer miyabei* Maxim. (U.S.G.S. slide no. 9087b) 3. *Acer pseudoplatanus* Linn. (U.S.G.S. slide no. 9626a) 4. *Acer velutinum* Boiss. (U.S.G.S. slide no. 9631) 5. *Acer caesium* Wall. (U.S.G.S. slide no. 8580) 6. *Acer trautvetteri* Medw. (U.S.G.S. slide no. 9629) 7. *Acer heldreichii* Orph. (U.S.G.S. slide no. 9617) 8. *Acer opalus* Mill. (U.S.G.S. slide no. 9622b) 9. *Acer obtusatum* Waldst. et Kitaibel. (H.U.P.B. slide no. 1022) 10. *Acer tauricolum* Boiss. et Bal. (H.U.P.B. slide no. 163) 11. *Acer hyrcanum* Fisch. et Mey. (U.S.G.S. slide no. 9618b) 12. *Acer monspessulanum* Linn. (U.S.G.S. slide no. 9620) 13. *Acer cinerascens* Boiss. (U.S.G.S. slide no. 9616) a: X12; b: X24 14. *Acer turkomanicum* Pojarkova. (H.U.P.B. slide no. 161) a: X12; b: X24 15. *Acer saccharum* Marsh. (U.S.G.S. slide no. 815) 16. *Acer grandidentatum* Nutt. (U.S.G.S. slide no. 1184c)



Text-fig. 8 Diagram illustrating the minor venation in the leaves of the sections Saccharina (continued), Integrifolia, Syriaca, Trifoliata and Lithocarpa. (all figures X12)

1. *Acer leucoderme* Small. (U.S.G.S. slide no. 7631) 2. *Acer nigum* Michx. (H.U.P.B. slide no. 1060) 3. *Acer oblongum* Wall. (U.S.G.S. slide no. 9) 4. *Acer buergerianum* Miq. (U.S.G.S. slide no. 7621) 5. *Acer paxii* Franch. (H.U.P.B. slide no. 250) 6. *Acer syriacum* Boisss. et Gaill. (U.S.G.S. slide no. 9628) 7. *Acer orientale* Linn. (U.S.G.S. slide no. 9624) 8. *Acer mandshuricum* Maxim. (U.S.G.S. slide no. 8605) 9. *Acer sutchuense* Franch. (H.U.P.B. slide no. 881) 10. *Acer griseum* (Franch.) Pax. (U.S.G.S. slide no. 8594) 11. *Acer triflorum* Komarov. (U.S.G.S. slide no. 8624) 12. *Acer nikoense* Maxim. (U.S.G.S. slide no. 8611) 13. *Acer villosum* Wall. (H.U.P.B. slide no. 884) 14. *Acer franchetii* Pax. (U.S.G.S. slide no. 7628) 15. *Acer diabolicum* Blume (H.U.P.B. slide no. 235)



Text-fig. 9 Diagram illustrating the minor venation in the leaves of the sections Laurina, Decandra and Pentaphylla. (all figures X12)

1. *Acer decandrum* Merr. (H.U.P.B. slide no. 160)
2. *Acer laurinum* Hassk. (U.S.G.S. slide no. 7632b)
3. *Acer pentaphyllum* Diels. (U.S.G.S. slide no. 8617)

which leaves are undivided, ovate or oval in general outline. Because of the foliar shape *A. distylum* had been once included in the section Indivisa (Pax, 1885; Koidzumi, 1911a) or in the section Integrifolia (Rehder, 1940). On the one hand, this species was included in the section Macrantha by Pojarkova (1933), and it was included in the section Spicata along with *A. nipponicum* by Momotani (1962a) due to the protein affinity of seeds. However, Ogata (1967) established a new section, considering all the morphologic characters of *A. distylum*. The veinlets of this species are almost lacking and rarely single (or very rarely weakly once branching) within quadrangular areoles. Thus, *A. distylum* was quite different in veinlet characters from the sections Spicata, Indivisa and Macrantha belonging to the first group. As later described, *A. distylum* is somewhat similar to the section Integrifolia, but is distinguishable in the areoles limited by thin veins.

(2) Sect. Parviflora Koidzumi
(Text-fig.6, 2; pl.5, fig.5)

The section Parviflora is also represented only by *A. nipponicum*, endemic to Japan. Leaves of this species are three- or five-lobed, and generally resemble those of some species of the section Macrantha. The veinlets are mostly single and rarely once weakly-branching (or very rarely lacking) within comparatively small areoles. *A. nipponicum* is generally similar in venation characters to *A. distylum*, but veinlets of *A. nipponicum* much well develop than those of *A. distylum*. Because these two species are common in many morphological

characters as described by Momotani (1962a) and Ogata (1967), they may be akin each other.

(3) Sect. Rubra Pax
(Text-fig.6, 3-5; pl.5, figs.6-8)

The section Rubra composed of three species, which are disjunctively distributed in Japan and eastern North America. These three species are common in many morphological characters, and have been consistently included in the Rubra by various authors. The venation characters are also similar among them: the freely-ending veinlets are mostly single and rarely lacking within quadrangular or pentagonal areoles, and in rare case shortly once forking. Based on the flower elements and seeds, the section Rubra is divided into two series by Ogata (1967). Although the minor venation pattern of these two series are almost indistinguishable, the series Rubra (*A. rubrum* and *A. pycnanthum*) are slender in the veinlets than the series Eriocarpa (*A. saccharinum*), and also are larger in the areoles.

(4) Sect. Platanoidea Pax
(Text-fig.6, 6-16; pl.6, figs.1-6)

Sixteen species belonging to the section Platanoidea are widely distributed from Europe to East Asia through western Asia. These species are well common in many characters, and have been nearly consistently included in the Platanoidea by many authors. As far as I investigated 12 species, the minor venation shows a typical character of the second group, excepting two species, although somewhat different in the size of areolation in each species. The veinlets are closely similar to those of the section Rubra: they are lacking or mostly single within the areoles. Two exceptional species, *A. longipes* and *A. turkestanicum,* are somewhat different in venation from other species of the Platanoidea; the freely-ending veinlets are thick, and are single or once branching.

(5) Sect. Campestria Pax
(Text-fig.7, 1-2; pl.6, figs.7, 8)

Three species of the section Campestria are disjunctively distributed in Europe, Caucasas and East Asia. These species have characteristic leaves and fruits: leaves are five-lobed with a few, large, obtusely-pointed dents on margin,

while two wings of fruit with globose seeds are spreading out with 180° or more angles. Though a Chinese species, *A. miotaiense,* is not yet examined, other two species are almost indistinguishable in venation including the veinlets from the sections Plantanoidea and Rubra. As the section Campestria had been treated as a series of the section Platanoidea by some authors, these two sections may be akin each other. Ogata (1967) emphasized these two section are different in ray of wood.

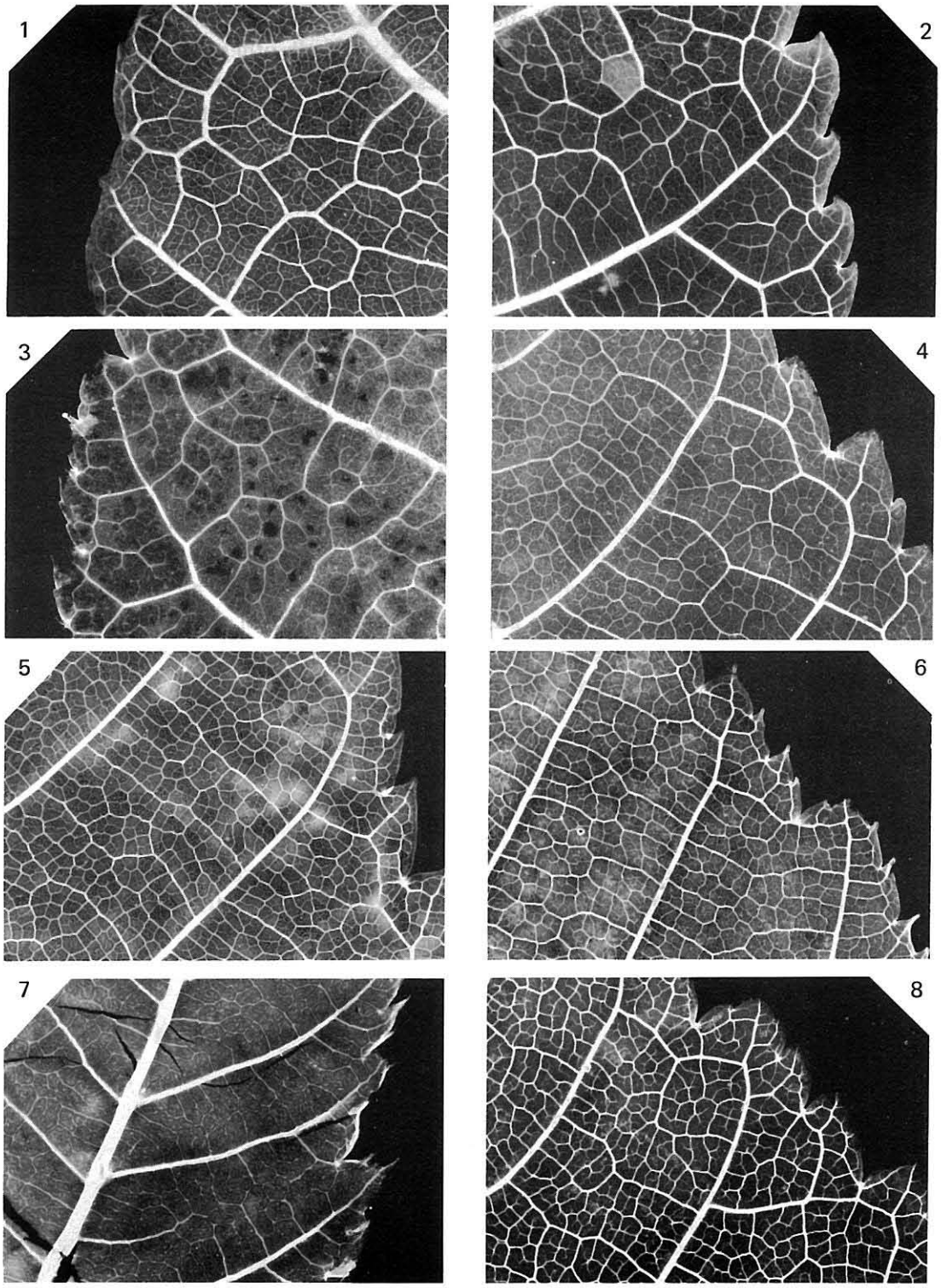
(6) Sect. Acer
(Text-fig.7, 3-7; pl.7, figs.1, 2)

The section Acer is composed of five species, which are common in their distribution in Europe, extending into Himalaya through Caucasas and Iran. This section includes *A. pseudoplatanus,* a type species of the genus *Acer.* All the species bear mostly five-lobed leaves with coarsely serrate margin. This section is subdivided into two series (Acer and Velutina), but the venation is indistinguishable between them. The fine veinlets are mostly lacking or rarely single within quadrangular areole.

(7) Sect. Goniocarpa Pojarkova
(Text-fig.7, 8-14; pl.7, figs.3-8)

Ten species belonging to the section Goniocarpa are mainly distributed in southern and southeastern Europe, partly extending into western Asia. All of these species are characterized by small, ultimate areolation, but are somewhat different in the freely-ending veinlets. The section Goniocarpa is divided into two series, Opulina and Monspessulana, by Ogata (1967). Most species of the Opulina are closely similar in venation characters to those of the section Acer, excepting for small ultimate areoles; the freely-ending veinlets are mostly

Explanation of Plate 1
(all figures X5)
Fig. 1 *Acer davidii* Franch. H.U.P.B. slide no. 845.
Fig. 2 *Acer insulare* Makino. H.U.P.B. slide no. 180.
Fig. 3 *Acer crataegifolium* Sieb. et Zucc. H.U.P.B. slide no. 229.
Fig. 4 *Acer pennsylvanicum* Linn. H.U.P.B. slide no. 980.
Fig. 5 *Acer morifolium* Koidzumi. H.U.P.B. slide no. 179.
Fig. 6 *Acer capillipes* Maxim. H.U.P.B. slide no. 1011.
Fig. 7 *Acer pectinatum* Wall. H.U.P.B. slide no. 885.
Fig. 8 *Acer rufinerve* Sieb. et Zucc. H.U.P.B. slide no. 237.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lacking or single. On the other hand, the species of the series Monspessulana show somewhat peculiar venation, compared with all other species of the second group. The veinlets of the Monspessulana are very irregular, and are mixedly composed of single to several times ramifying within the areoles. As already pointed out by Ogata (1967), these two series, Opulina and Monspessulana, are different in leaf shape and inflorescence, and so the section Goniocarpa may be necessary to further investigate on its taxonomy.

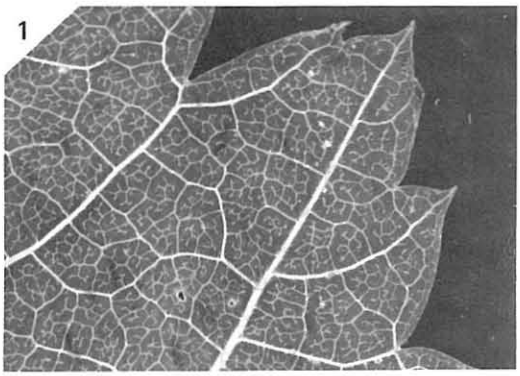
(8) Sect. Saccharina Pax
(Text-fig.7, 15-16; text-fig.8, 1-2; pl.8, figs.1-3)

The section Saccharina consists of five species living in eastern and central North America, and has been accepted without any essential revision by later authors since Pax (1885) established. These five North American species are closely similar in many essential characters, and have been distinguished by leaf shape, extension angles of two wings of fruit, penducle length and others. However, these characters are too graded to distinguish five species of the Saccharina; some of species (for instance, *A. leucoderme* and *A. barbatum*) have been considered as the varieties or even synonymies of *A. saccharum* by many authors. These five species are also closely similar in minor venation, excluding the size of areolation. Their freely-ending veinlets are mostly lacking or rarely single within quadrangular areoles, and show a close resemblance to those of the section Rubra.

(9) Sect. Integrifolia Pax
(Text-fig.8, 3-5; pl.8, figs.4-6)

Since Pax (1885) established the section Integrifolia, the species included in it has been variously discussed with some revisions by many authors. Most of

Explanation of Plate 2
(all figures X5)
Fig. 1 *Acer tchonoskii* Maxim. H.U.P.B. slide no. 876.
Fig. 2 *Acer micranthum* Sieb. et Zucc. H.U.P.B. slide no. 244.
Fig. 3 *Acer spicatum* Lam. H.U.P.B. slide no. 158b.
Fig. 4 *Acer ukurunduense* Trautv. et Mey. H.U.P.B. slide no. 238.
Fig. 5 *Acer japonicum* Thunb. H.U.P.B. slide no. 247.
Fig. 6 *Acer takeshimense* Nakai. H.U.P.B. slide no. 827.
Fig. 7 *Acer tenuifolium* Koidzumi. H.U.P.B. slide no. 737.
Fig. 8 *Acer sieboldianum* Miq. H.U.P.B. slide no. 246.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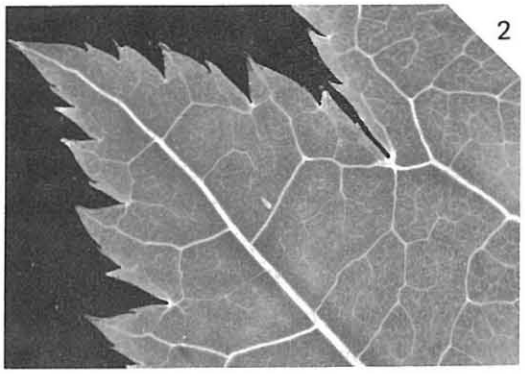
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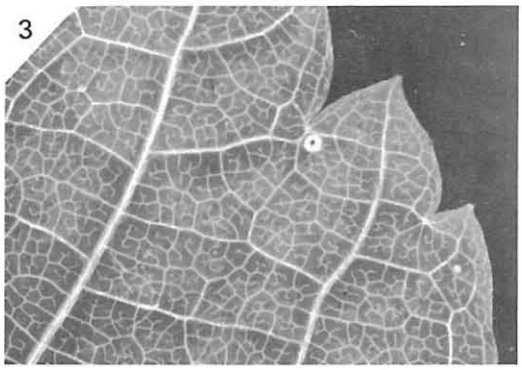
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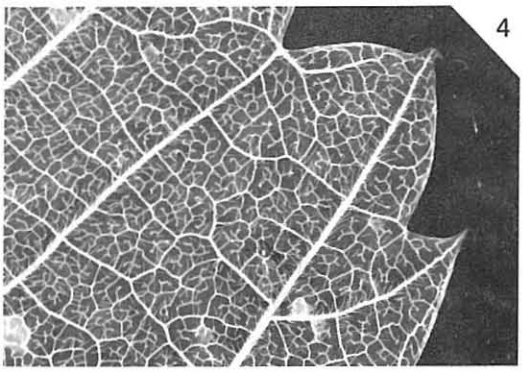
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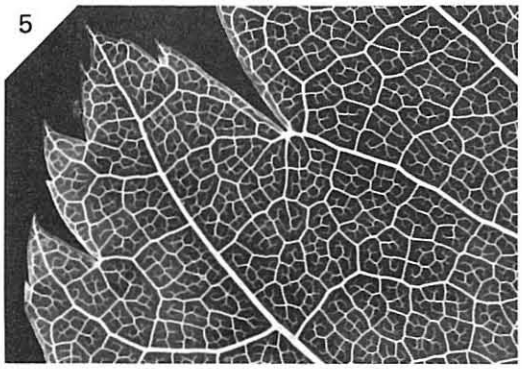
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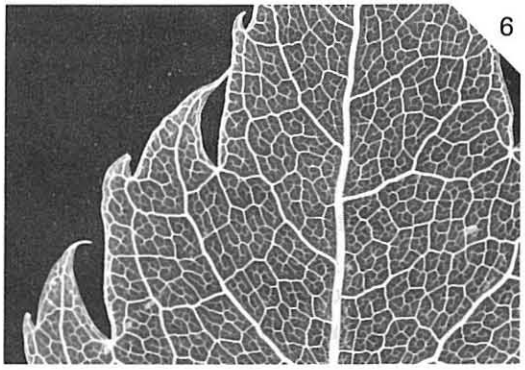
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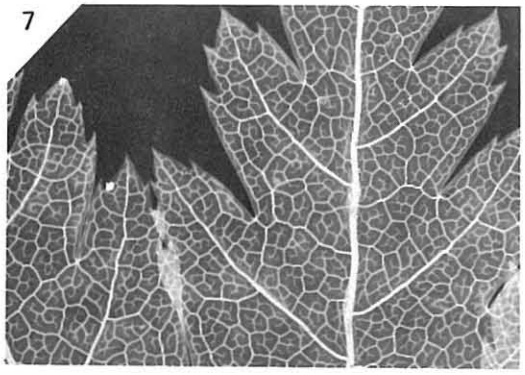
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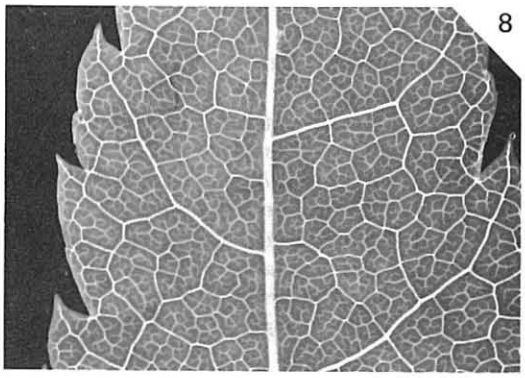
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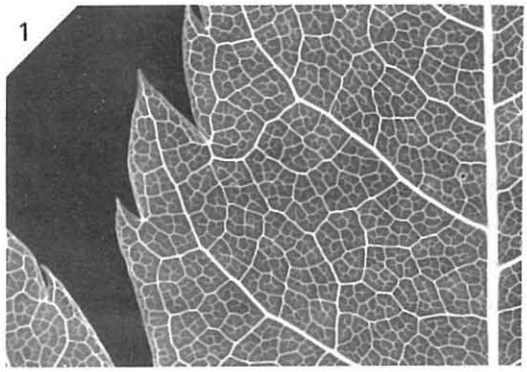
the species bearing oblong, entire-margined leaves were generally included in this section. Based on reinvestigation of all the morphologic characters, Ogata (1967) proposed that only three species, *A. oblongum, A. buergerianum* and *A. paxii,* belonged to the section Integrifolia. Actually, these three species show also a similar characters of venation: the ultimate areoles are generally small but surrounded by thick veins, while the veinlets are mostly lacking or very rarely single within the areoles. On the other hand, most of the species excluded from the previously-defined Intergrifolia show quite different venation character. For instance, *A. cordatum* once included in the Integrifolia (Pax, 1885; Momotani, 1963) is two or three times ramified in the veinlets, although it resembles *A. oblongum* in foliar shape and thick texture.

Three species belonging to the Integrifolia are now living in warm-temperate to warm regions of East Asia, extending into Himalaya.

(10) Sect. Syriaca Ogata
(Text-fig.8, 6-7; pl.8, figs.7, 8)

The section Syriaca established by Ogata (1967), is composed of four species now distributed from the eastern Mediteranean region to western Himalaya. Leaves of these species are usually three-lobed, thick-textured and remotely serrate in margin; they resemble superficially leaves of some species of the sections Integrifolia or Goniocarpa. Two Mediteranean species, *A. syriacum* and *A. orientale,* were examined. They are common in venation characters: the areoles are formed by thick veins, and the freely-ending veinlets are mostly lacking or very rarely single. With regard to the venation, the Section Syriaca is more related with the Integrifolia than the Goniocarpa. As the thick-textured leaves of the genus *Acer* are mostly thick even in the lower-order veins, the relationships between the sections Syriaca and Integrifolia should be further investigated. It is also noteworthy that the Syriaca and Goniocarpa are common in number of bud-scales as pointed out by Ogata (1967).

Explanation of Plate 3
(all figures ×5)
Fig. 1 *Acer circinatum* Pursh. H.U.P.B. slide no. 990.
Fig. 2 *Acer shirasawanum* Koidzumi. H.U.P.B. slide no. 182.
Fig. 3 *Acer serrulatum* Hayata. H.U.P.B. slide no. 341.
Fig. 4 *Acer schneiderianum* Pax et K. Hoffm. H.U.P.B. slide no. 883.
Fig. 5 *Acer pauciflorum* Fang. H.U.P.B. slide no. 882.
Fig. 6 *Acer heptalobum* Diels. H.U.P.B. slide no. 888.
Fig. 7 *Acer glabrum* Torr. H.U.P.B. slide no. 183.
Fig. 8 *Acer pubipalmatum* Fang. H.U.P.B. slide no. 880 (immature leaf).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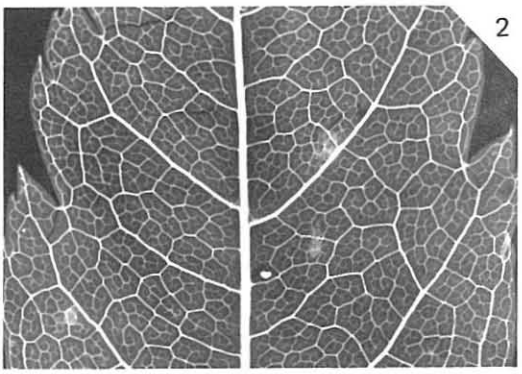
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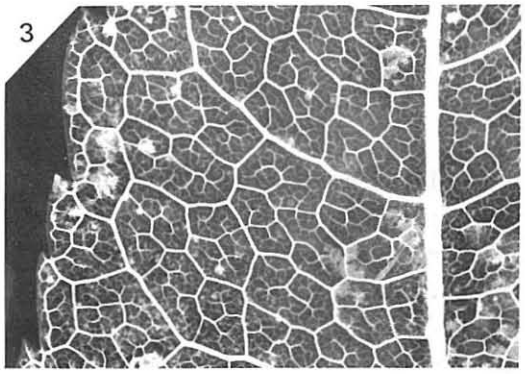
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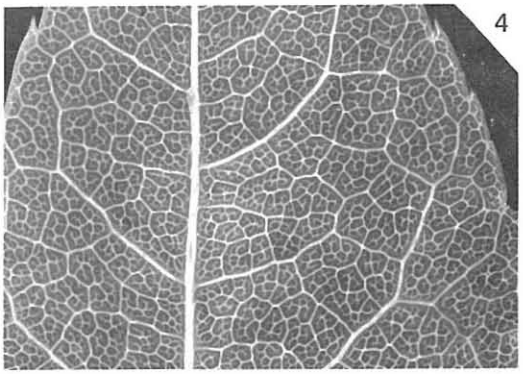
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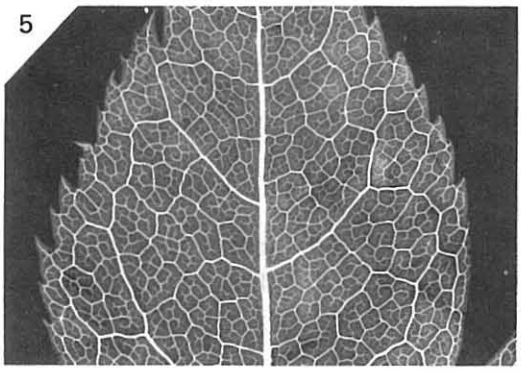
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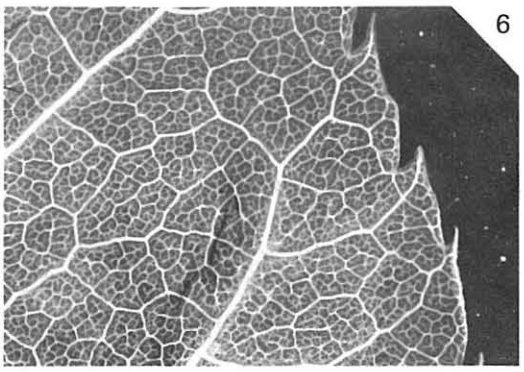
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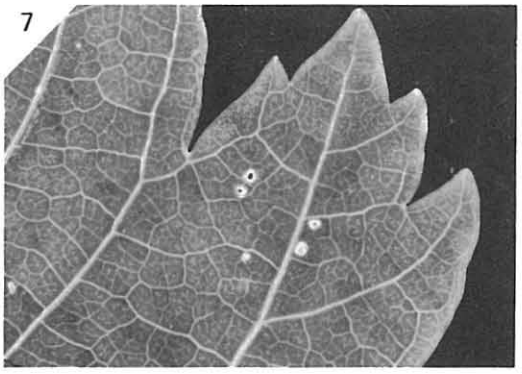
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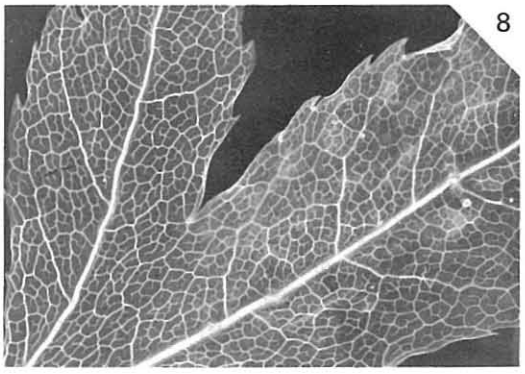
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(11) Sect. Trifoliata Pax
(Text-fig.8, 8-12; pl.9, figs.1-3)

The section Trifoliata is composed of five species, confined to East Asia in their modern distribution. Leaves of these species are trifoliate with oblong leaflets, which show typical venation characters of the second group; the freely-ending veinlets are mostly lacking or very rarely single within quadrangular or pentagonal areoles. This section was once subdivided into two series, Grisea and Mandshurica by Pojarkova (1933), but no considerable difference of minor venation is found between them, excepting for larger areolation in the Mandshurica.

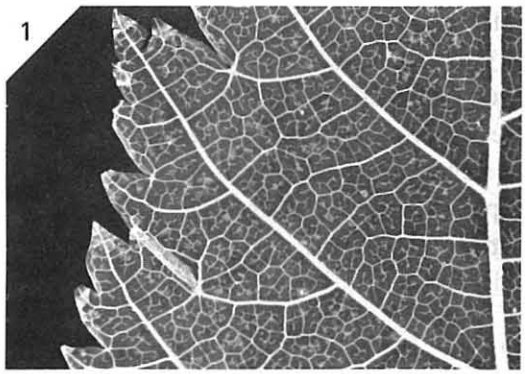
(12) Sect. Lithocarpa Pax
(Text-fig.8, 13-15; pl.9, figs.4, 5)

The five species are included in the section Lithocarpa, and are distributed in East Asia (Japan, China and Himalaya region). These species are represented mostly by three- or five-lobed leaves and also by nearly parallel two wings of fruits. As far as I examined three species (*A. villosum, A. franchetii* and *A. diabolicum*), the veinlets are mostly single or once ramified (very rarely lacking) within polygonal areoles. These venation features show close resemblance to those of the sections Campestria and Rubra, especially to the former.

(13) Sect. Laurina Ogata
(Text-fig.9, 1; pl.9, fig.8)

The section Laurina is represented only by *A. laurinum* now distributed in the tropical region of Southeast Asia. Because of oblong and entire-margined leaves, *A. laurinum* has been included in the section Integrifolia by most of the

Explanation of Plate 4
(all figures X5)
Fig. 1 *Acer argutum* Maxim. H.U.P.B. slide no. 241.
Fig. 2 *Acer stachyophyllum* Hiern. H.U.P.B. slide no. 996.
Fig. 3 *Acer negundo* Linn. H.U.P.B. slide no. 1101.
Fig. 4 *Acer acuminatum* Wall. H.U.P.B. slide no. 164.
Fig. 5 *Acer cissifolium* (Sieb. et Zucc.) K. Koch. H.U.P.B. slide no. 231
Fig. 6 *Acer ginnala* Maxim. H.U.P.B. slide no. 226.
Fig. 7 *Acer aidzuense* (Franch.) Nakai. H.U.P.B. slide no. 245.
Fig. 8 *Acer semenovii* Regel et Herder. H.U.P.B. slide no. 1009. (immature leaf)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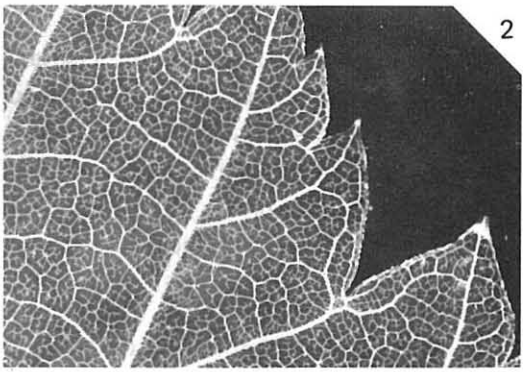
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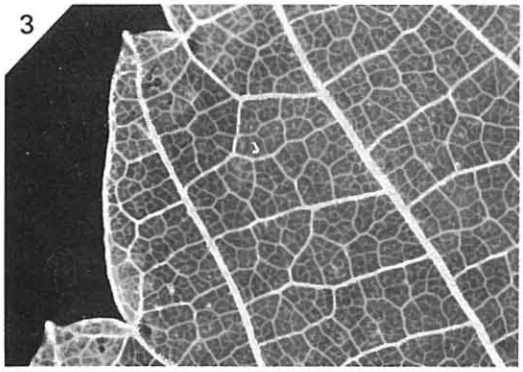
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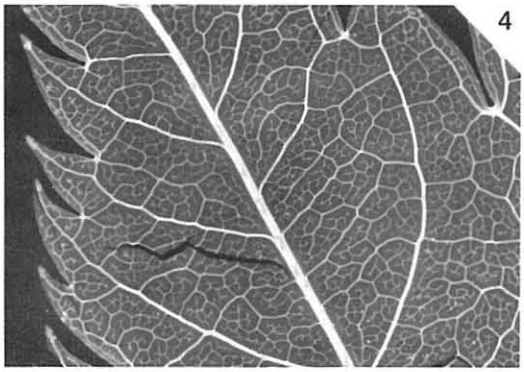
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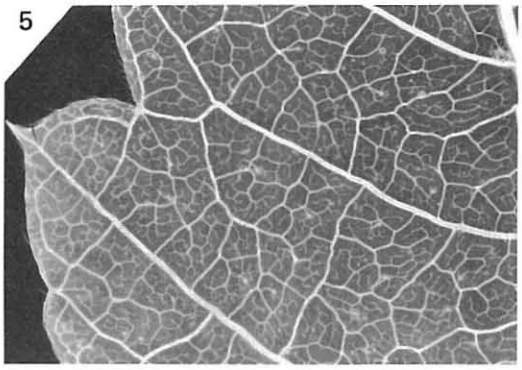
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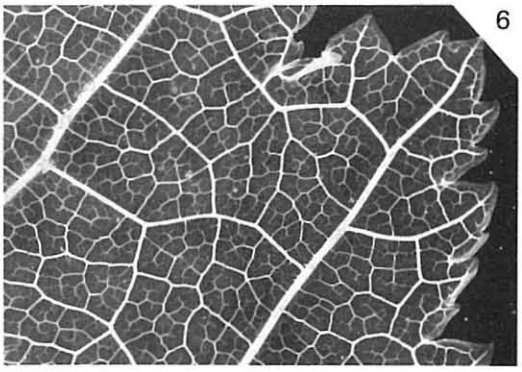
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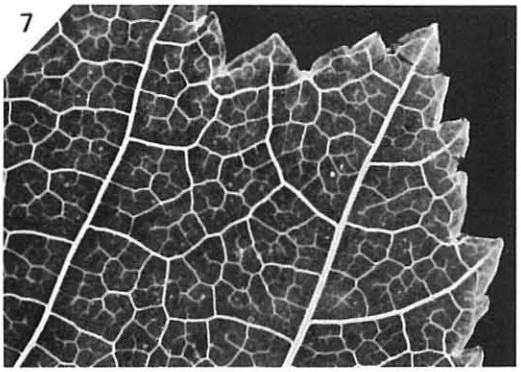
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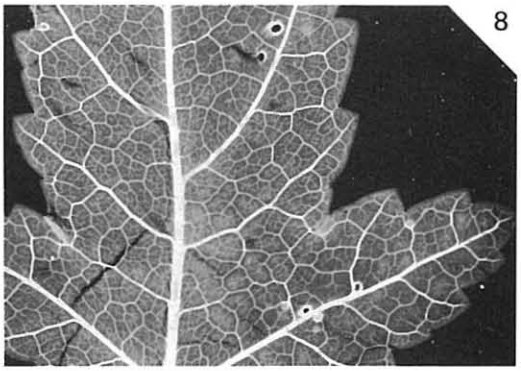
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authors (Pax, 1885; Pojarkova, 1933; Momotani, 1962b), but the section Laurina was established by Ogata (1967). In actual, this species is closely similar in minor venation to those of some species of the section Integrifolia, especially to *A. oblongum,* although the areoles are more than twice larger. The veinlets are mostly lacking and in rare case slenderly single within quadrangular or pentagonal areoles. The areoles of this species surrounded by thick veins, are largest among all the species of the genus *Acer.*

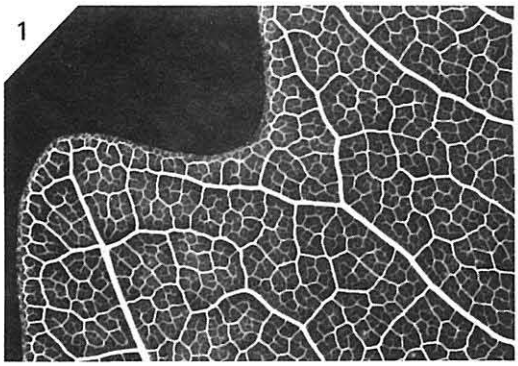
(14) Sect. Decandra (Hu et Cheng) Ogata
(Text-fig.9, 2; pl.9, fig.6)

The section Decandra is represented by one species, *A. decandrum,* which is endemic to Hainan Island, southwestern China. This species has oblong, entire-margined leaves, and has been included in the section Integrifolia along with the above-noted *A. laurinum.* The venation characters are similar to those of the sections Integrifolia and Lithocarpa, especially to the former, although somewhat larger in size of the areoles. Based on the sexuality, inflorescence and disc, Ogata (1967) considered *A. decandrum* to form an independent section.

(15) Sect. Pentaphylla Hu et Cheng
(Text-fig.9, 3; pl.9, fig.7)

The section Pentaphylla is represented only by *A. pentaphyllum* Diels, distributed in Szechuan and Yunnan, China. The leaves of this species are most peculiar in all the species of the genus *Acer*: leaves are usually digitately compound, with 5 to 7 leaflets which are lanceolate and entire-margined. The venation shows distinctly a character belonging to the second group: the freely-ending veinlets are mostly lacking, and rarely single within quadrangular or pentagonal areoles. These venation features are somewhat similar to those of

Explanation of Plate 5
(all figures X5)
Fig. 1 *Acer macrophyllum* Franch. H.U.P.B. slide no. 242.
Fig. 2 *Acer pubescens* Franch. H.U.P.B. slide no. 828.
Fig. 3 *Acer carpinifolium* Sieb. et Zucc. H.U.P.B. slide no. 227.
Fig. 4 *Acer distylum* Sieb. et Zucc. H.U.P.B. slide no. 230.
Fig. 5 *Acer nipponicum* Hara. H.U.P.B. slide no. 781.
Fig. 6 *Acer rubrum* Linn. H.U.P.B. slide no. 184.
Fig. 7 *Acer pycnanthum* K. Koch. H.U.P.B. slide no. 240.
Fig. 8 *Acer saccharinum* Linn. H.U.P.B. slide no. 501.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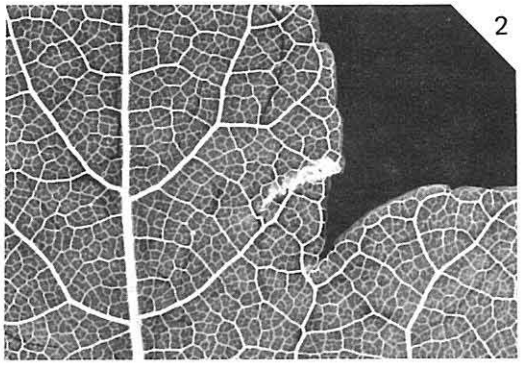
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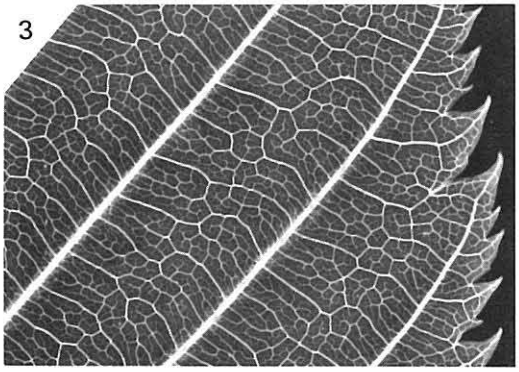
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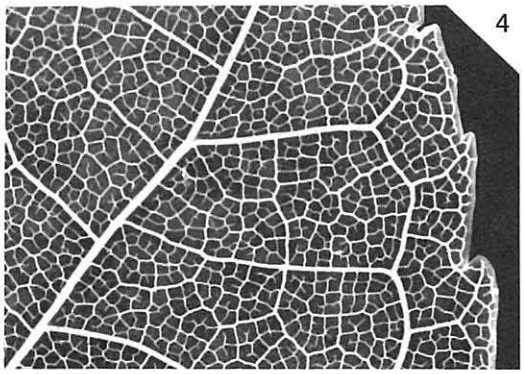
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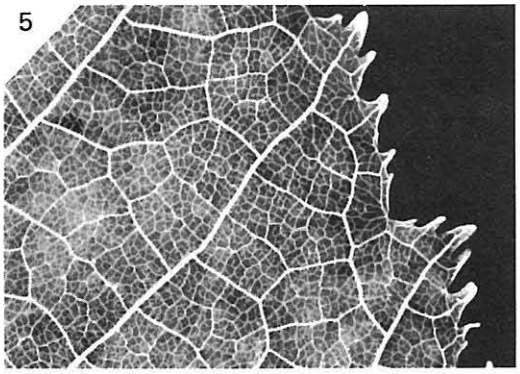
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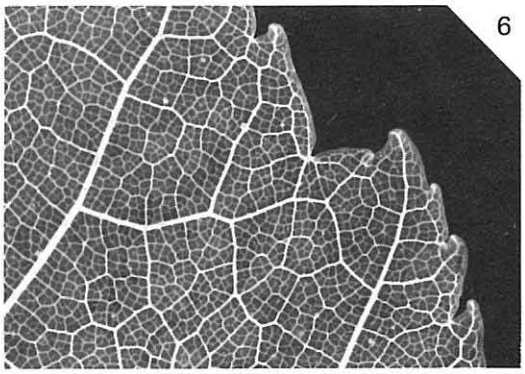
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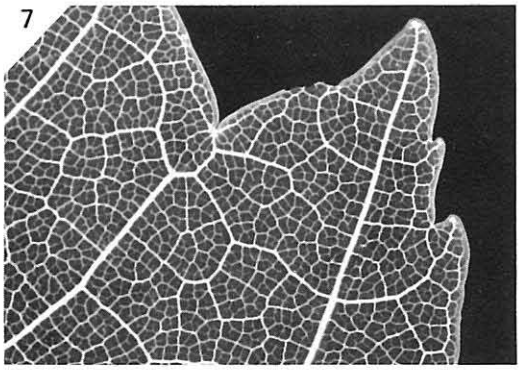
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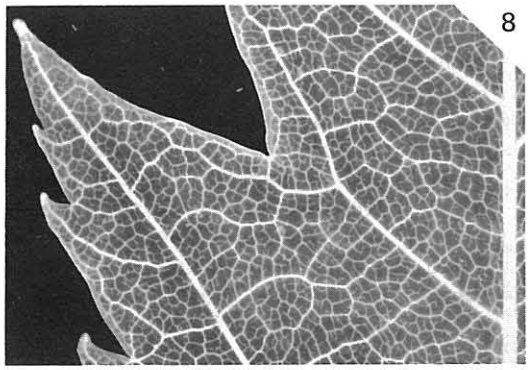
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the sections Saccharina and Platanoidea. Considering the veinlets together with size of areolation, *A. pentaphyllum* may be related to the Platanoidea, though it is far different in fruit characters.

The Formation of Free-ending Veinlets

One of the characteric features in the dicotylodonous leaves is very complicated vein system with finer reticulum. It has been generally accepted by many morphologists that these venation system reflects a growing process of leaves, and shows a certain pattern peculiar to each species through a certain ontogentic or phylogenetic process. The differentiation of venation system of leaves has been variously investigated since the end of last century, and especially this problem has been discussed by various workers since Foster (1952) reviewed on the ontogenetic standpoint.

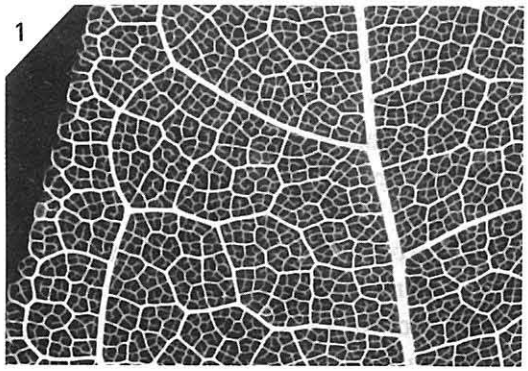
There seems to be general agreement concerning the histogenesis of the venation as a whole. In the dicotylodonous leaves the procambium of the leaf trace and of the midvein differentiate acropetally. Following the marginal growth of the leaf, the differentiation of the procambium of secondary veins, which is multiseriate in origin, also occurs from the midvein in the acropetal sequence. The procambial cells of tertiary and further lower-order veins appear between secondary veins (intercostal region). These intersecondary veins are uni- or biseriate in origin. The polygonal areoles are formed and subdivided several times by the differentiation of procambial cells of intersecondary veins. Thus, intersecondary veins delimit the ultimate areoles in which freely-ending veinlets are frequently observed in the mature stage.

With respect to the freely-ending veinlets treated mainly in my earlier chapter, there have been three different viewpoints, as follows:

(1) The majority of vein-endings appear after differentiation of procambium has ceased and during the phase of growth involving cell enlargment. During

Explanation of Plate 6
(all figures X5)

Fig. 1 *Acer catalpifolium* Rehd. H.U.P.B. slide no. 887.
Fig. 2 *Acer cappadocicum* Gleditsch. H.U.P.B. slide no. 249.
Fig. 3 *Acer tenellum* Pax. H.U.P.B. slide no. 877 (immature leaf).
Fig. 4 *Acer mono* Maxim. H.U.P.B. slide no. 248.
Fig. 5 *Acer platanoides* Linn. H.U.P.B. slide no. 45.
Fig. 6 *Acer truncatum* Bunge. H.U.P.B. slide no. 750.
Fig. 7 *Acer miyabei* Maxim. H.U.P.B. slide no. 239.
Fig. 8 *Acer campestre* Linn. H.U.P.B. slide no. 1099.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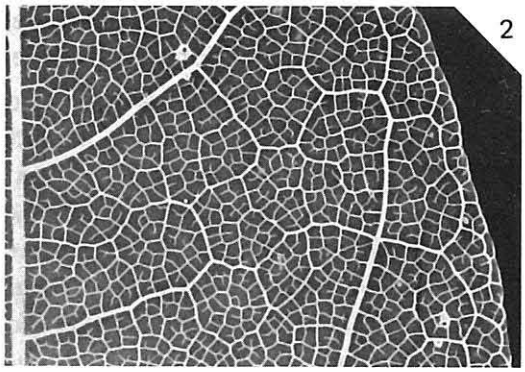
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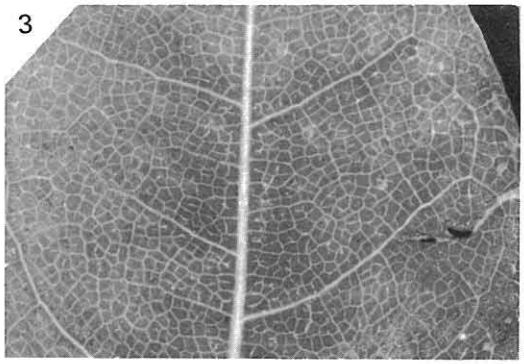
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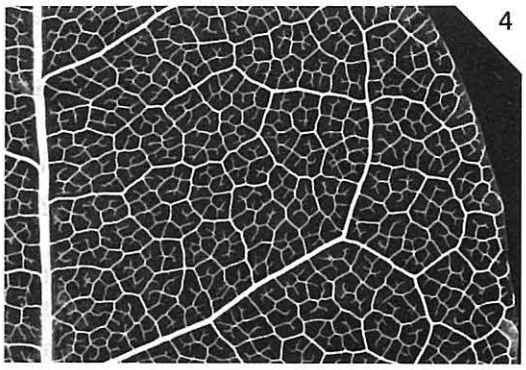
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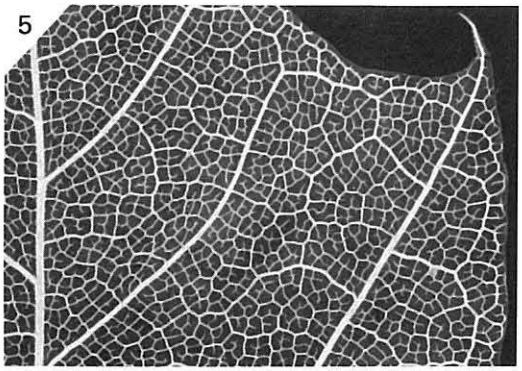
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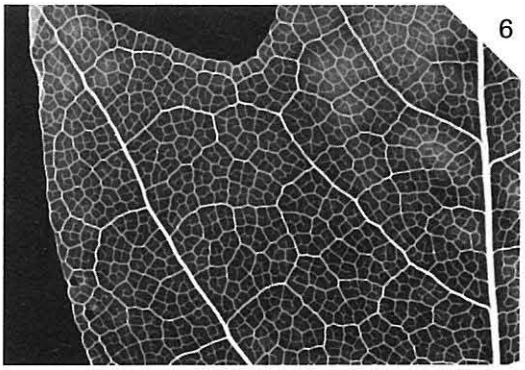
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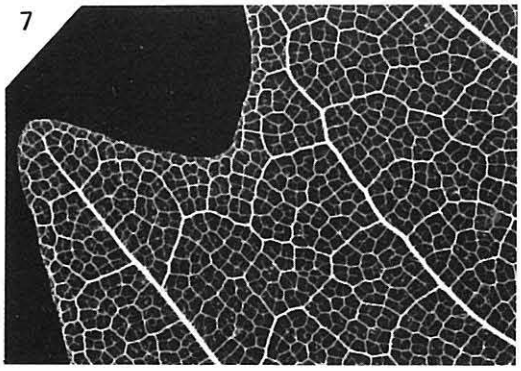
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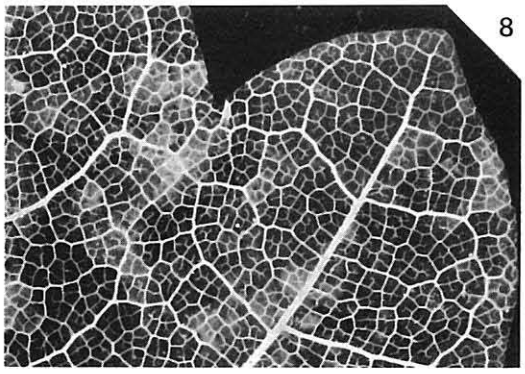
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leaf maturation the veinlets are under mechanical disruption or disconnection due to extending tension of leaf blade (Slade, 1957, 1959).

(2) The vein-endings develop through progressive differentiation of procambium from the ground meristem in the ultimate areoles of vascular reticulum. During active cell-division the vein-endings appear in the mosophyll surrounded by ultimate areoles. (Pray, 1954, 1955a, b).

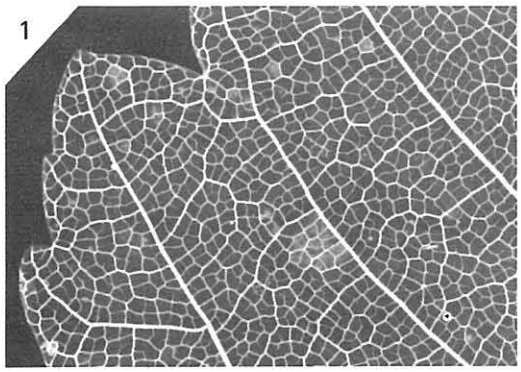
(3) Although vein-endings are formed through progressive differentiation, the vein-endings appear when the procambium of veins is unable to complet its potential course of development (for instance, forming areoles). It becomes only partially differentiated, and the potential procambial cells lying beyond the vein-endings become differentiated as mesophyll cell instead. (Hara, 1962; Lersten, 1965).

Among these three opinions regarding the origin of freely-ending veinlets, Slade's theory of "vein-breakage" has been recently not supported by most workers. It is not my purpose and also impossible for me to examine on the origin of ultimate veinlets in the genus *Acer,* because all the leaves were only cleared, not using paradermal and transverse sections. However, as far as I has investigated dicotyldonous leaves of more than 1000 species, few leaves shows any definite evidence for "vein-breakage" asserted by Slade. The ultimate veinlets appear to be progressively formed with ramification in most of dicotyledonous leaves. For instance, As observered in the first group of the genus *Acer,* the ramified veinlets terminating with gradually thinning tips (incomplete vascularization) within areoles, may show "progressive differentiation" stated by Pray. On the other hand, the veinlets with thick tips as observed in the second group of *Acer,* may represent "incomplete comissural vein", claimed by Hara and Lersten.

In any case, it is very important for us that all the species of the genus *Acer* are classified into two groups, based on the areolation and freely-ending veinlets. As these venation features are known to be nearly consistent in each

Explanation of Plate 7
(all figures X5)

Fig. 1 *Acer pseudoplatanus* Linn. H.U.P.B. slide no. 49.
Fig. 2 *Acer heldreichii* Orph. H.U.P.B. slide no. 168.
Fig. 3 *Acer obtusatum* Waldst. et Kitaibel. H.U.P.B. slide no. 1022.
Fig. 4 *Acer opalus* Mill. H.U.P.B. slide no. 166.
Fig. 5 *Acer tauricolum* Boiss. et Bal. H.U.P.B. slide no. 163.
Fig. 6 *Acer hyrcanum* Fisch. et Mey. H.U.P.B. slide no. 167.
Fig. 7 *Acer monspessulanum* Linn. H.U.P.B. slide no. 1037.
Fig. 8 *Acer turkomanicum* Pojarkova. H.U.P.B. slide no. 161.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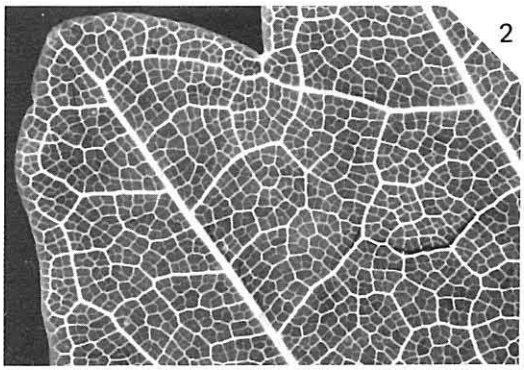
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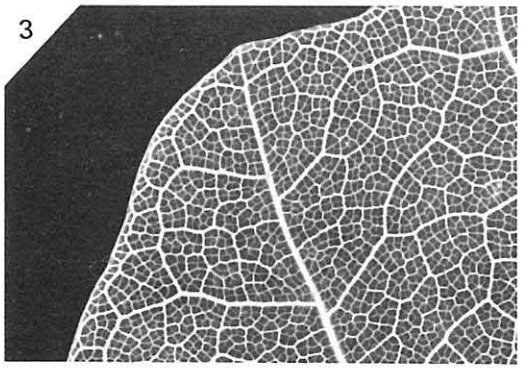
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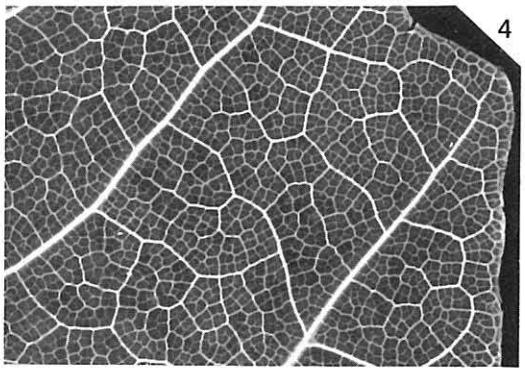
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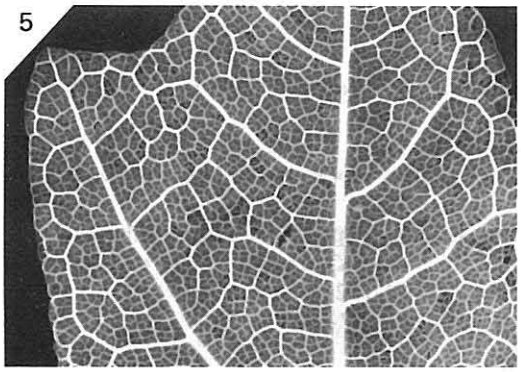
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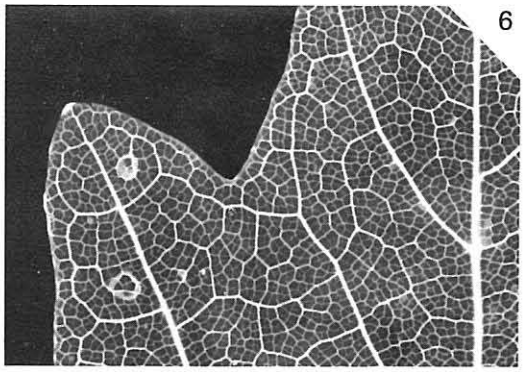
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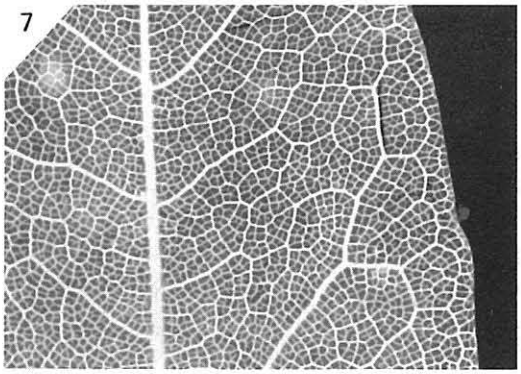
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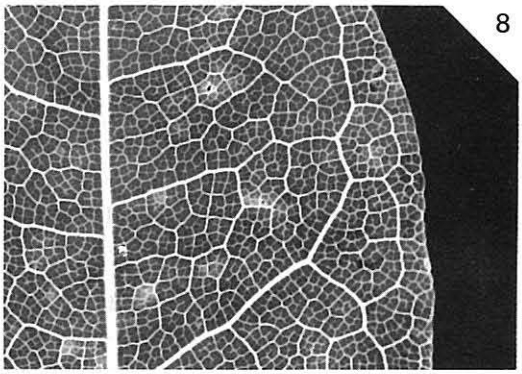
8

species, it seems effective for phylogetic investigation to compare fossil leaves with the extant species in venation system. Actually, many new knowledge on fossil species of *Acer* has been recently obtained by me (Tanai, 1977; Tanai & Ozaki, 1977). These taxonomical studies on fossil materials of the genus *Acer* in East Asia and North America will appear in later paper.

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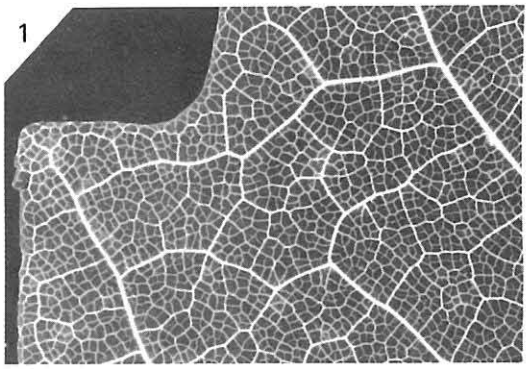
Explanation of Plate 8

(all figures X5)

Fig. 1 *Acer saccharum* Marsh. H.U.P.B. slide no. 236.
Fig. 2 *Acer leucoderme* Small. H.U.P.B. slide no. 999.
Fig. 3 *Acer nigrum* Michx. H.U.P.B. slide no. 1060.
Fig. 4 *Acer buergerianum* Miq. H.U.P.B. slide no. 250.
Fig. 5 *Acer paxii* Franch. H.U.P.B. slide no. 162.
Fig. 6 *Acer oblongum* Wall. H.U.P.B. slide no. 181.
Fig. 7 *Acer orientale* Linn. H.U.P.B. slide no. 169.
Fig. 8 *Acer syriacum* Boiss. et Gaill. H.U.P.B. slide no. 165.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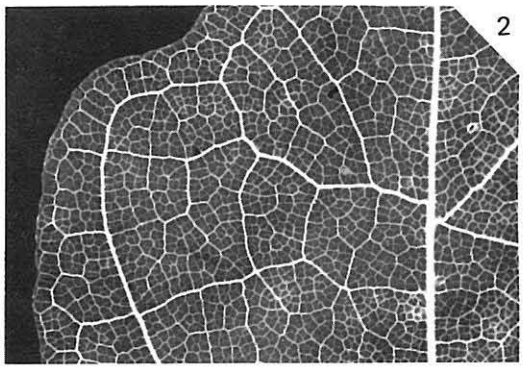
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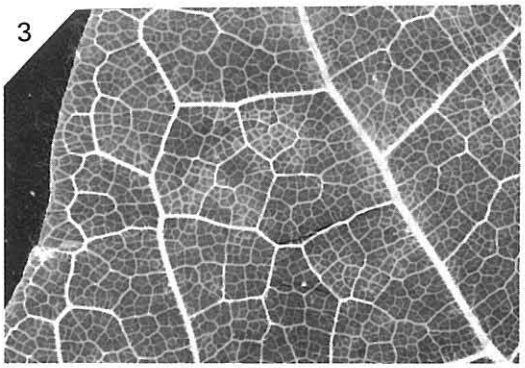
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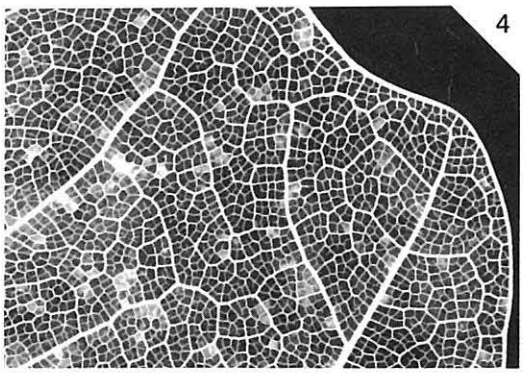
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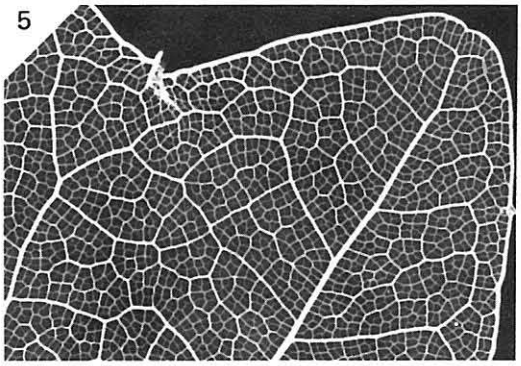
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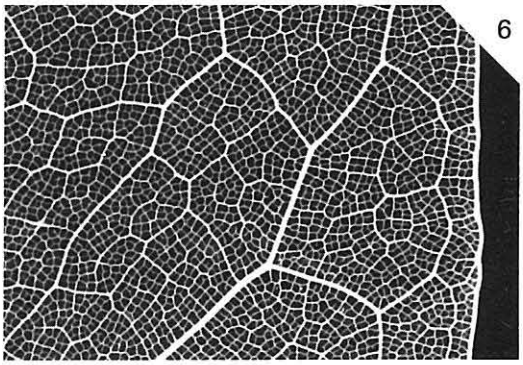
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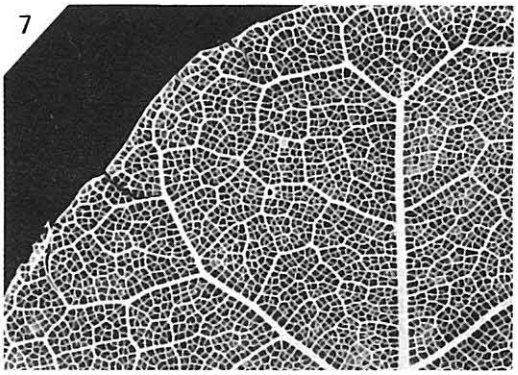
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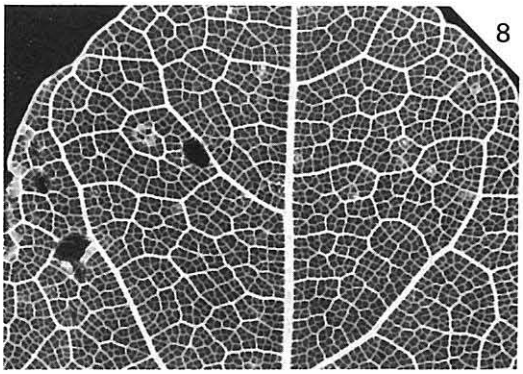
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Explanation of Plate 9

(all figures X5, excepting figures 7 and 8)

Fig. 1 *Acer sutchuense* Franch. H.U.P.B. slide no. 881.

Fig. 2 *Acer nikoense* Maxim. H.U.P.B. slide no. 228.

Fig. 3 *Acer triflorum* Kamarov. H.U.P.B. slide no. 232.

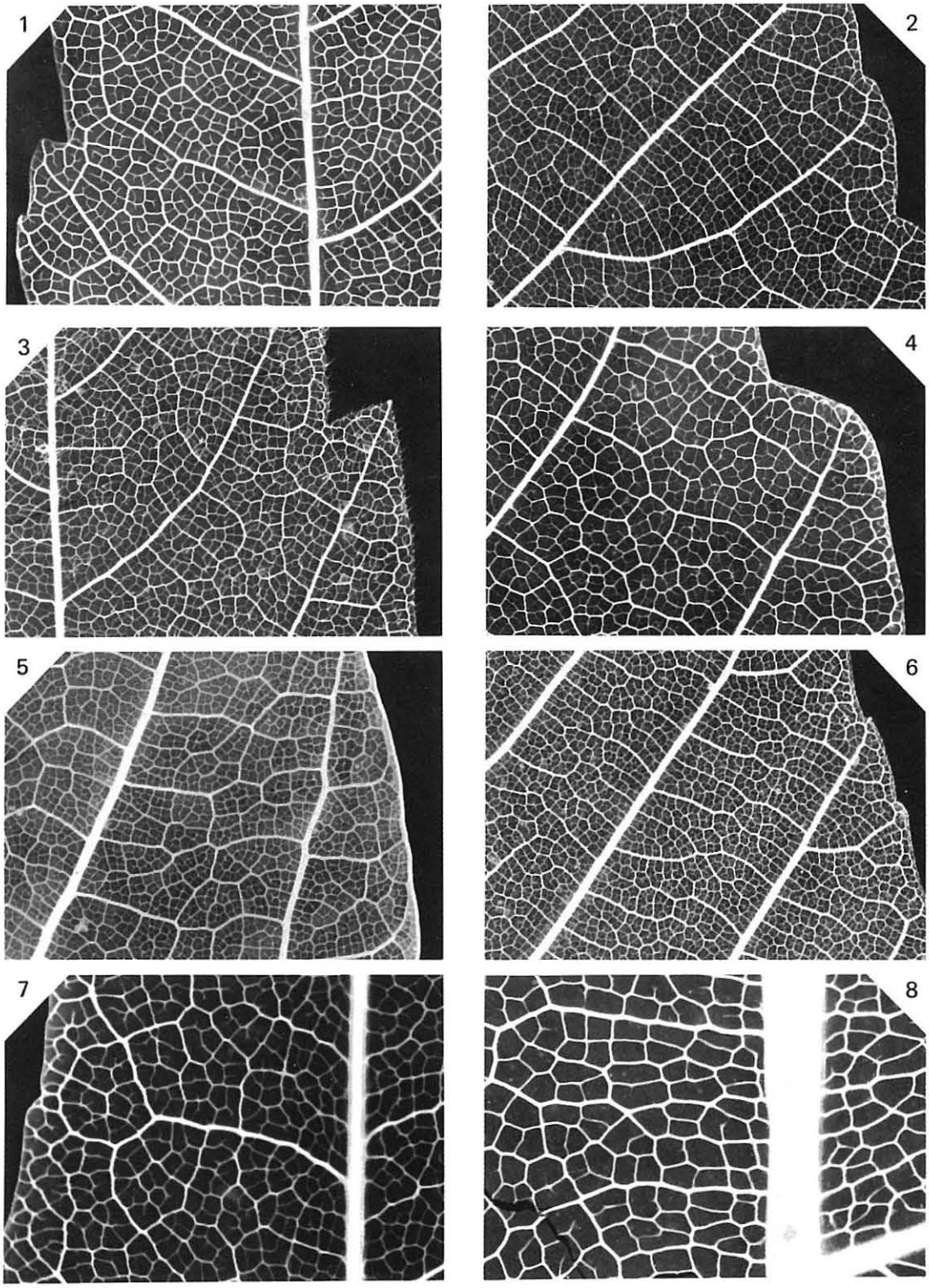
Fig. 4 *Acer diabolicum* Blume. H.U.P.B. slide no. 235.

Fig. 5 *Acer villosum* Wall. H.U.P.B. slide no. 884.

Fig. 6 *Acer decandrum* Merr. H.U.P.B. slide no. 160.

Fig. 7 *Acer pentaphyllum* Diels. U.S.G.S. slide no. 8617. X10.

Fig. 8 *Acer laurinum* Hassk. U.S.G.S. slide no. 7632b. X10.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