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Taxonomic Study of the Genus Acer, with Special Reference to the Seed Proteins I. Taxonomic Characters

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Introduction

The Aceraceae have been treated taxonomically by many investigators. According to recent opinions, in view of morphological and palaeontological taxonomy, this family belonging to Sapindales is related to Hypocastaneaceae, Staphyleaceae and Sapindaceae.

On the anatomical study of the seeds, CROIZAT (1941) proposed the following genealogical stem which is divided into two branches: one produces Sapindales, the other produces Aceraceae, Staphyleaceae and Hypocastaneaceae. According to BARNER's results (1927) by means of the serodiagnostic method, Acer insigne is related to Canarium commune of Burseraceae and Ricinus zanzibalensis of Euphorbiaceae as well as Sapindus.

The interspecific relations of the genus Acer were first discussed systematically by MAXIMOWICZ (1880). An excellent monograph of Aceraceae was published by Pax (1885-1886). Afterwards, many species, series and sections were added by more recent investigators. About 180 new species were published from 1900 to 1950, according to Index Kewensis. Many of them were deleted by other authors. At present, the following two genera have been recognized in Aceraceae: Dipteronia and Acer. The genus Dipteronia has two species. The genus Acer consists of about 150 species, which are classified into many groups, from 13 to 30. At the present period, Acer is known to have widely spread over the Northern Hemisphere. Even palaeoacers of Oligocene had been so differentiated as to be classified into one of the present sections. But the distribution of the fossils does not accord in detail with the that of the existing forms. Many of them have become extinct. For instance, while the sect. Rubra has many fossils widely distributed over the Northern Hemisphere, the existing section consists of A. rubrum and its allies from N. America and A. pycnanthum from Japan. The abundance of the extinct species is important to the phylogenetical considerations of Acer.

Even now, there are many problems not yet solved. For example, there are various conclusions among the subsequent investigators, concerning the extent and the phylogenetical relationship of Pax's sections. Therefore, the Aceraceae still have many taxonomic problems, though the family has been studied by many investigators.

The present writer studied on the seed proteins of cultivated Brassicae concerning the protein fractions by means of the antigen-antibody reaction, the turbidometric titration and the agarography. From his experimental results, it is suggested that the difference of protein fractions corresponds to that of relationships of the plants. In this work, the methods of fractionation are used to analyse the seed proteins of *Acer*. Adopting this new method of determining the affinities shown by proteins, the writer revised the taxonomic system of this plant group, under careful consideration of the reexamination of morphological characters.

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I. Taxonomic Characters

On the classification within the genus *Acer*, the length of scales of the bud, the differentiation of sexuality of the flower, the relative position of the stamens and the disc, the shape of inflorescence and the number of lobes of the leafblade, etc., have been valued.

Bud scale: Three different types of scales have been found in winter buds: 1) generally two-paired but rarely three-paired, 2) mainly four-paired, and 3) many-paired. In the species of two-paired scales, the scales of the inner pair are different from those of the outer pair and longer. Sometimes, in monstrosities, the scales of the inner pair accompany the leafblade at their apices. Therefore, it has been explained that most of the scales of the members of this genus are homologous to the petioles. In the leaf bud of *A. carpinifolium*, the inner scales are longer than the outer, with many parallel side-nerves.



Fig. 1. Bud scales.—1 and 2: A. carpinifolium.—3 and 4: A. buergerianum.—5, 6, 7, 8 and 9: Monstrosity of bud scales of A. negundo.



Fig. 2. Scars left by the bud scales and a leaf of *A. mono*.

Thus the scales of this species may be homologous to the leafblade. The monstrous scale is caducous (Fig. 1).

At the base of the twig of A. ginnala, there are sometimes a pair of entire leaves with reticulate nerves.

Though the scales of buds are caducous, we can count the scars left by the scales in herbarium specimens. The number of pairs is an important taxonomic character which may be observed in all seasons (Fig. 2).

Leaf: In this genus, leaves are always opposite and exstipulate. The anatomical structures of the leaves were investigated in detail by WARSOW (1908). The present author recognized that the distribution of crystals of calcium oxalate in the leaves was constant in each section.

MONACHINO (1960) reported on the folding methods of the leaves in winter buds. The writer has found that the pinnate nerves are already formed in the winter

bud in *A. car pinifolium*, while in the species reported by MONACHINO the nerves are formed in the palmate species, and in the unlobed species no pinnate nerves are formed in the winter buds.

The shape of leaves is variable to some extent. The descriptions include these variations and are obscure. But we can recognize the specificity of the shape of leaves. Any botanist can easily find the name of a certain species by merely looking at the figures of leaves in SCHNEIDER's Handbuch (1912). The nervations and the shapes of leaves are very important for the identification of herbarium specimens and fossils.

The shapes of some leaves of young trees of adventitious shoots are frequently different from those of the normal palmately lobed leaves. For instance, there are three deeply lobed leaves in *A. mono* and *A. palmatum*. In this case, there are small lobules at the base of the lateral pair. The lobules correspond to 5 palmate nerves.

In A. carpinifolium, the lowest nerve sometimes divides into two at the base. In the monstrosity having a lobule, the lowest nerve does not become the nerve of the side lobule. The lobule of the monstrous leaf of this species has two or three secondary nerves.

Generally, in the leaves of *Acer*, the lobules of a leaf lobe, the large incised serrations or the large sinuous dentations terminate the secondary nerves starting from the primary nerve. But the fine serrations do not terminate the secondary nerves. However there are many intermediate states among the dentations.

The following modes of serration at the tailed apex of a lobe are noted as a specific character; the one being serrate as in A. tegmentosum and A. argutum, and the other, entire as in A. acuminatum.

There are various kinds of hairs on the leafblade, on the petiole or on



Fig. 3. Bracteoles.—1: Male inflorescence of A. carpinifolium.—2: Female inflorescence of A. negundo.—3: Male inflorescence of A. diabolicum.

the nerve. For example, the hairs of *A. mono* are unicellular, straight or crisped. They are scattered on the nerve or tufted at the insertion of the nerve. HISAUCHI distinguished the varieties and subvarieties of *A. mono* by these characters of the hairs.

Inflorescence: There are various kinds of the inflorescences: compound raceme, raceme, panicule, corymb and umbel, etc. These may be classified into

the following two groups: one from compound raceme to simple many flowered raceme and then to a few flowered raceme, the other from compound raceme or panicule to many flowered corymb and then to a few flowered corymb.

The range of the sexuality of inflorescences is as follows: from andropolygamous to andro-monoecious, andro-dioecious and then to dioecious. The variation of inflorescences seems to be accompanied by the differentiation of the sexuality. The kinds of the inflorescences combined with the other characters have been frequently used for dividing the genus into sections.

The inflorescence is terminal on the leafy branchlet or on the leafless branchlet. In the latter case, the branchlet does not elongate, and the feature is called lateral.

The presence or absence of bracts and bracteoles was not treated as the important taxonomic character. Generally, a few bracteoles remain on herbarium specimens, because they are caducous. We can distinguish the following cases: without bracteoles, with the tuft of hairs instead of the bracteoles, with the ligulate bracteoles, with the lanceolate and ciliated bracteoles, and with the broad ovate bracteoles (Fig. 3).

Flower: The flowers are actinomorphous, hermaphlodite or unisexual. The elements of the flowers are usually pentamerous or rarely tetramerous, being represented by the formula, $K_sC_sA_{5+3}G_{(2)}$, but they are frequently excessive or defective. The flowers are rarely apetalous. Rarely, too, sepals are connate. A female flower is shown as $K_sC_sA_{abort}G_{(2)}$. A male flower is shown as $K_sC_sA_{5+3}G_{0}$. In the male flower of *A. diabolicum*, the petals and the sepals are adonate.

The stamens are bicyclic, generally 8, sometimes, 4, 10 or 12.

In case of the increase in number of the elements of a terminal flower in an inflorescence, the increased number should not be taken as the taxonomic character. But the frequency of the increase may be taken into account of the genealogical affinity.

The position of disc is considered as the important taxonomic character. By this character, PAX (1885) classified the genus *Acer* into four groups: *Extrastaminalia*, *Adiscantha*, *Intrastaminalia* and *Perygyna*. KOIDZUMI (1911) adopted the former three and distributed the members of *Perygyna* among them. The disc of *Intrastaminalia* is sinuated at the inside of the base of the stamen but is not connate on the outside, and often thickens on the inside. The disc of *Extrastaminalia* is connate each other at the outside of the base of the stamens which grow on the small cavities of the disc or grow on the inside of the disc. In the flowers of *A. mono*, it is difficult to decide whether the position of the disc is inside or outside of the stamens. This is regarded as extrastaminal, for the disc is connate on the outside of the stamens (KOIDZUMI classified *A. mono* in *Extrastaminalia*, on account of the stamens of the pistillate flower being inside of the disc). The disc of *A. pycnanthum* thickens and is sinuated on the inside of the stamens, so it should be regarded as intrastaminal, though

KOIDZUMI put this species in *Extrastaminalia*. Acer spicatum, A. ukurunduense and A. caudatum have been treated as to belong to *Extrastaminalia* for the reason that the disc thickens at the outside of the base of the stamens. But they are different from the other species of *Extrastaminalia*, on account of their profoundly sinuated disc. The disc of A. nipponicum is thin but secretes honey. HAYATA (1904) considers that the character of the disc has genealogical and ecological meanings (Figs. 4 and 5).

Sepal and petal are alternate. Their shape, existence or absence, free or connate, hairy or hairless, and their colour have been frequently used as distinguishing characters. In the petals and sepals, hairs on the margin and those on the nerves should be treated separately. Both the petal and the sepal are similar to each other in their shape and colour, e.g. *A. crataegifolium*. The petal is different from the sepal in their shape and colour, e.g. *A. palmatum*. The former is considered as primitive, and the latter as advanced. These occur on the different lines, polytopically.

The number of stamens is often used as one of the sectional characters. The filaments are hairy or glabrous. The hairs of the filaments are usually of the same kind as those of the disc. The shape and the scabrous surface of the anther become the distinguishing characters of the section *Palmatoidea*.

Carpels are two, connate. The ovary consists of two locules. There are two sessile ovules in each locule. The raphe is dorsal. The two ovules stand side by side or above and below. The ovaries are tomentose in many species. In some species, the ovaries become glabrous before their maturity. The hairiness is frequently used for the specific distinction. The style is bipartite or bilobate. There are intermediate forms between the two. The insides of the two branches of the style are stigmatiferous, and are finely and shortly laciniated. This character is common in this family.

Fruit: The fruit is an indehiscent dry one, composed of two one-seeded carpels, separating when ripe into mericarps, and provided with wings, i.e. samara. The features given by samara are useful in discriminating genera or species. The shape of a locule is closely connected with the shape of seed.

In the structures of the pericarps, we can distinguish three to five kinds of cell layers. The structures of pericarps may be divided into several pattern groups, differing from each other in the combination of different layers, though these pattern groups are not distinguished clearly, because of the existence of intermediates. In some cases, the pericarp, during its development, passes through several pattern groups. For example, in the young pericarp of *A. negundo* three layers are distinguished. The three layered pericarp is also found in the matured pericarp of *A. carpinifolium*. In *A. negundo* the upper layer is the epidermis, the middle layer is parenchymatous and the lower layer consists of two or three series of fibrous cells. In the middle layer, the shape of the parenchymatous cell with the mono-crystal of calcium oxalate can not be distinguished from that without the crystal. The matured pericarp consists



Fig. 4. Position of disc, shape of petal and shape of sepal.—From 1 to 9: A. mono.—1 and 2: Male flower.—3: Petals.—4: Sepal.—5,6 and 7: Female flower.—8: Petals.—9: Sepals.—From 10 to 14: A. buergerianum.—10, 11 and 12: Male flower.—13: Petals.—14: Sepals.—15 and 16: Female flower.



Fig. 5. Flowers of *A. pycnanthum.*—1: Winter bud.—2: Male inflorescence.—From 3 to 7: Male flower.—5: Disc.—6: Petal.—7: Sepal.—8 and 9: Female flower.—9: Disc.

of five layers; the layer of the epidermal cells, the sclerenchymatous cells, the parenchyma, the sclerenchymatous cells and the fibrous cells (Figs. 6 and 7).

The following species have four-layered pericarps: A crataegifolium, A. pennsylvanicum, A. tschonoskii, A. micranthum, A. pectinatum, A. insulare, A. kawa-kamii, A. capillipes and A. tegmentosum, etc.

The species having three-layered pericarp are A. spicatum, A. ukurunduense, A. caudatum, A. rufinerve, A. morifolium, A. rubescens, A. nipponicum, A. distylum, A. pycnanthum, A. rubrum, A. velutinum, A. herdreichii, A. trautvetteri, A. ginnala, A. aidzuense, A. tataricum and A. semenovii. It is interesting to note that most of these three-layered species were included in the section Spicata. For this reason, however, only the section Spicata can be claimed to be a natural group.



Fig. 6. Structure of pericarp.—1 and 2: A. negundo.—1: Young pericarp. —2: Matured pericarp.—3 and 4: A. carpinifolium.—5: A. ukurunduense.—6 and 7: A. nipponicum.—6: Matured pericarp.—7: Pericarp of sterile fruit.

Because, A. rufinerve, A. rubescens and A. morifolium are included in section *Macrantha*, which differs in several other characters from the section *Spicata*. And also A. pycnanthum and A. rubrum belong to the section Rubra. The section *Spicata* has generally been treated as a natural group. But the writer considers that this section (sensu ampl.) is composed of several primitive groups.

In the matured pericarp of *A. nipponicum*, the fibrous tissues are obscure. But in the pericarps of the sterile fruits or in the young pericarps, the fibrous tissues are visible. Thus the pericarp of *A. nipponicum* belongs to the same pattern group as that of *A. rufinerve*. In the matured pericarp of *A. nipponicum*, the testa and the pericarp closely contact with each other. Therefore, the embryo seems to be covered with one coat. Although the structure of the pericarp is not always distinct, it may be used as the prominent character of defining species or sections.

The mechanical strength of a hard locule chiefly depends on the ligneous sclerenchyma or on the fibrous tissue. The layer of the ligneous sclerenchyma is next to the fibrous tissue.

The vascular bundle lies in the parenchyma. In *A. mono* there are some plants which have thick parenchyma. In such plants the vascular bundle is found near the upper portion, but in *A. cappadocicum* it is found in the middle or lower portion. As for the nervation on a locule, the veins are numerous and fine in *A. mono*, and are obscure and thick in *A. cappadocicum*. In *A. miyabei* they are scarcely distinguishable. The nervation on the locule is an important specific character. It is, however, difficult to describe this character.

Seed: The seed has neither endosperm nor aril.

In some groups the outer layer of their testa consists of a layer of large cells. The cells of A. rufinerve are orange-red and the largest. Those of A. crataegifolium and its allies are a little smaller. Such cells are not observed in A. carpinifolium, A. negundo and A. cissifolium. The cells of A. campestre, A. miyabei, A. cappadocicum, A. platanoides, A. mono, A. truncatum and A. mayrii are orange-yellow and small. These cells are preserved even in the remains of Pleistocene or Pliocene.

The writer also considers the folding manner of the cotyledons to be important, following Pax's opinion (1885). The cotyledons of A. glabrum, A. rufinerve, A. rubescens, A. morifolium, A. nipponicum, A. velutinum, A. herdreichii, A. trautvetteri, A. opalus, A. buergerianum, A. oblongum, A. nikoense, A. griseum, A. diabolicum and A. macrophyllum are incumbent and circinate perpendicularly, those of A. palmatum, A. sieboldianum, A. japonicum, A. pseudosieboldianum, A. tenuifolium, A. shirasawanum, A. circinatum and the related species are incumbent and circinate horizontally, and those of A. carpinifolium, A. negundo, A. ginnala, A. crataegifolium, A. spicatum, etc., are accumbent (Fig. 8).

As for the external form of the locule, the following features are distinguished: plane (e.g. A. mono), somewhat plane (e.g. A. pectinatum), somewhat convex (e.g. A. miyabei), convex (e.g. A. rufinerve), keeled convex (e.g. A,





Fig. 7. Structure of pericarp.—1: The pericarps of A. barbinerve, A. tetramerum and A. acuminatum are similar to the pericarp of A. stachyophyllum.—2: The pericarps of A. capillipes, A. tegmentosum, A. kawakamii and A. insulare are similar to the pericarp of A. pectinatum.—3: The pericarps of A. morifolium and A. rubescens are similar to the pericarp of A. rufinerve.—4: The pericarps of A. spicatum and A. caudatum are similar to the pericarp of A. uhurunduense.—5: The pericarp of A. rubrum is similar to that of A. pycnanthum.—6: The pericarps of A. herdreichii and A. trautvetteri are similar to the pericarp of A. velutinum.—7: The pericarps of A. semenovii and A. aidzuense are similar to the pericarp of A. spicatum, A. semenovii and A. aidzuense are similar to the pericarp of A. spicatum, A. japonicum, A. tenuifolium, A. pseudosieboldianum, A. sieboldianum, A. circinatum, A. ishidoyanum, A. palmatum ssp. amoenum and A. palmatum ssp. matsumurae are similar to the pericarp of A. palmatum.—9: The pericarp of A. griseum is similar to that of A. nikoense.

; Fibrous Cells.

oblongum), nodose (e.g. A. velutinum) and reticulately sculptured (e.g. A. argutum). These are the important taxonomic characters. The same external form of the locule occurs polytopically in several taxonomic groups. For instance, both A. argutum and A. nikoense have ligneous pericarps. But they are distinguished from each other by many other characters. For example, concerning the anatomical characters of the pericarps, they are not equal to.

The feature of the disc is an important taxonomic character. Though there-



Fig. 8. Folding manners of cotyledons.—1: A. buergerianum.—2: A. rufinerve. —3: A. micranthum.—4: A. palmatum.—5: A. japonicum.—6 and 7: A. carpinifolium.—8 and 9: A. nikoense.

are only three types (extrastaminal, intrastaminal and without disc) the groups gathered by these characters differ from one another also in many other characters. So we consider the feature of the disc to be phylogenetically important.

Quantitative taxonomic characters: WOODSON (1947) succeeded in the classification of the genus Asclepias by means of a statistic analysis of the shape of the leaf. DING HOU (1955) applied this method to the genus Celastrus. The present writer treated some quantitative taxonomic characters of Acer by the statistic method.

The size of a samara and the ratio of the length of the locule against that of a wing were used as the characteristics in the key to the species. Although these features are often used for the identification of the species, they are not so decisive, in view of that they are quantitative and not qualitative. The quantitative characters may only be safely used in combination with the other characters. Their value as the taxonomic character depends on their frequency in a group.

Fruit: The length of the fruit and of the locule were examined in *A. mono.* Though the feature is variable within a single species, the ratio of the length of a locule to that of a wing can be used as a fixed character in classifying this species into several groups. In the measurement, the correlation coefficient of the two lengths was about 0.7. The correlation coefficient of a individual was 0.72: n=43. The ratio is useful for taxonomy, being measurable even on immature fruits.

The shape of the wings and the angle between the wings have been used as the specific characters. In some species these characters are not always constant. They are, however, fixed individually even there. The correlation coeficient of the width of the widest part and of the base of the wing is generally less than that of the lengths of the locule and the wing. In *A. cappadocicum* var. *indicum*, the correlation coeficient of the lengths of the locule and the wing is 0.88, and that of the width is 0.71. Thus the character of the width is inferior to that of the length as for constancy.

The mean value of the angles between the wings of A. mono is about 90° , the standard deviation of the angles is 15. So this character can not be used. But the corresponding value of A. miyabei is 185° , the standard deviation is 5. The character is, therefore, usefull in this species. But the characters of the lengths of locule and wing as well as of the width of wing are more important. Frequent distribution curve of the angles of a tree is not bilateral symmetry.

Leaf: Sometimes for the key within the genus *Acer*, the length and the width of a leafblade, the length of a petiole and their relative ratios are used. The writer treats these quantities as in fruits. The adult leaves are measured. The leaves of a long shoot or of an adventitious shoot (*A. ambiguum* DIPPEL non HEER was based upon the leaves of such shoot) or of a young tree are

avoided, because they are much different from the usual adult leaves.

The mean value of the leaves of the upper branches differs from that of the lower branches of the same tree, and also that of the leaves of the southern side differs from that of the northern side of the same tree. The mean value of the ratio of the length to the width of the leafblade of *A. mono* is about 0.9, the standard deviation is about 0.1. Generally, the relative ratio of the length to the width of the leafblade is not adequate for a distinguishing character. Nevertheless, the description of the ratio serves for the identification of species. For example, PAX's descriptions (1885) "latiora quamlonga" of *A. lobelii* subsp. *laetum* var. *indicum* and "aeque longa ac lata" of var. *colchicum* are valuable.

Petal and sepal: The comparison of the lengths between a sepal and a petal is described in most species. Unless ramarkable difference in length exists, this comparison is not useful. For example, the petals of A. micranthum are remarkably longer than the sepals. In this case, the difference is useful for identification. The petals and sepals of A. mono and A. cappadocicum were described both as "petala quam sepala equilonga" (by PAX and KOIDZUMI) or "petala quam sepala longiora" (by PAX). MAXIMOWICZ and GLEDITSCH did not describe them. In such cases, the difference is not acceptable for taxonomy. In A. mono and A. cappadocicum var. indicum, the petals are shorter than the sepals at the beginning of anthesis and the petals are longer than the sepals at the end of anthesis. On the scatter diagram of the correlation of length between sepals and petals, the line which corresponds to the regressive line makes a curve. During the anthesis, the petal elongates considerably, while it does not widen, so the ratio of the length to the width of the petal changes from 2:1 to 3:1.