Taiwania, **47**(3): 203-218, 2002

Phylogeny and Historical Biogeography of *Acer* I—Study History of the Infrageneric Classification[1]

Shing-Fan Huang[2,4], Robert E. Ricklefs[2], Peter H. Raven[3]

(Manuscript received 30 July, 2002; accepted 5 September, 2002)

ABSTRACT: Historical biogeography is a study of taxa in time and space including their origin, migration and diversification. This kind of study requires fossil data and an understanding of phylogenetic relationships. These requirements make *Acer* a good model to study because *Acer* 1) has a relatively complete fossil record, 2) contains many species, 3) is a major northern temperate floristic element, and 4) is well known. Because fossils are only confidently assigned to section or species group, section as a unit is suitable for tracing evolutionary history of *Acer*. However, the circumscription of section of *Acer* is different to each classification through the long history of studies. This work reviews and summarizes the studying history of *Acer*. Delendick in 1981concluded that the system of Ogata in 1967 and that of Jong in 1976 were superior to others except that most Jong's series should be raised to section. This work, therefore, follows Delendick's delineation of section except *Distyla* and *Parviflora*, which are combined as *Parviflora*, to elucidate the development of the circumscription of section based on the system of Pax in 1885 and 1886, Pojarkova in 1933, Momotani in 1962, Fang in 1966, Ogata in 1967, Murray in 1970, Jong in 1976, Delendick in 1990 and Xu in 1996.

KEY WORDS: *Acer*, **Infrageneric classification, Study history.**

INTRODUCTION

Historical biogeography is a study of the history of taxa in time and space including their origin, migration and diversification and explains how geological events or change of climate have shaped the distribution pattern of the extant taxa (Brundin, 1988; Myers and Giller, 1988). Revealing the history of a taxon that is dominant of a certain kind of vegetation, therefore, may provide insight for the history of the vegetation.

Plants of *Acer* are among the dominant temperate deciduous trees in Northern Hemisphere (Latham and Ricklefs, 1993). The habitats of northern temperate deciduous forest are now mainly in eastern North America (ENAM), eastern Asia (EAS) and western and central Europe where summer rain are maximum and the cold season is relatively short (Walter, 1973). This leads to the disjunctive distribution in northern temperate deciduous forest flora. The widely accepted process that explains the floristic similarity between disjunctive areas is that they are derived from common ancestor through floristic exchange between continents by ways of continental drift, land bridges and long-distance dispersal (Brown and Lomolino, 1998; Cox and Moore, 1993). Determination of the sister relationship of taxa in both disjunctive areas is the first step in studying disjunction (Raven, 1972). Thus a reconstructed phylogeny is required and the phylogeny may, especially, be revealed by molecular data (Avise, 1994; Hillis *et al.* 1996; Li, 1997; Riddle, 1996; Soltis *et al.* 1998). Two land bridges

1. Part of the doctoral thesis of the first author.
2. Department of Biology, University of Missouri-St. Louis, St. Louis, U.S.A.
3. Missouri Botanical Garden, St. Louis, U.S.A.
4. Corresponding author.

have been proposed to be responsible in contributing intercontinental exchange of the flora in the northern temperate areas. One is the Beringia and the other is the early Tertiary Atlantic land bridge (Hopkins, 1967; Manchester, 1999; McKenna, 1975; Raven, 1972; Taylor, 1990; Tiffney, 1985a, 1985b; Wolfe, 1975). Based on molecular phylogeny, conclusions have been made that the disjunctive pattern between EAS and NAM (North America) might have involved multiple historical events at very different geological times in different genera (Xiang *et al.* 1998; Wen, 1999). So the question for explaining disjunction is when and from which land bridge and by which mechanism does certain lineage have intercontinental exchange. Fossils are the direct evidence to reveal minimum age of certain lineage while they do not clearly reveal the relationship among organisms due to the incompleteness of the records (Manchester and Tiffney, 2001). In contrast, molecular data provide a robust hypothesized phylogeny and the molecular clock provides a way for estimating the timing of cladogenetic events (Avise, 1994; Li, 1997). The calibration of the timing of branching events from the reconstructed phylogeny is always assisted by applying the timing of geological events and the date of fossil records (Brown and Lomolino, 1998; Sanderson, 1998). Without fossils, the calibration of the timing will have no basis. Thus to trace a history of certain taxon requires the incorporation of fossils and phylogeny (Manchester and Tiffney, 2001; Tiffney and Manchester, 2001).

The genus *Acer* contains about 150 species in the northern temperate regions (Delendick, 1990; Gelderen *et al.* 1994). This genus is characterized by woody habit, opposite leaves, disc-nectar flower mainly with 8 stamens and two-carpelled, knife-shape-winged schizocarps. Because the leaves and fruits of *Acer* are relatively easy for recognition and many fossil leaves and fruits are well preserved through geological ages, there have been considerable works on fossil *Acer* and abundant fossil *Acer* are recognized (Boulter *et al.*, 1996; Mai 1995; Tanai 1983; Walther, 1972; Wolfe and Tanai, 1987). Thus there is potential to elucidate the intercontinental exchanges of this genus through Tertiary (Wolfe and Tanai, 1987; Manchester, 1999). However, without reliable phylogeny to reveal the relationship among the lineage, the proposed history may not correctly reflect the true history. Unfortunately, although the genus *Acer* has recieved much attention by many researchers, either carried out revisions (Delendick 1981, 1990; Gelderen *et al.*, 1994; Jong, 1976; Momotani, 1962b; Murray, 1970a; Ogata, 1967; Pax, 1885, 1886, 1902; Pojarkova, 1933; Wolfe and Tanai, 1987; Xu, 1996, 1998) or used certain evidence to examine or modify previous classification (Delendick, 1981, 1990; Jong, 1976; Mai, 1983, 1984; Momotani, 1962a; Ogata, 1967; Santamore, 1982; Tanai, 1978a, 1978b), the circumscription of sections are not consistent and the relationships among sections are not yet completely resolved. Further studies on the phylogeny of *Acer* are still needed. Recently, independent researches on the phylogeny of *Acer* based on molecular data had been carried out (Ackerly and Donoghue, 1998; Hasebe *et al.*, 1998; Suh *et al.,* 1996; Suh *et al.,* 2000; Pfosser *et al.*, 2002) either using markers of intertranscribed spacer (ITS) of nuclear ribosome DNA (nDNA), restriction fragment-length polymorphism (RFLP) of chloroplast DNA (cpDNA), or *trn*L intron and *trn*L-F intergenic spacer (IGS) (Pfosser *et al.,* 2002). Their works shed light on resolving the relationships among sections, but the resolution among sections is still poorly supported. Besides their works all suffer the problem of sampling regarding the representation of the genus. Thus a work to integrate all the available data to reconstruct a phylogeny in its entirety is needed.

Because only sections or species groups are confidently recognized in the fossil data of *Acer* (Manchester, 1999), section as a unit is suitable to trace evolutionary history of *Acer*. However, the circumscription of section is different to each classification through the long

history of studies of *Acer*. Therefore, the aim of this work is (1) to summarize the studying history of *Acer* and (2) to elucidate the development of the circumscription of section. In this way, later studies can be carried out by taking sections as hypothesized units and examine whether they are monophyletic groups, which represent common histories of species. Once the section is confirmed to be monophyletic, it then can be used as a unit to reconstruct the phylogeny, to elucidate the historical biogeography and to trace the evolutionary history.

Study history of the infrageneric classification

The genus *Acer* was established by Tournefort in 1719 (Jong, 1976). Linneaus (1763) cited 10 species, i.e., *A. tataricum, A. pseudoplatanus, A. rubrum, A. saccharinum, A. platanoides, A. pennsylvanicum, A. campestre, A. monspessulatum, A. creticum* (=*A. orientale*) and *A. negundo* in his book entitled 'Species Plantarum'. Among them, *A. pseudoplatanus* is considered as the type species of this genus. Since then, some important systematic studies were carried out by Lauth in 1781, Thunberg in 1793 and Spach in 1834 (Jong, 1976). Owing to the leaves being pinnate and the flowers without disk-nectar, *A. negundo* was considered to be a distinctive genus by earlier botanists such as Boehmer in 1760, de Candolle in 1824, Bentham and Hooker in 1862 (Ogata, 1967).

It was Pax (1885, 1886, 1902) who studied this genus in its entirety and laid a foundation for the later studies. He classified *Acer* into four groups, 13 sections and 17 series. His groups were based on the position of the nectar disk in flower. For example, the stamens inserting inside the disk named *Extrastamina*, inserting at the margin of the disk named *Intrastamina*, and inserting in the middle of the disk named *Perigyna*, and the absence of the disk named *Adiscantha*. Sections are then recognized within each group mainly by the features of leaves, such as compound vs. simple, and 1-3-lobed vs. 3-plural lobed. Four sections such as *Palmata*, *Rubra*, *Spicata*, and *Trifoliata* were placed in *Extrastamina*; section *Negundo* in *Adiscantha*; section *Indivisa* in *Intrastamina*; sections such as *Campestria*, *Glabra*, *Lithocarpa*, *Macrantha*, *Platanoidea* and *Saccharina* in *Perigyna*. Four series were proposed under section *Spicata*, namely, *Caudati*, *Spicati*, *Tatarici* and *Trifidi*.

Rehder (1905), studying the Chinese species of *Acer*, established a new section, *Arguta*. Later on, he (Rehder, 1941) followed Pax' s treatment but treated *Acer* into two sections, *Acer* and *Negundo,* by reducing Pax's and his section to series.

Koidzumi (1911) revised the species of *Acer* from Japan, the Ryukyu, Taiwan and Sakhalin and proposed some new sections, i.e., *Carpinifolia*, *Cissifolia, Diabolica* (=*Lithocarpa*), *Palmatoidea* (=*Micrantha*, included in *Macrantha*), and *Parviflora*. The former three sections were separated from Pax's sections *Indivisa*, *Trifoliata* and *Lithocarpa* respectively and the later two sections were separated from Pax's *Macrantha*. He also recognized two sectional groups, *Extrastamina* and *Intrastamina* by the position of the nectar disk.

Nakai (1915) revised the Korean species of *Acer* and proposed a new section, *Ginnala*, which was a synonym of the series *Tatarici* Pax. He recognized 3 subgenera, i.e. *Extrastamina*, *Amphistamina* and *Intrastamina*, by the position of the nectar disk.

Metcalf (1932), studying the Chinese species of *Acer* that belonged to the section *Integrifolia* sensu Pax, proposed two new series *Penninervia* and *Trinervia* to accommodate the species with entire leaf margin. The latter contains basal leaf venation forming tri-nerves and the former contains basal leaf veins not forming tri-nerves.

Pojarkova (1933) was the first person to criticize Pax's sections being heterogeneous without showing monophyly of the species group by mentioning the change of the

circumscription of section treated by Koidzumi (1911) and Nakai (1915). She also used the leaf anatomy studied by Warsaw in 1903 as evidence to prove the heterogeneity of Pax's section. Thus she proposed her own series and sections to accommodate species groups and related them in an evolutionary manners. She thought that there were two evolutionary lines in *Acer*. Therefore, the genus was classified into two groups, 17 sections and 32 series. Some new sections such as *Gemmata* (=*Acer*), *Goniocarpa*, *Microcarpa* (=*Spicata* plus *Sinensia p.p.*), *Trilobata* (=*Ginnala* plus *Integrifolia p.p.* and *Pubescentia*) and many new series were proposed such as *Crataegifolia, Grisea, Macrophylla, Manshurica, Micrantha, Monspessulana, Oblonga, Opulifolia, Picta*, *Pubescentia*, *Quinqueloba*, *Sinensia*, *Tegmentosa, Trautvetteriana*, *Velutina* and *Villosa*. Section *Platanioidea* and *Lithocarpa* were considered primitive by her and they evolved into two different lineages within *Acer*. They were primitive because their morphologies, i.e. lactiferous petiole and amphistaminate nectar-disk, were more similar to those from Sapindaceae, from which Aceraceae (includes *Acer* and *Dipteronia*) supposedly evolved. Since she considered her species groups shared the same history, thus she emphasized the use of series as a unit to discuss biogeography and evolution.

Hu and Cheng (1948), revising the Chinese species of *Acer*, proposed a new section *Pentaphylla* to accommodate the species *A. pentaphyllum* from south western China, and a new subsection *Decandra* to accommodate *A. decandrum* from Hainan, South China.

Momotani (1962a, 1962b) used seed proteins as markers to reconstruct the phylogeny of *Acer* and he classified *Acer* into three subgenera, 15 sections and 27 series. Aside from the conventional two groups proposed by Rheder (1949), *Acer carpinifolium*, belonging to *Indivisa*, was considered distinctive and was raised to a subgeneric status. He proposed a new series *Rufinervia* within section *Macrantha*. He also transferred section *Microcarpa* (=series *Sinensia*) under section *Palmata*.

Fang (1966, 1981) modified Pax's system by considering that the leaf character was more important than the position of the nectar disk. Thus he recognized two subgenera, *Acer* and *Negundo*, representing the lineage of simple and compound leaves. His system included 19 sections and 31 series. *Hyptiocarpa* was a new section proposed to accommodate *A. machilifolium* and *A. decandrum*. He also proposed many new series such as *Miaotaiensia*, *Fulvescentia*, *Catalpifolia*, *Pseudosieboldiana*, *Robusta*, *Buergeriana* and *Machilifolia*, but most of them were treated as synonyms by later researchers.

Not satisfied with the work of Momotani (1962b) due to the lack of entirety in studying the genus *Acer*, Ogata (1967) revised this genus based on the evidences of morphology, embryo and wood anatomy. Instead of nectar disk, he emphasized the number of bud scales and the inflorescence types for grouping species. He recognized six groups, 23 sections and 30 series. He illegally published a new section, *Syriaca*, as he put 'nom. provis.' after the new name. Plants of *Syriaca* were not familiar to him but distinguishable by the character of bud scales. He transferred the species of *Integrifolia* sensu Pax under 4 sections, i.e. *Integrifolia*, *Lauriana*, *Decandra* and *Palmata*. He did not cite *Hyptiocarpa* because he did not know Fang's work then. *Laurina* and *Decandra* were considered synonyms of *Hyptiocarpa* (Jong, 1976; Delendick, 1990). His sections except *Syriaca* were followed by many later researchers. He considered *Macrantha* as the most primitive section because it was in the supposed primitive group including *Distyla*, *Parviflora*, and *Spicata*, and it also contained relatively abundant species. This thinking may be influenced by Willis (1922) that the older the taxon the more diversified the taxon. He claimed that it was hard to postulate the relationships among sections because the linkages among sections were lost due to the long history of this genus.

Murray (1969, 1970a, 1970b, 1970c, 1970d, 1971a, 1971b, 1974, 1975, 1977, 1978, 1979), using morphological data only, classified *Acer* into seven subgenera, 24 sections and 35 series. His work collected all the names, including extant and fossil plants, and tried to delimit the species and species group's boundaries. By studying specimens, his species circumscription was broad due to combining many species into one species while species group's circumscription was narrow as he recognized many series. This reflects the fact that morphological variation is broad within the whole genus but variation is continuous within some entities. Because his classification is for taxonomic purpose, no attempt was made to relate these species groups. He proposed a new series, *Tonkinensia*, under section *Palmata*.

Jong (1976), emphasizing flower structure and sex expression, recognized 14 sections and 24 series. He compared the extant species of *Acer* with those from Sapindaceae and proposed the prototype of *Acer* and considered *Parviflora* (includes *Distyla*, *Parviflora* and *Spicata*), and *Palmata* to be the most primitive. Though he did not recognize any groups among these sections, he pointed out that *A. carpinifolium* might be distinctive from the others by its leaf venation. He proposed a new series, *Wardiana*, accommodating *A. wardianum*, under *Macrantha*. Later on, he (Jong, 1990; Jong, 1994) reviewed evidence especially from the chemical work of Delendick (1981, 1990) and proposed a revised system, mainly following his system proposed in 1976 except raising *Wardiana* to section and considered it to be intermediate between *Palmata* and *Macrantha*. Because characters of *Wardiana* such as bud scale is similar to *Macrantha*, while its fruit is similar to *Palmata* (Mai, 1984). However, Delendick (1990) rejected such arrangement and move its component species, *A. wardianum*, to the section *Palmata*. The authors agrees to move *A. wardianum* to *Palmata* because the flower is similar to *Palmata*, for example, brown petals and extrastaminate nectar (refer Fang, 1981).

Tanai (1978a, 1978b), a paleobotanist, studied the evidence of the leaf terminal venation of *Acer* and claimed that his evidence was most consistent with Ogata's (1967) system except the section *Syriaca*. He recognized two types of venation. One is recognized by the terminal veinlets being branched and the other is recognized by the terminal veinlets being forming anastomy or free but not branched. Thus *Integrifolia* and *Palmata* sensu Ogata (1967) can be easily distinguished by venation types of leaves. The terminal veinlets in the former are forming anastomy while those of the later are branched.

Delendick (1981, 1990) thoroughly reviewed the literature and classifications of the genus *Acer* and provided some new evidence such as leaf texture, pollen, germination type of seed, shape of cotyledon and especially chemical compounds (flavonoid) to examine the classifications proposed by earlier researchers. He concluded that Ogata's and Jong's systems were superior to others but many of Jong's series should be raised to sections. He accepted 21 sections and 23 series, which he classified into five groups using diverse evidence besides chemistry. Unfortunately, chemical compounds alone did not reveal clear relationship of each section.

Following the delineation of sections and series of Jong (1976), Mai (1983, 1984) used only fruit character to propose a classification of *Acer* and found it useful in delineating sections and series. He proposed four subgenera, 17 sections and 30 series.

Wolfe and Tanai (1987) reviewed the previous works and used morphology, especially variation of leaf terminal venation and fruit types, and anatomical characters to study the phylogeny of *Acer* including fossil and extant species. They classified extant species into four groups, 19 sections, and 21 series. The circumscription of the extant sections or series was based on those of Ogata (1967). They also discussed the evolutionary trend of characters and

proposed a prototype of *Acer*. They listed the primitive character state for 94 characters but they did not provide a data matrix for the entire genus. They recognized many fossil sections and thought that extant *Spicata* was the most primitive group.

Xu (1996) proposed a classification based on morphology. His system was influenced by Fang (1966, 1981), Ogata (1967) and Murray (1970a). He recognized four subgenera, 23 sections, 33 series and 200 species. Although he discussed the possible evolutionary trend of the morphological characters, he did not mention the works of Jong (1976) and Delendick (1981, 1990). He dismissed section *Spicata* and transferred its component species either under series *Tonkinense* of section *Microcarpa* or section *Rubra* separately. His circumscription of the series or section is not consistent with other authors after Ogata (1967).

Hasebe *et al.* (1998) reconstructed the phylogeny of *Acer* based on RFLP cpDNA. They sampled 64 species representing 17 sections sensu Ogata (1967) without the samples representing *Glabra*, *Hyptiocarpa*, *Indivisa*, *Macrophylla* and *Pentaphylla*. Their results showed that the delineation of sections were consistent with Ogata's system while relationships among sections could not be resolved.

Ackerly and Donoghue (1998) proposed a relationship among the sections of *Acer* based on ITS nDNA. Following Jong's (1994) sectional concept, 32 species were sampled representing most sections except *Pentaphylla*, *Hyptiocarpa* and *Trifoliata*. Their results showed that most sections were well defined except that *Palmata* should included *A. oblongum* that belongs to the section *Integrifolia* sensu Ogata (1967). However, the name associated with this sample was corrected as *A. fabri* that belongs to *Palmata* later by Suh *et al.* (2000). Thus the ITS data are consistent with the traditional grouping. A new finding of this work is that *A. rubrum, A. saccharinum* and *A. saccharum* form a clade while traditional thinking is that *A. saccharum* is better grouped with sections *Goniocarpa* and *Acer*. Suh *et al.* (2000) also used ITS to reconstruct the phylogeny of *Acer*. They filled the sampling gap of Ackerly and Donoghue (1998) by including species belonging to *Pentaphylla*, *Hyptiocarpa* and *Trifoliata*. A total of 28 species representing 14 sections sensu Jong (1994) were sampled. Basically, sectional delineation was consistent with traditional treatment except *A. argutum*, belonging to *Arguta*, was nested within *Macrantha*. Since this work did not incorporate the work of Ackerly and Donoghue (1998), further study based on ITS to incorporate all the samples is needed.

In order to study the origin of endemic species of *Acer* from small island in South Korea, Pfosser *et al.* (2002) reconstructed the phylogeny of *Acer* based on *trn*L intron and *trn*L-F intergenic spacer (IGS) cpDNA. They sampled 57 species representing 14 sections sensu Delendick (1990) without the samples representing *Glabra*, *Hyptiocarpa*, *Macrophylla*, *Negundo*, *Pentaphylla*, *Pubescentia*, *Rubra* and *Saccharina*. Using maximum parsimonious criterion and taking indels as additional characters, some sections were not consistent with traditional treatment, such as *Arguta*, *Ginnala* and *Lithocarpa*. The resolution between sections is poorly supported. A new finding of this work is that the traditional sister genus *Dipteronia* is nested within the clade *Acer*. However, we should be careful about this result since the delineation of some sections is away from the traditional ones while ITS nDNA and RFLP cpDNA are not.

Circumscription of the section of *Acer*

The following is the summary of the circumscription of section from the classification of Pax (1885, 1886), Pojarkova (1933), Momotani (1962b), Fang (1966), Ogata (1967), Murray (1970), Jong (1976), Delendick (1990) and Xu (1996). The standard circumscription of

section follows that of Delendick (1990) except *Distyla* and *Parviflora* that are combined as *Parviflora.*

Acer Sect. ***Acer*** Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 184. 1962; Fang in Acta Phytotax. Sinica 11(2): 150. 1966, p.p. excl. *A. macrophyllum*; Ogata in Bull. Tokyo Forests 63: 138. 1967; Murray in Kalmia 2: 5.1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 136.1976, p.p., excl. Ser. *Monspessulana* & *Saccharodendron*; Delendick in Mem. New York Bot. Gard. 54: 93. 1990; Xu in Acta Bot. Yunnanica 18(3): 283. 1996.

Acer Sect. *Gemmata* Pojarkova in Flora Syst. Pl. Vasc. 1: 236 & 312. 1933.
Acer Sect. *Spicata* Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p. quod est *A. caesium*, *A. helderichii*, & *A. pseudoplatanus*.

Acer Sect. ***Arguta*** Rehder in Sargen, Trees and Shrubs 181. 1905; Pojarkova in Flora Syst. Pl. Vasc. 1: 240 & 366. 1933; Fang in Acta Phytotax. Sinica 11(2): 181. 1966; Ogata in Bull. Tokyo Forests 63: 125. 1967; Murray in Kalmia 2: 6. 1970; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 290. 1996.

Acer Sect. *Glabra* Ser. *Arguta* (Rehder) Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 180. 1962; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 152.1976.
Acer Sect. *Indivisa* Pax in Engler, Bot. Jahrb. 7: 213. 1886, p.p., quod est *A. stachyophyllum*.
Acer Sect. *Lithocarpa* Pax in Engler, Bot. Jahrb. 7: 249. 1886, p.p., quod est *A. argutum*, *A. barbinerve* & *A. tetramerum*.

Acer Sect. ***Cissifolia*** Koidzumi in J. Coll. Sci Imp. Univ. Tokyo 32(1): 26. 1911; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Fang in Acta Phytotax. Sinica 11(2): 188. 1966; Ogata in Bull. Tokyo Forests 63: 128. 1967; Murray in Kalmia 2: 6. 1970; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 290. 1996.

Acer Sect. *Negundo* Ser. *Cissifolia* (Koidzumi) Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 188. 1962; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 151.1976.
Acer Sect. *Trifoliata* Pax in Engler, Bot. Jahrb. 7: 203. 1886, p.p., quod est *A. cissifolium*.

Acer Sect. ***Ginnala*** Nakai in Bot. Mag. Tokyo 29(339): 25. 1915; Fang in Acta Phytotax. Sinica 11(2): 151. 1966; Murray in Kalmia 2: 6. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 145.1976; Delendick in Mem. New York Bot. Gard. 54: 92. 1990; Xu in Acta Bot. Yunnanica 18(3): 284. 1996.

Acer Sect. *Spicata* Pax Ser. *Tatarica* Pax in Engler, Bot. Jahrb. 7: 182. 1886.
Acer Sect. *Trilobata* Pojarkova in Flora Syst. Pl. Vasc. 1: 324. 1933, p.p. excl. Ser. *Trifida*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 182. 1962; Ogata in Bull. Tokyo Forests 63: 129. 1967.

Acer Sect. ***Glabra*** Pax in Engler, Bot. Jahrb. 6:327. 1885; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 180. 1962, p,p., excl. Ser. *Arguta*; Murray in Kalmia 2: 6. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 152. 1976, p.p., excl. Ser. *Arguta*; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 284. 1996.

Acer Sect. ***Goniocarpa*** Pojarkova in Flora Syst. Pl. Vasc. 1: 347. 1933; Ogata in Bull. Tokyo Forests 63: 139. 1967; Murray in Kalmia 2: 6. 1970; Delendick in Mem. New York Bot. Gard. 54: 93. 1990; Xu in Acta Bot. Yunnanica 18(3): 283. 1996, p.p., excl. Ser. *Pubescentia*.

Acer Sect. *Acer* Ser. *Monspessulana* (Pojarkova) Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 137. 1976.
Acer Sect. *Campestria* Pax in Engler, Bot. Jahrb. 7: 219. 1886, p.p., quod est *A. italum, A. monspessulanum, A. obtusatum, A. orientale, & A. syriacum.*
Acer Sect. *Platanoidea* Pax Ser. *Monspessulana* (Pojarkova) Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 185. 1962.
Acer Sect. *Syriaca* Ogata in Bull. Tokyo Forests 63: 144. 1967.

Acer Sect. ***Hyptiocarpa*** Fang in Acta Phytotax. Sinica 11: 172. 1966; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 154. 1976; Delendick in Mem. New York Bot. Gard. 54: 94. 1990; Xu in Acta Bot. Yunnanica 18(3): 284. 1996.

Acer Sect. *Decandra* (Hu & Cheng) Ogata in Bull. Tokyo Forests 63: 153. 1967.
Acer Sect. *Integrifolia* Pax in Engler, Bot. Jahrb. 7: 207. 1886, p.p., quod est *A. niveum* (=*A. laurinum*); Pojarkova in Flora Syst. Pl. Vasc. 1: 238. 1933, p.p., quod est *A. garrettii, A. niveum & A. philippicum*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 185. 1962, p.p., quod est *A. garrettii & A. niveum.*
Acer Sect. *Laurina* Ogata in Bull. Tokyo Forests 63: 151. 1967.

Acer Sect. ***Indivisa*** Pax in Engler, Bot. Jahrb. 6: 328. 1885; Pax in Engler, Bot. Jahrb. 7: 213. 1886, p.p., excl. *A. davidii, A. distylum, A. hookeri, A. sikkimense, A. stachyophyllum & A. thomsonii*; Ogata in Bull. Tokyo Forests 63: 154. 1967; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 154. 1976; Delendick in Mem. New York Bot. Gard. 54: 91. 1990.

Acer Sect. *Carpinifolia* Koidzumi in J. Coll. Sci Imp. Univ. Tokyo 32(1): 26. 1911; Pojarkova in Flora Syst. Pl. Vasc. 1: 238. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 188. 1962; Murray in Kalmia 2:7. 1970; Xu in Acta Bot. Yunnanica 18(3): 290. 1996.

Acer Sect. ***Integrifolia*** Pax in Engler, Bot. Jahrb. 6: 327. 1885; Pax in Engler, Bot. Jahrb. 7: 207. 1886, p.p., excl. *A. cordatum, A. fabri, A. laevigatum, A. niveum, A. reticulatum*; Pojarkova in Flora Syst. Pl. Vasc. 1: 238 . 1933, p.p., excl. *A. cordatum, A. fabri, A. garrettii, A. laevigatum, A. niveum, A. philippinum & A. reticulatum*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 181. 1962, p.p., excl. *A. cordatum, A. fabri, A. garrettii, A. laevigatum, A. niveum & A. reticulatum*; Fang in Acta Phytotax. Sinica 11(2): 167. 1966, p.p., excl. *A. cordatum, A. garrettii, A. niveum, A. philippinum & A. reticulatum*; Ogata in Bull. Tokyo Forests 63: 142. 1967; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 152. 1976, p.p., excl. Ser. *Pentaphylla*; Xu in Acta Bot. Yunnanica 18(3): 285. 1996, p.p., excl. *A. cordatum, A. fabri, A. laevigatum & A. reticulatum.*

Acer Sect. *Microcarpa* Pojarkova Ser. *Buergeriana* Fang in Acta Phytotax. Sinica 11(2): 162. 1966, p.p., excl. *A. chapaense, A. fenzianum, A. liquidambarifolium & A. tonkinense.*
Acer Sect. *Oblonga* (Hu & Cheng) Delendick in Mem. New York Bot. Gard. 54: 92. 1990.
Acer Sect. *Spicata* Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p., quod est *A. coriaceum, A. paxii & A. trifidum* (=*A. buergerianum*)

Acer Sect. ***Lithocarpa*** Pax in Engler, Bot. Jahrb. 6: 328. 1885; Pax in Engler, Bot. Jahrb. 7: 249. 1886, p.p., excl. *A. argutum, A. barninerve & A. tetramerum*; Pojarkova in Flora Syst. Pl. Vasc. 1: 236. 1933, p.p., excl. Ser. *Macrophylla*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 187. 1962; Fang in Acta Phytotax. Sinica 11(2): 177. 1966; Ogata in Bull. Tokyo Forests 63: 147. 1967; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 150. 1976, p.p., excl Ser. *Macrophylla*; Delendick in Mem. New York Bot. Gard. 54: 94. 1990; Xu in Acta Bot. Yunnanica 18(3): 290. 1996.

Acer Sect. *Sterculiacea* Murray in Kalmia 2: 7. 1970.

Acer Sect. ***Macrantha*** Pax in Engler, Bot. Jahrb. 6: 328. 1885; Pax in Engler, Bot. Jahrb. 7: 244. 1886, p.p., excl. *A. parviflorum* (=*A. nipponicum*); P' arkova in Flora Syst. Pl. Vasc. 1: 238 & 344. 1933, p,p., excl. *A. distylum*, A. *parviflorum* & *A. wardii*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 150. 1962, p.p., excl. *A. wardii*; Fang in Acta Phytotax. Sinica 11(2): 173. 1966, p.p., excl. *A. distylum* & *A. wardii*; Ogata in Bull. Tokyo Forests 63: 111. 1967, p.p., excl. *A. wardii*; Murray in Kalmia 2: 7. 1970, excl. *A. wardii*; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 143. 1976, excl. Ser. *Wardiana*; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 286. 1996, p.p., excl. *A. wardii*.

Acer Sect. *Indivisa* Pax in Engler, Bot. Jahrb. 7: 213. 1886, p.p., quod est *A. davidii*, *A. hookeri* & *A. sikkimense*.

Acer Sect. ***Macrophylla*** (Pojarkova) Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 180. 1962: Ogata in Bull. Tokyo Forests 63: 138. 1967; Murray in Kalmia 2: 7. 1970; Delendick in Mem. New York Bot. Gard. 54: 94. 1990; Xu in Acta Bot. Yunnanica 18(3): 287. 1996.

Acer Sect. *Lithocarpa* Pax Ser. *Macrophylla* Pojarkova in Flora Syst. Pl. Vasc. 1: 236. 1933; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 150. 1976.
Acer Sect. *Spicata* Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p., quod est. *A. macrophyllum*.

Acer Sect. ***Negundo*** (Boehmer) Maximowicz in Bull. Acad. Imp. St. Petersburg. 26: 450. 1880; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Fang in Acta Phytotax. Sinica 11(2): 188. 1966; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 181. 1962, excl. Ser. *Cissifolia*; Ogata in Bull. Tokyo Forests 63: 126. 1967; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 151. 1976, p.p., excl. Ser. *Cissifolia*; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 291. 1996.

Acer Sect. ***Palmata*** Pax in Engler, Bot. Jahrb. 6: 326. 1885; Pax in Engler, Bot. Jahrb. 7: 198. 1886; Pojarkova in Flora Syst. Pl. Vasc. 1: 238. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 181. 1962; Fang in Acta Phytotax. Sinica 11(2): 143; Ogata in Bull. Tokyo Forests 63: 121. 1967; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 141.1976, p.p., excl. *A. crassum*, *A. lucidum* & *A. sino-oblongum*; Delendick in Mem. New York Bot. Gard. 54: 92. 1990; Xu in Acta Bot. Yunnanica 18(3): 288. 1996.

Acer Sect. *Integrifolia* Pax in Engler, Bot. Jahrb. 7: 207. 1886, p.p., quod est *A. fabri, A. laevigatum* & *A. reticulatum*; Pojarkova in Flora Syst. Pl. Vasc. 1: 238. 1933, p.p., quod est *A. cordatum, A. fabri, A.* laevigatum & A. reticulatum; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 185. 1962, quod est *A. cordatum, A. fabri, A. dimorphifolium, A. laevigatum* & *A. reticulatum*.
Acer Sect. *Macrantha* Ser. *Wardiana* Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 144.1976.
Acer Sect. *Microcarpa* Pajarkova Ser. *Sinensia* Pojarkova in Flora Syst. Pl. Vasc. 1: 325. 1933, p.p., excl. *A. hypoleucum* & *A. litsaefolium*; Fang in Acta Phytotax. Sinica 11(2): 150. 1966, p.p., excl. *A. nipponicum* & *A. pentapomicum*.
Acer Sect. *Microcarpa* Pojarkova: Murray in Kalmia 2: 7. 1970; Xu in Acta Bot. Yunnanica 18(3): 287. 1996, p.p., excl. *A. chapaense* & *A. stenolobum*.
Acer Sect. *Spicata* Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p., quod est *A. oliverianum* & *A. cambelli*.

Acer Sect. ***Parviflora*** Koidzumi in J. Coll. Sci Imp. Univ. Tokyo 32(1): 11. 1911; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 181. 1962; Ogata in Bull. Tokyo Forests 63: 116. 1967; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 145.1976, p.p., excl. Ser. *Spicata*; Delendick in Mem. New York Bot. Gard. 54: 91. 1990; Xu in Acta Bot. Yunnanica 18(3): 288. 1996.

Acer Sect. *Distyla* Ogata in Bull. Tokyo Forests 63: 115. 1967; Delendick in Mem. New York Bot. Gard. 54: 91. 1990.
Acer Sect. *Distyla* Murray in Kalmia 1: 41. 1969; Xu in Acta Bot. Yunnanica 18(3): 284. 1996.
Acer Sect. *Indivisa* Pax in Engler, Bot. Jahrb. 7: 213. 1886, p.p., quod est *A. distylum*; Koidzumi in J. Coll. Sci Imp. Univ. Tokyo 32(1): 11, p.p., quod est *A. distylum*.
Acer Sect. *Macrantha* Pax in Engler, Bot. Jahrb. 7: 244. 1886, p.p., quod est *A. parviflorum* (=*A. nipponicum*).
Acer Sect. *Macrantha* Pax Ser. *Parviflora* Pojarkova in Flora Syst. Pl. Vasc. 1: 238 & 345. 1933.
Acer Sect. *Macrantha* Pax Ser. *Crataegifolia* Pojarkova in Flora Syst. Pl. Vasc. 1: 238 & 345. 1933, p.p., quod est *A. distylum*.
Acer Sect. *Spicata* Pax Ser. Parviflora: Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 150. 1962.

Acer Sect. ***Pentaphylla*** Hu & Cheng in Bull. Fan. Mem. Inst. Biol. n.s. 1: 208. 1948; Fang in Acta Phytotax. Sinica 11(2): 184. 1966; Ogata in Bull. Tokyo Forests 63: 156. 1967; Murray in Kalmia 2: 7. 1970; Delendick in Mem. New York Bot. Gard. 54: 93. 1990; Xu in Acta Bot. Yunnanica 18(3): 288. 1996.

Acer Sect. *Integrifolia* Pax Ser. *Pentaphylla* (Murray) Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 143. 1976.

Acer Sect. ***Platanoidea*** Pax in Engler, Bot. Jahrb. 6: 327. 1885; Pax in Engler, Bot. Jahrb. 7: 233. 1886; Pojarkova in Flora Syst. Pl. Vasc. 1: 226. 1933, p.p., excl. Ser. *Pubescentia*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 184. 1962, p.p., excl. Ser. *Monspessulana* & *Pubescentia*; Fang in Acta Phytotax. Sinica 11(2): 143. 1966; Ogata in Bull. Tokyo Forests 63: 132. 1967; Murray in Kalmia 2: 7. 1970; Delendick in Mem. New York Bot. Gard. 54: 93. 1990; Xu in Acta Bot. Yunnanica 18(3): 288. 1996.

Acer Sect. *Campetria* Pax in Engler, Bot. Jahrb. 6: 327. 1885; Pax in Engler, Bot. Jahrb. 7: 219. 1886, p.p., quod est *A. campestre*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 182. 1962.

Acer Sect. ***Pubescentia*** (Pojarkova) Ogata in Bull. Tokyo Forests 63: 136. 1967; Delendick in Mem. New York Bot. Gard. 54: 93. 1990.

Acer Sect. *Campestria* Pax in Engler, Bot. Jahrb. 7: 219. 1886, p.p., quod est *A. pubescence*.
Acer Sect. *Microcarpa* Pojarkova Ser. *Buergeriana* Fang in Acta Phytotax. Sinica 11(2): 162. 1966, p.p., quod est *A. pilosum*.
Acer Sect. *Platanoidea* Pax Ser. *Pubescentia* Pojarkova in Flora Syst. Pl. Vasc. 1: 236 & 307. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 185. 1962.

Acer Sect. ***Rubra*** Pax in Engler, Bot. Jahrb. 6: 326. 1885; Pax in Engler, Bot. Jahrb. 7: 178. 1886; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 182. 1962; Ogata in Bull. Tokyo Forests 63: 130. 1967; Murray in Kalmia 2: 7. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 145. 1976; Delendick in Mem. New York Bot. Gard. 54: 94. 1990; Xu in Acta Bot. Yunnanica 18(3): 289. 1996, p.p., excl. *A. spicatum*.

Acer Sect. *Eriocarpa* Murray in Kalmia 2: 6. 1970.
Acer Sect. *Saccharodendron* Xu in Acta Bot. Yunnanica 18(3): 289. 1996, p.p., quod est *A. saccharinum*.

Acer Sect. ***Saccharina*** Pax in Engler, Bot. Jahrb. 6: 328. 1885; Pax in Engler, Bot. Jahrb. 7: 241. 1886; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 187. 1962; Ogata in Bull. Tokyo Forests 63: 141. 1967; Delendick in Mem. New York Bot. Gard. 54: 93. 1990.

Acer Sect. *Campestria* Pax in Engler, Bot. Jahrb. 7: 219. 1886, p.p., quod est *A. grandidentatum*.
Acer Sect. *Acer* Ser. *Saccharodendron* (Rafinesque) Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 187. 1976
Acer Sect. *Saccharodendron* (Rafinesque) Murray in Kalmia 2: 8. 1970; Xu in Acta Bot. Yunnanica 18(3): 289. 1996, p.p., excl. *A. saccharinum*.

Acer Sect. ***Spicata*** Pax in Engler, Bot. Jahrb. 6: 326. 1885; Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p., quod est *A. spicatum*; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 182. 1962, p.p., excl. Ser. *Parviflora*; Ogata in Bull. Tokyo Forests 63: 117. 1967; Murray in Kalmia 2: 8. 1970.

Acer Sect. *Caudata* (Pax) Delendick in Mem. New York Bot. Gard. 54: 93. 1990.
Acer Sect. *Microcarpa* Pojarkova Ser. *Spicata* (Pax) Pojarkova in Flora Syst. Pl. Vasc. 1: 236 & 339. 1933; Fang in Acta Phytotax. Sinica 11(2): 153. 1966.
Acer Sect. *Parviflora* Ser. *Ukurundensia* Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 145.1976.
Acer Sect. *Spicata* Pax Ser. *Caudata* Pax in Engler, Bot. Jahrb. 7: 182. 1886, p.p., excl. *A. caesium* & *A. campbellii*.

Acer Sect. ***Trifoliata*** Pax in Engler, Bot. Jahrb. 6: 326. 1885; Pax in Engler, Bot. Jahrb. 7: 203. 1886, p.p., excl. *A. cissifolium*; Pojarkova in Flora Syst. Pl. Vasc. 1: 240. 1933; Momotani in Kyoto Univ. Mem. Coll. Sci. ser. B. 29: 187. 1962; Fang in Acta Phytotax. Sinica 11(2): 184. 1966; Ogata in Bull. Tokyo Forests 63: 145. 1967; Murray in Kalmia 2: 8. 1970; Jong in Mededel. Landbouwh. Wagen. Nederland 76-2: 146. 1976; Delendick in Mem. New York Bot. Gard. 54: 94. 1990; Xu in Acta Bot. Yunnanica 18(3): 289. 1996.

Acer Sect. *Coleocarpa* Pax in Engler, Bot. Jahrb. 6: 328. 1885.
Acer Sect. *Emeiensis* Hsu in Acta Phytotax Sinica 23(1): 361; Xu in Acta Bot. Yunnanica 18(3): 291. 1996.

CONCLUSIONS

Overall, Pax(1885, 1886, 1902)'s work framed the structure of the systematic study of *Acer*. Since then, researchers contributed to the systematic study of *Acer* by proposing new delineation of species groups and adding new evidence to propose relationships among these species groups. It was not until the work of Ogata (1967) that the circumscription of most series or sections began to change. Murray (1970a) and Jong (1976) transferred Ogata's section *Syriaca* to its closely related species under *Goniocarpa*. This is supported by the leaf venation evidence (Tanai, 1978). Delendick (1981, 1990) agreed with Jong (1976) in most evolutionary explanations of morphological characters. Although the evidence of chemical compounds alone cannot reveal the relationships among sections of *Acer*, he (Delendick, 1981, 1990) proposes a phylogeny combining morphological data and his own chemical evidence. His system can be a basis for the study of relationship of each species group. The circumscription of sections is broad in the system of Jong (1976, 1994), which may be a

disadvantage to follow when one wants to study the phylogeny of *Acer* as the samples may not cover the variation of the whole genus. Revealing sectional relationship using molecular gene markers such as ITS nDNA (Ackerly & Donoghue, 1998; Suh *et al.* 2000), RFLP cpDNA (Hasebe *et al.*, 1998) and *trn*L intron and *trn*L-F IGS cpDNA (Psoffer *et al.* 2002) shed further light on solving this question. Nevertheless, thorough sampling and incorporating all the data available from previous studies is necessary for clarify systematic scheme of *Acer* and understanding the relationship among sections.

LITERATURE CITED

Ackerly, D. D. and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: a phylogenetic study of correlated evolution in maples (*Acer*). Am. Nat. **152**: 767-791.

Avise, J. C. 1994. Molecular Markers, Natural History and Evolution. Chapman & Hall, New York.

Boulter, M. C., J. N. Benfield, H. C. Fisher, D.A. Gee and M. Lhotak. 1996. The evolution and global migration of the Aceraceae. Phil. Trans. Royal Soc. London **351**: 589-603.

Brown, J. H. and M. V. Lomolino 1998. Biogeography 2nd ed. Sinauer Associates, Inc. Publishers, Massachusetts.

Brundin, L. Z. 1988. Phylogenetic biogeography. In: Myers, A. A. and P. S. Giller (eds.) Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions. pp. 343-369. Chapman and Hall, New York.

Cox, C. B. and P. D. Moore. 1993. Biogeography: an ecological and evolutionary approach. 5th. ed. Blackwell Scientific Publications. Oxford, London.

Delendick, T. 1981. A systematic review of the Aceraceae. PhD. Dissertation, City University of New York.

Delendick, T. 1990. A survey of foliar flavonoids in the Aceraceae. Mem. New York Bot. Gard. **54**: 1-129.

Fang, W.-P. 1966. Revisio Taxorum Aceracearum Sinicarum. Acta. Phytotax. Sin. 11: 139-189.

Fang, W.-P. 1981. Aceraceae. In: Fang, W.-P. (ed.), Flora Republicae Popularis Sinicae **46**: 66-273.

Gelderen, D. M. van, P. C. de Jong, and H. J. Oterdoom (eds.). 1994. Maples of the World. Timber Press, Portland, Oregon.

Hasebe, M., T. Ando and K. Iwatsuki. 1998. Infrageneric relationships of maple trees based on the chloroplast DNA restriction fragment length polymorphisms. J. Plant. Res. **111**: 441-451.

Hillis, D. M., C. Moritz and B. K. Mable. 1996. Molecular Systematics, 2nd ed. Snauer Associates Inc. Publishers, Massachusetts, U.S.A.

Hopkins, D. M. (ed.). 1967. The Bering Land Bridge. Standford University Press, Standford, California.

Hu, H. H. and W. C. Chen. 1948. New and noteworthy species of Chinese *Acer*. Bull. Fan Mem. Inst. Biol. n. ser. **1**: 199-212.

Jong, P. C. de 1976. Flowering and sex expression in *Acer* L. a biosystematic study. Mededelingen Landbouwhogeschool Wageningen Nederland **76**: 1-201.

Jong, P. C. de 1990. Flowering and evolution of *Acer*. International Dendrology Society Year Book **1990**: 42-47

Jong, P. C. de 1994. Taxonomy and reproductive biology of maples. In: Gelderen, D. M. van, P. C. de Jong, and H. J. Oterdoom (eds.), Maples of the World. Timber Press, Portland, Oregon.

Koidzumi, G. 1911. Revisio Aceracearum Japonicarum. Journ. Coll. Sci. Univ. Tokyo **32**: 1-75. Plate 1-33.

Latham, R. E. and R. E. Ricklefs. 1993. Continental comparisons of temperate-zone. In: Ricklefs, R. E. and D. Schluter (eds.), Species Diversity in Ecological Communities-Historical and Geographical Prospective. pp. 294-314. The University of Chicago Press, Chicago.

Li, W.-H. 1997. Molecular Evolution. Sinauer Associates Inc. Publishers. Massachusetts, U.S.A.

Linneaus. C. 1763. Species Plantarum. ed, 2. **2**: 1495-1497.

Metcalf, F. P. 1932. *Acer* (Section *Integrifolia* Pax) for southeastern China. Lingnan Sci. Journal **11**: 193-210.

Mai, D.-H. 1983. Studien an endokarpien europaischer und westasiatischer arten der gattung *Acer* L. (Aceraceae). Gleditschia **10**: 37-57.

Mai, D.-H. 1984. Die endokarpien bei der gattung *Acer* L. (Aceraceae)-eine biosystematische studie. Gleditschia **11**: 17-46.

Mai, D.-H. 1995. Tertiare vegetationsgeschichte Europas. Gustav Fischer Verlag Jena.

Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. Ann. Missouri Bot. Gard. **86**: 472-522.

Manchester, S. R. and B. H. Tiffney. 2001. Integration of paleobotanical and neobotanical data in the assessment of phylogeographic history of holarctical angiosperm clades. Int. J. Plant Sci. **162**(S6): S19-S27.

McKenna, M. C. 1975. Fossil mammals and early Eocene north Atlantic land continuity. Ann. Missouri Bot. Gard. **62**: 335-353.

Momotani, Y. 1962a. Taxonomic study of the genus *Acer*, with special reference to the seed proteins II analysis of protein. Mem. Coll. Sci. Univ. Kyoto, ser. B. **29**: 81-102.

Momotani, Y. 1962b. Taxonomic study of the genus *Acer* with special reference to the seed proteins. III. System of Aceraceae. Mem. Coll. Sci. Univ. Kyoto, ser. B, **29**: 177-189.

Murray, A. E. 1969. *Acer* notes (1). Kalmia **1**: 1-4.

Murray, A. E. 1970a. A Monograph of the Aceraceae. PhD. thesis. Pennsylnavia State University.

Murray, A. E. 1970b. A checklist of the species of *Acer*. Kalmia **2**: 22-24.

Murray, A. E. 1970c. A checklist of the species of *Acer*, in continuation. Kalmia **2**: 25-45.

Murray, A. E. 1970d. *Acer* infraspecific taxa. Kalmia **2**: 46-48.

Murray, A. E. 1971a. *Acer* infraspecific taxa. Kalmia **3**: 1-20, 21-28.

Murray, A. E. 1971b. Add to my *Acer* monograph. Kalmia 3: 21.

Murray, A. E. 1974. Himalayan maples. Kalmia **6**: 2-8.

Murray, A.E. 1975. Notes American maples. Kalmia **7**: 1-20.

Murray, A. E. 1977. New Asiatic taxa in Acer. Kalmia **8**: 2-12.

Murray, A. E. 1978. *Acer* notes No. 8. Kalmia 17-20.

Murray, A. E. 1979. Afrasian and European maples. Kalmia **9**: 2-40.

Myers, A. A. and P. S. Giller. 1988. Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions. Chapman and Hall, New York.

Nakai, T. 1915. Precursores ad Floram Sylvaticum Koreanum I. Aceraceae. Bot. Mag. Tokyo **29**: 25-30.

Ogata, K. 1967. A systematic study of the genus *Acer*. Bull. Tokyo Univ. Forest. **63**: 89-206.
Pax, F. 1885. Monograph der Gattung *Acer*. Bot. Jahrb. **6**: 287-347.
Pax, F. 1886. Monograph der Gattung *Acer*. Bot. Jahrb. **7**: 177-263.
Pax, F. 1902. Aceraceae. In: Engler, H. G. A. (ed.), Das Pflanzenreich. IV. **163**: 1-89
Pfosser, M. J., J. Guzy-Wróbelska, B. L. Sun, T. E. Stuessy, T. Sugawara and N. Fuji. 2002. The origin of species of *Acer* (Sapindaceae) endemic to Ullung island, Korea. Systematic Botany **27**: 351-367.
Pojarkova, A. I. 1933. Botanico-Geograpgical survey of the maples in USSR, in connection with the history of the whole genus. Acta Inst. Bot. Acad. Sci. USSR, ser. 1, **1**: 225-374. (Russian with English summary.)
Raven, P. H. 1972. Plant species disjunctions: a summary. Ann. Missouri Bot. Gard. 59: 234-246.
Rehder, A. 1905. The maples of eastern continental Asia. In Sargent, Trees and Shrubs **1**: 131-181.
Rehder, A. 1949. Bibliography of cultivated trees and shrubs. The Arnold Arboretum.
Riddle, B. R. 1996. The molecular phylogeographic bridge between deep and shallow history in continental biota. TREE **11**: 207-211.
Sanderson, M. J. 1998. Estimating rate and time in molecular phylogenies. In: Soltis, D.E., P. S. Soltis, and J. J. Doyle (eds.), Molecular Systematics of Plants II DNA Sequencing. Kluwer Academic Publishers, Massachusetts. Pp. 243-264.
Santamour, F. S. 1982. Cambial peroxidase isoenzymes in relation to systematics of *Acer*. Bull. Torr. Bot. Club **109**: 152-161.
Soltis, D.E., P.S. Soltis, and J.J. Doyle. 1998. Molecular Systematics of Plants II DNA Sequencing. Kluwer Academic Publishers, Massachusetts.
Suh, Y., H. J. Cho, S. Kim and C. W. Park. 1996. Comparative analysis of ITS sequences from Acer species (Aceraceae) in Korea. Journ. Plant Biol. **39**: 1-8.
Suh, Y., K. Heo and C. W. Park. 2000. Phylogenetic relationships of maples (*Acer* L.; Aceraceae) implied by nuclear ribosomal sequences. Journ. Plant Res. **113**: 193-202.
Tanai, T. 1978a. Taxonomical investigation of the living species of the genus *Acer* L. based on vein architecture of leaves. Journ. Fac. Sci. Hokkaido Univ. ser. IV. **18**: 243-282.
Tanai, T. 1978b. Taxonomical reinvestigation of the genus *Acer* L., based on vein architecture of leaves. Journ. Jap. Bot. **53**: 65-83.
Tanai, T. 1983. Revision of Tertiary *Acer* from East Asia. Journ. Fac. Sci. Hokkaido Univ. ser. IV. **20**: 291-390.
Taylor, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. Bot. Rev. **56**: 279-416
Tiffney, B. H. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. Journ. Arn. Arb. **66**: 73-94.
Tiffney, B. H. 1985b. The Eocene north Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. Journ. Arn. Arb. **66**: 243-273.
Tiffney, B. H. and S. R. Manchester. 2001. The use of geological and paleoontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. Int. J. Plant Sci. **162**: S3-S17.
Walter, H. 1973. Vegetation of the Earth. Springer Verlag, New York
Walther, H. 1972. Studien uber tertiare *Acer* mitteleuropas Abh. Staatl. Mus. Mineral. Geol., Dresden **29**: 1-309.
Wen, J. 1999. Evolution of eastern Asia and eastern North American disjunctions in flowering

plants. Ann. Rev. Ecol. Syst. **30**: 421-455.
Willis, J. C. 1922. Age and Area. Cambridge University Press, London.
Wolfe, J. A. 1975. Some aspects of plant geography of the northern temperate during the late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. **62**: 264-279.
Wolfe, J. A. and T. Tanai, 1987. Systematics, phylogeny, and distribution of *Acer* (Maples) in the Cenozoic of western North America. Journ. Fac. Sci. Hokkaido Univ. ser. IV. **22**: 1-246.
Xiang, Q.-Y., D. E. Soltis and P. S. Soltis. 1998. The eastern Asia and eastern and western North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. Mol. Phylog. Evol. **10**: 178-190.
Xu, T.-Z. 1996. A new system of the genus *Acer*. Acta Bot. Yunn. **18**: 277-292.
Xu, T.-Z. 1998. The systematic evolution and distribution of the genus *Acer*. Acta Bot. Yunn. **20**: 383-393.

槭樹屬植物之親緣關係及歷史生物地理 I—屬內分類系統之研究史[1]

黃星凡[2,4], Robert E. Ricklefs[2], Peter H. Raven[3]

(收稿日期：2002 年 7 月 30 日；接受日期：2002 年 9 月 5 日)

摘　　要

歷史生物地理學(historical biogeography)是研究分類群在時間及空間上之分布。 其研究內容包括分類群之誕生，散播，及分化。這類研究需借助化石証據，並需瞭解分類群內各個種間之親緣關係。槭樹屬植物具有下列四項條件符合這種要求：1)具有豐富的化石；2)包含很多物種；3)是北溫帶植物區系之主要元素之一； 4)廣為人知。因為槭樹植物之化石只能肯定的鑑定到組(section)，因此以組為單位來追溯槭樹植物之演化史是合適的。但是槭樹植物組之範圍大小，因研究者而異。故本文旨在回顧整理以前之研究來說明組範圍之變動以供為參考。Delendick 在 1981 年之文章中認為槭樹屬以下之分類系統以 Ogata 發表於 1967 年及 Jong 發表於 1976 年之系統最好，不過他認為很多 Jong 處理為系(series)之分類群應提升為組。因此本文除合併 *Distyla* 及 *Parviflora* 為 *Parviflora* 外，餘跟隨 Delendick 之系統以說明組範圍之變動。

關鍵詞：槭樹屬、屬內分類系統、研究史。

1.第一作者之部份博士論文。
2.美國密蘇里州立大學聖路易分校生物系。
3.美國聖路易市密蘇里植物園。
4.通信作者。