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The evolution and global migration of the Aceraceae

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SUMMARY

This article shows how a large palaeontological database (the Plant Fossil Record version 2.2, available on the Internet) can be used to draw evolutionary and migratory pathways. 2946 published records of the family Aceraceae have been found as leaf, fruit and seed, wood or pollen fossils, and their geographical and stratigraphical distributions are presented here in different graphical forms. Manipulation and analysis of the data have produced palaeo-geographic maps of these distributions, curves of the number of records in five global regions over the last 100 million years, and cladograms of taxa and their geography. The results give objective evidence which shows that early members of the family became well established on upland slopes of the north Pacific rim during the Palaeogene. Some of these early species migrated eastwards across Greenland to Europe before the North Atlantic opened to the Arctic. Later and larger migrations started in the Oligocene, from Asia westwards to central Europe, bringing a diversification in species both there and in the regions of origin.

1. THE *ACER* DATABASE

We have built a computerized database of the published fossil records assigned in the scientific literature to Aceraceae. Here we show our application of these to different analytical procedures such as occurrence and cladistics to help understand the global evolutionary patterns of the clade. We think that fossils attributed to the *Acer* family are particularly suitable for this treatment because there is an extensive literature of well-preserved material with clear morphological attributes. Many organs are well represented in the fossil record and the literature has good descriptions of most discoveries to help interpret the evolution and migration of the plants across drifting continents. Its fossil record has attracted so much attention that it is one of the few angiosperm families whose fossil and modern genera are allocated to the ranks of section and group. Wolfe & Tanai (1987) have created a number of sections for some of their older fossils and their cladogram of American data is tested here with additional information from Europe and Asia. The results of this accumulative review show patterns of evolution and migration within the family which we compare to those of previous theories.

The PFR database has 1391 occurrence records of megafossils attributed in the literature to Aceraceae, and the age and location of these are listed in table 1. They represent most of the published records of the leaves, fruits and seeds which are accessable on the Internet (http://www.uel.ac.uk./palaeo/). There are a further 1555 published records of pollen which are attributed to the family. These palynological assignations to Aceraceae are far less reliable than those for the leaves and seeds because the morphological features are indistinct and easily confused with those of other families. Also, pollen can be transported often many hundreds of kilometers away from the site of growth, a process which is relatively unusual for megafossils.

One purpose of this paper is to show how the new database can be used to help resolve biological and geological questions. So we describe the process of finding names and analysing them in different ways. However, users of this kind of database must be very cautious about the quality of the data and the different cultural and taxonomic attitudes its compilers represent. Here, every record in figure 1 has been checked accurately to represent the family in the literature, but to confirm the original specimens or illustrations of that literature is an impossible task. Not only are there 3000 sources of data in this work alone, but they are from different paradigms, generations, cultures and methods, and some material is lost. On the other hand, the use of very large sets of data might show trends and patterns through the noise: it is a new way of looking at things and work like this is to discover what might be seen. This paper introduces such a new approach to analyse palaeontological data.

2. EARLIER WORK ON ACERACEAE

Gelderen *et al.* (1994) have recently published a monograph entitled *Maples of the World*. The authors give substantial details of the horticultural features of the plants though they have written chapters on taxonomy and evolution and list more than 200 fossil

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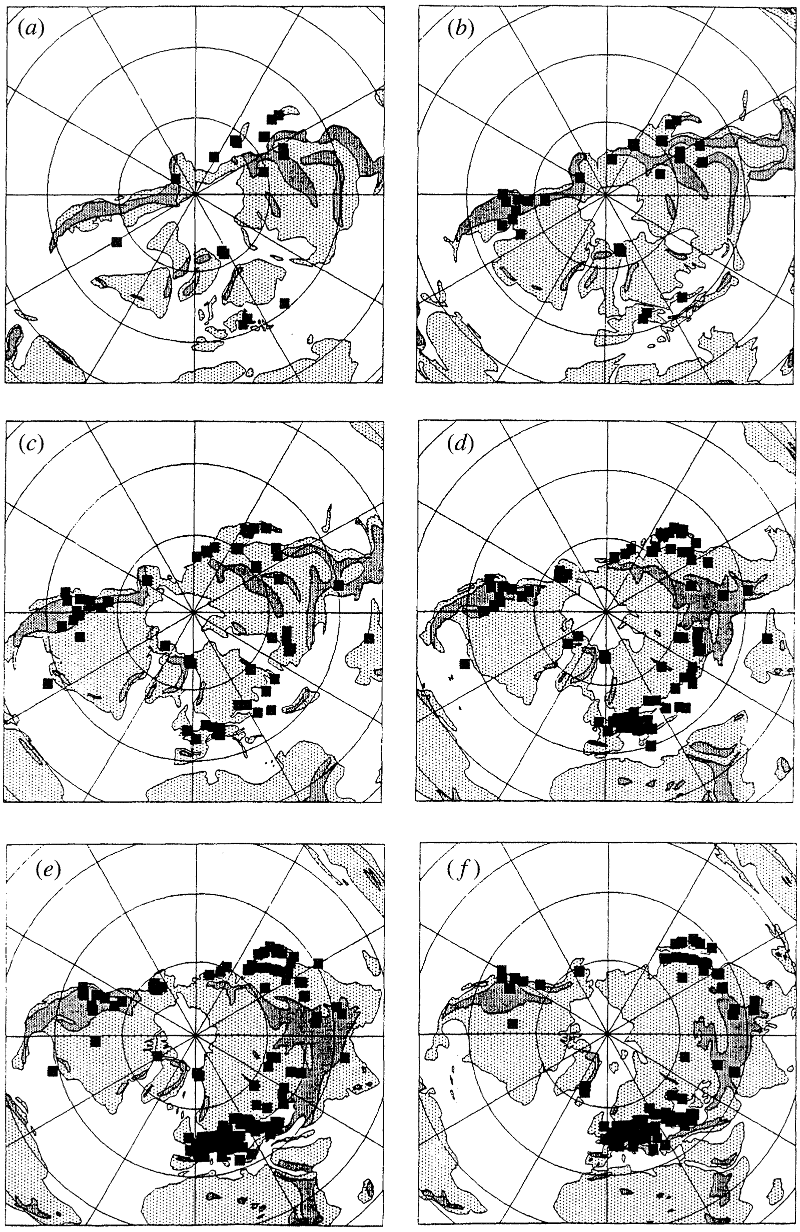

Figure 1. Palaeogeographic maps of the northern hemisphere at: (*a*) the Late Maastrichtian (66–65 Ma BP); (*b*) the Paleocene (65–56.5 Ma BP); (*c*) the Eocene (56.5–35.4 Ma BP); (*d*) the Oligocene (35.4–23.3 Ma BP); (*e*) the Miocene (23.3–5.2 Ma BP); and (*f*) the Pliocene (5.2–1.64 Ma BP), drawn from Smith (1992). The maps plot megafossil data searched from PFR2.2 and listed in table 1. The darker hatching represent mountain chains.

species of the modern genus (most are from America and were described a long time ago when the concepts of angiosperm evolution were very different from now). It is mentioned that the oldest known specimens of *Acer* are described from the Late Cretaceous of southern California. Wolfe & Tanai (1987) believe the first true maple is from the Late Palaeocene of Alaska & Kvacek (1994) concurs. Muller (1981) accepts an Oligocene first appearance of the more voluminous pollen record. Here we refer to older records of the family, going back into the Cretaceous, based on the opinions of the original authors. So this work is setting what are perhaps unreliable fossil records against the trends of a complete dataset and may pick out dubious identifications, though it is important to keep our minds open about the evolutionary scope of different taxonomic groups. Equally, our methods allow the constituency of established sections and their relationships to be tested and to re-examine the patterns of temporal appearance and geographic spread. This rests on our premise that logical, albeit fuzzy, patterns will emerge from natural systems.

The first major systematic treatment of the family was by Pax (1885) who created a number of groups and sections, with one to several species in each. Many subsequent authors have followed this taxonomic practice and fossils have been assigned (e.g. Walther 1972) to the groups and sections which were established on modern plant species. Furthermore, sections for fossil species have been created (Wolfe & Tanai 1987).

Taxonomic opinions differ with regard to the definition of these sections and groups, although some with distinct morphology are stable. Here we are trying to test whether or not these sections are of any value in helping to monitor the evolution of *Acer* through the Tertiary. If we are to believe in a monophyletic origin of *Acer* then these sections may enable us to plot the geneological changes through space and time. We can expect clear distributions of the sections in restricted areas at certain times. Maybe we will have got some of the assignations to the correct section wrong, and maybe there is a lot of missing evidence within the limited fossil record, but broadly we can expect to see good migratory and evolutionary patterns emerging.

The family's fossil history recorded in rocks from North America is reviewed in detail, with illustrations, by Wolfe & Tanai (1987). Their cladogram is based on 35 characters from modern and fossil species; it gives the impression that sections have evolutionary, phenotypic and geneological significance, with 12 newly conceived extinct sections at the lower nodes. Tanai (1983) revised the fossils from eastern Asia and presented useful stratigraphic range charts for most of the leaves. The central European record from Germany (Walther 1972) and Bohemia (Prochazka & Buzek 1975) is particularly rich and well described; other records from Europe tend to have fewer specimens and are described in literature listed in the bibliography.

3. SEARCHING AND PRESENTING THE DATA

Table 1 lists the age and locations of the megafossil records contained in the PFR2.2 database with the following names of fossils which we believe are associated with the clade: *Aceripollenites*, *Aceripollis*, *Acerites*, *Acerspora*, *Acer*, *Aceroxylon*, *Aceriphyllum* and *Aceraceae*. For each record the database has latitude and longitude coordinates, and the age range as the number of millions of years for each record, allowing palaeogeographic distributions to be plotted by the Atlas software (Smith 1993) which we have also adapted for the Internet. Figure 1 shows a set of palaeogeographic maps from 1.64–66 Ma BP with megafossil records plotted. More detail is shown in figure 2 where the time ranges are much shorter between 38–54 Ma. Pollen records are shown in the palaeogeographic maps of figure 3 from 1.64–112 Ma. The many vast areas on these maps where the Acer-clade data are absent do have terrestrial Cenozoic deposits, giving confidence to our plots of migration routes.

However, the database does have other sources of distortion due to anthropomorphic factors and a second method of presenting the information from the database attempts to take this into account. This is by plotting the number of occurrences recorded for each one million year interval through time. Our absolute plots of occurrence records through the last 100 Ma are shown in figure 4. Records from five northern hemisphere regions most compatible with continental movements (western North America, eastern North America, Europe, western Asia, eastern Asia) are plotted separately. Before we can make interpretations from such absolute curves it is important to check that it is showing real biological changes and is not too distorted by investigative noise.

This is manifest in different regions which have different qualities and quantities represented in the database, due to varying numbers of localities studied, sediments preserved, palaeontologists employed etc. Although it is possible to apply regional adjustment factors to recognize these influences, very little information is available to fix these features so that it is not possible to monitor the variations or take them into account by presenting relative values. The curves in figure 4 are of the absolute data with no adjustment, so for some regions the height of the curve is exagerrated. Also, the horizontal scales are often distorted by different stratigraphic scales and inaccurate age determinations. To help clarify the information the curves have been smoothed by Fourier techniques which have the effect of blurring the original data.

From the first occurrences of the Acer-clade in the Cretaceous until the end of the Palaeocene (or the Eocene away from the Pacific rim) there is no evidence of large numbers of individuals or species. Such quiescense is characteristic of other Arcto-Tertiary clades we have examined in this way and we explain it as a time of evolutionary consolidation. There is slight evidence here that the group was distributed over at least three of the regions recognized since Late Cretaceous times and has been widespread for most of its history.

The 50 or so records in western North America and eastern Asia during the Eocene can be seen on the relevant palaeogeographic maps in figure 1. Both the maps (figure 2) and the occurrence curves show the migration across western Asia to Europe after about 35 Ma. Thereafter all regions except eastern North America show a good number of records and diversification increased up to the time of deleterious Pliocene climatic cooling. The migration patterns shown here give objective confirmation of Kvacek's (1994) view that the family was firmly established in the upland vegetation of western North America and eastern Asia by the Middle Eocene. Also by this time some species had moved eastwards across the higher latitudes of America and across Greenland to Spitsbergen and Europe. Not until the Oligocene did the plants in Asia diversify to the west to become significant members of Neogene floras. The distribution points give evidence from both pollen and megafossils to show that many of the (especially early) records are from high latitudes as shown in Smith *et al.*'s 1994 maps. However, they do not represent particular sections or other groups of the clade, at least as they are currently defined. The megafossil record plots do not appear to have any value in separating out the geographic histories of the different sections.

Table 1. *List of national locations and geological ages of the megafossil records searched from the PFR2.2 database*

(Each species is allocated to a section at the determination of each author, whose name and reference can be found in PFR2.2. The two rows of numbers to the right of each column is the first and last appearance expressed as Ma BP, Harland 1990.)

Acer				
montanense	U.S.A., Montana	Eocene	56.5	35.4
postense	U.S.A., Oregon	Eocene	56.5	35.4
Arguta				
yoshiokaense	Japan	Miocene	6.6	5.2
yoshiokaense	Russian Far East, Primorye	Miocene	6.6	5.2
tottoriense	Japan	Late Miocene	10.4	5.2
yoshiokaense	Japan	Miocene	10.4	6.7
yoshiokaense	Russian Far East, Primorye	Miocene	10.4	6.7
yoshiokaense	Russian Far East, Primorye	Miocene	16.3	10.4
yoshiokaense	Russian Far East, Primorye	Oligocene	35.4	23.3
ivanofense	U.S.A., Alaska	Eocene	56.5	35.4
kryshtofovichii	Russian Far East, Sakhalin	Eocene	56.5	35.4
Campestria				
decipiens	East Ukraine	Mid Miocene	6.5	5.2
campestre	Germany	Miocene	6.6	5.2
decipiens	Austria	Miocene	6.6	5.2
palaeo-campestre	Austria	Miocene	6.6	5.2
protomiyabei	U.S.A., Alaska	Miocene	6.6	5.2
septilobatum	U.S.A., Idaho	Miocene	6.6	5.2
septilobatum	U.S.A., Nebada	Miocene	6.6	5.2
septilobatum	U.S.A., Oregon	Miocene	6.6	5.2
septilobatum	U.S.A., Washington	Miocene	6.6	5.2
campestre	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4
campestre	Germany	Miocene	10.4	6.7
cretnatifolium	Germany	Late Miocene	10.4	5.2
decipiens	Austria	Miocene	10.4	6.7
decipiens	Germany	Late Miocene	10.4	5.2
palaeo-campestre	Austria	Miocene	10.4	6.7
protomiyabei	U.S.A., Alaska	Miocene	10.4	6.7
septilobatum	U.S.A., Idaho	Miocene	10.4	6.7
septilobatum	U.S.A., Nevada	Miocene	10.4	6.7
septilobatum	U.S.A., Oregon	Miocene	10.4	6.7
septilobatum	U.S.A., Washington	Miocene	10.4	6.7
campestre	Poland	Middle Miocene	16.3	10.4
cretnatifolium	Germany	Middle Miocene	16.3	10.4
decipiens	East Ukraine	Mid Miocene	16.3	10.4
decipiens	Germany	Early Miocene	23.3	16.3
protomiyabei	North Korea	Early Miocene	23.3	16.3
rueminianum	Germany	Early Miocene	23.3	16.3
kushiroanum	Japan	Early Oligocene	35.4	29.3
Cissifolia				
lincolnense	U.S.A., Montana	Eocene	56.5	35.4
Columbiana				
medianum	Canada, British Columbia	Miocene	6.6	5.2
medianum	U.S.A., Idaho	Miocene	6.6	5.2
medianum	U.S.A., Nevada	Miocene	6.6	5.2
medianum	U.S.A., Oregon	Miocene	6.6	5.2
medianum	U.S.A., Washington	Miocene	6.6	5.2
niklasi	U.S.A., Idaho	Miocene	6.6	5.2
niklasi	U.S.A., Oregon	Miocene	6.6	5.2
niklasi	U.S.A., Washington	Miocene	6.6	5.2
medianum	Canada, British Columbia	Miocene	10.4	6.7
medianum	U.S.A., Idaho	Miocene	10.4	6.7
medianum	U.S.A., Nevada	Miocene	10.4	6.7
medianum	U.S.A., Oregon	Miocene	10.4	6.7
medianum	U.S.A., Washington	Miocene	10.4	6.7
niklasi	U.S.A., Idaho	Miocene	10.4	6.7
niklasi	U.S.A., Oregon	Miocene	10.4	6.7
niklasi	U.S.A., Washington	Miocene	10.4	6.7
oligomedianum	U.S.A., Oregon	Oligocene	35.4	23.3
eomedianum	U.S.A., Nevada	Eocene	56.5	35.4
powellense	U.S.A., Montana	Eocene	56.5	35.4
stockeyae	Canada, British Columbia	Eocene	56.5	35.4
Distyla				
protodistylum	Japan	Miocene	6.6	5.2
protodistylum	Japan	Miocene	10.4	6.7
protodistylum	China	Early Oligocene	35.4	29.3
Douglasa				
douglasense	U.S.A., Alaska	Eocene	56.5	35.4
Eriocarpa				
chaneyi	U.S.A., Alaska	Miocene	6.6	5.2
chaneyi	U.S.A., Idaho	Miocene	6.6	5.2
chaneyi	U.S.A., Nevada	Miocene	6.6	5.2
chaneyi	U.S.A., Oregon	Miocene	6.6	5.2
chaneyi	U.S.A., Washington	Miocene	6.6	5.2
ezoanum	Japan	Miocene	6.6	5.2
ezoanum	North Korea	Miocene	6.6	5.2
ezoanum	Romania	Miocene	6.6	5.2
ezoanum	Russan Far East, Primorye	Miocene	6.6	5.2
ezoanum	Russan Far East, Sakhalin	Miocene	6.6	5.2
ezoanum	U.S.A., Alaska	Miocene	6.6	5.2
ferrignoi	U.S.A., Oregon	Miocene	6.6	5.2
taggarti	U.S.A., Oregon	Miocene	6.6	5.2
whitebirdense	U.S.A., Idaho	Miocene	6.6	5.2
whitebirdense	U.S.A., Oregon	Miocene	6.6	5.2
whitebirdense	U.S.A., Washington	Miocene	6.6	5.2
chaneyi	U.S.A., Alaska	Miocene	10.4	6.7
chaneyi	U.S.A., Idaho	Miocene	10.4	6.7
chaneyi	U.S.A., Nevada	Miocene	10.4	6.7
chaneyi	U.S.A., Oregon	Miocene	10.4	6.7
chaneyi	U.S.A., Washington	Miocene	10.4	6.7
ezoanum	Japan	Late Miocene	10.4	5.2
ezoanum	Japan	Miocene	10.4	6.7
ezoanum	North Korea	Miocene	10.4	6.7
ezoanum	Romania	Miocene	10.4	6.7
ezoanum	Russian Far East, Primorye	Miocene	10.4	6.7
ezoanum	Russian Far East, Sakhalin	Miocene	10.4	6.7
ezoanum	U.S.A., Alaska	Miocene	10.4	6.7
ferrignoi	U.S.A., Oregon	Miocene	10.4	6.7
taggarti	U.S.A., Oregon	Miocene	10.4	6.7
whitebirdense	U.S.A., Idaho	Miocene	10.4	6.7
whitebirdense	U.S.A., Oregon	Miocene	10.4	6.7
whitebirdense	U.S.A., Washington	Miocene	10.4	6.7
ezoanum	Romania	Mid/Late Miocene	16.3	5.2
ezoanum	Russan Far East, S. Sakhalin	Early Miocene	23.3	16.3
ezoanum	U.S.A., Alaska	Early Miocene	23.3	16.3
chaneyi	U.S.A., Alaska	Oligocene	35.4	23.3
chaneyi	U.S.A., Washington	Oligocene	35.4	23.3
ezoanum	Russian Far East, Primorye	Oligocene	35.4	23.3
kenaicum	U.S.A., Alaska	Oligocene	35.4	23.3
tauroucursum	U.S.A., Nevada	Eocene	56.5	35.4
tiffneyi	U.S.A., Montana	Eocene	56.5	35.4
Glabra				
traini	Canada, British Columbia	Miocene	6.6	5.2
traini	U.S.A., Idaho	Miocene	6.6	5.2
traini	U.S.A., Nevada	Miocene	6.6	5.2
traini	U.S.A., Oregon	Miocene	6.6	5.2
traini	Canada, British Columbia	Miocene	10.4	6.7
traini	U.S.A., Idaho	Miocene	10.4	6.7
traini	U.S.A., Nevada	Miocene	10.4	6.7
traini	U.S.A., Oregon	Miocene	10.4	6.7

Table 1. (*Cont.*)

Gladriodea				
galbroides	U.S.A., Alaska	Early Miocene	23.3	16.3
florissanti	U.S.A., SW Montana	Oligocene	35.4	23.3
glabroides	U.S.A., Oregon	Oligocene	35.4	23.3
glabroides	U.S.A., SW Montana	Oligocene	35.4	23.3
becki	U.S.A., Oregon	Eocene	56.5	35.4
bosrivularis	U.S.A., Idaho	Eocene	56.5	35.4
cadaver	U.S.A., Nevada	Eocene	56.5	35.4
crookense	U.S.A., Nevada	Eocene	56.5	35.4
crookense	U.S.A., Oregon	Eocene	56.5	35.4
elkoanum	U.S.A., Nevada	Eocene	56.5	35.4
elwyni	U.S.A., Montana	Eocene	56.5	35.4
elwyni	U.S.A., Wyoming	Eocene	56.5	35.4
florissanti	U.S.A., Montana	Eocene	56.5	35.4
jarbidgianum	U.S.A., Nevada	Eocene	56.5	35.4
meyeri	U.S.A., Oregon	Eocene	56.5	35.4
milleri	U.S.A., Montana	Eocene	56.5	35.4
wehri	Canada, British Columbia	Eocene	56.5	35.4
wehri	U.S.A., Washington	Eocene	56.5	35.4
Indivisa				
subcarpinifolium	Japan	Late Miocene	10.4	5.2
Lithocarpa				
franchetii	Russian Far East, Primorye	Miocene	6.6	5.2
miofranchetii	China, Shandong	Miocene	6.6	5.2
franchetii	Russian Far East, Primorye	Miocene	10.4	6.7
miofranchetii	China, Shandong	Miocene	10.4	6.7
francheti	Russian Far East, Primorye	Miocene	16.3	10.4
miofranchetii	China	Miocene	16.3	10.4
franchetii	Russian Far East, Primorye	Oligocene	35.4	23.3
franchettii	North Korea	Oligocene	35.4	23.3
beckeri	U.S.A., Montana	Eocene	56.5	35.4
grantense	U.S.A., Montana	Eocene	56.5	35.4
Macrantha				
latahense	U.S.A., Oregon	Miocene	6.6	5.2
latahense	U.S.A., Washington	Miocene	6.6	5.2
miodavidii	China, Shandong	Miocene	6.6	5.2
miodavidii	Japan	Miocene	6.6	5.2
miodavidii	Russian Far East, Primorye	Miocene	6.6	5.2
miotegmentosum	Russian Far East, Primorye	Miocene	6.6	5.2
palaeorufinerve	Japan	Miocene	6.6	5.2
palaeorufinerve	Russian Far East, Primorye	Miocene	6.6	5.2
palaeorufinerve	U.S.A., Alaska	Miocene	6.6	5.2
palaerufinerve	Japan	Miocene	6.6	5.2
latahense	U.S.A., Oregon	Miocene	10.4	6.7
latahense	U.S.A., Washington	Miocene	10.4	6.7
miodavidii	China, Shandong	Miocene	10.4	6.7
miodavidii	Japan	Miocene	10.4	6.7
miodavidii	Russian Far East, Primorye	Miocene	10.4	6.7
miotegmentosum	Russian Far East, Primorye	Upper Miocene	10.4	5.2
miotegmentosum	Russian Far East, Primorye	Miocene	10.4	6.7
palaeorufinerve	Japan	Late Miocene	10.4	5.2
palaeorufinerve	Japan	Miocene	10.4	6.7
palaeorufinerve	Russian Far East, Primorye	Miocene	10.4	6.7
palaeorufinerve	U.S.A., Alaska	Miocene	10.4	6.7
palaerufinerve	Japan	Miocene	10.4	6.7
uemurae	Japan	Late Miocene	10.4	5.2
miodavidii	China	Miocene	16.3	10.4
koreanicum	North Korea	E.M Miocene	23.3	10.4
arcticum	East Russian Northwest	Oligocene	35.4	23.3
miodavidii	Russian Far East, Primorye	Oligocene	35.4	23.3
palaeorufinerve	Russian Far East, Primorye	Oligocene	35.4	23.3
tenuilobatum	France	Oligocene	35.4	23.3
arcticum	U.S.A., N.E. Washington	Eocene	50.0	38.6
arcticum	U.S.A., Washington	Eocene	50.0	38.6
arcticum	Northern Spitsbergen	Palaeogene	56.5	35.4
arcticum	Northern Svalbard	Eocene	56.5	35.4
arcticum	Northern Svalbard	Paleocene/Eocene	56.5	35.4
castorrivularis	U.S.A., Montana	Eocene	56.5	35.4
clarnoense	U.S.A., Oregon	Eocene	56.5	35.4
dettermani	U.S.A., Alaska	Eocene	56.5	35.4
aequilateralis	Russian Far East, Primorye	Early Paleocene	65.0	60.5
arcticum	Siberia, Yakutiya	Early Paleocene	65.0	60.5
arcticum	Russian Far East, Amur	Upper Cretaceous	88.5	65
arcticum	Russian Far East, Kamchatka	Upper Cretaceous	88.5	65
Macrophylla				
fatsiaefolia	Japan	Miocene	6.6	5.2
macrophyllum	U.S.A., Idaho	Miocene	6.6	5.2
macrophyllum	U.S.A., S.W. Nevada	Miocene	6.6	5.2
megasamarum	Japan	Miocene	6.6	5.2
megasamarum	U.S.A., Alaska	Miocene	6.6	5.2
megasamarum	U.S.A., Idaho	Miocene	6.6	5.2
megasamarum	U.S.A., Oregon	Miocene	6.6	5.2
megasamarum	U.S.A., Washington	Miocene	6.6	5.2
oregonianum	U.S.A., Idaho	Miocene	6.6	5.2
oregonianum	U.S.A., Oregon	Miocene	6.6	5.2
oregonianum	U.S.A. Washington	Miocene	6.6	5.2
fatsiaefolia	Japan	Miocene	10.4	6.7
honshuense	Japan	Late Miocene	10.4	5.2
macrophyllum	China	Late Miocene	10.4	5.2
macrophyllum	U.S.A., Idaho	Miocene	10.4	6.7
macrophyllum	U.S.A., S.W. Nevada	Miocene	10.4	6.7
megasmarum	Japan	Miocene	10.4	6.7
megasamarum	Russian Far East, Primorye	Upper Miocene	10.4	5.2
megasamarum	U.S.A., Alaska	Miocene	10.4	6.7
megasamarum	U.S.A., Idaho	Miocene	10.4	6.7
megasamarum	U.S.A., Oregon	Miocene	10.4	6.7
megasamarum	U.S.A., Washington	Miocene	10.4	6.7
oregonianum	U.S.A., Idaho	Miocene	10.4	6.7
oregonianum	U.S.A., Oregon	Miocene	10.4	6.7
oregonianum	U.S.A., Washington	Miocene	10.4	6.7
fatisiaefolia	U.S.A., Alaska	Early Miocene	23.3	16.3
grahamense	U.S.A., Alaska	Early Miocene	23.3	16.3
satsiaefolium	South Korea	Early Miocene	23.3	16.3
grahamense	Russian Far East, Kamchatka	Oligocene	35.4	23.3
megasamarum	U.S.A., Alaska	Oligocene	35.4	23.3
oregonianum	U.S.A., Oregon	Oligocene	35.4	23.3
osmonti	U.S.A., Oregon	Oligocene	35.4	23.3
osmonti	U.S.A., Washington	Oligocene	35.4	23.3
osmontii	Russian Far East, Kamchatka	Oligocene	35.4	23.3
alvordense	U.S.A., Montana	Eocene	56.5	35.4
alvordense	U.S.A., Oregon	Eocene	56.5	35.4
salmonense	U.S.A., Idaho	Eocene	56.5	35.4
salmonense	U.S.A., Montana	Eocene	56.5	35.4
salmonense	U.S.A., Oregon	Eocene	56.5	35.4
Manchesteria				
manchesteri	U.S.A., Oregon	Oligocene	35.4	23.3
axelrodi	U.S.A., Nevada	Eocene	56.5	35.4
Microcarpa				
ablaevii	Russian Far East, Primorye	Miocene	6.6	5.2

Table 1. (*Cont.*)

lebedevii	Russian Far East, Primorye	Miocene	6.6	5.2
miocaudatum	China, Shandong	Miocene	6.6	5.2
miocaudatum	Russian Far East, Primorye	Miocene	6.6	5.2
sinense	Russian Far East, Primorye	Miocene	6.6	5.2
ablaevii	Russian Far East, Primorye	Miocene	10.4	6.7
lebedevii	Russian Far East, Primorye	Miocene	10.4	6.7
miocaudatum	China, Shandong	Miocene	10.4	6.7
miocaudatum	Russian Far East, Primorye	Miocene	10.4	6.7
sinense	Russian Far East, Primorye	Miocene	10.4	6.7
lebedevii	Russian Far East, Primorye	Miocene	16.3	10.4
miocandatum	China	Miocene	16.3	10.4
ablaevii	Russian Far East, Primorye	Oligocene	35.4	23.3
lebedevii	Russian Far East, Primorye	Oligocene	35.4	23.3
miocaudatum	Russian Far East, Primorye	Oligocene	35.4	23.3
sinense	Russian Far East, Primorye	Oligocene	35.4	23.3
terneicum	Russian Far East, Primorye	Early Paleocene	65.0	60.5
Monspessulana				
monspessulanum	Germany	Miocene	6.6	5.2
pseudomonspessulanum	Caucasus, Gruzia	Miocene	6.6	5.2
pseudomonspessulanum	Caucasus, Krasnodar	Miocene	6.6	5.2
monspessulanum	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4
monspessulanum	Germany	Miocene	10.4	6.7
pseudomonspessulanum	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4
pseudomonspessulanum	Caucasus, Gruzia	Miocene	10.4	6.7
pseudomonspessulanum	Caucasus, Krasnodar	Miocene	10.4	6.7
pseudomonspessulanum	Romania	Late Miocene	10.4	5.2
Negundo				
heterodentatum	U.S.A., Alaska	Miocene	6.6	5.2
heterodentatum	U.S.A., Oregon	Miocene	6.6	5.2
knolli	U.S.A., Washington	Miocene	6.6	5.2
molallense	U.S.A., Oregon	Miocene	6.6	5.2
negundoides	U.S.A., California	Miocene	6.6	5.2
negundoides	U.S.A., Idaho	Miocene	6.6	5.2
negundoides	U.S.A., Nevada	Miocene	6.6	5.2
negundiodes	U.S.A., Oregon	Miocene	6.6	5.2
negundoides	U.S.A., Washington	Miocene	6.6	5.2
quercifolium	Austria	Miocene	6.6	5.2
heterodentatum	U.S.A., Alaska	Miocene	10.	6.7
heterodentatum	U.S.A., Oregon	Miocene	10.4	6.7
knolli	U.S.A., Washington	Miocene	10.4	6.7
molallense	U.S.A., Oregon	Miocene	10.4	6.7
negundoides	U.S.A., California	Miocene	10.4	6.7
negundiodes	U.S.A., Idaho	Miocene	10.4	6.7
negundoides	U.S.A., Nevada	Miocene	10.4	6.7
negundoides	U.S.A., Oregon	Miocene	10.4	6.7
negundoides	U.S.A., Washington	Miocene	10.4	6.7
quercifolium	Austria	Late Miocene	10.4	5.2
quericifolium	Austria	Miocene	10.4	6.7
quercifolium	Czechoslovakia	Late Miocene	10.4	5.2
quercifolium	East Ukraine/ Russia/Moldavia	Late Miocene	10.4	5.2
quercifolium	Germany	Late Miocene	10.4	5.2
quercifolium	Hungary	Late Miocene	10.4	5.2
quercifolium	Poland	Late Miocene	10.4	5.2
quercifolium	Romania	Late Miocene	10.4	5.2
quercifolium	Austria	Middle Miocene	16.3	10.4
quercifolium	Croatia/Bosnica/ Serbia	Miocene	16.3	10.4
quercifolium	Czechoslovakia	Middle Miocene	16.3	10.4
quercifolium	East Ukraine/ Russia/Moldavia	Miocene	16.3	10.4
quercifolium	Germany	Middle Miocene	16.3	10.4
quercifolium	Hungary	Middle Miocene	16.3	10.4
quercifolium	Poland	Middle Miocene	16.3	10.4
quercifolium	Romania	Miocene	16.3	10.4
quercifolium	Croatia/Bosnia/ Serbia	Early Miocene	23.3	16.3
quercifolium	Czechoslovakia	Early Miocene	23.3	16.3
quercifolium	Germany	Early Miocene	23.3	16.3
quercifolium	Hungary	Early Miocene	23.3	16.3
quercifolium	Romania	Early Miocene	23.3	16.3
cascadense	U.S.A., Oregon	Oligocene	35.4	23.3
cranei	U.S.A., Oregon	Oligocene	35.4	23.3
eonegundo	U.S.A., Nevada	Eocene	56.5	35.4
macginitei	U.S.A., Colerado	Eocene	56.5	35.4
macginitiei	U.S.A., Montana	Eocene	56.5	35.4
orbum	U.S.A., California	Eocene	56.5	35.4
sinoufluviatilis	U.S.A., Oregon	Eocene	56.5	35.4
Palmata				
sanctaecrucis	East Ukraine	Mid Miocene	6.5	5.2
integrilobum	Austria	Miocene	6.6	5.2
integrilobum	Germany	Miocene	6.6	5.2
nordenskioldi	China	Miocene	6.6	5.2
nordenskioldi	China, Shandong	Miocene	6.6	5.2
nordenskioldii	North Korea	Miocene	6.6	5.2
mordenskioldii	Russian Far East, Primorye	Miocene	6.6	5.2
protojaponicum	Japan	Miocene	6.6	5.2
integrilobum	Austria	Miocene	10.4	6.7
integrilobum	Germany	Late Miocene	10.4	5.2
integrilobum	Germany	Miocene	10.4	6.7
integrilobum	Romania	Late Miocene	10.4	5.2
nordenskioldi	China	Miocene	10.4	6.7
nordenskioldi	China, Shandong	Miocene	10.4	6.7
nordenskioldii	North Korea	Miocene	10.4	6.7
nordenskioldii	Russian Far East, Primorye	Upper Miocene	10.4	5.2
nordenskioldii	Russian Far East, Primorye	Miocene	10.4	6.7
nordenskoeldi	Japan	Late Miocene	10.4	5.2
protojaponicum	Japan	Miocene	10.4	6.7
protojaponicum	Romania	Late Miocene	10.4	5.2
protomatsumurae	Japan	Late Miocene	10.4	5.2
sanciae-crucis	Romania	Late Miocene	10.4	5.2
sanctae-crucis	Germany	Late Miocene	10.4	5.2
sanciae-crucis	Romania	Miocene	16.3	10.4
sanctaecrucis	East Ukraine	Mid Miocene	16.3	10.4
integrilobum	Germany	Early Miocene	23.3	16.3
integrilobum	Germany	Lower Miocene	23.3	16.3
nordenskioldii	Russian Far East, Sakhalin	Early Miocene	23.3	16.3
protojaponicum	Japan	Early Miocene	23.3	16.3
sanciae-crucis	Romania	Early Miocene	23.3	16.3
integrilobum	Austria	Oligocene	35.4	23.3
integrilobum	Caucasus, Gruzia	Oligocene	35.4	23.3
Parviflora				
browni	Canada, British Columbia	Miocene	6.6	5.2
browni	U.S.A., Oregon	Miocene	6.6	5.2
bornwi	U.S.A., Washington	Miocene	6.6	5.2
smileyi	U.S.A., Alaska	Miocene	6.6	5.2
smileyi	U.S.A., Idaho	Miocene	6.6	5.2
smileyi	U.S.A., Nevada	Miocene	6.6	5.2
smileyi	U.S.A., Oregon	Miocene	6.6	5.2
browni	Canada, British Columbia	Miocene	10.4	6.7
browni	U.S.A., Oregon	Miocene	10.4	6.7
browni	U.S.A., Washington	Miocene	10.4	6.7
smileyi	U.S.A., Alaska	Miocene	10.4	6.7
smileyi	U.S.A., Idaho	Miocene	10.4	6.7
smileyi	U.S.A., Nevada	Miocene	10.4	6.7
smileyi	U.S.A., Oregon	Miocene	10.4	6.7
smileyi	U.S.A., Oregon	Oligocene	35.4	23.3
smileyi	U.S.A., Alaska	Eocene	56.5	35.4

Table 1. (*Cont.*)

Platanoidea				
integerrimum	East Ukraine	Mid Miocene	6.5	5.2
laetum	East Ukraine	Mid Miocene	6.5	5.2
albopurpurascens	Germany	Miocene	6.6	5.2
amplum	Germany	Miocene	6.6	5.2
austriacum	Germany	Miocene	6.6	5.2
cappadocicum	Germany	Miocene	6.6	5.2
chiharae	Japan	Miocene	6.6	5.2
cinnamomifolium	Germany	Miocene	6.6	5.2
crenatifolium	Germany	Miocene	6.6	5.2
creticum	Germany	Miocene	6.6	5.2
divergens	Germany	Miocene	6.6	5.2
floridanum	Germany	Miocene	6.6	5.2
grandidentatum	Germany	Miocene	6.6	5.2
hyrcanum	Germany	Miocene	6.6	5.2
integerrimum	Caucasus, Abkhasia	Miocene	6.6	5.2
integerrimum	S. Poland	Miocene	6.6	5.2
integerrimus	S. Poland	Miocene	6.6	5.2
laetum	Caucasus, Gruzia	Miocene	6.6	5.2
laetum	S. Poland	Miocene	6.6	5.2
leucoderme	Germany	Miocene	6.6	5.2
miyabei	Germany	Miocene	6.6	5.2
mono	Germany	Miocene	6.6	5.2
monoides	Asia, Kazakhstan	Miocene	6.6	5.2
monoides	Russian Far East, Primorye	Miocene	6.6	5.2
oblongum	Germany	Miocene	6.6	5.2
oliverianum	Germany	Miocene	6.6	5.2
orientale	Germany	Miocene	6.6	5.2
orthopteron	Germany	Miocene	6.6	5.2
palaeoplatanoides	Japan	Miocene	6.6	5.2
palaeoplatanoides	Russian Far East, Primorye	Miocene	6.6	5.2
pictum	Russian Far East, Amur	Miocene	6.6	5.2
pseudomiyabei	Russian Far East, Primorye	Miocene	6.6	5.2
scottiae	U.S.A., Idaho	Miocene	6.6	5.2
scottiae	U.S.A., Nevada	Miocene	6.6	5.2
scottiae	U.S.A., Oregon	Miocene	6.6	5.2
scottiae	U.S.A., Washington	Miocene	6.6	5.2
subpictum	Austria	Miocene	6.6	5.2
subpictum	China	Miocene	6.6	5.2
subpictum	China, Shandong	Miocene	6.6	5.2
subpictum	Japan	Miocene	6.6	5.2
subpictum	North Korea	Miocene	6.6	5.2
syriacum	Germany	Miocene	6.6	5.2
trachyticum	France	Miocene	6.6	5.2
wilsonii	Germany	Miocene	6.6	5.2
albopurpurascens	Germany	Miocene	10.4	6.7
amplum	Germany	Miocene	10.4	6.7
austriacum	Germany	Miocene	10.4	6.7
cappadocicum	Germany	Miocene	10.4	6.7
chiharae	Japan	Miocene	10.4	6.7
cinnamomifolium	Germany	Miocene	10.4	6.7
crenatifolium	Germany	Miocene	10.4	6.7
creticum	Germany	Miocene	10.4	6.7
divergens	Germany	Miocene	10.4	6.7
floridanum	Germany	Miocene	10.4	6.7
grandidentatum	Germany	Miocene	10.4	6.7
huziokae	Japan	Late Miocene	10.4	5.2
hyrcanum	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4
jyrcanum	Germany	Miocene	10.4	6.7
integerrimum	Caucasus, Abkhasia	Miocene	10.4	6.7
integerrimum	Germany	Late Miocene	10.4	5.2
integerrimum	Romania	Late Miocene	10.4	5.2
integerrimum	S. Poland	Miocene	10.4	6.7
integerrimus	S. Poland	Miocene	10.4	6.7
laetum	Caucasus, Gruzia	Miocene	10.4	6.7
laetum	S. Poland	Miocene	10.4	6.7
leucoderme	Germany	Miocene	10.4	6.7
miyabei	Germany	Miocene	10.4	6.7
mono	Germany	Miocene	10.4	6.7
monoides	Asia, Kazakhstan	Miocene	10.4	6.7
monoides	Russian Far East, Primorye	Upper Miocene	10.4	5.2
monoides	Russian Far East, Primorye	Miocene	10.4	6.7
oblongum	Germany	Miocene	10.4	6.7
oliverianum	Germany	Miocene	10.4	6.7
orientale	Germany	Miocene	10.4	6.7
orthopteron	Germany	Miocene	10.4	6.7
palaeoplatanoides	Japan	Miocene	10.4	6.7
palaeoplatanoides	Russian Far East, Primorye	Miocene	10.4	6.7
pictum	Russian Far East, Amur	Miocene	10.4	6.7
platanoides	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4
pseudomiyabei	Russian Far East, Primorye	Miocene	10.4	6.7
rotundatum	Japan	Late Miocene	10.4	5.2
scottiae	U.S.A., Idaho	Miocene	10.4	6.7
scottiae	U.S.A., Nevada	Miocene	10.4	6.7
scottiae	U.S.A., Oregon	Miocene	10.4	6.7
scottiae	U.S.A., Washington	Miocene	10.4	6.7
subpictum	Austria	Miocene	10.4	6.7
subpictum	China	Miocene	10.4	6.7
subpictum	China, Shandong	Miocene	10.4	6.7
subpictum	Japan	Miocene	10.4	6.7
subpictum	North Korea	Miocene	10.4	6.7
syriacum	Germany	Miocene	10.4	6.7
trachyticum	France	Miocene	10.4	6.7
wilsonii	Germany	Miocene	10.4	6.7
integerrimum	East Ukraine	Mid Miocene	16.3	10.4
integerrimum	Germany	Middle Miocene	16.3	10.4
integerrimum	Poland	Middle Miocene	16.3	10.4
laetum	East Ukraine	Mid Miocene	16.3	10.4
laetum	Poland	Middle Miocene	16.3	10.4
palaeoplatanoides	Russian Far East, Primorye	Miocene	16.3	10.4
trachyticum	Poland	Middle Miocene	16.3	10.4
chiharae	Japan	Early Miocene	23.3	16.3
integerrimum	Germany	Early Miocene	23.3	16.3
integerrimum	Germany	Lower Miocene	23.3	16.3
monoides	Asia, Kazakhstan	Early Miocene	23.3	16.3
rotundatum	South Korea	Early Miocene	23.3	16.3
subpictum	Russian Far East, Sakhalin	Early Miocene	23.3	16.3
monoides	Asia, E. Kazakhstan	Lower Oligocene	35.4	29.3
monoides	Asia, Kazakhstan	Oligocene	35.4	23.3
palaeoplatanoides	Russian Far East, Primorye	Oligocene	35.4	23.3
rotundatum	Japan	Oligocene	35.4	23.3
rotundatum	North Korea	Oligocene	35.4	23.3
subpictum	North Korea	Oligocene	35.4	23.3
hueberi	U.S.A., Montana	Eocene	56.5	35.4
Princetona				
princetonense	Canada, British Columbia	Eocene	56.5	35.4
Republica				
ashwilli	U.S.A., Oregon	Oligocene	35.4	23.3
Rousea				
rousei	Canada, British Columbia	Eocene	56.5	35.4
Rubra				
trilobatum	Caucasus, E. Transcaucasus	Mid Miocene	6.5	5.2
trigilense	U.S.A., Alaska	Miocene	6.6	5.2
tigilense	U.S.A., Idaho	Miocene	6.6	5.2
tigilense	U.S.A., Nevada	Miocene	6.6	5.2
tigilense	U.S.A., Oregon	Miocene	6.6	5.2
tigilense	U.S.A., Washington	Miocene	6.6	5.2
tricuspidatum	Austria	Miocene	6.6	5.2
tricuspidatum	Central Germany	Miocene	6.6	5.2
tricuspidatum	Czechoslovakia	Miocene	6.6	5.2
tricuspidatum	Romania	Miocene	6.6	5.2
tricuspidatum	S. Poland	Miocene	6.6	5.2
tricuspidatum	Switzerland	Miocene	6.6	5.2
trilobatum	Austria	Miocene	6.6	5.2
trilobatum	Caucasus, E. Transcaucasus	Miocene	6.6	5.2
trilobatum	Caucasus, Gruzia	Miocene	6.6	5.2
trilobatum	Caucasus, Transcaucasus	Miocene	6.6	5.2

Table 1. (*Cont.*)

trilobatum	Caucasus, W. Transcaucasus	Miocene	6.6	5.2
trilobatum	Japan	Miocene	6.6	5.2
tigilense	U.S.A., Alaska	Miocene	10.4	6.7
tigilense	U.S.A., Idaho	Miocene	10.4	6.7
tigilense	U.S.A., Nevada	Miocene	10.4	6.7
tigilense	U.S.A., Oregon	Miocene	10.4	6.7
tigilense	U.S.A., Washington	Miocene	10.4	6.7
tricuspidatum	Austria	Late Miocene	10.4	5.2
tricuspidatum	Austria	Miocene	10.4	6.7
tricuspidatum	Central Germany	Miocene	10.4	6.7
tricuspidatum	Czechoslovakia	Late Miocene	10.4	5.2
tricuspidatum	Czechoslovakia	Miocene	10.4	6.7
tricuspidatum	East Croatia/ Bosnia/Serbia	Late Miocene	10.4	5.2
tricuspidatum	East Ukraine/ Russia/Moldavia	Late Miocene	10.4	5.2
tricuspidatum	France	Late Miocene	10.4	5.2
tricuspidatum	Germany	Late Miocene	10.4	5.2
tricuspidatum	Hungary	Late Miocene	10.4	5.2
tricuspidatum	Poland	Late Miocene	10.4	5.2
tricuspidatum	Romania	Late Miocene	10.4	5.2
tricuspidatum	Romania	Miocene	10.4	6.7
tricuspidatum	S. Poland	Miocene	10.4	6.7
tricuspidatum	Switzerland	Miocene	10.4	6.7
trilobatum	Austria	Miocene	10.4	6.7
trilobatum	Caucasus, Armenia	Upper Miocene	10.4	5.2
trilobatum	Caucasus, Armenia	Miocene	10.4	6.7
trilobatum	Caucasus, E. Transcaucasus,	Miocene	10.4	6.7
trilobatum	Caucasus, Gruzia	Miocene	10.4	6.7
trilobatum	Caucasus, W. Transcaucasus	Miocene	10.4	6.7
trilobatum	Japan	Miocene	10.4	6.7
trilobatum	Turkey-in-Europe	U. Miocene & L. Pliocene	10.4	3.4
tricuspidatum	Austria	Middle Miocene	16.3	10.4
tricuspidatum	Czechoslovakia	Middle Miocene	16.3	10.4
tricuspidatum	East Croatia/ Bosnia/Serbia	Miocene	16.3	10.4
tricuspidatum	East Ukraine/ Russia/Moldavia	Miocene	16.3	10.4
tricuspidatum	Germany	Middle Miocene	16.3	10.4
tricuspidatum	Hungary	Middle Miocene	16.3	10.4
tricuspidatum	Poland	Middle Miocene	16.3	10.4
tricuspidatum	Romania	Miocene	16.3	10.4
trilobatum	Caucasus, E. Transcaucasus	Mid Miocene	16.3	10.4
tricuspidatum	Czechoslovakia	Early Miocene	23.3	16.3
tricuspidatum	East Croatia/ Bosnia/Serbia	Early Miocene	23.3	16.3
tricuspidatum	East Eastern Bosnia	Early Miocene	23.3	16.3
tricuspidatum	Germany	Early Mioene	23.3	16.3
tricuspidatum	Poland	Early Miocene	23.3	16.3
tricuspidatum	Romania	Early Miocene	23.3	16.3
trilobatum	North Korea	E/M Mioene	23.3	10.4
trilobatum	Russian Far East, Sakhalin	Early Miocene	23.3	16.3
grosse-dentatum	Austria	Oligocene	35.4	23.3
ishikariense	Japan	Early Oligocene	35.4	29.3
kluckingi	U.S.A., Oregon	Oligocene	35.4	23.3
tigilense	U.S.A., Alaska	Oligocene	35.4	23.3
tricuspidatum	Asia, E. Kazakhstan	Lower Oligocene	35.4	29.3
tricuspidatum	Japan	Oligocene	35.4	23.3
tricuspidatum	Romania	Oligocene	35.4	23.3
trilobatum	Austria	Oligocene	35.4	23.3
trilobatum	East Belorussia	Oligocene	35.4	23.3
trilobatum	Russian Far East, Sakhalin	Oligocene	35.4	23.3
trilobatum	South East Russia	Oligocene	35.4	23.3
trilobatus	Asia, Kazakhstan	L. Eocene & E. Oligocene	38.6	29.3
ovipetrinum	U.S.A., Oregon	Eocene	56.5	35.4
Saccharina				
collawashense	U.S.A., Nevada	Miocene	6.6	5.2
collawashense	U.S.A., Oregon	Mioene	6.6	5.2
dasycarpoides	Czechoslovakia	Miocene	6.6	5.2
dasycarpoides	Germany	Miocene	6.6	5.2
dasycarpoides	Switzerland	Miocene	6.6	5.2
minutifolium	Canada, British Columbia	Miocene	6.6	5.2
minutifolium	U.S.A., Oregon	Mioene	6.6	5.2
palaeosaccharinum	Asia, Kazakhstan	Miocene	6.6	5.2
palaeosaccharinum	Austria	Miocene	6.6	5.2
pseudoginnala	Japan	Miocene	6.6	5.2
saccharum	Germany	Miocene	6.6	5.2
schorni	U.S.A., Idaho	Miocene	6.6	5.2
schorni	U.S.A., Nevada	Miocene	6.6	5.2
schorni	U.S.A., Oregon	Miocene	6.6	5.2
tyrellense	U.S.A., Idaho	Miocene	6.6	5.2
tyrellense	U.S.A., Nevada	Miocene	6.6	5.2
tyrellense	U.S.A., Oregon	Miocene	6.6	5.2
tyrellense	U.S.A. Washington	Miocene	6.6	5.2
palaeosaccharinium	Austria	Miocene/Pliocene	6.7	3.4
palaeosaccharinium	Bulgaria	Miocene/Pliocene	6.7	3.4
collawashense	U.S.A., Nevada	Miocene	10.4	6.7
collawashense	U.S.A., Oregon	Miocene	10.4	6.7
dasycarpoides	Czechoslovakia	Miocene	10.4	6.7
dasycarpoides	Germany	Miocene	10.4	6.7
dasycarpoides	Switzerland	Miocene	10.4	6.7
minutifolium	Canada, British Columbia	Miocene	10.4	6.7
minutifolium	U.S.A., Oregon	Miocene	10.4	6.7
palaeosaccharinum	Asia, Kazakhstan	Miocene	10.4	6.7
palaeosaccharinum	Austria	Miocene	10.4	6.7
palaeosaccharinum	Romania	Late Miocene	10.4	5.2
pseudoginnala	Japan	Miocene	10.4	6.7
saccharum	Germany	Miocene	10.4	6.7
schorni	U.S.A., Idaho	Miocene	10.4	6.7
schorni	U.S.A., Nevada	Miocene	10.4	6.7
schorni	U.S.A., Oregon	Miocene	10.4	6.7
tyrellense	U.S.A., Idaho	Miocene	10.4	6.7
tyrellense	U.S.A., Nevada	Miocene	10.4	6.7
tyrellense	U.S.A., Oregon	Miocene	10.4	6.7
tyrellense	U.S.A., Washington	Miocene	10.4	6.7
yamanae	Japan	Late Miocene	10.4	5.2
palaeosaccharinum	Asia, Kazakhstan	Early Miocene	23.3	16.3
palaeosaccharinum	Germany	Early Miocene	23.3	16.3
pseudocreticum	Germany	Lower Miocene	23.3	16.3
pseudoginnala	Japan	Early Miocene	23.3	16.3
dasycarpoides	Austria	Oligocene	35.4	23.3
palaeosaccharinum	Austria	Oligocene	35.4	23.3
pseudocreticum	East Europe	Oligocene	35.4	23.3
subplatanoies	Bohemia	Oligocene	35.4	23.3
Spicata				
brachyphyllum	East Ukraine	Mid Miocene	6.5	5.2
angustilobum	Germany	Late Miocene	10.4	5.2
brachyphyllum	East Ukraine	Mid Miocene	16.3	10.4
angustilobum	Germany	Early Miocene	23.3	16.3
engelhardtii	Germany	Early Miocene	23.3	16.3
angustilobum	Austria	Oligocene	35.4	23.3
articum	America	Oligocene	35.4	23.3
articum	Artic	Oligocene	35.4	23.3
articum	Eurasia	Oligocene	35.4	23.3
brachyphyllum	America	Oligocene	35.4	23.3
brachyphyllum	Artic	Oligocene	35.4	23.3
brachyphyllum	Eurasia	Oligocene	35.4	23.3
haselbachensis	Germany	Early Oligocene	35.4	29.3
oishii	Japan	Early Oligocene	35.4	29.3
articum	China	Eocene	56.5	35.4
articum	Russian Far East, Sakhalin	Early Paleocene	65.0	60.5
Spitza				
spitzi	U.S.A., Washington	Eocene	56.5	35.4
Stewarta				
hillsi	U.S.A., Washington	Eocene	56.5	35.4
stewarti	Canada, British Columbia	Eocene	56.5	35.4
Torada				
stonebergae	Canada, British Columbia	Eocene	56.5	35.4

Table 1. (*Cont.*)

stonebergae	U.S.A., Washington	Eocene	56.5	35.4
toradense	Canada, British Columbia	Eocene	56.5	35.4
washingtonense	U.S.A., Washington	Eocene	56.5	35.4
Trifoliata				
trifloriformis	Russian Far East, Primorye	Miocene	6.6	5.2
trifoliatum	China	Miocene	6.6	5.2
subnikoensefidium	Japan	Late Miocene	10.4	5.2
trifloriformis	Russian Far East, Primorye	Upper Miocene	10.4	5.2
trifloriformis	Russian Far East, Primorye	Miocene	10.4	6.7
trifoliatum	China	Miocene	10.4	6.7
trifloriformis	Russian Far East, Primorye	Oligocene	35.4	23.3
Trilobata				
hilgendorfii	Russian Far East, Primorye	Miocene	6.6	5.2
prototrifidium	North Korea	Miocene	6.6	5.2
prototrifidum	Russian Far East, Primorye	Miocene	6.6	5.2
subginnala	China	Miocene	6.6	5.2
hilgendorfi	Russian Far East, Primorye	Miocene	10.4	6.7
prototrifidium	North Korea	Miocene	10.4	6.7
prototrifidum	Russian Far East, Primorye	Miocene	10.4	6.7
subginnala	China	Miocene	10.4	6.7
prototrifidium	Russian Far East, Primorye	Miocene	16.3	10.4
hilgendorfii	Russian Far East, Primorye	Oligocene	35.4	23.3
prototrifdum	Russian Far East, Primorye	Oligocene	35.4	23.3
Veluntia				
velutinum	Caucasus, Armenia	U. Miocene & L. Pliocene	10.4	3.4

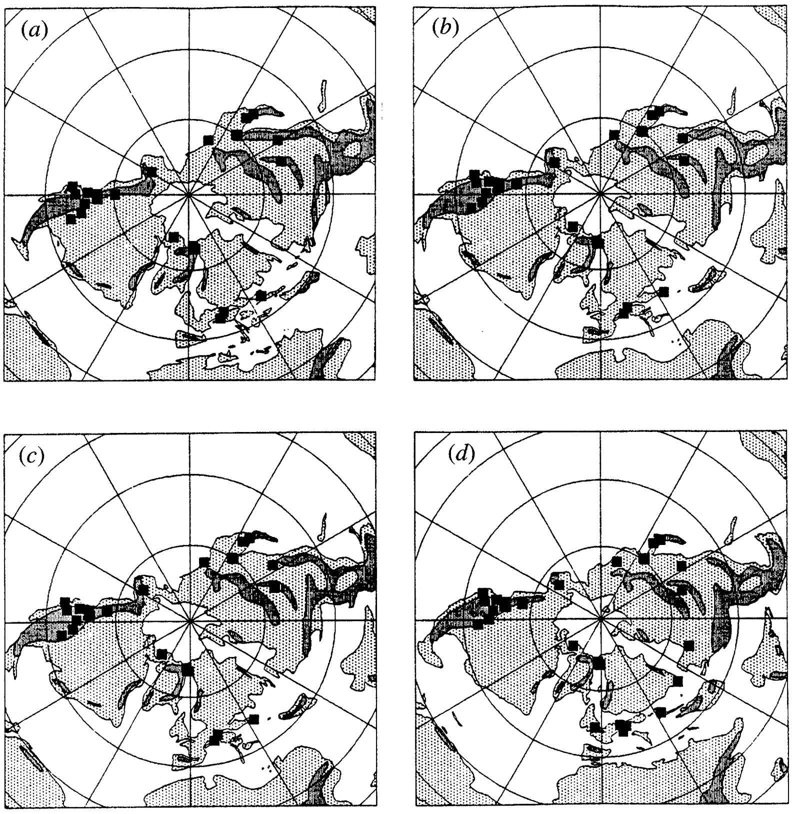

Figure 2. To see migrations in greater stratigraphic detail through the Eocene figure 1*c* above is redrawn for four separate time intervals. The movements across north Greenland can be seen to have led to the records in Europe. (*a*) 54–50 Ma BP; (b) 50–46 Ma BP; (*c*) 46–42 Ma BP; (*d*) 42–38 Ma BP.

4. PATTERNS OF MIGRATION AND EVOLUTION FROM CLADISTIC ANALYSES

Our records of Aceraceae occur in areas which are separated by geographical or ecological boundaries and here we analyse the relationships between these areas by comparing them with the taxa found there. The underlying tenet behind such cladistic biogeography (Platnick & Nelson 1978; Nelson & Platnick 1981; Humphries & Parenti 1986) is that major patterns of taxic relationships are reflected in vicariant biogeographic events, such as patterns due to major land-mass movement. Several such movements took place in the Cenozoic, not least the opening and closing of land bridges between eastern Asia and western North America, eastern North America and Europe, and eastern Asia and western Asia. If the patterns of branching on the cladogram of area relationship are

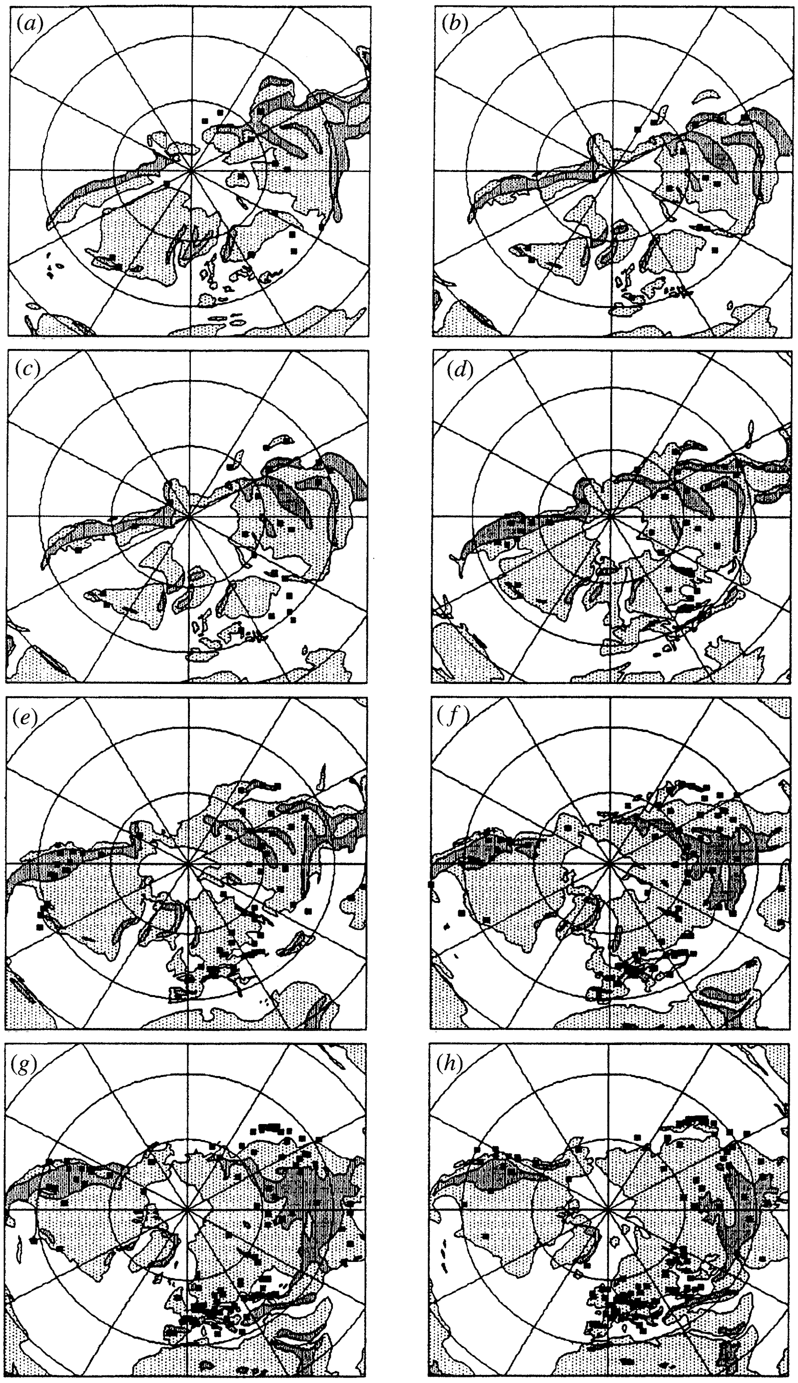

Figure 3. Eight palaeogeographic maps starting from Albian time presenting pollen data. Fossil pollen is often deposited far from its living home and so these maps show a more noisy picture than those of megafossil distribution in figure 1. However, in both sets of Palaeogene data there are strong associations of the records with major mountain ranges. (*a*)112–88.5 Ma BP; (*b*) 88.5–66 Ma BP; (*c*) 66–65 Ma BP; (*d*) 65–56.5 Ma BP; (*e*) 56.5–35.4 Ma BP; (*f*) 35.4–23.3 Ma BP; (*g*) 23.3–5.2 Ma BP; (*h*) 5.2–1.64 Ma BP.

reflected in those of the taxic cladogram, it is possible to identify the nodes of the cladogram as being due to a common history. The idea that disjunct distributions can be attributed to vicariance events encourages cladistic principles to be applied to biogeographic analysis.

The data we used for the cladistic analysis are listed in table 1. They were analysed using *Component* (Page 1993), a programme that compares cladograms using parsimony principles. Taxic cladograms and distributions are compared and generate the most parsimonious cladograms for the biogeographical area.

Where taxa occur in more than one area then the problems described above influence results by increasing the number of assumptions that have to be made when explaining the topology of the area cladogram. Extant *Acer* exhibit extensive widespread distributions (Wolfe & Tanai 1987; van Geldern *et al.* 1994). *Acer* has extensive non-vicariant histories, for example, the migration across land bridges such as that

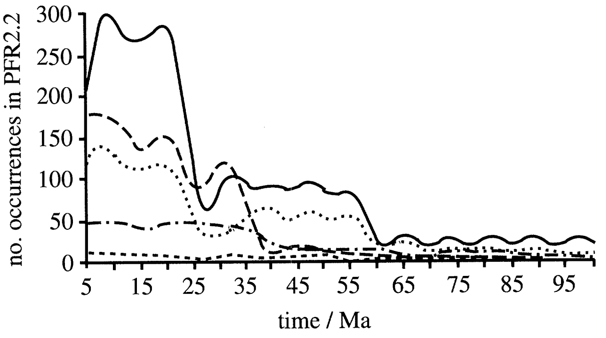

Figure 4. Absolute number of occurrences of *Acer* megafossils contained in PFR 2.2, over the last 100 Ma, for Europe (solid line), West Asia (long-dashed line), East Asia (dotted line), east North America (dot-dashed line) and west North America (short-dashed line). The vertical axis is the number of occurrences in PFR2.2. The curves have been smoothed by Fourier Tranformation Analysis (Boulter & Lhotak 1995).

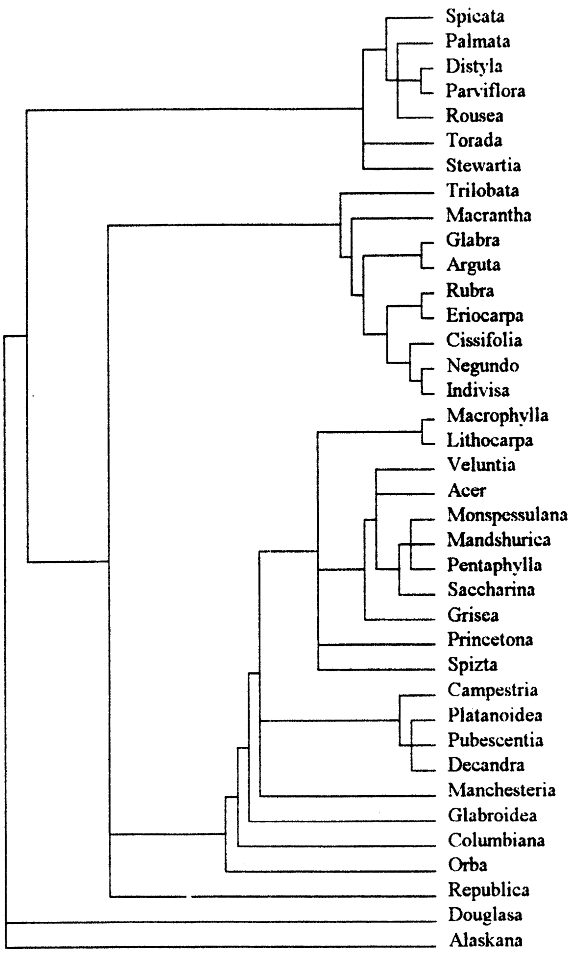

Figure 5. Wolfe & Tanai's (1987) cladogram of extinct and extant *Acer* sections upon which the present calculations are based.

between Alaska and Eastern Asia or eastern North America, Greenland and Europe. Biogeographic patterns of extant *Acer* sections might not provide sufficient resolution for a cladistic biogeographic investigation.

We have based our analysis of the data of *Acer* sections on the cladogram of fossil and extant taxa given in Wolfe & Tanai (1987). This cladogram was used to reconstruct the *Acer* cladograms for seven age ranges, shown below. The PFR database was queried for all *Acer* species present in the database at each age. The species were then assigned to their respective sections to produce a final database which included all the sections present with their geographical location at each age. From this, *Acer* records were selected that fitted within the age ranges used for the analysis (table 2).

Table 2 illustrates how only those records that fell within or close to the stratigraphic boundaries were included. Records from the PFR with low stratigraphic resolution were excluded. It can be seen that there are overlaps between the boundaries with respect to the selected age ranges, but these have been minimized. Cladograms for each age were re-drawn from the original (Wolfe & Tanai 1987) to include or exclude *Acer* sections according to their occurrence in the final database. It was then possible to analyse the data using *Component*. This requires that there be a cladogram to serve as a base-line, and that each taxon of that cladogram has a location. The original cladogram from Wolfe & Tanai (1987) (figure 5) and an example of one of the reconstructed cladograms (35 Ma plus; see figure 6) are given below.

The taxic cladograms were compared, as detailed above, using *Component* and the resulting area cladograms generated are shown in figure 7. These give the relationships of the geographical areas for each selected

Table 2. *Database record selection criteria*

(Component demands that clearly defined age ranges be used to calculate each cladogram, such as those ranges listed at the left. The PFR2.2 data has age ranges listed at the right. These allocations were used to prepare cladograms for each of the five time sequences; see figure 7)

selected age ranges used in analysis Ma	equivalent ranges from the PFR Ma
extant taxa	from Wolfe & Tanai (1987)
10–5	6.5–5.2, 6.7–3.4, 10.4–3.4, 10.4–6.7, 10.5–5.2
15–10	16.3–5.2, 16.3–10.4, 23.3–10.4
25–15	23.3–10.4, 23.3–16.3
35–30	35.4–23.3, 35.4–29.3, 38.6–29.3
40 plus	50–38.6, 56.6–35.4, 65–35.4, 65–60.5, 88–65

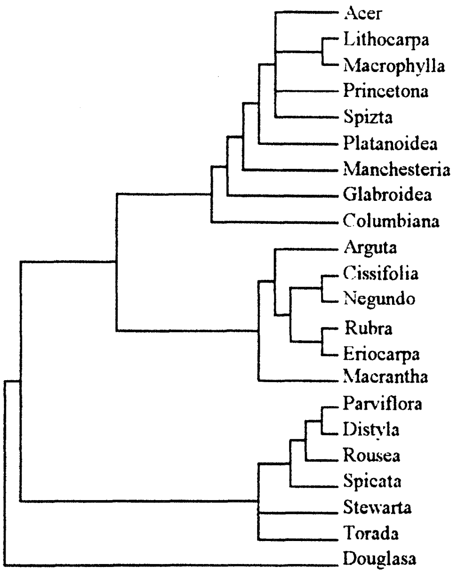

Figure 6. Cladogram reconstructed from figure 4 by *Component* adding occurrence data from Europe and Asia for records dated as being older than 35 Ma.

age. The ages to which each area cladogram corresponds are detailed in table 3.

From figure 7 it can be seen that 13 area cladograms were generated in total, and table 3 shows which ages they correspond to. The first two ages, extant taxa and 10–5 Ma BP each have a single most parsimonious area cladogram. The next two ages share the same nine area cladograms, whereas the final four ages share three. There is little agreement between the area cladograms of different ages, and within at least two of the ages there is a wide choice of possible arrangements. *Component* also compares the total possible area combinations (for a five branched cladogram this is 105), calculating the mean number of additions and losses and the standard deviation (s.d.) from that mean. From this the actual additions and losses can be compared with the mean less one s.d. to judge whether or not the results are significant. This can be seen in table 3 with the significant actual additions and losses being shown in italics. At 35–30 and 35 Ma BP plus, the number of losses of taxa needed to justify the area cladogram are greater that one would expect to get by chance.

Because of the wide range of area cladograms it is not possible to speculate about general biogeographic patterns shown by *Acer* sections, except that West and Eastern America tend to be more closely associated to one another in all but the area cladogram of extant taxa, where Western America is more closely associated with the Far East. This means that the data show that any vicariance patterns have been obscured by dispersal since the beginning of the clade's fossil record. We cannot infer too much from these results, especially when one considers both the nature of the data and the absence of a cladistic data matrix that would have allowed us to reanalyse the taxic cladogram at each time-slice.

There are several features of *Acer* biogeography and evolution that may account for the discrepancies between the area cladograms. Wolfe & Tanai (1987) postulated a complex history of dispersal and vicariant events that have contributed to the origin of the genus. They identify a diversification of the group in North America during the Eocene reaching a high level of sectional diversity in the late Middle to Late Eocene. In western North America the Middle Miocene saw the greatest diversity of *Acer* sections, followed by a subsequent decline. Wolfe & Tanai (1987) associate the extant Asian sections with the western North American taxa of the Eocene, implying dispersal from North America to Asia. This scenario fits only one area cladogram, figure 7*a*, in which western North America and the Far East are closely associated, probably by the Beringia land bridge. However, it must be noted that the cladogram that gave rise to the area cladogram 7(*a*) is composed of extant taxa only. Wolfe & Tanai (1987) thought that these Asian taxa re-entered North America by the Early Oligocene, but became extinct there by the Miocene.

There have been several hypotheses concerning the origin and biogeography of *Acer* (Deschênes 1970), but Wolfe (1981) examined the vicariance of the group in detail without using cladistic principles. He identified several patterns; an eastern Asia eastern North America pattern, another is a vicariant pattern in the section Palmata between eastern Asia and western North America. section Macrophylla, Wolfe postulates, is closely related to the Asian sections, and details several endemic sections throughout the range of *Acer*. However, Wolfe was using vicariance in a non-cladistic sense, including climatic differences and dispersal as vicariant events. Oterdoom (1990) briefly described *Acer* dispersal, and confirmed Wolfe's (1981) ideas, particularly the close association during the Miocene of eastern Asia and North America.

Our analysis has attempted to identify underlying cladistic vicariance events, but at the resolution of these data in their current form, any underlying patterns are hidden by a combination of incorrect fossil identification at the section level, over-broad biostratigraphic assignment and very widespread taxa. Assessment of sectional status even among extant *Acer* is difficult, and when doing so for extinct *Acer* specimens it is much harder. To compound the inaccuracies many of the original PFR records had to be discounted because their biostratigraphic range was too great to be any use to this analysis, and even the ones used caused problems by having stratigraphic ranges that overlapped two study age groups (see table 2).

None of the patterns of the area cladogram in this analysis show any conclusive patterns of biogeography and do not disprove the idea that the cladistic vicariance patterns have been obscured by many separate dispersions back and forward between continents (Wolfe & Tanai 1987; Wolfe 1981; Oterdoom 1990). This analysis will be repeated using a greater number of areas in the hope that this will separate taxa more completely by geography and thereby facilitate the identification of underlying biogeographic patterns.

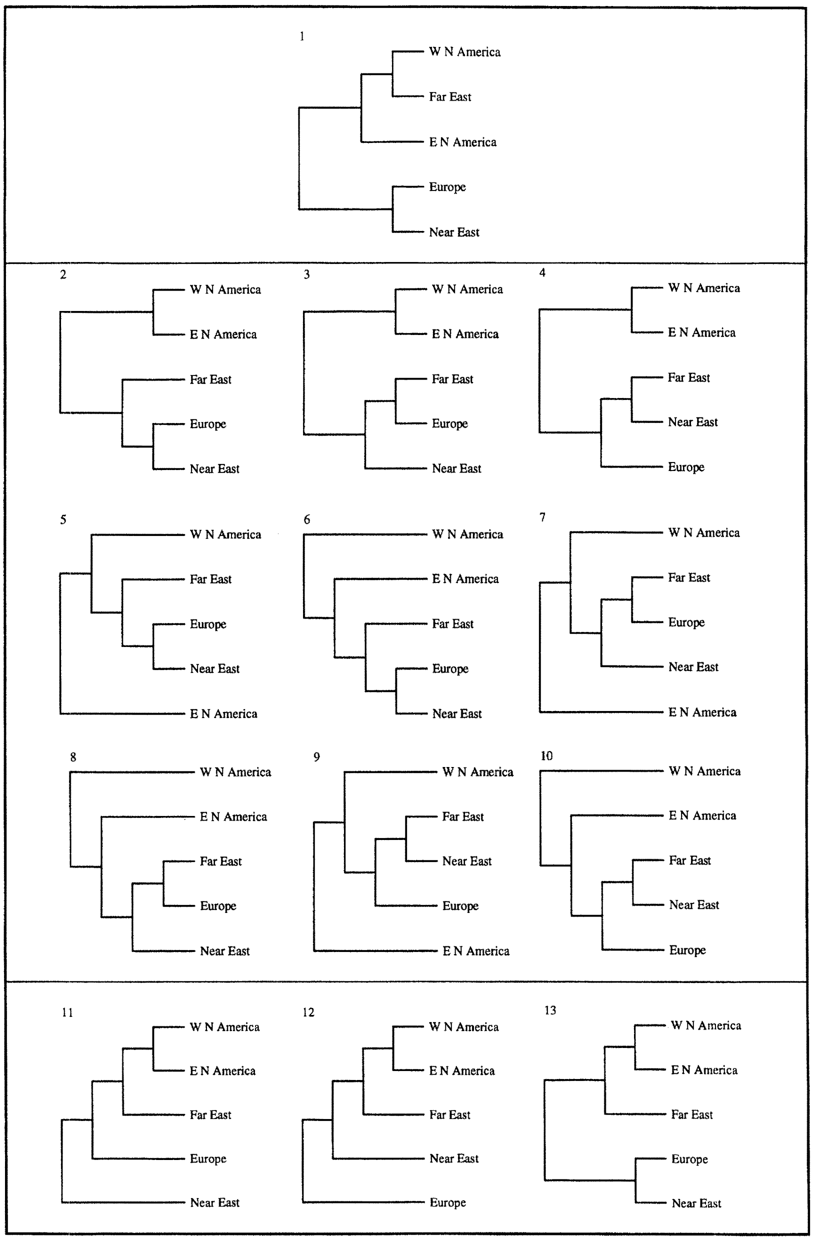

Figure 7. Thirteen area cladograms generated from *Acer* sections representing different ages which are coded in table 3. The first two stages, extant taxa and 10–5 Ma BP each have a single most parsimonious area cladogram. The next two stages share the same nine area cladograms, whereas the final four ages share three. There is little agreement between the area cladograms of different ages, and within at least two of the ages there is a wide choice of possible arrangements. *Component* also compares the total possible area combinations (for a five branched cladogram there are 105) calculating the mean number of additions and losses and the standard deviation from that mean. From this the actual additions andlosses can be compared with the mean, less one s.d. to judge whether or not the results are significant. This can be seen in table 3 with the significant actual additions and losses being shown in italics. At 35–30 and 35 plus Ma BP the number of losses of taxa needed to justify the area cladogram are greater than one would expect to get by chance.

5. CONCLUSIONS

This paper brings together about 3000 published data on the occurrence of fossils assigned to Aceraceae in the northern hemisphere. Their distribution is set out on palaeogeographic maps and time curves for different global regions, and then the data are compared to results from cladistic analysis of modern and fossil morphologies.

Our results show the likely place of origin of the group and its migration patterns through the Tertiary. They also suggest that any divisions of the clade into morphological groups of fossils older than about 35 Ma BP cannot be justified; that is the first part of the group's evolution does not show up in evidence that enables us to reconstruct any details. However, in the Neogene, sections of the group do comprise geographical and morphological entities. This may mean that the Aceraceae were busy establishing their genotypic identity until about 35 Ma BP, and that this did not show up in a stable or differentiated phenotype until later. A major climatic cooling began in the

Table 3. *Number of equally parsimonious area cladograms generated for each age and their addition and loss statistics*

(Statistically significant results are in *italics*. Area cladograms correspond to those in figure 7. The actual losses at 35–30 and 35 plus (28 and 42, respectively) are high, suggesting that the cladogram cannot be useful at these ages.)

age —— Ma	area cladograms	actual additions to reconciled cladograms	mean additions less s.d.	actual losses to reconciled cladograms	mean losses less s.d.
extant taxa	1	*58*	71.003	*34*	41.451
10–5	11	*72*	74.974	*25*	27.32
15–10	2–10	*42*	42.955	*9*	11.214
25–15	2–10	*42*	42.955	*6*	7.984
30–25	11–13	*67*	70.829	*19*	26.301
35–30	11–13	*73*	75.219	28	27.136
35 plus	11–13	*73*	77.874	42	32.451
40 plus	11–13	*73*	79.803	*33*	34.847

northern hemisphere at about this time and the physiological features which were evolving in the group may not have settled down to work properly until temperatures lowered. This hypothesis may also account for the high altitudes favoured by the earlier plants from the group, and for the migrations patterns shown here to have been across quite high latitude land bridges which would have been relatively cool territory for their time.

Our palaeogeographic plots show clearly that the group first came to prominance around the Pacific rim, most likely at high altitudes during the Early Tertiary. We hesitate to cite a first appearance because the fossil record is very incomplete and there is also a strong possibility that members of the clade were phenotypically unstable in their Late Cretaceous forms, as were the ancestors of so many other Arcto-Tertiary plants during adaptation to new ecosystems (Chaloner 1994). In the Eocene it is not possible to see vicariant development; for example, we have not been able to find evidence of one section developing on one continent and another section elsewhere. However, it seems that by Oligocene times the major evolutionary developments were complete and important morphological variation was evolved and distributed. sections are found from then onwards on every major continent of the northern hemisphere. In this study, with very much more data available than ever before, our results show no clear patterns until about 35 Ma BP when Recent structures start to show up. If our fossil record is in any way reliable the first half of the clade's existance comprised amorphous morphological character sets: the details used by modern taxonomists were still evolving.

This work started during one of the discussions at the NATO Advanced Research Workshop on *Reconstruction of North Atlantic Climate Change Using Extinct Plant Data* which the senior author directed in 1993. We are grateful to J. A. Wolfe for subsequent discussions and to M. Harley for checking the manuscript.

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