

How did Magnolias (Magnoliaceae: Magnolioideae) reach Tropical Asia?

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ABSTRACT. Extant magnolias (Magnoliaceae, Magnolioideae) have a classic disjunct distribution in southeast Asia and in the Americas between Canada and Brazil. Molecular analyses reveal that several North American species are basal forms suggesting that magnolias originated in North America, as indicated by their fossil record. We recognise four elements in their evolution: (1) Ancestral magnolias originated in the Late Cretaceous of North America in high mid-latitudes (45°–60°N) at low altitudes in a greenhouse climate. (2) During the exceptionally warm climate of the Eocene, magnolias spread eastwards, via the Disko Island and Thulean isthmuses, first to Europe, and then across Asia, still at low altitudes and high mid-latitudes. (3) With mid-Cenozoic global cooling, they shifted to lower mid-latitudes (30°–45°N), becoming extinct in Europe (*Yulania* was still present less than 2 mya.) and southern Siberia, dividing a once continuous distribution into two, centered in eastern Asia and in North America. (4) In the late Cenozoic, as ice-house conditions developed, magnolias migrated southward from both centres into moist warm temperate upland sites in the newly uplifted mountain ranges of South and Central America, southeast Asia, and the High Archipelago, where they diversified. Thus the late Cenozoic evolution of magnolias is characterised by impoverishment of northern, and diversification of southern species, the latter being driven by a combination of high relief and climate oscillations, and neither of the present centres of diversity is the centre of origin. Magnolioideae appear to consist of only the genus *Magnolia*.

Keywords. Magnoliaceae, *Magnolia*, fossils, DNA distribution, paleoclimate

Introduction

Understanding the present distribution (Fig. 1) and fossil occurrence (Fig. 2) of an ancient land-based group such as magnolias (subfamily Magnolioideae in the family Magnoliaceae) has to be done in relation to the historical disposition of land and global climate. For his Ph.D. (1956–59) Neil Opdyke studied the relationships between paleomagnetically determined latitudes and paleoclimates as inferred from temperature-sensitive deposits and from wind directions in eolian sandstones [Opdyke 1961a,b]. By placing such geological deposits at their original latitude, he was able to discuss possible past changes in climatic zones and in the positions of continents. Being able to do so is the key to unravelling the origin and paleogeographical dispersal of plant groups and individual species, in a way not available to earlier phytogeographers.

The genus *Magnolia* was described by Linnaeus in 1753 from material collected in what were then colonies of British North America. The type species is *Magnolia*

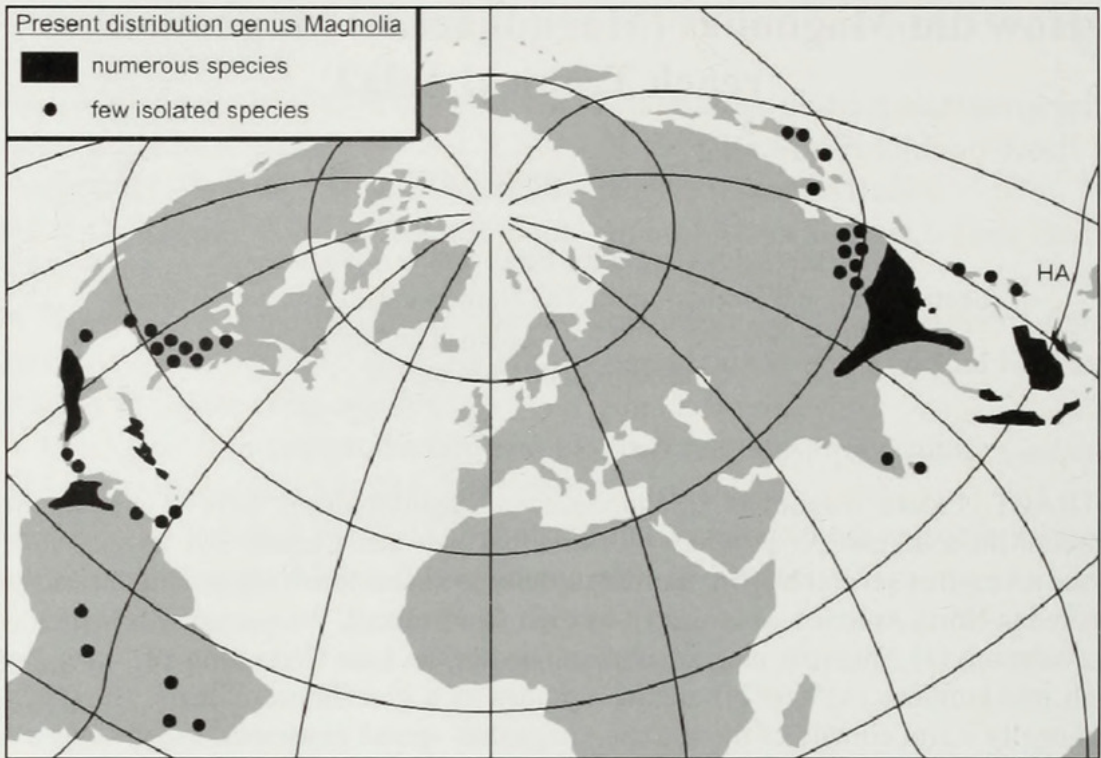


Fig. 1. Extant magnolias have a classic disjunct distribution in Southeast Asia and in the Americas between Canada and Brazil, and nowhere in between. (Source: Hebda & Irving 2004)

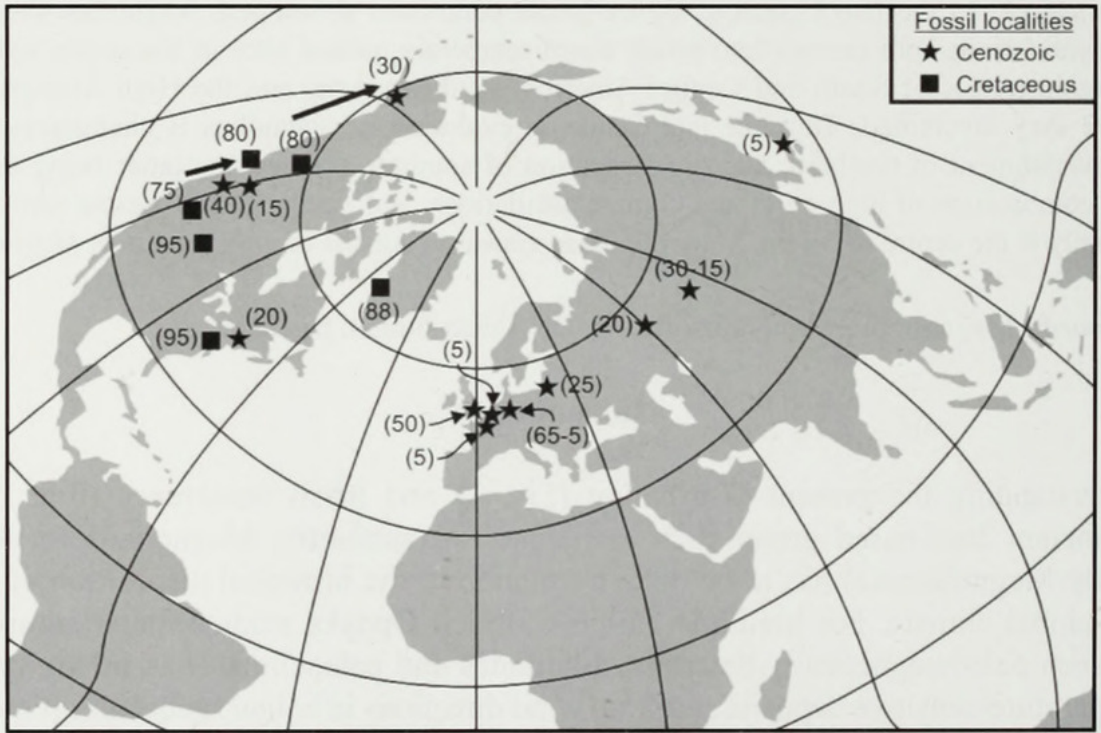


Fig. 2. Well established fossil occurrences of Cenozoic magnolias and Cretaceous ancestral taxa. Numbers in parentheses are approximate ages in millions of years. (Source: Hebda & Irving 2004)

virginiana L., the Laurel magnolia or Sweet bay. Magnolias are members of the Paleogene "boreotropical" flora. Magnolias flourished throughout the Cenozoic, and there are ancestral forms in the Late Cretaceous Epoch connecting them to one of the oldest lineages of flowering plants.

Taxonomy of modern Magnolias

Until recently, magnolias in the broad sense were divided among about half a dozen genera based on morphology and geographic isolation (Nooteboom 1993). There was much discussion concerning whether all these should be recognised as separate genera, the relationships among them, and the assignment of species to different genera (Nooteboom 1996, 2000). Recent studies of the position of flowers, the presence and absence of floral stipes (Figlar 2000), and especially of chloroplast DNA (cpDNA), have clarified relationships within the genus. Specifically, Figlar's study showed that morphological differences, once thought to separate *Magnolia* and *Michelia* L. are not valid, and cpDNA studies demonstrated that the variation within the genus *Magnolia*, as it was originally narrowly accepted, is greater than the variation among other closely related "genera" (Azuma et al. 2001, Kim et al. 2001).

This was later confirmed by study of nuclear DNA (Nie et al. 2008). For example, species in the old genus *Michelia* cluster closely with *Magnolia* species (Azuma et al. 2001, Kim et al. 2001). On the other hand, several species in the old section *Rhytidospermum* Spach, long considered to be indisputably magnolias, are, in fact, not closely related. Also, from the perspective of cpDNA as well as of nuclear DNA, western hemisphere (especially North American) species in the section *Rhytidospermum* appear to be the most diverse and basal in the cpDNA and in the nuclear DNA trees, suggesting that they could be relicts of the ancestral stock. Because there is evidence of ancient hybridisation, for instance several *Magnolia* species are polyploid, deep phylogeny cannot be deduced from chloroplast DNA, only from nuclear DNA.

Recent and historical geographical distribution of Magnolias

Molecular analyses reveal that several North American species are basal forms, suggesting that magnolias originated in North America, as indicated by their fossil record. We recognise four elements in their evolution.

(1) Ancestral magnolias originated in the Late Cretaceous of North America (Fig. 2) in the high mid-latitudes (45°–60°N), at low altitudes in a greenhouse climate.

Continental drift cannot be the sole factor in determining the distribution of extant magnolias, because reconstructing continents for Late Cretaceous and Paleogene epochs does not bring together the group's two principal zones of modern occurrence. Thus, Hebda & Irving (2004) made use of previous ideas concerning large changes

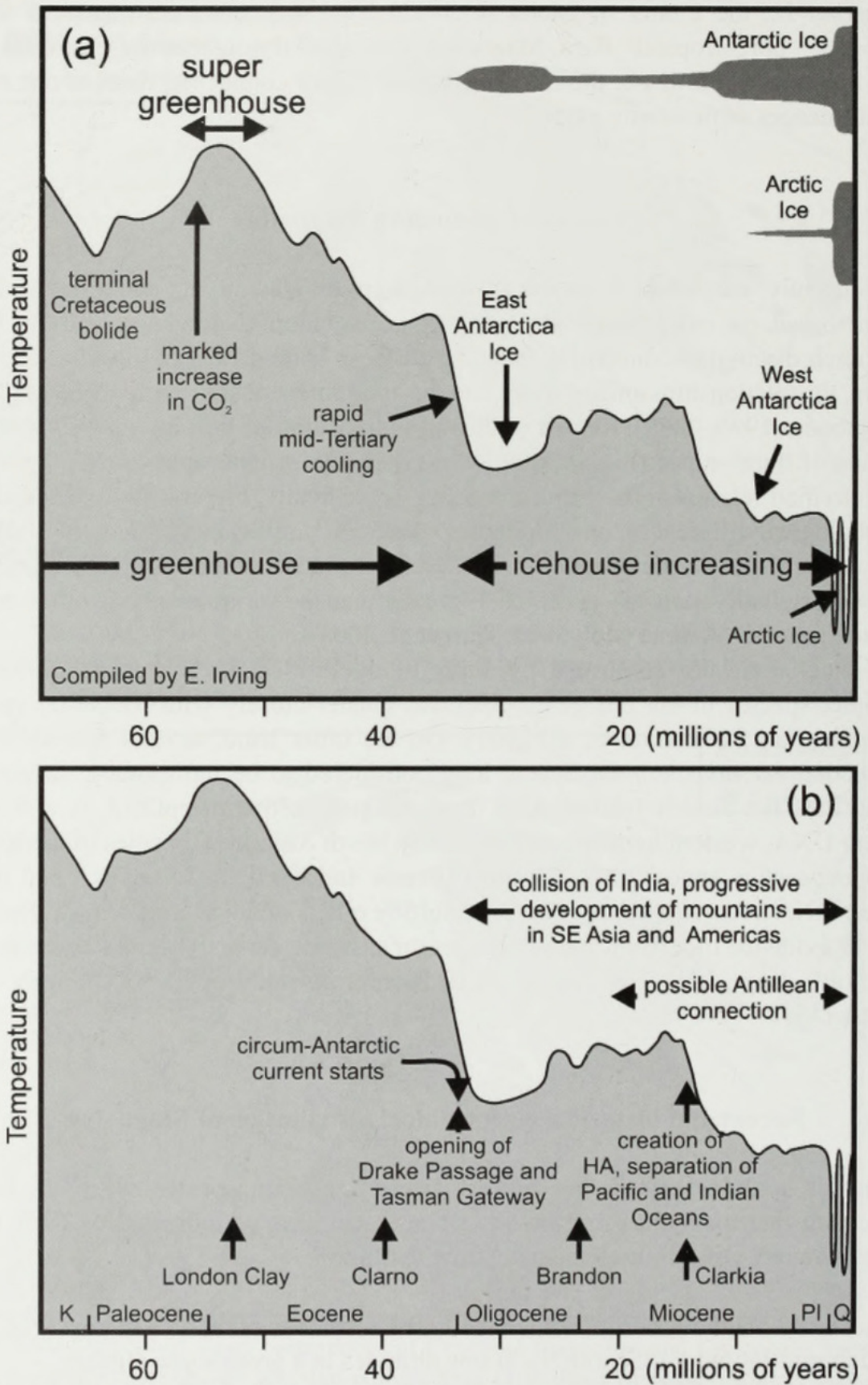


Fig. 3. Climatic (a) and paleogeographical (b) events during the past 70 Ma. HA = High Archipelago on the Sunda platform, PI = Pliocene, Q = Quaternary. (London Clay, Clarno, Brandon and Clarkia are notable fossil magnolia localities). Compiled by E.I. Irving from various sources.

in the past distribution of moist warm temperate climate, and in the development of upland habitat.

These changes are linked to the Mid- and Late Cenozoic evolution of global climate from a non-glacial (greenhouse) to a glacial (ice-house) regime and to the contemporaneous creation of regions of moist, warm temperate climate in the newly uplifted mountains of the Americas, southeast Asia, and the High Archipelago on the Sunda Platform (Fig. 3).

The history of land masses is shown in Fig. 4, based on plate tectonics (for positions of continental lithosphere), paleomagnetic evidence (for geographical grid), and the distribution of terrestrial and marine sediments.

(2) During the exceptionally warm climate of the Eocene (Fig. 4b), magnolias spread eastwards, via the Disko Island and Thulean isthmuses, first to Europe, and then across Asia, still at low altitudes and high mid-latitudes.

The Thulean land-bridge remained almost continuous until the Miocene, and the remnant Disko Island volcanoes may have reduced the obstacle of the Labrador Sea. Cross-Atlantic migration routes may, therefore, have been open but were less hospitable than earlier.

(3) With mid-Cenozoic global cooling, they shifted to lower mid-latitudes (30°–45°N), eventually becoming extinct in Europe and southern Siberia, dividing a once continuous distribution into two, and becoming centred in eastern Asia and in North America.

(4) In the late Cenozoic, as ice-house conditions developed, magnolias migrated southward from both centres into moist warm temperate upland sites in the newly uplifted mountain ranges of South and Central America, southeast Asia, and the High Archipelago (Fig. 4e).

Thus the late Cenozoic evolution of magnolias is characterised by impoverishment of northern, and diversification of southern, species, the latter being driven by a combination of high relief and climate oscillations, and neither of the present centres of diversity is the centre of origin.

The evidence from DNA

The divergence times for various major clades derived from a molecular (nuclear DNA) phylogenetic analysis of magnolias have been estimated by Nie et al. (2008). The relationship among the different groups is shown in Fig. 5. The major divergences include:

- *Liriodendron* L. and the rest of Magnoliaceae diverging c. 93 mya (*Liriodendron* then divided into two species c. 14 mya).
- The American section *Talauma* Baill., which is the base of all other magnolias, began diverging c. 54 mya. (The American species *Magnolia tripetala* L. is ancestral

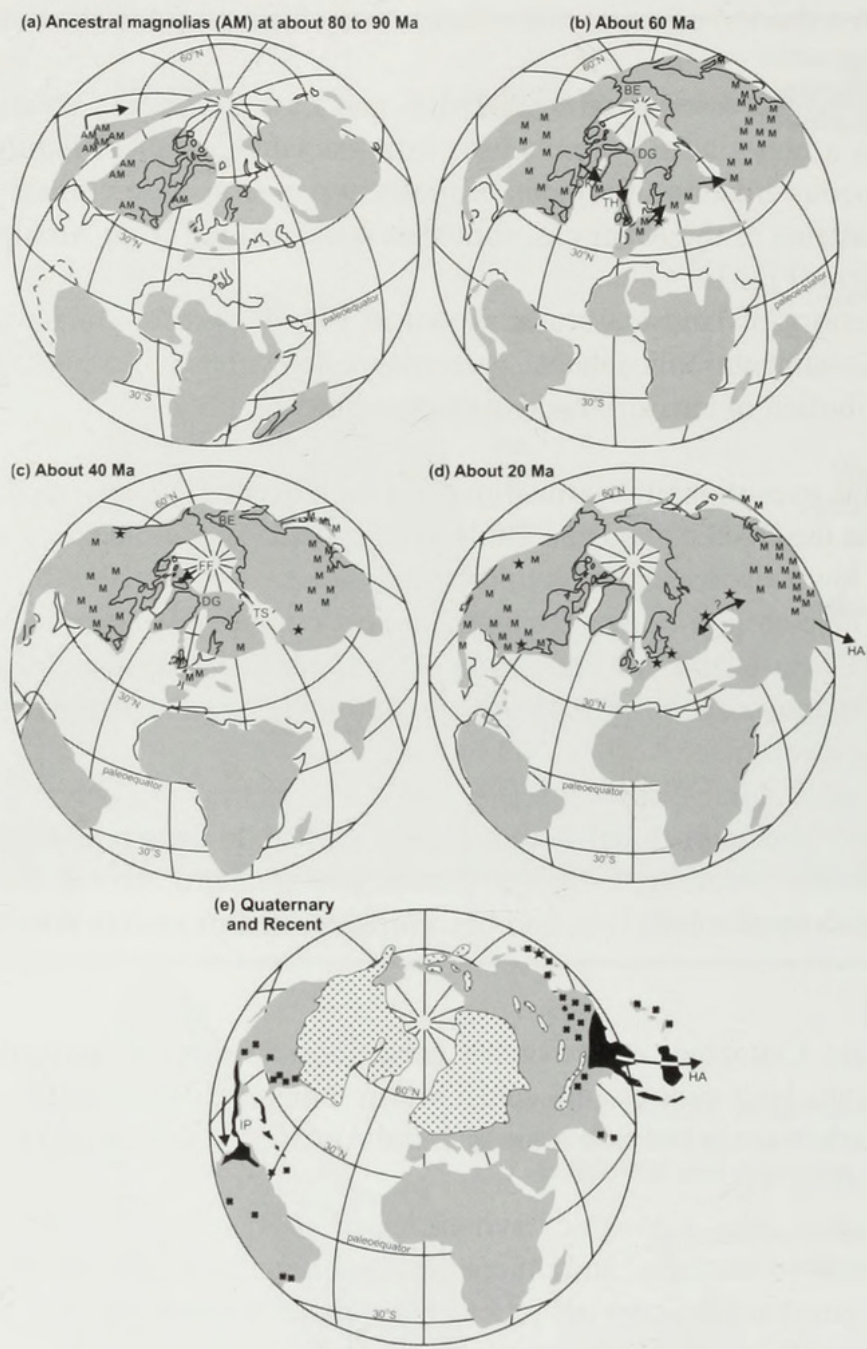


Fig. 4. **a.** Possible latest Cretaceous northward migration of Vancouver Island shown. **b.** Distribution of possible magnolia sites with respect to land bridges. **c.** Slight cooling about 40 million years ago and a beginning of magnolia migration southwards. **d.** About 20 million years ago, magnolias have become nearly extinct in Europe, but *Yulania* Spach. seeds are found until c. 2 mya (Hebda & Irving 2004, v.d. Hammen et al. 1971). **e.** The deciduous, temperate species are derived from evergreen warm-temperate species as an adaptation to the climate. (Source: Hebda & Irving 2004). BE = Bering land bridge; DG = De Geer Landbridge; FF = Fossil Forest, Axel Heiberg Island; HA = High Archipelago on the Sunda platform; IP = Isthmus of Panama; M = possible *Magnolia* site; TH = Thulean landbridge; TS = Turgai Street; * = fossil *Magnolia*; crosses indicate fewer (often more isolated) species; black areas indicate numerous species present; stippled areas are maximum glaciated cover.

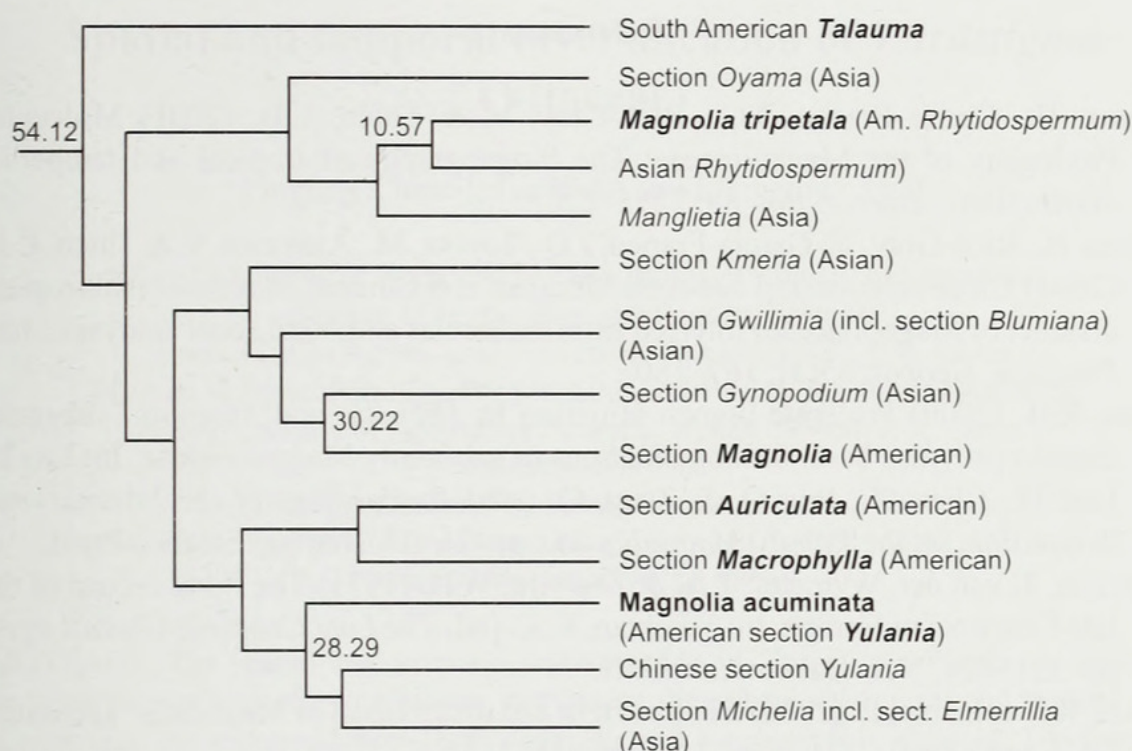


Fig. 5. A cladogram of the sections of which the nuclear DNA is known. Adapted from Fig. 6 of Nie et al. (2008).

to the other (Chinese) species of section *Rhytidospermum*, which began to diverge around 10 mya.)

— The Chinese *Magnolia sinica* (Y.W. Law) Nootboom and *Magnolia nitida* W.W. Sm. (section *Gynopodium*) are basal to section *Magnolia*, which diverged c. 30 mya. (This split happened probably in America. The American *M. virginiana* L. is basal to the rest of section *Magnolia*, which diverged as two groups c. 18 mya.)

— The American *Magnolia fraseri* Walter and *M. macrophylla* Michx., basal to both *Yulania* and *Michelia*, are clearly ancestral. *Magnolia acuminata* (L.) L., the only American *Yulania* species, is basal to both the rest of *Yulania* and *Michelia*, and diverged about 28 mya.

From such analyses, the resulting cladograms lead to the conclusion that Magnolioideae consists of only one genus, *Magnolia*. Even the subdivision into three subgenera is now obsolete. Apart from subg. *Magnolia*, only one other subgenus may be arguably recognised, *Yulania* Spach, consisting of five sections: the basal (American) sections *Auriculata* Figlar & Noot. and *Macrophylla* Figlar & Noot.; *Tulipastrum* (Spach) Figlar & Noot. with only the American *M. acuminata*; section *Yulania*; and section *Michelia*. Here the problem is that sections *Auriculata* and *Macrophylla* do not group morphologically with *Michelia* and *Yulania*.

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