On the evolution of *Magnolia*

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The genus *Magnolia* was named after the French botanist Pierre Magnol, who was the first to come up with the concept of plant families (Goetghebeur 2024). The name itself, *Magnolia,* was first published in 1703 in *Nova plantarum Americanarum genera* by Charles Plumier. In 1753 Carl Linnaeus described the first *Magnolia* in *Species Plantarum*, namely *Magnolia virginiana*, hence this species became the type species of the genus. From there onwards, species from North America were described, and later on those from Asia.

We now know that *Magnolia,* as part of the plant family Magnoliaceae, is closely related to the two-species genus *Liriodendron*. The main distribution of the genus is eastern Canada to Brazil, the Caribbean, India to the Kuril Islands and New Guinea, with the highest species diversity in warm temperate to subtropical areas (POWO 2024; Sutton 2022). The family Magnoliaceae is an old plant lineage, being part of the basal angiosperms before the split of the monocotyledons and the eudicotyledons (Goetghebeur 2024). This can be seen in the presence of ancestral characters: flowers have several whorls of tepals instead of petals and sepals and there are an undetermined number of stamens and apocarpic pistils spirally placed. The terminal flower bud is initially enclosed in stipules, known as perules in *Magnolia*. The genus evolved before the bees, hence is pollinated by beetles and has adapted tough and fleshy tepals and other floral parts to avoid damage by them.

Magnolia sensu lato or *sensu stricto*

In the past, the classification of *Magnolia* has been disputed frequently by taxonomists, because of the morphological homogeneity across the genus. Within Magnoliaceae, between two and 17 genera have been proposed, according to the lumping of species in big groups or splitting into smaller groups. Following Dandy (1927) for instance, *Magnolia* consists of nine separate genera with *Michelia, Magnolia* and *Talauma* among others, being a sister to the very distinct genus *Liriodendron*. In this mainly morphological classification, *Magnolia* is seen in the strict sense, or *sensu sticto*, and has been split from other closely related genera.

With new insights and the invention of better technologies in our molecular era, scientists have continued to discuss the classification and taxonomy of *Magnolia*. Recent studies have accepted a broader generic concept for *Magnolia,* to preserve monophyly and to be of more practical use by evolutionary biologists, horticulturists and botanists. Wang et al (2020) were able to suggest a new classification of Magnoliaceae based on phylogenetic studies that used whole chloroplast genomes of 86 species. These analyses showed the highest support for one big *Magnolia* genus, with two big clades consisting of 15 sections in total: *Gwillimia, Gynopodium, Kmeria, Macrophylla,*

Maingola, Magnolia, Manglietia, Michelia, Oyama, Rytidospermum, Splendentes, Talauma, Tuliparia, Tulipastrum and *Yulania*. One of these two big clades is tropical, uniting the Neotropical sections *Splendentes* and *Talauma* with the Asian *Gwillimia*. Only one of the 15 sections occurs in both Asia and the Americas, which is *Magnolia* Sect. *Rytidospermum* (Goetghebeur 2024). The paper discusses *Magnolia* in the broad sense, or *sensu lato*, with more than 300 species, hence incorporating different closely related genera. Wang et al (2020), provide a key to the different sections within *Magnolia s.l.*, see opposite. Some important morphological characteristics to recognise different sections are the manner of attachment of the stipules; plants being deciduous or evergreen; the opening of the anthers and the carpels; the branching pattern; the placement of the stamens; and the type of stomata (Goetghebeur 2024).

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Magnolia campbellii 'Darjeeling'

However, opinions between taxonomists remain divided and some Asiatic studies maintain the use of *Magnolia sensu stricto*. In horticulture too, some still use *Magnolia* in a more narrow sense. On Trees and Shrubs *Online*, groups of cultivars relevant to gardens are suggested as a useful criterion to cluster distinct plants with common characteristics (Christian 2024). An example is *M. campbellii* Mollicomata Group, with cultivars that have vivid purple, pink to nearly crimson flowers with the prized 'cup and saucer' form and flower later in the season than *M. campbellii* (Foster 2024).

Key to the sections of *Magnolia* (Wang et al 2020)

1	A Flowers false terminal (flowers on axillary brachyblasts)	Sect. ***Michelia***
	B Flowers terminal	2
2	A Plants with unisexual flowers	Sect. ***Kmeria***
	B Plants with bisexual flowers or androdioecious	3
3	A Young leaf blades open in bud	Sect. ***Gynopodium***
	B Young leaf blades conduplicate in bud	4
4	A Plants deciduous	5
	B Plants evergreen (except *M. decidua*)	10
5	A Leaves alternate, not in false whorls on the branches	6
	B Leaves arranged in false whorls on the branches	8
6	A Peduncles long, usually > 2 cm, and slender; fruits ellipsoid, not distorted	Sect. ***Oyama***
	B Peduncles short, < 2 cm, and robust; fruits cylindric to terete, more or less distorted	7
7	A Tepals white, pink, or purple; pronounced precocious flowering	Sect. ***Yulania***
	B Tepals green to yellow; precocious flowering less pronounced	Sect. ***Tulipastrum***
8	A Leaves cuneate to rounded or rarely subcordate at the base	Sect. ***Rytidospermum***
	B Leaves cordate to auriculate at the base	9
9	A Tepals without purple spot on base of adaxial surface	Sect. ***Tuliparia***
	B Tepals with purple spot on base of adaxial surface	Sect. ***Macrophylla***
10	A Ovules 4 to more in each carpel	Sect. ***Manglietia***
	B Ovules usually 2 in each carpel	11
11	A Stamens persistent	Sect. ***Maingola***
	B Stamens caducous	12
12	A Stipules free from the petiole	Sect. ***Splendentes***
	B Stipules adnate to petiole, or at least to the base of petiole	13
13	A Stipules only adnate to the base of the petiole (except in *M. virginiana,* stipules adnate to most of the petioles)	Sect. ***Magnolia***
	B Stipules usually adnate to 75%–100% length of the petiole	14
14	A Fruiting carpels beaked; endemic to tropical and subtropical Asia	Sect. ***Gwillimia***
	B Fruiting carpels mostly not beaked; endemic to the Neotropics	Sect. ***Talauma***

Down the course of evolution

Supporting arguments for the use of a broader species concept can be found in multiple areas of evidence. Firstly, there is an easy hybridisation of magnolias from species nested within different sections, as can be seen in the enormous number of cultivars, not only first generation, but also second


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and even further. In 2021, the *Magnolia* checklist (Lobdell 2020) reported 126 yellow flowering hybrids of *Magnolia*, which are a good example of the wide morphological variety of cultivars of multiple generations (Camelbeke 2024). The most important parent of these cultivars is *M. acuminata*, with late and inconspicuous green-yellow flowers or yellow with a blue wax in var. *subcordata*, and autumn colouration (Camelbeke 2024). Amongst the second parents is *Magnolia denudata*, with off-white flowers. *Magnolia fraseri* has greenish and creamy tepals, scented flowers, an auriculate leaf base and brown autumn colour, but has not yet been used as a parent. Cultivars are selected for bigger or more intensely coloured flowers, later or earlier flowering, better display of flowers, smaller plants, or plants with a narrower habit (Camelbeke 2024; de Spoelberch 2024). For true species, there is an overall morphological homogeneity within *Magnolia s.l.*, with minor differences illuminating a combination of specific characteristics for the different sections. This could be due to the slow evolutionary rate and the low number of polyploids within the genus, as these generate evolutionary novelty (Wang et al 2020).

Magnolia has a disjunct distribution, with representatives found in eastern North America to South America and south-eastern Asia. This distribution could be explained by what is known as the boreotropical flora concept (Dong et al 2021). The dispersion across different continents via higher latitudes (e.g. Bering Strait) would have been facilitated by warmer temperatures during the beginning of the Eocene (Azuma et al 2001). This was then followed by range restrictions, with this pattern of extending and restricting species distributions following climatic oscillations. This could also be an explanation for the amount of hybridisation within *Magnolia*, as already diverged taxa could have had secondary contacts (Dong et al 2021). By the end of the Oligocene, most of the sections within *Magnolia* were established (Dong et al 2021).



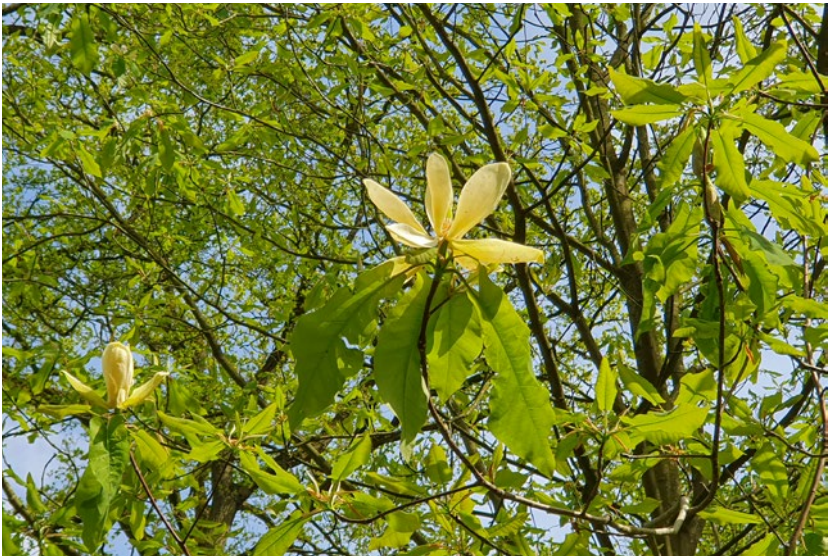
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Opposite: the off-white flowers of *Magnolia denudata*.

Right: *Magnolia acuminata* var. *subcordata*, with small yellow flowers with a blue wax.

Below: creamy flowers of *Magnolia fraseri*, with auriculate leaves.

Arboretum Wespelaar, Belgium



Magnolia today

Magnolia has become a tree of great importance in horticulture. So far, more than 1,000 cultivars have been selected (Lobdell 2020). Unfortunately, approximately 48% of magnolias in the wild are threatened, because of habitat loss due to agriculture and logging, followed by low levels of population

regeneration (Rivers et al 2016). Luckily, *Magnolia* seeds were sent to gardens in the British Isles more than 300 years ago (Gardiner 2024). They grew successfully and became a source for spreading plant material across the globe.

This article was inspired by talks given at a *Magnolia* study weekend at Arboretum Wespelaar in April, see pp.182–188.

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