Floral Ontogeny of Two Species in *Magnolia* L.

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**Abstract**

Floral ontogeny is described in two species of genus *Magnolia* (Magnoliaceae), *Magnolia albosericea* Chun et C. Tsoong, and *M. amoena* Cheng, representing subgenus *Magnolia* and subgenus *Yulania* in *Magnolia*, by using scanning electron microscope (SEM). The sequence of initiation of floral organs is from proximal to distal. The three distinct outermost and middle organs are initiated in sequence, but ultimately form a single whorl, thus their ontogeny is consistent with a sepal interpretation. The last three tepals (petals) alternate with the preceding tepal whorl. The members of androecium and gynoecium arise spirally, although the androecium shows some intermediacy between a spiral and whorled arrangement. The carpel primordia initiate in group of four to five. The order of stamen initiation within each tier is not determined. The floral ontogeny is remarkably homogeneous between the subgenus *Magnolia* and subgenus *Yulania* that does not support the resuming of genus *Yulania*.

**Key words:** floral ontogeny; *Magnolia albosericea*; *Magnolia amoena*; subgenus *Magnolia*; subgenus *Yulania*.


Magnoliaceae has been considered to be one of the earliest flowering plant. This family is a well-defined and horticulturally important basal angiosperm family of about 230 species of trees and shrubs characterized by large flowers with numerous tepals and fertile parts inserted separately on an elongated axis. More than 80% of species of Magnoliaceae are distributed in subtropical and tropical regions of eastern Asia; the remainder occurs in America, indicating a relictual tropical disjunction (Azuma et al. 2001). Renewed debate on the systematics of the family has been stimulated by several recent cladistic analyses, both morphological (Li and Conran 2003) and molecular (Shi et al. 2000; Kim et al. 2001), but several outstanding questions remain.

Dandy (1927) proposed the first comprehensive taxonomic treatment of Magnoliaceae, which recognized ten genera distributed in two tribes: Liriodendraceae (sole genus *Liriodendron*) and Magnolieae, including *Magnolia*, *Manglietia*, *Michelia*, and six smaller genera. Subsequent authors have proposed several different infrafamilial taxonomic schemes, but all of them divide the family into two subfamilies, of which one, Liriodendroideae, includes the sole genus *Liriodendron*, and the other, Magnolioideae includes a variable number of genera. Law’s (Law 1984) Magnolioideae included two tribes: Magnolieae, with terminal flowers, and Michelieae, with axillary flowers. Nooteboom (1985) and Cheng and Nooteboom (1993) reduced genera of Magnolioideae first to six genera (Cheng and Nooteboom 1993) and later to two, and discarded all tribes and subtribes (Nooteboom 2000).

The large magnolia flower was once considered to represent the primitive floral type (the Ranalian hypothesis), based mainly on the existence of many fossil forms. However, recent improved understanding of phylogenetic relationships, together with new fossil discoveries, have demonstrated that small flowers with relatively few organs predominate in basal angiosperms; the large flowers of Magnoliaceae are now normally regarded as relatively specialized within this grade (for reviews see Crane et al. 1994; Endress 1994). Earlier work on floral ontogeny in Magnoliaceae includes investigations of the floral apex and carpel of *Michelia fuscata* Blume (Tucker 1960, 1961). This research work demonstrated the floral apex ontogeny and phyllotaxis of the carpel by microtome sections under...
light microscope (LM), of which the spatial reconstruction was obtained by comparing sections afterwards. van Heel (1981, 1983) only described the carpel development in *Magnolia stellata* Sieb. et Zucc. and *Michelia montana* Blume under SEM based on bigger flora buds, but unfortunately did not have access to primordial stages. A brief floral ontogeny in *Liriodendron tulipifera* L. and *Magnolia denudata* Desr. was also included (Erbar and Leins 1994; Leins and Erbar 1994; Leins 2000). Little information about the early flora apex and initiation of perianth and stamens was provided in their studies. A floral ontogenetic investigation could provide more characters for discussing the relationships of the family. Here floral ontogeny of subgenus *Magnolia* and subgenus *Yulania* were examined in detail, in order to fill the gaps in our current knowledge of the family and place them in a systematic context.

**Results**

**Floral morphology**

Flowers are solitary, bisexual, and haplomorphic, i.e. with spirally arranged organs inserted separately onto an elongated axis. A ring of three bract-like structures surrounds the flower; these are normally interpreted as sepals. The perianth consists of normally nine free tepals which surround numerous free stamens and carpels respectively (Figures 1, 2).

**Floral development**

At initiation, the floral apex is circular (Figures 3, 4) in two species examined, and subsequently develops three sepals surrounding a triangular floral primordium (Figures 5, 6). During subsequent floral development the shape of the floral apex varies from flat during perianth initiation to highly convex at later floral stages. The later convex shape of the apex is maintained through appendage initiations. Tepals, stamens and carpels are initiated in groups at slightly different levels around the periphery of the apex. The members of each group of organs are initiated closely in time.

The three outer tepals are initiated in sequence but ultimately form a single whorl. At this stage, the shape of the floral primordium changes circular form to triangular. The second whorl of three semicircular tepal primordia are initiated at the tips of the three angles formed by the triangular floral primordium and alternate with the outer tepal whorl. One of them is initiated slightly earlier than the other two. Similarly, the innermost third whorl of three perianth primordia differ slightly from one another in time of initiation and alternate with those of the middle whorl and hence are opposite those of the first whorl (Figures 6–8). Thus, the tepals are initiated in spiral acropetal succession, but are trimerously whorled; the internodes between petals seldom elongate. There is a considerable difference in size between primordia of the first and the second whorl during early stages. Following completion of tepal initiation, the central floral primordium is more or less circular.

Stamen primordia are initiated slightly later than the third whorl of perianth primordia. One or two stamen primordia arise opposite the first tepal primordium (Figure 9). Stamens are initiated acropetally, successively and rapidly around the base of the apex (Figures 10–14). We could never observe a regularly spiral sequence of stamen primordia. The order of stamen initiation within each tier is not determined. During stamen development, the floral apex displays its greatest height and diameter.

When all stamen primordia have been initiated and begun to broaden, the remaining floral apex becomes slightly flatter. Some rounded bulges are initiated in groups of four to five, which are larger than the stamen primordia (Figures 15, 16). Carpel primordia are free and initiated alternately in acropetal succession. During carpel initiation, the floral apex gradually diminishes in height and diameter. There is no differentiation of stigma and style at this stage. In older buds of two species examined here, stamens and carpels are arranged spirally on the flower axis (Figures 17, 18).

**Figures 1–8.** Mature flowers and development of the tepals (SEM).

1. Flower of *Magnolia albosericea* Chun et C. Tsoong.
2. Flower of *M. amoena* Cheng.
3. Floral apex of *M. albosericea*.
4. Floral apex of *M. amoena*.
5. Differentiation of three outer tepals surrounding the triangular floral apex (*M. albosericea*).
6, 7. Differentiation of the second tepal whorl, one slightly earlier than the other two (*M. amoena*).
8. Differentiation of the third tepal whorl (*M. albosericea*).

f, floral apex; t1, tepal of first whorl; t2, tepal of second whorl; t3, tepal of third whorl. Bars, 100 µm.

9. Differentiation of stamens, opposite the first tepal primordia (arrow) (*M. albosericea*).

10. Differentiation of stamens (*M. amoena*).

11, 12. Acropetal differentiation of stamens. At this stage the floral apex reaches its greatest height and diameter (*M. albosericea*).

13, 14. Acropetal differentiation of stamens (*M. amoena*).

f, floral apex; s, stamen primordium; t2, tepal of second whorl; t3, tepal of third whorl. Bars, 100 µm.
Plantefol (1948) suggested two hypotheses concerning the placement of petals, stamens and carpels on the receptacle. One was that the “generative centers” proliferate at the level of the petals to produce many “floral helices”. This inferred that apical growth continues in the flower. Another suggestion was that after petal initiation, the remaining productive surface of the floral apex subdivided simultaneously into numerous small plaques, which implied that no further apical growth occurs in the floral apex. As described above, it is obvious that apical growth continues during floral development in *Magnolia*, but the floral apex gradually diminishes in diameter and height during carpel initiation. The results correspond with Tucker’s (1961) observations on *Michelia fuscata*. Thus, the flower of Magnoliaceae is not a “true” determinate structure, since it does not...
not terminate in an organ or organ whorl, as in typical eudicot flowers. Rather, the floral meristem achieves determinacy by gradual diminution (Tucker 1960), as with the indeterminate apex of racemose inflorescences.

Genus *Yulania* Spach was established by Spach in 1839. It was later treated as subgenus or section in genus *Magnolia* (Dandy 1950). Recent researches revealed that subgenus *Yulania* has a closer relationship with genus *Michelia* instead of *Magnolia* (Figlar 2000). Fu (2001) and Gong et al. (2001) suggested that the genus *Yulania* should be resumed based on morphological differences and procreant insulation. However, floral ontogeny is remarkably homogeneous between these two subgenera. The similarity exists both in the style and the sequence of the initiation of all floral parts. These results support the classification that genus *Magnolia* consists of subgenus *Magnolia* and subgenus *Yulania*.

Based on the observation, tepals arranged in a more or less whorled structure surrounding more or less spirally arranged fertile organs, although the androecium show some intermediacy between a spiral and whorled arrangement. Erbar and Leins (1994) observed a similar intermediate organization in *Magnolia denudata* and *Liriodendron tulipifera*, and suggested that a whorled condition is derived from a spiral one in basal angiosperms (Erbar 1983, 1988; Erbar and Leins 1983, 1994). In some Magnoliidae not examined here, such as genus *Pachylarnax*, *Dugandiodendron*, and *Woonyoungia* (Li and Conran 2003) the carpel number is reduced to less than ten, and arranged in whorls. For example, van Heel (1983) described early carpel formation in *Michelia montana*, which is unusual in possessing only two to four stalked carpels arranged in pairs.

One outstanding question of floral morphology in Magnoliidae is whether the outmost organs represent bracts, as indicated by their mature structure, or sepalas, as Ueda (1986) proposed. The three distinct outermost organs are initiated in sequence, but ultimately form a single whorl; thus their ontogeny is consistent with a sepal interpretation.

Materials and Methods

Specimens at a range of developmental stages were collected from the Magnolia Garden at the South China Botanical Garden, the Chinese Academy of Sciences. Voucher specimens of samples collected were deposited in the herbarium of South China Botanical Garden (IBSC). Two species were investigated: *Magnolia albosericea* Chun et C. Tsoong, (subgenus *Magnolia*, section *Gwillimia*) (IBSC: FX Xu 02008), *Magnolia amoena* Cheng (subgenus *Yulania*, section *Yulania*) (IBSC: FX Xu 02002).

Material was fixed in formalin acetic alcohol (FAA: 70% alcohol, formaldehyde and glacial acetic acid in a ratio of 85:10 : 5). For scanning electron microscope (SEM) examination, buds were dehydrated in an ethanol series. Dehydrated material was then critical-point-dried using a Baltec CPD 030 critical point drier, mounted onto SEM stubs using double-sided adhesive tape, coated with platinum using an Emitech K550 sputter coater, and examined using a JEOL cold field emission JSM-6360LV at 4–5 kV.

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References


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