

Floral anatomy of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar (Magnoliaceae): recognition of a partial pentamery

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ABSTRACT

Floral anatomy of the endemic Chinese species *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar was studied in order to clarify its disputed relations within the family Magnoliaceae. Its most striking feature is a change in floral merosity, clearly demonstrated by the vasculature, the three perianth whorls being often pentamerous, while only the gynoecium might be considered as trimerous. Interestingly the androecium exhibits an intermediate condition, as the stamens are supplied by 15 vascular trunks, a pattern reminiscent of that previously described in *Meiocarpidium* Engl. & Diels (Annonaceae), with two levels of 15 trunks each. Perianth pentamery, almost completely lacking sclerenchyma at anthesis, as well as a sharp separation in the vascular supply of the perianth and sexual parts, characterize unmistakably this species from all other known Magnoliaceae, even though its relationship with *Magnolia* sect. *Manglietia* is otherwise strengthened by stamen and carpel pattern. This very unexpected pentamery – somewhat comparable to that of the monocot genus *Pentastemona* Steen. – is briefly discussed. The value of vascular anatomy as an additional but essential source of data to complement the standard phyllotactic and ontogenetic approaches used for the flower, is emphasized again.

KEY WORDS

Magnoliaceae,
Magnolia,
Manglietia,
Sinomanglietia,
cortical vascular system
(CVS),
floral anatomy,
merosity,
pentamery.

RÉSUMÉ

Anatomie florale Magnolia decidua (Q.Y.Zheng) V.S.Kumar (Magnoliaceae): reconnaissance d'une pentamérie partielle.

L'anatomie florale de l'espèce endémique chinoise *Magnolia decidua* a été étudiée, afin de préciser ses affinités discutées à l'intérieur des Magnoliacées. Le fait le plus marquant est le changement de mérie dans la fleur, bien démontré par la vascularisation, les trois verticilles périnthaires étant le plus souvent pentamères, tandis que le gynécée peut être interprété comme trimère. L'androcée, de façon remarquable, montre une situation intermédiaire, où les étamines sont irriguées par 15 troncs vasculaires, selon un modèle rappelant celui précédemment décrit chez *Meiocarpidium* Engl. & Diels (Annonaceae), avec deux étages de 15 troncs chacun. La pentamérie périnaire, l'absence presque complète de sclérenchyme à l'anthèse, ainsi que la séparation nette des vascularisations des pièces périnthaires et sexuées, caractérise sans aucun doute cette espèce de toutes les autres Magnoliaceae connues, même si ses affinités avec *Magnolia* sect. *Manglietia* apparaissent évidentes par la structure des étamines et des carpelles. La signification de cette pentamérie tout à fait inattendue – assez comparable à celle de *Pentastemona* Steen. dans les Monocotylédones – est brièvement discutée. L'intérêt de l'anatomie vasculaire florale est une nouvelle fois souligné, comme donnée complémentaire – mais essentielle – aux approches phyllotaxiques et ontogénétiques classiques.

MOTS CLÉS

Magnoliaceae,
Magnolia,
Manglietia,
Sinomanglietia,
systèmes vasculaires
corticaux,
anatomie florale,
mérie,
pentamérie.

INTRODUCTION

The endemic Chinese genus *Sinomanglietia* was established by Yu in 1994 for four specimens collected in Jiangxi Province (Mingyue Mountain, Yichun City) between 1988 and 1993. A full description – including flowers and mature fruits – was provided for the single species, *S. glauca* Z.X.Yu & Q.Y.Zheng (Fig. 1, under the accepted name *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar; Yu 1994). The genus was at that time placed very near *Manglietia* Bl., especially because of the numerous ovules in each carpel (Tiệp 1980). However it differs by its deciduous (vs persistent) leaves, its floral bud enclosed in a single (vs several) bract, and its fruits (follicles) gradually dehiscent from top to bottom of the gynoecium on the full length of the inner (ventral) carpel side and almost so along the dorsal suture.

A perianth of 15 tepals (up to 18, according to Xiao & Xu 2006) was originally indicated, but this feature was readily interpreted as five whorls of three tepals each, referring to the three wide

outer tepals. Such a pattern is odd in Magnoliales as it seems rather uncommon to encounter more than three trimerous whorls (e.g., four in the recently revised annonaceous genus *Fenerivia* Diels; Deroin 2007).

The genus *Sinomanglietia* was subsequently merged under *Manglietia* (*M. decidua* Q.Y.Zheng), and synonymized under *Magnolia* by Sampath Kumar in 2006 (as *M. decidua* (Q.Y.Zheng) V.S.Kumar, see also Xia *et al.* 2008). These nomenclatural changes, although consistent with DNA sequence analysis (Azuma *et al.* 2001; Wang *et al.* 2006; Nie *et al.* 2008), were unfortunately made without any sound parallel morphological analysis.

More recently, two other – and much larger – populations of *Magnolia decidua* (yet named *Sinomanglietia glauca*) were discovered in Hunan Province (Yongshun City), about 450 km away from those in Jiangxi. They were recognized as genetically separate, a pattern that likely evolved since the Quaternary glaciation (habitat fragmentation and demographic bottlenecks, according to Zhang *et al.* 2009).



FIG. 1. — Flowers of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar at anthesis (left) and in bud (right). Courtesy of Dr Xin-Chun Lin (Zhejiang Forestry University).

MATERIAL AND METHODS

Four flower buds of *Magnolia decidua* were collected in the garden of Jiangxi Agricultural University, fixed in FAA (90 parts 70% ethanol, 5 parts glacial acetic acid, 5 parts stock formalin; no vouchers), kindly sent by Pr. Yu Zhixiong (JAU), then kept in a preservative fluid (glycerol/95% ethanol/water).

One bud was processed in a 10% aqueous solution of H_4FN during 48 h in order to remove siliceous bodies – often recorded in magnoliaceous cell walls (Nooteboom 1985) – then dehydrated through a *t*-butyl series and embedded in paraffin (melting point: 58–60°C). Serial transverse sections were cut at a thickness of 25–50 μ m and stained with Toluidine blue after Sakai (Gerlach 1984). Floral vasculature was reconstructed by drawing the serial sections using a camera lucida and then superimposing tracing papers on them.

One bud was cut lengthwise by hand in order to check the vascular connections between the floral whorls. Sections were cleared in a 20% aqueous solution of commercial sodium hypochlorite,

washed in 10% acetic acid, then lightly stained in Malachite green, cleared in toluene and observed in paraffin oil.

RESULTS

PEDICEL HISTOLOGY

In cross-section, below the point of calyx insertion and from the outside, the pedicel (*c.* 5 mm in diameter) exhibits the following tissues (Fig. 2A): a thin but strongly cutinized epidermis lined with a 1–2-layer collenchymatous hypodermis; then 9–11 layers of an annular and lignified collenchyma; finally 30–40 layers of a spongy cortex formed by cellulosic parenchyma cells in which are spread *c.* 12 bundles. The stele is made up of *c.* 60 elliptical bundles, unequal in size and coarsely arranged in a crown, separated by rays 1–3 cells in thickness. All bundles are provided with phloem fibres and a cambial zone at anthesis. The pith resembles the cortex, but appears solid, with scattered minute brachysclereid clusters. No diaphragm is formed at this stage.

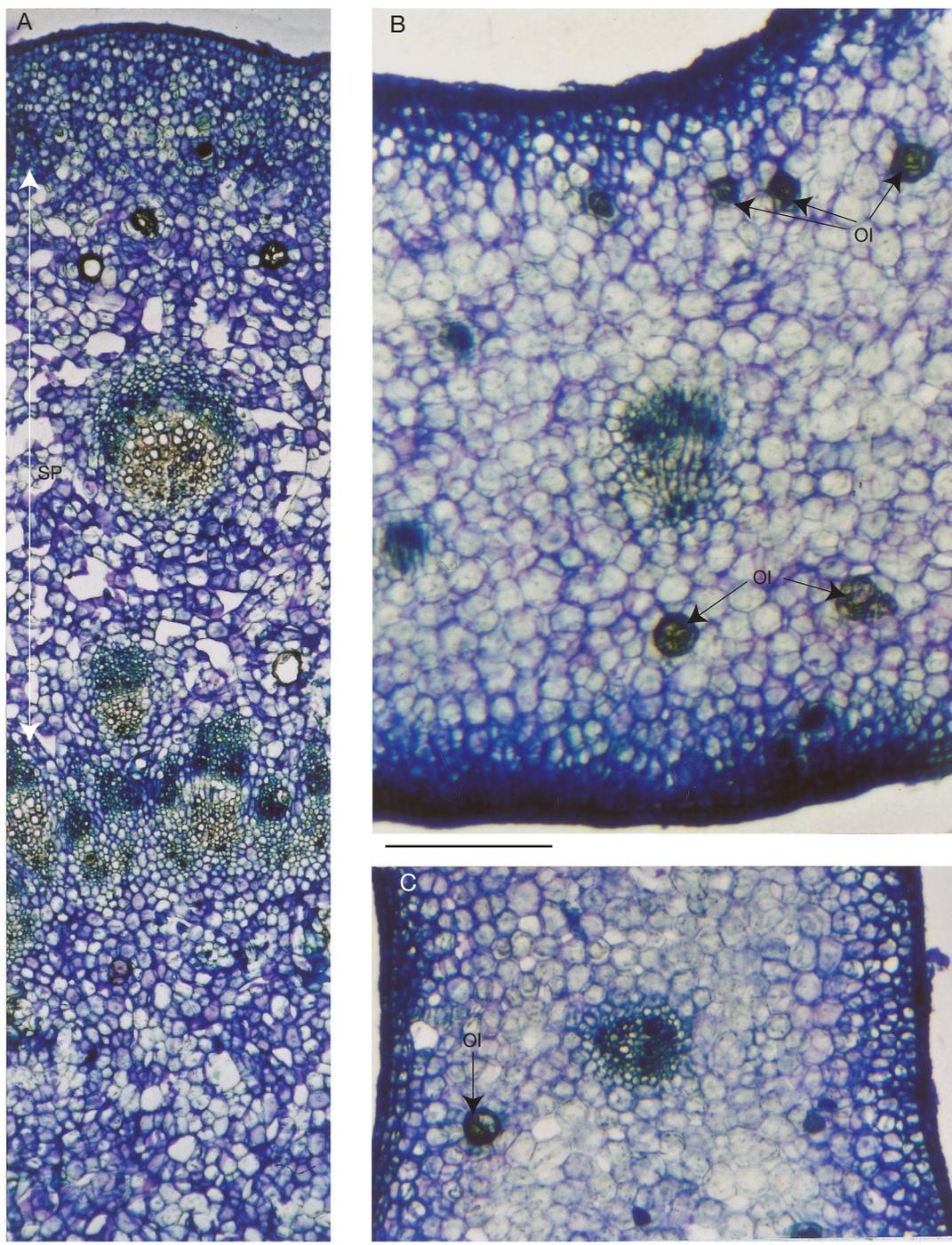


FIG. 2. — Histological details of the flower of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A**, pedicel in cross-section; **B**, **C**, sepal and petal. Abbreviations: **OI**, oil cell; **SP**, spongy parenchyma. Scale bars: 250 μ m.

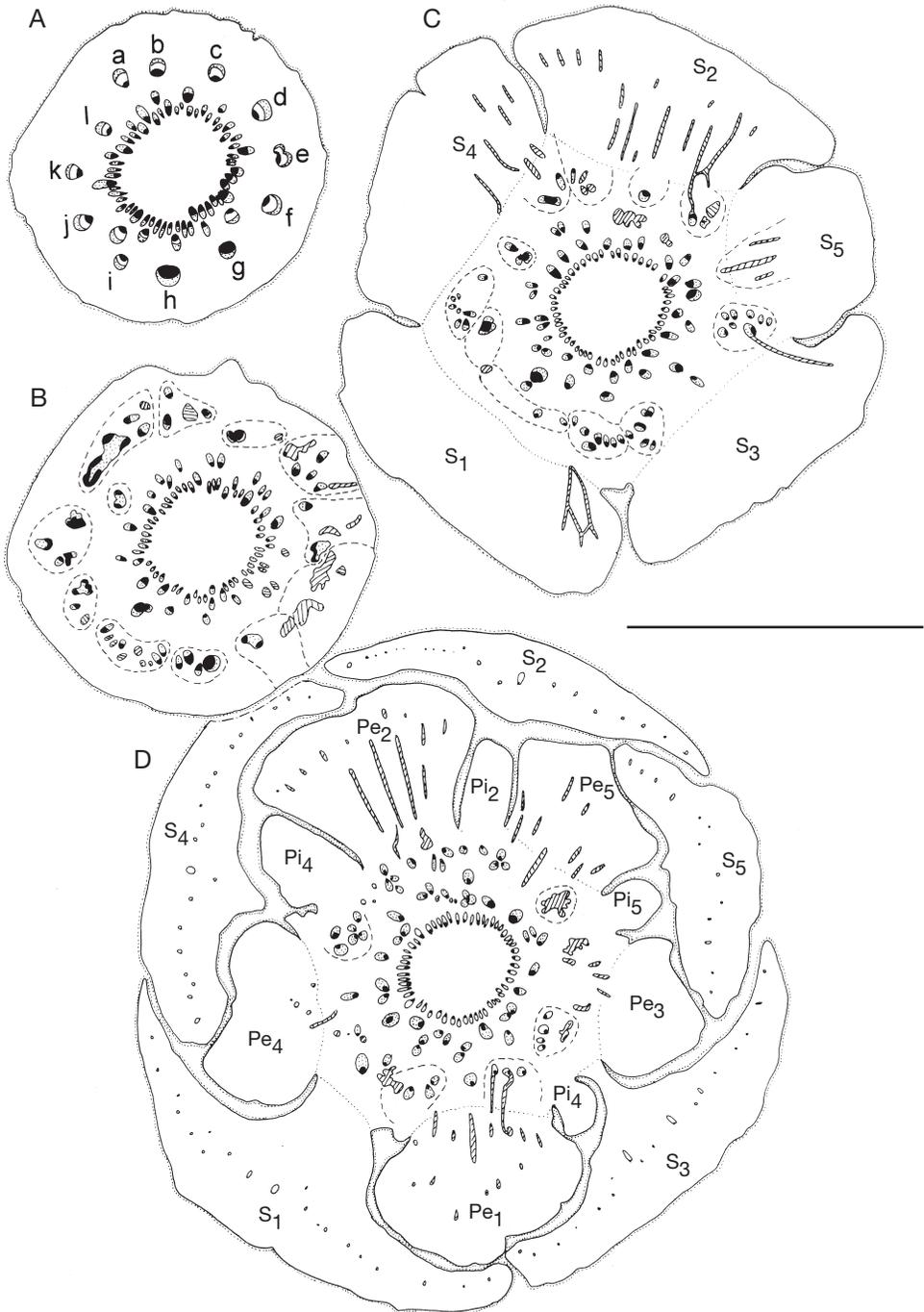


FIG. 3. — Transverse sections of the receptacle showing the floral vasculature of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A**, top of the pedicel; **B-D**, at the perianth level. **Stippled area**, phloem; **black area**, xylem; **hatching**, oblique bundles. Broken lines surround branches from the same bundle. Abbreviations: **a-l**, bundles of the outer cortical vascular system (CVS); **Pe_n**, outer petal; **Pi_n**, inner petal; **S**, sepal. Perianth members are numbered according to the observed 2/5 aestivation. Scale bar: 5 mm.

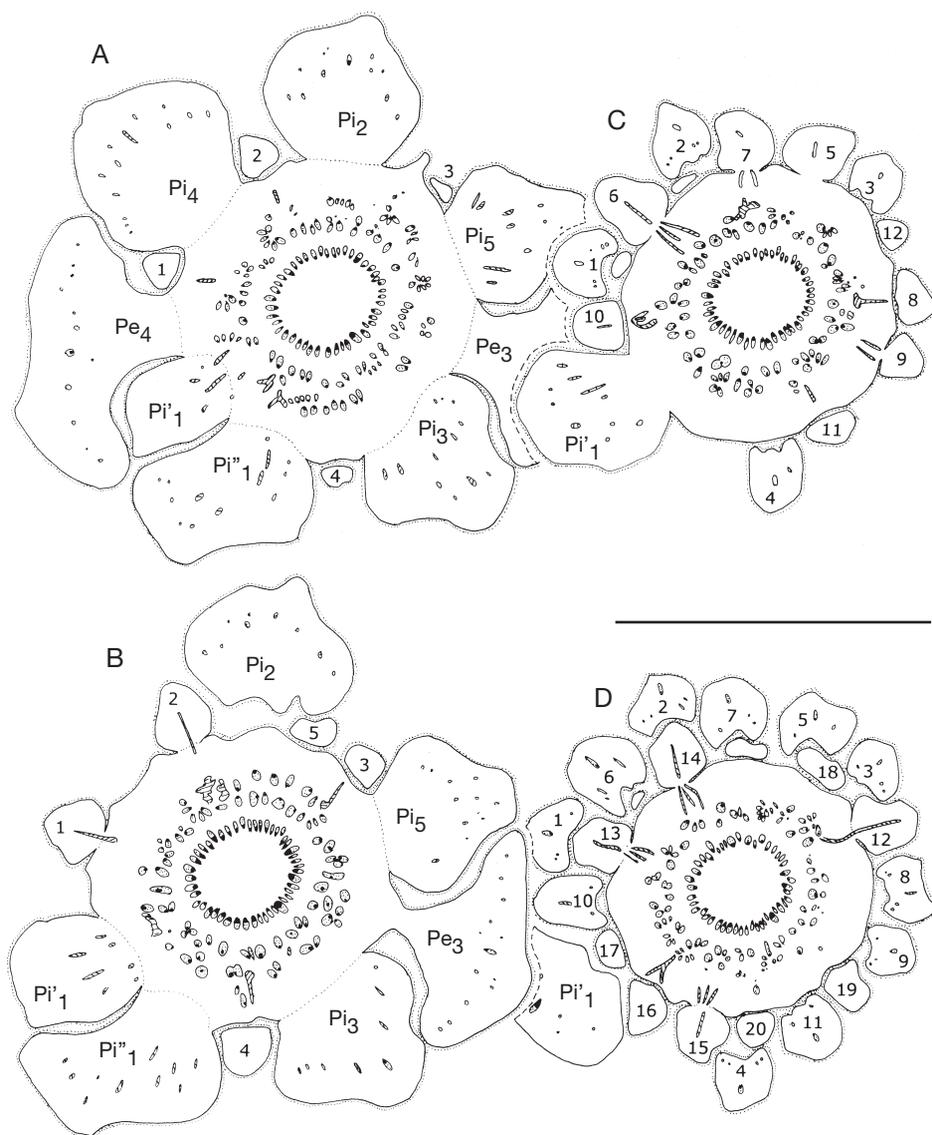


FIG. 4. — *Magnolia deciddua* (Q.Y.Zheng) V.S.Kumar: **A-D**, androecial vasculature. All stamens are numbered in their apparent insertion order. Abbreviations: **P_e**, outer petal; **P_i**, inner petal. Scale bar: 5 mm.

VASCULATURE OF THE RECEPTACLE

At the base of the receptacle, the stele is ordered in two concentric crowns (Fig. 3A), i.e. a cortical crown of *c.* 12 bundles (a-l) and a central one of *c.* 60 bundles, somewhat irregular in outline due to *c.* 10 protruding bundles. The whole outer crown splits into several sections (Fig. 3B) and supplies a

major part of the calyx vasculature and the lateral traces of the petals, while protruding bundles are emitted as a second lax crown, providing mainly the median petal bundles (Fig. 3C, D). Thus the outer crown may be described as an incomplete perianth cortical vascular system (CVS). Moreover, the perianth is remarkable by its pentamerous pattern

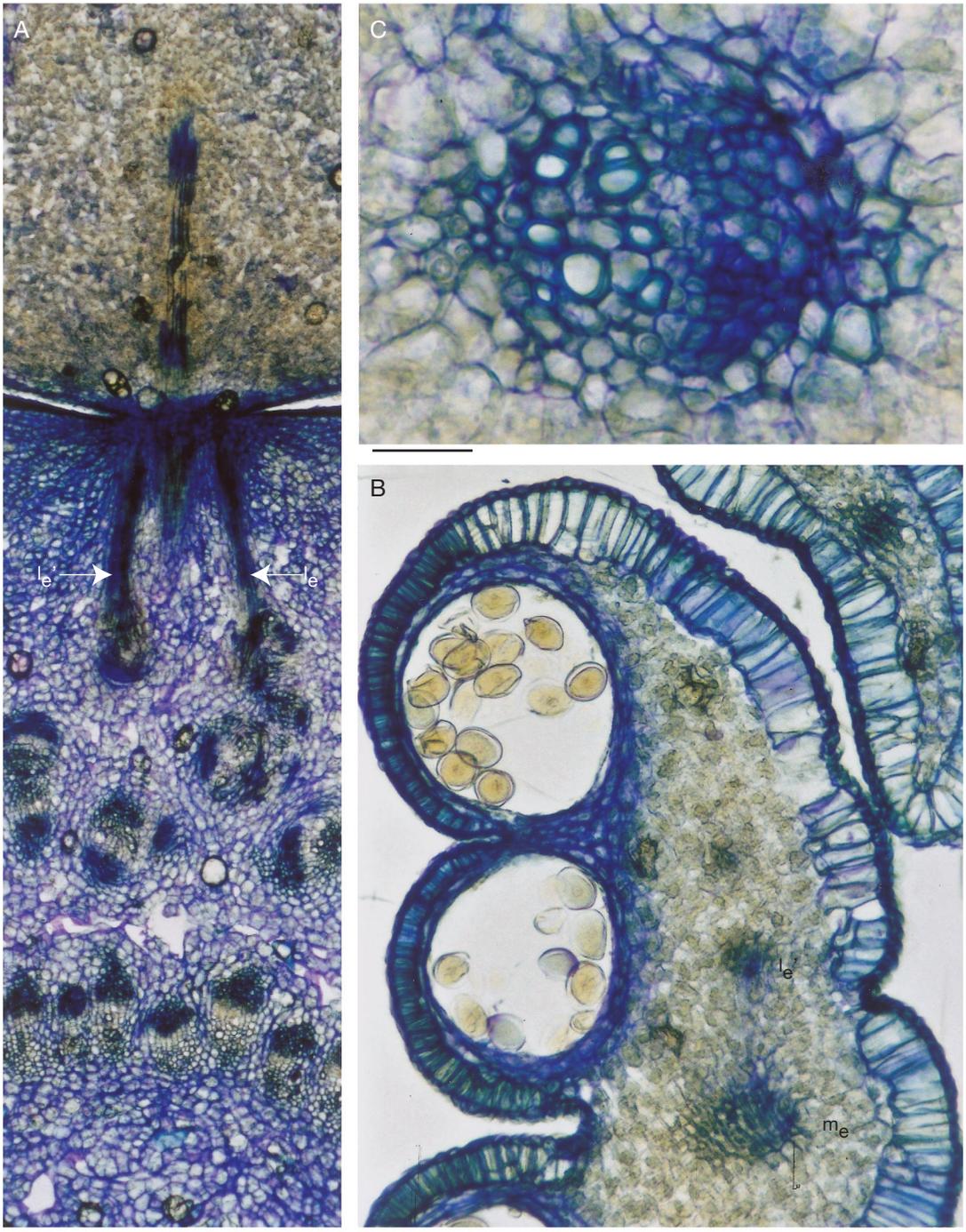


FIG. 5. — Androecial histology of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A**, detail of the stamen insertion on the androgynophore in cross-section; **B**, anther histology (half cross-section); **C**, median stamen bundle. Abbreviations: l_e, l_e', lateral stamen bundles; m_e, median stamen bundle. Scale bars: A, 250 µm; B, 100 µm; C, 25 µm.

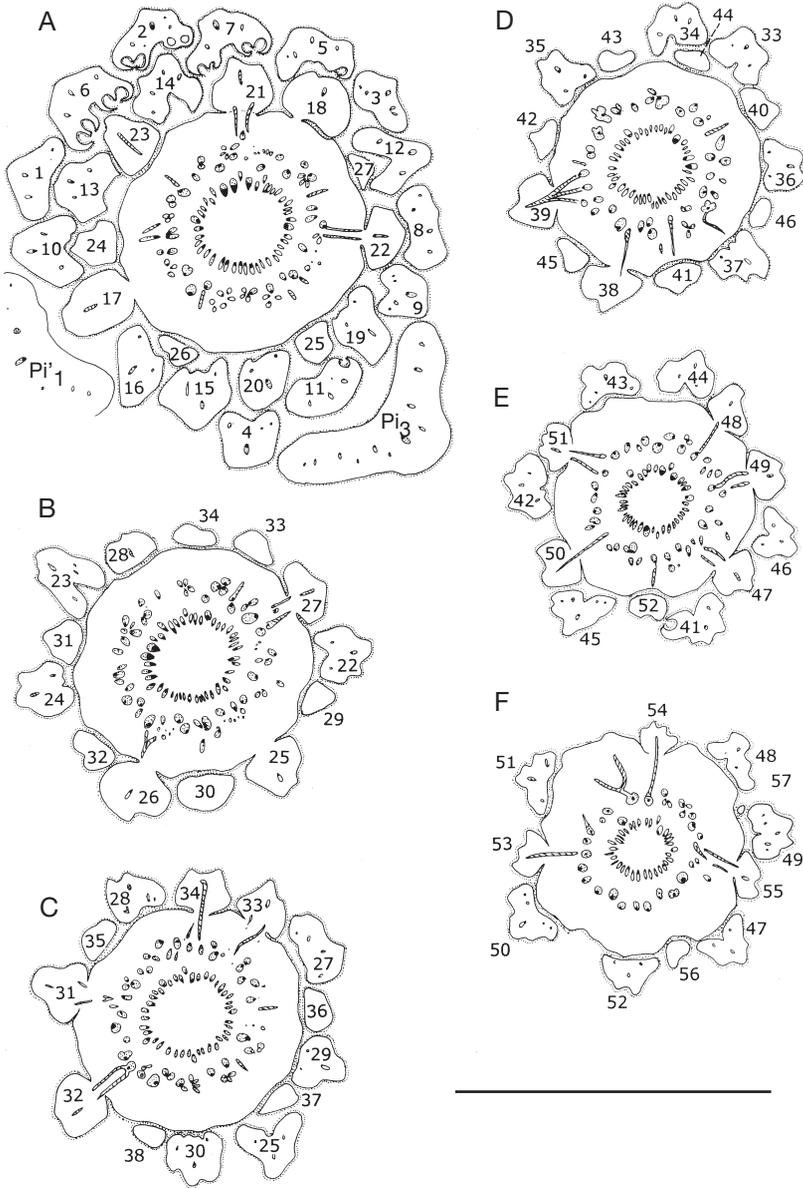


FIG. 6. — *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A-F**, androecial vasculature (continued from Figure 4). Only innermost stamens are drawn from section B. Scale bar: 5 mm.

(5 sepals, 5 outer petals, and – in this flower – 6 inner petals with P_{11} obviously duplicated in P_{11}' and P_{11}'' ; Fig. 10A), as previously recognized (Yu 1994). The sepals appear fundamentally supplied by 5 traces (S_3 in Fig. 10A), while all petals have 3

traces. The perianth vasculature is thus fairly condensed for a member of Magnoliaceae.

At a more distal level, but just below the top of the receptacle, a third crown breaks up from the central stele, and is made up by 15 inverted

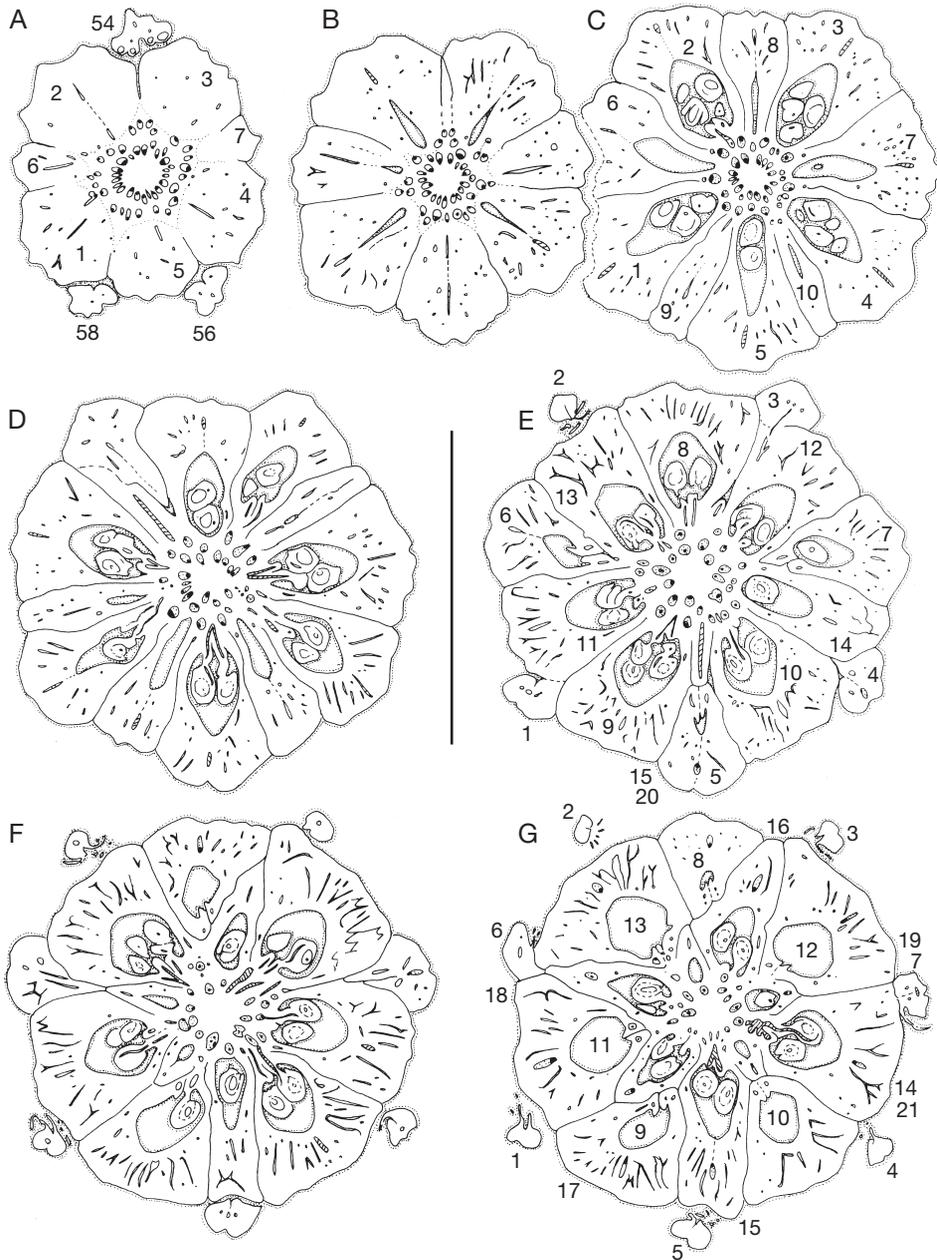


FIG. 7. — *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A-G**, gynoecial vasculature. All carpels are numbered in their apparent insertion order in some sections. Scale bar: 5 mm.

bundles (with xylem outside; Fig. 10A, t_{1-15}). These are vascular trunks, at first supplying stamens along the whole androgynophore (Figs 4;

6), with each stamen fed by 3 strands emitted by the same trunk (Fig. 5A). Moreover, it is noteworthy that 58 (very near 60) stamens are

reported in this flower, i.e. a theoretical number of 4 stamens per trunk.

Twenty one carpels are inserted at the top of the receptacle (Fig. 7), more or less arranged in three whorls, the two outer (here with 14 carpels) wholly supplied by the 15 trunks (i.e. inner CVS). As characteristic for Magnoliaceae (Ozenda 1949; Canright 1960), each carpel has 3 traces: a median bundle fused to both the placentary ones, and 2 lateral bundles. The traces are wholly fused in a single complex bundle, except for carpel 1, whose median and subsequent placentary bundles are emitted by the central stele (Fig. 10B). The third – upper – carpel whorl (Fig. 9A–C) is wholly linked to the central stele, without any apical remnant, so that lateral bundles of adjacent carpels are more or less fused (Fig. 8A, B).

There are about 4–6 pendulous anatropous ovules borne in 2 rows in the locule and provided by a short synplacentary bundle fused to the median carpel bundle. The lateral bundles reach the base of the erect stigma (Fig. 9D), which is at first unifacial then extends above an inner receptive epidermis covered with long mucilaginous hairs (Fig. 8C) before splitting into two tongue-like lobes (Fig. 9E, F).

The ovary wall is histologically rather undifferentiated at this pre-anthetical stage, except for the dense branching of the lateral and median bundles, which is usual in the family (Canright 1960).

STAMEN HISTOLOGY

At the base of the locules and from the outside, the anthers exhibit the following tissues (Fig. 5B): an unbroken epidermis, somewhat thinner at the level of the pollen sacs, made up by round, papillose, cutinized cells; a fibrous layer (i.e. endothecium) showing on the abaxial connective side a progressive transition to a palisade-like hypodermis, with cells twice as thick, and less lignified, in places even anticlinally divided. This layer is lacking on the very narrow adaxial connective side. The pollen sacs are wholly introrse and protruding, and surrounded by 1–3 layers of collenchymatous cells that stain deep purple with Toluidine blue. The tapetum is no more recognizable at this stage, while pollen grains appear mature with two obvious nuclei. The core of the laminar connective is a spongy parenchyma

made of cells with a dense, granular, and hardly stainable oily content, among which are scattered a dozen secretory cells 2–4 times as large and with a resinous content. Three collateral bundles supply the connective: a median one, elliptic in outline, with thick xylem and phloem (c. 10 vessels and 10 sieve-tubes) surrounded by a crown of sclereids (Fig. 5C), especially in the upper half of the anther; two lateral bundles, more or less circular and half to a third the size, with only 2 or 3 vessels and sieve-tubes, and fusing to the median bundle at different levels below the top of the locule. The connective is extended and tongue-like, its histological features are unaltered, but the hypodermis is unbroken, the parenchyma appears firmer and the complex bundle extends inside.

DISCUSSION

For the most part, the floral anatomy – especially vasculature – of *Magnolia decidua* (Fig. 10) conforms to the pattern recognized in Magnoliaceae, i.e. the high number of stele bundles (c. 60 > 40) in the pedicel (Deroin 1997), and the occurrence of two concentric CVS, in addition to the central stele (Skipworth & Philipson 1966; Ueda 1986; Deroin 1999). The outer bundle (Fig. 10A) is connected to the upper bract (Ozenda 1949), supplying here the whole perianth, whose parts are mainly 5-traced. The inner CVS (Fig. 10B) irrigates the androecium and the 2 lower whorls of the gynoecium. The upper whorl of carpels is fed by the central stele as a rule in Magnoliaceae (Canright 1960; Xu & Rudall 2003).

The stamens of the material studied resemble those of many *Magnolia* species, their laminar connectives being covered by an unbroken epidermis and endothecium (Canright 1952; Skvortsova 1958; cf. previous developmental study by Xiao & Yu 2004). However, the 3-traced condition, with an apical fusion of lateral nerves to the median – thus building a simple brochidodromous venation – is very similar to that described in *Magnolia* sect. *Manglietia* (Tiệp 1980). Each carpel is connected (Ozenda 1949; Canright 1960) by 5 traces (i.e. a median bundle, 2 mediolateral ones – all three

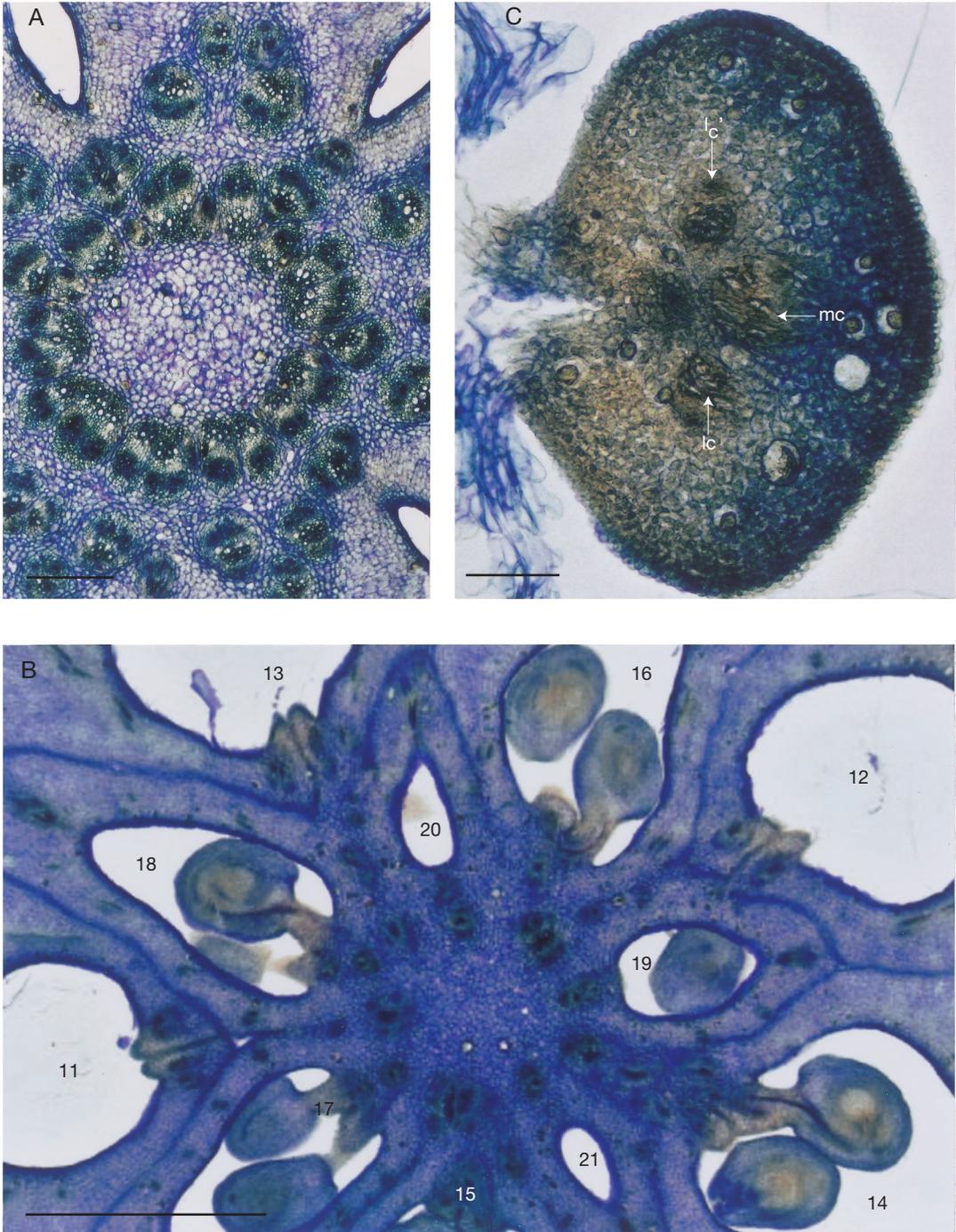


FIG. 8. — Gynoecial histology of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A**, detail of the central vasculature; **B**, cross-section of the gynoecium, showing the insertion of upper carpels (numbered as in Figures 6G and 8B) and ovules; **C**, detail of stigma. Abbreviations: l_c , l'_c , lateral carpel bundles; m_c , median carpel bundle. Scale bars: A, 250 µm; B, 1 mm; C, 100 µm.

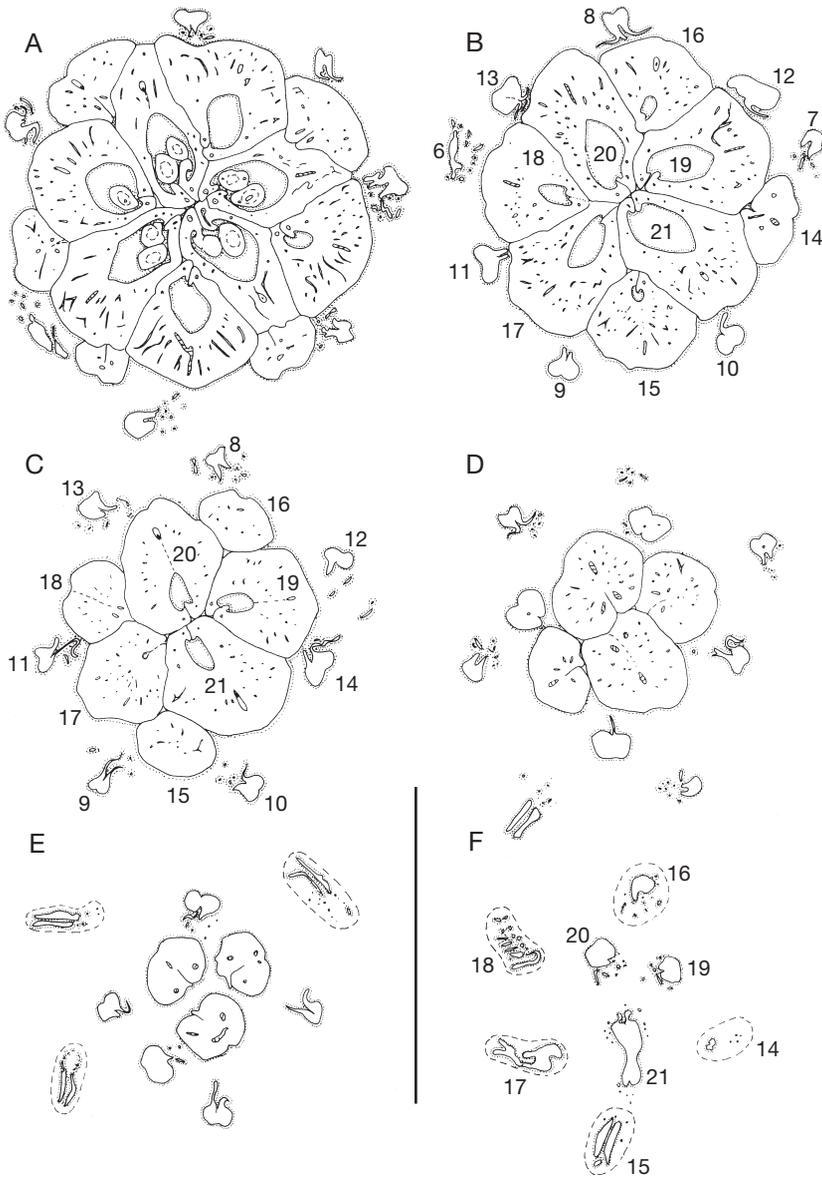


FIG. 9. — *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A-F**, gynoecial vasculature (continued from Figure 2). Scale bar: 5 mm.

spreading in the stretched stigma – and 2 lateral bundles fused to each other in a short synlateral bundle, itself fused to the median bundle base), which is the usual condition in Magnoliaceae. An anatomical study of the mature fruit axis of this species (under the name *Sinomanglietia glauca*; Yu

et al. 1999) showed 26 to 29 vascular bundles, a number consistent with that found here for the central stele at the base of the gynoecium (*c.* 34, see Figure 6F), as some bundle fusion seems to occur. Interestingly, vascular bundles split at the level of the pedicel during fruit set (Deroin 1997).

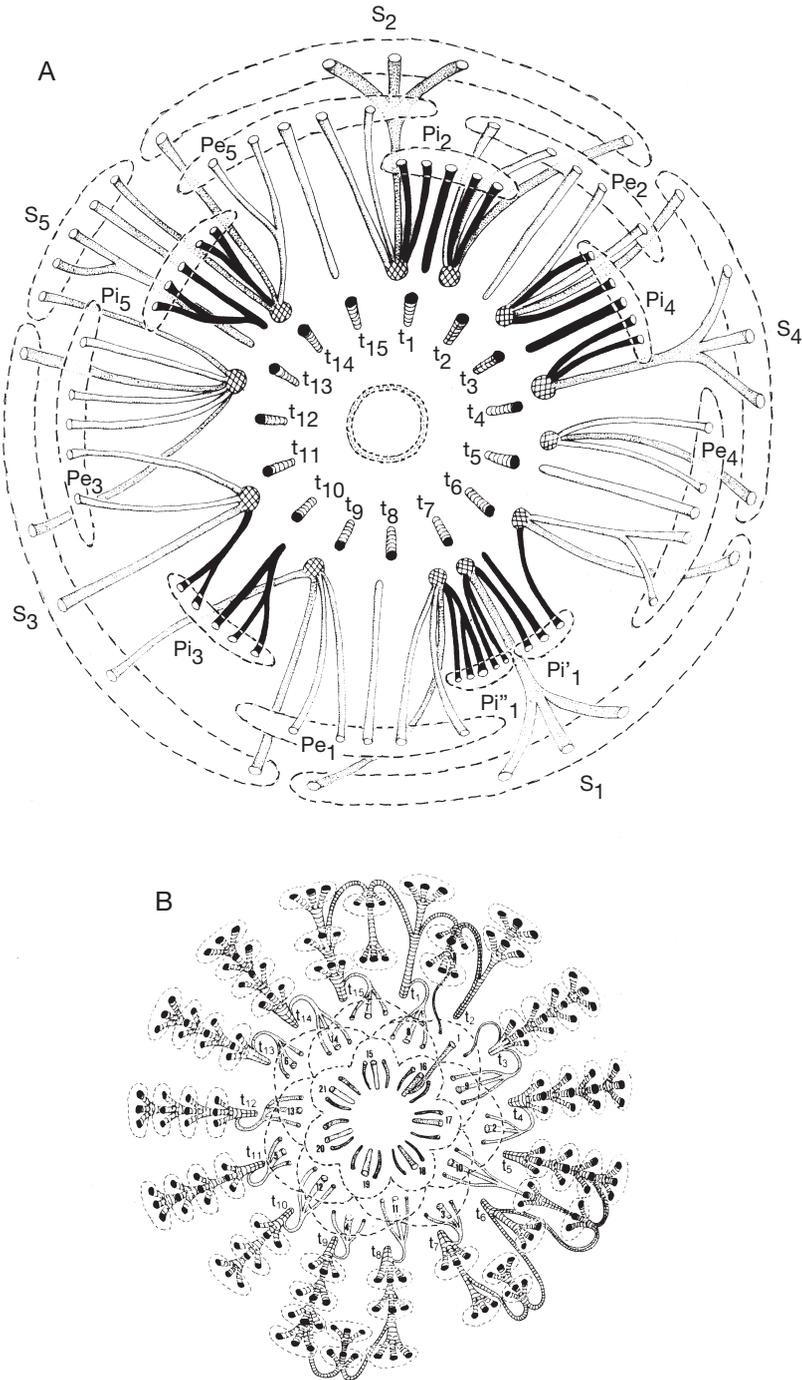


FIG. 10. — Vascular diagram of *Magnolia decidua* (Q.Y.Zheng) V.S.Kumar: **A**, at the perianth level; **B**, at androecium and gynoecium levels. **Stippled area**, sepal bundles; **white area**, outer petal bundles; **black area**, inner petal bundles; **hatching**, stamen bundles; **cross-hatching**, cortical vascular systems (CVS). Abbreviations: **P_e**, outer petal; **P_i**, inner petal; **S**, sepal; **t**, vascular (mainly stamen) trunk.

The gynoecium – and fruit – axis is to be interpreted as a synstipe, as in other Magnoliaceae (Deroin 1999), the so-called “carpels” in fact being nothing other than the upper ovuliferous part of individual carpels.

Some floral features of *Magnolia decidua* are more uncommon for Magnoliaceae:

1) a weak sclerenchyma is present at anthesis, as frequently seen in some Annonaceae, e.g., *Isolona*, *Monodora* (Deroin & Couvreur 2008) or *Tous-saintia* (Deroin 2000), but not at all in *Magnolia* and *Liriodendron* studied to date (Laborie 1888). However, a fibrous sheath with thick (c. 15 µm) cell walls is formed during the fruiting stage, as is common for Magnoliaceae (Yu *et al.* 1999);

2) a sharp separation between the vasculature of the perianth and sexual parts, due to the fact that lateral stamen bundles are also emitted by the inner CVS and are not fused to petal bundles, as in e.g., *Magnolia grandiflora* (Skvortsova 1958, and Fig. 11). Such a condition was already recognized by Hiepkö (1965) in *M. acuminata*, where stamens are mainly fed by 6 cortical vascular trunks;

3) the most outstanding feature is obviously the pentamery of the perianth vasculature of the two flowers examined, without any known equivalent in Magnoliaceae, heretofore always defined by its trimerous flowers (Nooteboom 1985). The vascular diagram (Fig. 10A) suggests that a pentamerous calyx evolved by a secondary intercalation of two narrow sepals (S_4 and S_5) in a typical trimerous calyx, but the double corolla appears already well restructured. Moreover, a pentamerous pattern might even be recognizable in the androecium, supplied by 15 vascular trunks and comprising c. 60 stamens. The androecium of *Magnolia decidua* is thus interestingly both trimerous and pentamerous. Such a puzzling feature can be linked with the monotypic genus *Meiocarpidium* Engl. & Diels, likely basal in Annonaceae, in which the stamens are supplied by 2 concentric crowns of 15 trunks each (Deroin 1987).

Conversely, the gynoecium of *Magnolia decidua* is easier to interpret as most likely trimerous. For greater convenience, we consider here to represent 3 “whorls” of 7 carpels each, the lower two ones supplied by the inner CVS, while the upper one is fed straight by the central stele (Fig. 10B).

The occurrence of pentamery in monocots was already shown in 1982 by van Steenis for the genus *Pentastemona* Steen. (Stemonaceae). As in *Magnolia decidua*, the gynoecium remains trimerous (a unilocular ovary with 3 parietal placentas) so that floral pentamery is not complete. The transition from trimery to pentamery (or tetramery) in any case appears anyway difficult and “extremely rare both in monocotyledons and in dicotyledons”, as emphasized by Kubitzki (1987).

CONCLUSIONS

The results presented here bring to the fore significant consequences from several points of view:

1) vasculature is of significance for understanding floral architecture in Magnoliales, but due to its complexity and technical problems, it is too rarely considered and often wholly overlooked in the most recent papers (such as Xu & Rudall 2003) attaching a too much weight to ontogeny and phyllotactic features, i.e. to external morphology, which depends to some extent from constraints in space optimization. Anthotaxis of *Magnolia* was fully analyzed by Zagórska-Marek (1994), who demonstrated that alternate and whorled phyllotaxis are not fundamentally different patterns, as they intergrade one into another by dislocation or fusion of parastichies. These might result – according to Zagórska-Marek – from the stochastic behaviour of the meristem and the subsequent displacement of the growth center, which moreover often induces inversion of the ontogenetic helix. Vascular analysis appears likewise to be a good tool for drawing up the correct merical pattern, but is commonly neglected (Kubitzki 1987). It is, however, noteworthy that trimery and pentamery coexist in the androecium of *Magnolia decidua*, as well as in *Meiocarpidium* (Annonaceae), because meristic patterns are likely not so exclusive as often thought;

2) conversely, floral vasculature was put forward in several pluriaxial interpretations of Magnoliales flowers (Melville 1963, 1969; Meeuse 1972) based on rather rudimentary studies of cleared longitudinal sections only. Contrary to Canright’s (1960) claim, clearings may be misleading and should be

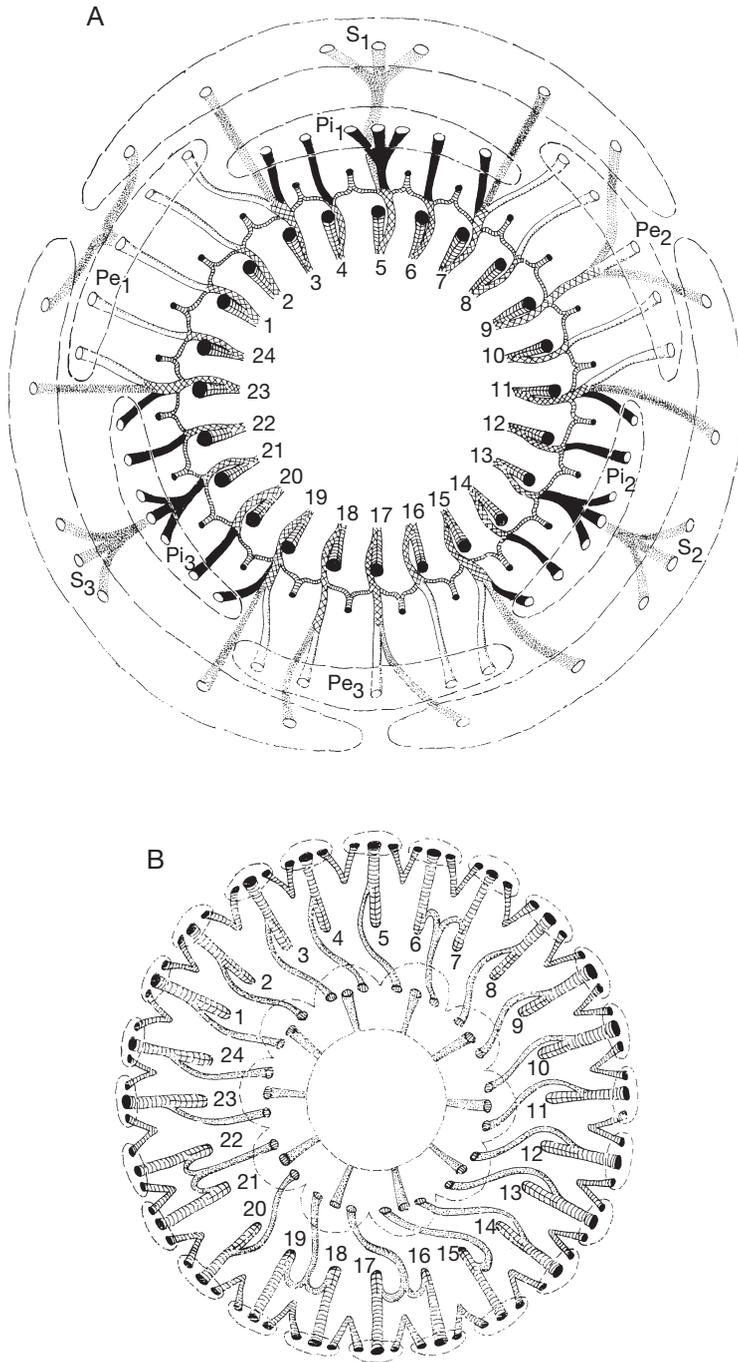


FIG. 11. — Vascular diagram of *Magnolia grandiflora* L. (Skvortsova 1958 and personal observation on hand sections of an anthetical flower, cultivated individual from Draveil, France): **A**, at the perianth level; **B**, at androecium and gynoecium levels; for convenience, only one whorl is drawn for each. Same legend and abbreviations as Figure 9.

used carefully, above all as a check of the vascular diagram reconstructed from seriate transverse sections. Some significant bundles, especially those which connect neighbouring whorls, might be overlooked because of their thinness, even when stained. On the other hand, clearings lead to a confusion of functional units (e.g., CVS) with morphological units (e.g., axes);

3) *Magnolia decidua* is wholly characterized by its unique trend toward floral pentamery, combined with uncommon features such as deciduous leaves, little-differentiated sclerenchyma at anthesis and numerous ovules (Yu 1994). This outstanding combination of characters might have evolved as a result of a long isolation in the mountains of southeastern China. We hypothesize that perianth pentamery is not an ancestral trait in this taxon, but rather a reversal, as tri- and tetramerous whorls rarely occur in this species (Zhang pers. comm.) while pentamery occurs sporadically in some flowers of *Magnolia* (*Michelia*) *champaca* (L.) Figlar and *M. baillonii* Pierre (Richard Figlar pers. comm.). The androecium and gynoecium of *M. decidua* exhibit patterns much closer to trimery. Interestingly, the most recent ontogenetical research demonstrates the unstable nature of pentamery in basal angiosperms (Ronse De Craene *et al.* 2003) and the probable – and until now neglected – role of dimery. A morphogenetical study of the flower of *M. decidua* should be very enlightening for understanding this meristic transition.

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