Those Amazing Magnolia Fruits

Richard B. Figlar

Unlike people who are interested in growing nut trees like *Juglans* or fruit trees such as *Malus*, those who cultivate magnolias are mainly interested in the flowers, not the fruits. Though some fruits of magnolia species are quite ornamental, I find the fruits to be most useful for studying the differences (or similarities) between species or groups of species of *Magnolias*. Taxonomists have long had a similar interest in observing fruits of Magnoliaceae and they have often used those differences or *perceived* differences in fruit characters to justify their systems for classification of Magnoliaceae.

When James E. Dandy codified his system of Magnoliaceae in 1927, he based much of his classification on fruit characters. This basis remained virtually unchanged for the rest of his life, for example (adapted from Dandy 1964):

A. Fruiting carpels dehiscent, not fleshy,

- B. Carpels free, in fruit dehiscent along the dorsal suture,
  - C. Ovules 4 or more in each carpel .... ***Manglietia***
  - C. Ovules 2 in each carpel (rarely 3-4 in the lower carpels) .... ***Magnolia***
- B. Carpels concrescent at least at the base, in fruit circumscissile and woody, the upper portions falling away either singly or in irregular masses, the lower portions persistent with suspended seeds; stipules adnate to the petiole .... ***Talauma***

A. Fruiting carpels indehiscent, concrescent to form a fleshy syncarp; etc .... ***Aromadendron***

As new species were discovered, taxonomists often followed Dandy's guidelines regarding fruit characters, which resulted in the creation of even more Magnoliaceae genera based on relatively minor variations in the fruits. This list includes *Manglietiastrum* (concrescent carpels, dehiscing completely by the ventral suture, partially via the dorsal suture of the carpels and partially along their line of junction), *Tsoongiodendron* (concrescent carpels, circumscissile, the upper portions falling away, or dehiscing via the dorsal suture), and others such as *Pachylarnax* and *Paramichelia*.

Later (1985) Nooteboom concluded that,"the concrescence of the carpels has apparently developed independently in different lineages of Magnoliaceae... therefore concrescence of carpels alone is not an acceptable character for delimitation of genera." Recently (Kim et al., 2001; Azuma et al., 2001), molecular biologists also found that Dandy's concept of fruit characters seemed to have little to do with molecular (DNA) affinities among Magnoliaceae taxa. Thus, it appeared that Dandy and his followers may have been misguided with their perception of Magnoliaceae fruit anatomy, or they may have simply failed to correctly observe the dehiscence process itself.

So, how does this dehiscence process work? In researching the literature I have not yet found a suitable explanation of what actually occurs when *Magnolia* fruits (including *Talauma*) ripen and dehisce seeds. Moreover, the terminology used in describing fruiting characters, that is, concrescent or connate vs. free carpels, ventral suture vs. basal attachment etc., is often misleading or inaccurate. Thus, the goal for this project is to examine and describe in detail the process of dehiscence of a "typical" *Magnolia* fruit and a "typical" *Talauma* fruit. For a typical *Magnolia* fruit I selected *Magnolia grandiflora* and for the talauma I used *Magnolia hodgsonii* (also known as *M. liliifera* var. *obovata*). I will also attempt to describe my observations as precisely and unambiguously as possible.

Pre-dehiscent (ripe) fruits of *Magnolia grandiflora* were gathered this past autumn from my own plants at Pomona NY, and similarly ripe fruits of *M. hodgsonii* were generously provided by fellow Magnolia Society member, William T. Drysdale of Riverside California.

Magnolia grandiflora

When the fruit was removed from the tree, its carpels were still tightly fused together and the individual carpels had not yet begun to split to release seeds. This fusion *between* the carpels (along their line of junction) is often referred to as "concrescence" or "connation." (Note: Contrary to Dandy's observations, concrescent carpels occur in all Magnoliaceae lineages except in most species of subgenus

Michelia where the carpels are free (not fused) throughout their development.) Also, the outer (dorsal) part of the carpels—the tissue between the hollow carpel pocket that contains the seeds and the outer dorsal wall—is moderately fleshy, or about as firm as an apple. This tissue is called the *mesocarp*. In *M. grandiflora* the mesocarp is relatively thin, but in some species, especially *M. macrophylla*, the mesocarp can be very thick, up to 0.4 in (1 cm) (see Figure 1).

Within a few days the carpels begin to separate. With a pocketknife I removed one of these carpels for further observation. On the outside surface of the carpel sidewall is an odd textured surface that looks something like lizard skin. This *tesselate* surface represents the footprint of where the adjacent carpels had previously been fused to it (see Figure 2).

At about the same time as the carpels begin to separate, they also begin to split along the *longitudinal* suture. The part of this longitudinal suture (or line of dehiscence) that runs from the stylar beaks inward toward the axis of the fruit is defined as the *ventral* suture. The part that goes from the stylar beak down across the dorsal face, then finally inward to meet the axis, is called the *dorsal* suture. The base of the carpel is adnate (attached) to the axis of the fruit. Sometimes taxonomists mistakenly refer to this attachment as the ventral suture.

In some carpels, dehiscence is initiated along the ventral suture, then it proceeds to split along the dorsal suture (Figure 3). In other carpels the splitting begins along the dorsal suture, then may or may not propagate completely through the ventral suture. Eventually carpel movements cease and the seeds are presented hanging via funicular threads from each carpel.

This dehiscence process seems to be facilitated, if not completely controlled, by the drying of the carpel tissues and the degree of the resultant shrinkage. Since the mesocarp is initially relatively fleshy, it shrinks to a greater degree than the thinner laminar carpel sidewalls. Thus, as the drying continues, more free space is made available between the carpels. This in turn allows the splitting carpels to bend (flare) outward without obstruction until the carpel is completely open and presenting the seeds. Occasionally, this process is impeded slightly by an adjacent carpel. In those cases, the opening can still be sufficient for the seed to be presented, however, the split may not have propagated through the entire ventral suture. For the same reason, in other cases, the ventral suture may be entirely open, while the dorsal suture may only be partially split.

Finally, the seeds have fallen away and the drying movements of the tissues have come to rest. The fruit has become a stiff woody remnant of what now appears to consist of free open carpels that remain attached to an axis.

Magnolia hodgsonii

Initially the *M. hodgsonii* fruit gives the same visual impression as the previously described *M. grandiflora* fruit except for the conspicuous lenticels on the skin (*exocarp*) of the fruit. The carpels are connate and no splitting was detected along the longitudinal sutures. However, upon handling the fruits, it is immediately apparent that the mesocarp is quite woody and hard (Figure 4).

Within a few days most of the carpels begin to separate from each other but not as much as in *M. grandiflora*. Moreover, there is no noticeable splitting along the longitudinal suture. Thereafter, the fruits begin to "fall apart" circumscissile, such that all but the adnate bases of the individual carpels seemingly break off, leaving the familiar seeds suspended by their funicular threads from the carpel bases (see Figure 5). Most of these carpel pieces fall away individually.

Looking more closely at the anatomy of the drying (still dehiscing) fruit, it is plain to see that the carpels that are still attached to the fruit are at least temporarily locked in place, their mesocarps unable to shrink further, while other tissues within the fruit (carpel sidewalls, axis, etc.) have experienced greater shrinkage. It appears that since the unyielding mesocarp can no longer shrink at the same rate as the other tissues, the relatively thin carpel sidewalls become tensile stressed and weakened, leading to their eventual breakage at their weakest point near the carpel bases. Thus, the carpel pieces fall away.

When I examined the fallen carpel pieces closely, it was evident that in each case the ventral suture had started to split from near the stylar beak to its former attachment near the base. Similarly, the bottom part of the dorsal suture had partially split along its inward seam near its attachment to the base. However, this longitudinal splitting was unable to continue to propagate through the dorsal

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Figure 1
Fruit cross section of *M. macrophylla* (right) ~~(left)~~ showing thick 0.4 in (10 ~~cm~~ MM) mesocarp compared to the relatively thin mesocarp of *M. grandiflora* ~~(right)~~ (left).

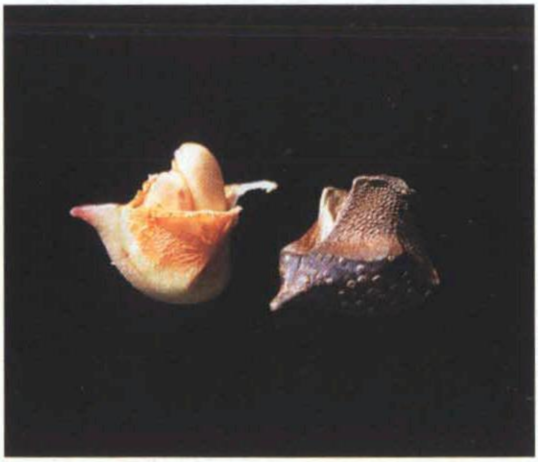

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Figure 2
"Backwards" dehiscent carpels of *M. hodgsonii* ~~(left)~~ (right) and *M. grandiflora* ~~(right)~~ (left)

face, undoubtedly due to the resistance afforded by the thick woody mesocarp.

As these individual pieces continued to dry, the carpel sidewalls began to flare outward at the opening, just as they do in *M. grandiflora,* except here it gives the visual impression of being dehiscent "backwards." (Interestingly, if nearly ripe carpels of *M. grandiflora* are forcibly removed from the axis before they are given a chance to longitudinally dehisce, they too will dry and flare outward at the base just as the *Talauma* carpels (see Figure 2).) Overall, the anatomy of the fruit of *M. hodgsonii* is still quite the same as in *M. grandiflora*. Even the tesselate surface of the outer part of the carpel sidewall is clearly evident just as it is on the carpels of *M. grandiflora.*

Discussion

From this experiment it is now clear to me that the *Talauma* type of dehiscence is essentially the same process as the *Magnolia* type. The process is initiated when the fruit's tissues begin to dry out and shrink, causing varying degrees of carpel separation and longitudinal splitting. This separation and splitting may continue uninterrupted to release the seeds (via the longitudinal suture), or it may be

Figure 3
Fruits of *M. acuminata* showing initiation of carpel separation and dehiscence along the ventral suture and partial through the dorsal suture.

interrupted but still facilitate the breaking away of the carpel parts to release the seeds. The more woody and/or thick the mesocarp, the more likely that this separation/splitting process gets interrupted or impeded.

This also may explain why both kinds of dehiscence can occur in some Magnoliaceae taxa such as in *Magnolia cylindrica*. In *M. cylindrica*, the mesocarp is slightly woody and noticeably thicker than in fruits of other *Yulania* species. Here, some carpels may separate and split longitudinally with little or no interruption, while in others, the splitting is impeded and the carpel parts break away as in typical *Talauma*. Still, some carpels dehisce both ways simultaneously. Evidently, in *M. cylindrica* the resistance of the mesocarp to splitting and separating is more or less in balance with the tensile strength of the carpel walls. As a result, some carpels break away Talauma-like while others dehisce longitudinally.

Figure 4
Ripe, pre-dehiscent fruits of *M. hodgsonii* (left four) and *M. grandiflora* (right).

Except for Spongberg (1998), most taxonomists were probably unaware of the nature of the fruits of *M. cylindrica*. Otherwise, some may have attempted to describe it as a new genus as had been done with *Manglietiastrum, Tsoongiodendron, Paramichelia, Aromadendron,* and *Pachylarnax*. Herbarium specimens of fruits of most of these taxa show that their fruit form and dehiscence can easily be explained by slight variations in degree of lignification and thickness of the mesocarp of the carpels.


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Figure 5
Dehiscing fruits of *M. hodgsonii*. Splitting of ventral suture can be seen on some of the still-attached carpels.

In James Canright's 1960 analysis, *The comparative morphology and relationships of the Magnoliaceae. III. Carpels,* he states that while "the occurrence of sclereids (lignification) in the gynoecia (of *Magnolia*) was found to be the exception, rather than the rule… the lack (or existence) of sclereids is not a reliable generic character…" This study seems to affirm Cartright's statement, while it also exposes some flaws in Dandy's observations regarding fruits and their dehiscence. Like many taxonomists of his time, Dandy had perhaps relied too much on his observations of dried fruits in the herbarium. This probably accounts for his categorizing the carpels in *Magnolia, Manglietia* and *Alcimandra* as free rather than concrescent, since the degraded remains of fruits in the herbarium can be perceived as finally consisting of "free" carpels. Evidently, he must have overlooked the tesselate surfaces on the sides of the carpels as well, since this would have provided ample evidence of carpel concrescence.

It's also unclear why Dandy described *Aromadendron* fruits as being *fleshy* and *indehiscent*. I have seen dried fruits of *Magnolia (Aromadendron) elegans* at the NYBG herbarium, and the woody remnants would suggest that the ripe carpels had not been fleshy and indehiscent. Others who have examined freshly collected ripe *M. elegans* fruits have found them to be woody and lenticellate (Keng, 1978) as well as dehiscent, similar to *M. hodgsonii*.

Even though it is now evident that woody carpels carry little or no taxonomic weight regarding relationships within Magnoliaceae, why did the character develop independently in so many separate lineages? Curiously, nearly all Magnoliaceae lineages with thick woody mesocarps are endemic to tropical climates. Perhaps the thick woody carpels are an ecological adaptation for providing protection from water loss during summer droughts, or from seed predators such as *Leptoglossus* and other fruit puncturing insects.

Acknowledgment

The author thanks William T. Drysdale of Riverside California for providing fresh fruits of *Magnolia hodgsonii*, without which this project could not have been completed within this short period of time. In 1991 Mr. Drysdale published an excellent account of growing this tree in Vol. XXVI, No. 2, of the *Magnolia*, the Journal of the Magnolia Society, entitled, "The Lordly *Talauma*."

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Other Fruit Specimens Studied

Magnolia (Elmerrillia) ovalis de Vogel & Vermeulen 7064	NYBG
Magnolia (Aromadendron) elegans Forest Res. Institute, no. 99351	NYBG
Magnolia (Aromadendron) elegans Krukoff, no. 4213	NYBG
Magnolia (Paramichelia) baillonii No. 4130	NYBG
Magnolia (Manglietiastrum) sinica (orig. type specimen)	SCIB
Magnolia (Talauma) dodecapetala my collection	MGA
Magnolia (Tsoongiodendron) odora my collection via Zhongshan Univ.	MGA

The Gallery: A Selection of Photographs Submitted by Members

This new hybrid (tentatively named M. 'Aurora') is a result of a cross made in the mid 90s between M. 'Pink Surprise' and M. 'Daybreak.' M. 'Pink Surprise' is a cross of M. 'Galaxy' and Phil Savage's M. 'Toro', while Augie Kehr's M. 'Daybreak' is a cross of M. 'Woodsman' and a Gresham Hybrid. (Augie was uncertain about the pollen parent of M. 'Daybreak,' but with its glowing pink color and the M. *campbellii* characteristics of its prodigy, it is my belief that M. *veitchii* may be part of its genetic background.)

The magnolia bloomed for the first time in mid-May of 2002, about a week later than either of its parents. It continued to bloom until the end of June. The flower has nine tepals and holds its upright, cup-shaped form until the tepals fall. The color is a deeper pink than either of its parents. This magnolia has the color and shape of M. *campbellii* and is hardy into at least Zone 5. M. 'Aurora' has very good seed fertility and extremely good pollen fertility. All flowers pollinated with Aurora pollen formed huge carpels. Who knows—next year I may try it on M. *grandiflora*.

The picture of the three magnolias shows M. 'Pink Surprise' on the top, the new hybrid on the left, and M. 'Daybreak' on the right. The tree is still quite small, but appears to have the columnar growth habit of M. 'Daybreak'.

Bud wood is very limited, but two nurseries will be supplied this summer with more extensive distribution to occur later.

Photographs and text submitted by Dennis Ledvina, Green Bay, WI USA

The Gallery, cont.

Frank Galyon submitted this photo of himself shown with his hybrid, M. 'Frank's Masterpiece.'

M. 'Frank's Masterpiece' (M. × soulangeana 'Deep Purple Dream' × M. 'Paul Cook') is a tree with strong apical dominance and branches with a semi-weeping character. The flowers are ten to 11 inches across and have eight or nine tepals. Individual tepals are five inches long and four inches wide. The outside color of the tepals is very deep red purple, deeper and more red than 'Deep Purple Dream.' Frank produced this hybrid and named and selected it in 1997. M. 'Frank's Masterpiece' appeared on the list of Magnolia Cultivar Registrations in Magnolia, Issue 63 (Winter 1998).

The photograph was taken by Robert W. Hendricks.

Your Letters...

More about the M. 'Daybreak' mixture

I recently received a copy of Jim Gardiner's new book, *Magnolias A Gardener's Guide* and found on page 69 a picture of *Magnolia* 'Daybreak.' I don't believe that this is the right tree.

In October 1999, Dr. August E. Kehr put a message in *Magnolia*, the Journal of the Magnolia Society. It read that there has been a mixture in *Magnolia* 'Daybreak.'

He explained that in 1993 that he had received a few plants of *M.* 'Daybreak' from a tissue culture laboratory. He planted them and grew them for observation and after a few years he started noticing a big difference in these trees. In 1999, Dr. Kehr saw these trees bloom and the blooms were purple instead of pink. These were clearly not *M.* 'Daybreak.'

I believe the picture in Jim Gardiner's book is the purple blooming mixture that Dr. Kehr is talking about.

I have a tree of *M.* 'Daybreak' in my yard and I know that it is the true one, because I went to Dr. Kehr's place in Hendersonville, NC and got scion wood from the mother tree.

Dr. Kehr explained that the real *M.* 'Daybreak' had a dull upper surface on the leaves and that the false tree had shiny leaves and that the real one had only slightly pointed leaves where the false one had sharp pointed leaves.

My tree checked out to be the real *Magnolia* 'Daybreak', so the photo accompanying this letter is a picture of the true *M.* 'Daybreak.'

I noticed as I was taking the photos, that the flowers had a heavenly fragrance and I will have to say that it is the best of the 200 magnolia varieties that we have.

Only the flowers that had advanced to where the stamens had recurved from their tight form and where ready to dehisce had the fragrance, so the fragrance must be coming out of the stamens.

This photo was taken on April 28, 2001; that is when *Magnolia* 'Daybreak' blooms in middle Tennessee.

Thank you Dr. Kehr for creating such a wonderful tree.

Terry Pennington
38 Walling Hill
McMinnville, TN 37110

Olav Kallenberg of Norway took this dramatic photo of the new Mark Jury hybrid, *M.* 'Black Tulip.'