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Arnoldia Circulation Manager
The Arnold Arboretum
125 Arborway
Boston, MA 02130-3500

Nancy Rose, *Editor*
Andy Winther, *Designer*

Editorial Committee

Phyllis Andersen
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Michael S. Dosmann
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Front cover: Fruit of Oriental bittersweet (*Celastrus orbiculatus*), a notoriously invasive vine.
Photo by Peter Del Tredici.

Inside front cover: Read about the complex flowering and pollination process of sweetbay magnolia (*Magnolia virginiana*) starting on page 19. Photo of *M. virginiana* × *virginiana* 'Milton', accession 779-87-A, by Michael S. Dosmann.

Inside back cover: In midwinter, wintersweet (*Chimonanthus praecox*) bears wonderfully fragrant flowers. This species is marginally hardy at the Arboretum and in severe winters (like the current one) the flower buds may be killed. This photo by Michael S. Dosmann of the Arboretum's single specimen (accession 236-98) in bloom is from January 2012, a mild month in a very mild winter.

Back cover: Fruit of American bittersweet (*Celastrus scandens*). Photo by Nancy Rose.

Untangling the Twisted Tale of Oriental Bittersweet

Peter Del Tredici

It's amazing that the details of the introduction of one of eastern North America's worst invasive plants, Oriental bittersweet (*Celastrus orbiculatus* Thunb.), are essentially unknown. According to Alfred Rehder in his seminal *Manual of Cultivated Trees and Shrubs* (1927) the vine was introduced into cultivation from Asia in 1860, but he offered no specific details about who the responsible party was. Since then, most authors have simply taken Rehder at his word and repeated the 1860 date without question (or attribution). More recently, some botanists have cited 1879 as the date of introduction of Oriental bittersweet into North America based on an 1890 article by Charles S. Sargent, but again with only minimal details. The purpose of this article is to fill in this void in the early history of the plant, especially now that it has become such a ubiquitous—and highly destructive—member of our flora.

A Brief History of Oriental Bittersweet

The first species of *Celastrus* to be described was the American or climbing bittersweet (also called waxwork or stafftree), native to eastern North America, and named *C. scandens* by Linnaeus in 1753. The second was Oriental bittersweet, *C. orbiculatus*, native to Japan, Korea, and China and originally published in 1784 by Linnaeus's student, Carl Peter

Thunberg, in his ground-breaking *Flora Japonica* under the name *Celastrus articulatus*. Some ninety-seven years later, the Russian botanist Carl Maximowicz pointed out that this name was actually a misprint of *Celastrus orbicula-*



Oriental bittersweet, in yellow fall foliage, scrambles to the top of a tall eastern cottonwood (*Populus deltoides*) in Bussey Brook Meadow at the Arnold Arboretum.

tus, Thunberg's intended name, which he used in the index of *Flora Japonica* as well as in the original manuscript pages of the book. It took years of back and forth debate among botanists to straighten out the confusion caused by this simple typographical error, but *C. orbiculatus* is now universally accepted as the correct scientific name for Oriental bittersweet.

In *Flora Japonica* Thunberg also described a second Japanese species of bittersweet, *C. punctatus*, with smaller, more ovate leaves than *C. orbiculatus*, a different pedicel (flower stalk) structure, and rough white lenticels on its stems. Shortly after this plant entered cultivation in the mid- to late 1800s, it too became engulfed in a taxonomic debate, specifically as to whether it was a "good" species or just a variety of *orbiculatus*. Alfred Rehder, writing in L. H. Bailey's massive *Cyclopedia of American Horticulture* (1900), officially reduced *C. punctatus* to a variety of *C. orbiculatus*, with shorter petioles and smaller, thicker, elliptic leaves. This reduction in status was widely accepted in botanical publications for many years, most notably in the English version of Jisaburo Ohwi's *Flora of Japan* (1965), which described variety *punctatus* as "a southern phase, abundant usually near seashores, although transitional with the typical phase [*orbiculatus*]."

The traditional view of Oriental bittersweet taxonomy underwent a change in 1955 when Ding Hou, a freshly minted Ph.D. from Washington University in St. Louis, published his revision of the genus *Celastrus* in the *Annals of the Missouri Botanical Garden*. Hou reviewed the tortured history of Thunberg's two bittersweets and concluded they were both valid species. He also reviewed the taxonomy of the two *Celastrus* species described and illustrated in 1860 by Eduard von Regel, the Director of the St. Petersburg Botanical Garden: one was a "new" species that he christened *C. crispulus*, the other was Thunberg's species, *C. punctatus*. Writing in *Plantae Wilsonianae* in 1915, Alfred Rehder had expressed the opinion that both of Regel's plants belonged to the species *C. orbiculatus*—*crispulus* was a synonym and *punctatus* a variety—a determination that formed the basis for his citing 1860 as the date of Oriental bittersweet's introduction into cultiva-

tion. Ding Hou looked at the same article and reached a very different conclusion—Regel's *crispulus* was synonymous with Thunberg's *punctatus* and his *punctatus* was really Thunberg's *orbiculatus*. According to Hou's interpretation, Rehder was right about 1860 as the date for the introduction of *Celastrus orbiculatus*, but wrong about which of Regel's two species was the true Oriental bittersweet.

In the years following its publication, Ding Hou's revision of the genus *Celastrus* has stood the test of time. The current online *Flora of Japan Database Project*, for example, treats *C. punctatus* as a semi-evergreen species native to the warm-temperate or subtropical parts of the country, while the deciduous species *C. orbiculatus* is found in more northerly cool- and warm-temperate zones. Similarly, the English version of the *Flora of China*, which describes twenty-five species of *Celastrus*, includes both *C. orbiculatus* and *C. punctatus*. The former is widely distributed in the eastern and northeastern parts of the country, mainly north of the Yangtze River, while the latter is restricted to southeast China and Taiwan.

Introduction Into Europe

Eduard von Regel's 1860 *Gartenflora* article is significant for three reasons: 1) it is the first report of the cultivation of Oriental bittersweet outside of Asia; 2) it contains the first scientific illustrations of both *Celastrus orbiculatus* and *C. punctatus*; and 3) it unequivocally states that *C. punctatus* (= *C. orbiculatus* according to Hou) had "only recently been imported" into European gardens by the famous naturalist Philipp von Siebold.

Siebold is an important and colorful figure in the early history of European involvement in Japan. His spectacularly illustrated *Flora Japonica*—co-authored with Joseph Zuccarini and published in thirty volumes between 1835 and 1870—is a botanical landmark. Siebold was a Bavarian physician who spent six years (1823 through 1829) in Japan working for the Dutch government, teaching and practicing medicine, and making a significant collection of Japanese flora and fauna. His sojourn ended when he was imprisoned for political reasons (the unauthorized possession of a strategically important



Fig. 1-5. *Celastrus crispulus* Rgl.
 , 6. *punctatus* Thbrg.

map of Japan) and forced to return to Holland in 1830. He did, however, manage to leave with a boatload of herbarium specimens and living plants, which he cultivated in his garden in Leiden. Siebold managed to return to Japan in August 1859 but was forced to leave in 1862. Again, he returned to Leiden with a collection of Japanese plants that he added to the "Jardin D'Acclimatation," which he had established in the 1830s (Spongberg 1990). He published a nursery catalogue for the garden in 1863 that listed an astounding 838 species and varieties of plants for sale, mainly from Japan and China. Included among the entries was "*Celastrus punctatus* Thbg." at the price of 1 or 2 francs, presumably depending on the plant's size. Based on this catalogue listing and on Regel's article from 1860, we can now say that Siebold probably collected seeds of *C. orbiculatus* (which he called *C. punctatus*) in the fall of 1859—at the start of his second visit to Japan—and sent them to colleagues in Europe for cultivation. Siebold's 1863 nursery catalogue listing appears to be the first recorded public offering of *C. orbiculatus* outside of Asia.

Introduction Into North America

On the other side of the Atlantic, Oriental bittersweet made its horticultural debut in the Kissena Nurseries catalogue first published in 1886 or 1887. The Kissena Nurseries were established by Samuel B. Parsons in 1871 as the successor to the earlier nursery he had established with his brother Robert in 1840 in Flushing, New York. The nursery specialized in ornamental trees and shrubs and was the first nursery in the United States to introduce Japanese maples into commerce and to propagate and distribute hardy evergreen rhododendrons (Meehan 1887). The Arnold Arboretum library has two virtually identical copies of the Kissena Nurseries "Descriptive Catalogue of Hardy Ornamental Trees, Flowering Shrubs and Vines." One of them has "1887?" penciled on it while the other is marked "Probably issued Spring, 1889." Both of the catalogues are 94 pages long and both include the identical entry for Oriental bittersweet on page 53: "*Celastrus punctatus*, Japan. Leaves marked with points of white. 75 cts." (This reference to "points of white" is probably a misinterpretation of



Portrait of Samuel B. Parsons from Meehan, 1887.

the word *punctatus*, which Thunberg used in reference to the prominent white lenticels on the stems.) In the *Rhododendron* section of the catalogue, on page 78, there is a reference to "a recent published paper from C. M. Hovey, whose experience in this plant is well known, he states that he bought in 1884 [should read 1844], in England, a number of *Rhododendrons* supposed to be hardy." A search of the literature from this period turned up Hovey's article in the December 1885 issue of *The American Garden*, which makes spring 1886 the earliest possible date for the publication of the Kissena Nurseries catalogue.

***Celastrus paniculatus*.** Japan. A large-leaved, climbing vine. 50 cts.

— ***punctatus*.** Japan. Leaves marked with points of white. 75 cts.

— ***scandens* (Bitter Sweet).** America. Fine leaves, turning a bright yellow color in early fall, clusters of orange capsuled fruit. Very strong grower, well suited to cover rocks and trunks. 35 cts.

The listings for *Celastrus* from Parsons's 1887 Kissena Nursery Catalogue.



A remnant row of katsura trees (*Cercidiphyllum japonicum*) in Kissena Park, Flushing, New York, the former site of S. B. Parsons's Kissena Nurseries, photographed in November 2013.

The first horticultural description of Oriental bittersweet in America did not come until a few years later, in a *Garden and Forest* article by John G. Jack (1889). Under the heading "Notes from the Arnold Arboretum," Jack described *Celastrus articulata* (noting that the name should be *C. orbiculata*) and stated that it "has inhabited the Arboretum for several years, having been sent here from the Parsons' Nursery at Flushing [New York]." Jack was enthusiastic about its ornamental attributes: "The fruit is smaller than that of our American species, but it is very brilliantly colored, and, as it is produced here in the greatest profusion

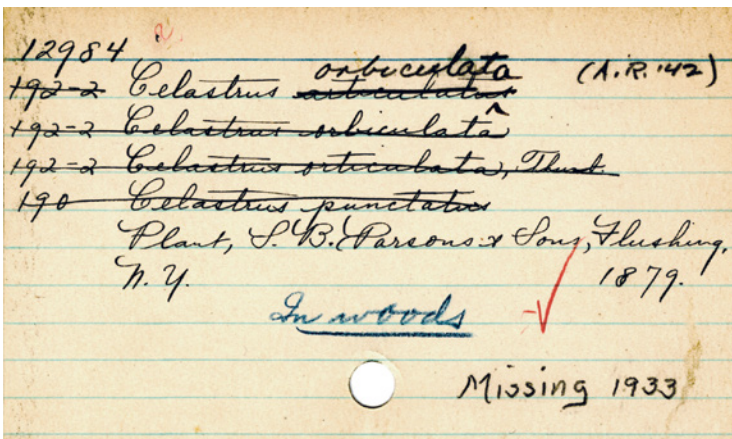
along the whole length of the spur-like lateral branches, it makes a great show after the leaves have fallen, remaining fresh and bright until nearly the end of winter. *C. articulata* is a hardy and vigorous plant, growing rampantly when once established in rich soil, and then sometimes producing stems twelve or fifteen feet long during a single season, and immense masses of foliage."

Remarkably, no more than three weeks later, in a letter to the editor of *Garden and Forest*, a writer who signed his name only as "S." described the elegant estate of Charles A. Dana on the tiny island of Dosoris in the town of Glen Cove on the north shore of Long Island, New York. The description goes into great detail about the fabulous garden plantings—especially the conifers—but one sentence stands out, "A seawall is built all around the island, and it is draped and festooned with Matrimony vine [*Lycium barbatum*], our native Bitter-sweet, a Japanese species of the same genus (*Celastrus articulatus*) and *Periploca Graeca*, which are planted on the top." While nothing can be said for sure about when the Oriental bittersweet on Dosoris was planted, the fact that it received such a prominent mention suggests that Mr. Dana's plants were well established and that he probably got them from Samuel Parsons, whose Kissena Nurseries were only twenty miles away in Flushing.

A little more than a year after these two articles appeared, in the November 12, 1890, issue of *Garden and Forest*, Charles S. Sargent wrote an article featuring *Celastrus articulata* under the heading of "New or Little Known Plants." The article described the morphology of the plant in detail and was accompanied by an illustration of the plant drawn by the Arboretum's botanical illustrator, Charles Faxon. Sargent praised its ornamental fruit "which, as long as they remain on the plants, nearly hide it from view" and reported that the Arboretum's first plant was received from Samuel Parsons in 1879.



Illustration of *Celastrus orbiculatus* by Charles Faxon from Sargent's 1890 article in *Garden and Forest*.



Arnold Arboretum accession card for *Celastrus orbiculatus* accession 190 from Samuel Parsons.

A check of the Arboretum's old card file system revealed that accession 190 had indeed been sent to the Arboretum by Samuel Parsons in 1879 under the name *C. punctatus*. In their articles, both Jack and Sargent changed the specific epithet to *articulata* instead of *punctatus*. Whether they did this because they thought the two species were synonymous or because they thought the plant was misidentified is unclear, but the latter explanation is more likely. Remarkably, the card file also revealed that seeds of "*Celas-*



Herbarium specimen from Arnold Arboretum accession 190-1, a plant raised from a cutting from the original plant from Parsons.

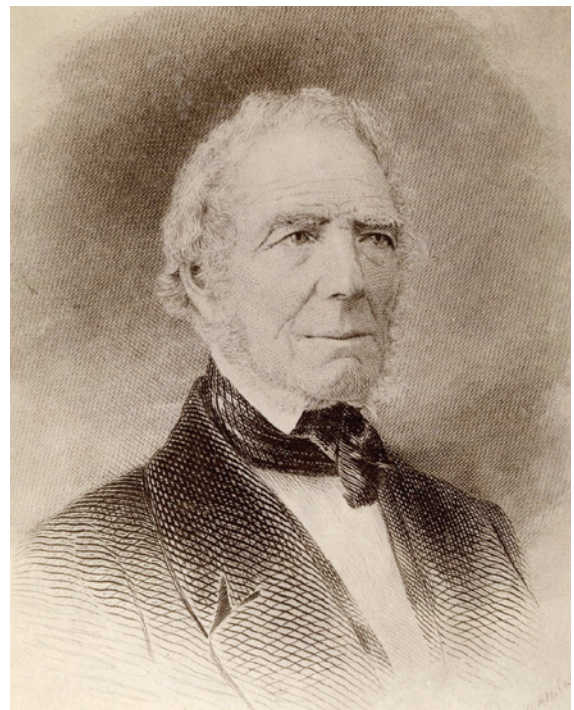
trus articulatus" (accession 192) were received by the Arboretum on March 2, 1880, from the Agricultural College in Sapporo, Japan, less than a year after Parsons sent the Arboretum a plant of "*C. punctatus*." Fortunately the Arboretum possesses herbarium specimens of both of these accessions, one from accession 190-1, which originated from a cutting collected on October 20, 1887, from Parsons's original plant, and the other from one of the original Sapporo plants collected on October 26, 1888. Both herbarium specimens are labeled "*articulata*" and both are in fruit, but only the Parsons specimen has leaves on it. As far as I have been able to determine, they are both *Celastrus orbiculatus*.

Who Sent the Seeds?

The unanswered question about the introduction of Oriental bittersweet into North America boils down to this: Where did Samuel Parsons get his plants? One possibility is that they came from Dr. George Rogers Hall, an American physician who lived in Japan from 1855 through 1861 and introduced many Japanese plants (including many collected by Siebold) into North America (Spongberg 1990). In March of 1862, upon his return to the United States, Hall hand-delivered a large shipment of Japanese plants and seeds to Parsons, who breathlessly described unpacking them in *The Horticulturist*. While there is no mention of *Celastrus* in the article, the door of possibility is left slightly ajar with the statement that the shipment contained "a large number of other tree and shrub seeds." But this seems an unlikely source for bittersweet given that it would have necessitated a seventeen year time lag before its distribution to the Arnold Arboretum. In addition, a comprehensive article titled "Ornamental Vines" by Josiah Hoopes in *The Horticulturist* (July 1874) describes American bittersweet (*Celastrus scandens*) and one of Hall's notorious introductions, Japanese honeysuckle (*Lonicera japonica*), but makes no mention of Oriental bittersweet.

The available evidence—what little there is—suggests that Thomas Hogg, Jr. was the source of Parsons's Oriental bittersweet seeds. Hogg served as the United States marshal assigned to the Japanese Consulate from 1862 to 1869

and later as an advisor to the Japanese Customs Service from 1873 through 1875. Hogg's father, Thomas, Sr., had immigrated to New York City from London in 1821 and established one of the first nurseries in the area. When Thomas, Sr. died in 1854, his two sons, James and Thomas, Jr., took over the business. During his diplomatic appointment in Japan, Hogg used the opportunity to send a number of Japanese plants—most notably variegated hostas and Japanese irises—to the family nursery in New York as well as to other horticulturally minded individuals in the northeast (Sargent 1888, 1894; Whitehead 2011). Hogg interacted with various Japanese nurseries as well as the European botanists who were working in Japan at the time, most notably Carl Maximowicz who lived in Japan from 1860 through 1864 and collected numerous plants—including Oriental bittersweet—for the St. Petersburg Botanical Garden (Bretschneider 1898). In a letter to his brother James (published in *The Horticulturist* in 1863), Hogg described their relationship: "There is a Russian Botanist (Mr. Macimovitch) now here making a collection of living



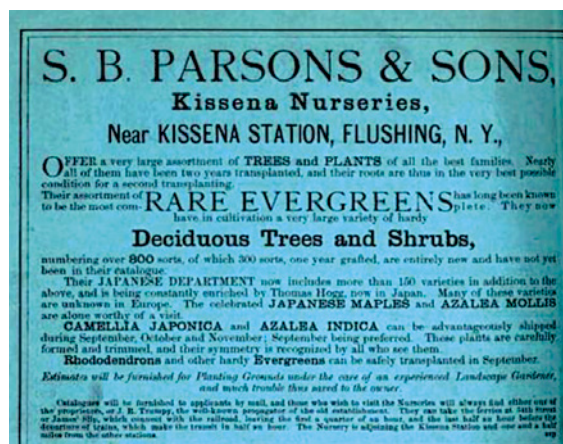
Portrait of Thomas Hogg, Jr.

COURTESY OF THE GRAY HERBARIUM OF HARVARD UNIVERSITY

and dried plants for a Society in St. Petersburg. He has been in the country three years, and is now about returning home by the way of Nagasaki. He has been very industrious, and has procured many valuable things. I frequently call upon him, and find him very communicative, and have obtained much valuable information from him."

During his second sojourn in Japan, Hogg worked as an advisor for the Japanese Customs Service, a position that allowed him more freedom to travel around the country and collect plants than he had had during his first trip (Sargent 1893). He again sent plants and seeds to numerous horticulturists, including Samuel B. Parsons, a fact that was documented in September 1875 in an article about Kissena Nurseries written by Josiah Hoopes: "Adjoining this block of fine specimens is a suite of cold-frames well filled with the largest collections of Japanese plants to be found,—not only in the United States, but in Europe as well. They were sent home by that indefatigable collector Thos. Hogg, now a resident of Japan." Parsons himself acknowledged Hogg's contributions in an advertisement on the back cover of the February 1876 issue of *Gardener's Monthly and Horticulturist*, which announced that "Their Japanese Department [of Kissena Nurseries] is being constantly enriched by Thomas Hogg, now in Japan." In the absence of any direct reference to the importation of Oriental bittersweet, these statements by Hoopes and Parsons are critically important because they provide a likely explanation for how and when *Celastrus orbiculatus* arrived in North America: collection in Japan by Thomas Hogg, Jr. in the fall of 1874; propagation by Samuel B. Parsons in 1875; distribution to the Arnold Arboretum in 1879; nursery sales in the early 1880s followed by the first North American catalogue listing in 1886 or 1887.

The rapidity of Oriental bittersweet's distribution was such that by 1893—less than twenty years after its collection in Japan—J. G. Jack reported that it "is now found in a good many gardens." And C. S. Sargent, in his book *Forest Flora of Japan* (1894) referred to Oriental bittersweet as "now well-known." In this same book, he makes the interesting observation that



Kissena Nursery advertisement on the back cover of the February 1876 issue of *Gardener's Monthly and Horticulturist* referring to Thomas Hogg sending plants from Japan.

"its leafless branches, covered with fruit, are sold in the autumn in great quantities in all Japanese towns, where they are used in house decorations"—a tradition similar to their current use on Thanksgiving tables and Christmas wreaths in the eastern United States.

By 1901 (and probably earlier), plants of "*Celastrus articulata*" were available directly from Japan via the Yokohama Nursery Company for 20 cents (gold) each or ten for \$1.80, and by 1907 the Biltmore Nursery in Asheville, North Carolina was offering 1½- to 2-foot-tall plants of *Celastrus orbiculatus* for 15 cents each, \$1.50 per dozen, or \$10 per hundred—an 80% drop in price from its initial public offering (75¢) in the Kissena catalogue some twenty years earlier.

The Era of Distribution and Promotion

In 1898, Sir Joseph Dalton Hooker, Director of Kew Gardens (and a good friend of Charles Darwin), reported in *Curtis's Botanical Magazine* that the Arnold Arboretum sent seeds of Oriental bittersweet to Kew in 1891. According to Hooker, the seedlings grew vigorously and flowered for the first time six years later, in June 1897, and fruited in November. Remarkably, this plant returned to North America when, according to George Nash writing in *Addisonia* in 1916, the New York Botanical Garden raised Oriental bittersweet plants "from seed

Thomas Hogg, Jr.'s Plant Introductions

Thomas Hogg, Jr. introduced many Japanese plants—both wild species and horticultural selections—to North America. Among his most famous are the old-fashioned variegated hostas ‘Decorata’ and ‘Undulata Albomarginata’, numerous Japanese maple cultivars, and the golden thread-leaved cypress (*Chamaecyparis pisifera* ‘Filifera Aurea’). Writing in the *Transactions of the Massachusetts Horticultural Society for the Year 1880*, Samuel B. Parsons, Jr. wrote, “Mr. Hogg has given us possibly more new Japanese plants than any collector since the time of Robert Fortune’s famous horticultural explorations.”

While I’ve been unable to locate a comprehensive list of Hogg’s introductions, the horticultural literature of the late nineteenth century is rife with references to them. The most important sources are an article by Hogg himself in *Gardener’s Monthly and Horticulturist* in 1879 (GMH), the 1887 Kissena Nurseries catalogue (KN), and Charles Sprague Sargent’s writings in *Garden and Forest* (GF) from 1888 to 1897 and *The Forest Flora of Japan* (FFJ) in 1894. From these four references, I’ve compiled the following list of Hogg’s woody plant introductions from Japan. No doubt persistent digging will add more species to this list in the future. Introduction years are from Rehder’s *Manual of Cultivated Trees and Shrubs*.

PLANT	YEAR OF INTRODUCTION	REFERENCE
Veitch fir, <i>Abies veitchii</i>	1874	Sargent FFJ, p. 83
Katsura tree, <i>Cercidiphyllum japonicum</i>	1864 or 1865	Hogg GMH 21: 53
Sweet autumn clematis, <i>Clematis terniflora</i>	1864?	Sargent GF 3: 621
Kousa dogwood, <i>Cornus kousa</i>	1874	Sargent FFJ, p. 47
Yeddo euonymus, <i>Euonymus hamiltonianus</i> var. <i>sieboldianus</i>	1865	Sargent FFJ, p. 26
Japanese winterberry, <i>Ilex serrata</i>	1866	Sargent FFJ, p. 25
Kobus magnolia, <i>Magnolia kobus</i>	1865	Sargent FFJ, p. 10; GF 6: 65
Japanese umbrella magnolia, <i>Magnolia obovata</i>	1865	Sargent FFJ, p. 9; GF 1: 305
Oyama magnolia, <i>Magnolia sieboldii</i>	circa 1865	Parsons KN, p. 24
Japanese photinia, <i>Photinia villosa</i>	1865	Sargent GF 1: 67
Kudzu, <i>Pueraria lobata</i>	—	Sargent GF 6: 504
Japanese hydrangea vine, <i>Schizophragma hydrangeoides</i>	—	Hogg GMH 21: 53
Stachyurus, <i>Stachyurus praecox</i>	1865	Sargent FFJ, p. 18
Japaneses stewartia, <i>Stewartia pseudocamellia</i>	1868	Sargent GF 9: 34
Sapphireberry, <i>Symplocos paniculata</i>	1865	Sargent GF 5: 89
Siebold viburnum, <i>Viburnum sieboldii</i>	—	Sargent GF 2: 556; Parsons KN, p. 50



Sapphireberry



Japaneses stewartia



Kousa dogwood



Color illustration of *Celastrus orbiculatus* from *Curtis's Botanical Magazine*, 1898, vol. 124 [ser. 3, vol. 54]: tab. 7599.

secured in 1897 from the Royal Gardens, Kew, England." Nash also noted that the painting that accompanied the article "was prepared from a vine growing on some small trees in the rear of the Museum building of the New York Botanical Garden. It was of accidental occurrence there, and perhaps originated from seed carried by the birds from the large specimen in the viticetum [a place where vines, especially grapevines, are cultivated] but a short distance to the east"—the very plant that had come from Kew Gardens in 1897. So the cycle is complete: bittersweet seeds went from the wilds of Japan to Flushing to Boston to England and then back to New York where they began to naturalize!

Oriental bittersweet was a relatively rare cultivated plant towards the end of the nineteenth century, mainly confined to the properties of wealthy horticultural enthusiasts. With its dramatic fruit display and rampant growth, however, the plant was destined for popularity, and the staff of the Arnold Arboretum, as it had done earlier, was leading the charge. E. H. Wilson, writing in his 1925 book about the Arnold Arboretum, *America's Greatest Garden*, described the plant in glowing terms, "On the left ascending the Bussey Hill road, is another arresting feature. It is merely a dense tangle of Japanese Bittersweet (*Celastrus articulata*) but how beautiful!—a mass of clear yellow foliage and a wild profusion of fruits with deep yellow husks cracked open, disclosing the clustered seeds clad in jackets of cinnabar-red." Later on he notes that some of the Arboretum's boulders of

granite and conglomerate were covered with Oriental bittersweet "whose stems are coiled and twisted into an intricate clump of growth, picturesque at all season of the year." No doubt he was referring to plants that E. J. Palmer later reported finding on the south side of Hemlock Hill in his 1935 publication, *Supplement to the Spontaneous Flora of the Arnold Arboretum*.

While Wilson was an admirer of Oriental bittersweet, the Arboretum's longtime horticulturist, Donald Wyman, was its true champion. He wrote about the plant in various Arnold Arboretum publications in 1939, 1944, and 1950 as well as in a number of other horticultural publications, and described it in his best-selling *Shrubs and Vines for American Gardens*, published in 1949. Wyman's 1944 article was a survey of the use of rapidly growing vines in the United States, which concluded



PETER DEL TREDICI

A tangle of fruiting Oriental bittersweet on a stone wall in Cornwall, Connecticut.

that Oriental bittersweet grows well in most regions of the country, other than the coastal southeast and the arid west, and that a panel of eminent horticulturists considered it to be among the most ornamental of the ninety-one vines under observation.

Wyman's 1950 paper is particularly interesting because he looks specifically at the fruiting habit of three bittersweet species in relation to their complex flower structure. Based on a series of bagging experiments, he postulated that pollen of either American (*C. scandens*) or Oriental (*C. orbiculatus*) bittersweet could pollinate the other. He also reported the existence of a "polygamo-dioecious" clone of Oriental bittersweet at the Arnold Arboretum with self-fertile, perfect flowers. Wyman concluded his paper by admonishing nurserymen to stop growing *Celastrus* "indiscriminately" from seed and start "growing only pistillate [female] plants from cuttings and budding on each plant one or two buds of the staminate plant."

Wyman's report of the hybridization between American and Oriental bittersweet was not the first. Three years earlier, Orland White and Wray Bowden of the University of Virginia had reported the successful creation of hybrids between American and Oriental bittersweet, but only when *C. scandens* was used as the seed (female) parent. White and Bowden's 1947 paper is also noteworthy because it offered an early warning about the invasive tendencies of Oriental bittersweet, noting that it "has escaped from cultivation in Virginia and the New York Botanical Garden, where it has become almost a pest, as it readily germinated from seed and is widely distributed by birds eating the berries and voiding the seeds."

The Era of Invasiveness

Donald Wyman reiterated his enthusiasm for the ornamental value of Oriental bittersweet in his article in the October 1, 1964, issue of *American Nurseryman*, but tempered it with the caveat that "bittersweet vines are vigorous twiners and can become vicious pests." This warning, alas, was too little, too late.

In 1973, David Patterson published a short article on the "Distribution of Oriental Bittersweet in the United States," which was

abstracted from his recently completed Ph.D. thesis at Duke University. The article was blunt about the serious threat posed by Oriental bittersweet and the fact that, following its initial introduction, the plant was "popularized as an ornamental by the Arnold Arboretum." Sparring no one, he also noted its distribution by the National Arboretum in Washington, D.C., in 1966 and 1967 to nurseries and public gardens in 30 states as well as its recommended use for highway bank plantings in New Jersey, Rhode Island, and Massachusetts. He concluded his article with the prescient note that "There are no indications that Oriental bittersweet has reached the limits of its potential range in the United States. In the future, unless planting and distribution are discouraged, it may become as serious a pest as Japanese honeysuckle."

While most of Patterson's work on the physiological ecology of *Celastrus orbiculatus* has been superseded by modern research, his history of the plant's spread as a naturalized species is a classic example of the exponential growth of an invasive species, beginning with the earliest collection of a spontaneous plant in Cherry Grove, Maryland in 1912. By 1940, naturalized Oriental bittersweet had been collected at 16 sites in six states, and by 1970 it was reported from 84 sites in 19 states. Today it is reported from thousands of sites in at least 25 states.

Following Patterson's ground-breaking work, dozens of articles have been published on all aspects of the plant's biology, many of them focusing on its competitive displacement of American bittersweet in areas where the two species overlap. While there is considerable debate about the mechanisms driving this displacement, there can be little doubt that Oriental bittersweet is the more adaptable of the two species in terms of its growth potential, its tolerance of soil disturbance and low light, and its greater production of both pollen and seed. One study, published in 1999 by Jean Fike and Bill Niering of Connecticut College, documented how a lone plant of *Celastrus orbiculatus*—over a forty-year period—completely altered the trajectory of the typical old-field succession process in New London, Connecticut. In another study based on data from greater New



"A botanical boa constrictor"—Oriental bittersweet strangling a black locust tree.



Oriental bittersweet root suckers.

Oriental Bittersweet Life History

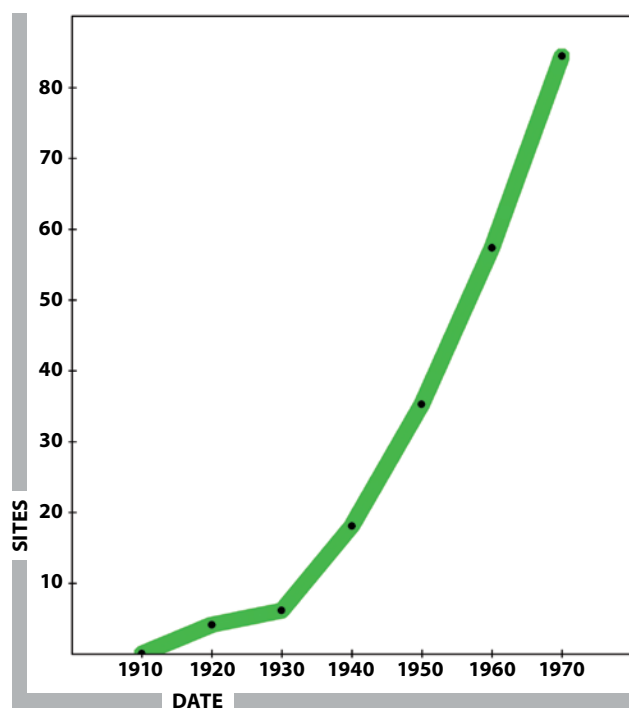
Celastrus orbiculatus is a high-climbing vine with stems that can grow up to 15 feet long in a single season and 60 feet long at maturity. It lacks tendrils and climbs by means of twining shoots that can eventually strangle the trunk of its host tree—not unlike a botanical boa constrictor (Lutz 1943). Oriental bittersweet produces simple, alternately arranged leaves that are highly variable in shape—from round or egg-shaped to oblong or elliptical; they are smooth with wavy, slightly toothed margins and tips that taper to a long or short point. Bittersweet roots are shallow growing and bright orange (a good field identification characteristic) and are used as an anti-inflammatory in traditional Chinese medicine. Any piece of root that is left behind after pulling or cutting the stems will give rise, Medusa-like, to numerous sucker shoots. This root-suckering capacity makes it extremely difficult to control Oriental bittersweet in landscapes where it has become established (Dwyer 1994).

Oriental bittersweet produces small, greenish flowers that typically become unisexual by the developmental failure of either the male or the female organs, thus making the plant functionally dioecious (Brizicky 1964). Occasionally a plant will develop both unisexual and perfect flowers (polygamodioecious), leading to individual specimens that are functionally monoecious (Wyman 1950; Hou 1955). The inconspicuous flowers are insect pollinated (mainly by bees) and produced on lateral branches in May and June. Following pollination, female plants produce round green fruits (capsules) that become highly conspicuous in the fall when they turn yellow and then split open to reveal seeds covered with a scarlet aril. A wide variety of birds (both native and exotic) feed on the brightly colored fruits and disperse the seeds across the landscape. Seedlings are common under the trees and shrubs where birds roost at night and seeds can remain viable in the soil for several years (Dwyer 1994).

Oriental bittersweet is highly adaptable and grows under a variety of light and soil conditions. Compared with the native *C. scandens*, the seedlings and young root sprouts of *C. orbiculatus* are extremely shade tolerant and can persist in the forest understory for a long time waiting for a light gap to develop (Leicht and Silander 2006). The plant is notorious for its ability to strangle and overwhelm nearby trees and shrubs and can cause serious damage in forests (Fike and Niering 1999). Oriental bittersweet was widely planted for ornamental, erosion control, and wildlife habitat purposes in the United States in the 1950s through 1970s and is now considered an invasive species throughout much of eastern North America. A recent publication from New Zealand (Williams and Timmins 2003) documented the spread of Oriental bittersweet in northern portions of that country, beginning in 1975.

York City, researchers at the Brooklyn Botanical Garden documented the concurrent decline of *Celastrus scandens* and increase of *Celastrus orbiculatus* over the past hundred and twenty years (Steward et al. 2003).

In a very recent Ph.D. thesis, David Zaya (2013) of the University of Illinois, Chicago, determined that when the two bittersweet species grow side by side in the wild, 1) the Oriental species hybridizes *asymmetrically* with its American cousin such that 51% of the seedlings produced by *C. scandens* were hybrids while only 1.6% of those of *C. orbiculatus* were; and 2) the rate of hybridization of *C. scandens* varies directly with its proximity to *C. orbiculatus*. In controlled crosses between the two species, Zaya found that pistillate plants of *C. scandens* were twenty times more likely to produce hybrids when pollinated with *C. orbiculatus* pollen than vice versa, confirming earlier reports that hybridization between the two species is mainly unidirectional. Remarkably, he also calculated that Oriental bittersweet produces up to 200 times more pollen per individual plant than *C. scandens*. In short,



From David Patterson's 1973 Ph.D. thesis, this figure shows the cumulative number of naturalized sites from which Oriental bittersweet was collected between 1910 and 1970.

American bittersweet, through a mechanism that Zaya refers to as "pollen swamping," is slowly being hybridized into oblivion by Oriental bittersweet.

Conclusion

The rise of Oriental bittersweet and the concurrent demise of its American cousin is a story that goes to the dark heart of the human relationship with nature—things "go oft awry" not from bad intentions but from ignorance. Without thinking much about it, we have globalized our environment in much the same way we have globalized our economy. Certainly the Arnold Arboretum has learned from its past mistakes and is now much more careful about promoting plants that have the potential to become invasive species. But the fact is that climate change—acting in concert with urbanization and globalization—has made the world much more complicated and less predictable than it was back in the days of Sargent, Jack, and Wilson. Across the planet, cosmopolitan ecosystems are displacing native vegetation at an alarming rate but at the same time many of these non-native species are growing vigorously on highly disturbed or badly contaminated land. It's a bittersweet conundrum that the plants that grow best under such conditions are seldom the ones we want.

Acknowledgements

The author would especially like to thank Anner Whitehead for her assistance in tracking down the connection between Thomas Hogg and Samuel Parsons, Lisa Pearson of the Arnold Arboretum Library and Archives for tracking down several obscure references, and the librarians at the New York Botanical Garden and the L. H. Bailey Hortorium at Cornell University for providing access to their Kissena Nurseries catalogues. This article is dedicated to the memory of Dr. Leslie Mehrhoff of the University of Connecticut, Storrs, who was deeply interested in all plants, regardless of their invasive tendencies.

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A curtain of Oriental bittersweet foliage.

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Peter Del Tredici is a Senior Research Scientist at the Arnold Arboretum.

***Magnolia virginiana*: Ephemeral Courting for Millions of Years**

Juan M. Losada



MICHAEL DOSMANN

The Arnold Arboretum's magnolia collection currently holds 157 accessions of native and non-native magnolias.

At the end of the seventeenth century, Henry Compton, the Bishop of London and a man known for his passionate love of gardening, sent the Reverend John Banister on a missionary trip to the New World. Banister arrived in Virginia in 1678 and, in addition to his clerical work, collected many new plant species for Bishop Compton. Among these was a tree species never before seen in Europe, specimens of which were planted and flourished near Fulham Palace, the Bishop's residence. After observing these specimens, botanist Philip Miller recorded the first written reference to this species in his book, *The*

Gardeners Dictionary. Miller was not only the chief gardener of the Chelsea Physic botanic garden, the second oldest in Britain, but also a plant collector and conservationist who cultivated many exotic species. Interestingly, the garden was visited by Linnaeus during his trip to England in 1736. Miller was influenced by the new system of classification that Linnaeus proposed, to the extent that he organized the garden following the Linnaean system. In 1753, Linnaeus included for the first time in his world renowned work *Species Plantarum* the specimens that Miller observed at Fulham Palace, with the name *Magnolia virginiana*.

Magnolia virginiana is a woody flowering plant native to the east coast of the United States, growing from Florida and Texas to Pennsylvania, New Jersey, and Massachusetts, the northernmost point in its range. Because of its preference for marshes and moist areas, *M. virginiana* was called swamp bay magnolia or swamp laurel. It is most commonly known as sweetbay magnolia and has been integrated into the local lore and culture where it grows. For example, early inhabitants made a tincture from its bark to use in chronic rheumatism and a medicine to treat coughs, colds, and fevers.

The Arnold Arboretum hosts an important collection of both native and non-native magnolias. In 1919, Charles Sargent studied the distribution of *Magnolia virginiana* from North Carolina to Florida and Texas, noticing for the first time the southern form, *M. virginiana* var. *australis* (note that current taxonomy lumps this variety back into *M. virginiana*). In the *Bulletin of Popular Information*, Sargent described the flowering of *M. virginiana*, then also listed as *M. glauca*, in this way: "... the flowers are small, cup-shaped, creamy-white and delightfully fragrant, and continue to open in succession from the middle of June until August. In all North America there is not a more delightful shrub to plant in the garden, or one that will give larger returns in beauty and fragrance...." Its form, flowers, and attractive leaves (glossy dark green with silvery white undersides) make this species valuable as an ornamental tree in gardens, parks, and other areas. *Magnolia virginiana* specimens at the Arboretum bear flowers continuously throughout summer, pervading the evening air with their marvelous sweet, lemony fragrance.

Magnolias and the Evolution of Flowers

All magnolias belong to the large plant family Magnoliaceae, within the relatively ancient order Magnoliales. Until the end of the last century, plant biologists considered Magnoliales to be among the oldest flowering plants, based on the morphology of the flowers, the characteristics of the pollination process, and some aspects of the internal anatomy of the wood. However, with the addition of research using molecular markers, and a vastly improved fossil record of the earliest flowering plants, it is



NANCY ROSE

Magnolias bear conelike aggregate fruits. At maturity, the individual follicles open, revealing seeds covered with scarlet arils. Seen here is a fruit of *M. virginiana* × *virginiana* 'Milton', accession 779-87.

now known that the first flowering plants were mainly shrubs, lianas, and aquatic plants such as water lilies.

While Magnoliales diversified early compared to more derived angiosperms (the latest estimations date the emergence of the order around 95.5 million years ago), they are now considered ancient but distinctly specialized flowering plants. The fossil record establishes that magnolias have remained relatively unaltered for millions of years, and have been widespread in tropical and subtropical climates. The early expansion and diversification of flowering plants led to the colonization of all types of environments. The biological forces behind this rapid diversification have posed a challenge to plant biologists for decades. However, it appears that the development of novel reproductive structures—flowers—played a significant part.

Before the emergence of flowering plants, gymnosperms (conifers, ginkgos, etc.) domi-

nated terrestrial ecosystems. Both gymnosperms and angiosperms are seed plants, and seeds are the product of fertilized ovules. Herein lies the main difference between both plant groups: while gymnosperms have their ovules exposed or “naked,” flowering plants developed maternal tissues to shelter their ovules. Despite the more complicated new arrangement of the ovules, flowers increased the efficiency of sexual reproduction and opened up many new opportunities for coevolutionary relationships between flowering plants and insect pollinators. Flowers became key evolutionary innovations, opening a door for innumerable new reproductive strategies that can be seen throughout the great diversity of flowering plants.

Sexual Reproduction and Flower Receptivity

In 1694, Rudolf Jakob Camerarius published his discovery that plants undergo sexual reproduction. Flowers are the reproductive parts of angiosperms, performing two main functions: they act as a showy display to attract pollinators, and they bear the germ lineages (gametes). The germ lineages are housed inside of a number of tissues specialized for either dispersal (for the male gametes) or protection (for the female gametes). The contact of both male and female gametes in most flowering plants involves the transfer of pollen between individuals, which is a task often carried out by insect pollinators. The first major studies on plant pollination were done by Kölreuter (1733–1806), but Darwin was also interested in pollination and breeding systems, writing two books on the topic: one on insect pollination of orchids (*Fertilisation of orchids*, 1862) and another on selfing and outcrossing in plants (*The effects of cross and self fertilisation in the vegetable kingdom*, 1876). The end of the nineteenth century and the beginning of the twentieth century saw an upsurge of studies on the reproductive biology of flowering plants, showing that the amazing diversity of flower morphologies are directly tied to the myriad of pollination and fertilization processes that flowers undergo to produce offspring.

A bisexual flower bears both male and female germ lineages in its reproductive organs. The pollen grains that will produce male gametes

are formed within the anthers. The female gametes are housed within special structures called female gametophytes within multi-layered structures (the ovules), which are further enclosed by the pistil tissues. The whole of the female reproductive structure is known as a gynoecium. The typical gynoecium is composed of three contiguous reproductive tissues, from the apical part to the base of the gynoecium: the stigma, the style, and the ovary. The first contact between male pollen grains and female flower tissues occurs on the stigma, a specialized receptive tissue exposed at the tip of the gynoecium. On the stigma, pollen grains hydrate and then germinate, producing a pollen tube containing the two sperm cells that elongates in a tip-oriented growth within the pistil tissues to reach the ovules. Once a tube penetrates an ovule, the two male gametes are discharged into the female gametophyte where a process known as double fertilization takes place. One of the sperm cells fuses with the egg cell, while the other one fuses with another female gamete. The former fusion will produce the embryo while the latter will give rise to the endosperm, which becomes the tissue that nourishes the developing embryo. In general terms this double fertilization process to form a new generation is shared by all flowering plants.

As might be imagined, coordinating all of the events between mothers and fathers in flower-



Bees visiting a flower of *Magnolia grandiflora* at the Arnold Arboretum. Nitidulidae beetles are considered the natural pollinators of magnolias, but bees are also possible pollinators, though their effectiveness as magnolia pollinators is still under debate.

ing plants is a highly sophisticated and complex process. In each species, a dialog between male and female components of the reproductive equation is carried out by species-specific molecular interactions. The gynoecium of flowers, far from being a passive actor during the pollination process, plays an active role in the recognition and regulation of pollen tube growth on its journey through the pistil. On one side, the pistil tissues have the ability to distinguish between pollen grains from different species and impede their germination, in a mechanism known as interspecific incompatibility. On the other hand, germination of very similar pollen grains is also blocked in many species, and this is called self-incompatibility, which prevents self-fertilization and promotes a mixture of different genetic material from individuals of the same species (remember, Darwin wrote a whole book about this topic!).

The recognition of pollen grains/tubes by maternal tissues of flowers has been revealed at the molecular level. Pollen grains/tubes bear proteins that are unique to the species, acting as molecular fingerprints. Those proteins can be recognized by counterparts in the gynoeceal tissues. Depending on whether they can interact or not (and thus whether or not the pollen grain is acceptable), it allows a maternal flower tissue to allow or deny pollen tube elongation. Therefore, the reception of pollen grains is decisive in the fertilization process. However, the stigma is not always ready, and pollen grains have to

reach the stigma at the right time—when this tissue is mature. If a pollen grain lands on a stigma before or after the surface is receptive, it is not likely to germinate and thus fertilization is not achieved (no seed is formed). The time frame in which a stigma allows pollen germination is referred to as stigmatic receptivity. This parameter varies between different plant groups and acts as an important filter during plant evolution—and as will be seen in *Magnolia virginiana*, the dance between male and female requires some remarkably interesting dialog.

Flower Receptivity in *Magnolia virginiana*

Magnolia virginiana flowers provide an excellent arena to study both the process and evolution of sexual reproduction in plants. As a member of an ancient lineage of flowering plants, *Magnolia virginiana* has many characteristics that are thought to be relatively ancient in flowers. At the time of pollination, the central and most distal part of the flower looks conelike. This is the female part of the flower and is made up of numerous carpels, each of which terminates in a stigma which will ultimately receive pollen. Each stigma connects directly with a single ovary. Below the female portion of the flower are a very large number of colorful and showy stamens, the organs that produce pollen.

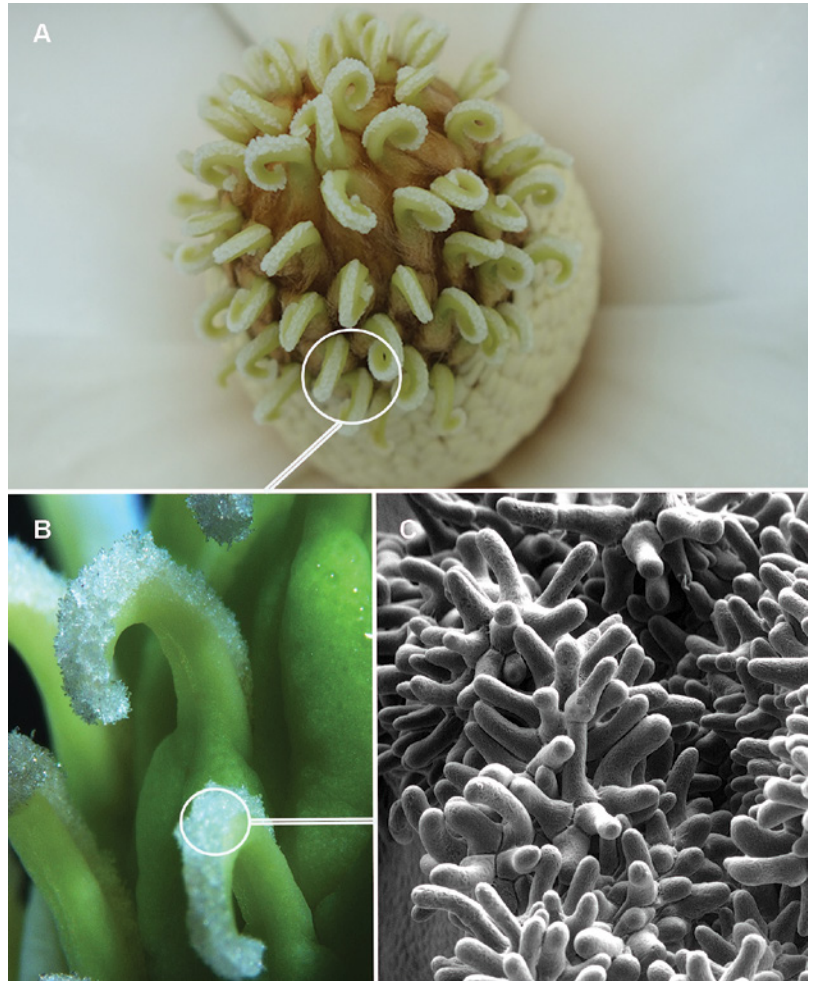
The presence of male (stamens) and female (gynoecea) organs in a single flower can lead to a very high probability of pollen moving



Magnolia virginiana protogynous flowering cycle. (A) The first flower opening (the female phase) occurs the first evening, and the stigmas (maternal tissues) are exposed to receive pollen grains (containing male gametophytes). (B) Four to five hours later, the inner tepals close and form a chamber enclosing the stigmas; this lasts for around 24 hours. (C) The cycle is completed the second evening with the male phase; the flower reopens at the same time that anthers open and shed pollen. This protogynous cycle (the female function precedes the male function) is a temporal separation that prevents the flower from self-pollinating. However, flowers opened at both male and female phases occur on the same plant, so cross-pollination between flowers of the same plant is possible.

within a flower—self pollination (the equivalent of marrying a very close relative). But in *Magnolia virginiana* (and in other *Magnolia* species), a temporal separation of the activities of the male and female parts of individual flowers acts to diminish the possibility of inbreeding. The temporal separation of both sexes is manifested as a protogynous flowering cycle (proto = first, gynoecium = female parts, or “ladies first”), and is delimited by floral movements. As a result, the female phase precludes the male phase and they do not overlap, thus creating a two day flowering cycle. Flowers open the first day at dusk (opening takes around 20 minutes and can be observed by just staring patiently at the right flower) as females with wet, sticky stigmas that receive pollen grains, and then close when night falls. They remain closed until the evening of the following day, when flowers reopen in the male phase, at which point stamens shed pollen. During the stage in which the flower remains closed, the flowers generate heat in order to give shelter to their main pollinator, beetles. The ability for flowers to produce heat is common to all magnolias (and other members of the family), and so is thought to be an ancestral character for the lineage. Other pollinators, such as bees, have been observed to act as pollinators for these plants, but little is known about how effectively they transfer pollen from flower to flower.

The timing of flower movements affects reproductive performance and points to the importance of a rhythm. This rhythm could be associated with pollinator behavior, in our case mainly bees and bumble bees, and possibly beetles. Our research project with *M. virginiana* at the Arnold Arboretum started with the observation of this cycle and pollinator inter-



Female phase of *Magnolia* flowers. (A) A *Magnolia* flower shows multiple gynoecia at the first flower opening. **(B)** Detailed view of the hooked stigmas that have bright, sticky surfaces ready to receive pollen grains. **(C)** Scanning electron micrograph of the stigma surface in *Magnolia virginiana*, showing the fingerlike cells (papillae) that form an intricate network for pollen grain gathering.

actions, recorded with time-lapse photography under controlled conditions. The resulting video is available online:

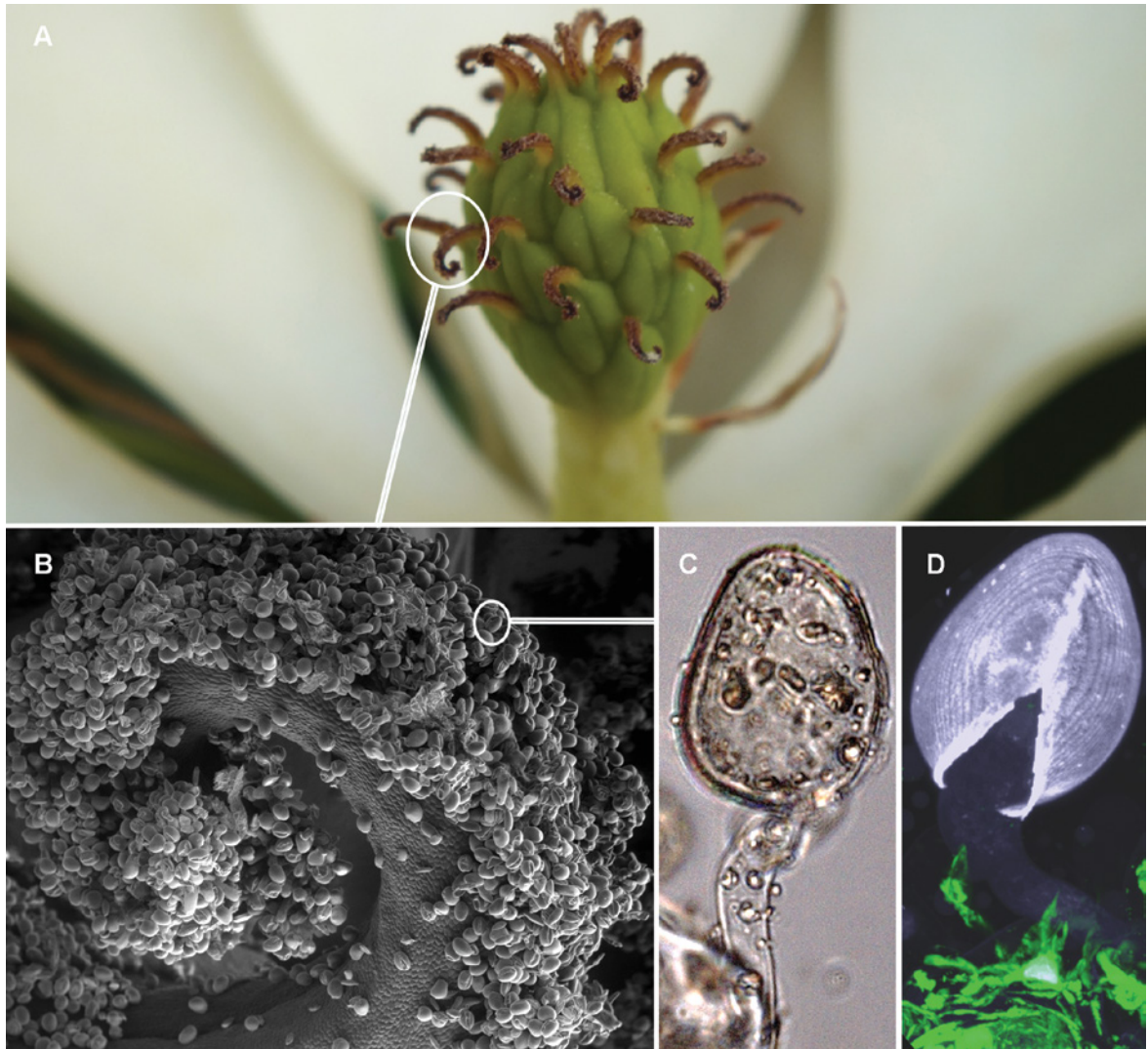
<http://www.youtube.com/watch?v=Ja3GjyJ98uI>

A few studies in the reproductive biology of the genus *Magnolia* suggested that the period of female receptivity was connected to these flower movements, but exact timing was unknown. Our investigations in the Arboretum with controlled pollinations in the laboratory confirmed those suggestions, and showed that stigmatic receptivity is remarkably short.

Stigmas of *M. virginiana* are only ready to allow pollen grain germination for a few hours following the first flower opening. As soon as the flowers close, the stigmas lose the capacity to allow pollen grain germination.

With a better understanding of the time frame of stigma receptivity in *M. virginiana*, the question remained as to what molecules

are involved in the communication between the male pollen grains and the stigmatic tissue. Our previous work with apple (*Malus*) flowers established what factors are involved in the reception and acceptance of compatible pollen (pollen that is not being rejected), and what their effect was on fruit production. We found that a group of glycoproteins (complex molecules



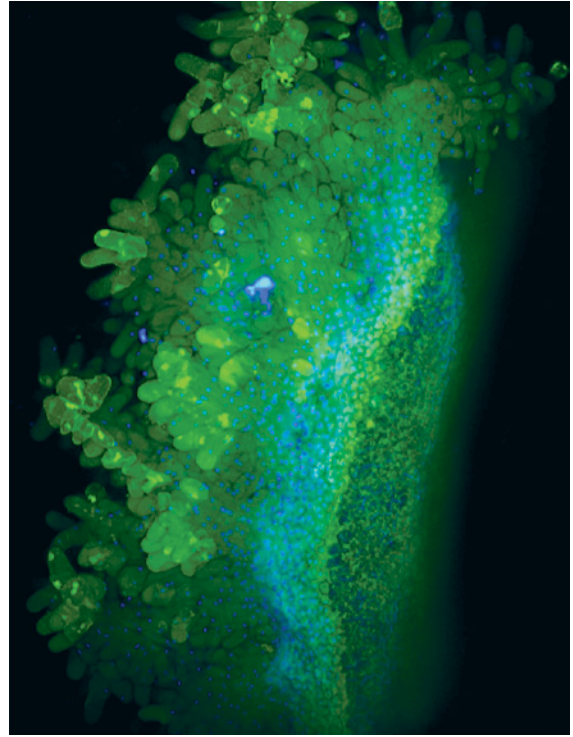
Male phase of *Magnolia virginiana* flowers. (A) Stigmas showing a brown coloration the second day of flower opening. (B) Scanning electron microscopy of a hand-pollinated stigma of *Magnolia virginiana*; many pollen grains are seen between cells of the stigma surface before germination. (C) Light micrograph of a single germinated pollen grain on the *Magnolia* stigma showing the pollen tube and other associated materials on its surface. (D) Laser confocal microscope view of a germinated pollen grain on the stigma of *Magnolia virginiana*: the white part is the pollen grain coat (exine), opening at the bottom to allow pollen tube emergence. The fluorescent green shows glycoprotein revealed by using the immunolocalization technique.

composed of two organic units: small amino acid backbones, and large sugar moieties where the functional capacity resides), which have numerous functions in plants such as acting as mediators in cell-to-cell communication, were secreted towards the apple stigma surface precisely at the time of receptivity. Furthermore, these glycoproteins are known to control plant cell elongation processes, and could be involved in pollen tube elongation. Their conspicuous presence in female tissues of apple flowers prompted us to wonder whether ancient lineages of angiosperms (flowering plants) would use similar molecular mechanisms.

Microscopy evaluation of *Magnolia virginiana* stigmas showed that the nutrient movements in stigmatic tissues followed a precisely defined cycle, and that the secretory products on the stigma surface were mainly saccharides (short chains of sugars, based on the binding of individual units such as glucose or fructose). Furthermore, by using antibodies (immunolocalization) specific for the glycoproteins that were also present in apple stigmas, we detected these molecules during the short period of stigmatic receptivity in *M. virginiana*. This suggests that in *M. virginiana*, as in apple, specific glycoproteins mark the short time frame that flowers are able to allow pollen grain germination on the stigmatic surface. This work showed for the first time in a member of the Magnoliaceae that maternal tissues bear glycoproteins during pollen reception, and hinted at their involvement in pollen tube elongation towards the ovules.

Combined, all this data offers new perspectives on how different flowering plants control the production of offspring. The presence of common nutritive factors secreted from the female tissues at times of pollen reception in very distantly related species points to a possible conserved mechanism across all angiosperms. But also, it sheds light on the molecular crosstalk during initial stages of male–female interactions in seed plants. The stigma appears to be a unique tissue with a crucial function during the reproductive process.

Yet our results point to unresolved questions on the stigmatic behavior in other primitive flowering plants, where few studies have been performed. Understanding the molecules that



In this image of a *Magnolia virginiana* stigma surface the cell nuclei appear in blue and glycoproteins in fluorescent green. The fluorescence of glycoproteins is achieved by immunolocalization, a technique that tags specific parts of proteins with monoclonal antibodies that specifically bind them. A secondary antibody bearing a fluorescent label is then added to bind the primary one, thus allowing observation of the protein location in plant tissues under a fluorescent light/laser microscope.

mark receptivity can give insight into the complex mechanisms that flowers have to recognize the male counterparts and promote their growth. In order to figure out how these mechanisms may have influenced the evolution of this lineage, we plan to compare how different female tissues of the style and ovary can control pollen tube growth, and we plan to include a wider range of taxa in this study. The finely-tuned mechanism of flower receptivity in *Magnolia virginiana* displays the amazing capacity for precision during angiosperm reproduction. The coordination of pollinator activity, flowering cycle, and molecular performance offer an effective system in the time frame of only a few hours for possible interaction.

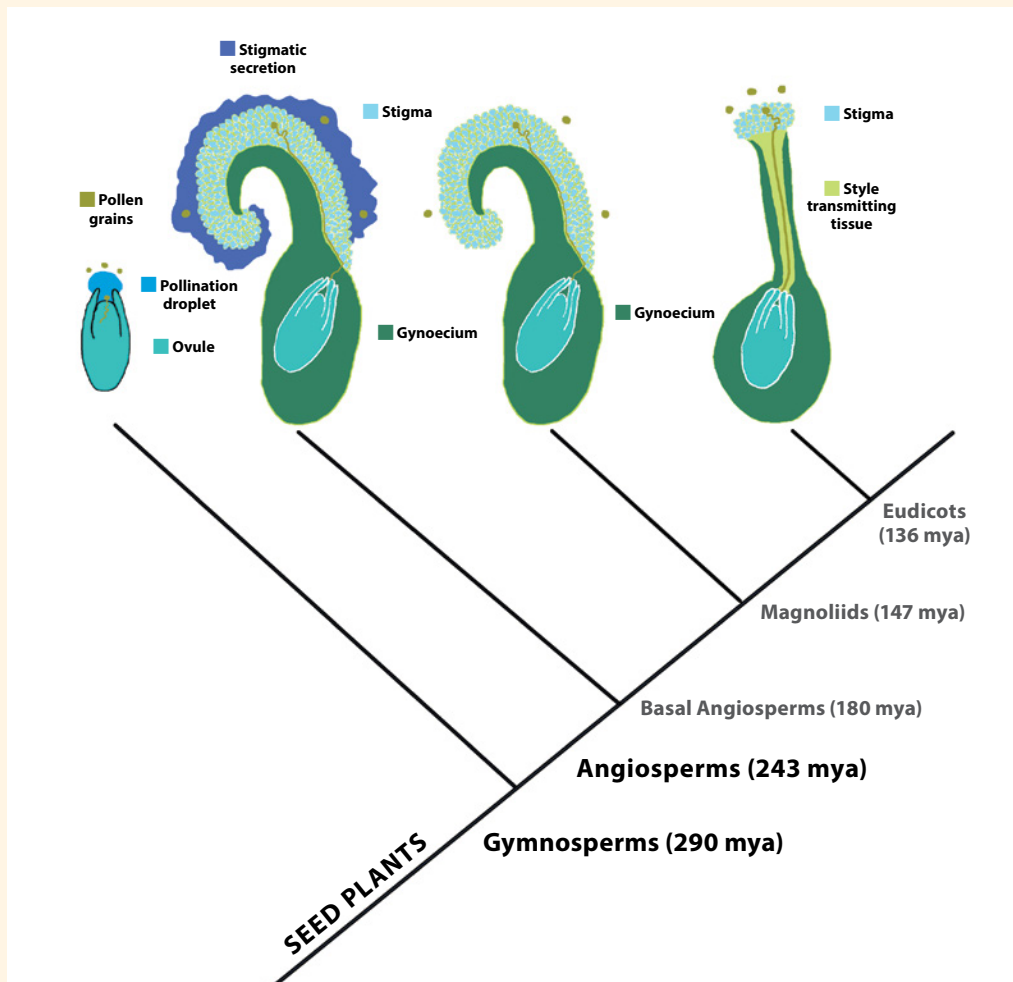
Long ago, Bishop Compton and many royal European families recognized the beauty and pleasant scent of *Magnolia virginiana* flowers

The Evolution of Pollen Receiving Structures in Seed Plants

SHOWN HERE are illustrations of longitudinal median sections of different maternal tissues receiving pollen grains in seed plants. The associated cladogram shows the estimated time of emergence for general seed plant lineages (mya=millions of years ago).

The earliest group shown is the gymnosperms, which arose around 290 million years ago, and are characterized by naked ovules that have a liquid secretion at their ovule tips (the pollination droplet) directly catching pollen grains. Those pollen grains germinate following contact with ovule tissues. In contrast, angiosperms evolved around 243 million years ago, and most basal flowering plants had already developed maternal tissues surrounding their ovules. Among them, the apical part (the stigma) establishes the first contact between maternal tissues and paternal pollen grains. In the basal angiosperm lineages (Amborellales, Nymphaeales, and Austrobaileyales), the stigmas produce a copious secretion at their surface for pollen reception. More evolved but still relatively early divergent angiosperms show large stigmatic surfaces and a wet appearance, but lack a copious secretion. Pollen grains can develop different pollen tube lengths depending on the area of the stigma where they are deposited. Finally, in most evolved angiosperms (in a broad sense), stigmas tend to reduce their area, whereas larger styles developed, and a specialized central transmitting tissue is the arena for pollen tube elongation towards the ovules.

These illustrations emphasize the importance of the stigma during the first male–female recognition in flowering plants, but also the gradual physical separation between ovules and stigmatic tissues during flower evolution.



when they included this species in their palace gardens. However, they missed the equally remarkable story behind what was happening within those flowers: the impressive coordination of floral movements and molecular interactions that created the ephemeral female phase, a short time for a courtship repeated every blooming period for millions of years.

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Juan M. Losada is a Putnam Scholar and a Postdoctoral Fellow at the Arnold Arboretum.

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Wish You Were Here

Nancy Rose

Long before email, Twitter, or Instagram, postcards were the medium of choice for sending brief messages and colorful images to friends and family. Simple cards, mostly used for advertising, were first introduced in the United States in the 1860s but were not especially popular since they required the same postage as letters. In 1873, the United States Postal Service (USPS) introduced official “postal cards,” plain cards with a printed stamp. The postage cost was one cent, half the rate for letters. However, non-USPS cards still required the full two-cent rate.

The rise of souvenir postcards can be traced to the 1893 World’s Columbian Exposition in Chicago, where vendors offered USPS postal cards with the addition of full color images of Exposition sights printed on the front. Finally, in 1898, an Act of Congress allowed privately printed postcards to mail at the same rate as USPS cards. Over the following decade the popularity of postcards soared, starting to decline only with trade and tariff issues prior to and during World War I (most postcards of the time were printed in Germany) and the increasing prevalence of telephones in the 1920s.

Given the beauty of the Arnold Arboretum it’s not surprising that it has been featured on many postcards over the years. The Arboretum archives hold a folder full of these historical postcards, some of which are presented below.

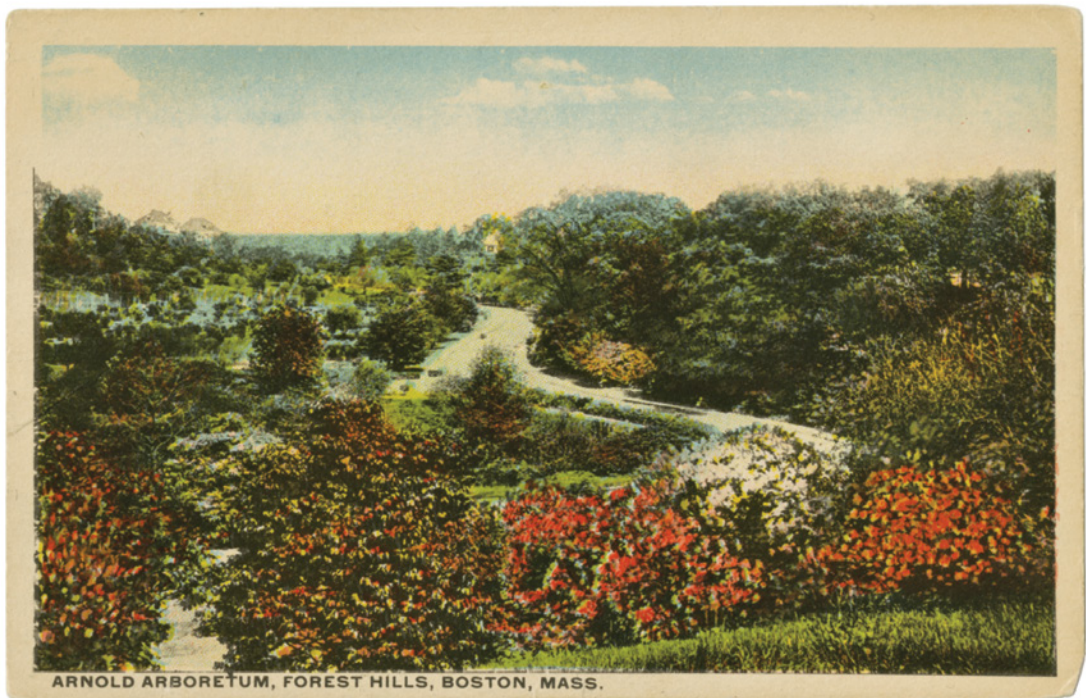
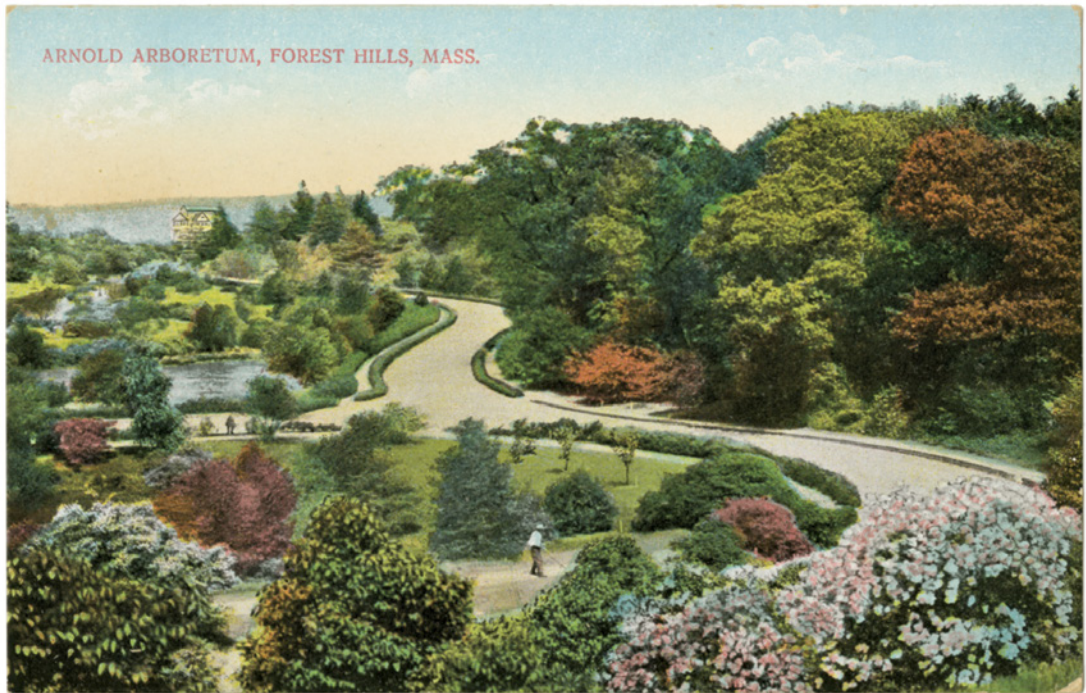


Linen style postcards were introduced in 1931. They are notable for the fabric-like texture embossed on the paper and their crisp, bright colors. This postcard of the Arboretum’s Hunnewell Building (then simply called the Administration Building) was likely produced in the 1930s but was clearly based on a 1921 black-and-white photograph made by Alfred Rehder (the vine coverage on the building matches precisely!).



One hundred forty characters or less?

Prior to 1907, postal regulations allowed only the mailing address to be written on the stamped side of cards. On many souvenir cards, whose main appeal was the colorful image on the front, this left only a narrow strip at the bottom for a personal message. This may have inspired concise composition (the upper card reads “With kind regards, hope you are all well, from your friend Jemima Cook”) or very tiny lettering. The lower card shows the pre-1907 admonition against writing messages on the stamped side but by 1910, the year it was postmarked, the sender’s message—“Dear Grandpa, Mamma send[s] her love and hopes you are well”—was perfectly legal.



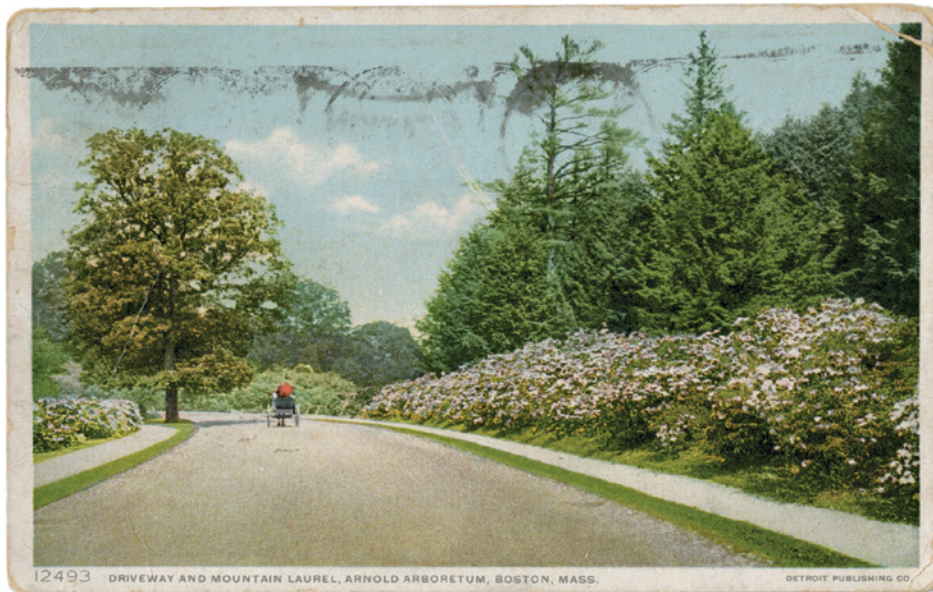


In living color

The original postcard boom was in part related to the development and proliferation of chromolithography in the latter nineteenth century. Using multiple lithographic stones or plates to apply layers of color, this printing process greatly increased the availability of high quality but affordable color prints. The best quality chromolithograph postcards were printed in Europe, primarily Germany. Hand colored images could be printed in all their glory on postcards, though printers could be variable in color quality. Among the Arboretum cards, some show fairly natural colors while others have little resemblance to the actual landscape.

These two cards (facing page) show the same view from within the Arboretum's lilac collection on Bussey Hill, looking east toward the ponds and Forest Hills gate. The top card was made in Germany circa 1906–1914 by Reichner Brothers, a printing company that also had offices in Boston and produced many cards showing sights in the Northeast. The tinted image takes liberties with actual colors but at least shows some pale purple lilac flowers, while the tinted halftone card below it, printed in the 1920s by M. Abrams in Roxbury (part of Boston), inexplicably paints the lilacs bright orange.

Different printers sometimes used the same images for their postcards. The cards above show the striking difference between black-and-white and hand colored versions of the same photograph of Bussey Brook at the base of Hemlock Hill.



This postcard with very naturalistic coloring (minus the smeared cancellation mark) shows Hemlock Hill Road, looking east toward Rhododendron Dell. It was printed in 1908 or 1909 by the Detroit Publishing Company (DPC), known for their high quality postcards made with the Swiss-invented photochrom process that allowed the direct transfer of photo negatives to lithographic printing plates (DPC used the trademark name “Phostint” on their cards). Arboretum visitors today can still see the the bank of mountain laurels (*Kalmia latifolia*) at the foot of Hemlock Hill (seen on the right side of the card) and the large white oak (*Quercus alba*, accession 286-2011) seen on the left.



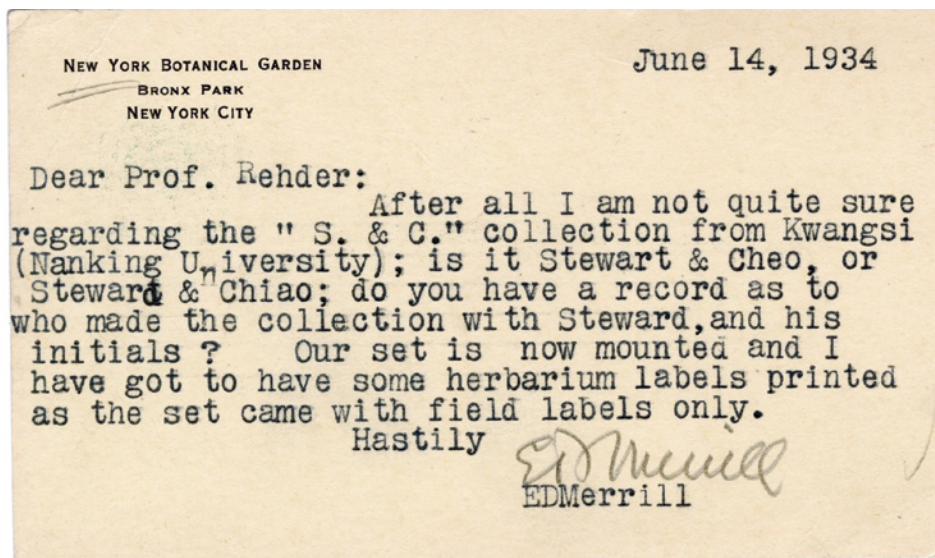
New inks and photo processes ushered in the modern Photochrome (or Chrome) era of postcards in 1939. These brightly colored photographic postcards are still the standard today, sending “Greetings From ...” around the world. The Arboretum produced its first color postcards in 1954, a series of seven images of spring flowering in the collections made by staff member Heman Howard. Many more colorful postcards featuring images from staff and volunteers were produced in subsequent years. Shown here, a popular 1989 card showing a view of autumn foliage and the Boston skyline from atop Peters Hill.



Where in the Arb?

Hundreds of thousands of postcards featuring everything from local taverns to the Grand Canyon have been printed over the past 100-plus years. Thanks to long-standing appreciation of postcards as collectors' items, a surprising number of these bits of paper have been preserved. Postcards have come to be recognized as valuable research materials for historians of architecture, landscapes, and other natural and man-made features, including places like the Arboretum. It's particularly interesting to see the same view over the years: Seen here, a beautiful circa 1907–1912 postcard (top) shows the Bussey Brook watershed, looking west towards the sunset, and a late 1980s card made from a similar vantage point.





Beyond vacation greetings

The Arboretum archives also hold postcards of a more practical nature within its correspondence files, especially those of Alfred Rehder. Voluminous folders show that Rehder corresponded frequently with colleagues from around the world as well as across town at the Harvard University campus in Cambridge. Postcard correspondence (the work email of the day) from Rehder's files includes a Harvard request for updated academic publications lists, notes from a nurseryman who was wild-collecting seeds in Arizona, messages from Europe related to his work on the *Bradley Bibliography*, and a note from a Swiss forestry researcher thanking Rehder for mentioning his work in the *Journal of the Arnold Arboretum*. Seen above, a note from E. D. Merrill at the New York Botanical Garden (he later became director of the Arnold Arboretum) requesting collection details for some herbarium specimens, and at left, a colorful card from Venezuela sent by botanist Leon Croizat, a former Arboretum colleague of Rehder's. Croizat underlined and added an exclamation point to the word "fauna" in the postcard's caption (*Pintoresca vista de la fauna Venezolana*), no doubt because the image shows Venezuelan flora rather than fauna.



We regret the error

Poor spelling and misinformation did not originate with the internet—even the early postcard era had its share of errors. At left, a card incorrectly names the Arboretum’s Bussey Hill as “Buzzy Hill,” while the rather unappealing card below labeled “Scene in Arnold Arboretum” appears to be the entrance to nearby Franklin Park instead.

Suggested Reading

Prochaska, D. and J. Mendelson, eds. 2010. *Postcards: Ephemeral Histories of Modernity*. University Park: Pennsylvania State University Press.

Stevens, N. ed. 1995. *Postcards in the Library: Invaluable Visual Resources*. New York: Haworth Press.

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Nancy Rose is the editor of *Arnoldia*.



Chimonanthus praecox: A Redolence of China

David Yih

On a raw, wintery day last February, I traveled from Connecticut to visit the Arnold Arboretum, impelled by curiosity. In 1977, my father, at the behest of the poet Donald Hall, had written a series of vignettes for *The Ohio Review* recalling the China he had left more than thirty years earlier. Among these was a nostalgic essay in which he sought to convey a feeling for Chinese esthetics as exemplified by *Chimonanthus praecox*, known in China as *la mei*. Its English common name, wintersweet, encapsulates two notable features of the plant: its membership in that small fraternity of temperate shrubs that bloom in winter and the remarkable fragrance of its flowers. I had recently learned that a specimen grew at the Arboretum and wanted to experience this fragrance for myself.

No account of wintersweet fails to mention the scent of its blossoms. But, as my father's essay points out, the resources of the English language are scarcely adequate to describe the smell of flowers. His attempt begins by contrasting wintersweet with gardenia, orange, and locust, whose scents "have something sensual in them that makes you feel restless, as if there were something missing in your life." The wintersweet's fragrance is something "entirely different, because it is ethereal, spiritual, otherworldly." This distinctive scent had set off a Proustian tumult of memories when my father happened to visit a botanical garden while living in Geneva, in 1964:

"As I wandered about I suddenly smelled a remembered fragrance ... In the tepid sun and the breeze, I suddenly recalled my grandfather's house with its two wintersweet trees, my middle school in Soochow with its ancient garden, and the hills of the Chia-ling River. My mind was drunk with memories of people who had gone out of my life and of sceneries I should in all likelihood never see again."

Chimonanthus belongs to Calycanthaceae, a small family whose members are found primarily in East Asia and North America. Endemic to montane forests in China, *Chi-*

monanthus praecox has been cultivated for over a thousand years. A great number of cultivated varieties exist in China, where it is grown as a garden shrub, a potted plant, and for flower arrangements. When the Sung dynasty poet Huang T'ing-chien composed a poem in praise of *la mei*, the plant attained instant fame and popularity in the capital, Kaifeng. Fan Chengda included it in his botanical treatise, *Fancun meipu* (Fan-Village plum register), circa 1186. According to the custom of associating a plant with each month of the lunar calendar, *la mei* is the flower of the twelfth month; its blooming thus coincides with the Chinese New Year.

The Arnold Arboretum's lone specimen (accession 236-98) was grown from seeds received from a botanical garden in Belgium. Wintersweet is marginally cold hardy in USDA Zone 6 (average annual minimum temperature 0 to -10°F [-17.8 to -23.3°C]), so the plant was carefully sited in a protected microclimate on the south side of Bussey Hill. In colder winters flower buds may be damaged or killed, but in good years the hardy visitor who ventures into the Explorers Garden in January will come upon the pendant, waxy yellow blossoms picturesquely scattered along leafless branches and find the air charged with the heady scent for which the plant is known.

The chemical components of wintersweet's fragrance are under intensive study in Asia, where as many as 161 compounds have been identified in the scent. Little wonder, then, that opinions vary as to how best to describe it. Last winter, the Arboretum's *Chimonanthus* struggled to bloom in freezing temperatures, but my companions and I did find many plump, globose flower buds and a few open flowers to sniff. Among our varied reactions: spicy, minty; like hyacinth or mock-orange; like a steaming cup of jasmine tea—welcome sensations on a chilly day in the dead of winter.

David Yih is a writer, musician, and member of the Connecticut Botanical Society.



