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Front cover: Sarracenia leucophylla growing in the bog garden at the Atlanta Botanical Garden. The species name was published by Rafinesque in 1817. Photo by Daniel Mosquin.

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Inside back cover: Flowers and developing fruits of *Dipelta floribunda*. Photo by Nancy Rose.

Back cover: Trunk of the type tree of *Metasequoia glyptostroboides* in Modaoqi, western Hubei, China. Photo by Zsolt Debreczy and István Rácz.

Constantine Rafinesque, A Flawed Genius

Daniel Mosquin

Stenanthium was first proposed as a subgenus of *Veratrum* L. by Asa Gray in 1837. Rafinesque had already suggested this group be recognized as its own genus, named by him as *Anepsa*, in 1832. When it was generally agreed upon that this group of species should indeed be considered its own genus, Rafinesque's earlier contribution was disregarded, and Gray's *Stenanthium* was conserved instead. Pictured here is *Stenanthium occidentale* A. Gray.

Viburnum rafinesqueanum—to a teenaged boy in Manitoba beginning to learn the scientific names of plants, this moniker stood out. *Poa pratensis*? Meadow grass or Kentucky bluegrass (*pratensis* = "of a meadow"). *Caltha palustris*? Marsh marigold (*palustris* = "of a marsh"). *Aquilegia canadensis*? Canada columbine or red columbine. *Viburnum rafinesqueanum*? Here was a mess of near-impenetrable letters, a poetic delight to my ears when recited, which I soon learned honored a man named Rafinesque. A few years later in a floristics lecture, the good-natured eye-rolling reaction of the professor to my question about Rafinesque started a broader curiosity about the man.

Constantine Samuel Rafinesque was among the great American naturalists of the nineteenth century. He was also among the most controversial and eccentric natural history personalities of his time. In the course of four decades, he offended nearly every establishment botanist in the United States, leading to a disdain that persisted among these botanists and succeeding generations of their students. As one result, his contributions to botany and other natural history sciences were downplayed or ignored for many decades beyond his death in 1840. His reputation has been mended somewhat since the mid-nineteenth century, as those he interacted directly with passed away and several twentieth-century historians critically examined his life and work. What emerges is that the man was a flawed genius, whose inability to work within the bounds of scientific convention necessarily led to lower recognition than he would otherwise have deserved.

To immediately give an idea of Rafinesque and aspects of his personality, it is perhaps best to learn of his many roles in his own words:

> "Versatility of talents and of professions, is not uncommon in America; but those which I have exhibited in these few pages, may appear to exceed belief; it is a positive fact that in knowledge, I have been a Botanist, Naturalist, Geologist, Geographer, Historian, Poet, Philosopher, Philologist, Economist, Philanthropist ... By profession, a Traveller, Merchant, Manufacturer, Collector, Improver, Professor, Teacher, Surveyor, Draftsman, Architect, Engineer, Pulmist [one who treats pulmonary diseases], Author, Editor, Bookseller, Library, Secretary ... and I hardly know myself what I may not become as yet: since whenever I apply myself to any thing, which I like, I never fail to succeed if depending on me alone, unless impeded and prevent by lack of means, or the hostility of the foes of mankind."

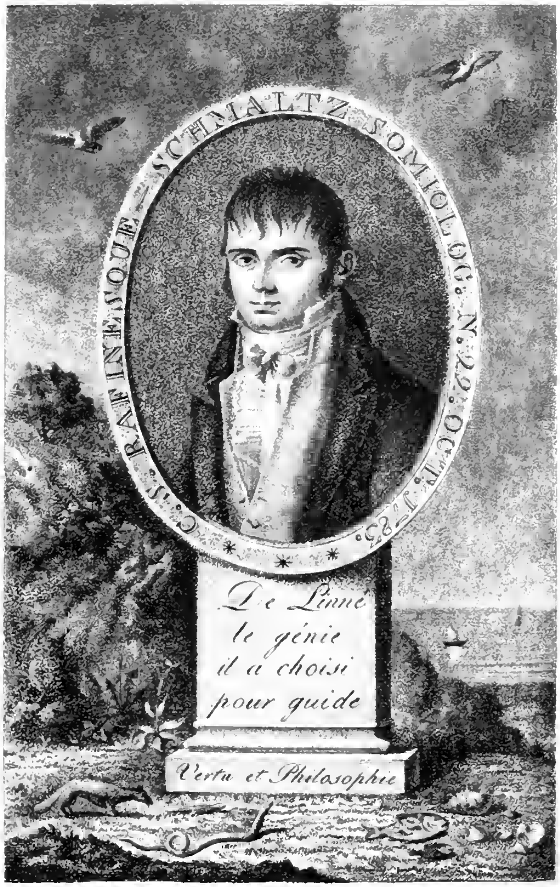

Image of Constantine Rafinesque on the frontispiece of his 1815 publication *Analyse de la nature.*

RAFINESQUE'S LIFE

Rafinesque was Turkish-born to a French father and a mother of German descent on October 22, 1783. He was reared in Marseilles, France, by his mother and his father's family; his father was a merchant trader who spent much time abroad. In 1792, his family fled to Italy to escape the French Revolution. A year later, his father died during a yellow fever epidemic in Philadelphia. Rafinesque returned to France in 1797, where he remained until 1802.

At the age of 19, he landed in Philadelphia for three years, where his passion for botanizing the United States started immediately. He asserted that the brassicaceous *Draba verna* L. he picked up after stepping off the ship was a new species, as he generally believed that American counterparts of well-known European species could not be the same species. It is also in Philadelphia where he began to write books and papers. In 1805, he returned to Italy where he resided for a decade (occasionally living under the name Constantine Samuel Rafinesque Schmaltz, in order to avoid anti-French sentiment). Here, he married in 1809, had a daughter born in 1811 and an infant son who perished in 1814. A return to the United States was made in 1815, though the boat he was traveling on was shipwrecked off Long Island and he lost much of his collections and notes. Rafinesque lived in New York for three years, and helped to found the Lyceum of Natural History of New York. In 1818, a brief residence of under two years was made in Philadelphia, before undertaking a posting as Professor of Natural History at Transylvania University in Lexington, Kentucky, from 1819 to 1826. Post-professorship, he returned to Philadelphia for the remainder of his life. On September 18, 1840, he died of stomach cancer.

TAXONOMIC CONTROVERSIES

Botanist, taxonomic scholar, and former director of the Arnold Arboretum Elmer Drew Merrill completed the voluminous *Index Rafinesquianus* in 1949 wherein he attempted the Herculean task of compiling the botanical work

Enemion hallii (A. Gray) J. R. Drummond & Hutchinson is a member of the Ranunculaceae (buttercup family). The name *Enemion* was published in 1820 by Rafinesque. The *Flora of North America* account for the genus states: "North American taxonomists tend to retain the North American species in *Isopyrum* L. whereas taxonomists elsewhere recognize *Enemion*."

Rafinesque proposed the genus *Olsynium* in 1836. While occasionally used by other taxonomists (especially in the early twentieth century), the name did not receive widespread use until the late twentieth century. Instead, this species was typically placed in *Sisyrinchium*. *Olsynium douglasii* (A. Dietrich) E. P. Bicknell (seen here) was published in 1900.

of Rafinesque. Merrill seems to be ultimately sympathetic to Rafinesque, declaring:

> "It is doubted if in the entire history of descriptive biology there is any other author who has suffered more from the weight of authority than Rafinesque. The leading biologists of his time, both in Europe and in America, ignored his numerous nomenclatural proposals to an extraordinary degree, whether he was correct in his conclusions or not."

However, from the perspective of a taxonomist, Merrill also states:

> "After years of effort devoted in part to a consideration of the unending series of problems in botany alone, raised by Rafinesque's work, my frank conclusion is that in taxonomy and nomenclature we would have been infinitely better off today had Rafinesque never written or published anything appertaining to the subject."

How did Rafinesque engender such a conclusion? The answer begins with the nomenclatural system developed by Carl Linnaeus, the father of modern taxonomy. Prior to Linnaeus, the names of species were descriptive Latin polynomials (i.e., multiple words were used as a name). Linnaeus simplified this system to the consistent use of binomials, with the first word representing the genus or group (e.g., *Acer*, the maples) and the second representing the specific epithet (e.g., *rubrum*, or red). Combined with the author who first (validly) published the name, a species name is created, for example, *Acer rubrum* L. (L. is an abbreviation for Linnaeus). Linnaeus's system quickly became adopted by other scientists and remains in widespread use today.

A later addition to the Linnaean system was the concept of type specimens. The underlying idea of type specimens is that a name (an abstract notion) must be connected to a physical object, which provides an example of the taxon. Most often this type specimen is a dried herbarium specimen, but it can also be an illustration. Type specimens provide taxonomists with a way to re-examine the specimens that led to the establishment of a new species or presently define a species (in instances where a species was named prior to the concept of typification or where the type specimen was lost

The genus *Lomatium* was proposed in 1819. It did not see much use for the next century, as critics declared it too close to the name *Lomatia* R. Br. (Proteaceae). Coulter and Rose briefly adopted it in a 1900 monograph of the Umbelliferae, but it didn't see widespread use until 1920 when Macbride pointed out that, according to the rules of botanical nomenclature, it was a valid generic name despite the similarity to *Lomatia.* Seen here, *Lomatium brandegeei* (Coult. & Rose) J.F. Macbr. is native to British Columbia and Washington.

due to fire or other disasters), a nod to the principle of reproducibility in the scientific method.

An additional, and critical, concept to understanding the controversy surrounding Rafinesque is that the Linnaean system makes no attempt to define the boundaries of taxa. Though a hierarchical framework is provided, the questions of "What is a species?" or "What constitutes a genus?" are left to the determination of taxonomists. This leeway gives the taxonomist much latitude in determining what might constitute a taxon. If the taxonomist errs on making too broad of a definition (i.e., "lumps" too much variability within a taxon), it increases the likelihood that her or his work will be revised by the next taxonomist to examine the taxon. Similarly, if the taxonomist errs on making too narrow of a definition (i.e., "splits" a group into separate taxa based on too little variability), the likelihood of revi-

Parnassia glauca was one of a number of species published posthumously in 1840, in Rafinesque's *Autikon Botanikon.*

Though its center of diversity is in California, the genus *Ceanothus* has several central to eastern North American species including *Ceanothus herbaceus* (seen here), which was described and named by Rafinesque in 1808.

sion is again increased. An accurate, stable, and useful representation of taxa is the goal, though "lumpers" and "splitters" disagree on how best to reach that ideal.

Finally, it is also necessary to know the nomenclatural concept of "priority." Priority is the principle that the first valid publication of a name for a taxon establishes the name when that taxonomic entity is recognized. At its most basic application, this idea resolves which name should take precedence when multiple names for a taxon have been published. In the modern age with peer review, ready access to a significant amount of published literature, and digitized herbarium specimens, it is an infrequent occurrence for a taxonomist to rename an already-named taxon. In the early nineteenth century in the United States, however, communication about newly described species (of which there were many) was difficult and only readily accessed in major centers. Different authors contemporaneously giving separate names to the same taxon was a frequent occurrence, which later taxonomists resolved using the principle of priority.

The controversy surrounding the botanical work of Rafinesque was in large part a matter of his flooding the published literature with names, sometimes accompanied by poor descriptions. Often, it was claimed (and sometimes rightly so) that he did not need to see a specimen to ascribe it a new name. He was a splitter without equal:

> "Altho' this attempt may astonish or perplex some timid Botanists, my labors will be duly appreciated ere long, and my increasing efforts to improve the science meet with a kind reception from the new improving school. The axiom that a multiplication of names enlarges our ideas, holds true in all cases and sciences, since they are based on facts or mental entities. Some Linneists have vainly tried to discredit on generic

> reform, and called us Genera-mongers. We may in return call them Genera-shufflers, who want to squeeze plants into improper genera, and delay improvements by opposing the corrections of botanical blunders. It is to them that we owe the superfluity of synonyms: they often shuffle plants into 3 or 4 Genera, as Linnaeus did for *Heliopsis*, until it must at last form a Genus of itself. It is a fact that almost all plants of doubtful Genera, are types of peculiar ones; the chances of it increase, as they are shifted."

With the establishment of the Linnaean system and the publication of *Species Plantarum* as the nomenclatural benchmark, Linnaeus is credited with the valid publication of a large number of genera and species. Linnaeus described about 1,440 genera, and most of these names are still in use today. By contrast, the splitter Rafinesque described approximately 2,700 genera—of these, no more than 50 or 60 are applied to recognized genera today (yet, had priority been applied, he would be credited with at least 160). Linnaeus also generated almost 9,000 binomials (species names), and again, the large majority of these are in use today. Rafinesque did not quite match Linnaeus in this category. Of the 6,700 or so species names published by Rafinesque, fewer than 300 are generally accepted.

Rafinesque's proclivity to deem the most minor variations as new species (and sometimes new genera) created work—much more work—for anyone who later attempted to publish a new species, write a monograph, or clarify names in a taxon. To give an example, *Clintonia* is a genus named by Rafinesque (and still recognized today). Before Rafinesque erected a new genus for this group in 1832, its species were variously recognized as being in *Dracaena* (the first published name was in 1789), *Convallaria*, and *Smilacina*. According to *The Plant List* (drawing on information from the World Checklist of Selected Plant Families), 41 names have been published within *Clintonia* (the actual number is likely higher). Working with a dataset of 35 names of "High Confidence Level" ("applied to the status of name records derived from taxonomic datasets which treat the whole of the taxonomic group in question on a global basis and have been peer reviewed"), 30 are at the species rank (5 below the species level). Five of the species names are confidently recognized as "Accepted" species, and a single name for a recently described (1993) Asian species remains unresolved. The remaining 24 names are listed as synonyms, i.e., names that are considered to be already represented within the concept of a different name. Of these 24 synonyms, 19 were published by Rafinesque. Examples of species recognized by Rafinesque but generally regarded as minor variations within *Clintonia uniflora* (Sol.) Raf. include *Clintonia angustifolia* Raf. (a narrow-leaved entity), *Clintonia biflora* Raf. (a two-flowered entity), and *Clintonia ciliata* Raf. (presumably with fine hairs along the margins of an organ like a leaf or petal).

If a taxonomist were to discover what she/he believes to be a new species of *Clintonia*, the taxonomic work involved would require at a minimum comparing it against the type specimens of other members of the genus and reviewing the taxonomic literature to ensure a previously published name and description (including all synonyms) does not conform to the purported new species. In practice, the taxonomist would further compare it against additional specimens of each species in order to properly account for variation within each species. In order to name a new species in *Clintonia*, the work required would involve reviewing all of Rafinesque's names and descriptions to determine if he had named the entity first. For a relatively simple group of species like *Clintonia* (5 accepted species), the task would be difficult in modern times, and very difficult at the time of Rafinesque. For more taxonomically complicated genera, like *Trillium*, Rafinesque made the difficult near-impossible. There are about 38 recognized species of *Trillium* in North America, with more than two-thirds of these from eastern North America. Rafinesque is presently responsible for 3 of these accepted names, though he described an additional 31 species and 67 varieties.

This onslaught of published names of additional genera and species in many eastern North American plant groups, sometimes poorly described, was not well received. Amos Eaton, a botanist and author of the 1817 *Manual of Botany for the Northern States*, was generally

Four of the five recognized species of *Clintonia*, clockwise from above: *Clintonia borealis* (Sol.) Raf., the type species of the genus erected by Rafinesque in 1832; *Clintonia umbellulata* (Michx.) Morong, first named by Michaux as *Convallaria umbellulata* in 1803, then eventually transferred by Morong into *Clintonia* in 1894 after residing in a number of other genera; *Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth, transferred into *Clintonia* by Kunth in 1850; and *Clintonia andrewsiana* Torr., first described and published in 1857 after Rafinesque's proposal of *Clintonia* became generally accepted.

sympathetic to Rafinesque and considered him a friend. However, in 1817, he wrote to his student John Torrey:

> "I am glad Mr. Rafinesque has not set you all wild. Why can not he give up that foolish European foolery, which leads him to treat Americans like half-taught school boys? He may be assured, he will never succeed in this way. His new names with which he is overwhelming the science will meet with universal contempt."

Eaton accurately predicted the ultimate approach by much of the botanical establishment—ignore much of Rafinesque's work, to the extent that the principle of priority was overridden in many cases to exclude Rafinesque's contributions.

Asa Gray, the pre-eminent American botanist of the nineteenth century, contributed to the practice of discounting Rafinesque. Though he was charitable towards Rafinesque's earlier work, Gray's influence cemented the rejection of Rafinesque's ideas about new genera and species when he wrote the following about Rafinesque after his death:

> "Many of Rafinesque's names should have been adopted; some as a matter of courtesy, and others in accordance with the strict rule.... One who, like Rafinesque, followed the easy rule of founding new genera upon all these species, could not fail to make now and then an excellent hit; but as he very seldom knew the plants themselves, he was unable to characterize his proposed genera, or to advance our knowledge respecting them in the slightest degree. In his later publications, this practice is carried to so absurd an extent as entirely to defeat its object ... A gradual deterioration will be observed in Rafinesque's botanical writings from 1819 to about 1830, when the passion for establishing new genera and species, appears to have become a complete monomania".

ON EVOLUTION

Another area where Rafinesque generated controversy was in his ideas about how species and genera were formed. One of the reasons Rafinesque named so many species and genera was because (in his own words, from 1832), "The truth is that Species and perhaps Genera also, are forming in organized beings by gradual deviations of shapes, forms and organs, taking place in the lapse of time," and that "every variety is a deviation which becomes a species as soon as it is permanent by reproduction."

Originally published as *Saxifraga ranunculifolia* by Hooker in 1832, Rafinesque clearly disagreed. He erected the genus *Hemieva* in 1836 to segregate this species, but was ignored. In 1879, Asa Gray named a new genus and species *Suksdorfia violacea*. In 1891, H. Engler assigned *Saxifraga ranunculifolia* to *Suksdorfia*. Recent phylogenetic studies suggest *Suksdorfia ranunculifolia* is within a distinct genus, so *Hemieva ranunculifolia* (Hook.) Raf. was resurrected in the second edition of *The Jepson Manual* (2012), a major taxonomic reference.

Rafinesque's ideas were informed by Adanson from 1763, to whom he gives credit:

> "Adanson ... was like Linnaeus, Necker and myself (in fact like all acute observers) a strenuous supporter of the doctrine that Species were unlimited, and increasing by the natural process of semination, deviation, variation, hybridization and such. Whence he concluded that we could hardly ascertain the primitive types of species, that many known to ancient Botanists were lost or no longer found, while new ones were evolved in mountains, groves, fields, and gardens."

Austrian botanist Josef August Schultes honored Rafinesque in 1830 with the publication of *Viburnum rafinesquianum*, known commonly as downy arrowwood.

To give context, the dogma of the time was that species were fixed entities, unchanging. Nearly all of Rafinesque's contemporaries used Rafinesque's descriptions of evolutionary trees and the formation of new genera and species as proof that his ideas in all areas (including taxonomy) were to be shunned. Gray also made note of this in his obituary of Rafinesque, reminding others of how Rafinesque strayed from the dogma of the time:

> "According to his principles, this business of establishing new genera and species will be endless; for he insists, in his later works particularly, that both new species and new genera are continually produced by the deviation of existing forms, which at length give rise to new species."

In 1859, Darwin published *On the Origin of Species*, with his theory of evolution by natural selection. Gray became an evolutionist.

RAFINESQUE'S LEGACY

Upon Rafinesque's death, his belongings were junked or sold, including his plant collections and some of the over one thousand papers and books he authored. He died a pauper, with the money generated from the sale of his belongings not even covering the cost of his burial.

Proof of Rafinesque's genius resides in the 160 or so genera he would have established had the principles of priority been followed. That he would have surpassed ten percent of Linnaeus's total named genera, in a country that had already been relatively well explored, is testament to his keen observational skills and botanical acumen. Had he more credibility with his peers, his ideas on the formation of new genera and species may have invited additional exploration from other brilliant biological minds of the time, perhaps advancing the science of evolutionary biology by decades. Historians continue to mend his reputation, such that one of Rafinesque's statements seems prophetic: "Time renders justice to all at last."

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A Quarter-Century Perspective on the Center for Plant Conservation Collections at the Arnold Arboretum

Abby Hird

Given the array of current threats to biodiversity (including habitat destruction, pollution, climate change, and invasive species), it is no surprise that roughly one out of every three plant species in the world is threatened with extinction. As native habitats are changing and disappearing, ex situ conservation (preservation of species outside their natural habitat as living plants, seeds, or other viable tissue) efforts are even more vital to the successful conservation of plants.

Public gardens, numbering more than 700 in the United States alone (BGCI 2012), offer valuable resources, facilities, and horticultural expertise that support conservation efforts. These ex situ refuges also allow visitors a unique chance to learn about and observe threatened species firsthand. While these important plant collections serve as insurance policies against extinction for many species, the recent North American Collections Assessment found that only 39% of North America's threatened species are currently cultivated in public gardens; clearly, there is much opportunity to increase rare plant conservation collections (Kramer et al. 2011). In addition to increasing the number of threatened species in ex situ collections, broadening genetic diversity within those collections will support meaningful conservation applications.

During my Putnam Fellowship from 2008 to 2010 I worked with Arboretum Curator of Living Collections Michael Dosmann to assess the conservation potential of the

Flowers and fall foliage of *Amelanchier nantucketensis*.

Coppery new foliage and yellow flowers of *Diervilla sessilifolia*.

living collections in the Arnold Arboretum. We started with the formal conservation collections maintained as a partnership with the Center for Plant Conservation (CPC) (Hird and Dosmann 2010). We knew the CPC collections were well-constructed collections of threatened species, but we didn't know how they had fared since their establishment nor what priorities we should keep in mind for future collections development. The following is a summary of our findings and the lessons we learned along the way.

Collecting, maintaining, and preserving plant biodiversity was a founding principle of the Arnold Arboretum in 1872 and remains at the core of the Arboretum's activities today. Charles S. Sargent, the Arboretum's first director, initiated the creation of one of the most extensive temperate woody species collections in the world. This long-standing commitment to collections development remains a core value of the Arboretum. Today, the Arboretum's rich and dynamic botanical collections serve active research and education programs, and represent an invaluable repository of preserved genetic resources.

The CPC was founded in 1984 through a collaboration among 18 botanical gardens and arboreta as a network aimed at the "establishment of a permanent, well-documented, and accessible collection of rare and endangered native plant taxa of the United States" (CPC 1984). The Arnold Arboretum played a key leadership role in jump-starting the effort by housing the first CPC office and building the first CPC collections. Now headquartered at the Missouri Botanical Garden in St. Louis, the CPC has grown to a nationwide network of 38 botanical institutions. This network works to preserve 772 critically endangered North American species that compose the CPC National Collection of Endangered Plants. Each participating institution is assigned species relevant to their institution and region, monitors remaining wild populations, and collects and maintains genetically sound, long-term ex situ collections to support research, education, and, ultimately, species survival.

As a CPC participating institution, the Arnold Arboretum is obligated to follow a set of eight management guidelines (facing page) described in the CPC Handbook (CPC 2007). The Arboretum meets and exceeds most CPC guidelines, especially in the areas of collections data management and research. These guidelines are associated with detailed information including original wild collection data, germination and propagation protocols, health conditions of each specimen through time, and cultural requirements for each species. However, a variety of challenges have prevented the Arboretum from fulfilling certain guidelines, such as meaningful seed storage and reintroduction of species.

CPC COLLECTIONS MANAGEMENT GUIDELINES (CPC 2007)

1. Taxa should be proposed and accepted by the CPC Science Advisory Council for inclusion into the National Collection.
2. Propagative materials should be collected from the wild in accordance with CPC guidelines and should be maintained in protective storage.
3. A usable seed storage and germination protocol should be developed for the taxon and initial seed viability should be determined if possible.
4. Horticultural techniques for ex situ cultivation should be established and documented, and the taxon should be successfully raised to reproductive maturity.
5. Adequate propagules and data should be stored in at least two separate secure sites
6. An initial baseline germination test should be conducted on stored seed accessions of the taxon, and viability should be retested at appropriate intervals, using enough seed if possible to detect statistically valid declines in viability.
7. Collaborative research agreements to be established for taxa as necessary and appropriate.
8. Legitimate reintroduction programs or experimental reintroductions are encouraged.

In total, the Arboretum has assisted in the conservation efforts of 24 threatened CPC species by collecting wild germplasm and maintaining those plants in the living collections

MICHAEL DOSMANN

Fothergilla major **bears fragrant, bottlebrush-like flowers in spring.**

Table 1. Historic and Contemporary CPC Collections at the Arnold Arboretum
(current in bold)

SPECIES	FAMILY	NatureServe G-Rank1	Year of Transfer	Living (as of 06/15/12) Lineages/ Accessions/ Plants
Abies fraseri	**PINACEAE**	**G2**	**Pending**	**5/7/9**
Amelanchier nantucketensis	**ROSACEAE**	**G3Q**	**–**	**14/14/47**
Buckleya distichophylla	SANTALACEAE	G3	2005	1/1/1
Clematis viticaulis	RANUNCULACEAE	G2	2005	0/0/0
Conradina verticillata	LAMIACEAE	G3	1993	0/0/0
Corema conradii	EMPETRACEAE	G4	2005	1/1/1
Diervilla rivularis	**CAPRIFOLIACEAE**	**G3**	**–**	**8/26/26**
Diervilla sessilifolia	**CAPRIFOLIACEAE**	**G4**	**–**	**14/26/33**
Fothergilla major	**HAMAMELIDACEAE**	**G3**	**–**	**15/16/27**
Gaylussacia brachycera	**ERICACEAE**	**G3**	**Pending**	**2/3/3**
Hudsonia montana	CISTACEAE	G1	*	0/0/0
Ilex collina	**AQUIFOLIACEAE**	**G3**	**–**	**14/14/25**
Kalmia (Leiophyllum) buxifolia	ERICACEAE	G4	2005	1/1/2
Magnolia pyramidata	**MAGNOLIACEAE**	**G4**	**Pending**	**0/0/0**
Paxistima canbyi	CELASTRACEAE	G2	2005	0/0/0
Prunus alleghaniensis	ROSACEAE	G4	2005	3/3/3
Prunus alleghaniensis var. *davisii*	ROSACEAE	G4Q	*	1/1/1
Rhododendron austrinum	ERICACEAE	G3	1995	2/2/2
Rhododendron prunifolium	**ERICACEAE**	**G3**	**–**	**9/10/28**
Rhododendron vaseyi	**ERICACEAE**	**G3**	**–**	**21/21/40**
Spiraea virginiana	**ROSACEAE**	**G2**	**–**	**42/44/44**
Torreya taxifolia	TAXACEAE	G1	2010	10/10/14
Viburnum bracteatum	**ADOXACEAE**	**G1G2**	**–**	**3/6/10**

NatureServe 2012; see textbox on facing page for explanation of ranks.

* Species not assigned to the Arnold Arboretum, but is part of the CPC National Collection and living in the Arboretum.

About NatureServe G-ranks and Threat Levels

NATURESERVE'S Global Conservation Status Ranks (G-ranks) are the most comprehensive source of conservation information on species native to the United States or Canada (NatureServe 2012). G-ranks can be used to gauge the "level of need" for each species, which is useful when prioritizing collections curation and development activities such as repropagations, voucher collection, or backup germplasm distribution at an institution. Thus, *Torreya taxifolia* with a G-rank of G1 (Critically Imperiled) has the greatest conservation need (the most threatened in the wild, with the fewest remaining wild populations) among current CPC species and first priority in collections management decisions; while *Diervilla sessilifolia* with a G-rank of G4 (Apparently Secure) has a relatively lower conservation need.

Global Rank Categories

GX: Presumed Extinct, GH: Possibly Extinct, G1: Critically Imperiled (5 or fewer populations remain), G2: Imperiled (very few remaining populations), G3: Vulnerable (relatively few remaining populations), G4: Apparently Secure (common; widespread and abundant), Q: Questionable Taxonomy, GNR: Unranked, GNA: Not Applicable

(see Table 1). A majority of the Arboretum's CPC collections began via collecting expeditions to the southeast and northeast regions of the United States in the late 1980s and early 1990s by Rob Nicholson, then plant propagator for the Arnold Arboretum (Nicholson 1996). At the time of this assessment there were 13 species assigned to the Arnold Arboretum. Many of the current and historic CPC species collected by the Arboretum originate from the southeastern United States, and some have experienced cold hardiness issues in the Northeast. In the past 15 years, due to significant decline in health and numbers of living accessions, about half of the original CPC species have been transferred to more appropriate institutions closer to their native range and with more compatible climates.

PLANTS IN THE ARNOLD ARBORETUM'S CPC COLLECTIONS

Abies fraseri: The Fraser fir is well-known in the Christmas tree industry due to its spirelike crown and fragrant foliage. Reaching heights of up to 25 meters (82 feet), this species is native to the Smoky Mountain Range and is unique because it grows at high elevations. It is severely threatened in the wild by the invasive balsam wooly adelgid (*Adelges piceae*) introduced from Europe. In 1876, Asa Gray first collected a wild plant for the Arboretum (accession 1522), which did not survive. Since then, several specimens were unsuccessfully introduced to the the Arboretum. A collecting trip in 1985 supported the establishment of the CPC collection of this species, which have suffered excessive losses due to incompatible climate and spider mite infestations. The Arboretum maintains 6 specimens from 3 states (Virginia, North Carolina, and Tennessee).

Amelanchier nantucketensis: The Nantucket shadbush is a stoloniferous shrub which forms dense colonies in its restricted native habitat along the northeastern Atlantic coast. Flowers usually open in May but are small and hard to notice. Threats to this species include overcrowding by other plant species, harmful management practices such as fire suppression, and uncontrolled land development of coastal habitat. The Arboretum maintains specimens collected in the 1980s from New York, Massachusetts, and Maine. A large group was successfully transplanted during the Bradley Rosaceous Collection renovations in 2009 and now thrives near Dawson Pond.

Diervilla rivularis: The mountain bush honeysuckle is an arching shrub 1 to 2 meters (3.3 to 6.6 feet) tall and wide, very similar in appearance to *D. sessilifolia*, and forms colonies by rooting where the tips of its branches touch the ground. Small yellow flowers appear in July and attract insect pollinators. Its native range extends from the Blue Ridge to the Appalachian Plateau of the southeastern United States. This species is threatened in the wild by habitat destruction from logging and crowding by invasive species. The Arboretum maintains vigorous specimens from one location in Georgia, which are cut back every 2 to 3 years to maintain them as individual plants.

Diervilla sessilifolia: The southern bush honeysuckle is a sprawling shrub, 1 to 2 meters (3.3 to 6.6 feet) tall and wide, very similar in appearance to *D. rivularis*, except that the leaves are sessile (stalkless) on its arching branches. Native from Georgia to the Blue Ridge in Virginia, this species is threatened by construction, development, and crowding by invasive species. The Arboretum currently maintains healthy specimens from Georgia, North Carolina, and Tennessee in the Leventritt Shrub and Vine Garden, and near the top of Bussey Hill.

NANCY ROSE

Showy fall foliage color of *Fothergilla major*.

Fothergilla major: The mountain witchalder, or large fothergilla, is a dense, colonizing shrub known to reach up to 6 meters (19.7 feet) tall in the wild. Fragrant, creamy white bottlebrush-like flowers emerge in May and make this a popular landscape plant. It is native to six states in the southeastern United States, and is threatened by land development. The Arboretum has successfully cultivated this species since 1876. Specimens from North Carolina and Georgia currently thrive here.

Gaylussacia brachycera: The box huckleberry is a slow-growing evergreen shrub native to the Mid-Atlantic United States; it grows in dense, self-incompatible clonal colonies. The oldest plant in North America is a colony of this species growing in Pennsylvania, thought to be about 5,000 years old. Small white tubular flowers resemble other species in the heath family. This species is threatened by irresponsible land development and management practices, and invasive species. Charles Sargent first brought this species to the Arboretum from Pennsylvania in 1905. Since then, several specimens have grown in the collections. The Arboretum currently maintains two specimens including one collected from Tennessee; both are growing well in the Leventritt Shrub and Vine Garden.

Ilex collina: The longstalk holly is a multi-stemmed shrub to 3 meters (9.8 feet) tall that produces large, red to yellow berries on female plants. This species is native to North Carolina, Virginia, West Virginia, and possibly Tennessee, and is threatened by land development. There is taxonomic doubt as to whether this is a synonym of *I. longipes* or not. The Arboretum maintains specimens from all states except Tennessee, and this species thrives in cultivation.

***Magnolia pyramidata*:** The pyramid magnolia grows 3 to 7 meters (9.8 to 23.0 feet) tall, and produces creamy white flowers that give it potential as an ornamental landscape plant. It is native to a limited range along the coastal plain of the southern and southeastern United States, and is threatened by land development. The Arboretum does not currently have specimens in the living collections, but had grown two lineages from Texas that were removed in 2001 when it was determined that the specimens were not *M. pyramidata*.

***Rhododendron prunifolium*:** The plumleaf azalea is one of the showiest native azaleas, and may reach up to 6 meters (19.7 feet) tall in the wild. It has glabrous leaves and bears clusters of red-orange flowers in July and August. It is native to Alabama and Georgia and is threatened by logging and low seedling numbers in the wild. The Arboretum currently has specimens from two locations in Georgia, and is responsible for introducing this species into cultivation in the early 1900s via plant collector T. G. Harbison.

***Rhododendron vaseyi*:** The pinkshell azalea is an upright shrub known to grow up to 5 meters (16.4 feet) tall in the wild. Scentless (and frost resistant) pink flowers emerge in April prior to leaf bud break, providing striking ornamental value. This species is native to North Carolina, and is threatened by land development and illegal collecting in the wild. The Arboretum introduced it to cultivation in 1880, and maintains several specimens from North Carolina which thrive in the Boston climate.

***Spiraea virginiana*:** The Virginia meadowsweet is a 1- to 2-meter-tall (3.3 to 6.6 feet) shrub that forms dense clumps of upright, arching stems with cream colored inflorescences in May. This species is endemic to the central and southern Appalachians, where its sporadic populations are threatened by competition with fast growing herbs and vines, habitat destruction including dam construction, and lack of sexual reproduction. Plants were first collected by the Arnold Arboretum in 1919 by T. G. Harbison in

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A Fraser fir cone.

North Carolina (accession 10160), grown at the Case Estates, and then repropagated via cuttings and brought to the main Arboretum grounds in 1988, where the lineage still exists today. When this CPC collection was established in the mid-1980s and 1990s, the Arboretum amassed one of the most extensive ex situ collections of this species in the world, composed of plants from all states where it is currently known to grow. Two groups were recently transplanted to beds near the South Street and Mendum Street gates.

***Torreya taxifolia*:** Once a towering tree of 15 meters (49.2 feet) or more, the stinking cedar (named for its pungent, sharp needles) is native to Georgia and Florida, and is now one of the most threatened conifers in the world because of a fungal disease. The few remaining wild individuals have been reduced to root suckers.Until 2010, the Arboretum maintained 33 specimens from known remaining populations.

A stand of Fraser fir killed by balsam wooly adelgid.

This collection suffered severe attrition because the species is poorly adapted to the Boston climate. In 2010 the collection was successfully transferred to the Atlanta Botanical Garden (see textbox on page 22).

***Viburnum bracteatum*:** A shrub to 3 meters (9.8 feet) tall with spreading branches and sharply-toothed leaves, this viburnum species is well adapted to the Boston climate. There is some taxonomic question whether this species should be included as part of *V. dentatum*. It is native to Alabama, Georgia, and Tennessee, and has long been noted as naturally rare in the wild. It is currently threatened by limestone quarrying. The Arboretum first introduced it to cultivation in 1904 and maintains specimens from Tennessee and Georgia.

CPC COLLECTIONS REVIEW

Prior to this collections review, we had only anecdotal information about the CPC collections at the Arnold Arboretum. Staff members had made annual field checks of the CPC specimens, so there was a lot of information stored in BG-BASE (the curation database). We knew basic information such as which species grew well in certain areas of the Arboretum and which were problematic for maintenance, but we did not know certain things such as which CPC species were truly thriving (versus barely surviving) in the Arboretum's cultivated environment, and which CPC species were adequately represented as a collection to support conservation activities. We also wanted to develop directions for the care and maintenance of the CPC collections, an important step in determining curatorial and horticultural priorities for future development. Curatorial reviews

NANCY ROSE

Colorful fruit on a female plant of *Ilex collina* at the Arnold Arboretum.

Magnolia pyramidata has a limited native range in the United States.

NANCY ROSE

***Rhododendron vaseyi* puts on a spectacular spring floral show in shades of pink.**

of each CPC species were done by compiling all relevant plant records, conservation, and historical information in order to accurately assess the current value and future conservation potential of each collection. This process brought to light several ways to guide the management and development of the Arnold Arboretum's CPC collections (Hird and Dosmann 2010). Described in more detail below, we looked at the major collections factors: lineages, accessions, plants, and supporting documentation.

Lineages

The number of unique genetic lineages (i.e., plant material collected from one or a few individuals in one location; clonal reproduction can extend a lineage through time) of a species in an ex situ collection reflects the potential genetic diversity available for research and conservation efforts (including reintroduction of plants to the wild). Genetic diversity allows for evolutionary adaptation of a species, and healthy plant populations typically have high levels of genetic diversity, allowing them to survive a variety of environmental pressures. Conservation collections should be managed with the aim of preserving as much genetic diversity as possible, as an insurance policy in case the gene pool of natural populations diminishes or disappears. Sampling standards have been developed to ensure the greatest genetic diversity is captured in ex situ collections of rare species (see Table 2; Falk and Holsinger 1991). For rare species with three or fewer populations remaining in the wild, 100% of these populations should be sampled and preserved in ex situ collections. For rare species with four or more populations remaining in the wild, approximately 80% of the populations should be preserved in ex situ collections. The Arnold Arboretum's CPC species mostly fall into the latter category, so an appropriate sample size for a majority of these collections is at least four or five unique populations. This can guide lineage development both within and among populations.

A few species such as *Spiraea virginiana* have a fairly wide genetic base at the Arboretum, but a few of the more-threatened species such as *Abies fraseri, Gaylussacia brachycera,* and *Viburnum bracteatum* are not adequately represented to support effective conservation. Notably, lower lineage numbers for some CPC species like *Abies fraseri* are a result of high attrition from lack of adaptability to the Arboretum's climate.

Accessions

The number of living accessions (i.e., plants from a single lineage, acquired by one means of propagation at one time) for each species further demonstrates the depth of each collection and sheds light on lineage redundancy within the living collections. With limited resources and space, the Arboretum sets a collections goal to have 2 to 3 accessions per unique lineage for most types of plants (species, etc.) in the living collection (Living Collections Committee 2007). When comparing the total number of living accessions to the total number of living lineages, each CPC species is represented by 1 to 2 accessions per lineage. This assessment showed that both of the *Diervilla* species had a higher number of accessions per lineage, demonstrating redundant clones within the same lineages. To maintain appropriate accession-to-lineage ratios for the CPC collections, we identified lineages and accessions that could be bulked up via clonal propagation and others that could be "thinned" by sending back-up material to other institutions.

Table 2. Recommended Number of Populations in a Rare Plant Sampling Program for Capturing Genetic Diversity at the Population Level (Falk and Holsinger 1991)

Number of Extant Populations	Number of Populations Sampled
1	1
2	2
3	3
4	3-4
5	3-5
>5	4-5

COURTESY OF MT. CUBA CENTER

Rhododendron prunifolium **bears red-orange flowers with prominent red stamens.**

Plants

Health conditions through time and total numbers of living plant specimens give an indication of how well a species grows in the Arboretum and can provide guidance for collections management. At the time of this assessment in 2009, most CPC specimens were healthy. However, management needs were further considered for species with significant proportions of specimens in fair or poor condition, such as *Torreya taxifolia*, *Amelanchier nantucketensis*, and *Abies fraseri*. Also, *Magnolia pyramidata*, with no living plants represented in the collection, was prioritized for a collection transfer or germplasm acquisition.

By using the Arboretum collections standard of maintaining an average of 2 plants per unique accession (Living Collections Committee 2007), we identified collections redundancy or deficiency for each CPC species. As we analyzed accession-to-lineage ratios, we also compared the total number of living accessions with the total number of living plants

Finding a Home for *Torreya taxifolia*

TORREYA TAXIFOLIA, once a towering giant in the forests of Georgia and Florida, has been diminished to twig-like sprouts by an obscure fungal disease over the past century. It is now one of the most threatened conifers in the world. Several ongoing conservation efforts strive to understand the pathology of the disease and find effective management and reintroduction strategies. Several ex situ collections of the species have been aimed at conserving the narrowing genetic diversity of extant wild populations as well as producing seeds and cuttings for research.

A large-scale ex situ effort began in 1985, funded by the CPC and the Arnold Arboretum (Nicholson 1996). Rob Nicholson and Mark Schwartz collected cuttings from 163 wild lineages of *T. taxifolia* and then distributed resulting plants to 10 institutions in North America and Europe in the early 1990s. Using a 1996 Arboretum inventory of 156 of the original lineages as a foundation, we conducted an international inventory of this species in 2009 and tracked down all possible specimens that originated from the original CPC material.

Fortunately most of the lineages had been preserved among the institutions surveyed (a benefit of backing up collections). But about 20% were represented by only one or a few remaining plants per lineage, and about 40% of lineages existed only at one or two institutions. Lessons learned from this long-term ex situ effort include ensuring a collection holder has appropriate horticultural know-how, climatic compatibility, and staff commitment for successfully maintaining a collection. For example, a loss of 70% of unique lineages at the Arnold Arboretum was observed from 1989 to 2009. This loss is attributed to incompatible climate, poor adaptability to container nursery conditions, and human error (staff changeover, labeling errors, etc.). Further, 5 of the 8 institutions still maintaining the original *T. taxifolia* germplasm required accession data cleanup and several specimen identifications were determined lost or unknown due to accidental dissociation with accession numbers, labels, or records.

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Foliage of *Torreya taxifolia*.

This long-term ex situ conservation effort demonstrates how living collections can contribute to the collective conservation power of public gardens. As a result of the 2009 ex situ inventory for *T. taxifolia*, redistribution of germplasm has occurred among collection holders to preserve and back up ex situ maternal lines at multiple institutions. Further, this inventory led to a successful transfer of this important CPC collection from the Arnold Arboretum to the Atlanta Botanical Garden in 2010.

per species, also taking into account specimen health. This allowed us to identify specific plants in need of repropagation, removal, or relocation. One particularly successful example of making management decisions to improve plant health is the *Amelanchier nantucketensis* specimens in the Bradley Rosaceous Collection (BRC). Poor health had been recorded for these plants for several years, and during bed renovations in the BRC they were transplanted to new beds near Dawson Pond. This location's higher soil moisture has resulted in improved health for the plants. A common issue identified for *Amelanchier nantucketensis*, both *Diervilla* species, and *Spiraea virginiana* was maintaining individuals of these mass-forming species. As a result, these specimens were put on a pruning schedule to prevent uncontrolled spreading and suckering.

Since the Arboretum's primary goal with the CPC collections is preservation of living germplasm, long term survival of the CPC plants is a top priority. Collections management at the Arboretum includes the preservation of unique lineages through clonal repropagation if needed. Sometimes plants brought to the Arboretum are not well-suited to survive in the collections for reasons such as lack of compatibility to cultivation or the local climate. Species whose records show high levels of lineage or plant loss, such as *Torreya taxifolia*, likely represent poor compatibility with Arboretum conditions, making them potential candidates for transfers to institutions better able to cultivate them.

Supporting Documentation

The geographic, temporal, and environmental details about the source of an accessioned living plant are referred to as the passport data, which are curated in the Arboretum's plant records. Passport data can make collections more valuable for conservation, education, horticulture, and research by associating valuable habitat or biological information with each specimen. For wild-collected plant material the value of a collection increases with the amount of passport data. This can range from coarse geographic information such as country and state to highly local information such as soil type or altitude of an original collection location.

Additional supporting documentation may include observations, voucher herbarium specimens, images, verifications, and recorded instances of collections use (for tours, publications, and educational projects involving a species). Herbarium specimens and images offer long-term genetic and biological information that can enhance understanding and aid in conservation of a threatened species. The Arnold Arboretum Cultivated Herbarium sets a goal to document the living collections with vegetative, flowering, and fruiting material per unique lineage (Curatorial Department 2009).

This CPC assessment identified gaps in passport data and supporting documentation for each species. In addition to augmenting geographic passport data for many CPC accessions, we also established herbarium specimen and image collecting targets, as well as past verifications that could be entered into the plant records database.

COLLECTIONS ENHANCEMENT PRIORITIES

The Arboretum has taken a number of positive steps following this assessment to improve and more effectively manage the CPC collections, making them more valuable and accessible for research, education, and conservation. Individual species reviews allowed us to create a prioritized master list of recommended curatorial and horticultural actions based on collections goals and needs.

Accomplishments include enhancements in plant records information through the addition of county names, latitude and longitude, or other location information when possible. Voucher and image collection has also been a priority for the curatorial department, and over 350 herbarium specimens have been collected to further document the CPC collections. Recommended repropagations, removals, and relocations have been completed, including repropagation of two *Abies fraseri* specimens which are failing in the collection; addition of new lineages (*Rhododendron vaseyi*); removal of non-wild-origin plants and acquisition of new wild-origin lineages (*Rhododenron prunifolium*); planting out of nursery stock (*Torreya taxifolia*); and removal of redundant specimens

MICHAEL DOSMANN

Rhododendron vaseyi flowers.

to send as back-up material to other institutions (*Amelanchier nantucketensis, Spiraea virginiana*). Successful relocations of *Spiraea virginiana* and *Amelanchier nantucketensis* to other locations in the landscape have improved plant conditions and horticultural management of these collections. Horticultural practices identified and implemented during this assessment include applying horticultural oil to *Abies fraseri* to control spider mite outbreaks, cutting back of both *Diervilla* species and *Spiraea virginiana* to maintain specimens as individuals, and pruning of suckering roots to maintain individual specimens of *Amelanchier nantucketensis.* There were also several wild-origin lineages that were historically not included in the Arboretum's CPC collections, so these valuable specimens were formally reported to CPC and added to the annual inventory process for close monitoring and care in the future. After failed viability tests, we discarded a short-term seed collection of several CPC species (*Amelanchier nantucketensis, Diervilla sessilifolia, Ilex collina, Rhododendron vaseyi, Spiraea virginiana*) and storing garden-origin seed was discontinued. We streamlined the annual CPC collections inventory and data reporting processes by setting up automatic reports in BG-BASE. We also identified future acquisition targets for under-represented populations of several of the CPC species. To encourage broader awareness of the Arboretum's CPC collections we created a web page of CPC species highlights and have given several public tours focused on CPC species. Perhaps our biggest success was the official transfer of the *Torreya taxifolia* CPC collection to a more appropriate location and garden.

FUTURE OPPORTUNITIES

Going forward, there are a lot of exciting opportunities for the Arboretum to maintain and enhance genetic diversity of the CPC collections and further meet the CPC collection management guidelines. This may include wild-collecting additional plants or seeds for long-term seed storage and continuing to identify institutions that could receive backup germplasm of the Arboretum's CPC collections. Within the Arboretum, archival research for additional wild-collection information and digitization of species verification records may enhance plant records data. Incorporation of specific horticultural needs into the *Landscape Management Plan* (Horticulture Department 2012) would encourage close monitoring of CPC collections by staff horticulturists. Opportunities to further share information about CPC collections through classes, tours, and web applications present exciting possibilities.

Of top priority are additional collection transfers for *Abies fraseri, Gaylussacia brachycera,* and *Magnolia pyramidata.* These collections have not thrived at the Arboretum so transfer to a more appropriate institution or region of the United States would ultimately support the long-term survival of these species. Appealing to the CPC and identifying potential receiving institutions, are the first steps. Once remaining collections are stabilized and appropriate species are transferred, new acquisitions of Northeastern threatened woody species can be considered as potential CPC collections in the future. This regional focus for CPC

Spiraea virginiana sources revealed through molecular study

IN THE SUMMER of 2008, leaf tissue samples of all living specimens were sent to Jessica Brzyski, then PhD candidate at the University of Cincinnati, who was researching reproduction of *S. virginiana.* In the summer of 2009, Jessica visited the Arboretum as a Deland Award recipient and conducted controlled pollinations to determine the level of self-compatibility and out-crossing ability for *S. virginiana.* She was able to provide a summary of her molecular studies using the leaf tissue, which provided clarification on some of the questionable paternities of a few living specimens at the Arboretum, some of which had grown into large masses in recent years. The controlled pollinations were inconclusive, as 2009 was an extremely rainy summer and most of the pollinations were completed in the rain. However, the molecular information helped us re-identify specimens that came from the same populations as other specimens with known identities.

USDA-NRCS PLANTS DATABASE

Spiraea virginiana **from Britton and Brown's** ***An illustrated flora of the northern United States, Canada, and the British Possessions*, 1913.**

species would bring conservation work closer to home and likely result in increased success for threatened species grown, maintained, and utilized at the Arnold Arboretum.

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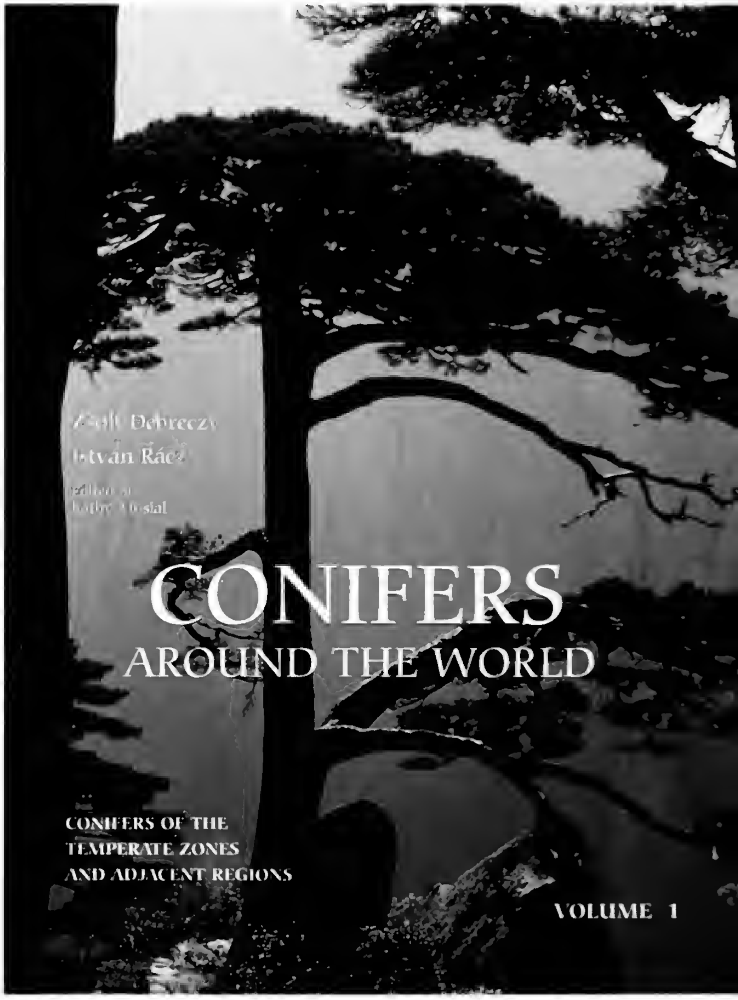
Book Review: *Conifers Around the World*

Peter Del Tredici

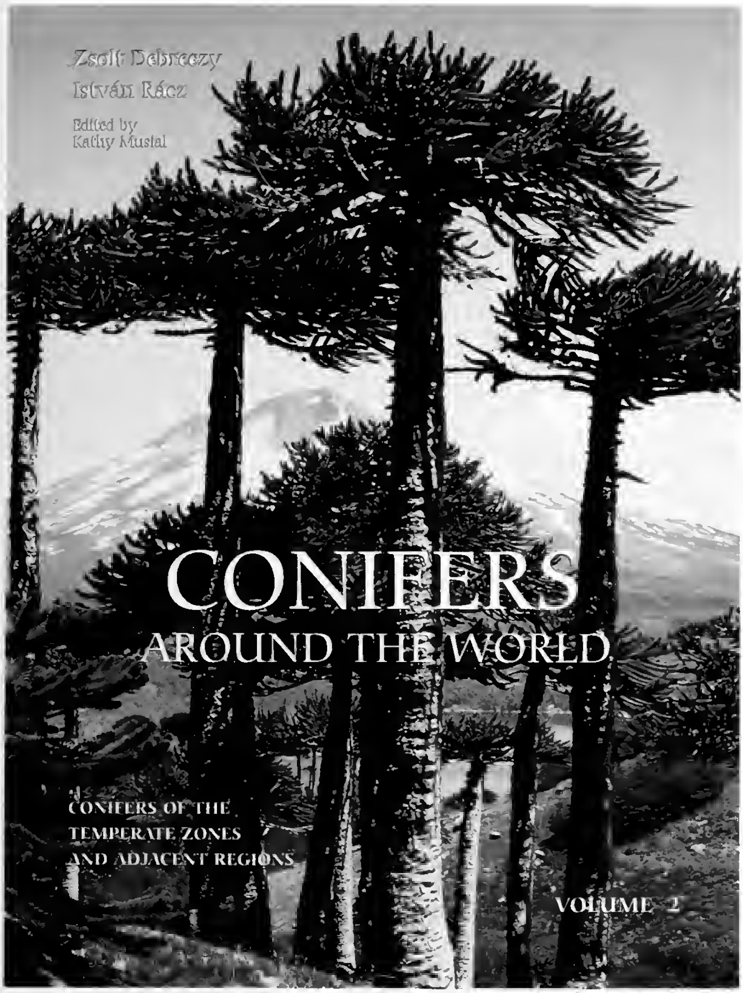
Conifers Around the World
Zsolt Debreczy and István Rácz,
edited by Kathy Musial
Budapest: DendroPress Ltd., 2011.
Two volumes—1,089 pages, 474 range maps, 1,300 line drawings, and more than 3,700 color photographs.
ISBN 978-963-219-061-7



Weighing in at fourteen pounds, the two volumes of *Conifers Around the World* are a botanical tour de force that harkens back to the days when plant books were lavishly illustrated with colorful plates that were as beautiful as the objects they were describing. In the context of the modern digital age, when print publications are generally described as dead, this gorgeous, full-color, large-format book (12.5 x 9.5 inches) is definitely an anachronism.

The production of this amazing 1,089-page work has been a long-term labor of love by its Hungarian authors, Zsolt Debreczy and István Rácz, who were in residence at the Arnold Arboretum as Mercer Fellows from 1988 through 1991 when they were just embarking on their project. The book describes over 500 conifer species and subspecies (in 56 genera) native to temperate or warm-temperate regions of the world. The focus is on plants as they exist in nature, with only an occasional mention of cultivars. The full-color photos of conifers growing in their native habitats form the core of the book and, given the time and effort required to make them, are its most remarkable feature. This is especially true of rare conifers from China and Mexico, known from only a location or two in remote mountain ranges.

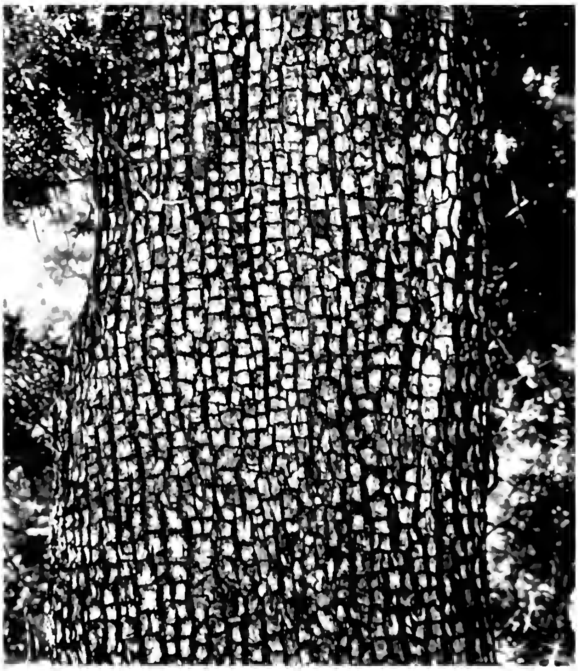
The basic format of the book is straightforward, with one full page devoted to each species. The top quarter of each page consists of a concise technical description of the plant, which includes information about distribution, habitat, associated species, human uses, and conservation status. The lower three-quarters of the page is taken up with four or five photos illustrating the needles, cones, branch structure, and overall growth habit of the species in its native environment. The high quality of these photos—which are worth thousands of words—allows the authors to keep the descriptive text to a bare minimum. In addition to the 500-plus species treatments, separate sec-



the book as well as making the English text completely clear and readable.

The overall organization of the book takes some getting used to, with plants arranged by the continents they are native to (and within each continent, alphabetically by genus and species). Volume 1 covers four geographical areas: Europe and adjacent regions, continental Asia and Hainan, Japan and adjacent islands, and Taiwan. Volume 2 includes six regions: western North America, eastern North America, Mexico and Central America, West Indies and Bermuda, Chile and Argentina, and Australia and Tasmania. This eclectic geographical arrangement reflects the authors' wider purpose of presenting the modern distribution of conifers in a geological context—specifically on the Arcto-Tertiary Geoflora (ATG) concept. This idea was introduced in the late 1800s to help explain the disjunct distribution patterns found in many closely related plants, most famously of those found growing in eastern Asia and eastern North America, by postulating a unified flora that covered the temperate zones in the northern hemispheres during the late Cretaceous and early Cenozoic. The ATG concept was developed at a time before geological time scales were accurately known and well before the advent of modern molecular systematics which allows for direct calculation of the age of species divergence. In short, the ATG concept works at a general level of explaining the distribution of various forest "types" (e.g., temperate broadleaf deciduous forest, mixed conifer broadleaf forest, etc.), but doesn't work all that well at explaining the distribution patterns of the individual species that compose these forests. By using a geographical rather than a taxonomic arrangement of plants, the authors bring climate, geology, and geological history to the foreground as determinants of modern conifer distribution patterns. This arrangement also enhances the sense of place for each region, and gives one a sense of actually visiting the areas where the trees are growing. On the negative side, this arrangement results in the

tions of the book cover species ranges (474 maps reproduced from other sources); lengthy descriptions and numerous photographs of typical conifer habitats, arranged by continent; and a highly unusual "bark gallery" consisting of 648 color photos that augment the photos in the species treatments. And finally, there is a 130-page introduction that describes the history, morphology, ecology, taxonomy, biogeography, and evolution of conifers along with a complete listing and description of conifer families (written by Robert Price). This introduction could easily be expanded into a stand-alone book about conifer morphology and natural history. An early version of *Conifers Around the World* was published in Hungarian in 2000 (*Fenyők a Föld Körül*), but it is a pale shadow of the present English version. No doubt the editor, Kathy Musial of the Huntington Botanical Garden, played a major role in expanding the scope of



Bark gallery images, clockwise from upper left: *Abies pindrow*, *Larix decidua* var. *decidua*, *Podocarpus nivalis*, *Juniperus deppeana* var. *deppeana*.

JEFF BISBEE

This specimen of *Cupressus arizonica* var. *arizonica* displays two types of bark: scaly, persistent ribs on the main trunk, and detaching leathery plates on the lateral branches.

A *Juniperus flaccida* photographed in Big Bend National Park, Texas.

spatial separation of closely related species (e.g., those within *Taxodium*) that are growing in separate regions.

The taxonomy used in the book, for the most part, follows the accepted botanical classification used by most conifer authorities, but Debreczy and Rácz do not shy away from expressing their own opinions when they disagree with standard texts. The near total absence of any references to modern molecular taxonomic research or of cladograms that show the genetic (i.e., evolutionary) relationships among related taxa are indicative of the book's firm rooting in traditional, herbarium-based taxonomy. While it is clearly the authors' prerogative to take this approach, it leaves one with the impression that the book is stuck in something of a time warp. There is one curious anomaly in the book: a twelve-page appendix devoted to the convoluted taxonomic history of *Pinus apulcensis,* the so-called Apulco ravine pine from southern Mexico. Why this species, with its tiny range, should occupy ten times much more space than any other species in the book is unexplained by the authors and left this reviewer thinking that a little molecular analysis might have been helpful in clarifying the confused taxonomic situation.

That being said, however, the book is a truly remarkable resource that all serious conifer aficionados will want to own—not only for its exquisitely beautiful illustrations, but also for the vast amount of information about conifer biology, ecology, and taxonomy that it brings together under a single roof. What I particularly like about the book is how the authors' intimate personal experience with the trees shines through on every page—they have actually seen all (or virtually all) of the plants they describe and are generously sharing their experiences with the reader. While the book does a remarkable job at capturing the grandeur of the conifer kingdom, one hopes that it does not inadvertently become its epitaph in a world that is suffering mightily from the ever-expanding impacts of resource extraction, land transformation, and climate change.

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

FOLLOWING ARE TWO SPECIES EXCERPTS (reproduced at a reduced size) FROM *CONIFERS AROUND THE WORLD*

Tsuga dumosa

Tsuga dumosa (D. Don) Eichler 1887 [illegible]

Himalayan Hemlock, Yunnan Tieshan, Ba Shing, Tengre Salla

[illegible] *dumosa* is the westernmost of the Asian hemlocks, ranging through the Himalayas from [illegible] Sichuan [illegible] marginally occurring in Tibet–Xizang (2300–3500 m). The Yunnan stands, once distinguished as *T. yunnanensis*, have needles [illegible]. *T. dumosa* can easily be distinguished from most other hemlocks by its often whiplike, partly pendulous terminal shoots and needles longest [illegible] in the genus and strikingly pruinose white below. One of the most typical components of the Himalayan mid- and upper-elevation coniferous forests, it appears in mixed deciduous–evergreen broad-leaved forest dominated by Himalayan Live Oak and Tree Rhododendron. Its main zone is farther up, in its central and eastern range associating with *Abies densa*, *A. spectabilis*, *Larix griffithii*, and *L. himalaica*, in the west with *A. gamblei*, *A. pindrow*, *Cedrus deodara*, and *Picea smithiana*, with *Taxus contorta* or *T. wallichiana* var. *wallichiana* in the lower canopy layers.

TREE [illegible] 40 m [illegible] 2.7 m) with typically long free trunk and wide-spreading branches forming a rounded or spreading crown. **BARK** [illegible] in old trees evenly covered by scaly plates, detaching in thick plates and small scales; fresh exposed bark changing from [illegible] to gray. **BRANCHLETS** maturing from yellowish green to light brownish [illegible] yellowish white hairs [illegible]. **NEEDLES** [illegible] 3.5 cm) often distantly set, pectinately outspreading, falcate only on long shoots, evenly tapering to fine [illegible] emarginate apices, often [illegible] serrate [illegible] pruinose green above (adaxially), later shiny green, with 2 bright white stomatal bands below (abaxially). **CONES** [illegible] cm) ovoid [illegible] scale apices (apophyses) slightly striate, slightly recurved at margins, otherwise thin, maturing from pruinose green or bluish to shiny brown

Pinus lambertiana **Douglas, 1827**

Sugar Pine

The cyclitol-containing sweet resin of *Pinus lambertiana*, declared by John Muir to be "the best of sweets, better than maple-sugar" was once gathered by Indians, who also consumed its large tasty seeds. The tallest and most massive pine species in the world, *P. lambertiana* rules the coniferous landscape with its huge horizontally wide-spreading branches, their tips weighed down by the heavy cone clusters. Up to 63 cm, the long-stalked pendent cones are the longest in the genus; only *P. ayacahuite* (<40 cm), *P. strobiformis* (<48–60 cm), and *P. veitchii* (<50 cm) of Mexico are comparable. Distributed from northern Oregon along the Cascade Range, the adjacent Klamath Mountains southward through the Coast Ranges, and in the Sierra Nevada south to the Sierra San Pedro Mártir in Baja California (330–3200 m). *P. lambertiana* associates with almost all conifers of the west, most typically *Abies lowiana*, *A. magnifica*, *A. procera*, *P. jeffreyi*, *Pseudotsuga menziesii* var. *menziesii*, and *Sequoiadendron giganteum*, in mountain chaparral with lower canopy and shrub layers dominated by oaks, manzanitas, and madrones.

Haploxylon White pine with 5 needles. TREE (40–60<81 m × 1–3.5 m) with conical to flat-topped crown and horizontally wide-spreading main branches. **BARK** smooth, gray, with conspicuous lenticels, later breaking to narrow ridges, finally to long scaly plates, changing from cinnamon-brown to gray or dark gray. **BRANCHLETS** thick, pubescent, changing from green to tan, eventually gray. **NEEDLES** (5–10 cm) rather short, thick (thickest of the white pines, <2 mm), flexible, gray on inner surface (adaxially). **CONES** (15–55<63 cm) long-stalked, oblong-cylindrical, tapering at both ends, maturing yellowish-brown, persistent for months before falling, seeds large (1–2 cm), winged.

1/4

Dipelta floribunda: A Shrub of Subtle Beauty

Michael Dosmann

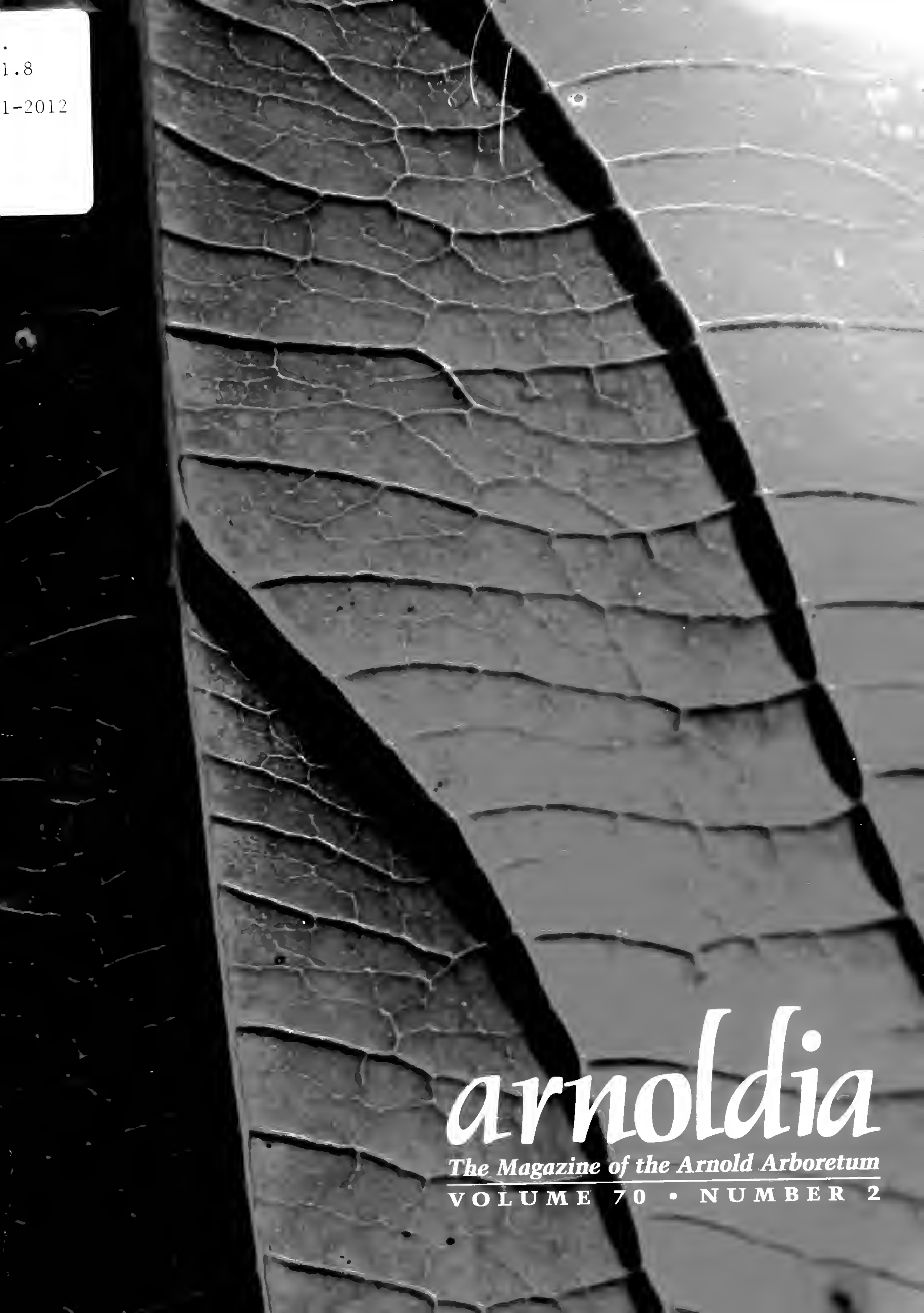
In the horticultural world, it is not uncommon to hear plant lovers laud a particular plant's endless weeks of flowering, months of dazzling autumn leaf color, and flamboyant, persistent fruits the size of golf balls. I can appreciate plants like that, and yet sometimes I want something subtler. English novelist George Meredith wrote that "Speech is the small change of silence," and as I apply that maxim to the garden I find that I am drawn toward plants that possess quiet interest. One such plant is *Dipelta floribunda*, the rosy dipelta, a shrub native to central and western China.

The Arboretum has cultivated rosy dipelta for over a century, the first seeds coming to the Arboretum in February 1911 from E. H. Wilson's collection from Fang Hsien, western Hubei, the previous October. He made the collection from plants growing in "sunny places" at altitudes of 1,200 to 1,800 meters (3,937 to 5,905 feet). Seventy years later, the Arboretum received its latest accessions of this species, collected in Hubei during the 1980 Sino-American Botanical Expedition. Plants from two separate accessions from the 1980 SABE grow in the Arboretum, as does one large plant (accession 14514-B) from the Wilson accession. The Explorers Garden atop Bussey Hill serves as perhaps the best place to see these plants, though there is also another fine mass planting of rosy dipelta along Peters Hill Road.

Dipelta floribunda bears fragrant, pinkish-white flowers, typically blooming in early May. Each tubular corolla comprises five fused petals, with the two upper lobes forming a top lip, while the basal three lobes form a lower lip. Yellow pigment splashes along the lips and throat of the flower, no doubt serving as nectary guides for the bees that pollinate the flowers. At the base of the corolla are greenish bracts that increase in size as the growing season advances, surrounding the fruits (two-seeded achenes) as they mature. The round, 1-inch-wide, papery bracts provide a bit of late summer interest—particularly as they blush a tawny pink—and also aid in the wind dispersal of the seeds. A casual examination of *Dipelta* reveals similarities with *Kolkwitzia amabilis*, beauty bush, also introduced by Wilson. The two genera are closely related to each other within Caprifoliaceae, the honeysuckle family; their flowers look similar, though *Kolkwitzia* fruits have but a single seed and lack *Dipelta*'s papery bracts.

Rosy dipelta is a large, vase-shaped shrub that typically attains a height of 12 to 15 feet (3.7 to 4.6 meters) and a width of 6 to 8 feet (1.8 to 2.4 meters). The leaves are lanceolate and rather coarse, and tend to abscise in the autumn with little effective color change. But when they do drop from the plant they reveal another bit of quiet interest. With a few years of age, the bark of the stems begins to shed in long, vertical, tawny-white strips. In the garden, some may think this somewhat messy (plantsman Michael Dirr muses that "the entire matrix ... assumes the presence of a pile of sticks"). However, I like this trait for both its tactile quality and its visual appeal in the winter. An undulating row of several of these fine shrubs at the back of a mixed perennial border provides an excellent backdrop, particularly when they are pruned to remove lower branches. Mix in several beauty bushes to extend the flowering season a few weeks, add a *Heptacodium miconioides* (seven-son flower) to provide late summer blooms, and enjoy all three of them for their habit and bark interest.

Michael Dosmann is Curator of Living Collections at the Arnold Arboretum.



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The ARNOLD ARBORETUM of HARVARD UNIVERSITY

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Front cover: So, why *do* some leaves turn bright red in autumn? Learn more about this mystery, starting on page 2. Photo of *Cornus sericea* 'Ruby' by Nancy Rose.

Inside front cover: The flowers and fruits of over 170 plant species appear in sixteenth-century frescoes in Rome's Villa Farnesina, providing a treasure trove of information to present-day horticulturists. A number of the genera depicted in the Villa also grow at the Arnold Arboretum, including *Sorbus*. Photo of *Sorbus aucuparia* by Nancy Rose.

Inside back cover: The bumpy, softball-sized fruit of Osage orange (*Maclura pomifera*) matures in early autumn at the Arboretum. Photo by Nancy Rose.

Back cover: Autumn color under the microscope: this cross section of a sugar maple (*Acer saccharum*) leaf reveals red and yellow pigments. Photo by David Lee.

The Mystery of Seasonal Color Change

David Lee

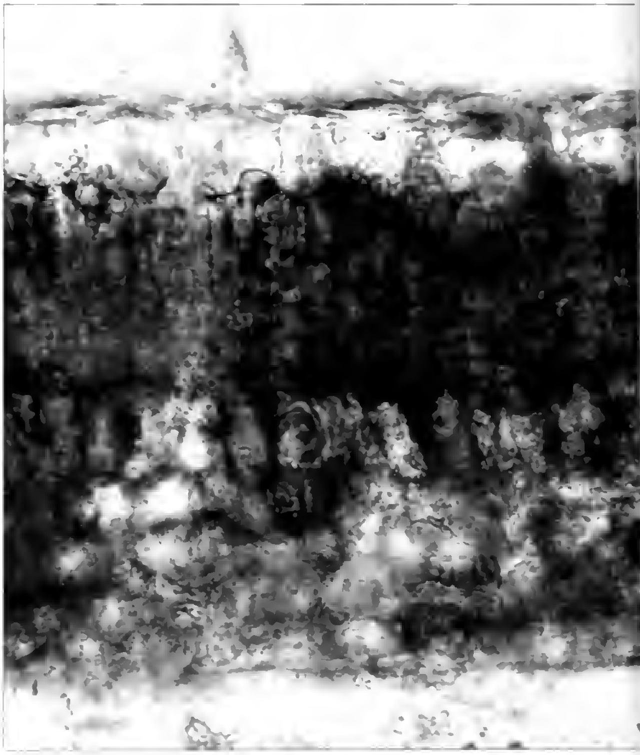
... the gods are growing old;
The stars are singing Golden hair to gray
Green leaf to yellow leaf,—or chlorophyll
To xanthophyll, to be more scientific ...

Edwin Arlington Robinson *(Captain Craig)*

Throughout New England each autumn—early October in some parts and as much as three weeks later in others—the pageant of color change in our forests unfolds. Though less noticed, in the springtime these forest canopies take on delicate pastel colors as buds swell and leaves expand. In the last 15 years, our understanding of the science behind color change has begun to emerge, with two different but not mutually exclusive hypotheses being formulated and defended. I have been involved in the research and debate on these color changes, and why that is so is a bit of a mystery in itself. After all, I grew up on the cold desert of the Columbia Plateau in Washington State, where the predominant colors were the grays of sagebrush and other pubescent shrubs. Occasionally I visited the forests of the Cascade Range to the west, witnessing the dark greens of conifers, occasional yellows of cottonwood, birch, and willow in the autumn, with just a few splashes of the reds of the Douglas maple (*Acer glabrum* var. *douglasii*). I did enjoy the autumn colors of the mid-Atlantic and Midwest forests as a graduate student and post-doctoral fellow, but was too busy in the laboratory to think much about that color.

Then I moved to tropical Asia—Malaysia specifically—and took notice of the differences in tropical rainforest vegetation, which I have been studying ever since. I was particularly struck by the red colors of leaves, both on the undersurfaces of understory plants and the expanding leaves of giant trees (so colorful that from a distance they looked to be in flower). Yet, few of

A red maple leaf shows developing red autumn color along with still-green sections.



This micrograph of a red maple (*Acer rubrum*) leaf shows that it contains both red anthocyanins and yellow xanthophylls.

the leaves turned red before falling from trees, and the canopies remained green because leaf fall was staggered. I began studying that red color—which led me back to the autumn reds of New England forests.

A PALETTE OF PIGMENTS

As poet Edwin Arlington Robinson partly described, the colors of leaves are the products of pigments produced in their internal tissues. Chlorophylls produce greens, xanthophylls produce yellows and oranges, and anthocyanins (left out by Robinson) produce reds. The leaf tissue is like the thick paper employed in watercolor painting. If you consider that most of the leaf consists of cellulose fibers, the similarities are particularly strong. The interior leaf volume, with its numerous air chambers facilitating the exchange of gases that supports photosynthesis, strongly scatters light, allowing some to reflect and some to be transmitted through the leaf. The leaf pigments are then like the soluble pigments in watercolors, and color is produced subtractively. Chlorophyll produces a green color because it absorbs light in the blue and red wavelengths. Xanthophylls produce yellow because they absorb blue into green, and anthocyanins red because they absorb even more green into blue. These pigments can combine to produce oranges (yellow and red), or even brown (green and red). The colors of spring and autumn are produced by these pigment combinations in leaves.

When I was a college student of botany in the 1960s, the textbooks taught us that autumn colors were produced by the loss of chlorophyll unmasking the yellows of xanthophyll and reds of anthocyanin pigments, and that the colors had no function. To me, this did not seem right for the reds of anthocyanins, because I knew that these pigments are quickly synthesized in leaves. When I began to work at Florida International University in Miami in 1980, I turned my attention to the young leaves of mango and

ALL IMAGES BY THE AUTHOR

A red maple glows in autumn color at the edge of Connor Pond, between the towns of Petersham and Barre in central Massachusetts.

Autumn color in forests along the Deerfield River in the Berkshire Mountains of western Massachusetts.

cacao, where anthocyanins are produced when developing leaves are rapidly expanding. We showed that the anthocyanins disappear when the leaves mature and that they do not effectively protect against ultraviolet (UV) damage (then the ruling hypothesis about anthocyanins' function in leaves). However, the importance of the inhibition of photosynthesis by high levels of solar energy, in leaves not able to process this excess energy, was a newly appreciated facet of leaf physiology—and anthocyanins could function as a sunscreen to protect against this damage. Kevin Gould, now at Victoria University of Wellington, in New Zealand, came to Miami to work with me on this problem for a year. Kevin, along with FIU colleagues and me, pursued this hypothesis in understory plants with red undersurfaces (where shade-adapted plants are particularly vulnerable to damage from flecks of sunlight) and published a short paper in the journal *Nature* in 1995. Kevin went on to become the global expert on anthocyanin function in leaves.

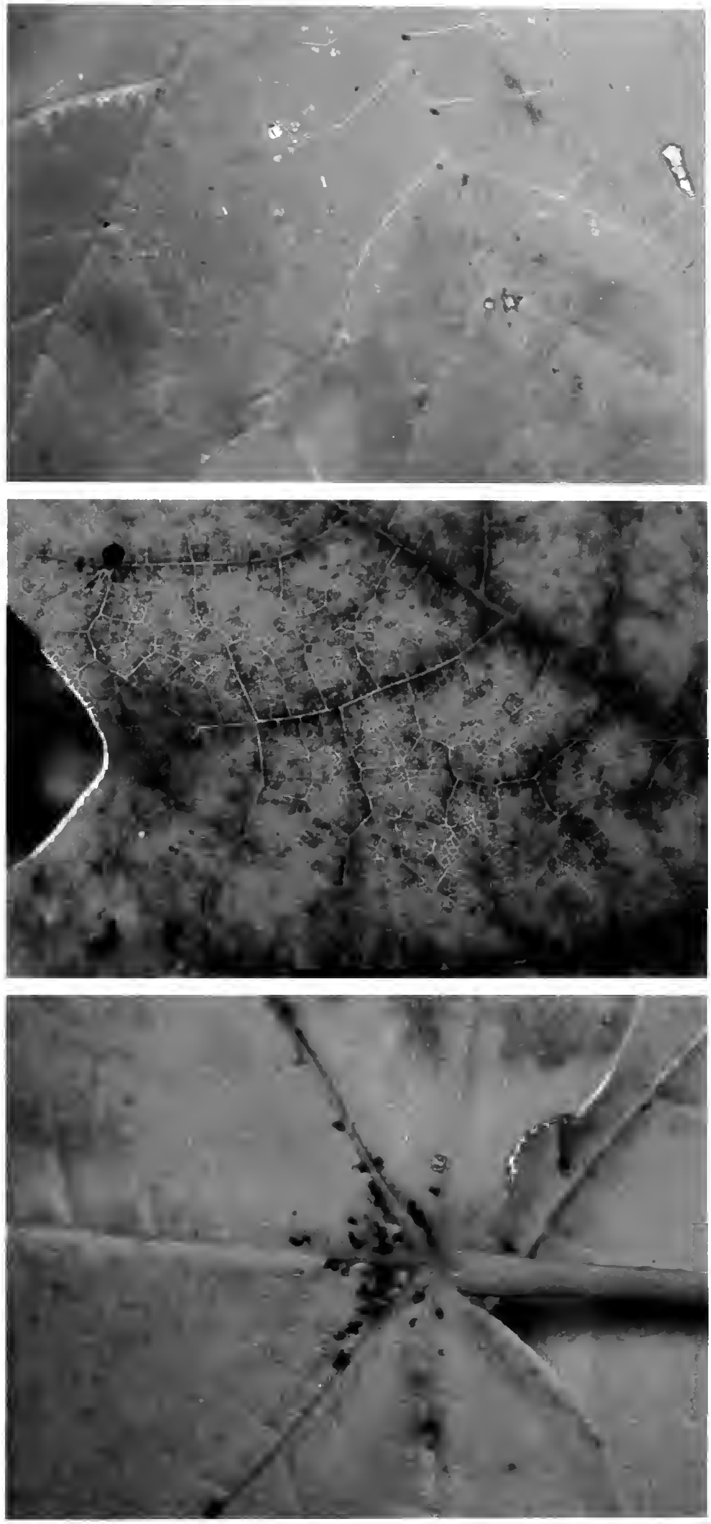
RESEARCH AT HARVARD FOREST

I had thought that the *Nature* article would promote more interest and research in this phenomenon, but little happened. It was then that I turned my focus towards autumn colors. That was a phenomenon universally appreciated, and a powerful economic driver of tourist business in New England during the autumn months; I have observed Route 2, running west out of Cambridge, Massachusetts, turn into a parking lot of buses loaded with international tourists in the middle of October.

In 1997, during a conference on "Hinduism and Ecology" at the Harvard Divinity School, I had dinner with Missy Holbrook who was then a junior faculty member at Harvard (and an old friend) to discuss research on autumn foliage. At the time I thought that red leaf coloration during the autumn meant the synthesis of protective anthocyanin pigments during senescence. The riddle was that protection during leaf senescence made no sense; the leaves were about to die. The advantage had to go to the entire tree for the following year, and we speculated that the advantage could be to protect the leaves during the process of the breakdown of chlorophyll. Leaves carefully disassemble the chlorophyll and associated proteins during senescence, and much of the nitrogen-containing compounds are resorbed in the woody tissues for use the following spring.

We discussed a plan of action, and Missy supported my application for a Bullard Fellowship at the Harvard Forest in Petersham, Massachusetts, which I used from late summer through early winter in 1998 and 2004. During those sojourns in central Massachusetts, with frequent cultural trips to Cambridge and Boston, I observed the changes in the forest pretty much every day, and made observations and physiological measurements of leaves during the process of leaf senescence and color change. When the snow started falling in early December, I high-tailed it back to balmy Miami.

Missy and I collaborated with her Ph.D. student Taylor Feild (now at the University of Tennessee) and Harvard Forest scientist John O'Keefe, who had been observing the phenology (when trees leaf out, when they flower and fruit, and when the leaves change color and fall from the trees) of common tree species at the forest starting in 1991. We found that most of the trees and shrubs (62 of 89, or 70%) produced anthocyanins during senescence, starting when leaves had already lost about half of their chlorophyll. Such leaves appeared red, red-orange, bronze, and even brown in color. The precise colors depended on the mixtures of anthocyanins, chlorophylls, and xanthophylls. We studied the changes in pigment composition and physiology in leaves of individuals of 16 species, 8 with anthocyanins and 8 whose leaves turned yellow (they had residual xanthophylls but no anthocyanins). We found that anthocyanin concentration during senescence was correlated with lower nitrogen content, consistent with the prediction that more nitrogen could be resorbed by the woody

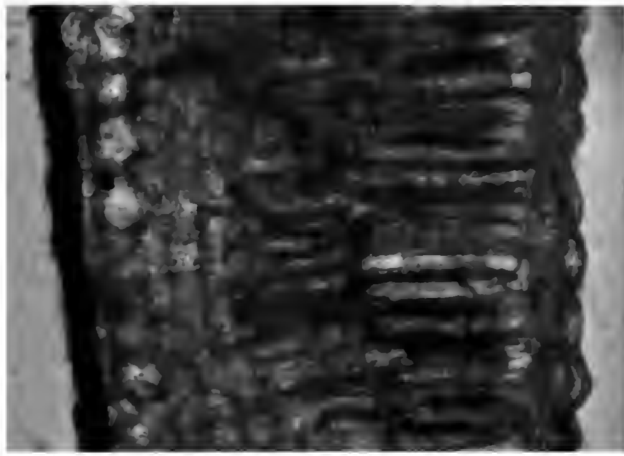


Autumn leaf color in sugar maple (*Acer saccharum*) varies between (and even within) individual specimens.

tissue. We also reported that the timing of leaf fall varied between species, but was pretty consistent within species from year to year. However, with more data collected, John and other collaborators have been able to show that leaves are forming earlier and senescing a bit later—the early influence of climate change. We also conducted some shading experiments and showed that reduced solar radiation retarded leaf senescence (and anthocyanin production) in red leaves.

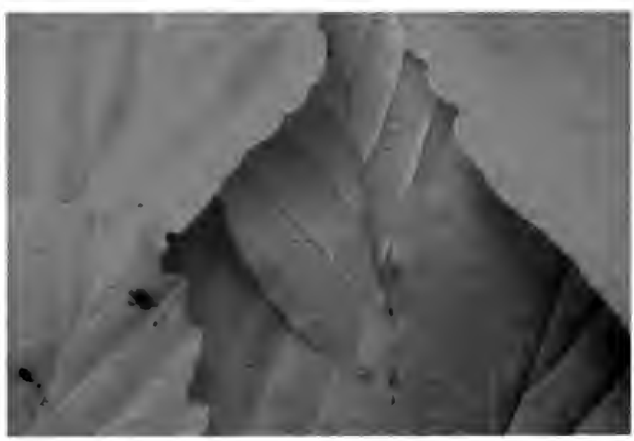
Following Taylor's lead, we examined the physiology of leaves of red-osier dogwood (*Cornus sericea*) during senescence and obtained clear evidence of photoprotection by the anthocyanins accumulating in the vacuoles of the photosynthetic cells, additional support for this hypothesis. At about the same time that Taylor's paper came out, William Hoch and colleagues published a review of this hypothesis in considerable detail, and then two years later published the best evidence of the photoprotection hypothesis, using green- and red-senescing varieties of three common shrubs, Elliott's blueberry (*Vaccinium elliottii*), red-osier dogwood, and Sargent viburnum (*Viburnum sargentii*), showing that the anthocyanin-lacking mutants resorbed significantly less anthocyanin than the red anthocyanin-containing varieties.

About the time we were initially pursuing this research, William Hamilton, the famous evolutionary biologist known for his research on sexual selection, had proposed a radically different explanation. He argued that colorful leaves could serve as a warning to potential herbivores, specifically aphids, advertising the toxicity or low palatability of the leaves. Thus warned, the aphids would avoid those trees during the autumn and would lay their eggs on un-advertised (green) trees, thereby favoring the growth of the autumn-red or yellow trees the following year. Their initial evidence for this hypothesis was primarily for yellow leaves, and was based on existing literature. Hamilton, along with Sam Brown and Marco Archetti, began to test the hypothesis, but Hamilton tragically died in Africa from malaria in 2000. This hypothesis particularly stimulated Marco Archetti to tenaciously search for evidence supporting it.

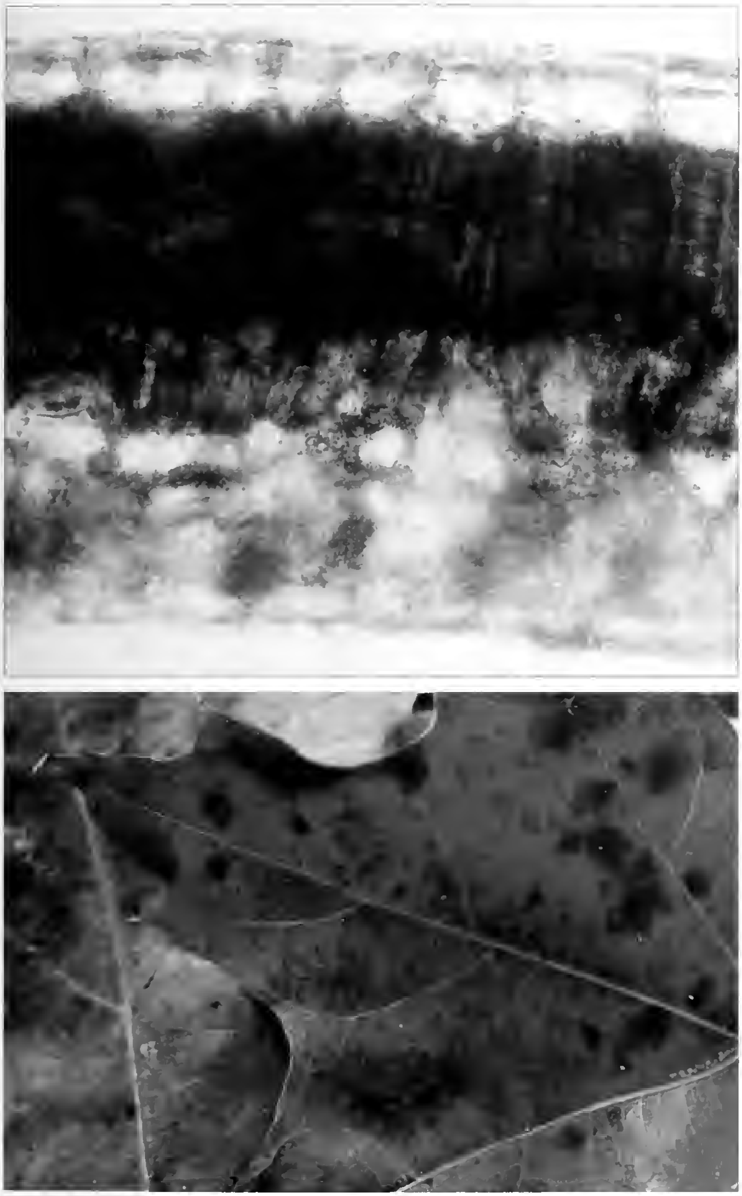


A micrograph of an aspen (*Populus tremuloides*) leaf shows chloroplasts containing yellow xanthophylls.

Black gum, also known as sour gum or black tupelo (*Nyssa sylvatica*), is noted for developing bright red-orange to red-purple autumn leaf color.



Common witchhazel (*Hamamelis virginiana*) displays yellow autumn color, as do most birch (*Betula*) and beech (*Fagus*) species.



Inside and outside views of autumn leaf color in red oak (*Quercus rubra*).

DUELING HYPOTHESES

Publications supporting the two hypotheses stimulated additional research, along with a number of speculative reviews. A little animosity arose between proponents of these two views, even though the hypotheses were not mutually exclusive. To Marco's credit, he convened a meeting at Oxford in March 2008, with researchers from both "camps" present. That created (1) some good will, (2) the understanding that we didn't know much about either hypothesis (which is often the fuel for disagreement and animosity), (3) the most exhaustive review on the subject (see the citation at the end of this article), and (4) an exhortation that we should produce the missing data that would more critically test the hypotheses.

Because it involves animals, the co-evolution hypothesis has attracted the most research. When we observe color, we automatically think of signaling—as from attractive flowers to pollinators, and from colorful fruits to dispersers. Conversely, in the physiological hypothesis, color is merely the by-product of protective absorption at specific wavelengths we can't see.

We now know that color, particularly yellow against a green background, repels visits by aphids, at least in the few trees that have been examined, especially European birch (*Betula pendula*). The evidence for red leaves is more controversial. Although there is some evidence of aphids avoiding red leaves, these insects seem not to have visual receptive cells sensitive in the red wavelengths. Limited evidence supports the contention that repelling aphids reduces egg laying, decreases activity of these sucking insects the following year, and increases seed production. Marco's strongest supporting evidence is from wild apples, where autumn aphids lay more eggs on green rather than red leaves.

Another weakness is a lack of evidence of reduced palatability, greater toxicity, or less nutrition in yellow or red leaves, although such leaves would likely be more advanced in senescence and thus less nutritious than green leaves. A model of the kind of research needed was published in 2011 by Kevin Gould and colleagues in a New Zealand tree, horopito (*Pseudowintera colorata*), that has red leaf margins. They found a toxic plant molecule, polygodial, was associated with red edges, and the combination dramatically reduced attacks by insects feeding on the edges of the leaves.

The evidence for the physiological hypothesis has not increased appreciably since Hoch's paper, although the photoprotective function of anthocyanins is now widely accepted. Reactive chlorophyll catabolite (RCC), a chlorophyll breakdown intermediate, may be especially important, and anthocyanins nicely intercept the wavelengths that activate this molecule. So, we're pretty much in the dark about the mechanism of photoprotection by anthocyanins.

MORE QUESTIONS ABOUT COLOR

Much that we have recently learned about autumn coloration does not neatly fit with either of these hypotheses. For instance, Niky Hughes, now at High Point University in North Carolina, has shown the protective activity of anthocyanins in *evergreen* shrubs that turn reddish in the winter and return to green color the following spring. Examples of such shrubs in New England woods include cranberry (*Vaccinium macrocarpon*), swamp laurel (*Kalmia polifolia*) and wintergreen (*Gaultheria procumbens*).

Anthocyanins have additional physiological activity; they are extremely strong antioxidants. The consumption of blueberries (loaded with anthocyanins) is now seen as an anti-aging strategy, promoted by blueberry grower cooperatives and other marketeers. The importance of such activities in aging leaves is unclear, however. The reactive oxygen species (ROS) implicated in cell death and aging are produced in the chloroplasts, but during autumn color production anthocyanins are pumped into cell vacuoles, far from chloroplasts. In the vacuoles, they might react with hydrogen peroxide, but the physiological importance is unclear.

Paul Schaberg and colleagues at the United States Forest Research Laboratory in Burlington, Vermont, have been measuring changes in sugar maple (*Acer saccharum*) leaves during the autumn. Sugar maples display some of the brightest foliage in the forest during the autumn, but colors vary between green, yellow, orange, and red between—and even within—tree crowns. They have observed that leaves that will become red have lower nitrogen concentrations, that red leaves have higher sugar and starch concentrations, and that red leaves tend to be retained longer than other leaf colors.

In addition to woody plants, some herbaceous plants also change color during the autumn. I have been observing these changes, collaborating with John O'Keefe, at the Harvard Forest and nearby areas. There, the percentage of herbs with leaves turning red is much lower than for shrubs and trees.

The production of color by trees during the autumn is strongly influenced by their evolutionary histories. Trees have evolved different strategies for dealing with the stress of senes-

Hobblebush (*Viburnum alnifolium*), a native woodland shrub, has autumn foliage color ranging from coral-pink to burgundy.

Though more subtle than in autumn, reddish color is also common in spring on expanding leaves, as seen here in woods near Beaverkill, New York.

cence, or the pressures of herbivory. Many maples and oaks produce red colors during the autumn, and birches and beeches produce yellows. Hoch has shown that the birches resorb nitrogen as well as the species with red anthocyanins, so there are likely to be other protective mechanisms that have evolved. The color production in geographically distant forests also varies greatly. Among the most spectacular color displays are autumn forest scenes in New England, and also in the southern Appalachians (residents of the Great Smoky Mountains region think their colors are the most beautiful!). However, European forests produce little red, and a lot of yellow. Although red and yellow colors are produced in virtually all deciduous trees in New England, in other forests leaves may stay green. Isreali botanist Simca Lev Yadun has speculated that variation in color production may be the result of the different tree species in particular forests, and their evolutionary histories.

Past and future climates may affect color production by determining the distributions of different trees in forests. Diseases may also remove species and change the colors during autumn. For New England forests, I expect that a century ago there was much more yellow in the autumn color palette. The rapid decline of the American chestnut from chestnut blight and the loss of American elms from Dutch elm disease removed the autumn yellows of these large and often dominant trees from forest canopies. Oaks are now threatened by sudden oak death, maples by Asian longhorned beetle, and ashes by emerald ash borer; losses of these genera could remove many reds and purples from the autumn palette in the future. Finally, temperature increases, greater at higher latitudes, may remove trees essential to our autumn colors; the sugar maple (our single greatest source of oranges and reds) may not survive in a warmer southern New England, but will move farther north in eastern Canada. Then sassafras (*Sassafras albidum*), with its bright coral and red autumn leaves, may become more common farther north.

New England forests also produce colors in the springtime, pastel pinks and yellows as buds break open and delicate young leaves spread their blades. Although I suspect that young red leaves are common among trees of New England forests, I have not systematically collected such information. The majority of trees in forests of Israel, Finland, and Japan produce young red leaves, and a minority of these trees produce red autumnal foliage. Also, red leaves in the spring are not good predictors of red colors in the autumn, suggesting different functions by colors produced in spring and the autumn.

I hope that this discussion about the science behind seasonal colors heightens your appreciation of the autumn pageantry as you rake colorful leaves from your lawn or take a country drive. Maybe some of you would just as soon enjoy the autumn colors without knowing anything about chlorophylls, xanthophylls, and anthocyanins. Walt Whitman would have agreed, for he wrote:

> *About birds and trees and flowers*
> *and water-craft; a certain free margin, and*
> *even vagueness—perhaps ignorance,*
> *credulity—helps your enjoyment of*
> *these things, and of the sentiment of*
> *feather'd, wooded, river, or marine*
> *Nature generally. I repeat it—don't want*
> *to know too exactly, or the reasons why.*

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Inside Plants: An Engineer's View of the Arnold Arboretum

Lorna J. Gibson

Gardeners tend their plants to produce a beautiful display in the garden or to harvest fruits and vegetables. Botanists study the anatomy, life cycles, and evolution of plants. Engineers, too, are interested in plants, although from a different perspective. Historically, engineers have been interested primarily in wood, because of its widespread use in everything from furniture to boats to buildings. But more recently, engineers have recognized that plants are very effective at resisting the loads they are subjected to (for instance, from the wind or from their own weight). Today, engineers study plants to learn what features make them so effective mechanically, with a view towards "bio-inspired design" of engineering materials and structures that exploit these features. In this article, I will take you for a walk through the Arboretum and describe a variety of plants and how they work from an engineering perspective.

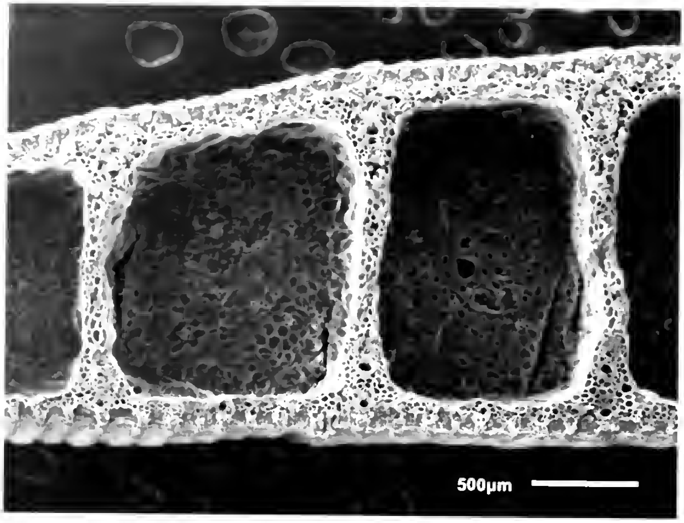
ROBERT MAYER

Cattails (*Typha* spp.) growing in the Meadow at the Arnold Arboretum.

THE TOUR BEGINS

Across from the Hunnewell Visitor Center, east of Meadow Road, lies the Meadow, a marshy area largely filled with cattails (*Typha* spp.). The leaves stand close to vertical and reach an impressive height, often over 6 feet tall. As you walk past, you can see the leaves bend in the wind; occasionally, a sparrow or red-winged black bird lands on the stem or its fuzzy, cylindrical seed head and bends that over, too. If you look at the leaves up close, you can see that they have fibers running along their length; if you draw your thumbnail across the width of the leaf you can feel the ridges of the fibers. How do the long, thin leaves stand up so tall?

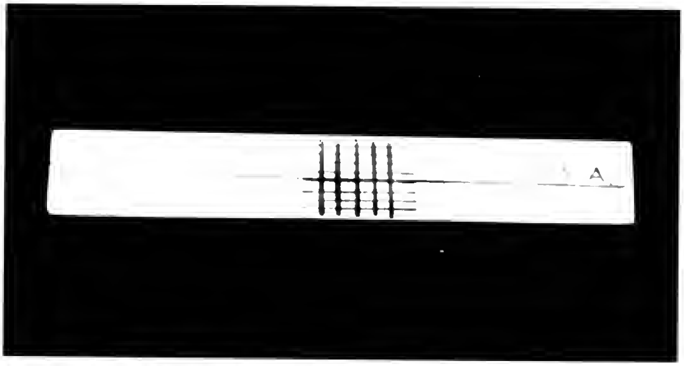
A look at the cross section of a cattail leaf reveals the answer. The cross section shows two outer faces connected by a number of ribs. At the very outer top and bottom surfaces, you

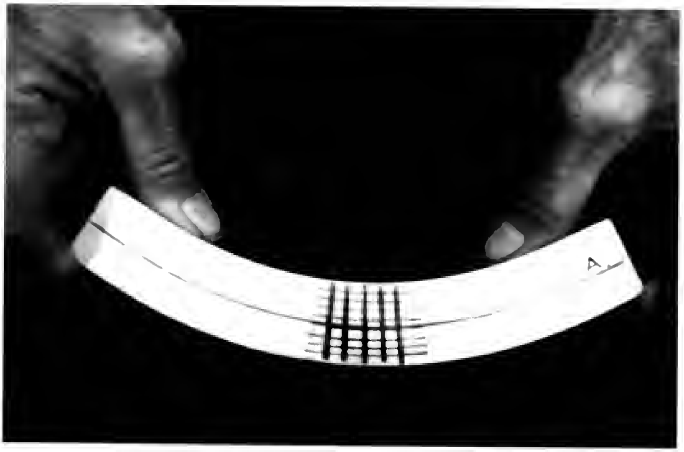


In cross section, under a scanning electron microscope, this cattail leaf has a structure resembling I-beams.

can see small ridges that correspond to the fibers you can feel with your thumbnail. The ribs and outer surfaces of the leaf act mechanically in the same way as a steel I-beam in a building. The more material that one has away from the center of a beam, the more resistant it is to bending deflections and internal loads. Think of a 12-inch-long wooden ruler that is 1 inch across and 1/8 inch thick. It's much easier to bend the ruler if you are pressing on the 1-inch face than if you turn it and press on the 1/8-inch face. The separation of the outer surfaces of the leaf by the ribs increases the resistance to bending, in the same way as the separation of the flanges (outer plates) of a steel I-beam by the web (the inner vertical section).

Long, tapered leaves are typical of monocotyledonous plants such as cattails, irises,

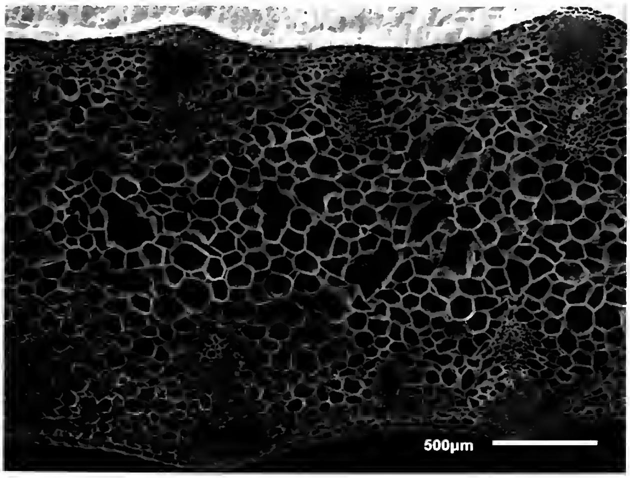




The Mechanics of Bending

PLANT LEAVES and stems, as well as tree trunks and branches, typically bend, either from the wind or from their own weight. If we look at a bent rubber beam on which we have marked a rectangular grid, we can see that the vertical lines rotate about the middle of the beam when it is bent. The horizontal lines on the top half of the beam get shorter and shorter the further they are away from the middle of the beam and, correspondingly, the horizontal lines on the bottom half of the beam get longer and longer the further they are away from the middle of the beam. The top half of the beam is in compression (pushing) while the bottom half is in tension (pulling) and the very middle sees no internal force at all. The material at the top and bottom surface of the beam is the most compressed or stretched, and sees the highest internal loads. The outer faces of the cattail leaves and the dense fibers at the top and bottom of the cross section of iris leaves resist the high internal loads at the outermost part of the leaves.

The swordlike leaves of bearded iris have a "sandwich structure" that increases their resistance to bending.



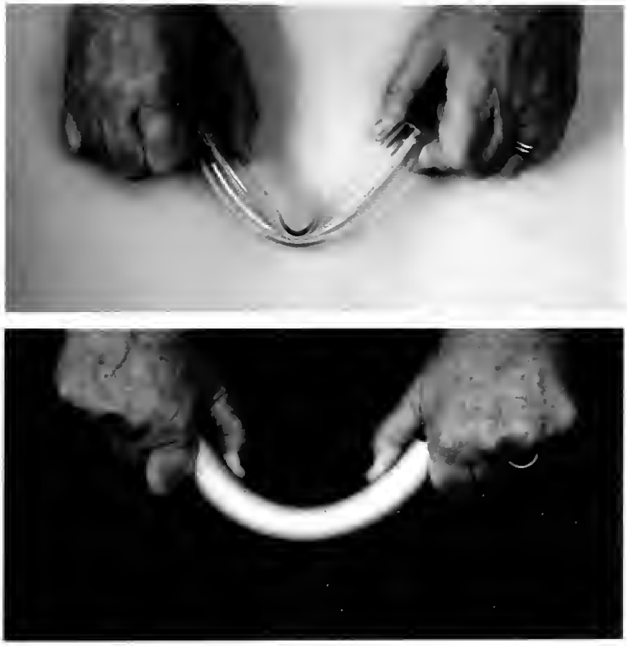
DON GALLER, MIT

Dense outer fibers (schlerenchyma) are separated by foamlike parenchyma in this iris leaf cross section.

and grasses. A cross sectional view of an iris leaf shows that it has large dense fibers (called sclerenchyma) at the outer surface and a thick inner layer of foamlike cells (called parenchyma). When the leaf is bent, the dense fibers carry most of the high internal loads at the outside of the leaf. The separation of the denser, stiffer fibers by the inner foamlike layer increases the resistance of the iris leaf to bending. Engineers make use of the same concept (a "sandwich structure") in the design of downhill skis, lightweight panels for aircraft, and the blades of windmills, which often have two outer skins of carbon-fiber-reinforced plastic separated by a foam (or sometimes an engineering honeycomb) core.

SUPPORTING ACT

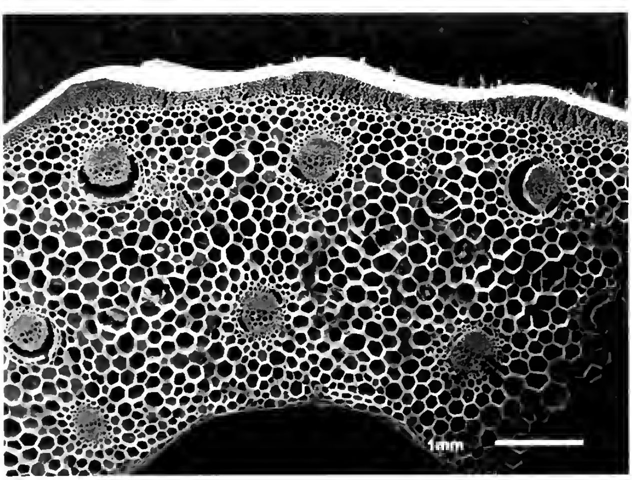
If we walk back towards the Arborway Gate and look along Willow Path, we see the huge leaves of the butterbur (*Petasites japonicus*). How does the stem support such large leaves without falling over? The stem bends under the weight of the leaf and from wind acting on the leaf. The stem is roughly circular in cross sec-



LORNA J. GIBSON

An empty tube kinks when bent, but the foam-filled tube resists kinking.

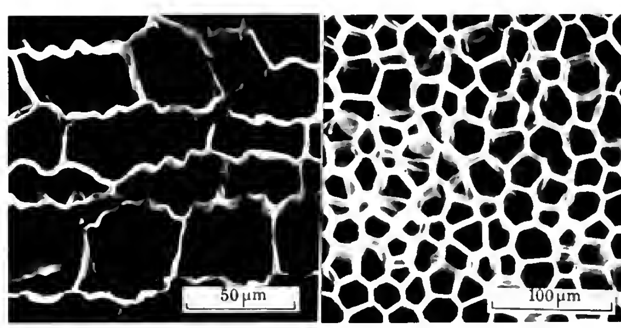
Butterbur leafstalks must support very large leaves (often 2 feet or more in diameter).



Cross section of a butterbur leafstalk.

tion, so that it can resist bending in any direction equally. If we look at a cross section of the stem in a scanning electron microscope, we see that it has a dense outer layer surrounding an inner foamlike layer of cells that are reinforced with bundles of fibers. At the center of the stem is a void. This combination of foamlike cells surrounded by a thin, denser outer layer is common in plant stems and is often called a "core-rind" structure. The dense outer layer resists most of the internal loads from bending on the stem, which are highest at the outer extremity of the stem. The inner foamlike core also plays a role: it helps resist kinking of the stem. The dense outer cylindrical shell of the stem is a little like a drinking straw. When a straw is sufficiently bent, it tends to fail by forming a crease or kink in the middle. If the drinking straw is filled with foam and then bent, the foam pushes back against the kinking, increasing the straw's resistance to this type of failure (see photos on page 13, lower right). The interior foamlike cells in the butterbur stem also help resist kinking by pushing back against the outer layer if it tends to kink inwards.

Slightly further along Meadow Road we pass by the cork trees (*Phellodendron* spp.) with their thick, deeply grooved bark. If you press your thumbnail into the bark you'll notice that it is quite soft and springy. Cork stoppers, such as those used in wine bottles, come from the bark of a different tree, however: the cork oak, *Quercus suber*, that grows in Mediterranean climates, particularly in Portugal and Spain. Remarkably, unlike most other trees, after the

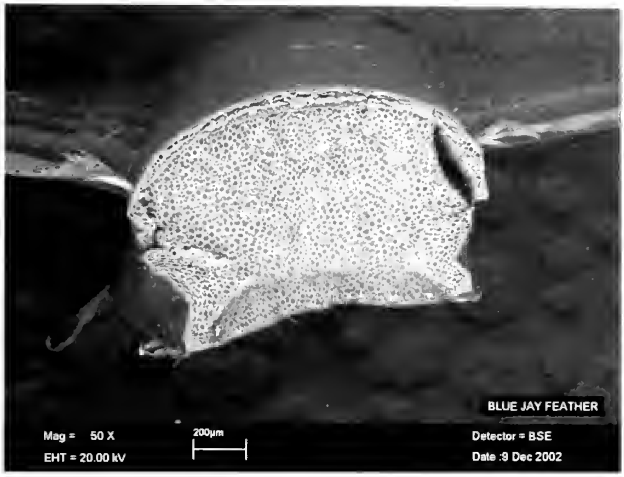


Scanning electron microscope images of cork oak (*Quercus suber*) cells.

Birds of a Feather

BIRD FEATHER quills have a similar structure to iris leaves. As the bird's wings beat in flight, the feather is bent up and down, so that the bending loads are highest on the top and bottom of the quill. A sandwich structure, with dense faces at the top and bottom of the quill, would seem to be an ideal option. But bird feathers also have to resist twisting, or torsion, and the foam-filled closed tubes are adept at this. (You can try this simple experiment: take a drinking straw and twist it. Now cut a slit along the length of the straw and twist it again. The straw is much better at resisting twisting when the cross section is closed and intact.) As with the butterbur, the foamlike core also helps resist kinking failure of the dense outer layer of material in the feather quill.

Blue jay (*Cyanocitta cristata*).



DON GALLER, MIT

Cross section of a blue jay feather.

bark of the cork oak is removed, it regrows, allowing harvesting of cork every 10 to 15 years. The cork cells are like little bellows: they are roughly box-shaped, but with corrugations running in one direction. When you compress the cork in the direction of the corrugations, they simply fold up, like a bellows, so that they do not expand in the lateral direction. This feature of cork is one reason cork works well at stoppering bottles. A rubber stopper, on the other hand, bulges out laterally when compressed, making it difficult to press into a bottle; for this reason, rubber bottle stoppers are always tapered.

TREES = WOOD

When we think of the Arnold Arboretum, we think of trees. And when engineers think of trees, they inevitably think of wood. Wood is one of the structural materials used for the longest time in human history and is still one of the most widely used. The oldest known wooden boat is Cheops's 4,600 year old barge, found dismantled in a pit next to the Great Pyramid in Egypt. In the late 1600s, eastern white pines (*Pinus strobus*) from New England were a strategic resource for the British Royal Navy. The tall, straight trunks of the pines were used as masts for ships; the taller the mast, the more sail area, the larger the ship, and the more cannons it could carry. And most houses in North America are still wood framed.

North American woods are divided into hardwoods (deciduous trees that drop their broad leaves annually) and softwoods (conifers with needles that are typically, but not always, evergreen). While hardwoods tend to be denser and harder than softwoods, that is not always the case: for example, Douglas fir, a softwood,


The tall, straight trunks of white pine were once used for ship masts.

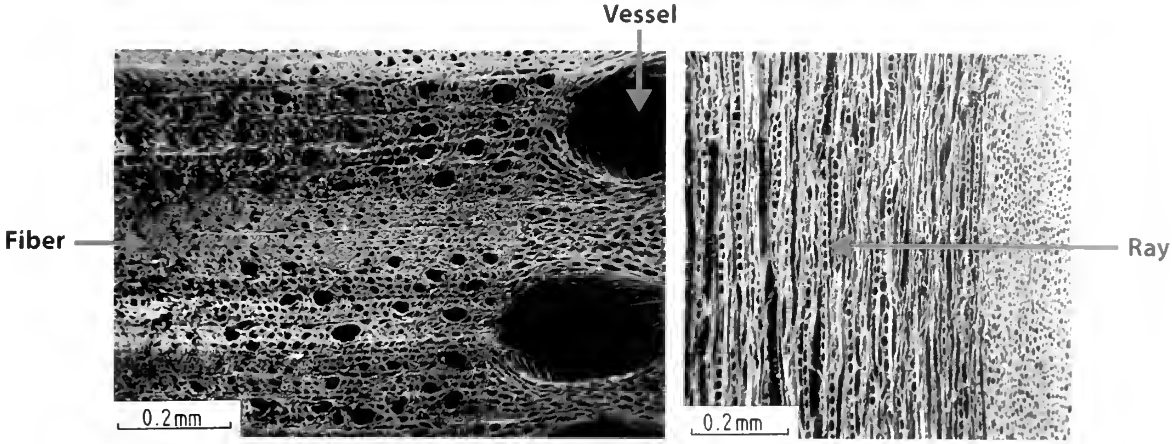
is denser and stronger than quaking aspen, a hardwood.

Up Bussey Hill Road, past the lilac collection, and past the turnoff to Bussey Hill, we come to the shady Oak Path, with its many species of magnificent oak trees (*Quercus* spp.). Oaks and other hardwoods have three types of cells: *fibers* that provide structural support, larger diameter *vessels* that conduct water and sap up and down the tree, and *rays* that store sugars: all three are visible in the images of the cross-section and longitudinal section of oak. The fibers and vessels, which make up the bulk of the cells, run longitudinally along the trunk and branches of the tree.

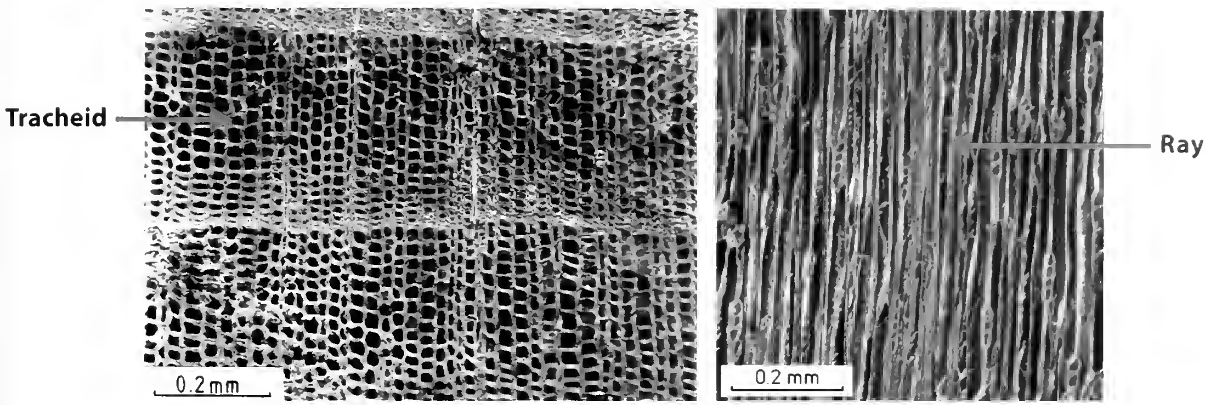
Walking across the grass towards Valley Road, we next come to the Conifer Path, with its hemlocks, pines, spruces, and firs. Softwoods have two types of cells: *tracheids*, which make up the bulk of the cells and provide structural support and conduct fluids (via small holes called pits along their sides), and *rays*, which again store sugars.

To a first approximation, the structure of both hardwoods and softwoods resembles a honeycomb, with roughly square, instead of hexagonal, prismatic cells. Forces applied to wood are largely carried by the fibers in hardwoods and by the tracheids in softwoods. Since these wood cells resemble an elongated honeycomb, the mechanical properties of woods can be modeled, to a first approximation, as a simple honeycomb with identical cells. It is well known that the stiffness and strength of woods are much higher along the grain than across the grain; the reason for this can be explained by modeling the wood cells as a honeycomb.

When a model honeycomb is loaded in compression (pushing) along the length of the cells (along the prism axis), the cell walls simply compress, and the stiffness and strength just depend on the amount of material in the cross section, or the fraction of the area that is solid. Wood cells loaded along the grain in compression also simply shorten axially, just like the honeycomb model. Using the honeycomb model, we see that the stiffness and strength of wood along the grain, too, depend on the fraction of the area of the cross section that is solid; for prismatic cells as in the honeycomb and



Oak wood, cross section and longitudinal section.

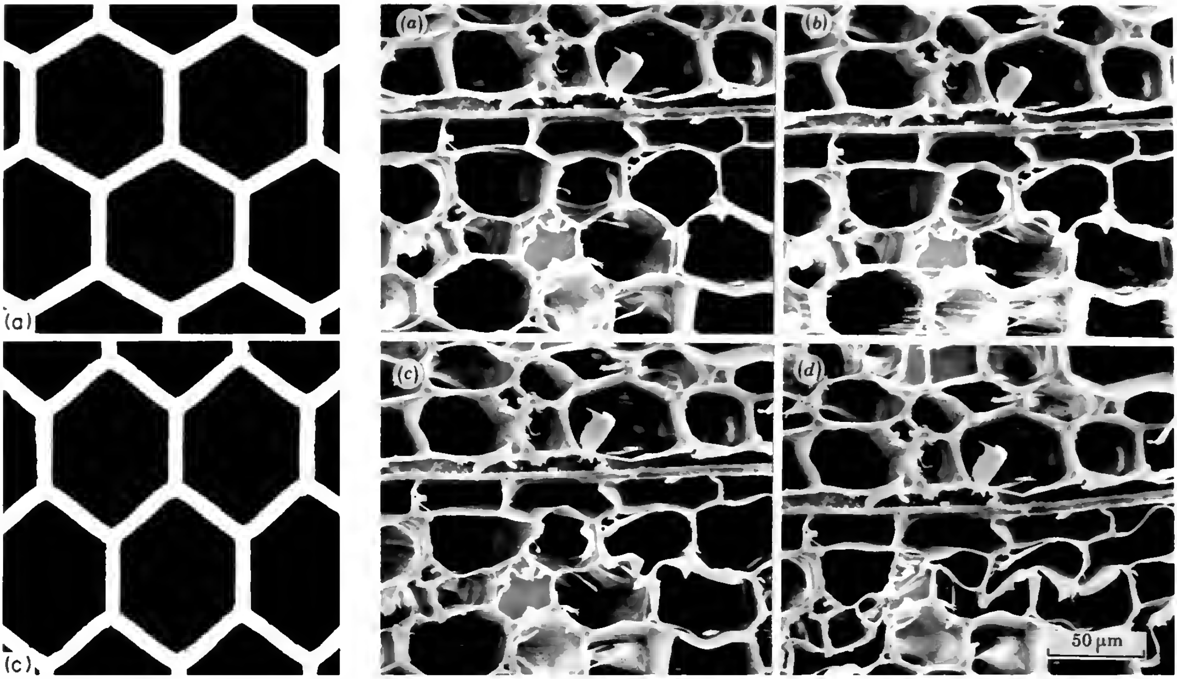


Cedar wood, cross section and longitudinal views.

wood, this is equivalent to the fraction of the volume that is solid.

In contrast, when a model honeycomb is loaded across the cells, it is much easier to deform the honeycomb, as the cell walls bend. Wood cells loaded across the grain also bend in a manner similar to the honeycomb; this can be seen most easily in a low density wood like balsa (*Ochroma pyramidale*) (see upper right images on page 18).

If you take a ruler and bend it, it deforms much more than if you rest one end on a table and compress it from the opposite end with the same load. It is also less strong when bent: it is much easier to break the ruler in bending than by compressing it on end. We have already seen how, in a bent beam, the amount that the material stretches or compresses increases as the distance up or down from the middle of the beam increases: the thickness of a beam plays a greater role in resisting deflection or internal loads than the width. When loaded across the grain, the wood cell walls bend, giving much lower stiffness and strength across the grain than along the grain. This effect can be analyzed in more detail to show that the stiffness of woods loaded across the grain depends on the cube of the volume fraction of solid, and the strength (loaded across the grain) depends on the square of the volume fraction of solid. This leads to the great difference in the stiffness and strength in woods when loaded along and across the grain, a difference that is greater in lower density woods, such as pine, than in high density woods, such as oak. For instance, in Eastern white pine the compressive strength



A rubber honeycomb model shown unloaded (top left) and, when loaded in compression from the left, with bent cell walls (bottom left). The set of four images (right) shows the same area in a piece of balsa wood under increasing load in a vice in a scanning electron microscope. The top left image (a) is unloaded, and images (b), (c), and (d) are at increasing compressive load.

along the grain is about 11 times that across the grain while in white oak the compressive strength along the grain is about 7 times that across the grain.

THE END OF THE TOUR

At the end of the Conifer Path, off to the right near Centre Street, is a group of bamboo accessions (mostly *Phyllostachys* spp.). Bamboo is a member of the grass family and is exceptionally fast-growing. Moso bamboo (*Phyllostachys edulis*), native to China, can grow 3 feet in a day and the stem, or culm, can have a 6-inch diameter. While the initial growth is remarkably fast, it takes several years for the stem to mature and fully densify and lignify. In countries where it is indigenous, it has been used traditionally for houses and other small structures.

A cross section through a bamboo culm shows vascular bundles surrounded by dense sclerenchyma tissue and separated from one another by ground tissue of low density parenchyma cells. There is a radial density gradient: towards the periphery of the culm there are more vascular bundles (and each one is denser) than at the inside surface of the culm. As we have already seen, placing dense material away from the center of a beam (where the deformation and internal loads are zero) increases the resistance of the beam to bending. Bamboo culms are

Cross section of bamboo stem.

typically loaded in bending from the wind—the increase in denser material towards the outside of the cross section increases the resistance of the culm to bending deflections and loads, compared with a section with the same amount of material evenly distributed across the section.

On our walk through the Arboretum, we have seen a variety of plants with different internal structures. Plants are often mechanically efficient, using material to resist internal loads where they are greatest. Engineers studying the mechanical behavior of plants take inspiration from them for the design of engineering materials and structures.

NANCY ROSE

Stems of a bamboo, *Phyllostachys makinoi*.

Acknowledgements

Bamboo SEM figure is from Gibson, L. J., M. F. Ashby, G. N. Karam, U. Wegst, and H. R. Shercliff. 1995. The mechanical properties of natural materials II: microstructures for mechanical efficiency. *Proceedings of the Royal Society of London* A450: 141–162.

Cork SEM figure is from Gibson, L. J., K. E. Easterling, and M. F. Ashby. 1981. The structure and mechanics of cork. *Proceedings of the Royal Society of London* A377: 99–117.

Oak and cedar SEMs and balsa images are from Easterling, K. E., R. Harrysson, L. J. Gibson, and M. F. Ashby. 1982. On the mechanics of balsa and other woods. *Proceedings of the Royal Society of London* A383: 31–41.

Rubber honeycomb model figure is from Gibson, L. J., M. F. Ashby, G. S. Schajer, and C. L. Robertson. 1982. The mechanics of two-dimensional cellular materials. *Proceedings of the Royal Society of London* A382: 25–42.

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Fruits and Nuts of the Villa Farnesina

Jules Janick


The loggia of Psyche in the Villa Farnesina. The paintings on the ceiling depict scenes from the love story of Cupid and Psyche.

In 1505, an extremely wealthy Sienese banker named Agostino Chigi (1466–1520) decided to build a new home for himself that was to be the most splendid in Rome. A banker to popes and kings, Chigi's modus operandi was to lend money and, in return, obtain monopolies for such things as importation of grain or production of alum from mines. He often accepted jewelry for "security." He was in a sense a pawnbroker and a wheeler-dealer who structured his deals so he couldn't lose. He became the richest man in Europe. Chigi was a courtier, very well connected, and truly a Renaissance man. Although not particularly well educated, he bought into humanism, a Renaissance movement that had rediscovered Latin and Greek writings and the mythical legends of the pagan world, was absorbed with nature, and was intensely concerned with the human condition.

Chigi built the most splendid residence in Rome to honor and glorify himself. Chigi's villa, now known as the Villa Farnesina (it was sold to Cardinal Farnesina by Chigi's heirs after they burned through their inheritance), is located on the West Bank of the Tiber in the district now known as the Trastevere, southeast of the Vatican and east of the Orto Botanico. Here Agostino Chigi, the Magnificent, received artists, poets, princes, cardinals, and the pope in opulence and pomp. At one famous dinner the silver and gold plates were thrown into the Tiber after use—but into nets. The building was an evocation of the classical world, with the rooms filled with paintings and statues, opulent furnishings, and a garden called the *viridiarium*, a repository of rare plants. Each room is decorated with a different theme, but this article will concentrate on the loggia, now known as the Loggia of Psyche, originally a veranda or gallery with one wall open to the outside.

The Loggia of Psyche was decorated under the management of Raphael Sanzio (1483–1520), the boy wonder of the high Renaissance and a rival to Michaelangelo Burotti. As judged by

Richly detailed festoons painted by Giovanni Martini da Udine contain thousands of botanical images.

the decorations of his home, Chigi was more interested in the sensuality of the pagan world than on the artistic representation of suffering, torture, and death of the medieval Christian tradition. The decorations—painted between 1515 and 1517—involve love and marriage, perhaps in anticipation of Chigi's marriage to his longtime mistress in 1519, one year before his death. The loggia is presented as a tentlike pergola with images of two large tapestries painted on the ceiling as a roof, depicting a scene of the Council and the Banquet of the Gods—the climax of the Cupid and Psyche story. The arches of the ceiling are divided into spandrels that contain scenes of the heavenly adventures of Venus, Cupid, and Psyche, alternating with severies that illustrate cherubs bearing trophies of the gods.

The Cupid and Psyche myth is based on the first novel that comes down to us from antiquity, known as the *Metamorphoses* (or *The Golden Ass*) of Apuleius, written in the second century but translated to Latin in 1469. The story, which was to become immensely popular, concerns the marriage of Cupid (mischievous God of Love) to the beautiful mortal Psyche ("soul") leading, after tribulations and trials, to the divinity of Psyche. The underlying theme of the story is that "love conquers all."

These Raphael frescoes illustrating the heavenly adventures of Cupid and Psyche are stunning, but for botanists and horticulturists an even greater treasure is found on the ribs enclosing the loggia's spandrels and severies. Here, the elaborate festoons and wreaths painted by Giovanni Martini da Udine (1487–1564) contain thousands of images of individual fruits, vegetables, and flowers, encompassing over 170 species (Caneva 1992a,b). The festoons have been deconstructed by scanning the images and collating each species, which makes it possible to examine genetic variability within species. For this article, I will concentrate on images within the festoons of selected horticultural crops, specifically maize, pome fruits, nuts, eggplant, cucurbits, and legumes. It is of particular historical interest that the festoons contain what may be the earliest known European images of maize, pumpkins, and squash from the New World, barely a quarter century after Columbus's encounter with the Americas, providing evidence of the rapid diffusion of these crops into Europe.

THE CROPS

Maize

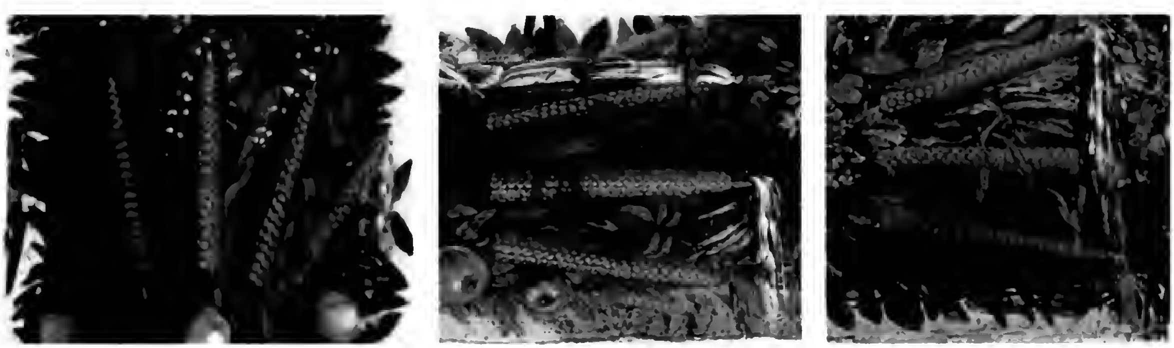
There are a total of eight groups (28 ears) of maize (*Zea mays*) scattered throughout the festoons. A close examination of the maize ear images suggest that they are painted with some artistic license (Janick and Caneva 2005). Despite the presence of some atypical characteristics (as compared to United States cornbelt maize), the attribution is based on the combination of characters including kernel size and color, ear type (10 and 12 rows are depicted), the presence of white,

The strange tripartite extensions of the ear tips in image are suggestive of rudimentary tassels.

Leonhard Fuchs 1542 woodcut of maize (*Zea mays*)was previously thought to be the first European depiction of the species.

yellow, and reddish silks, and the long, narrow leaves typical of maize. In addition, the historical evidence supports the conclusion that these images may be the earliest representation of maize in Europe, fully a quarter century earlier than the famous woodcut of Leonhard Fuchs labeled *Turcicum Frumentum* (Latin) and *Türckisch korn* (German), presumed to have been the first European image. The depiction of leaves suggests that maize was grown and seen by the artist, probably in the *viridarium*, a repository for rare plants at Chigi's villa, although the original drawings were probably made from detached ears. It seems obvious that most of the multiple ears within the same group are copies of a detached prototype ear. The shank depictions are probably invented since there appears to be an attempt to hide them in most images and those that are drawn are obviously botanically incorrect. Since maize ears have paired spikelets, the preponderance of interlocking kernels is disconcerting. One explanation is that a lack of synchrony of silk receptivity and pollen shed in these nonadapted exotics could cause pollination gaps leading to plump, round seed, and perhaps the artist filled in the voids in an attempt to portray perfection.

Maize has been cultivated in Spain, Portugal, and Italy for five centuries and selection and isolation have produced various races differing in maturity and phenotype. Characteristics of the maize ear phenotypes depicted in the images from the Farnesina can be found in races from Spain (Sanchez-Monge y Parellada 1962), Portugal (Costa-Rogrigues 1971), and Italy (Istituto sperimentale per la Cereali-



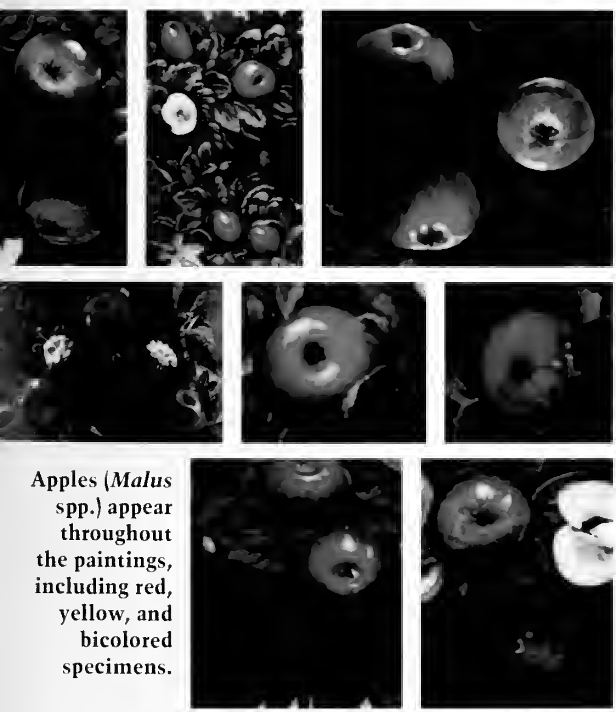
Though the ears don't look exactly like modern American cornbelt maize (note the irregular kernel orientation in these images), they are clearly identifiable as maize.

coltura 2002). The resemblance of the maize images painted in Italy between 1515 and 1519 to races of maize in Spain, Portugal, and Italy is confirmatory evidence for the early origin of some of these races. There is direct evidence that maize seeds reached Rome in 1594. A letter from Peter Martyr D'Anghiera, an Italian teacher connected with the Spanish court, to Cardinal Ascoanio Sforza, vice-chancellor of the papal court, describes news of the early returning ships from the second voyages of Columbus and encloses seed of maize (McNutt 1912; Janick and Caneva 2005).

Pome Fruits

Five types of pome fruits are illustrated in the festoons: apple (*Malus*: 97 fruits of cultivated apple and 21 fruits of wild apple); pear (*Pyrus*: 78 fruits of European cultivated pear and 21 of wild pear); quince (*Cydonia*: 31 fruits), medlar (*Mespilus*: 27 fruits), and hawthorn (*Crataegus*: 30 fruits in two clusters). The number of images are indicative of the relative popularity of these fruits in Renaissance Italy.

Of the apple fruits (*Malus* × *domestica*), 34 were solid red, 43 red–yellow bicolored, and 20 were yellow. A few show fungal spots. The cultivated apples all resemble modern types in shape and color. There were also three groups of small apples or crabapples (*Malus sylvestris*), each with multiple fruits (21 total) in clusters. One cluster consisted of 7 bicolored fruits, one had 5 red fruits, and the other had 7 dark purple fruits.



Apples (*Malus* spp.) appear throughout the paintings, including red, yellow, and bicolored specimens.

Examples of pears in the festoons.

Of the pears (*Pyrus communis*), 45 were red–yellow bicolored and 33 were yellowish. The preponderance of red fruits is much different from present day distribution of pear cultivars in Europe, where most are green, yellow, or russet. There were three cluster of small wild pears (*Pyrus pyraster*) totaling 21 fruits, all of varying degrees of red color.

There were 31 images of large quince (*Cydonia oblonga*) fruits, all lobed. Some were obviously mature, with an old gold color, a few were reddish, while others, obviously immature, were whitish or light yellow. All of the quince resemble the "golden apple" as described by Pliny: "cleft with incisions and has a color verging on gold" (Roach 1985).

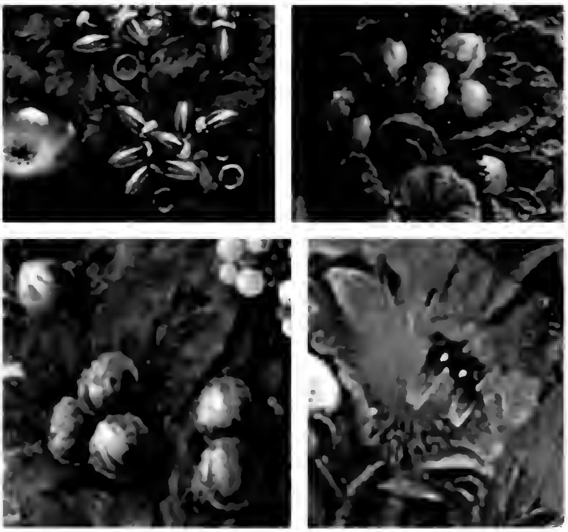
The 6 groups of medlars (*Mespilus gemanica*) totaled 27 fruits, which were small and of the same type. They fit Pliny's description for the small and aromatic 'Anthedon', one of the three types of medlars in ancient Rome. Medlars are still found in Italian markets but are usually larger than the ones illustrated in the festoon.

There are two groups of hawthorn (*Crataegus oxyacantha,* a synonym for *C. laevigata*). They show sprays of fruits, one dark purple with about 22 fruits and the other bright red with 8 fruits.

Left to right. Quince, medlar, and hawthorn fruits.

Nuts

Acorns, chestnuts, hazelnuts (filberts), pinenuts, and walnuts, are illustrated on the ceiling. Acorns appear among the 8 groups of English oak (*Quercus robur*) and 4 groups of *Q. virgiliana.* European chestnuts are pictured in 3 groups of *Castanea sativa.* European hazelnuts appear in 4 groups of *Corylus avellana* and two groups of *C. maxima* (which some taxonomists lump in with *C. avellana*). Edible pinenuts are



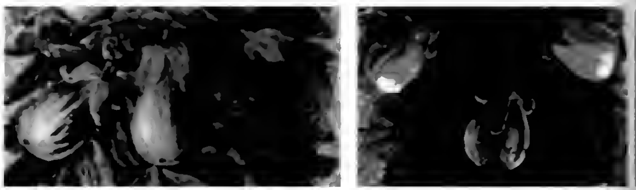
Clockwise from upper left. Acorns, hazelnuts, chestnuts, and walnuts are depicted in the paintings.

The cones of Italian stone pine (*Pinus pinea*) hold large, edible nuts.

represented by 11 groups of Italian stone pine cones (*Pinus pinea*). There are also depictions of English (or Persian) walnuts (*Juglans regia*) in 6 separate groups.

Eggplant

There are a total of 21 images (30 fruit) of eggplant (*Solanum melongena*). The fruits are very similar and are characterized by varying degrees of purple pigmentation and white undercolor.



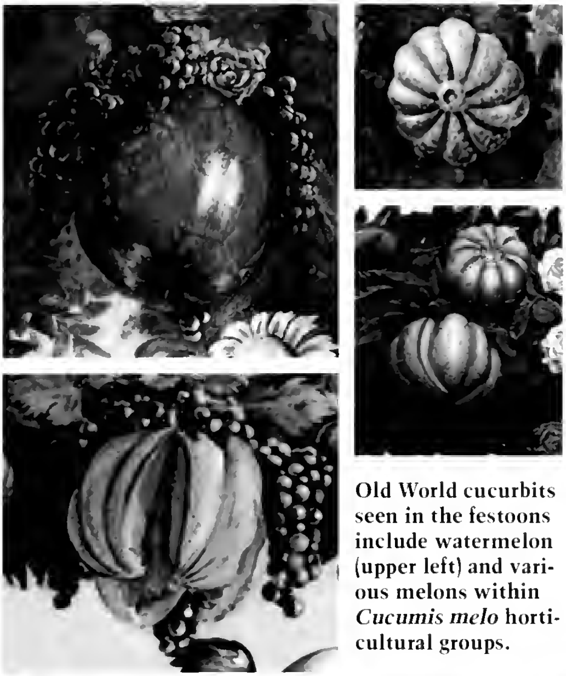
Eggplant images include several yellow, fully mature specimens.

In some cases the eggplants are deep yellow, indicating maturity. Most of the fruits are club shaped.

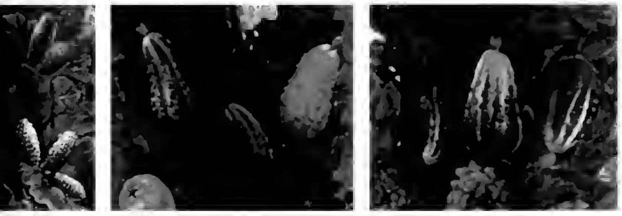
Cucurbits (Old World Species)

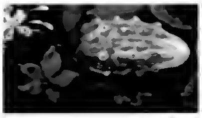
Cucurbit fruits from Old World species are well represented (Janick and Paris 2006). Images include *Citrullus lanatus* (watermelon), *Cucumis melo* (melon), *Cucumis sativa* (cucumber), *Ecballium elaterium* (squirting cucumber), *Lagenaria siceraria* (bottle and serpentine gourd), and *Momoridica balsamina* (bitter gourd).

The four watermelon images, each with a single fruit, represent a single type with small, round, striped fruit similar to modern ice-box types. In contrast, the 16 melon fruits include three horticultural groups: Cantalupensis (12 fruits), Reticulatus (3 fruits of two types), and Flexuosus (single fruit). The Cantalupensis types represent four extant cultivars ('Cantalun', 'De Bellegarde', 'Noir des Carmes', and 'D'Alger'), indicating high genetic variability.



Old World cucurbits seen in the festoons include watermelon (upper left) and various melons within *Cucumis melo* horticultural groups.





The cucumbers in the paintings look like typical modern pickling types. There is also one image of squirting cucumber (upper left).

The cucumber images (13 groups, 25 fruit) all resemble the type known as "American Pickling." There is a single image of the so-called squirting cucumber.

Two types of *Lagenaria* fruit associated with white flowers are included: the inedible bottle gourd (var. *fiasco*) which is used largely for utensils, and the serpentine or club-shaped gourd (var. *longissima*), called cocuzza in Italy, that is edible when immature and still consumed in Sicily. There are 9 fruits of bottle gourds with slight variation in color and neck morphology. There are 19 groups (22 fruits) of cocuzza with subtle differences in shape based on the thickness of the calyx end suggesting that some might be hybrids of *fiasco* and *longissima* types. Cocuzza are widely displayed in Renaissance

Depictions of *Lagenaria siceraria* gourds include both the bottle type (with a broad, round base) and serpentine type (long, slender form).

art, probably because of their phallic shape and association with the worship of Priapus, god of orchards and vineyards and the personification of the male generative organ (Morel 1984; Janick 2004).

Finally, there are 3 images (9 fruits) of bitter gourds, known also as balsam apple (*M. balsaminia*) and balsam pear (*M. charantis*). Fruits are reddish and slightly warty, with a pointed end.

Cucurbits (New World Species)

Of particular interest for the festoon images are representatives of two species of New World cucurbits: *Cucurbita maxima* (fall and winter squashes and pumpkins) and *Cucurbita pepo*

New World cucurbits seen in the paintings include large pumpkin or squash types of *Cucumis maxima* (upper left) and small gourd type examples of *C. pepo*.

(pumpkins, summer squash, and gourds). Some of these fruits were identified as *C. moschata* by Caneva (1992) but this may be a misattribution. There are 9 fruits of *C. maxima* of two types: brilliant orange, furrowed fruit with a protruding stylar end reminiscent of the turban gourds; and white, furrowed, round pumpkins, now called "show pumpkins" in the United States. The images of *C. pepo* are of two types: a large orange pumpkin type and 11 clusters (about 17 fruits) of striped, oviform to pyriform gourds.

Legumes

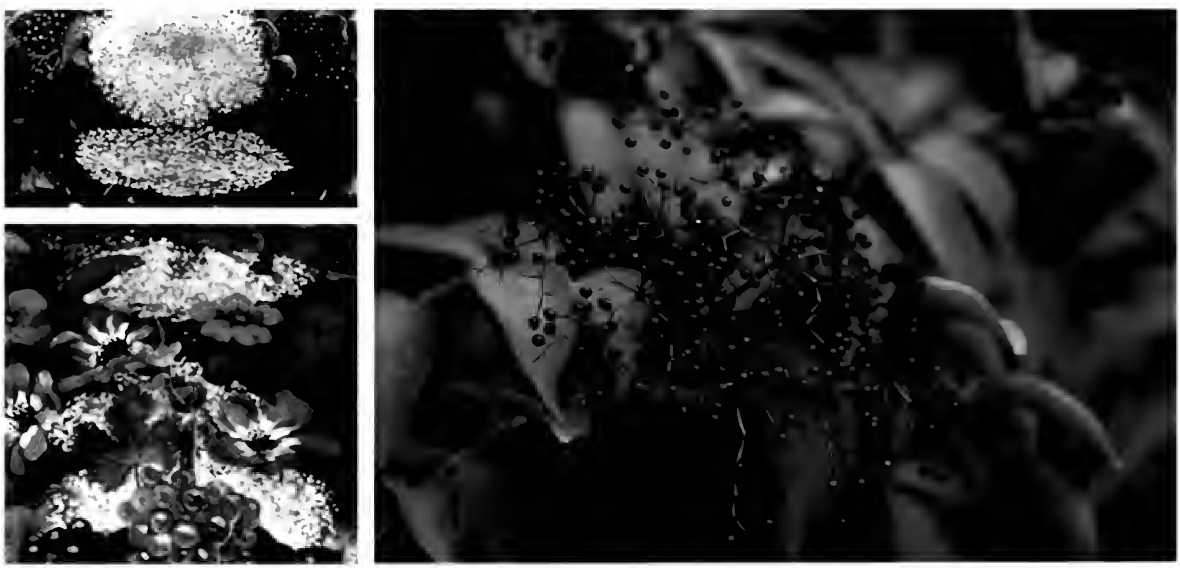
Six genera of legumes are represented in the festoons including: *Cassia* (1 image, 4 pods); *Ceratonia* (3 groups, 8 pods); *Trifolium* (1 image, flower only); *Phaseolus* (2 groups, 5 pods); *Pisum* (1 group, 3 pods); and *Vicia* (four groups, 15 pods). If *Phaseolus*, a New World species, is indeed represented, (the attribution is open to question) this is still not the first representation of *Phaseolus* in Europe. An image of *Phaseo-*

Legume genera include (clockwise from upper left) *Phaseolus*, *Pisum*, *Viscia*, *Cassia*, and *Ceratonia*.

Pictured Plants at the Arnold Arboretum

IT IS INTERESTING to note that many of the woody plant genera found in the ceiling of the Loggia are represented in the collections of the Arnold Arboretum, including the following:

Castanea	*Cydonia*	*Morus*	*Quercus*	*Sambucus*
Cornus	*Hedera*	*Pinus*	*Ribes*	*Sorbus*
Corylus	*Juglans*	*Prunus*	*Rosa*	*Vaccinium*
Crataegus	*Mespilus*	*Pyrus*	*Rubus*	*Vitis*



NANCY ROSE

Elderberry (*Sambucus* spp.) images from the Villa Farnesina (upper left: flowers and fruit; lower left: flowers mixed with flowers of *Anemone coronaria* and grapes) and the Arnold Arboretum (right).

lus is found in an illustrated manuscript, *Livre d'Heures d'Anne de Bretagne*, painted between 1503 and 1508 by Jean Bourdichon (ca. 1457–1521) (Camus 1894; Zevan 1997; Bilimoff 2001).

LEGACY OF THE VILLA FARNESINA

The images of the Cupid and Psyche legend and the botanical festoons found in Chigi's villa demonstrate the vigor of the Renaissance humanists in promoting art and science in the beginning of the sixteenth century. The beautiful art work is still admired after 500 years and accounts for a significant flow of tourist money into Italy. These images also contain significant scientific interest, especially within horticulture and agriculture, since they provide information on the genetic diversity of many horticultural plants as well as information about the dispersal of New World plants in Europe.

Chigi, in whose villa the images were displayed, may be a pivotal figure in the dissemination of New World plants in the Mediterranean Basin. He had a garden of rare plants (*viridiarium*), was well know to Cardinal Sforza and Pope Alexander VI, was influential in the affairs of the Vatican and the Republic of Venice, and was directly involved in the Mediterranean trade, especially between Venice and Turkey, through his monopolies concerning alum and cereals (Gilbert 1980). We owe a debt to Giovanni da Udine for his skill in illustrating what may be the first images of maize and New World cucurbits in Europe, and for leaving a breathtakingly beautiful visual record of crop diversity in the high Renaissance.

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Additional images can be seen at:
http://www.hort.purdue.edu/newcrop/udine/info.html

Jules Janick is the James Troop Distinguished Professor in Horticulture at Purdue University, West Lafayette, Indiana.

Maclura pomifera: Neither Apple Nor Orange

Jon Hetman

Though I confess that plants held little sway among my childhood interests, a few specific trees stand out in my early recollections, all due to their memorable fruits. A seemingly ancient apple tree in a neighbor's front yard was a climbing favorite, and bore small, mottled green fruits that were a delight to eat as long as you didn't overindulge. Behind my grandparent's garage in central Florida, a moss-covered orange tree provided fragrant spring flowers and slightly sour fruits that remain indelible sensations of my youth. But the fruits that perhaps fascinated me most belonged to an Osage orange tree that grew near my elementary school—large, hard as baseballs, and looking to us like green brains, the bumpy orbs with their citrusy aroma were a delightful mystery that inspired a number of ingenious games of our own design.

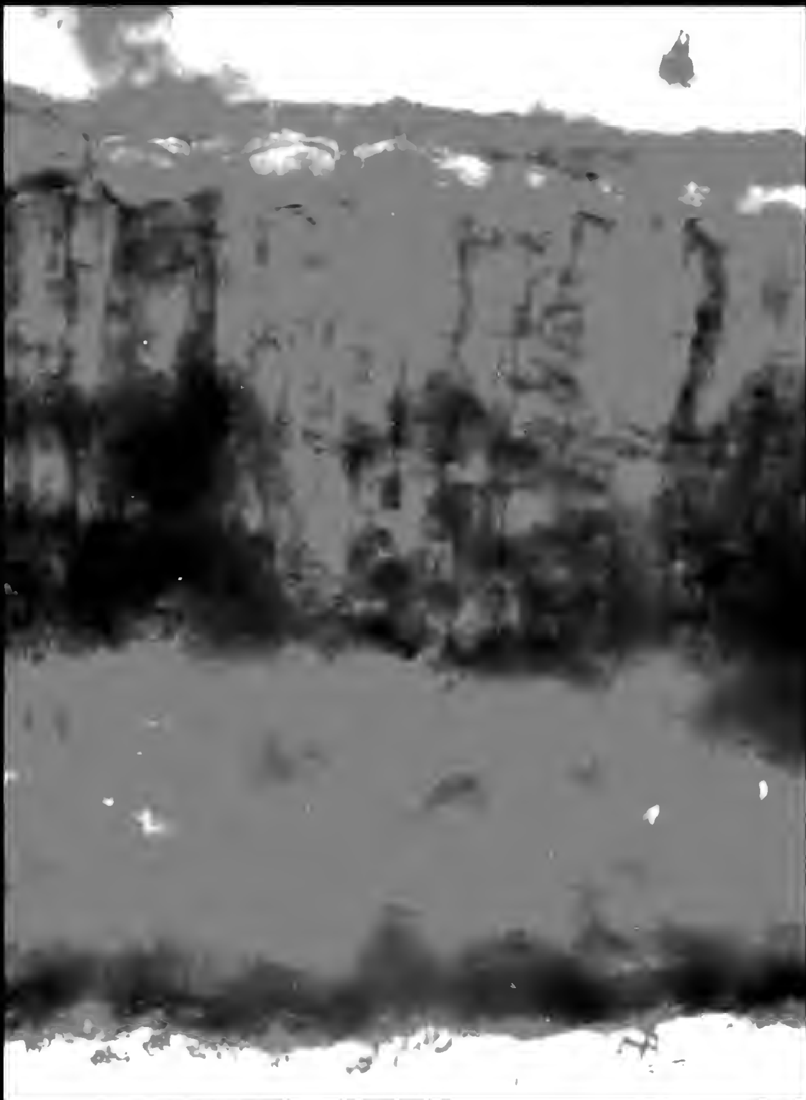
In earlier days, Osage orange (*Maclura pomifera*) garnered significant interest among people of its native Oklahoma, Arkansas, Missouri, and Texas, though for very different reasons. Hunters in the Osage tribe fashioned war clubs and bows from the tree's bright yellow heartwood, which proved stronger than oak and as tough as hickory. Early settlers in the American frontier called it the hedge apple, planting it in thicket-like rows so that the thorny, interlacing branches sheltered fields from wind and provided an impenetrable animal barrier. As historian Paul Landacre famously described it, an Osage orange hedge was "horse-high, bull-strong, and pig-tight."

For me though, even as an adult, it's the fruits of these dioecious trees that really excite the imagination. If you cut one in half—and you may need a saw to do so—you'll discover a tough, pithy core surrounded by a couple hundred small seeds. Like other members of the Moraceae (mulberry family), *Maclura* bears a true multiple fruit composed of numerous separate ovaries, each developing from a separate female flower. In fact, the fruit's distinctive bumps—and their accompanying black, hairlike styles—rise from the fruit's numerous, tightly-packed ovaries. Though squirrels rip into fallen fruits to consume the seeds, nothing else seems to find these forbidding fruits the least bit appetizing. Nothing, that is, that still exists. In her book *The Ghosts of Evolution,* author Connie Barlow suggests that mammoths, mastodons, and other large herbivores of the North American plains ate *Maclura* fruits and were its dispersal agents before humans evolved their own interests in the plant.

Although the exact details of the original collection of this monotypic species remain murky, we know that *Maclura* was among the botanical specimens gathered by Lewis and Clark on their transcontinental expedition of the American West. By studying saplings subsequently cultivated in the Philadelphia garden of Bernard McMahon, Constantine Samuel Rafinesque produced the first botanical description of the tree in 1817, naming it *Ioxylon pomiferum,* or "poison apple." Perhaps unaware of Rafinesque's classification, Thomas Nuttall offered his own description the following year, honoring American geologist William Maclure with its generic epithet and proposing *aurantiaca* ("orange colored") as its specific epithet. Nearly a century later, Germany's Camillo Karl Schneider argued for the name that has stuck to this day, pairing Nutall's generic *Maclura* with a derivation of Rafinesque's specific, *pomifera.*

Coincidently, this Teutonic connection to *Maclura* is compounded in the Arboretum's most spectacular accession (471-36-B) of the plant, a female obtained in 1936 from the Hermann A. Hesse Nursery of Weener, Germany. Growing today on a steep bank near the Centre Street wall across from Faulkner Hospital, the tree exhibits the criss-crossing, nearly horizontal branching that once made the species so desirable as a hedging plant. It is 36 feet (11 meters) tall and its two trunks have diameters at breast height of 14 and 16 inches (36 and 40.5 centimeters). Visit it in autumn, when its limbs bend beneath the weight of its fruits and its glossy leaves turn yellow, and you'll likely acquire fond associations of your own with this most singular of American fruiting trees.

Jon Hetman is the Arnold Arboretum's Communications and Stewardship Officer.



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Front and back covers: On page 11, curatorial colleagues Michael Dosmann and Tony Aiello continue their "Quest" series, this time searching for hardy southern live oak (*Quercus virginiana*). Photo of an impressive specimen of southern live oak growing in Lake Kissimmee State Park, Florida, courtesy of David Price, Bok Tower Gardens.

Inside front cover: Blue flag iris (*Iris versicolor*) is one of many species recorded in a recent floristic survey of the Middlesex Fells, a unique nature preserve within the Boston metropolitan area. Photo by Nancy Rose.

Inside back cover: This Arboretum specimen of Dahurian birch (*Betula dahurica*, accession 1015-80-A) is of interest for its ornamental traits and its conservation value. Photo by Nancy Rose.

Pink lady's-slipper (*Cypripedium acaule*) flowers and fruits prolifically after fires, taking advantage of the extra sunlight and extra nutrients from the ash.

that collided with coastal New England and Canada. The resulting geological features are a complex of felsic lava hills (including Pine Hill) in the south, and plutonic domes of granite (including Bear Hill) in the north. The middle section of the Fells differs in having an overlay of metasedimentary rock. The southeast corner features a steep scarp along the North Boundary Fault, with panoramic views of the Boston Basin. One of the more intriguing geological features is the Medford Dike, a narrow valley of dark, mafic rock between Pine and Little Pine Hills, and the site of nineteenth-century quarries. The gritty gabbro rock from the quarries is called grus, and was used to line the paths of the Public Garden in Boston. There are also swarms of dark black Jurassic dikes, some of which can be seen in the cut side of Pine Hill along Interstate 93. Evidence of the glacial epochs remains in the form of numerous large erratic boulders, striations on the exposed bedrock, and the thin, stony glacial till soils. These poor soils, along with the steep topography, made farming so difficult that few people made their home there. The main use of the Fells was for timber and firewood, resulting in its forests having been cut over many times by 1894. It is noteworthy that despite this, there are areas that have many trees over 3 feet (0.9 meter) DBH (diameter at breast height), the largest one being a red oak (*Quercus rubra*) at Bellevue Pond with a DBH of 4.8 feet (1.5 meters).

About one quarter of the Fells is water, mainly in the form of reservoirs, which provide drinking water for the surrounding communities. The largest is Spot Pond, a glacial kettle pond of 294 acres, so named in 1631 by Governor Winthrop for its many small islands. This, and several other open and covered reservoirs, are operated by the Massachusetts Water Resources

Authority. The three reservoirs on the western side of the Fells were created out of the large Turkey Swamp before the reservation was set aside, and are owned (along with the adjacent land) by the town of Winchester. All of these reservoirs were included in both the original floristic survey of 1894–1895 and our recent 2003–2011 survey headed by Bryan Hamlin. Most streams in the Fells are small, but Spot Pond Brook had enough drop in elevation to provide water power for many small-scale industries. The Fells falls within the Mystic River watershed, which makes up over half of the Boston Basin Ecoregion. This ecoregion includes the city of Boston, and has had 80% of its land developed. The Fells and Lynn Woods represent the only large blocks of native forest left in this ecoregion, forming isolated islands of natural vegetation in a densely populated area.

The climate is in USDA Plant Hardiness Zone 6a (average annual minimum temperature -5 to -10°F [-20.6 to -23.3°C]), with average annual precipitation around 41 inches (104 centimeters). Climate change is evidenced by increasing temperatures in the Northeast; the Boston area has been warming at a rate of 0.5°F each decade since 1970, which has significantly extended the growing season. Photographic records made during the nine years of this survey support this, documenting increasingly earlier bloom times. Average annual precipitation in the Northeast increased 8% in the twentieth century, mainly occurring in the last forty years. The proximity of Interstate 93 and the densely populated surrounding towns contribute to local air pollution, which can have a particularly negative effect on sensitive lichens. Doug Greene and Elizabeth Kneiper recently surveyed the lichens in the Fells and found 110 taxa, indicating that the forest is doing a good job of purifying the air.


MIKE RYAN

Ridgetop Pitch Pine–Scrub Oak communities are a very common prioirity habitat on rocky summits, especially in the southern portion of the Fells.

A STORIED HISTORY OF BOTANIZING

The Middlesex Fells provides a forest panorama of changing seasons for the thousands of Boston area commuters who drive through it on either Interstate 93 or State Route 28 (the old Andover Turnpike), both of which bisect it. It was on the latter road that William Boott arrived in the 1850s to stay at a hotel on the south end of Spot Pond and become the first to botanize the area. Before it was made into a reservoir, Spot Pond was shallow with a muddy bottom, which is reflected in the greater diversity of aquatic plant taxa Boott collected compared to today. Lorin Dame and Frank Collins would follow in his footsteps

A rocky summit along Rock Circuit Trail in Middlesex Fells, looking northeast to nearby Boston suburbs.

in the 1880s, collecting plants for their *Flora of Middlesex County, Massachusetts.* After them came the fern specialist, George Davenport, whose favorite haunt was Pine Hill in Medford, the home of Elizur Wright, who pioneered the preservation of the Fells.

When the Metropolitan Park System was created in 1894, amateur botanist and landscaper Warren Manning, who worked for the Olmsted company, was given the job of organizing a floral survey of all four reservations. He brought together twenty volunteers to conduct field work and collect plant specimens. Among them, amateur botanist William Rich of Boston was the chief collector in the Fells. The well-respected local botanist Walter Deane was then hired at the end of 1895 to compile a "preliminary" flora from the survey's sightings and specimens. Deane based his 1896 *Flora of the Blue Hills, Middlesex Fells, Stony Brook, and Beaver Brook Reservations of the Metropolitan Parks Commission, Massachusetts* on the sixth edition of *Gray's Manual of Botany*, published in 1890, and consulted with Drs. Fernald and Robinson of Harvard University's Gray Herbarium. For our survey we relied mainly on Haines's 2011 *Flora Novae Angliae* in draft and published form.

In the winter of 1895–1896 Deane helped found the New England Botanical Club (NEBC) in response to the collaboration between amateur and professional botanists, most of whom didn't know each other prior to the survey. The newly formed NEBC herbarium eventually provided a home for the survey vouchers, including over 300 Fells specimens. I am currently engaged in creating a database, including images, of all the survey vouchers through a Museum and Library Services Grant. The specimens will then be linked to archival materials in the library, such as Manning's letters to surveyors and Deane's card file of sightings and specimens. For the current Fells survey over 350 specimens were collected, which will also be deposited in the NEBC herbarium.

In 1917, Nathaniel Kidder, then president of the NEBC, proposed a follow-up survey to the Deane *Flora*. He was unsuccessful in getting support for the project, and so pursued it on his own from 1919 to 1924. Kidder focused on collecting the plants that had been reported in 1896 but hadn't been vouchered with herbarium specimens, and new plants that hadn't been reported. Although he never produced a report of his work, his specimens represent a valuable contribution to our knowledge of the reservation's flora, documenting new arrivals and overlooked plants, and verifying the *Flora* sightings.

RECENT FLORISTIC SURVEYS

Deane's *Flora* reported a high level of biodiversity in the Fells, but a 1996 article by Drayton and Primack indicated an alarming loss of species. The article was based on a centennial study of part of the western Fells, done in the early 1990s by Brian Drayton for his master's degree. In the early 2000s, Bryan Hamlin began to question the validity of the 1996 report, after finding many of the "missing" plants in the area of study. As a result, he began a systematic resurvey of the entire Fells, assisted by Betty Wright, Don Lubin, and others. At an NEBC meeting in 2006, Bryan Hamlin told me that he was working on a new flora of the Fells, and I agreed to help him with the difficult graminoid taxa—the grasses, rushes, and sedges. Over time, the current survey became a community effort among members of the NEBC, with a long list of local botanists contributing their expertise, very much like the original collaboration that led to the formation of the Club.

For his survey, Drayton excluded ferns, graminoids, and aquatic taxa. Comparing the same set of plants from the same area, our survey found 564 taxa (355 native), while Drayton and Primack only reported 331 taxa (244 native) with a "loss" of 155 taxa since the Deane *Flora.* Our survey was able to find 105 of these reportedly lost taxa, 83 of them within their study area. The most likely reason for this large discrepancy was that Drayton's survey consisted mainly of a single person surveying for only 300 to 400 hours over three years, versus our team effort of about 2,000 hours over nine years.

Drayton's work was also hindered because he wasn't allowed to collect specimens, which could lead to misidentifications. A large study of surveying techniques found errors of misidentification averaged about 5%, and that overlooking plants averaged 17%. After examining the Deane *Flora* vouchers, we found about a 4% error rate in misidentification. As stated in our *Rhodora* article, "The level of expertise of the surveyors, the level of teamwork, and man-hours spent surveying all affect accuracy."

For the 1890s survey, Manning defined four frequency categories—common, frequent, occasional, and rare—that the surveyors then reported according to their individual qualitative assessments. In order to create a quantitative measurement of frequency, we divided the Fells into eight approximately equal-sized sectors. Based on the number of sectors in which a plant was found, it was scored as common when found in seven to eight sectors; frequent in five to six; occasional in three to four; and rare in one to two. In order to obtain these data we conducted what were in effect eight mini-surveys. Our examination of Deane's *Flora* and vouchers showed 680 vascular taxa (570 native, 110 non-native) for 1896, while our survey found 868 taxa (563 native, 305 non-native). This comparison of the two survey totals shows a tripling of non-native plants. While there was little net change in native plant numbers, there was a significant change in the composition. One hundred twenty-five native taxa that were reported in 1896 were not found by our survey, while we discovered or reconfirmed 119

BRYAN HAMLIN

The parastic American squawroot was singled out by Deane as being the rarest plant in the Fells. It has since increased significantly in frequency, as we found it in five out of eight sectors.

new native plants. Remarkably, the relative number of plants in each frequency category was very similar for both surveys. This equilibrium in frequency and native plant numbers is indicative of a robust and dynamic ecology that is capable of supporting a high level of native diversity over time, despite the influx of non-native plants. It compares very favorably to other urban areas that have been recently surveyed, such as the Massachusetts towns of Needham and Worcester, which have experienced losses of 24% and 17% of native taxa, respectively, and more closely aligns with the rural flora of the Greater Mount Holyoke Range at 4.5%.

There are over 100 Vernal Pools in the Fells with a great diversity of hydrology, making the Fells a hotspot for this priority habitat.

ECOLOGICAL CONSIDERATIONS

In order to better understand the diversity of the plants we were finding, we also included a survey of the plant communities. This was greatly aided by the descriptions in the 2001 Natural Heritage and Endangered Species Program (NHESP) Classification of the Natural Communities of Massachusetts. To determine which community types existed, various ecological criteria were observed in 100-square-meter (1,076.4-square-foot) plots, including elevation, slope, aspect, hydrology, bedrock, and soils, as well as the presence and abundance of plants occurring there. It was possible to make historical comparisons with the current communities using a 1905 map titled "Forest Plan for Middlesex Fells Reservation, 1896" prepared by Olmsted and Olmsted, which outlined where various woody plant associations had occurred.

Over thirty different habitats were documented in the Fells, ten occurring in wetlands and twenty in the uplands. Nine of these habitat types were priority communities, those which are considered for monitoring and protection by the state. Four of

Nodding ladies'-tresses (*Spiranthes cernua*) varied in abundance from year year during the recent Fells surveys.

these were not previously known to occur in the Boston Basin Ecoregion, and two of them were newly designated during the course of this survey. One of these was Sugar Maple-Oak-Hickory Forest, which is similar to Rich Mesic Forest, and only occurs on the south side of Bear Hill. The most prominent priority habitats were Rocky Summits, Pitch Pine Scrub Oak Communities, and Vernal Pools. Over 100 vernal pools of varying size and hydrology have been identified, making the Fells a hotspot for vernal pools.

The great diversity of habitats in the Fells can be accounted for by the diversity of geology and topography, in turn resulting in a high diversity of plants. Given the loss of land and the changing habitats over time, it is not surprising that there would be a significant change in the composition of the flora. The cessation of logging has allowed the forest to mature, with some areas starting to approach the characteristics found in old growth forest. Within the forest matrix, frequent anthropogenic fires continue to create a patchwork mosaic of different aged successional growth contributing to diversity. These burns have been kept small by the suppression of fires since the 1920s, which, along with increasing rainfall, has led to the overall favoring of mesophytic plants like beech and maple. During our survey a beaver dammed Whitmore Brook, creating a pond and marsh out of a red maple swamp, which resulted in an influx of new plants. Our survey found wetlands plants to be particularly opportunistic in responding to varying water levels and habitat succession.

Studies of urban forests have found that the rarer plants with low population numbers are more susceptible to local extirpation. In the Fells about 60% of the taxa that were rare in 1896 are still extant, and almost half of those have increased in frequency. There are two state-listed rare species and eleven others which are watch-listed as potentially becoming rare in the state. Most of these rarer plants are herbaceous; woody plants are generally more abundant and more persistent. Some of the rare plants are ephemeral in nature, depending on successional habitats, and can come and go in a single season. We observed that orchids like


NANCY ROSE

Wild columbine (*Aquilegia canadensis*) is common in woodlands throughout the eastern United States and Canada, including Middlesex Fells.

nodding ladies'-tresses (*Spiranthes cernua*) that were locally abundant in one year often went dormant and were very scarce the next. Other rare plants are restricted by only growing in habitats that are uncommon in the Fells.

One of the factors that contributed to loss of plant populations was the replacement of the native oak forest around the Winchester Reservoirs with non-native evergreens. Another factor was construction. When Interstate 93 was built through the middle of the Fells in the late 1950s it destroyed a large area that included the only large fen habitat. A less obvious yet important negative factor is fragmentation caused by recreational overuse. There are 36 miles of fire roads and 75 miles of trails in the Fells, with a large proportion of these trails being created by users, resulting in very few large trailless areas. This extensive network of trails is an avenue for invasive plants to become widely established, evidenced by their abundance along the trails.

Invasive vines such as Oriental bittersweet, porcelainberry, and English ivy (pictured here) smother the native herbaceous ground cover and can also climb and overtop trees and shrubs.

One year after it was cleared of English ivy, this area is already beginning to recover as the native ground cover regrows.

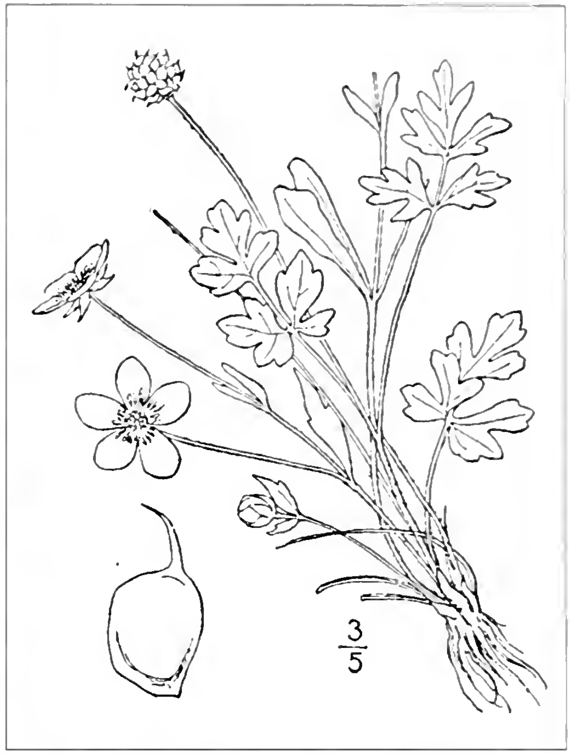

Illustration of early buttercup (*Ranunculus fascicularis*) from *An illustrated flora of the northern United States, Canada, and the British Possessions* by Britton and Brown, 1913. The single small population of early buttercup growing on Bear Hill was crowded out by invasive plants despite efforts to save it.

This is because foot traffic spreads seeds, and birds often use trail openings to travel, depositing seeds along the way.

The Fells is an island surrounded by a cultivated urban area, such that non-native plants are constantly entering from nearby plantings. Some of these plants are highly destructive of habitats, chief among them being vines such as Oriental bittersweet (*Celastrus orbiculatus*), porcelainberry (*Ampelopsis glandulosa* var. *brevipedunculata*), and English ivy (*Hedera helix*), which completely smother all other vegetation. Despite the inroads of invasive plants, the Fells has so far proved to be a robust system that has sustained a high diversity of native plants. The concern we have, though, is that without a significant effort to contain the increasing spread of invasive plants, native diversity may be severely reduced. Already, the locally rare early buttercup (*Ranunculus fascicularis*) has succumbed to invasive plants.

Diseases have also contributed to altering the forest ecology, with chestnut blight reducing American chestnut (*Castanea dentata*)—once a towering forest tree—to sprout growth, and beech bark disease beginning to reduce the fruiting of American beech (*Fagus grandifolia*) trees. The loss of both chestnut and beech fruit has had a negative impact on wildlife. Invasive insects like the hemlock woolly adelgid have also had a huge impact on the forests. Just as at the Arnold Arboretum's Hemlock Hill, these insects have decimated entire groves of mature hemlocks in the Fells, resulting in their replacement with a successional habitat of young sweet (black) birch (*Betula lenta*). On the other hand, the arrival in the Fells of the beneficial beetles (*Galerucella* spp.) that eat purple loosestrife (*Lythrum salicaria*) has helped reverse the advance of this invasive plant, which was dominating wetlands. Although the deer population is relatively small, it still has had a negative effect on native lilies, which are also eaten by the non-native scarlet lily beetle (*Lilioceris lilii*). Other insects that pose potential future threats to the Fells forest include the emerald ash borer (*Agrilus planipennis*) and Asian longhorned beetle (*Anoplophora glabripennis*). Research in biological controls is ongoing and may eventually aid in controlling these highly destructive insects.

THE NEVER-ENDING FLORA

With our current survey of the Fells we have endeavored to make good use of Manning's intention to provide future generations with a long-range understanding of its dynamic flora. The Fells is a constantly changing system in which plants come and go, and for that reason no survey is ever 100% complete. In the year since we concluded the survey, we have found a further 23 taxa, 9 native and 14 non-native. This reflects the reality of overlooking, especially of difficult taxa like the graminoids and hard-to-detect rare plants like the three-lobed violet (*Viola palmata*), which we walked by dozens of times before noticing it. The high number of additional non-native plants we found confirms our observation that these are continuing to arrive at a rapid pace, but the finding of more native plants also supports the existence of a robust mature ecology in equilibrium. While past policies of passive forest management have allowed it to evolve naturally, a more active management would aim to protect sensitive priority habitats, reduce fragmentation through trail closures, and remove invasive plants.

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The Quest for the Hardy Southern Live Oak

Michael S. Dosmann and Anthony S. Aiello

Southern live oaks (*Quercus virginiana*) draped with Spanish moss line the roa at Wormsloe, a historic colonial estate in Savannah, Georgia.

It's no secret that individual plants within a species can vary in appearance—just peruse the range of Japanese maples (*Acer palmatum*) for sale at your local nursery. All belong to a single species, yet show diversity in traits like growth habit, foliage color, and leaf shape. It's also old news that individuals can vary according to provenance (geographic source); winter hardiness is frequently noted as one of those variable physiological traits. Although he was not the first to note this phenomenon, botanist and plant explorer Joseph Hooker provided an early description in1853. In an introductory essay preceding his notes on the flora of New Zealand, he described differences in the hardiness of Himalayan plants, "depending upon the altitude at which they were gathered." Specifically, "some of the seedling Pines whose parents grew at 12,000 feet appear hardy, whilst those of the same species from 10,000 are tender. The common scarlet *Rhododendron* of Nepal and the North-west Himalaya is tender, but seedlings of the same species from Sikkim, whose parents grew at a greater elevation, have proved perfectly hardy." A few years ago, we wrote about C. S. Sargent's interest in acquiring cedar of Lebanon (*Cedrus libani*) germplasm that would prove to be hardy in Boston (Aiello and Dosmann 2007). He succeeded by obtaining seeds from Turkey, and those plants and others from that region have fared notably well in Philadelphia and Boston as well as colder climes, while accessions from other provenances have failed.

The cedar of Lebanon story points out the ongoing importance of plant exploration, a vital component of the missions of our respective arboreta. When adding accessions, we want to capture as much variation as possible within a species, so we often collect from multiple populations within a species' range. This is standard practice for species in our core, or high-priority, collections that are already well adapted to our local Arboretum conditions. However, for species like *C. libani* that are not typically winter hardy in our climate, we must seek specific provenances that may hold hardier populations.

One of those marginally hardy species that has evaded our grasp so far is the southern live oak (*Quercus virginiana*), whose massive, gnarled form—often draped in Spanish moss

(*Tillandsia usneoides*)—conjures up images of the antebellum South. This oak often exceeds 50 feet (15.2 meters) in height, but it is the spread that typically draws our attention. Almost always wider than tall, the colossal sweeping branches of old trees are a marvel. The common name "live oak" refers to the typically evergreen leaves, stiff and shiny on the top, and gray-tomentose on the bottom. However, during particularly cold spells the species may shed some of its leaves and is regarded as brevideciduous. Tolerant of drought as well as soil salinity and salt spray, southern live oak is often categorized as a "tough plant," aside from winter hardiness issues.

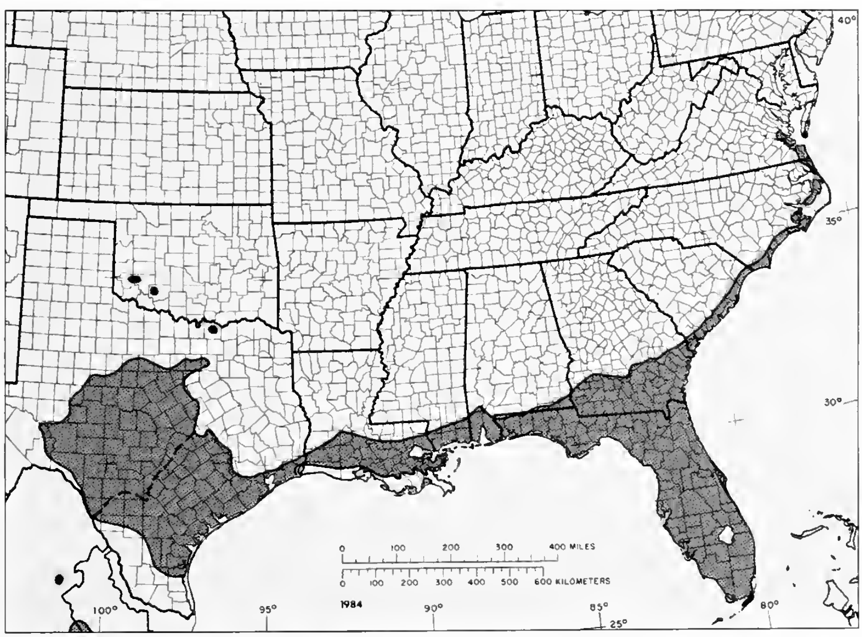
Quercus virginiana has leathery, usually evergreen leaves.

ALL PHOTOS BY THE AUTHORS UNLESS OTHERWISE INDICATED

THE QUEST BEGINS

In 140 years of acquiring and testing species from all over the temperate world, the Arnold Arboretum has never even *attempted* to grow *Q. virginiana*. That the Arboretum had tried—and failed—to establish hardy plants in the collection is one thing, but to never even try? That was a surprise. The situation was similar at the Morris Arboretum, where *Q. virginiana* acorns were received in the mid-1950s as part of the ambitious Michaux Quercetum project. Acorns from several collections germinated and were planted in the oak nursery, but none of these survived to be grown on because, "mortality during the first winter [in the nursery] was extremely high, and no trees survived the second winter" (Santamour 1960). With this history at both arboreta, we determined that it would be worth the effort to document and collect from trees that, like the special provenance of *C. libani* in Turkey, might be hardy for us in our respective regions.

Southern live oak is native to the southeastern United States, with a range that extends from central Texas and a few populations in southwest Oklahoma, all along the Gulf Coast and Florida peninsula, turning northward to follow the coasts of Georgia, South Carolina, North Carolina, and southern Virginia. Flint (1997) noted that while the species' useful range as a landscape plant is USDA Zone 8b (average annual minimum temperature 15 to 20°F [-9.4 to -6.7°C]), it can tolerate colder extremes like Zone 7b (average annual minimum temperature 5 to 10°F [-15 to -12.2°C]) but is unlikely to attain its full size and landscape value because of ice and snow damage. Recent research from



The native range of _Quercus virginiana_, from _Silvics of North America_, USDA Handbook 654.

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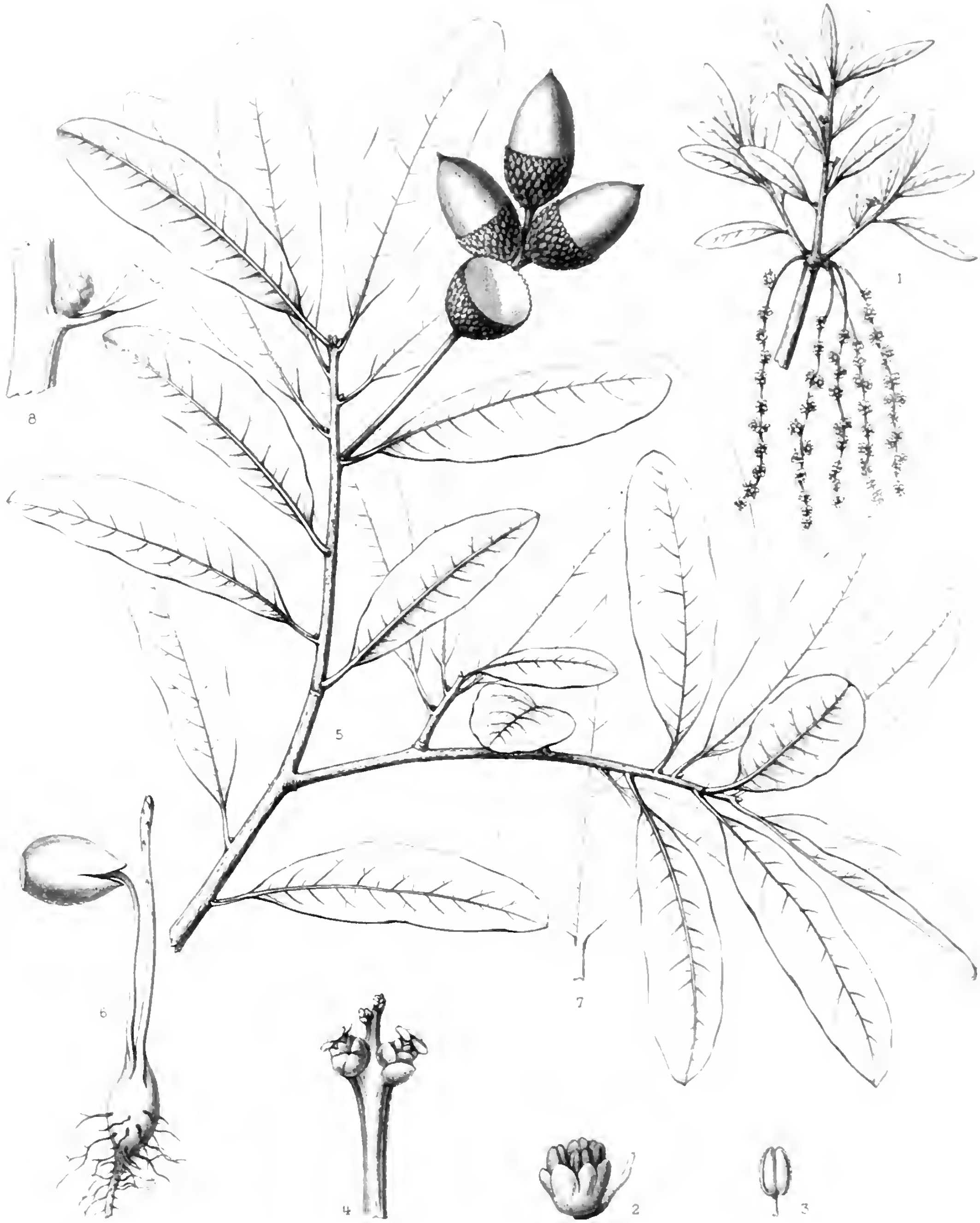


C. E. Faxon del.

Rapine sc.

QUERCUS VIRGINIANA, Mill.

A. Riocreux direx.

Imp. J. Taneur Paris.

Botanical illustration drawn by Charles Faxon, from *The Silva of North America* by Charles Sprague Sargent.

the lab of Jeannine Cavender-Bares at the University of Minnesota has yielded interesting information on its ecology. Her lab found that *Q. virginiana,* like many other temperate species, varies in leaf and stem hardiness as a function of latitude: the more northern populations possess greater hardiness (Cavender-Bares 2007; Cavender-Bares et al. 2011; Koehler et al. 2012). In these studies, the lowest temperature that plants were exposed to (and survived) was 14°F (-10°C), which is still warmer than the average annual minimum temperatures found in Philadelphia (Zone 7a, 0 to 5°F [-17.8 to -15°C]) or Boston (Zone 6b, -5 to 0°F [-20.6 to -17.8°C]).

We feel there is potential to grow this species in our collections, or at least make the attempt. For one, our average annual minimum temperatures have risen because of climate change and urban heat island effects (see textbox). Although this hardly places us in the banana belt, it warrants an attempt to grow *Q. virginiana.* Also, the northernmost population sampled by Cavender-Bares was from Goose Creek State Park, North Carolina, where notably cold temperatures have occurred (down to 9°F [-12.8°C] in 1904). Surely if these populations survived that weather event, they likely possess greater hardiness than was indicated in experimental testing. Lastly, our review of various checklists, atlases, and other resources revealed that natural populations could be found around Norfolk and Virginia Beach, Virginia, (particularly First Landing State Park), as well as a few points northward—over 90 miles north of the Goose Creek sampling sites.

We wanted to collect germplasm from the most northerly natural populations in Virginia. Because some of these populations are near (or even within) urban areas, it is especially important to collect acorns and grow the seedlings elsewhere in case these populations become threatened by development in the future. During our planning, we also learned of notable trees that were either remnant natural populations or planted specimens that had survived frigid winters. These included old specimen trees growing in Hampton and Williamsburg (where it reached -7°F [-21.7°C] in 1985), and Richmond (-12°F [-24.4°C] in 1940). Even if these trees were planted (and therefore did not represent a wild source), their potential hardiness makes them valuable. And for a few of them, their extreme age suggests they were derived from now-extirpated local populations.

TO RICHMOND

Our short trip (October 20th to 24th, 2012) to explore the Eastern Shore of Virginia started in Richmond and finished in Virginia Beach. Our first collection site was the campus of the University of Richmond, home of the Spiders. Upon arrival, we were impressed by the well groomed landscape, despite having hosted a football game the day before (they beat James

Immature (green) and fully ripe (brown) acorns of southern live oak.

Tony Aiello measures the diameter of one of three mature southern live oak specimens growing in Bryan Park.

Madison University, 35 to 29). We commented that either the students were notably well behaved, or the landscape services department worked through the evening hours.

Using directions provided by Professor of Biology John Hayden, we were able to easily find the various specimens, many of which had been planted in the last few decades. Although we had seen the occasional *Q. virginiana* before, this site gave us our first chance to really observe the species in depth. Our first two collections were from trees growing near Westhampton Lake. The first tree, rounded and spreading in form, was about 15 feet (4.6 meters) tall and twice as wide; we estimated that it had been growing in that location for 10 to 15 years. And it was loaded with acorns, most with bright yellowish green nuts and tawny brown caps. However, a few had started to turn the typical mature color, a rich burgundy-brown. The branches were dense, with short internodes, and thickly set with leathery, oblong to oval leaves. Considering their form and (brevi)evergreenness, we thought they would make great screens. As was our protocol for the entire trip, we gathered germplasm in the form of acorns, made herbarium vouchers from cut twigs (complete with the acorns), and of course jotted down copious collection details that pertained to the trees as well as the local conditions and environment. The second collection was from a nearby tree, smaller and younger than the first, but similar to another six growing nearby. Undoubtedly the campus was trying to establish a grove of these trees in this area. Before leaving the University, we located and collected from two trees, older than the first, which were growing near a dining hall.

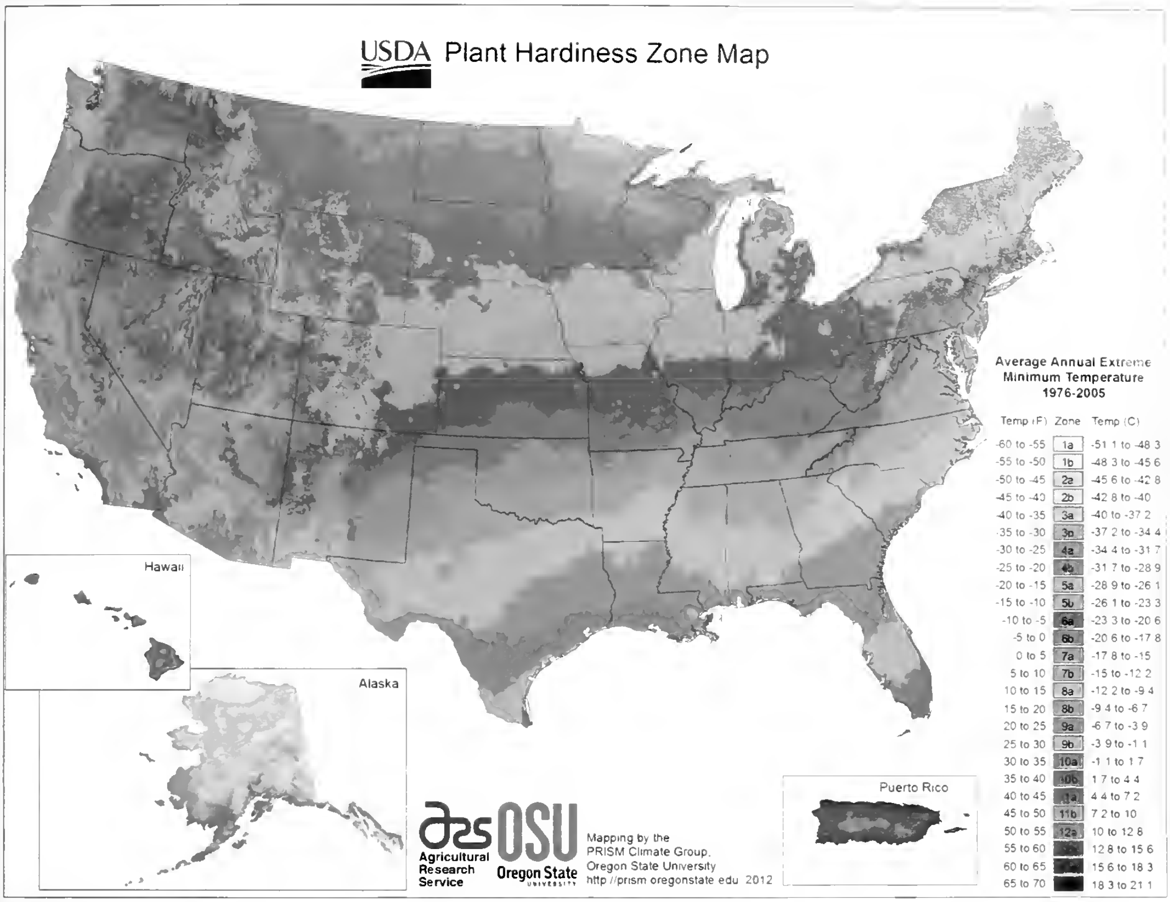
Changes in Plant Hardiness Zones

IN JANUARY 2012, the United States Department of Agriculture unveiled its new Plant Hardiness Zone Map (PHZM) (http://planthardiness.ars.usda.gov/PHZMWeb/), a development that was long anticipated by gardeners and researchers. Like its earlier incarnations, the new PHZM provides guidelines to predict a region's average annual minimum temperature, a vital statistic in determining whether or not a plant may survive the winter in a particular area. Last updated in 1990, the map now features a number of significant features. For one, it has gained interactivity through a Geographic Information System (GIS) that enables users to zoom in at regional and state levels; it also has a tool to identify a zone by zip code. Data quantity and quality represent marked improvement in the map's reliability— the new PHZM utilizes 30 years (1976–2005) and a wider geographic sampling of weather station data. (In comparison, the 1990 PHZM used data from only a 13-year period, 1974–1986, and fewer stations.)

Compared with the 1990 version, zone boundaries in the new edition have shifted in many areas, typically about a half-zone warmer from their previous designation (although some have shifted to a colder zone). Some of the changes are the result of the new, more sophisticated mapping methods and greater numbers of station observations, which has greatly improved accuracy, especially in mountainous regions. Additionally, in urban and suburban regions, the cities themselves can greatly influence temperature, resulting in heat islands that make them significantly warmer than their rural surroundings.

The data solidify the reality of climate change, suggesting even greater unpredictability with regard to future weather patterns and environmental conditions. The implications are significant not just for the natural world and those who study it, but also for gardeners. Warmer temperatures in the colder months can lead to further pest and disease outbreaks, as both are better able to survive in mild winters. Plants at the southern limits of their adaptability may eventually be negatively impacted to the point where they are useful solely at more northern sites.

On the positive side, warmer zones allow for an expanded palette of plants that gardeners can reliably grow. For instance, in Philadelphia there is now a better chance of growing traditional southern favorites such as crape myrtle (*Lagerstroemia* spp.), southern magnolia (*Magnolia grandiflora*), and Japanese camellia (*Camellia japonica*). In New England, the change in hardiness may

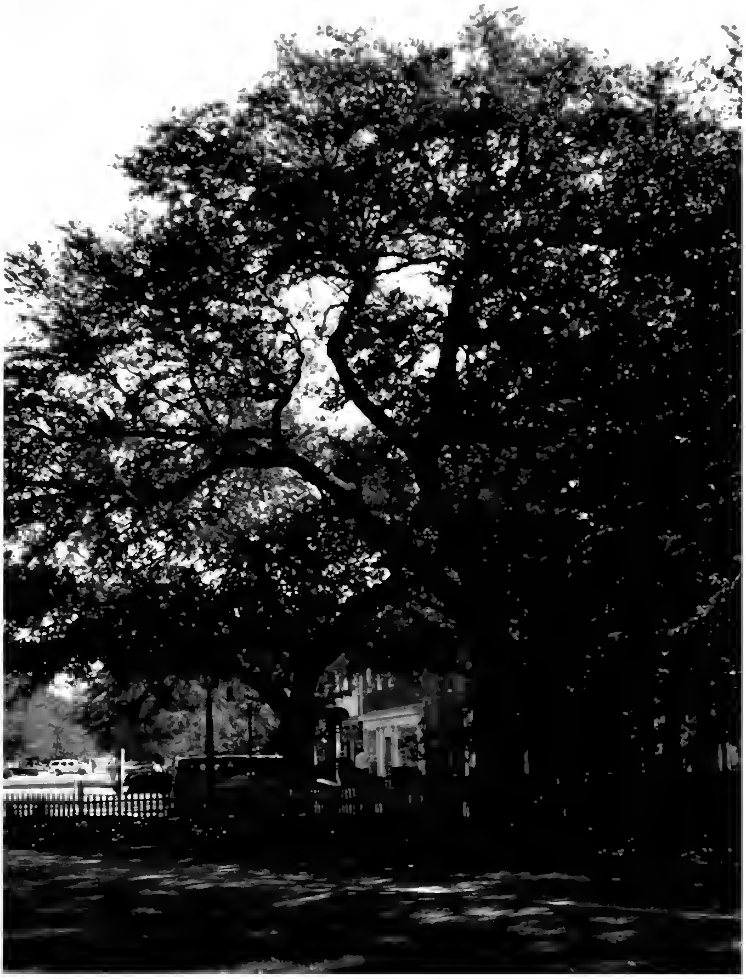


allow gardeners to reliably grow *Stachyurus praecox* and *Chimonanthus praecox*, which are currently hardy only in protected microclimates. And, if we are lucky, Philadelphia and Boston can add *Quercus virginiana* to that list.

Our next destination—after an amazing lunch at Buz and Ned's BBQ—was Bryan Park, a historic Richmond landscape founded in 1910. We expected to find small, rounded trees similar to those we had found at the University earlier in the morning. However, what we did find were three very large individuals, just down the hill from the Gatekeeper's House on the park's northeast side. Heights ranged from 30 to 40 feet (9.1 to 12.2 meters); each was rounded, usually twice as wide as tall, and with gnarled, twisting stems and branches. Only two of the trees (with dbh values of 35 and 39 inches [89 and 99 centimeters], respectively) bore acorns. Although we do not have any records to confirm this, based on their size we assume that the trees date back to the founding of Bryan Park and approach the 100 year mark. If so, they certainly would have survived the frigid winter of 1940.

TO WILLIAMSBURG

We departed Richmond in the early morning of October 22nd, and by 9:00 a.m. arrived at our next destination: the College of William and Mary in Williamsburg. Beth Chambers, curator of William and Mary's herbarium, was a great help to our efforts. Prior to our arrival,



Two mature southern live oaks east of the Wren Building on the College of William and Mary campus.

she scouted the numerous southern live oaks on campus, and even collected a few acorns in case there were none to be had by the time we arrived. She also accompanied us during collecting, providing assistance as well as anecdotes about the trees and buildings of this historic campus and neighboring colonial village. There were numerous southern live oaks planted on the campus, and their history dates to even before the founding of the university in 1693. The Corner Live Oak, a famous tree on campus, had served as a prominent boundary marker until its removal in 1943. Its age was estimated to be about 300 years at that time. Prior to its removal, acorns were collected and the progeny were planted around campus, including a prominent line along Landrum Drive (Mathes 1992).

The southern live oak legacy is also preserved in an 1836 watercolor of the Wren Building, a prominent campus edifice named after the famous architect Sir Christopher Wren, who *may* have designed it. When we arrived at the Wren Building, we were greeted by a towering *Q. virginiana* on the southeast corner. Although it had few accessible acorns, just to the east were several other large trees, the tallest nearly 40 feet (12.2 meters) in height. We collected seeds and vouchers from three of these specimens, two of which appear in a photograph from about 1875 (http://www.history.org/foundation/journal/Winter11/old_williamsburg/#3). A number of trees also grew off campus, in the Colonial Williamsburg section of town. We made two additional collections from these town trees, and also made the interesting discovery of the Compton oak, *Quercus × comptoniae*, a hybrid between *Q. virginiana* and *Q. lyrata* (overcup oak). We ascertained its identity from Terry Thon, a basket maker for Colonial Williamsburg, who has been routinely collecting acorns from it for years. This tree was an impressive specimen with a dbh of 60 inches (152.4 centimeters) and a spread of 100 feet (30.5 meters), and we were anxious to make a collection, too. [Editor's note: We'll have more on the Compton oak in a future issue of *Arnoldia*.]

THE OAKS OF FORT MONROE

During the trip's planning stage, Michael Dosmann spoke to Christopher Beagan of the National Park Service's (NPS) Olmsted Center for Landscape Preservation. Christopher described the amazing oaks of Fort Monroe and insisted that we visit this population and others near Hampton. He shared a few photos of the trees and we were instantly interested. He put us in touch with one of his NPS colleagues, Eola Dance, who is the Chief of Visitor Services and

A grove of old southern live oaks at the edge of the Parade Ground of Fort Monroe.

The moat surrounding Fort Monroe contributed to its defenses; mature southern live oaks can be seen growing within the fort's interior, above and to the right of the casement.

Resources Management at the Fort. We were thankful for the lead.

Perched at the ocean's edge, the Fort has a rich history that dates to the early seventeenth century. It had been occupied by the military until its recent decommissioning in 2011, and it is now a National Monument. The massive six-sided stone structure is the largest of its kind in North America: 63 acres of land surrounded by walls and an impressive moat. Construction of the current Fort took 15 years to complete and the final phase (finished in 1843) was overseen by Robert E. Lee. In an ironic twist, such was its fortitude that it was never lost to the Confederacy.

We arrived in the late afternoon of the 22nd to meet Eola, who enthusiastically showed us around the facility and explained some of its fascinating history. We also returned on the morning of the 24th to visit with her, as well as Joshua Gillespie and Robert Kelly of the Fort Monroe Authority. Inside the buttressed edifice we found a composite of former army barracks, period officer quarters, office and training facilities, storage buildings, a chapel, and a museum, as well as nearly 350 southern live oak specimens scattered throughout. Perhaps the most impressive is a large grove that grows along the south and west edge of the interior parade ground. Some trees stood as lone sentries, while others grew in small groups, sometimes arching over the sidewalks and defying gravity. Most were no taller than 35 to 40 feet (10.7 to 12.2 meters), and all had dramatic, ethereal forms, the result of decades and even centuries of difficult environmental conditions including drought, intense heat, and salt spray (even inside the fort's walls). No doubt, the grandest of these was the Algernourne Oak, a leviathan estimated to be over 450 years old. This tree has a basal diameter of 90 inches (228.6 centimeters), with two massive leaders diverging about 3 feet (0.9 meters) above the ground. True to the species' form, the tree's height is around 60 feet (18.3 meters), but its spread is nearly 100 feet (30.5 meters).

The acorns on all the oaks at Fort Monroe were few and far between, so we collected only herbarium vouchers from this representative population. We assumed that these trees produced few acorns because of the exposed, hot and dry location, and the droughty summer. That same exposed and hot nature of the fort is probably the reason these trees still exist. People needed shade, and because few other trees were capable of growing in such an environment, this remnant natural population was left in place and even allowed to regenerate (perhaps with a bit of assistance from the local inhabitants). Standing

Michael Dosmann at the base of the Algernourne Oak at Fort Monroe.

The Algernourne Oak at Fort Monroe is estimated to be over 450 years old.

in the parade ground, we imagined ourselves dressed in full uniform, performing drills and marching for hours under the hot sun and dry, salty breeze—those trees would be considered sacred! The trees were in remarkably good condition considering their age, size, and the heavy impact of human activities on the site. Many of them showed the marks of time but they were mostly healthy and growing well, a testament to the resilience of southern live oaks.

Tony Aiello stands near a cluster of *Osmanthus americanus* along the namesake Osmanthus Trail at First Landing State Park.

FIRST LANDING

We dedicated the 23rd to surveying the flora of First Landing State Park, which lies on Cape Henry between Norfolk and Virginia Beach. Its current name, changed from Seashore State Park in 1997, acknowledges this site as the location where the Virginia Company first landed in 1607 prior to settling Jamestown. The park covers about 3,000 acres, and comprises eight upland plant community types that range from dune crests to mesic forests (Clampitt 1991). Our initial foray was into the mesic forests where several of our non-oak collecting targets were to be found: devilwood (*Osmanthus americanus*) and swamp bay (*Persea palustris*). Like southern live oak, these two species of shrubs or small trees are near or at their northernmost ranges in Virginia. And, for reasons similar to our quest for hardy southern live oak germplasm, we were anxious to locate and collect from these species.

MIKE HOGAN, HTTPS://IT.AUBURN.EDU/SFWS/SAMUELSON/DENDROLOGY

Devilwood (*Osmanthus americanus*) bears sweetly fragrant flowers in the spring.

Finding them was quite easy thanks to our earlier planning conversations with Erik Molleen of the Virginia Department of Conservation and Recreation; the fact that there was an Osmanthus Trail in the park was also helpful. *Osmanthus americanus* specimens were numerous and scattered throughout the understory. They became easy to identify from a distance because their glossy green leaves are arranged oppositely, as with other members of the olive family (Oleaceae). At the Arnold Arboretum, this species has proven to be quite a challenge to cultivate because of cold hardiness issues. One clone, a cultivated lineage from Spring Grove Cemetery in Cincinnati, Ohio, has been reliably hardy in Boston. Likewise a plant at the Morris Arboretum has survived but not thrived since it was received from a local nursery in 1962. Wild-provenance material has long been a target because of the species' botanical and ornamental appeal. Its broadleaved evergreen foliage provides winter interest, and the small, creamy white flowers in spring are a delight to the nose; their mellic scent beckons from great distances. We were able to collect fruits—bright green drupes at this stage—from many trees in the woodland.

Persea palustris also dotted the understory, and, like devilwood, has large, elliptic, evergreen


COURTESY OF BOBBY HATTAWAY, WWW.

Mini-avocados? Immature fruits of *Persea palustris* bear a slight resemblance to their large-fruited relative, the avocado (*Persea americana*).

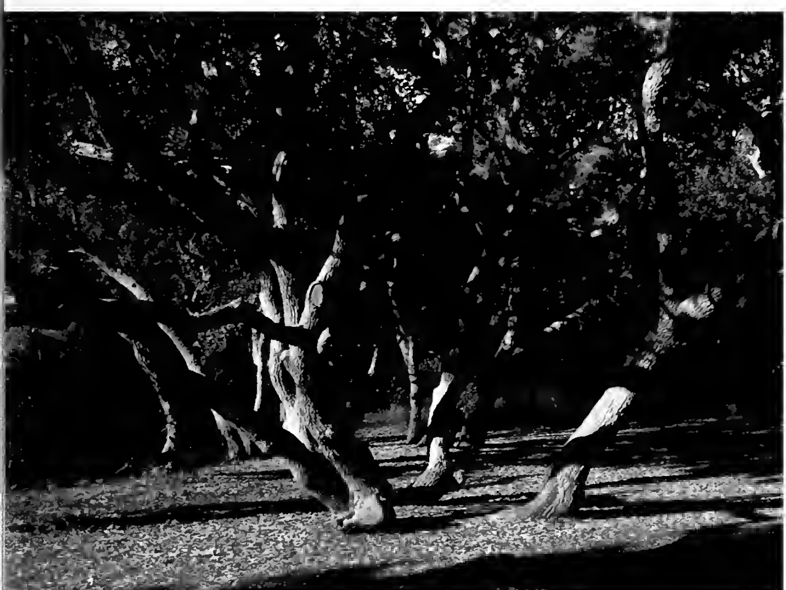
The ghostly white Indian pipe (*Monotropa uniflora*) blooms above the fallen cones of loblolly pine (*Pinus taeda*).

leaves. However, the leaves are coarser in texture and borne alternately in this member of the laurel family (Lauraceae), and the fruits (also drupes) were an eye-catching purplish blue at this stage. With only a bit of imagination, it is easy to see the kinship to *Persea americana*, the avocado. However, with drupes less than ½ inch long, they wouldn't yield much guacamole.

Many other plant species caught our eyes. Sand hickory (*Carya pallida*) grew in and along the higher ridges. This species was also on our target list, but there were very few fruits to be found; those we did stumble upon were on the ground and of poor quality. While scouring the ground, it was a treat to see Indian pipe (*Monotropa uniflora*), the nodding white flowers and stems appearing like dancing apparitions among the pine cones. Looking up, we noticed many leaves of sourwood (*Oxydendrum arboreum*) at their peak for autumn color, the brilliant reds and oranges echoed in the near-spent needles of bald cypress (*Taxodium distichum*). These bald cypress trees were impressive, conjuring up images of great swamps, and yet we were only a few hundred meters from sand dunes and the ocean (a reminder of how quickly landscapes change). Because the water level was down considerably, their buttressed trunks and knees were exposed to reveal an amazing network of lignified stalagmites. Throughout the woodland landscape, Spanish moss draped across the limbs and branches like overloaded Christmas tree tinsel. As with southern live oak and devilwood, southeast Virginia marks the northern edge of the native range for this rootless member of the pineapple family (Bromeliaceae).

After a brief lunch, we explored the shoreline of First Landing, a strip considerably different than what we saw in the morning. The morning site was lush and diverse, but this sandy strand was quite the opposite. Oaks—primarily

The water table was down considerably at First Landing State Park, exposing the buttressed trunks and knees of the bald cypress (*Taxodium distichum*).



Multistemmed and low branching *Quercus virginiana* at First Landing State Park.

southern live oak plus some bluejack oak (*Q. incana*)—dominated this landscape to create a band of dense vegetation that was pruned by the salt-laden winds into interesting forms and habits. As we had seen with the cultivated plants, the live oak trees were wider than tall (but rarely over 20 feet [6.1 meters] in height) and frequently had multiple stems and a low-branching form. One of the larger trees we found had three stems measuring 12.5, 17, and 21 inches (31.8, 43.2, and 53.3 centimeters) in diameter at 12 inches (30.5 centimeters) above the ground. Despite the stressful environment, trees were healthy and there was noticeable regeneration of young seedlings in the understory, which is always a good sign. Rather than focus on individual trees at this site, we maximized the amount of genetic variation in the collection by gathering acorns from 12 trees. Some trees were so fecund and at perfect ripeness that we could easily shake the branch and scores of the nuts would drop from their caps.

NEXT STEPS

Although the fieldwork is complete, the data are in the databases, and the herbarium specimens are mounted, much work remains ahead of us. Each of our institutions is hard at work germinating the seeds from the various collections made on the trip—twelve separate *Q. virginiana* collections, plus one each of the *Persea*, *Osmanthus*, and *Q.* × *comptoniae*. We plan to try several different methods to successfully coax the oaks into cultivation. For starters, we captured a wide swath of variation during our trip—one never knows just which germinating seedlings from which populations will be the ones to survive. Because young plants are less cold hardy than older ones, we plan to hold some seedlings in containers for a few years before planting them into nurseries. And, because each of our arboreta has microclimates that are warmer than our nursery areas, we also plan to plant some young plants directly into those microclimates, skipping the nursery altogether. For marginal species such as these, success often is achieved by those who hedge their bets.

Southern live oaks and sea grasses growing along the dunes of First Landing State Park.

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Mark Catesby: Pioneering Naturalist, Artist, and Horticulturist

David Yih

This April marks the 301st anniversary of naturalist Mark Catesby's arrival in Williamsburg, Virginia, to begin the first of two exploratory sojourns he would make in the American colonies. A dabbler in watercolors from a family of provincial English lawyers, Catesby was twenty-nine when he stepped off the ship to begin the adventure that would determine the course of his life and culminate in his monumental work on North American flora and fauna, *The Natural History of Carolina, Florida, and the Bahama Islands.* The lavishly illustrated work would be hailed in the *Philosophical Transactions* of the Royal Society of London as "the most magnificent work ... since the art of printing has been discovered" (Mortimer 1748). It would stand as a benchmark in American natural history throughout the eighteenth century and be deemed "the most splendid of its kind that England had ever produced" (Pulteney 1790).

Though little documentation of Catesby's early life exists, it is generally supposed that his interest in the natural world had been stimulated by his uncle Nicholas Jekyll, an avid gardener who introduced the young man to John Ray, "the foremost English naturalist of the late seventeenth century ... whose systems would dominate English natural history until the adoption of Linnaean classification" (Frick 1974). The best glimpse into Catesby's preoccupations as he first arrived in America to visit his sister's family and have a look around comes in his own words:

> "... my Curiosity was such, that not being content with contemplating the Products of our own Country, I soon imbibed a passionate Desire of viewing as well the Animal as Vegetable Productions in their Native Countries; which were Strangers to England. Virginia was the Place (I having Relations there) suited most with my Convenience to go to, where I arriv'd the 23d. of April 1712. I thought then so little of prosecuting a Design of the Nature of this Work, that in the Seven Years I resided in that Country, (I am ashamed to own it) I chiefly gratified my Inclination in observing and admiring the various Productions of those Countries, only sending from thence some dried Specimens of Plants and some of the most Specious of them in Tubs of Earth, at the Request of some curious Friends ..." (Catesby 1731)

Perhaps Catesby could afford to be a bit modest by the time he wrote these prefatory words of his celebrated magnum opus. In reality, when he returned to England after seven years in the colonies, he "brought with him an extensive knowledge of New World flora and fauna as well as an impressive cache of drawings of animals and plants never before seen by English naturalists" (Meyers and Pritchard 1998). These were sufficient to attract the interest of the eminent English botanist William Sherard, who happened to be in the process of organizing sponsors to send a naturalist across the Atlantic to explore and document the living wonders of America, especially those that might have scientific, economic, ornamental, or curative value. Whom to send on this mission was an issue yet to be resolved. But an ability to render accurate images of the new finds would be a significant qualification. Impressed by Catesby's work, Sherard wrote to an acquaintance, "He designs and paints in water colours to perfection."

Catesby got the job, and with the support of a dozen backers—including a number of aristocrats as well as the President and several members of the Royal Society—set out on his second journey, arriving in Charleston, South Carolina, in 1722. With the funds and trust that were now invested in him, he threw himself into

The Mock-Bird and Dogwood Tree
Northern mockingbird (*Mimus polyglottos*) and flowering dogwood (*Cornus florida*)

A Note About the Images

THE IMAGES in this article were scanned from the Arnold Arboretum's copy of Catesby's *Natural History of Carolina, Florida, and the Bahama Islands.* Our copy is the revised edition published in 1754. It was purchased for $50.00 in February 1912 with funds provided by Francis Skinner, a friend and neighbor of Charles Sprague Sargent. This copy had previously been in the library of Venetian botanist Francesco Rizzo Patarol.

Catesby's book used Latin polynomials (multi-word descriptive phrases) to identify the plants and animals, the accepted practice before Linnaeus's system of binomial plant names became widely established. Linnaean binomials were added to the third edition (1771), and over the years researchers have provided more accurate identification and nomenclature. For the images that appear in this article, the first line of each caption gives the common names (or the first part of the Latin polynomial if listed only that way) as they appear in Catesby. The second line provides the modern common and scientific names from Reveal (2012).

his work, resolving never to visit the same area twice during the same season. The frequent clamoring of his impatient backers for specimens sometimes hampered his efforts at what he saw as the main thing to be accomplished: an illustrated record of the plants and wildlife of America. But he persevered and for four years ranged from coastal plains to Appalachians and from the Carolinas south through Georgia, Florida, and the Bahamas, collecting, documenting, and painting as he went.

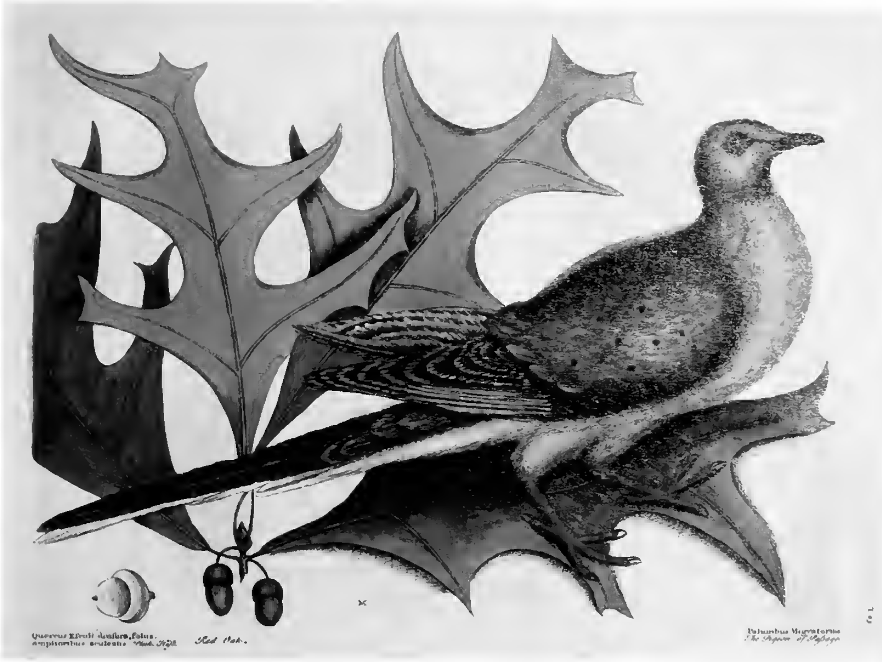
Upon his return to England in 1726, Catesby took a job as a nursery horticulturist and began work on the great book he envisioned. The project would take more than twenty years to complete. And he would have to publish it himself. In a practice common at the time, Catesby solicited subscribers by issuing a prospectus describing the proposed publication and his qualifications for undertaking it. Subscribers would make advance payments, and these would help defray the costs of producing the books. Catesby gave persuasive evidence of the worthiness of his project by listing in the prospectus the names of the twelve eminent men who had sponsored his second trip and by publicly exhibiting the drawings and watercolors he had brought with him from the colonies. Ultimately, 155 persons and institutions signed on, enough to set the project in motion.

In order for the illustrations to be printed, they would have to be engraved into copper

The Blue Bird and *Smilax non spinosa, humilis*
Eastern bluebird (*Sialia sialis*) and sarsaparilla vine (*Smilax pumila*)

The Globe-Fish and *Cornus, foliis Salicis Laureae acuminatis* (upper) and *Phaseolus minor lactescens flore purpureo* (lower)

Checkered pufferfish (*Sphoeroides testudineus*), lancewood (*Nectandra coriacea*), and red milk-pea (*Galactia rudolphioides*)



The Pigeon of Passage and the Red Oak
Passenger pigeon (*Ectopistes migratorius*) and turkey oak (*Quercus laevis*)

plates. Catesby had hoped to have the work done by the expert engravers of Amsterdam or Paris, but given the number of plates involved—220 would grace the finished work—the expense proved prohibitive. Undeterred, he studied the technique of etching with Joseph Goupy, a French printmaker and art instructor then living in England, and proceeded to etch all of the plates himself. He published the work in installments of twenty plates with accompanying bilingual English–French text. Sherard supplied the Latin polynomials, which were the brief descriptive phrases used as species names before Linnaeus' binomial (genus + specific epithet) system came into general use. Upon the completion of each new segment, Catesby presented it to the Royal Society, which was, itself, a subscriber. When he presented the fifth installment in 1732, the one hundred plates that would comprise the first volume of the two-volume work were finished. Within a few months, Catesby was formally nominated and duly elected a Fellow of the Royal Society.

The publication of Catesby's *Natural History*, the first illustrated account of North American flora and fauna, was ultimately completed in 1747 with the addition of the twenty-plate appendix to the second volume. (The title page of the first edition gives the publication date as 1731, so citations often indicate that year rather than 1747.) The first volume had been dedicated to the wife of England's King George II, Queen Caroline, for whom Carolina was named. Queen Caroline having now died, Catesby dedicated Volume II to another avid gardener and patroness, Princess Augusta, wife of Frederick, Prince of Wales. The gardens at the couple's country retreat would later form the basis of the Royal Botanic Gardens at Kew, founded in 1760. Catesby himself survived the completion of his *Natural History* by only two years. A revised edition was published posthumously, in 1754, and a third edition, providing Linnaean binomials for the species, came out in 1771.

As set forth on its title page, the *Natural History* presents examples of "*... Birds, Beasts, Fishes, Insects, and Plants: Particularly the Forest-Trees, Shrubs, and Other Plants, Not Hitherto Described, or Very Incorrectly Figured by Authors ...*" The first known depictions of a succession of eels, butterflies, and frogs leap, flutter, and writhe from the pages, together with snakes of all stripes and birds of all feathers. The ghost of the passenger pigeon looks out from its page. The species was still so numerous when Catesby encountered it that flocks would "break down the limbs of Oaks with their weight" (they were prodigious consumers of acorns, he notes) "and leave their Dung some Inches thick under the Trees they roost on." (Catesby 1731) Catesby's 111 bird images have led to a perception of him as a kind of overshadowed precursor of Audubon, yet the bulk of what is portrayed in the work belongs to the plant kingdom: 171 species. Richard Howard (director of the Arnold Arboretum from 1954 to 1977) and George Staples were able to

The Cacao Tree
Cacao (***Theobroma cacao***)

loba), cucumbertree magnolia (*Magnolia acuminata*), umbrella magnolia (*Magnolia tripetala*), sourwood (*Oxydendrum arboreum*), blackjack oak (*Quercus marilandica*), and water tupelo (*Nyssa aquatica*). Though not cold-hardy enough to be grown in New England, another plant having a Catesby illustration as its type deserves mention: the cacao tree (*Theobroma cacao*), whose seeds are the source of chocolate.

As if attempting an accounting of the flora and fauna of a large swath of the continent were not enough, Catesby includes in the *Natural History* a lengthy essay, "An Account of Carolina and the Bahama Islands," in which he discusses the region's climate, soils, habitats, hydrology and geology—including notable fossil finds—as well as Native American culture. He also enumerates the crops grown in the colonial southeast, assessing their suitability and economic potential there, and provides extensively annotated lists of many wild species not illustrated. For good measure, Catesby records recipes for making caviar and pickled sturgeon and describes the process of making tar from pine trees.

Later critics have found flaws in Catesby's work. He sometimes interpreted the differing appearances of juvenile and adult birds as representing members of different species. And though his depictions were broadly accurate, they lacked accuracy in finer details. The work of G. D. Ehret, the botanical illustrator who contributed three illustrations to the *Natural History*, shows a greater attention to details such as venation, as compared with Catesby's relatively stylized renditions. In addition, some inaccuracies resulted from the direct transfer of drawings onto the copper plates. Because printing reverses the image engraved on the plate, creating a mirror image,

match modern scientific names to all but two species (Howard and Staples 1983). They also noted that "Catesby's plates appear to be the types of twenty-five recognized [plant] taxa, of which twenty-one were described by Linnaeus and four by subsequent authors." (A "type" is one particular exemplar that embodies the defining characteristics of a taxon and is permanently associated with it; in botany, a type may consist of either an herbarium specimen or an illustration.)

Specimens of several taxa on Catesby's type list currently grow in the Arnold Arboretum's collections, including pawpaw (*Asimina tri-*

The Painted Finch and the Loblolly Tree
Painted bunting (*Passerina ciris*) and loblolly bay (*Gordonia lasianthus*)

The Blue Gross-beak and the Sweet Flowering Bay
Blue grosbeak (*Passerina caerulea*) and sweetbay magnolia (*Magnolia virginiana*)

The Blueish Green Snake and *Frutex baccifer, verticillatus*
Rough green snake (*Opheodrys aestivus*) and American beautyberry (*Callicarpa americana*)

the direction of twist shown in the twining of Catesby's sweet potato plant (*Ipomoea batatas*) is incorrect. Catesby himself recognized that his artistic skills were limited by his lack of expertise in perspective but felt that his flat depictions were sufficient for the purpose of delineating species.

In time, his work was superseded by the achievements of later generations, and Catesby's renown faded. "After the American Revolution, interest in Catesby's work, as with most things American, waned in England. And as the scientific community became increasingly specialized,... Catesby's generalist approach fell into disfavor. By the time John James Audubon set off to paint in South Carolina nearly a century later, Catesby had been almost forgotten." (Amacker)

In recent decades, however, a new appreciation of Catesby's contribution has emerged. With the perspective of two-and-a-half centuries, it has become clear that Catesby's work was innovative and ahead of its time. He broke from the stilted bird profiles typical of the times to include dynamic images of birds in motion. The bald eagle in full swoop, bearing down upon its prey in the very first plate is an example. He was the first to depict birds against botanical backgrounds. More importantly, in choosing these backgrounds, he made a conscious effort to depict ecological relationships, frequently showing birds with the plants on which they feed or in which they nest. His texts go beyond describing morphology to reveal behavioral and ecological characteristics. In the case of birds, he often commented on aspects of nest-building, feeding, and migratory behaviors. He authored the first scientific paper (Catesby 1746-7) to accurately address the phenomenon of bird migration (earlier theories had birds hibernating in caves or under water during the winter months). For these reasons, and in consideration of the many new bird species he brought to light, Catesby has been called the founder of American ornithology (Frick 1974).

Apart from his contributions to natural history, Catesby, throughout his career, maintained an active presence in transatlantic horticultural affairs, participating not only in the importing of interesting American plants into Europe, but in the adoption of useful exotic crops in the colonies, and the transfer of plants among the colonies. His last work, the *Hortus Britanno-Americanus*, published posthumously in 1763, became part of a movement embraced by British gardeners who planted "American gardens"—naturalistic "wilderness" plantings designed to evoke, albeit in a carefully controlled manner, the wildness of the American continent. "Catesby himself ... asserted that, in the half-century in which he was active, more plants were imported into England from the British colonies in North America than during the previous one thousand years from all other parts of the world." (O'Malley 1998)

The Yellow Breasted Chat and *Solanum triphyllon flore hexapetalo*
Yellow-breasted chat (*Icteria virens*) and spotted wakerobin (*Trillium maculatum*)

In the course of his transatlantic horticultural activities, Catesby may have had a hand in the naming of a genus with which the Arnold Arboretum has a special relationship, *Stewartia*. (The *Stewartia* collection is one of six that the Arboretum curates as a member of the North American Plant Collections Consortium, with the goal of broad acquisition and long-term preservation of *Stewartia* germplasm.) Upon receiving specimens of a new shrub from a correspondent in Virginia, Catesby planted them at the nursery where he worked in Fulham, England. As Spongberg and Fordham (1975) relate, "The plants flowered in May of 1742, and it is suspected that Catesby, recognizing their ornamental value and botanical interest, gave plants of the new shrub to John Stuart, the third Earl of Bute, for the botanical garden he was helping to establish at Kew." Subsequently, Linnaeus named the genus in honor of Stuart in 1746.

It is a telling testament to the importance of Catesby's work that scholars and scientists continued to acknowledge his pioneering efforts

Steuartia

Silky camellia (*Stewartia malacodendron*) [Ed. note: Though he named the genus in honor of John Stuart, Linnaeus spelled it as *Stewartia.* This is still the generally accepted spelling, though some taxonomists spell it as *Stuartia.* Catesby's spelling seems to split the difference.]

long after his death. In his *Species Plantarum* (1753), Linnaeus cited Catesby ninety-five times (Ewan 1974). Thomas Jefferson cited Catesby in the table of North American birds he included in his *Notes on the State of Virginia* (1785) to contest a French naturalist's assertion that American species lacked variety. Lewis and Clark studied the *Natural History* in preparation for their explorations, as did Alexander von Humboldt. And Catesby has been immortalized in the scientific names of many American organisms. Our bullfrog was named *Rana catesbeiana*, in 1802. Catesby has four reptiles named for him and a number of plants, including (with the naming botanist's name appended) *Lilium catesbaei* Walter, *Gentiana catesbaei* Walter, *Quercus catesbaei* Michaux (a synonym of *Q. laevis*), *Clematis catesbyana* Pursh, *Trillium catesbaei* Elliott, and *Leucothoë catesbaei* (Walter) A. Gray (a synonym of *L. axillaris*).

A few genera also bear Catesby's name. The Dutch botanist Gronovius had already named the lily-thorn genus, *Catesbaea*, for Catesby during his lifetime. In 1968, the monospecific genus *Catesbya* was erected by J. E. Böhlke and D. G. Smith for *Catesbya pseudomuraena*, an eel inhabiting the reefs of the Bahamas. In naming the new genus the authors explicitly paid tribute to "Mark Catesby, whose [work] marks the beginning of our knowledge of Bahaman fishes" (Böhlke & Smith 1968).

In the end, Catesby's artwork had a new triumph. Purchased by George III in 1768, the original watercolors and drawings that were the basis for Catesby's *Natural History* etchings were placed into books and shelved in the Royal Library at Windsor Castle. There they remained, all but forgotten, for well over two centuries. In 1997, they were at last unbound for conservation work. A new book of reproductions was published, and selections were assembled into two international traveling exhibitions. One went to the United States, where it was displayed at a succession of four museums before finishing its tour back in the United Kingdom at the Queen's Gallery in London; the other visited four sites in Japan. For the first time since the 1720s, the public could view and appreciate the original images Catesby had trekked through the wilds of America to bring home.

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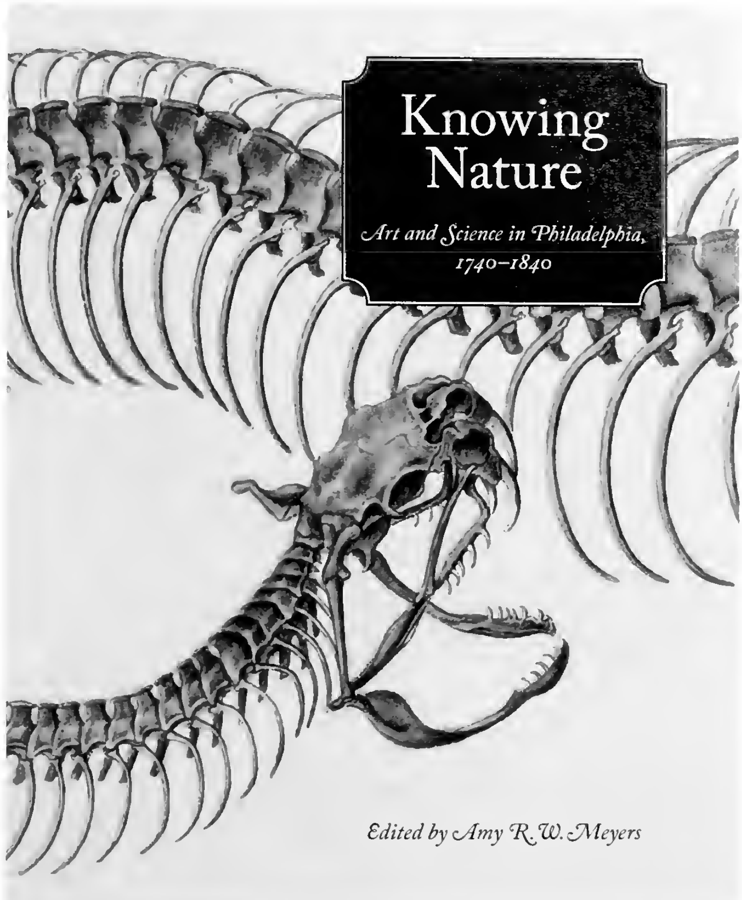
Book Review: *Knowing Nature: Art and Science in Philadelphia, 1740–1840*

Peter Del Tredici



Knowing Nature: Art and Science in Philadelphia, 1740–1840
Edited by Amy R. W. Meyers with the assistance of Lisa L. Ford
New Haven: Yale University Press, 2012. 417 pages.
ISBN 978-0-300-1104-0

It's hard to fully appreciate this high quality, large format (10 by 12 inches) book without actually picking it up and thumbing through its stunningly beautiful pages. It is at once a graphic and an intellectual tour de force that examines the passion for the arts, sciences, and culture that characterized Britain and America during the dynamic years from 1740 to 1840, immediately before and after the American Revolution. The thirteen historians who contributed articles to the book come from a variety of backgrounds and specialties, but all are experts in their fields and share a deep passion for their subjects. Together they have created a portrait of this time period that overwhelms the reader with many exquisite eighteenth-century illustrations of plants, animals, human anatomy, architecture, and decorative arts.

Perhaps because so many of the contributors are art historians or curators (the editor is the Director of the Yale Center for British Art), the book has the look and feel of a museum exhibition. More than anything else, the book presents the art and artifacts of the era in their historical context such that their deeper social meaning becomes visible. Nowhere is this more apparent than in the chapter by Alexander Nemerov on "The Rattlesnake," which discusses a spectacularly beautiful illustration once thought to have been drawn by Benjamin Smith Barton, but now attributed to the British-born architect Benjamin Henry Latrobe. Not only does Nemerov carefully dissect the drawing and relate it to Latrobe's architectural work but he also explores the symbolic significance of the rattlesnake during the period of the American Revolution.

A common thread that runs through the book is the life and work of William Bartram, as seen most clearly in the articles by Joel Fry and Amy Meyers who, taken together, create a masterful portrait of the scientific, horticultural, and artistic context in which he worked. More than any other historical figures, the Bartrams (father John and son William) personify the complex and highly fruitful interchange between Europe and North America both before and after the Revolution. I was particularly fascinated by the

One of the images of ginseng in the book is *The Whip-Poor-Will and the Ginseng, or Ninsin of the Chinese* from Catesby's *Natural History of Carolina, Florida, and the Bahama Islands.*

story of John Bartram's involvement in the discovery of ginseng in Pennsylvania (1739) and his efforts to collect plants for his patron, Peter Collinson, who was interested in establishing a business exporting American ginseng from England to China. While I have read about this story before, the six beautiful images of ginseng (including a botanical specimen collected by Bartram) that illustrate Janice Neri's chapter on the China trade give this version a vitality that text alone does not provide.

Mark Laird's chapter on "The American Connection in Georgian Pleasure Grounds" traces how the interest in and importation of North American plants and animals into England changed the nature of designed English landscapes. In a similar vein, I found Lisa Ford's chapter about François-André Michaux's *North American Sylva* particularly enlightening. She not only discusses the history of this incredibly beautiful and scientifically seminal work, but also the story behind its creation, including a copy of the questionnaire that Michaux used when gathering information about the local uses and distributions of native trees. Again, her discussion of the larger rationale for producing such a lavishly illustrated book, namely that Napoleonic France was anxious to replant its forests after centuries of unchecked exploitation, puts the focus not just on the object itself but its historical context. Alicia Weisberg-Roberts contributes a chapter on the relationship between eighteenth-century textile design and Philadelphia natural history, and James Green deftly covers the salient details in the important transition between hand coloring and color printing in natural history books.

The second to last chapter of the book covers the pictorial history of the Lewis and Clark expedition and the role played by eminent citizens of Philadelphia, including Benjamin Smith Barton, Benjamin Rush, Caspar Wistar and Charles Willson Peale, whose natural history museum housed many of the animal skins and skeletons Lewis and Clark collected on their journey. The last chapter of the book is devoted to an analysis of how the work of Philadelphia naturalist John Goodman (author of *Rambles of a Naturalist*) and *Birds of America* creator John James Audubon "democratized" the subject of natural history, making it accessible to a much wider audience. In short, this wonderful book puts the panorama of early American natural history studies into its proper social and historical context in a most beautiful and elegant way.

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

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Betula dahurica: A Special Birch Tree

Hugh McAllister

In the United Kingdom, *Betula dahurica* has a reputation for not making a well-shaped tree, as it often suffers repeated dieback and poor growth because of late spring frosts and inadequate summer heat. One specimen in the Arnold Arboretum (overhanging the road on Bussey Hill) shows the typical "witches' broom" growths caused by such repeated dieback, but most trees of *B. dahurica* in the Arboretum have made good specimens. Particularly noteworthy is a tree of Japanese origin (accession 1015-80-A) just off Conifer Path near the bamboo collection. Dahurian birch is noted for its peeling, papery bark (similar to river birch, *B. nigra*) and this specimen has particularly attractive shaggy curls that have a redder color on their inner surface than some other Arboretum specimens. The color of the inner surface contrasts nicely with the creamy white of the outer surface of the curls and the unpeeled sections of bark on the branches.

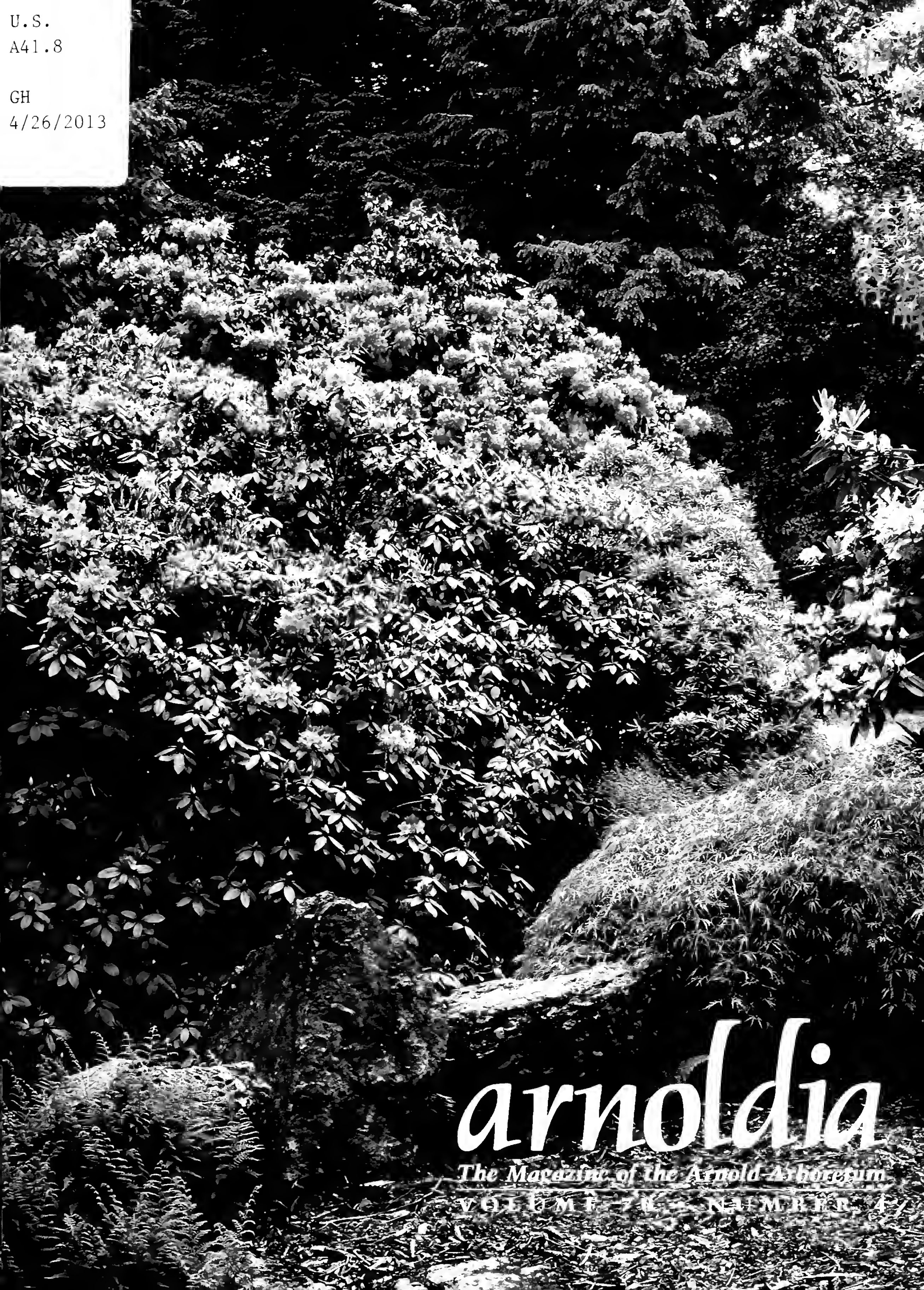
Betula dahurica is native to China, Japan, Korea, eastern Mongolia, and far eastern Russia. Accession 1015-80-A is of special interest since *B. dahurica* is endangered in Japan, being known primarily from a small population near Nobeyama in Nagano Prefecture in the central part of the main island of Honshu (where this accession was collected). There is another small population in the northern island of Hokkaido and one on Iturup in the Kurile Islands, which were Japanese before being occupied by Russia at the end of World War II. Of genetic interest, these offshore island populations are hexaploid (6 times the base number for birches of $x=14$) with a chromosome number of $2n=84$, whereas the extensive populations on the Asiatic mainland all appear to be octoploid with $2n=112$. This means that the island populations are unlikely to interbreed freely with the mainland populations, are genetically distinct, and, if they can be recognized by their appearance, should be named as a distinct species.

Three cuttings from the tree in the Arboretum have been rooted and are now growing in the nursery. The only other known trees from the Nobeyama provenance in cultivation are a single tree at Dawyck, a satellite garden of the Royal Botanic Garden Edinburgh in southern Scotland, and six trees at Ness Gardens, the University of Liverpool Botanic Gardens near Chester in northwest England. Trees from this provenance grow far better in the United Kingdom than any from continental Asia, presumably because of the greater similarity of our climate to the maritime climate of Japan.

Since the Nobeyama trees are genetically distinct and rare in the wild, they are clearly of conservation significance and efforts should be made to have breeding populations for seed production in cultivation. Most species of birch are self-incompatible (self-sterile), so at least two different seedling trees are needed for seed production. Fortunately we have this at Ness and, despite the large number of other birch species in the surrounding garden, seedlings from the cultivated trees seem to be mostly coming true (i.e., are not hybrids with other species).

Accession 1015-80-A is producing some viable seeds, so it will be interesting to sow this and see what the seedlings are. If the parent tree is totally self-incompatible then all the seedlings will be hybrids. No known hybrids of *B. dahurica* have ever been reported, and certainly no hybrids of the Nobeyama provenance, so, if we can identify what the other parent(s) might have been, it will tell us what other species *B. dahurica* can hybridize with. Any such hybrids could be of horticultural interest since *B. dahurica* may be resistant to bronze birch borer. Alternatively, accession 1015-80-A could have a limited degree of self-compatibility (resulting in a low percentage of viable seeds) and at least some of the seedlings could be the result of self-fertilization. This could result in some dwarf or other abnormal growth forms as a result of inbreeding depression—this is the probable mode of origin of many dwarf conifers. No doubt this species, and the Japanese provenance in particular, will continue to be studied, conserved, and propagated at the Arnold Arboretum, Ness Gardens, and other botanical institutions.

Hugh McAllister is an honorary lecturer at the University of Liverpool and was recently a Sargent Award visiting scholar at the Arnold Arboretum.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Front cover: Rhododendron Dell at the Arnold Arboretum. Photo by Nancy Rose.

Inside front cover: Gymnosperms all bear reproductive structures known as cones, but the cones vary greatly within the group. Seen here is the female cone of *Encephalartos ferox*, a cycad in the Zamiaceae. Photo by Michael Calonje, Montgomery Botanical Center.

Inside back cover: Fragrant abelia (*Abelia mosanensis*), accession 591-2003, growing in the Arboretum's Leventritt Shrub and Vine Garden. Photo by Nancy Rose.

Back cover: Illustration of *Ginkgo biloba* (then better known as *Salisburia adiant[h]ifolia*) from Siebold and Zuccarini's *Flora Japonica*. The first plates for the book were published in 1835 but the full publication was not finished until 1870. From the Archives of the Arnold Arboretum.

Beyond Pine Cones: An Introduction to Gymnosperms

Stephanie Conway

Gymnosperms are an intriguing group of plants, yet in many ways they are not well known. Most people can recognize a pine, with its familiar woody cones, but they may not know that this and other conifers are gymnosperms. Or, they may think that conifers are the *only* plants in the gymnosperm group. Undoubtedly the often large-flowered angiosperms (flowering plants) are the better known group within the seed plants, but gymnosperms are well worth a look.

So what are gymnosperms and what makes them so intriguing? There are four groups of plants that make up the gymnosperms: the well-known conifers, plus the lesser known cycads, ginkgo, and the order Gnetales. These groups are so different from each other that it would be hard to immediately recognize them as related. In fact, exactly how they are related to each other is not entirely clear, but most studies put cycads and ginkgo at the base of a gymnosperm evolutionary tree (meaning that they are the simplest, evolutionarily), and conifers and Gnetales as more evolutionarily advanced.

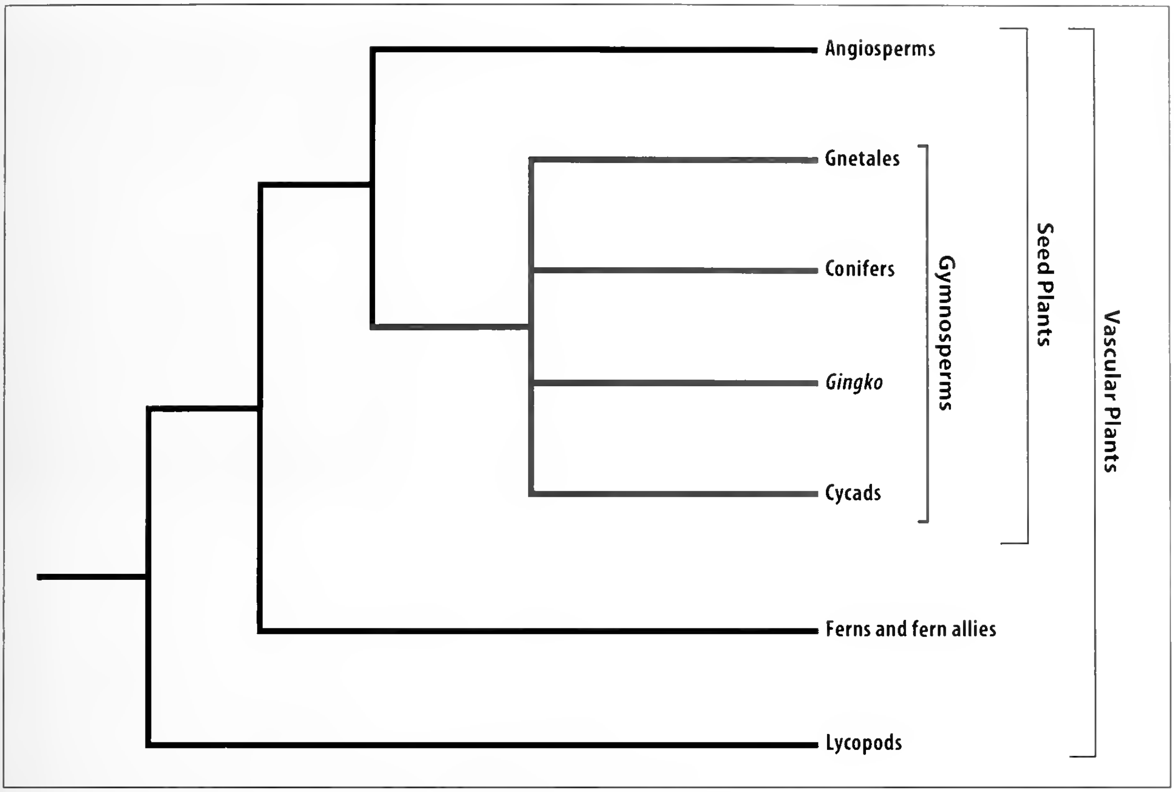
KEITH KANOTI, MAINE FOREST SERVICE, BUGWOOD.ORG

Pine cones are perhaps the most familiar gymnosperm cone type. A mature eastern white pine (*Pinus strobus*) cone is seen here.

What does it mean to be a gymnosperm? The most common feature across all four groups is that the ovule (which becomes the seed) is naked (unprotected) prior to fertilization. In comparison, the angiosperms have ovules that are protected by a layer of tissue called a carpel. The word gymnosperm comes from ancient Greek and means "naked seed." This naked state of the ovule is a unifying feature of the gymnosperms (there are also some shared vegetative features such as wood anatomy), but often these ovules are not visible to the naked eye. This is perhaps what makes them so intriguing: How does this translate to the more common feature that we can see, the cone? How did these evolve? And how does the cone tell the story of the evolution of the gymnosperms?

GYMNOSPERM ROOTS

The ancestors of gymnosperms most likely evolved from a group of plants called the seed ferns (pteridiosperms), which are known only from the fossil record. These were the first plants to reproduce by seeds, despite looking deceptively like ferns. (True ferns reproduce from spores rather than seeds.) Early seed plants bore their seeds directly on leaves or branches, without any specialized structures like cones. From this starting point we can begin to see how the naked ovules and cones of living gymnosperms evolved. The four lineages of gymnosperms each have a unique set of cone characteristics, and comparisons with the naked eye are extremely difficult. In fact, even comparisons between well-known conifer groups are challenging. To understand



STEPHANIE CONWAY

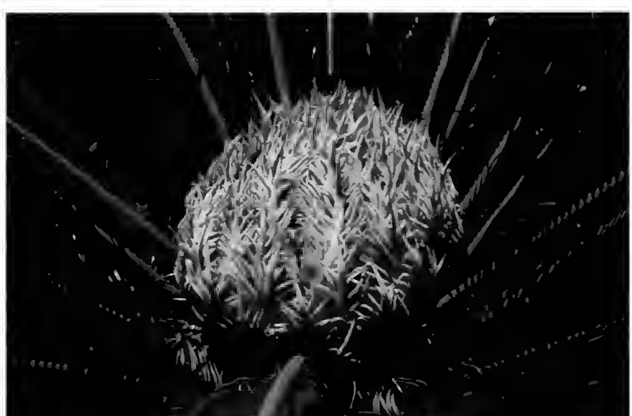
Phylogeny chart showing the relationship of gymnosperms to other plant groups.

the elusive relationship between these cone types, it helps to examine the distinct paths of evolution that each gymnosperm lineage took from the seed fern ancestral condition, how all retained the character of a naked ovule and yet ended up with very different looking reproductive structures.

CYCADS

Cycads are a very ancient lineage of plants with a fossil record that extends back at least 280 million years. They were once very common across most of the planet and were a prominent plant group in the age of the dinosaurs, but they have since retreated to the tropics and sub-tropics. As is the case for all the gymnosperm lineages, it's important to remember that when we look at the cycad taxa growing today we are seeing the survivors of a once very successful plant group. These "leftovers" include 3 families of cycads: Cycadaceae, Zamiaceae, and Stangeriaceae, which contain about 11 genera and 250 species in total.

Cycads have unique characteristics that set them apart from the rest of the gymnosperms and make them unique among all seed plants. They have a single, typically unbranched trunk with the leaves all bunched together in a crown at the top of the plant. This features makes them look superficially like palm trees, a fact reflected in the common name of one cycad that is often grown as a house plant, sago palm



MICHAEL CALONJE, MONTGOMERY BOTANICAL CENTER

The female cone of *Cycas revoluta*. Note that the sporophylls resemble leaves and are all bunched together at the crown, similar to the leaves. Young ovules are formed on the lower portion of the sporophylls and are very exposed or naked.

(*Cycas revoluta*). Some cycads have trunks that can grow partially or fully underground, others have long, straight trunks and can grow quite tall—up to 18 meters (59 feet) in the Australian cycad *Lepidozamia hopei*. The leaves of cycads are pinnate, with leaflets arrayed in two rows on either side of the rachis. This pinnate leaf form is not found in any other gymnosperms.

Cycads are dioecious, meaning that there are separate male plants that produce pollen cones and female plants that produce seed cones. The cones of cycads are typically large, with many fertile, leaflike organs (sporophylls) that are aggregated into cones. Both cone types are simple, which in botanical terms means the sporophylls are attached directly to the cone axis or column and have no other leaves or bracts associated with them. The simple nature of both the seed and pollen cones is important to the interpretation of the evolution of the cone in cycads. Many botanists believe this shows that the cycads represent an early line of evolution that took a different path from the rest of the gymnosperms. The morphology of the seed cone is quite variable within the cycads, but the *Cycas* type of cone is considered primitive within the cycad group. In this genus, the ovules are borne on the edges of sporophylls, and these sporophylls form in a crown at the top of the plant, similar to the leaves. The sporophylls do in fact resemble young leaves, only these "leaves" have ovules along their edges. Before pollination, the *Cycas* cone represents the best example of a naked ovule within the gymnosperms, as the ovules are very much exposed to the air. The rest of the cycads have ovules born on scalelike structures, some with leaflike structures along the margin, but many without any leaflike morphology at all. The pollen cones of cycads are similar to seed cones, and pollen is born on the lower surface of scalelike structures.

STEPHANIE CONWAY

Zamia furfuracea **female cones with bright red seeds attached to scalelike sporophylls. Note the lack of leaflike portion of the scale, as compared to *Cycas* sprorophylls.**

MICHAEL CALONJE, MONTGOMERY BOTANICAL CENTER

Cycas maconochiei **cones have leaflike sporophylls with green ovules along the margins. Note that in this species the sporophylls are less leaflike than in *Cycas revoluta* but are still bunched together in the crown.**

It is generally believed that in the ancestral type, cycads bore ovules directly on leaves. Over time, these fertile leaves evolved into a condensed and simplified form—the cycad cone. In *Cycas*, the leaflike structure was somewhat retained, but in more advanced cycads there was further reduction and elimination of the leafy parts, resulting in the scale-type cones found in *Zamia* and other cycads. The fact that the cones are "simple" is important to this interpretation since it means that we can recognize the evolution of the cycad cone from a *leaf* with ovules rather than a *branch* with ovules. This distinction is important and, as we'll see, shows that the cycad cone and the conifer cone had quite different evolutionary beginnings. But first, let's look at the fascinating *Ginkgo biloba*, which, in terms of cone morphology, is often considered an intermediate between cycads and conifers.

GINKGO

Gingko biloba is the sole living species of the once widely distributed order Ginkgoales and is often called a "living fossil." This plant has fascinated botanist for centuries because it represents a unique set of characteristics that alludes to both the cycads and conifers but which represents a unique lineage within the gymnosperms. Ginkgo's flat, fan-shaped leaves are its most distinctive feature; the leaves on the plant's long shoots are typically two-lobed, hence the specific epithet *biloba*. Unlike the cycads, adult trees are heavily branched and have a broad crown.

The fertile structures in gingko are unique as well, with little to make a comparison to either the cones of cycads or conifers easy. The male

PETER DEL TREDICI

A *Ginkgo biloba* tree in fall color at Forest Hills Cemetary in Boston.

PETER DEL TREDICI

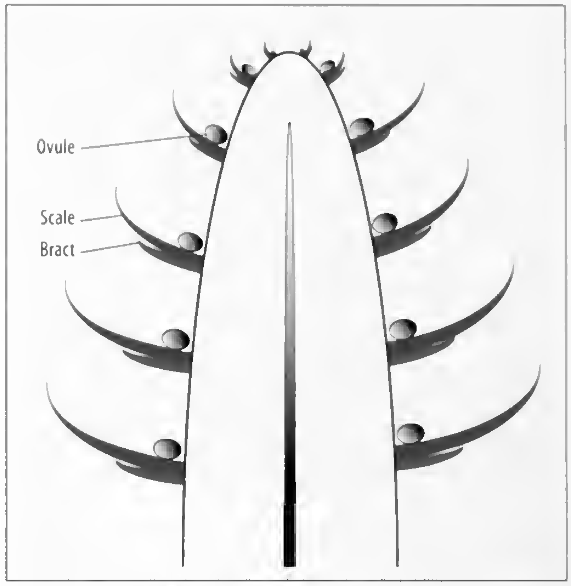
The female cones of *Ginkgo biloba* are generally thought to have evolved from a branch, but all that remain are the long stalks with terminal ovules (seeds) with a thin fleshy covering.

KEVIN NIXON

Male ginkgo cones (strobili) bear many pollen-producing organs along a central stalk.

pollen cones (strobili) are simple structures that arise at the base of leaves on the short shoots. They have longish stalks with lots of pollen-producing organs attached directly to the stalk. Female cones (strobili) also arise at the base of leaves on the short shoots and consist of a stalk and two terminal ovules.

The fossil record is large and variable for Ginkgoales, so there is much debate about the ancestor of ginkgo. This makes the interpretation of the cone difficult. However, the most common interpretation of the female reproductive structure of ginkgo is that it is an extremely reduced and modified branch, so highly reduced that only the stalk and the two terminal ovules remain. While the entire evolutionary history of gingko is still not entirely settled, the interpretation is important because it will direct our understanding on the relationships of all seed plants.



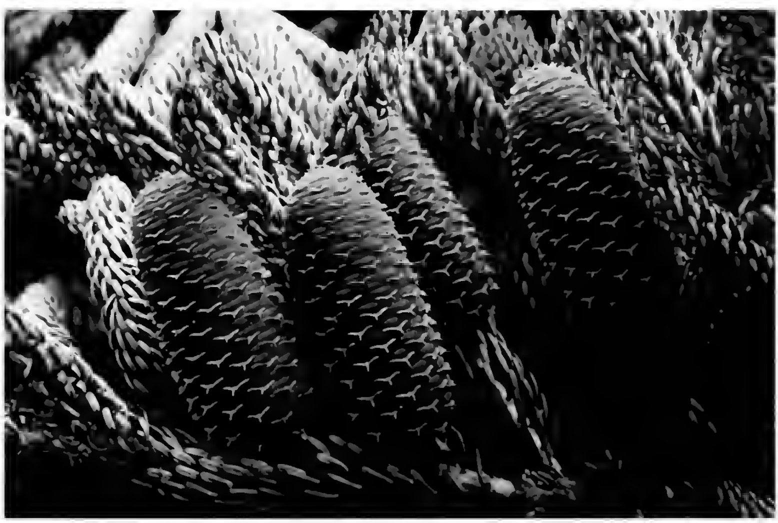
STEPHANIE CONWAY

The bract–scale structure of a pine cone.

CONIFERS

Conifers are the most conspicuous group of gymnosperms, containing 7 families and more than 600 species. They tend to dominate forests in the Northern Hemisphere and have a rich and diverse existence in the Southern Hemisphere, but are reduced in numbers in most tropical environments. Conifers are such a highly variable group that this whole article could be spent summarizing their general characters. Instead we shall just look at a few interesting examples.

The pollen cones of conifers are always simple, that is, the organs that produce pollen are attached directly to the cone axis without other associated leaves or bracts. The story of the female seed cones is much more complicated and a curious person only needs to go outside and look at various conifer cones to sense the issues at hand. For example, how does the cone of a juniper (*Juniperus*) compare to that of a fir (*Abies*)? How about *Calocedrus* compared to *Cephalotaxus*? And what about *Taxus*, is that even a cone?



PETER DEL TREDICI

The large, attractive cones of this Korean fir cultivar (*Abies koreana* 'Silberlocke') have long yellow bracts with pointed tips. These bracts can be seen protruding from below the brown scales.

Our current understanding of the conifer cone comes mostly from a Swedish paleobotanist named Rudolf Florin. Prior to Florin (and many others who also contributed), there was no cohesive interpretation of the different parts of the cone in different families and how they could have evolved from a single ancestor. Florin's theory is centered on the fact that the female cone of *Pinus* is a compound structure. This means that each cone has a single, central column or axis, to which other "columns" are attached. Each of these attached columns has its own set of organs attached to it. In other words, you can break up a cone into a number of individual units, and each unit has a complete, replicate set of organs. Each one of those units is made up of a bract, a scale, and ovules. The bract is on the outside, and the scale is on the inside. This scale is sometimes called the ovuliferous scale because it is where the ovules are formed and where eventually the seed develops. The fact that the scale where the ovules are formed sits at the base of the bract is important because therein lies the fundamental compound nature of the cone.

'oung female Douglas-fir (*Pseudotsuga menziesii*) cones sit pright on the branch and display prominent pink bracts (at his stage the scale cannot be seen). The more mature male ollen cones (hanging downward) have pollen organs attached irectly to the cone axis.

oung cone of northern Japanese hemlock (*Tsuga diversifolia*) ith large green and purple scales. The much smaller bracts (white ith brown tips) can be seen on the scales closest to the stem.

Florin proposed that in the ancestor of the conifers, seeds were formed on widely spaced branches, each branch with a number of fertile scales that bore stalked ovules. Each branch formed at the base of a bract. He proposed that over evolutionary time these branches transformed to have fewer and fewer scales until there was only one, that the ovules lost their stalks, and that the single remaing scale became more and more fused to the bract. So the interpretation is that each unit (an individual bract-scale complex) that we break off a cone is all that remains of a once large branch.

Most of the other genera in the pine family (Pinaceae) have fundamentally the same bract-scale complex but with different shapes and sizes of the bracts and scale. In *Pinus* for example, the bracts are small and inconspicuous compared to the scales, whereas in Douglas-

PETER DEL TREDICI

The most prominent feature of this young *Sciadopitys verticillata* cone is the large white scales, with the smaller brown bracts hidden underneath.

firs (*Pseudotsuga*), as well as certain species of *Abies* and hemlock (*Tsuga*), the bracts are long and conspicuous, often forked, and the scales are small. In cases where the bracts or scales are small and inconspicuous, it is very difficult to see them at all, except in early stages of development, and sometimes only with a microscope.

In umbrella pine (*Sciadopitys verticillata*, the sole species in Sciadopityaceae) the scales are the main feature of the mature cone. The bract is only apparent early in development and becomes fused with the scale during further growth, becoming almost indistinguishable. However, in Araucariaceae, a Southern Hemisphere family, there is no apparent ovuliferous scale at any time during development; instead, the ovules are borne directly on the bracts. In such groups where there is no ovuliferous scale, this scale is considered to have been lost over evolutionary time. In other families of conifers the story is more complicated, and comparisons between adult cones of different groups stretches Florin's model to its limits.

The cypress family (Cupressaceae) is a large and diverse group that also shows great diversity in cone types within the family. In *Sequoia*, *Sequoiadendron*, and *Metasequoia*, the ovuliferous scale only appears as a small mound of tissue at the base of the ovules very early in development. The cones of *Cupressus* and *Chamaecyparis* are similar to each other, with four or more opposite pairs of woody bracts and nothing that resembles an ovuliferous scale. *Juniperus* forms what looks like a berry, but in fact the "berry" is the completely fused, swollen bracts that have become soft and pulpy after fertilization. Before full ripening the seamlike outlines of the bracts can often be seen in the flesh. Again, no traces of an ovuliferous scale can be found. In some juniper species the cones are reduced to a single seed per cone. This extreme level of reductions is often associated with reproductive advantage since the single ovule occupies the prime position for fertilization and the colored bracts serve to attract birds and other animal dispersers. Thus, this simplified cone with a minimal number of organs is considered evolutionarily advanced.

Cupressus tonkinensis **has a female cone with woody bracts that open to release the seeds.**

The purple bracts of the berrylike cones of Eastern red cedar (*Juniperus virginiana*) swell and become fleshy. A glaucous waxy coating gives the cones a blue cast.

The female cones of *Podocarpus macrophyllus* have a single seed covered in a fleshy bract and scale; the receptacle below will swell and become red when mature.

PETER DEL TREDICI

The fleshy olive-shaped female cones of *Cephalotaxus fortunei.*

ROBERT VIDEKI, DORONICUM KFT., BUGWOOD.ORG

Cones of *Taxus* (*T. baccata* is seen here) are so different that they are hard to compare to other conifers. In this species, the seeds are formed terminally on the end of short stems, and a swelling at the base of the ovule develops into a fleshy red aril that covers the seed and also attracts seed dispersers. On the younger green cone the single terminal seed can be seen with the fleshy aril just starting to develop.

The large Southern Hemisphere family Podocarpaceae also developed a berrylike cone, with fleshy parts to aid dispersal and minimal numbers of seeds per cone. However, this family has a unique cone type that looks nothing like the cones of *Juniperus*. The cones typically consist of a number of sterile bracts and one fertile bract on which the ovule arises on a structure called the epimatium, which is considered the evolutionary equivalent to the ovuliferous scale. In *Podocarpus*, the bracts at the base of the cone also swell into an often colorful "receptacle" that, as in *Juniperus*, probably serves in attracting animals for dispersal.

Plum yew (*Cephalotaxus*) also has fleshy, single-seeded cones that look suspiciously like olives. The early development of *Cephalotaxus* shows a lack of ovuliferous scales, and instead the ovules form on the bracts in a manner similar to other conifers. However, the bracts grow out to cover the seed in a fleshy covering that, as seen in *Podocarpus*, presumably aids in animal dispersal of the seed.

Taxus is the final example of a female conifer cone and it's one that does not fit within Florin's theory of conifer cone evolution. The female reproductive structure of *Taxus* does not have ovules on bracts or scales; instead, it has a single terminal ovule. This ovule sits at the end of a short branch, and an outgrowth at the base of the seed becomes a fleshy red aril that partly covers the seed. Florin himself was so convinced of the fundamentally different nature of the cone structure in Taxaceae that he placed the family in a different order, the Taxales. This implied that Taxales had different ancestors than the rest of the conifers, therefore making the conifers not a natural group. This was a controversial theory, and other researchers have since shown it to be unlikely. Instead, researchers have proposed that the terminal cone may be related to the more advanced cones of the Cupressaceae, including various species of *Juniperus* with single terminal ovules. However, how and from where the *Taxus* type of cone evolved (if considering the conifers as a monophyletic group) has not yet been satisfactorily resolved and remains something of a mystery.

Ephedra viridis, commonly known as green ephedra or Mormon tea, grows in the southwestern United States. It is very drought tolerant and often grows in association with creosote bush and sagebrush.

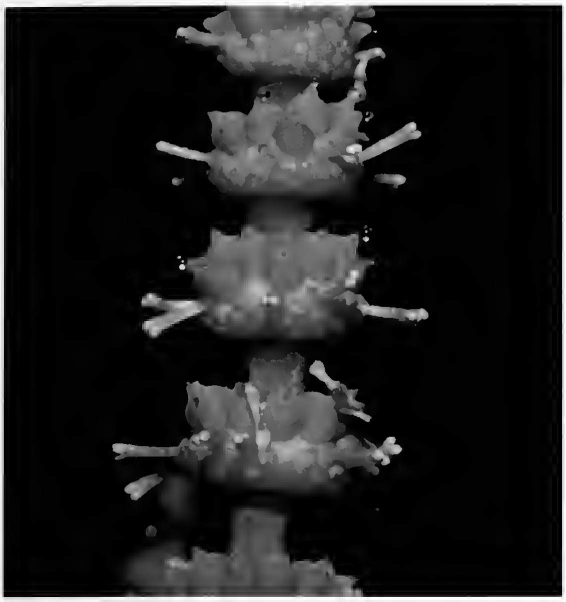
Ephedra sinica female cone with ovules in the uppermost fertile bracts. The ovules are secreting a pollination drop, the pollen capturing mechanism of gymnosperms.

GNETALES

The Gnetales are perhaps the most enigmatic group of the gymnosperms, which, considering the mysteries we have already encountered, is no minor statement. Their phylogenetic position within the seed plants remains unresolved and their morphology is puzzling. This order of plants is made up of 3 families—Ephedraceae, Gnetaceae, and Welwitschiaceae—each with a single genus. Many features of these plants are so different that at first glance it is hard to believe they are related, but a few shared features do keep these plants united as a group. These features include an advanced type of water conducting cell called a vessel, which is similar to the type found in flowering plants, as well as the compound and complex nature of both the pollen and the seed cones.

Ephedraceae comprises about 35 species of *Ephedra* and is found mostly in dry, desert-type climates. Almost all species are small, spindly shrubs, although a few grow like vines and one species in Brazil is a small tree. The leaves of

KEVIN NIXON



A male cone of *Gnetum gnemon* with rings of pollen organs below rings of sterile female ovules, some with pollination drops present.

he seed cones on this female *Gnetum urens* have matured nd only one red, fleshy seed has developed from each cone. bove the seed on the right you can see the nodes where the ther ovules would have formed, but have failed to develop.

Ephedra are generally scalelike, or occasionally longer and needlelike, and all are joined at the base to form a sheath around the stem. Most species of *Ephedra* are dioecious (separate male and female plants). The pollen cones of *Ephedra* have a pair of bracts at the base of the cones, and the cones themselves are made up of a series of bracts, each with its own fertile shoot. This makes these cones compound structures in the same fashion as the seed cones of conifers. The female cones are also compound. The cones have a pair of bracts at their base, and the cones themselves are also made up of a series of bracts. The uppermost bracts have ovules in their axes, although often only one develops into a seed.

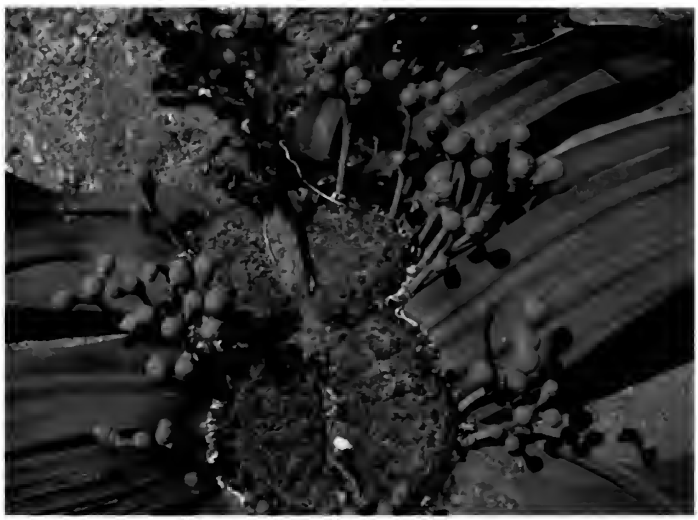
Gnetaceae has only one genus, *Gnetum*. Most *Gnetum* species are tropical vines, though one of the most widely studied species, *Gnetum gnemon*, is a tree. *Gnetum* species occur in parts of Asia, South America, and Africa as well as some Pacific Islands. If you were to walk past one in the tropics you would be hard pressed to recognize it as a gymnosperm because the leaves are broad, flat, and have netlike veins, making it look much more like a flowering plant (angiosperm). *Gnetum* cones are also very distinct from typical conifer cones and they form fleshy seeds that look like berries. Both the cones that produce pollen and those that produce seeds are compound structures and unique among gymnosperms. In *Gnetum gnemon* they are long and have distinct nodes where the fertile structures are formed. The pollen cones have bracts that cover the nodes, and underneath these a number of pollen organs are enclosed within two fused structures. Above this ring of pollen organs there are often aborted female ovules, which has lead many botanists to consider the cone of *Gnetum* to be primitively flowerlike. The seed cone also is on a long axis, with the fertile structures occurring on the nodes. There are bracts that cover a ring of 8 to 10 ovules. Each ovule is surrounded by 3 bractlike structures that form envelopes around the ovule.

Welwitschiaceae consists of only one species, *Welwitschia mirabilis*, which may be one of the strangest plants on the planet. It grows only in the Namib Desert of Angola and Namibia and produces just two huge leaves from a short, woody, unbranched stem. The leaves grow an average of 8 to 15 centimeters (3 to 6 inches) per year, and often are split and twisted at their ends, forming a tangled mass. Some *Welwitschia* leaves have been measured at up to 6 meters (19.7 feet) long. The plants survive in the desert by developing a huge taproot that may extend down nearly 2 meters (6.6 feet). A few plants have been estimated to be close to

2,000 years old. The cones of this odd plant develop from buds on the woody crown between the two leaves. Both the pollen cones and seed cones are compound and consist of two rows of opposite bracts. In the base of these bracts the fertile shoot emerges. Pollen cones bear 6 pollen organs that have fused bases. These are enclosed by 2 sets of bractlike structures. There is an aborted ovule in the middle of the apex. The seed cones are similar in design to the pollen cone; the outer bracts are not fused and inner bracts are long and fused and form an envelope over the ovule.

DONNA TREMONTI

Male cones of *Welwitschia mirabilis* are composed of numerous bracts, each with protruding pollen organs.



GILLIAN COOPER DRIVER

Female cones of *Welwitschia mirabilis* form on the woody crown and are made up by a number of bracts with enclosed ovules.

The Gnetales are particularly challenging to botanists because they seem to jump around within the phylogeny of seed plants depending on the type of study being carried out. This makes it difficult to confirm theories about the evolution of their cones. They have at various times been aligned with angiosperms, in part due to the organization of the cones; *Gnetum* and *Welwitschia* especially lend themselves to comparison with flowers because of the organization of their pollen and seed strobili. Also, the presence of bracts that envelope the ovule means that the ovule is not necessarily naked, as in the rest of the gymnosperms. However, an equally valid interpretation is the placement of Gnetales within the gymnosperms as sister to the conifers, which makes comparisons of the bracts and scales of conifers relevant. Where Gnetales sits in the phylogeny of seed plants is significant because their placement affects the evolutionary concepts for all of the shared features of the gymnosperm cone. A resolution of their evolutionary position would likely come from the fossil record, but the fossil record for the Gnetales is poor, or at least very few fossils have been correctly identified as belonging to this group. Taken altogether, the most recent evidence from fossils, morphology, and genetics places the Gnetales as nested within the gymnosperms, but just where exactly within this group remains controversial.

GYMNOSPERM EVOLUTION

As a group, the gymnosperms present a diverse and beautiful lineage of plants whose morphology tells a superb, if not fully understood, evolutionary story. The structure and function of the cone has only been briefly covered here,

An adult *Welwitschia mirabilis* plant growing in the Messum River area in Namibia.

but the common theme across all the lineages has been an evolution towards simplifying the reproductive structure. This has been achieved in a variety of ways and with different results. Cycads reduced the leafy portion of their cones down to a scale. Ginkgo reduced a large branch to a single stalk with two ovules. Conifers tended towards simplifying the branch complex to just a bract, or getting rid of the traditional cone altogether, and 4 out of the 7 conifer families developed a fruitlike structure as well as reducing the seed number. Gnetales began experimenting with having both seed and pollen structures within a single cone.

While a pine cone may be the best known representative of gymnosperm reproductive structures, it is in fact only a small part of the gymnosperm story. The current, living assemblages of gymnosperm groups are really only relicts of what once was a gymnosperm dominated world, so the task for us is to understand the whole narrative of dominance and decline. The gymnosperms of today are incredibly important since they represent 4 out of the 5 extant lineages of seed plants (angiosperms are the fifth lineage) and botanists continue to study exactly what gymnosperms are and how they evolved. Current research includes phylogenetic stud-

Male cones of *Pinus muricata* are simple, with a bract at the base of each cone and the pollen organs attached directly to the cone axis.

The young female cones of *Pinus longaeva* have long pink scales above smaller bracts.

ies using data sets from thousands of species and multiple genes to tease apart relationships both at the species level and between distant lineages. Genetic studies of, for example, how the genes that determine flowering in angiosperms are related to the genes that determine cone formation in gymnosperms, and morphological studies on the evolution of the different parts of the gymnosperm cone continue with modern techniques. Such mysteries of the gymnosperms have fascinated botanists for centuries and will continue to do so for many years to come.

Resources

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Rediscovering Rhododendron Dell, Part 1

Kyle Port

A pile of plant record labels, mysteriously stripped from accessioned plants in the Arboretum's Rhododendron Dell, sent Manager of Plant Records Kyle Port on a mission to assess, verify, and relabel the collection

In this issue, Kyle reports on the early history of Rhododendron Dell, and in the next issue he will write about the multi-layered curatorial process involved in the Rhododendron Dell project.

One hundred forty years ago, a triumphant rhododendron show bloomed on the Boston Common. For a nominal fee, attendees were ushered under tents where plants from private collections, including those of Arnold Arboretum director Charles S. Sargent and the event's sponsor, H. H. Hunnewell, were arranged. Rhododendron hybrids imported from Anthony Waterer (Knap Hill Nursery, Woking, England) garnered considerable attention. The revelation that *R.* 'Album Elegans' and a few other cultivars were hardy outdoors in the Boston area soon fostered planting trials beyond conservatory walls, specifically in the bur-

EDITORIAL NOTES
Rhododendron Show at Boston

The Rhododendron show on the Boston Common was a sight never to be forgotten—the finest in colors and display of choice varieties this country has ever beheld. It was with considerable difficulty the bare privilege was secured from the common council, to exhibit upon the Common; and next, it was believed to be almost impossible to transport and successfully flower so many plants as would be needed to produce the desired effect. Thanks, however, to the untiring energy of Mr. H. H. Hunnewell, Charles S. Sargent and E. S. Rand, jr., every difficulty was surmounted, and for the entire month of June the denizens of that city saw a collection of Azaleas and Rhododendrons of rare value and great beauty ...

Two large tents were erected, one about 60 by 100 feet, the other 100 by 300 feet, and the plants transplanted from their native home and conservatories of Mr. Hunnewell and Mr. Sargent, and placed in the natural soil of the Common. Within the tents were laid out, first, an avenue of 100 feet in length, bordered with Palms and rare Ferns; this led to the Rhododendron beds and walks. In the center of the large tent were three raised beds; the first, 15 by 30 feet; the second, 50 by 80 feet; the third, 15 feet in diameter. Walks also surrounded all the beds, which were lined with specimen plants. Imagine all this space and beds filled solidly with masses of Rhododendrons in full bloom, bearing flowers of most royal size, and delicate as well as glowing and brilliant colors, and it would seem to be but a vision of the garden of Paradise.

... most of them [rhododendrons] are fit for in-door greenhouse culture only, many being but just imported from the Knapp [Knap] Hill nursery of Anthony Waterer, Woking England.

Luther Tucker
The Horticulturist, and Journal of Rural Art and Rural Taste,
Volume 28, August 1873

The alluring white-flowered *R.* 'Album Elegans' (hybridized by Waterer, pre-1847) was one of the first large-leaved, evergreen rhododendrons proved hardy in Massachusetts. This Arboretum accession of the cultivar was photographed by Ralph W. Curtis in June 1932.

The burgeoning Rhododendron Dell is seen in this Autochrome glass slide from 1934.

Staff members of the Arnold Arboretum have collected, researched, and written extensively about *Rhododendron*, covering a myriad of species and hybrids. So prolific were early Arboretum contributors that the Royal Horticultural Society bestowed the Loder Rhododendron Cup on C. S. Sargent in 1924, E. H. Wilson in 1927, and Alfred Rehder in 1936.

geoning landscapes of the Arnold Arboretum, which had been established just the year before. More importantly, the friendships forged at the Boston show guaranteed that the most sought after rhododendron hybrids of the day would become accessible for viewing and study, free of charge, to anyone who journeyed to the Arboretum.

A suitable location for cultivating these large-leaved rhododendrons was found in a wind sheltered two-acre area between the northern contours of Hemlock Hill and Valley Road, through which Bussey Brook flows. Eventually named Rhododendron Dell, the existing soils—Hinckley sandy loam and Scio very fine sandy loam—proved adequate. Stands of eastern hemlock (*Tsuga canadensis*), intentionally left by the previous land owner Benjamin Bussey (1757–1842), provided an ideal amount of shade. And above all, the site allowed for cold air to sink away toward low-lying Bussey Brook Meadow.

The new hybrids were not immediately planted in Rhododendron Dell; instead, the first plantings on the site were of the hybrids' North American parent species, which included *R. catawbiense, R. maximum,* and *R. minus*. It is likely that the only remaining plants from these early plantings exist in a mass planting of *R. maximum* accessions 23020 and 23021. These accessions actually comprise a number of accessions that were interplanted over the years and became indistinguishable from each other. The oldest of these *R. maximum* accessions was obtained as seeds in 1880 from Benjamin Marston Watson's Old Colony Nurseries and Seed Warehouse in Plymouth, Massachusetts.

In 1886, the first *R. catawbiense* hybrids from Anthony Waterer were planted in Rhododendron Dell. Some of these hybrid cultivars had been featured in the tents of the 1873 rhododendron show on Boston Common, but now they were being planted outdoors to see how they would fare. Among these inaugural cultivars, *R.* 'Purpureum Grandiflorum' (accession 2804) and *R.* 'Album Grandiflorum' (accession 2805-A) survive to this day. Subsequent introductions such as *R.* 'Mrs. Harry Ingersoll' (accession 6202-C, acquired in 1891) epitomize the allure these hybrid rhododendrons had upon so many. Their survival at the Arboretum solidified a resolve to develop, evaluate, and maintain a collection for the ages. As Sargent wrote to Anthony Waterer in February 1911, "I think that we should have here a correctly named standard set of the hardy hybrid Rhododendrons as so many people depend on the Arboretum for information on such a subject."

While the majority of the early acquisitions of hybrids in Rhododendron Dell were those of Anthony Waterer and his cousin, John Waterer, a number of other international hybridizers are also represented. Fel-

KYLE PORT

Rhododendron catawbiense **'Grandiflorum'**

KYLE PORT

Rhododendron **'Mrs. Harry Ingersoll'**

KYLE PORT

Rhododendron **'Echse I'**

Rhododendron 'Duke of York'

low Englishman G. Paul provided *R.* 'Duke of York' (accession 22616-A, 1921 lineage from a 1915 introduction), and in 1908 German T. J. Rudolf Seidel sent, among others, *R.* 'Echse I' (accession 6175-B), which has bright reddish purple flowers with wavy-edged petals.

In 1919, the federal government's passage of Quarantine No. 37 governing the importation of nursery stock halted shipments of plants by steamer directly to Boston. The Arboretum had a nearly exclusive reliance on overseas suppliers at the time, but this quarantine forced relationship-building closer to home. North American nurseries, hybridizers, and hobbyists stepped up to meet the challenge and became reliable allies in the development of the Rhododendron Dell collections.

Kyle Port is Manager of Plant Records at the Arnold Arboretum.

For a great opportunity to explore the Rhododendron Dell in bloom, join us there for

COLLECTIONS UP CLOSE: RHODODENDRON RAMBLE

on Sunday, June 2, 1:00 to 3:00 p.m.

This free event includes walking tours with knowledgeable Arboretum staff and fun science activities for kids.

BOOK EXCERPT

Ginkgo: The Tree That Time Forgot

Peter Crane

Editor's Note: In his new book, noted botanist Peter Crane has gathered a vast trove of information on the ginkgo, undoubtedly one of the most loved trees in the world. Exploring topics ranging from paleobotany to evolutionary biology, plant exploration, and human culture, the author presents fascinating tales from the ginkgo's very long history on Earth. Printed here by permission of the publisher is Chapter 21, "Extinction." (Don't worry, ginkgophiles—Chapter 22 is "Endurance.")

Ginkgo: The Tree That Time Forgot
Peter Crane
Yale University Press, 2013. 408 pages.
ISBN: 978-0-300-18751-9

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Extinction

Many rivers to cross
But I can't seem to find my way over.
—Jimmy Cliff, "Many Rivers to Cross"

Given its long fossil history, the presence of ancient ginkgo across much of the Northern Hemisphere for most of the past 65 million years is not so surprising. Ginkgo and its extinct relatives were seemingly nearly everywhere on the planet for eons, and despite their clear decline about 100 million years ago, ginkgo managed to persist in many places. However, looking back from today, the fact that ginkgo was growing wild in Bulgaria and Greece just 5 million years ago nonetheless seems strange. It reminds us that not so long ago the world was a very different place. In the grand sweep of geologic time the distribution of animals and plants on our planet has changed rather quickly; where they live and grow now bears a strong imprint of history.[1]

Fossil floras from the Late Miocene and Pliocene provide irrefutable evidence that in addition to ginkgo, there were many other plants in western North America and Europe between about five million and fifteen million years ago that no longer grow there. In terms of the trees the vegetation in these areas was much richer then than now. For example, fossils from the fill of an ancient sinkhole at Willershausen near

Göttingen, Germany, show a mix of broadleaved and coniferous forests. On richer soils broadleaved forest included species of maple, birch, hickory, beech, ash, oak, and elm among about thirty-four tree species. Conifer forest included many trees that no longer occur today in Europe but can be found growing in the warm temperate forests of eastern Asia: the umbrella pine, for example, as well as the Chinese swamp cypress, the katsura, the dawn redwood, and the hardy rubber tree. Like ginkgo, in Europe, they all disappeared relatively recently.

In North America, fossil evidence from Clarkia, Idaho, shows exactly the same pattern. Again, the Chinese swamp cypress and the katsura are both present, along with the dawn redwood and the China fir. All of these plants are today restricted to eastern Asia. At both Clarkia and Willershausen there was also the Cathay silver fir, a rare conifer discovered as a living plant only in 1955. Today it has a scattered and restricted range in southwestern China. After about five million to fifteen million years ago, these plants were never seen in Europe and North America again, but somehow they managed to persist in the East.[2]

It is hard to understand exactly when and how these species were eliminated from Europe and North America because in most cases the fossil record is not sufficiently complete to provide a detailed picture of how their distribution gradually changed from being widespread in the past to being much more restricted today. We can, however, get some idea of how they may have fared by tracing the fate of a few of their associates that have especially distinctive pollen grains. Pollen grains are produced and preserved in the fossil record in vast numbers, and when they are sufficiently diagnostic of a particular tree, and readily recognized in fossil assemblages, they can be used to get a fine-grained look at how that plant fared as global climates deteriorated.

Particularly instructive is the history of the Caucasian wingnut, a tree in the walnut family that has especially distinctive pollen grains. These pollen grains disappear and reappear through successive glacial and interglacial phases in southern Britain. After each of the first few glacial advances up to about 500 thousand years ago, pollen grains of the Caucasian wingnut reappear in the intervening warm interglacials. These plants seem to have been forced south by successive glacial advances, but they evidently migrated back again into Britain, presumably from the south and east, as the climate warmed. However, these distinctive pollen grains are last seen in Britain during the Hoxnian interglacial between about 374 thousand and 424 thousand years ago. For some reason, in the two most recent interglacials, the Eemian, which lasted from about

114 thousand to 130 thousand years ago, and the present Holocene, which began about 10 thousand years ago, the Caucasian wingnut never made it back.[3]

It would be wonderful if we could follow the history of ginkgo in a similarly detailed way, but unfortunately its pollen grains are too easily confused with those of other plants. However, the example of the Caucasian wingnut does raise a potentially important but unanswered question concerning the ecology of ancient ginkgo: having been displaced from particular places by changing climates, did it have the ability to recolonize? Colder and drier climates may have progressively restricted ginkgo's geographic range, but why did it not bounce back? Surely it should have been able to recolonize those places where it obviously grows so well today.

In most plants, the ability to colonize an area depends on the effectiveness with which seeds are dispersed. Seed dispersal provides plants with the ability to emulate an animal and move from one place to another, albeit much more slowly, generation by generation. The fruits and seeds of many plants show specializations to increase the effectiveness of dispersal, from the parachute-like fruits of dandelions that are blown along by the wind to the seeds of blackberries that are gobbled up along with the fleshy fruits in which they develop and are dispersed in the droppings of birds. A key question in the case of ginkgo is whether one of the factors responsible for its decline over the past few million years was a poor system for dispersing its seeds.

In 1982 the tropical ecologist Dan Janzen and the paleontologist Paul Martin published a provocative article with an arresting title: "Neotropical Anachronisms: The Fruits the Gomphotheres Ate." Their central idea flowed from the observation that many of the common plants in Guanacaste National Park in Costa Rica, where Janzen had worked for many years, appeared to have no natural means of dispersing their seeds. They noted that this was particularly the case for some of the plants in which the fruits and seeds were relatively large, such as guanacaste itself and another legume tree, divi-divi. Today, the fruits and seeds of these trees are eaten by horses and cattle, but these animals have been introduced by people from elsewhere only relatively recently. There are no indigenous animals that appear capable of dispersing them. Janzen and Martin argued that this mismatch arose because these plants had been dispersed in the past by animals that are now extinct. The plants had survived, but the animals capable of dispersing their seeds had not.

Janzen and Martin suggested that such plants used to be dispersed by the large mammals that once inhabited South and Central America but disappeared relatively suddenly, perhaps as a result of hunting by humans, climate change, or both factors acting together, about ten thousand years ago. These now-extinct animals would have included the gomphotheres, massive extinct relatives of modern elephants, that were obviously plant eaters and flourished in Central America for most of the past five million years. Living alongside them were other fruit eaters like ground sloths, glyptodonts, extinct horses, extinct bears, giant armadillos, flat-headed peccaries, and others. Janzen and Martin's point was that the gomphotheres, along with other extinct large mammals, probably played an important role in the ecosystems of Central America over the past few hundred thousand years and that their relatively recent extinction has left us trying to understand an ecosystem that is missing some of its most important parts.[4]

What was most important about Janzen and Martin's idea was its focus on the importance of history for interpreting the world around us. The survival of the plants, after the extinction of the gomphotheres and other animals that may have dispersed them, was an accident of history. In effect the evolutionary histories of the plants and their associated animals were now out of phase. With some slight rhetorical license, Janzen and Martin called those plants that had lost their dispersal agents the "living dead." The implication was that without the dispersers with which they had evolved, their days were numbered.[5]

Janzen and Martin's ideas proved hugely influential, and in 1984 my paleobotanical colleague Bruce Tiffney of the University of California, Santa Barbara, suggested that something similar might have happened in the history of ginkgo. Bruce argued that ginkgo, like Janzen and Martin's tropical trees, was also one of the "living dead," a plant that had lost its dispersers. He speculated that the strange and strong-smelling ginkgo seed might have been a specialization for attracting dinosaurs, or perhaps early kinds of mammals that are now extinct.

Of course, an idea like this is hard to prove, but it does begin to hint at another reason, other than local extinction due to climate, as to why living ginkgo very nearly went extinct. The apparent migration around fifteen million to twenty-five million years ago of ginkgo into eastern and southeastern Europe, areas where it was not previously present, seems to suggest that dispersal was still possible long after the demise of dinosaurs and ancient extinct mammals. However, Bruce's point was nevertheless a good one. A lack of effectiveness in the dispersal of ginkgo seeds may have played a part in its progressive restriction, and the fact that this may reflect more recent extinctions, rather than ancient extinctions at the time of the dinosaurs, is in some ways beside the point.

Unfortunately, even though its smelly seeds are one of its most well-known and distinctive features, we know very little about how seed dispersal works in living ginkgo. However, germination does improve after the fleshy seed coat has been removed—for example, by passing through the gut of an animal. In one of the potentially wild ginkgo populations in China it is also documented that the seeds are eaten by a wild cat, and in Japan they are eaten by badgers. Dogs are sometimes attracted to them too. A friend recalls his dog feasting on ginkgo seeds one autumn on the University of Minnesota campus. It would be helpful to have more information on the kinds of animals attracted to ginkgo seeds today, but even if various mammals are known to collect and eat ginkgo seeds, this is not quite the same as knowing that ginkgo has a reliable seed disperser.[6]

If Bruce is broadly correct, and sometime toward the end of the Mesozoic, or more likely during the Cenozoic, ginkgo lost the animals on which it depended for dispersal, then the effects of climatic restriction would have been greatly amplified. It would have meant that ginkgo, unlike the Caucasian wingnut, for example, was not able to easily recolonize areas from which it had been displaced. It would have continually lost ground, and its populations would have become smaller, moving it ever closer to what conservationists sometimes call the extinction vortex. Colder or perhaps drier climates would have eaten away at ginkgo's once widespread geographic range, and limited powers of dispersal would have reduced ginkgo's ability to recolonize. The effect would have worked like a ratchet; once ginkgo lost ground it was unable to take it back. In North America and Europe the impact over the past few million years may have been especially pronounced if, as seems likely from the fossil evidence, the geographic extent of ginkgo in those areas had already been reduced by climatic drying and other vegetational changes. The mountains and valleys of southern and western China may have provided a greater variety of potential refuges.

Whatever the reason, the pattern of regional extinction could not be clearer. Ginkgo has a more or less continuous record in Asia beginning with the early fossils described by Zhou Zhiyan and his colleagues more than 200 million years ago. It continues through the Jurassic and Cretaceous, to the presence of ginkgo in fossil floras from the Pliocene of Japan. However, in Europe and North America the pattern is different. Here the fossil record of ginkgo is also deep but it is abruptly truncated relatively recently.[7]

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EXTINCTION

These insights provide a clear example of the importance of fossils to fully understand how our modern world came to be. The natural world is full of patterns, some of them completely unexpected, that can be explained only by reference to history, and as I never tire of saying to my students, if you want to understand the way anything is today, whether it is a plant, a person, an ecosystem, an organization, or a country, then you need to understand its history. It is a mantra that is hardly original, but one that is easily forgotten in our modern preoccupation with the here and now. In biology, these kinds of historical complications are the reason why we ignore evolution, and the direct historical evidence that comes from paleontology, at our peril.

In particular, the fossil record of ginkgo and similar plants helps make sense of a somewhat enigmatic observation made by botanists since the time of Linnaeus: that there are surprising similarities between the plants of eastern North America and eastern Asia. Highlighted at the end of the eighteenth century by the Italian botanist Luigi Castiglioni, and then later by the American Thomas Nuttall, the full extent of these similarities did not become clear until the work of the great nineteenth-century American botanist Asa Gray.[8]

Gray and his contemporaries were at a loss to explain how the pattern had come about. For Darwin, writing to Gray at Harvard in 1856, this was one of the "many utterly inexplicable problems" of botanical geography. Darwin was completely puzzled about why there should be stronger similarities between the flora of eastern North America and eastern Asia than between the floras of eastern and western North America. The fossil record shows beyond doubt, just as Gray later inferred, that these seemingly strange and widely separated occurrences are the result of regional extinction, especially in Europe and western North America, of plants that were once much more widespread. In the case of ginkgo regional extinction went even farther; the species was completely eliminated from Europe, from eastern and western North America, and also from Japan. Even in China its extinction was very nearly total.[9]

21. Extinction

1. Epigraph: From Jimmy Cliff's album *Jimmy Cliff,* 1969, Trojan Records. For more information on the Early Pliocene fossil vegetation in southern Europe, see Kovar-Eder et al. (2006).

2. The Willershausen flora is especially rich; more than 130 species have been collected, representing more than one hundred different kinds of plants. See Straus (1967); Ferguson (1967); Ferguson and Knobloch (1998).

3. Like ginkgo, the Caucasian wingnut has been reintroduced by people into many of the places where it once grew; there are large specimens of the Caucasian wingnut at Kew, for example, that date from the late nineteenth century. The nearest native populations are in the Caucasus, with its closest relative, a similar species native to China.

4. The gomphotheres may have persisted until as recently as six thousand years ago in present-day Colombia; see Rodríguez-Flórez et al. (2009). For a complete list of now-extinct large herbivores of Central America, see Janzen and Martin (1982, 21).

5. For a popular discussion and elaboration of Janzen and Martin's idea, see Barlow (2002).

6. Known foragers of the seeds of living ginkgo include the catlike *Paguma larvata* in China and the Japanese badger *Nyctereutes procyonoides.* Rothwell and Holt (1997) note the improved germination rates of seeds scarified by passing through the digestive tract of badgers.

7. By the end of the Pliocene, ginkgo had disappeared from the fossil record everywhere except perhaps for a small area of southern Japan; see Uemura (1997).

8. Castiglioni had visited North America between 1785 and 1787, and also had consulted *Flora Virginica,* published by Gronovius in 1739 and 1743, and Thunberg's *Flora Japonica* published in 1784: see Spongberg (1993). Asa Gray at Harvard was a frequent correspondent and staunch supporter of Darwin in North America. Darwin's letter to him on "botanical geography" was written on October 12, 1856. New information that Gray had at his disposal included Siebold's *Flora Japonica* as well as specimens brought back from the Rodgers-Ringgold Expedition (1853–1856), also known as the

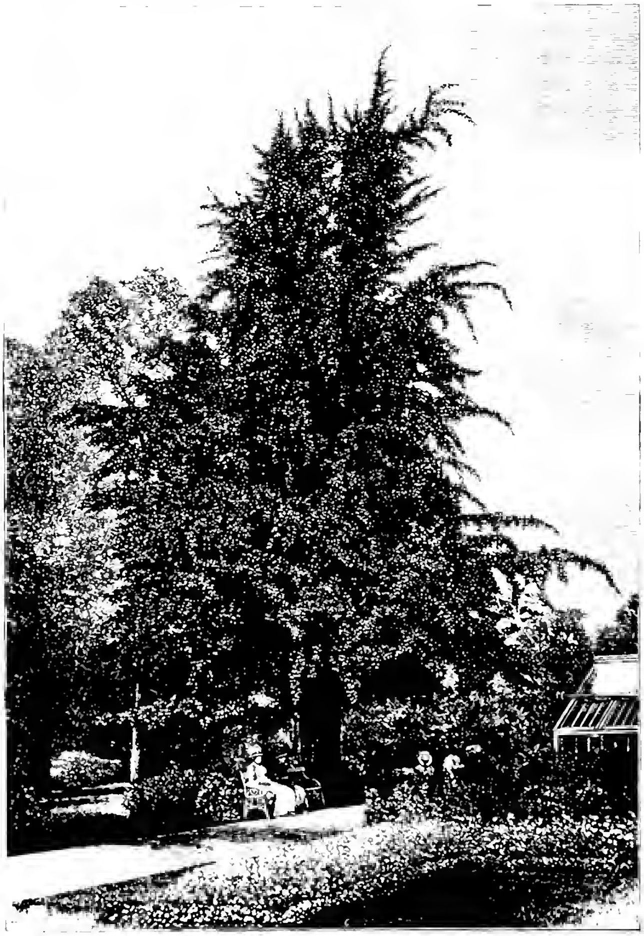
North Pacific Exploring and Surveying Expedition, a United States scientific and exploring project with the broader purpose of finding shorter trade routes for merchant ships in the Pacific; see Cole (1947). Also available were specimens brought back from Japan by Charles Wright.

9. Gray (1859, 422) listed about 580 Japanese species "which have particular relatives in other and distant parts of the northern temperate zone," along with the corresponding plants in the floras of Europe; central and northern Asia; western North America; and eastern North America. To explain the widely separated but highly similar floras of eastern Asia and eastern North America, Gray suggested that before the glacial epoch, the flora of the North Temperate Zone had been relatively homogeneous and that regional extinction during the Ice Ages resulted in greater losses from western North America and Europe. In some cases the impact of regional extinction was less pronounced. The sweet gum, for example, has widely separated remnants not only in eastern Asia and eastern North America, but also in southeastern Europe.

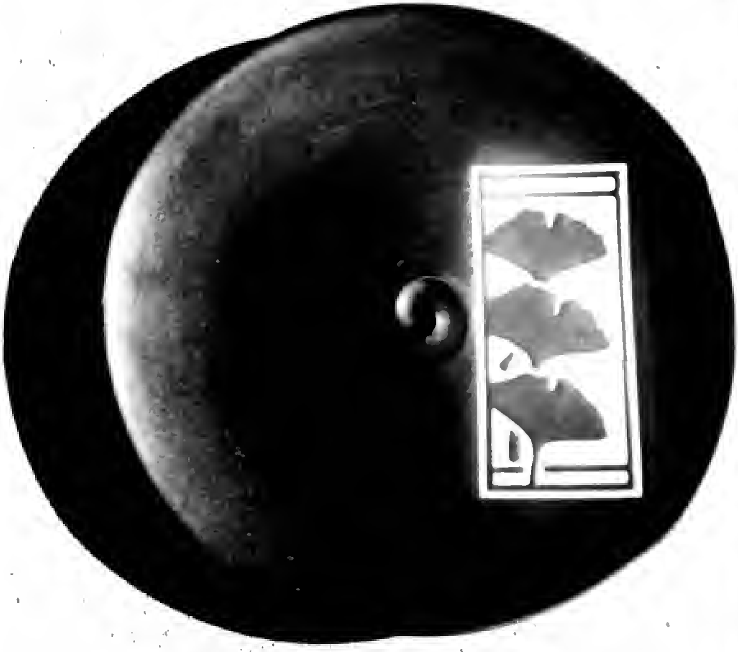
GINKGOPALOOZA

Peter Crane's book inspired us to gather a few ginkgo images. These pages show just a few of the aspects that make ginkgo such a fascinating plant.

AN ARTFULLY ESPALIERED GINKGO graces a wall of the Sterling Morton Library at the Morton Arboretum (right). At about 55 years old, this ginkgo is a youngster compared to the "Old Lion" ginkgo at the Royal Botanic Gardens, Kew. That venerable tree was planted in 1762 and is seen here in an engraving that originally appeared in the British publication *Gardeners' Chronicle* in March 1889 (lower left), and in a photograph from May 2010 (lower right).



PEOPLE LOVE GINKGOS. Clockwise from upper left: This wonderful 1921 E. H. Wilson photograph shows a woman hugging an enormous ginkgo at the Temple of the Yellow Dragon, Kuling (Su-shan), China (Wilson recorded the tree at 100 feet tall and with a trunk circumference of 19.5 feet, measured at 3 feet above ground level). Ginkgos stand behind a Buddha statue at the Sensō-ji temple in Tokyo. Over 100 (possibly 200) ginkgo cultivars have been selected, including those with dwarf, fastigiate, weeping, and globe-shaped habits as well as different leaf forms ('Variegata' is seen here). Ginkgophiles enjoy the golden glow under a ginkgo alleé along Icho Namiki (Ginkgo Avenue) in Tokyo.



THE GINKGO LEAF'S simple but elegant shape and unique dichotomous venation make it a work of art in itself. Over many centuries its iconic form has appeared on everything from street signs to silverware to shampoo bottles. Shown here (clockwise from upper left) are a live leaf, a plate from Japan, the 1916 woodblock print *Crow and Ginkgo Leaves* by Japanese artist Watanabe Seitei, a pair of silver sugar tongs, and a decorative wall tile.

2012 Weather Summary

Sue A. Pfeiffer

Temperatures were again above average in 2012; this was the first year in local recorded weather history that all 12 months had above average temperatures (in 2011, all months except for November were above average in temperature).

JANUARY began with warm temperatures, but a cold front moved in on the 4th and 5th, dropping the low to 10°F. Temperatures rebounded until a second cold front passed through on the 15th and 16th; the low of 6°F, which occurred on both nights, was the low temperature for the year. Overall the month was warm with an average temperature above freezing, almost 8°F warmer than the previous year. Snowfall was well below average—only 4.8 inches accumulated. Most of this snow fell between the 17th and the 22nd, and by the 26th, the snowpack had completely melted. Despite the lack of significant snow accumulation, January was damp and dreary as we received some type of precipitation on 16 out of 31 days.

FEBRUARY was warm and extremely dry. High temperatures in the 40s and 50s occurred on 24 of 29 days and on only one occasion was a high below freezing recorded (28°F on the 13th). Only trace amounts of snowfall were recorded and the ground remained bare for the entire month. February was pleasant and calm except for one storm that passed through on the 25th, dropping 0.52 inches of rain and bringing along wind gusts over 50 mph. This storm provided most of the precipitation for the month as only 0.68 inches fell, well below the 30-year historical average of 4.24 inches. These warm temperatures and dry conditions allowed the horticulturists and arborists access to the collections to prune and mulch.

MARCH began with 4 days of precipitation that fell as a rain-snow mix, delivering some much-needed moisture to soils. This storm brought 1.73 inches of rain equivalence, including 1.8 inches of snow, but by March 6th all snow had melted away. The remainder of the month was dry; the month's total precipitation of 1.99 inches fell far below the 30-year historic average of 5.58 inches. The lack of snowfall in November and December of 2011, coupled with the below average precipitation during February and March and above average temperatures, left soils extremely dry. March was also a month of extreme temperatures—from the 18th to the 23rd we reached temperatures from 75°F to a record high of 82°F, which forced many plants into full

JON HETMAN

An incredibly mild winter led to very early bloom at the Arboretum, including these magnolias in flower on March 22, 2012.

bloom. These extreme highs were followed by extreme lows as temperatures dipped to 25°F and 26°F on March 26th and 27th respectively. These frosty conditions caused visible damage to many plants in full bloom, turning petals brown. The average high temperature for the month was 54°F, 10°F warmer than the 30-year historic average of 44°F. According to NOAA's National Climate Data Center, March 2012 was the warmest month on record in all of the lower 48 states; 15,000 weather related records (7,755 daytime records and 7,517 nighttime records) were broken and at least one record was broken in each of the 50 states.

APRIL was another warm month, with the average high temperature 6°F above the average and a record setting high temperature of 90°F on April 16th. Warm temperatures lead certain plants into early flowering but caused visible stress to others. The lack of moisture during the first three weeks was evident as buds dried up and fell off; twig dieback was observed on young shrubs and plants with shallow root systems. On April 23rd, 2.81 inches of much-needed precipitation fell. Following this rain event, many plants leafed out almost immediately, greening up the landscape. This spring was highly unusual, marked with lack of precipitation and high temperatures.

MAY provided typical spring weather; precipitation was frequent as we received rain 14 out of the first 17 days. This much-needed moisture continued the greening of the landscape as leaves emerged and plants recovered from earlier drought conditions. Warmer temperatures during April allowed many plants to flower earlier than usual, including those in our famous lilac collection. Fortunately, cooler temperatures during early May sustained lilac blooms until Lilac Sunday on May 13th. We reached a high of 85°F on the 27th and a low of 42°F on the 11th. Both temperature and precipitation were slightly above the historic averages.

JUNE began with six straight days of rain, cloudy conditions, and cooler temperatures with highs in the 50s and 60s (far below the mid 70s average for the month) and overnight lows in the 40s. A fast-moving storm came through on the 8th, delivering thunder, lightning, and an additional 0.41 inches of precipitation in a relatively short period of time. Minor damage was reported, with tree limbs down and a lightning strike on a mature white pine, which resulted in its decline and eventual removal. This opening week brought 2.24 inches of rain in total, leaving soils plenty moist. Mid-June saw temperatures return to normal with mostly sunny conditions. Temperatures continued to rise as we experienced a record breaking 3-day heat wave from the 20th to the 22nd with temperatures reaching 95°F. This sudden increase in temperature caused recent transplants to flag. Relief from the heat came on the afternoon of June 22nd as a thunderstorm delivered 0.67 inches of rain. Steady precipitation continued on the 24th and 25th and later that evening a violent thunderstorm delivered 2.43 inches of rain along with minor damage to the collections. Already moist soils could not absorb this rapidly falling rain, resulting in flooding and erosion damage in the collections and on secondary gravel roads. Overall, the cool temperatures early in the month were balanced by the heat wave during the latter part of the month, leaving us with above average temperatures for the month. Rainfall was 6.10 inches, well above the average of 4.31 inches for the month.

JULY was the warmest month of the year with highs mostly in the 80s and 90s. The month started off sunny and warm with minimal precipitation and consistently high temperatures in the 80s. A 6-day heat wave (temperatures 90°F or higher) occurred from July 13th to the 18th, peaking at 95°F on July 17th. Humidity was also high and the heat index reached above 100°F. Both people and plants were stressed; recent transplants, in particular, required vigilant monitoring and supplemental irrigation. A cold front moved in during the afternoon of the 18th bringing an evening of thunderstorms, hail, and a spectacular lightning show. The system dropped 1.53 inches of rain and brought with it more bearable temperatures in the 70s and low 80s. Storms on the 24th and 29th provided additional precipitation.

AUGUST was sunny, hot, and humid. Rain on the 1st and 2nd (1.21 inches total) and the monthly high temperature (92°F) on the 3rd lead to very high humidity—98%—during the first week. Several thunderstorms with intermittent rainfall from the 11th through the 18th delivered an additional 1.6 inches of precipitation. The remainder of the month provided ideal summer conditions—sunny days with high temperatures in the mid 80s and lows in the 60s. Arboretum visitation increased as these comfortable conditions set in. Overall it was a fairly typical August, with average high temperatures 5°F warmer than normal and below average precipitation.

SEPTEMBER rainfall was slightly below average and temperatures were slightly above average. We received 3.90 inches of rainfall this month, most of which fell during four well-spaced events on the 5th, 9th, 18th–19th, and 29th, providing consistent moisture to plants throughout the month. The storm that passed through on the evening of the 18th and into the 19th brought strong winds, with gusts of over 30 mph recorded. Temperatures were slightly above average; the high of the month was 85°F on the 8th and the low was 41°F on the 24th. The grounds continued to look lush and showed no signs that fall was on the way.

SUE A PFEIFFER

A large sugar maple (*Acer saccharum*) limb broke and fell near the Centre Street Gate on September 8, 2012, a windy day with gusts over 20 mph.

OCTOBER started off with consistent rain events during 13 of the first 16 days but provided only 0.96 inches of rain in total. The first frost occurred on the 12th, ending the growing season at 194 days. The monthly high was 80°F on the 16th and the low was 31°F on the 12th. The main weather event of the month was the arrival of Superstorm Sandy, which was initially predicted to hit Boston head on. As the late season hurricane moved up the east coast its path shifted to the south as it swung around and plowed straight into the New Jersey–New York (Long Island) areas during the evening of the 29th. At the Arboretum, the storm arrived

JIM PAPARGIRIS

Autumn color was in full swing at the Arboretum on October 24, 2012.

with light rain and increasing winds on the 29th; a maximum wind gust of 25.3 mph was recorded in the early afternoon. On Monday, conditions intensified with wind gusts from 30 mph to a maximum of 50.3 mph (recorded at 2:15 and 2:30 p.m. at the Weld Hill Research Building). Sustained winds ranged from 20 to 23 mph throughout the afternoon. At 8:45 p.m. wind speed and gusts dropped suddenly and the atmospheric pressure and air temperature began to rise. We were very fortunate not to receive a direct hit from Superstorm Sandy, but there was some damage at the Arboretum. About two dozen trees were lost; many of these were older and located in natural areas. Despite the storm's 2.66 inches of rain, precipitation for the month remained below the 30-year historic average of 4.69 inches.

NOVEMBER was a relatively dry month with only 1.46 inches recorded (well below the 4.76 inch average). Half of that rain equivalence came from the winter's first snowfall, 2.5 inches overnight on the 7th–8th. Temperatures in the 50s quickly melted the snow. This storm brought high sustained winds with gusts over 30 mph on both days. A warm front brought temperatures into the mid 60s from the11th through the 13th, but this warm weather did not last as more seasonal temperatures in the 40s and low 50s set in for the remainder of the month. Overall temperatures were slightly above the historic average. We reached a high of 67°F on November 12th and a low of 26°F on the 29th.

DECEMBER was an extremely wet month with variable temperatures. We received a total of 7.11 inches of precipitation, of which 6.08 inches fell during the second half of the month. Most of the total precipitation arrived as rain except for 4 inches of snow on the 30th. Two large storms passed through bringing high winds and heavy rain; the event of December 21st and 22nd brought wind gusts of 35 mph and 30 mph and 0.8 inches of rain while the storm on the 27th brought gusts of over 40 mph and 2.49 inches of rain. We reached our highest temperature of 60°F on December 10th and the average high temperature for the month was 44.2°F, more than 5°F warmer than average. Daily high temperatures did not dip below the freezing mark until the final day of the year, when we reached only 29°F and had a low of 16°F. What a way to end this unusually warm year—with one of the coldest days of 2012!

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Arnold Arboretum Weather Station Data • 2012

	Avg. Max. (°F)	Avg. Min. (°F)	Avg. Temp. (°F)	Max. Temp. (°F)	Min. Temp. (°F)	Precipi-tation (inches)	Snow-fall (inches)
JAN	41.1	24.2	32.7	59	6	3.62	4.80
FEB	44.3	25.9	35.1	57	13	0.68	
MAR	54.0	35.6	44.8	82	19	1.99	1.80
APR	62.3	41.1	51.7	90	29	3.54	
MAY	68.5	52.4	60.5	85	42	4.14	
JUN	74.9	56.9	65.9	95	47	6.10	
JUL	85.2	65.0	75.1	95	56	3.23	
AUG	83.8	64.0	73.9	92	53	2.92	
SEP	74.1	54.3	64.2	89	41	3.90	
OCT	64.4	46.1	55.3	80	31	4.28	
NOV	48.0	33.6	40.8	69	26	1.46	2.50
DEC	44.2	30.3	37.1	60	16	7.11	4.10

Average Maximum Temperature . . . . 62.1°F

Average Minimum Temperature . . . . 44.1°F

Average Temperature . . . . 53.1°F

Total Precipitation . . . . 42.97 inches

Total Snowfall in 2012 . . . . 13.39 inches

Snowfall During Winter 2011–2012 . . . . 8.79 inches

Warmest Temperature . . . . 95°F on June 20, June 22, and July 17

Coldest Temperature . . . . 6°F on January 15 and January 16

Last Frost Date . . . . 29°F on April 1

First Frost Date . . . . 31°F on October 13

Growing Season . . . . 194 days

Growing Degree Days . . . . 3294.5 days

The Sweet Smell of Spring: *Abelia mosanensis*

Nancy Rose

Someday I really want to publish a scratch-and-sniff issue of *Arnoldia*, providing a "by the nose" tour of the Arnold Arboretum. I'd probably skip the less pleasant odors—skunk cabbage, ripe ginkgo cones, the stinkhorn fungi that pop up in mulched planting beds—in favor of the many truly wonderful scents to be found here. While pleasant fragrances occur from winter (e.g., the flowers of *Hamamelis mollis* 'Princeton Gold') through autumn (e.g., falling *Cercidiphyllum japonicum* leaves), the floral explosion from mid-spring to early summer brings the peak sniffing season.

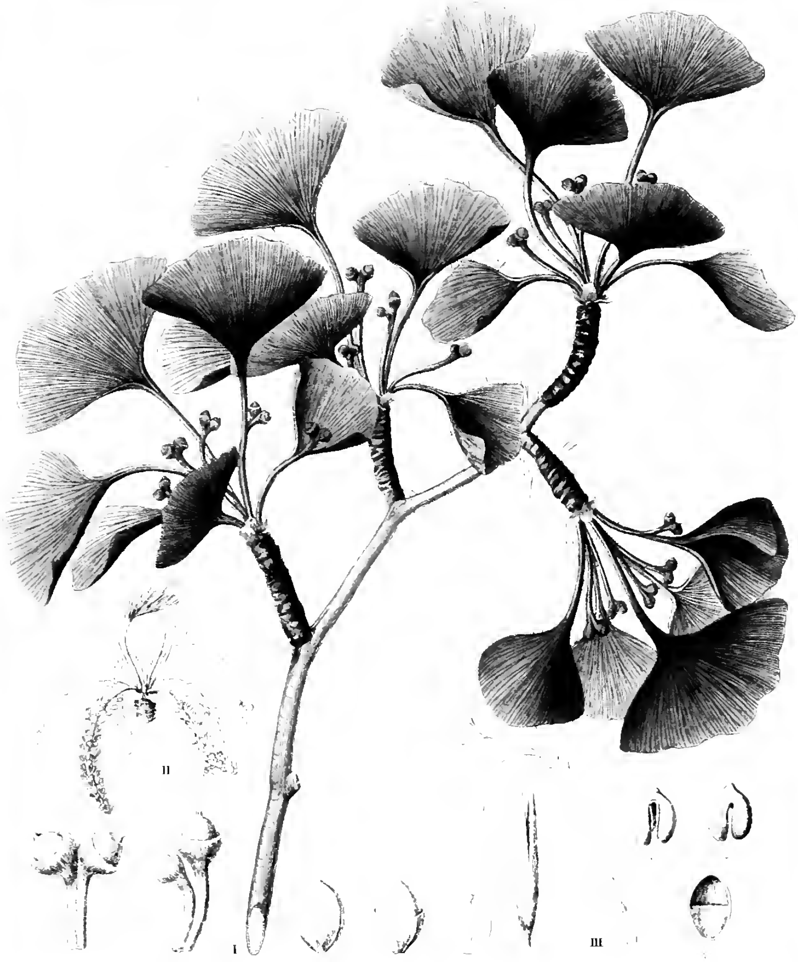
Come May, there are plenty of sweet-smelling flowers to stick my nose into but my current favorite is the aptly named fragrant abelia (*Abelia mosanensis*). This deciduous abelia is less well known than glossy abelia (*Abelia* × *grandiflora*), an evergreen or semi-evergreen hybrid species that, with its many cultivars, is a popular landscape plant, particularly in the southeastern quarter of the United States. Fragrant abelia is a somewhat rangy shrub, forming a loose mound of slender, arching stems and reaching a height of 4 to 6 feet (1.2 to 1.8 meters), possibly taller, with an equal or slightly greater width. Its bright green, ovate leaves often have a bronze or reddish tint when emerging. Some sources claim that fragrant abelia has showy red-orange autumn foliage, but specimens at the Arboretum have turned pinkish brown at best.

Fragrant abelia blooms in May to early June at the Arboretum. Flowers are borne in short terminal panicles. The flower buds are rich reddish pink and open to white, funnelform flowers with 5-lobed corollas. The obovate sepals often have an attractive pink tint and persist long after the flowers fall. The fruit is a leathery achene topped by the persistent sepals. But back to the flowers. They are marvelously fragrant, but it's difficult to put into words exactly what the fragrance is (this is where I need that scratch-and-sniff feature). References variously compare the fragrance to lilacs, lilies, hyacinths, and Korean spice viburnum (*Viburnum carlesii*). I think I'd go with the best-scented common lilac (*Syringa vulgaris*), maybe 'President Lincoln', plus a hint of orange blossom, a drop of lily-of-the-valley (*Convallaria majalis*), and a shot of tropical fruit.

The Arboretum has a limited history with *Abelia mosanensis*. The species is native to Korea but was not collected by Ernest Henry Wilson on his expeditions there (in fact, the species name was not published until 1926, eight years after Wilson's last visit to Korea). During an October 1977 plant collecting expedition to South Korea, Arboretum botanists Steven Spongberg and Richard Weaver collected *Abelia mosanensis* seeds in the Seoul National University Forest near Kwangyang in Cholla-Namdo Province. Arboretum greenhouse records indicate that the seeds were sown but there was no germination. We currently have three specimens of fragrant abelia at the Arboretum, all growing in the Leventritt Shrub and Vine Garden. There are two individuals of accession 282-2003, which were purchased as container-grown plants from Spring Meadow Nursery in 2003. There is one plant of accession 591-2003, which was grown from seeds received from the Academy of Science in Salaspils, Latvia. The seeds were offered in the Academy's Index Seminum (seed exchange list) and were collected from cultivated plants growing at a garden in Latvia.

Fragrant abelia is available from a number of commercial sources. It is considered cold hardy through USDA zone 5 (average annual minimum temperature -20 to -10°F [-28.9 to -23.3°C]) and grows best in full sun or partial shade and moist, fertile, somewhat acidic soil. Though perhaps not the tidiest or most handsome of shrubs, it is worth growing just for the delicious fragrance of its flowers.

Nancy Rose is a horticulturist and the editor of *Arnoldia*.



SALISBURIA adiantifolia