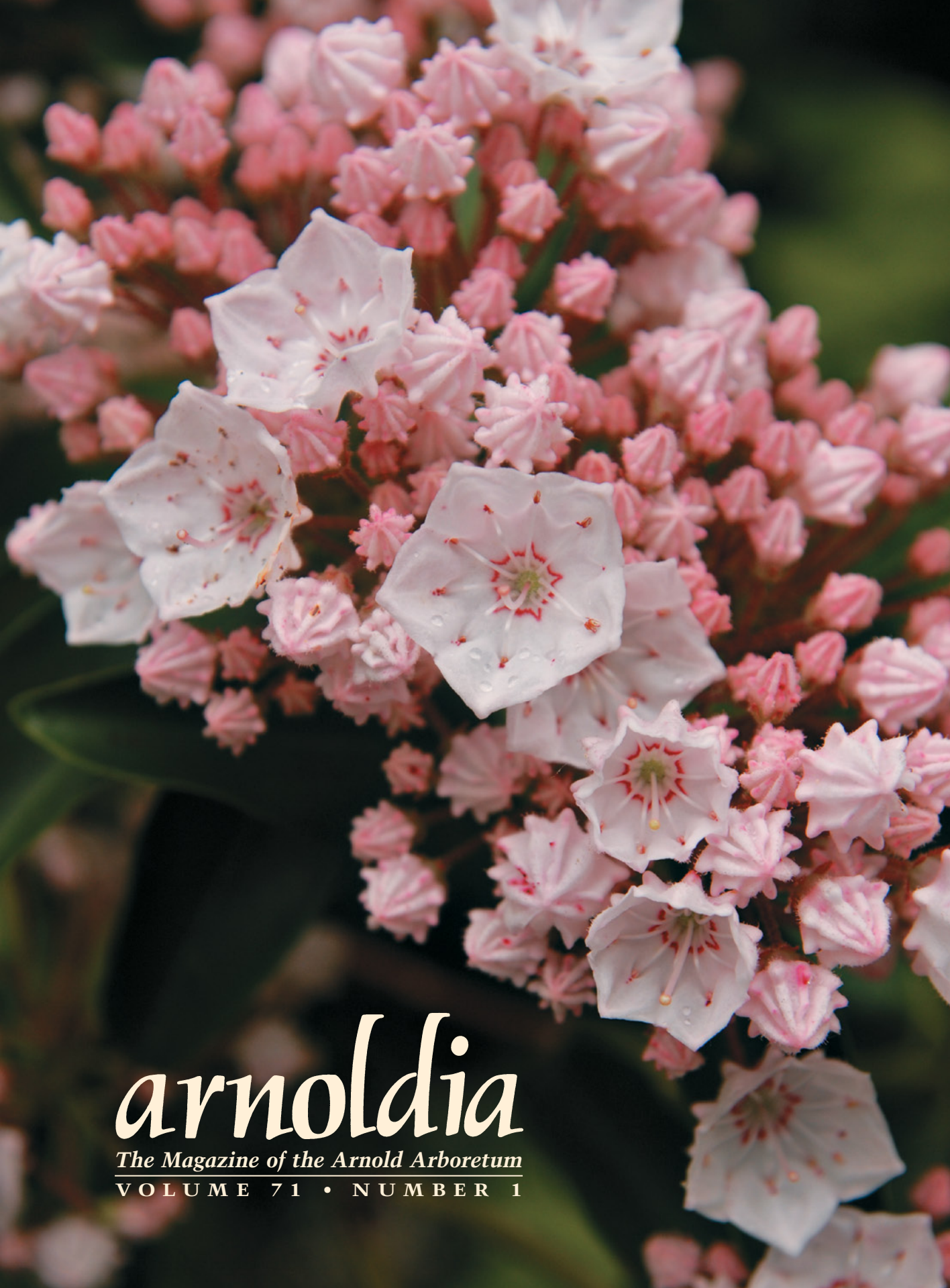

arnoldia

The Magazine of the Arnold Arboretum

VOLUME 71 • NUMBER 1

arnoldia

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VOLUME 71 • NUMBER 1 • 2013

Arnoldia (ISSN 0004–2633; USPS 866–100) is published quarterly by the Arnold Arboretum of Harvard University. Periodicals postage paid at Boston, Massachusetts.

Subscriptions are $20.00 per calendar year domestic, $25.00 foreign, payable in advance. Remittances may be made in U.S. dollars, by check drawn on a U.S. bank; by international money order; or by Visa, Mastercard, or American Express. Send orders, remittances, requests to purchase back issues, change-of-address notices, and all other subscription-related communications to Circulation Manager, *Arnoldia,* Arnold Arboretum, 125 Arborway, Boston, MA 02130-3500. Telephone 617.524.1718; fax 617.524.1418; e-mail arnoldia@arnarb.harvard.edu

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Postmaster: Send address changes to
Arnoldia Circulation Manager
The Arnold Arboretum
125 Arborway
Boston, MA 02130–3500

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The ARNOLD ARBORETUM of HARVARD UNIVERSITY

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Mutants in our Midst

William E. Friedman

What is horticulture? At its core, it is a human celebration, whether conscious or unconscious, of the very fact of evolution. It is thousands of years of detecting and rejoicing in the rare: the selection of the novel form that somehow pleases the human aesthetic or serves to feed the world. Although often overlooked, many of the wonderful horticultural varieties that grow in botanical gardens (as well as in backyard gardens) are premier examples of the amazing and ongoing process of evolution: random mutations that lead, *on the rarest of occasions,* to novel and desirable biological characteristics—as opposed to novel and neutral or undesirable characteristics.

Charles Darwin was an avid consumer of horticultural literature and information, and was a frequent correspondent with the most eminent horticulturists of the nineteenth century. Over the course of his life, he wrote 55 notes and articles in the *Gardeners' Chronicle and Agricultural Gazette,* one of the most widely circulated horticultural periodicals of his time. He covered everything from how pea and bean flowers are pollinated (Darwin 1857, 1858, 1866) to the origin of variant forms of roses in cultivation (Darwin 1868). He wrote of his observations of and interest in the origin of double-flowered forms (Darwin 1843) and variegated leaves (Darwin 1844). No horticultural phenomenon was beyond his interest. Indeed, Darwin looked to the world of horticulture and plant domestication in order to gain critical insights into the generation of variation and the process of natural selection that underlie evolutionary change. In essence, Darwin was intensely interested in mutants in our midst.

EVOLUTION AT THE ARBORETUM

The Arnold Arboretum of Harvard University hosts a remarkable collection of more than 15,000 accessioned woody temperate plants distributed in over 2,000 different species. This living collection contains wild-collected trees, shrubs, and vines, as well as a spectacular set of horticultural varieties whose very presence is the result of human discovery and propagation of desirable variants. Many of these horticultural varieties are the result of the never-ending process of spontaneous mutations that occur in all organisms and serve to create novel

GEOFF BRYANT

Charles Darwin wrote about many horticultural topics including variegated pelargoniums, which were very popular in the Victorian era. 'Mrs. Pollack', seen here, was introduced in 1858.

> **"Florists have attended in some instances to the leaves of their plant, and have thus produced the most elegant and symmetrical patterns of white, red, and green, which, as in the case of the pelargonium, are sometimes strictly inherited."**
>
> **— Charles Darwin, *The Variation of Animals and Plants Under Domestication*, 1868**

Variety, Form, or Cultivar?

HOW TO NAME a variant plant is the topic of some taxonomic debate and often results in multiple versions of the plant's name. As taxonomic understanding and interpretation changes through the years it often results in changed nomenclature, reflected in the *International Code of Nomenclature* and the *International Code of Nomenclature for Cultivated Plants*. A quick reference search finds the white-flowered redbud mentioned in this article listed as *Cercis canadensis* var. *alba, Cercis canadensis* f.[forma] *alba,* or *Cercis canadensis* 'Alba'(a cultivar name). The same range of synonyms are found for the mutant *Kalmia latifolia* (var. *polypetala,* f. *polypetala,* or 'Polypetala') featured later in the article. To add to the confusion, in common usage the words "variety" and "form" are often broadly applied ("I like pink varieties of roses") or used when referring to a cultivar. For this article, I have used the scientific names as they appear in the Arboretum's collections database.

PAUL W. MEYER, MORRIS ARBORETUM

Eastern redbud (*Cercis canadensis*) blooms throughout its canopy, producing a spectacular spring display.

traits—the very stuff of evolution. These variant plants, referred to as "sports," arise in a single generation and have undergone a dramatic change in phenotype (the biological properties of the organism) from the parent plant and species. Typically, sports are discovered as a single branching system on a tree or shrub that differs significantly in its morphology, coloration, or other biological properties from the rest of the parent plant. The source of the biological novelty is random mutation, and subsequent vegetative propagation (e.g., grafting, rooting of cuttings, tissue culture) allows the new form to be cloned for further dissemination.

Since arriving at the Arnold Arboretum in January 2011, I have fallen in love with these wonderful horticultural results of random genetic mutations and the creation of novelty

in plants. And in turn, I have come to see the Arboretum (and all botanical gardens) as among the best places to actually observe evolution, and importantly, how evolution works. A walk in any woodland would indeed expose the rambler to mutant forms of plants, but most of these would be so subtle as to evade the senses of all but the most acute observer. On the other hand, a walk through the Arboretum essentially concentrates the opportunity to witness the results of evolution—many of our horticultural gems are representatives of the even rarer forms of mutations that are dramatic and easily observable. In this article, I will examine two cases of mutants in our midst at the Arboretum. Each is the result of what is likely to be a single genetic mutation that caused a major change in the color or morphology of the plant that bears the aberrant copy of the gene.

THE REDBUD AND THE ORIGIN OF NOVEL FLOWER COLOR

> "A long list could easily be given of "sporting plants;" by this term gardeners mean a single bud or offset, which suddenly assumes a new and sometimes very different character from that of the rest of the plant. Such buds can be propagated by grafting, &c., and sometimes by seed. These "sports" are extremely rare under nature…"
>
> Charles Darwin, *On the Origin of Species,* 1859

> "Many cases have been recorded of a whole plant, or single branch, or bud, suddenly producing flowers different from the proper type in colour, form, size, doubleness, or other character. Half the flower, or a smaller segment, sometimes changes colour."
>
> Charles Darwin, *The Variation of Animals and Plants under Domestication,* 1868

The eastern redbud, *Cercis canadensis* (pea family, Fabaceae), is a widely distributed small tree species native to the eastern and midwestern United States from Connecticut south to Florida and over to Oklahoma and parts of Texas. Every spring, it can be counted on for its clusters of pink and magenta flowers that appear throughout the leafless canopy just prior to the production of new leafy shoots. The Arnold Arboretum has more than twenty accessioned specimens of *Cercis canadensis.* One of these trees (accession 10-68-B), however, has had something remarkable occur—it has undergone a spontaneous (and random) mutation that changes the color of the flowers from the normal ("wild-type") pink and magenta to mostly white.

MILES SAX

About a decade ago, a mutation that eliminated most of the synthesis of red pigmentation in flowers occurred on a branch of an Arboretum redbud (*Cercis canadensis,* accession 10-68-B), producing pink-tinged white flowers on that branch.

For several decades after its establishment in the Arboretum collections, this specimen produced the characteristic clusters of pink and magenta flowers on all of its two-year and older woody branches. However, beginning about ten years ago (see below for details on how this was determined), one of the branches on this tree began to produce flowers that are

WILLIAM E. FRIEDMAN

This cluster of flowers shows both the normal (pink and magenta) and the mutant (whitish) forms found on the Arboretum's mutant redbud.

mostly, but not entirely, white. It was not, however, until the spring of 2009 that these aberrant flowers were first noticed by Arboretum staff. The flowers are beautiful, and novel and rare in a way that every lover of new horticultural forms can appreciate. Now, every year, this redbud continues to produce the typical pink and magenta flowers on most of its shoot systems, with whitish flowers on a single lateral set of branches that bear the mutant gene that results in altered flower color.

Interestingly, this is by no means the first horticultural variant of the eastern redbud to sport white flowers. A widely grown one, *Cercis canadensis* 'Alba' (often referred to as *C. canadensis* f. *alba* from its earlier botanical description) can be found in gardens throughout the United States. It has pure white flowers, with no trace of red pigmentation. Although it has not been scientifically studied, it is very likely that the mutation that created 'Alba' was one that "broke" or entirely suppressed the expression of the biochemical pathway to produce red pigmentation in these plants. Even young leaves, which typically have a purplish

WILLIAM E. FRIEDMAN

(Top to bottom) normal redbud flower with full red pigmentation; one of the mutant flowers, with pink splotches on the petals and a lighter pink calyx showing that some red pigmentation is still expressed; and a flower of 'Alba', with distinctly green sepals and white petals lacking any red pigmentation.

WILLIAM E. FRIEDMAN

This white flowered cultivar of redbud (*Cercis canadensis* 'Alba', accession 372-2001-A) produces flowers that are pure white, with no evidence of any red pigmentation.

or reddish hue in normal eastern redbuds, are green in 'Alba', suggesting that red pigmentation from anthocyanins is lacking from these plants. Another white-flowered cultivar of eastern redbud, 'Royal White', also lacks red pigmentation in its flowers and young emerging leaves.

Both 'Alba' and 'Royal White' arose on separate occasions when a parent plant underwent a spontaneous mutation that disabled the biochemical pathway that produces the red pigment anthocyanin. 'Alba' originated in the nursery of John Teas and Son in Carthage, Missouri, around the turn of the last century (Rehder 1907; Anonymous 1922). Both the Arnold Arboretum and the Missouri Botanical Garden acquired this cultivar in 1903. Sadly, the Arboretum's specimen perished in 1930, perhaps a reflection of the greater sensitivity to cold of this cultivar. 'Royal White' was discovered as a seedling in Bluffs, Illinois, in the 1940s. For each of these white-flowered redbud variants, it might well have been the case that had no one observed the mutant form, natural selection would have culled this variant from the gene pool as a consequence of its being less fit than its red-pigmented cousins. Flower color is an important biological attribute and in the case of redbuds in a state of nature, almost certainly affects rates of insect pollination. A variant lacking the standard red pigmentation might still be visited by bees and other insects, but perhaps at lower rates. In addition, anthocyanins may also serve as photoprotectants for plants. Young leaves, while expanding to mature size, can be very sensitive to high light levels, and red pigmentation can serve an important role in helping these tender leaves to avoid being sunburned and permanently damaged (Close and Beadle 2003).

In the case of the remarkable eastern redbud with the whitish flowers at the Arboretum, the genetic mutation has caused these flowers to lose most, but not all, of their red pigmentation. A careful examination of the mutant flowers shows that there is still red pigmentation present, although in significantly lesser amounts. The calyx (the collective term for the sepals of a flower) is pink with streaks of green. This is similar to the calyx of the normal flowers, except that in a normal flower (found on the rest of the tree), the calyx appears to contain more anthocyanins that render it more deeply pigmented.

The petals of the mutant redbud flowers also show something rather interesting. At first glance the flowers appear white, but a closer look under the microscope demonstrates that there are often small patches of pink pigmentation on the petals. The banner petal (upper center petal) often displays relatively strong expression of magenta in radiating streaks that lie between the veins of this specialized petal. Interestingly, returning to examine the normal flowers reveals that the banner petal, while clearly pink, also has more intense zones of deep magenta that radiate out and lie between the veins. This is true on the tree's non-mutant flowers, as well as on flowers of other standard redbuds (Robertson 1976). A pattern of red streaking is characteristic of what are commonly called nectar guides, displays

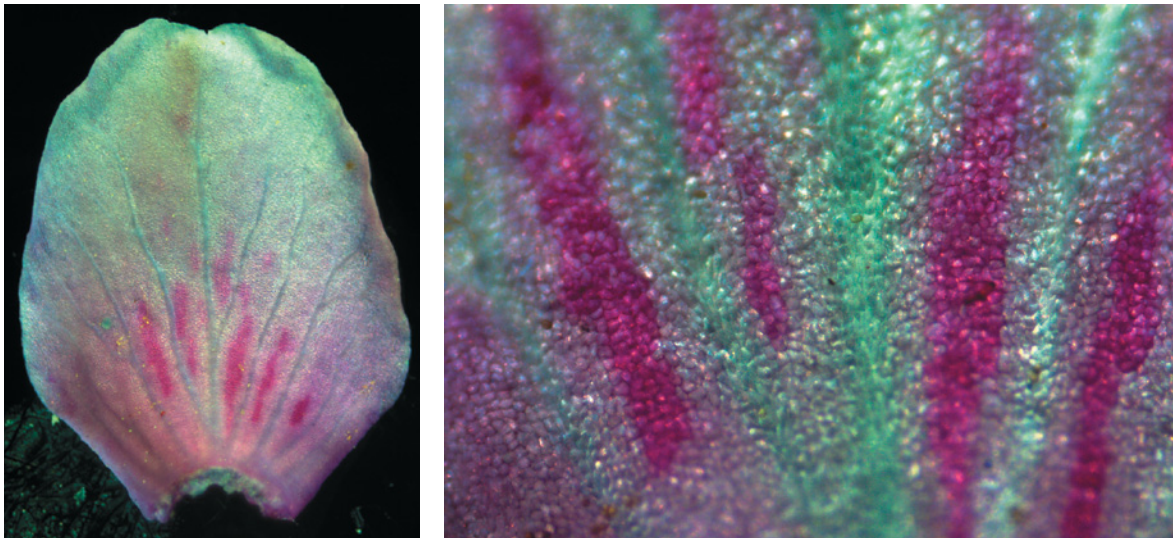
of pigmentation that help insect pollinators orient properly as they approach the flower during pollination. Nectar guides are much the same as the lighting on an airport runway, helping the airplane pilot to properly approach the landing strip.

Finally, in the mutant redbud flowers the female reproductive parts, particularly the style and stigma, differ in pigmentation from the wild type. In normal redbud flowers, the style displays a reddish color, as a consequence of the expression of the biochemical pathways to create anthocyanins. Under the microscope, it becomes evident that the mutant flowers have styles that lack any obvious red pigmentation.

What does all of this mean? It suggests that unlike 'Alba' and 'Royal White', which appear to have entirely lost the ability to create anthocyanins (at least in the flowers and young leaves), the Arboretum variant has a mutation that alters *where* the anthocyanins are produced. In other words, it still makes red pigmentation, but the cellular machinery that might otherwise produce this pigmentation throughout the petals and the style is no longer turned on in these places.

How do we know when and where this remarkable single mutation occurred in the Arboretum redbud variant? The answer lies in a basic knowledge of how plants grow and a specific knowledge of an unusual pattern of flowering that can be found in redbud trees. At the tip of every branch of every tree, there is a small group of cells that remains perpetually embryonic and undifferentiated. These cells form the apical meristem, and are similar to stem cells in humans. Every year this small population of cells divides, and in dividing creates the new tissues that will differentiate into stems and leaves. If a mutation occurs in one of the cells of the apical meristem, this mutation may come to populate some or all of the cells, and hence the differentiated stem, leaf, and flower cells that are descended from this mutant apical meristem.

In the Arboretum's mutant redbud, the mutation that reduced the production of anthocyanins in the flowers of this tree can be found on a set of branches that are all descended from an original mutant meristem of the growing tip of a single shoot. The ability to determine when this mutation occurred in a shoot apical meristem can be deduced because of a specific and somewhat unusual characteristic of all redbud trees. Redbuds exhibit a phenomenon known as cauliflory (Owens et al. 1995). Translated literally, cauliflory means flowering on stems. However, in botanical usage, cauliflory refers to the production of flowers on older woody stems. A careful examination of redbud trees reveals



WILLIAM E. FRIEDMAN

This banner petal of a mutant flower clearly shows magenta lines that act as nectar guides for insects (a close-up of the nectar guides under the compound microscope is seen at right).

WILLIAM E. FRIEDMAN

Redbud's trait of cauliflory (production of flowers on older stems) helped with determining when the mutation that eliminated most of the synthesis of red pigmentation in flowers occurred in this tree.

clusters of flowers that can be found along all of the branching systems (except for the current year's new shoots) and even the trunk of the tree. It is the phenomenon of cauliflory that makes redbuds so spectacular when they flower. Rather than having flowers restricted to the newest growth of the plant, flowering in redbuds is spread throughout the entire leafless canopy.

In the photo above, you can see two clusters of flowers on an old branch of our mutant redbud tree. One of the clusters of flowers is wild type, with a magenta calyx and typical pink petals. Just inches away, another cluster of flowers can be seen with a lighter pink calyx and petals that are almost exclusively white. This tells us that the population of cells making new magenta and pink flowers each year are different from the nearby population of cells making largely white flowers. Years ago, when the shoot apical meristem was growing at this point, the mutation that reduced production of anthocyanins in flowers occurred. From that point forward, all of the cells of the subsequent shoots contained the mutation creating the whitish flowers. Because of cauliflory, the tree continues to produce flowers on parts of the shoot system that in other kinds of plants would no longer produce flowers. And this allows us to infer that about ten years ago, a mutation occurred in the cells of the growing tip of the shoot when it was located between the typical cluster of magenta and pink flowers and the more distal cluster of mutant white flowers.

THE MOUNTAIN LAUREL AND THE ORIGIN OF NOVEL FLOWER FORM

> "We have before us a novel and specially interesting monstrosity which is described by these terms. It was discovered by Miss Bryant, at South Deerfield in this state [Massachusetts], and we are indebted to her, through a common friend, for the specimens before us. Among the shrubs of *Kalmia latifolia* which abound in a swamp belonging to Col. Bryant, a few have been noticed as producing, year after year, blossoms in singular contrast to the ordinary ones of this most ornamental shrub, and which, indeed, are more curious than beautiful. The corolla, instead of the saucer-shaped and barely 5-lobed cup, is divided completely into five narrowly linear or even thread-shaped petals. These are flat at the base, and scarcely if at all broader than the lobes of the calyx with which they alternate, but above by the revolution of the margins they become almost thread-shaped, and so resemble filaments. This resemblance to stamens goes further; for most of them are actually tipped with an imperfect anther; that is, the corolla is separated into its five component petals, and these transformed into stamens."
>
> Asa Gray, 1870

Kalmia latifolia, mountain laurel, is a member of the heath family (Ericaceae) and close kin to rhododendrons and azaleas. It is a beautiful evergreen shrub whose natural distribution extends from the panhandle of Florida north to Maine and southern Ontario. In spring, moun-

tain laurels produce an abundance of flowers in terminal panicles. In the wild, flowers of *Kalmia latifolia* are white to pink, with showy cup-shaped corollas. Hundreds of cultivars have been selected; these variants have flowers ranging from white to deep red, many with banded or speckled patterns. But, the "monstrosity" described above (initially as *Kalmia latifolia* var. *monstrosa,* later as *K. latifolia* f. *polypetala,* and now generally referred to as the cultivar 'Polypetala') is not a color mutant. Rather, it is a variant with an altered morphology of the petals. Instead of forming a sympetalous (fused sets of petals) corolla, 'Polypetala' has narrow, unfused individual petals. This is the form of mountain laurel first described by Harvard Professor of Botany Asa Gray in 1870, as a consequence of the keen collecting eye of one Miss Mary Bryant of South Deerfield, Massachusetts.

It did not take long before specimens of this unusual morphological mutant came to Harvard University. A specimen of *Kalmia latifo-*

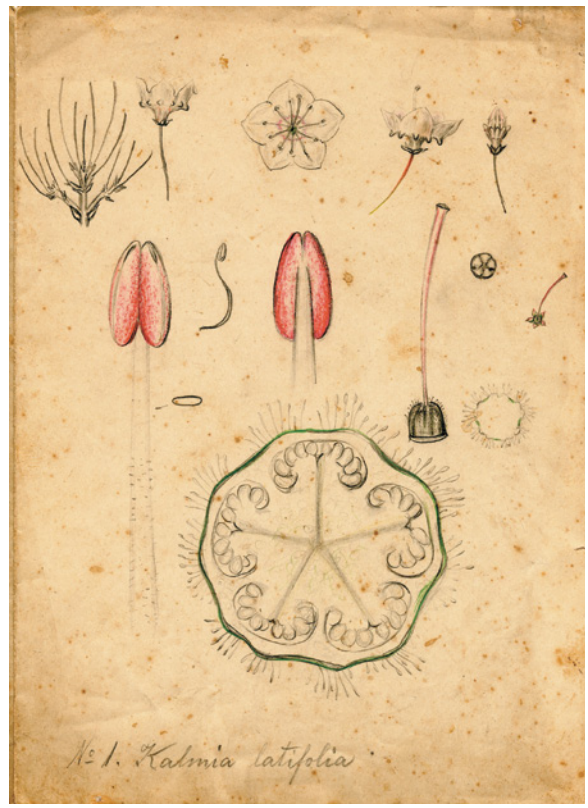
KYLE PORT

In this inflorescence of *Kalmia latifolia* 'Polypetala' many of the flowers have yet to open. The dark red coloration at the tips of the filiform petals is associated with the unusual production of pollen-producing anthers on these mutant petals. Also note the reflexed normal stamens jutting out between the petals.

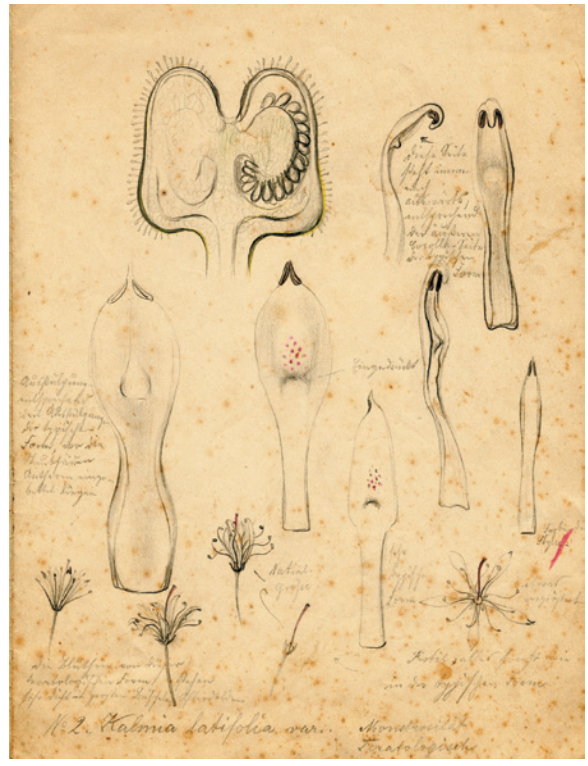
NANCY ROSE

Inflorescences of *Kalmia latifolia* 'Polypetala' create a markedly altered and attractive appearance when the plant is in flower (the plant seen here is the original 1885 accession from South Deerfield, Massachusetts). Flowers of a normal ("wild-type") *K. latifolia* are seen at far left in the photo.

GLASS MODELS: THE WARE COLLECTION OF GLASS MODELS OF PLANTS, HARVARD UNIVERSITY, ROSE LINCOLN/ARNOLD ARBORETUM



DRAWINGS: COLLECTION OF THE RAKOW RESEARCH LIBRARY, THE CORNING MUSEUM OF GLASS



Rudolph Blaschka made drawings for glass models from several plants at the Arnold Arboretum, including *Kalmia latifolia* 'Polypetala' (labeled as var. Monstrositat on the drawing at right). The exquisite glass models of the normal (top) and mutant (bottom) forms of mountain laurel can be seen at the Harvard Museum of Natural History.

lia 'Polypetala' from the Harvard University Herbaria notes that it was collected in the Botanic Garden at Harvard (in Cambridge) in 1884. Another 1891 herbarium sheet in the Harvard University Herbaria comes from a grafted specimen that was introduced into the Arnold Arboretum in 1885 (accession 2458). Finally, and quite wonderfully, one of the extraordinary models in Harvard's famed glass flowers (formally, the Ware Collection of Glass Models of Plants) was based on observations and collections of the Arboretum specimen of *Kalmia latifolia* 'Polypetala'. In the summer of 1895, Rudolph Blaschka—of the father (Leopold) and son (Rudolph) team that created the glass flowers—came to the Arboretum to sketch and observe this mutant pioneer. The glass model of *Kalmia latifolia* 'Polypetala' (one of over 800 models created by the Blaschkas between 1886 and 1936) can be viewed at the Harvard Museum of Natural History. And, after all of these years, six of the seven original living plants from the 1885 accession (2458-A, B, C, E, F, G) still survive and thrive on the grounds of the Arboretum.

In 1907, another cluster of mountain laurels with unfused petals was found along roadsides in Leverett, Massachusetts, near Mount Toby (Stone 1909). The mutant petals of these plants were reported *not* to produce anthers at their termini, as is the case with the 'Polypetala' discovered by Miss Bryant and first described by Asa Gray. Arboretum botanist Alfred Rehder suggested that this discovery was evidence of the independent origins of these petal mutants in different naturally occurring populations (Rehder 1910). However, it is possible that this description was in error. In the University of Massachusetts Herbarium, there are six specimens of the 'Polypetala' form of mountain laurel (in flower) that were collected between 1910 and 1932 on Mount Toby, and all of them show anthers at the tips of the mutant petals. Perhaps these oddly placed anthers were not initially observed in the report from 1909. Nevertheless, it is worth noting that 'Polypetala'-like forms of *Kalmia latifolia* have also been found growing in the wild in North Carolina (Ebinger 1997) and elsewhere. These variants appear to be fundamentally different from those of the South Deerfield and Mount Toby populations, as they are reported to lack anthers on the tips of the unfused (apopetalous) petals. Clearly there are at least two different and independently formed (evolved) variants with the unifying feature of forming unfused petals—not unlike the multiple evolutionary origins of white-flowered redbuds.

Asa Gray's description of the 'Polypetala' type of *Kalmia* refers to the notion that the petals have been "transformed into stamens." In evolutionary terms, this is a statement worth examining. Close observation with a hand lens (or under the microscope) of the "petals" of the South Deerfield plant reveals that each one bears a pair of pollen-producing structures at its distalmost end (collectively, an anther). As might be expected, pollen can be found within and then dispersed from these anomalous anthers. Normally, the stamens of *Kalmia latifolia* comprise a long filament terminated by a reddish anther that produces pollen. A defining characteristic of the floral biology of *Kalmia* species is that the ten stamens insert themselves into ten pouches in the petals of the cup-like corolla, creating a mechanical tension. Visitation by an insect pollinator trips the catapult and the anther flings pollen with enough force to throw it three to six inches away from the flower, but usually directly onto the body of the pollinator, where it will be transported to the next flower to effect pollination (Ebinger 1997).

In the 'Polypetala' *Kalmia* from South Deerfield, the "petals" still produce a pouch about midway along the length of the organ. However, the disruption to the normal morphology of these flowers precludes the proper insertion of the ten normal stamens into these pouches. Thus, as the flower expands towards anthesis (the opening of the flower), the ten normal stamens proceed through their typical pattern of physical reflexing, but never find the petal-borne pouches. The "petals" also bear much of the typical pinkish-red markings that create some of the brilliant spots or circumferential bands on the corolla of normal flowers. As such, the South Deerfield 'Polypetala' "petals" may best be thought of as chimeric organs—part petal and part stamen—while some of the other 'Polypetala'-like variants that lack anthers on their unfused petals may best be viewed as

mutations that have only changed the form of the petals from broad and fused to more narrow and unfused.

Interestingly, over the course of the last thirty-five years, molecular biologists have uncovered some of the basic genetic controls that determine whether a floral organ will differentiate into a sepal, petal, stamen, or carpel (the female seed producing organ). The scientific literature is filled with instances where geneticists have created mutant forms of flowers in which petals have been replaced with stamens, or stamens have been transformed into carpels (Coen and Meyerowitz 1991; Mathews and Kramer 2010). Along the way, floral mutants have also been created in the laboratory with chimeric or hybrid structures that blend petals with stamens, as appears to be the case in the South Deerfield 'Polypetala'. The floral mutants that scientists have created in the laboratory are a wonderful echo of the myriad naturally occurring mutations in nature that have produced many of our beloved horticultural variants.

As with the case of the Arboretum's mutant redbud, it is possible that a mutation in a "normal" mountain laurel growing in South Deerfield, Massachusetts occurred in a shoot apical meristem that then produced a branching system bearing the mutant gene. From there, seeds produced by the mutant branching system might have yielded descendants with the novel form of corolla. Alternatively, a mutation could have occurred either in the gamete lineage or young embryo of a mountain laurel plant, as appears to have been the case with the 'Royal White' cultivar of redbud trees, where the aberrant type arose as a seedling. In this case, a new variant plant would have appeared in a single generation with flowers that all bore the linear, unfused petals.

If this seems unlikely, it is worth noting that Queen Victoria, who was a carrier for the genetic mutation that confers hemophilia (a carrier does not have hemophilia, but can transmit the disease to her descendants), appears to have acquired a mutant copy of this gene either as a gamete or as a zygote (assuming she was not the illegitimate daughter of a hemophiliac biological father) or to have undergone a mutation in her own cells that produced eggs (Potts and Potts 1995). We know this because

PHOTOS BY WILLIAM E. FRIEDMAN

A bee with heavily laden pollen baskets on its hind legs visits flowers of a *Kalmia latifolia* with the normal cup-shaped, fused-petal corolla. Note the ten pollen-producing anthers held in pockets on the corolla; physical contact (typically by a pollinator) unsprings the anthers, which catapult a shower of pollen.

A 'Polypetala' petal (top) shows a stripe of pink pigmentation that correlates with the inner pink ring seen in normal flowers. The red patch at the right (distal) end is where the "misplaced" pollen-producing anthers form. A normal pollen-producing stamen from the mutant flower is seen below the petal.

In normal *Kalmia latifolia* flowers the ten stamens reflex backwards and insert into the ten pockets in the cup-shaped corolla, but in 'Polypetala', seen here, they are unable to find their normal spot and reflex backwards between the separate petals. Note the deep red anthers at petal tips.

family history and modern genetics make clear that the gene for hemophilia did not exist in her family prior to her conception. Mutations happen in gametes (or gamete-producing cell lineages), and zygotes and the organisms that develop from the act of fertilization will exhibit the consequences of the new mutation. Recent sequencing of whole genomes of human families indicates that each of us carries roughly 75 new simple genetic mutations ("single nucleotide variants" in the parlance of geneticists) that neither of our parents was born with (Campbell et al. 2012; Kong et al. 2012).

Whether the mutation that created a new chimeric corolla form in the South Deerfield *Kalmia latifolia* took place in the immediate decades before Miss Bryant found the monstrous plants, we will never know. It could be that this mutation was present in this local population of mountain laurels for hundreds if not thousands of years, unseen by human eyes. And for all we know, this mutation might ultimately mark the beginning of a new species of *Kalmia* over the course of time. In either case, it took a wandering (and observant) naturalist to discover this product of the evolutionary process, this biological gem, and bring it to the attention of a professional botanist. One can only imagine the delight of Miss Bryant upon finding this unique type of mountain laurel!

CLOSING THOUGHTS ON BOTANICAL GARDENS AS SHOWPLACES OF EVOLUTION

And so we come back to the concept of botanical gardens and horticultural variants as exemplars par excellence of the process of evolution. In populations of redbuds around the world, mutations are constantly occurring. The same is true for mountain laurels (and humans). These mutations might create selectively favored traits such as resistance to drought, or tolerance to cold, neither of which can be seen by the human eye. Most of the genetic mutations in redbuds and mountain laurels (indeed, all organisms) will probably have little if any effect on the fitness of the plant. Some will be deleterious, and these genes will ultimately be purged from the population. In evolutionary terms, it is always easier to "break" something than to create a novelty that improves fitness.

Botanical gardens are filled with examples of spontaneous mutations, many of which evolved and were discovered in our own lifetimes. These are the very same kinds of mutations that occur constantly in nature and have served as the raw materials that gave rise to humans, oak trees, and plasmodial slime molds—all descended and transformed over the course of billions of years from a single-celled common ancestor of all of life on Earth. The raw ingredients of evolution writ large are all around us. And if we look carefully, we can observe the process of evolution by simply walking through a botanical garden, or one's own backyard. Mutant forms of redbud and mountain laurel, as well as myriad other "sports," are an important reminder that we live in a beautiful and profoundly evolutionary world.

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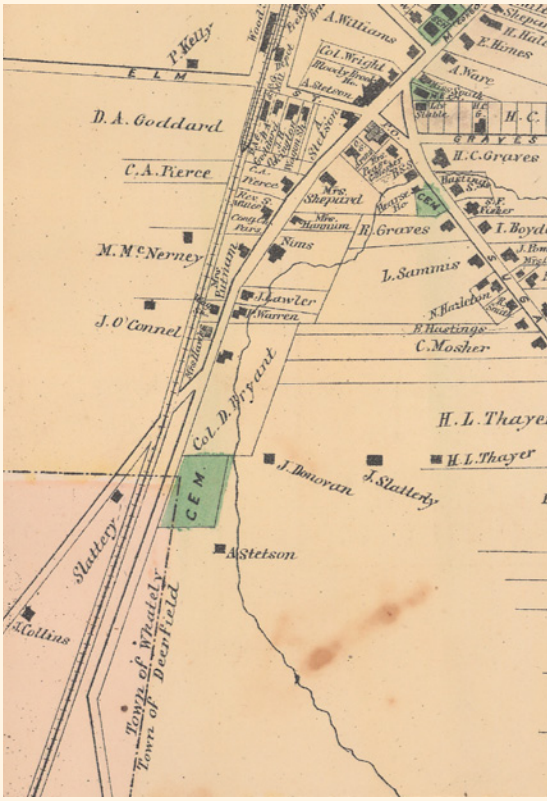
POSTSCRIPT: One question that lingered after all of the historical research on *Kalmia latifolia* 'Polypetala' was whether any of the mutant plants (or their descendants) that were originally found on Colonel Bryant's property were still in existence. A map of the South Deerfield, Massachusetts, area from 1871 showed exactly where this property was located. Fortunately, this map could be cross-correlated with modern maps to show where Miss Bryant collected the mutant plants.

On June 22, 2013, I drove to South Deerfield to hunt the wild mutant *Kalmia*. The old home that once belonged to Colonel Bryant still stands and is well cared for. Regrettably, the land around the original six acres has not had a kind interaction with humans. The barren area on the other side of the brook was home to a pickle factory for many years. The town also installed a major sewer line that is buried alongside the brook. While I found lots of poison ivy and a modest amount of undergrowth beneath some maples and hemlocks, there were no *Kalmia* plants, mutant or otherwise, to be seen.

After my visit to South Deerfield, I drove around the base of Mount Toby. There, I spotted several spectacular populations of mountain laurel in full bloom. My ramble in the woods did not turn up any mutant flowers. Next year, with a bit of time and coordination with the University of Massachusetts Herbarium, we will try to explore the Mount Toby area and search more thoroughly for the 'Polypetala' form of *Kalmia latifolia*.



MAP COURTESY OF WARDMAPS LLC, CAMBRIDGE, MA. WWW.WARDMAPS.COM

This section from an 1871 map of South Deerfield, Massachusetts, shows Colonel Bryant's property, where the mutant mountain laurel was discovered, near the center.

The loss of the mountain laurel population from which Miss Bryant collected the 'Polypetala' mutant is a stark reminder of the incredible importance of botanical gardens as refugia for rare and endangered plants, whether entire species, threatened local populations, or unusual mutant forms. It is a very fortunate thing that Miss Bryant's monstrosity was propagated and cared for at the Arnold Arboretum. Otherwise, it might well have disappeared from the face of the earth without a second thought.

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Rediscovering Rhododendron Dell, Part 2

Kyle Port

"They [hoodlums] deliberately twist off the metal labels from trees and shrubs, so that valuable information is sometimes lost forever and the yearly replacement bill is terrific. They break hundreds of unopened flower buds off the Rhododendrons in the early spring."

—Edgar Anderson, Arnold Arboretum arborist , June 4, 1932

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Planted in close proximity to one another, *Rhododendron* 'Old Port' 990-56-B (a catawbiense hybrid with "vinous crimson" flowers, seen here) was incorrectly labeled as *R.* 'Red Head' 329-91-A (with "orient red" flowers). A description published by the Royal Horticultural Society was used to verify the only remaining plant as 'Old Port'; a lack of indumentum on the undersides of the leaves distinguishes it from 'Red Head'.

The Arboretum's plant records attest to episodes of vandalism, arson, theft, and other willful shenanigans that have occurred in the living collections over the years. In 2010, a pile of plant record labels was found in Rhododendron Dell. This intentional—and completely unsanctioned—removal of labels from numerous specimens by an anonymous person(s) can certainly be considered a major transgression. But, to quote Albert Einstein, "In the middle of difficulty lies opportunity," and this act of vandalism initiated an unplanned curatorial review that has advanced our understanding of the rhododendron collection and further fostered its use.

In response to the identity crises in Rhododendron Dell, a multi-year collection review was conceived. Identity verification and field work (e.g., labeling, photographing) was timed to coincide with peak flowering. Winter months were dedicated to auditing and digesting the raft of secondary documentation (e.g., records, articles, herbarium specimens, images) amassed over the collection's 141-year history. Through

each of these periods, real-time observations about the collection were recorded in curatorial databases.

The initial assessment of the collection was sobering. Many labels were missing and others had been haphazardly rehung by non-Arboretum staff. Since it was the dead of winter when the errant labels were found, the rhododendron flowers—the hallmark structures used to verify these cultivars—were months away from opening. Partial identities were confirmed using the leaf characteristics of a few scattered lepidote rhododendrons and some elepidotes with indumentum. But without flowers, determinations and label hanging had to wait until spring.

FLOWERING FACILITATES FIELD WORK

Imaging

The window of opportunity to study flowers in Rhododendron Dell is finite. Depending on weather conditions, flowers can remain for days or wither soon after opening. To overcome the challenges of flower senescence, we used digital cameras to capture thousands of new diagnostic images over the past three years. This provided the first comprehensive image archive of the collection. Paired with in-field observations, the images have helped us positively identify specimens and will eventually become a valuable online resource. We will continue to add rhododendron images to the archive over time.

Inventory field checks

Persistent field observations render the best results. Over the past three growing seasons, detailed observations of Rhododendron Dell plants have been catalogued in curatorial databases. Prior to these efforts, the last major curatorial review was undertaken in 1990. Regular, systematic review of collections and their secondary documentation (e.g., maps) will likely reduce the need for time-consuming curatorial inputs in the future.

Lepidopteran on an Elepidote

FOR IDENTIFICATION purposes, rhododendrons can be divided into two broad groups, lepidotes and elepidotes. Lepidote rhododendrons have small scales on the undersides of their leaves ("lepid" is the Greek root word for "scale"). They also typically have small leaves and grow as small shrubs. Elepidote rhododendrons do not have leaf scales, usually have large leaves, and grow quite large. Some elepidotes have indumentum (dense, felted hairs) on the leaf undersides; color and density of the indumentum can be a key to identification.

Seen here, an eastern tiger swallowtail butterfly (*Papilio glaucus*) rests on an elepidote rhododendron. Butterflies and moths are in the insect order Lepidoptera, which references the tiny scales that cover their wings (and bodies).

The gorgeous cultivar 'Brookville' was introduced in 1959 by the Westbury Rose Company based in Long Island, New York.

On larger specimens, new record labels have been attached to lower trunks with screws.

Labeling

Following the imaging and field checks, hundreds of new anodized aluminum records labels were embossed and placed in Rhododendron Dell. Many are mounted on three-inch stainless steel screws at the base of large stems. Additional records labels have been hung on branches for easy retrieval. In addition to these, prototypes of larger photo-anodized aluminum display labels were tested over the peak flowering periods. Feedback regarding these labels has been overwhelming positive and the roll-out of permanent signage is expected in 2014.

Mapping

The current maps of Rhododendron Dell are being revised. Vector data (e.g., points, lines, and polygons) representing plants and hardscape features are being re-collected using global posistioning system (GPS) equipment. These technologies allow for decimeter-accurate field mapping and update the triangulation and submeter-accurate data collection of the past. Note that interactive maps of Arboretum collections are available at http://arboretum.harvard.edu/plants/collection-researcher/

WINTER AUDITS AND RECORDS REVIEW

Nomenclatural review

In advance of label production, we undertook a comprehensive review of rhododendron nomenclature. A total of 103 cultivar names were standardized following *The International Rhododenron Register and Checklist* (Royal Horticultural Society 2004). This effort revealed inaccuracies in spelling, punctuation, and use of synonymy for 20 elepidote cultivars. In addition to these edits, the name records in BG-BASE (collections management software) were appended with hybridizer, introducer, parentage, awards, descriptions, and common name as found in the aforementioned resource. We have used this information to create new display labels and have updated online resources.

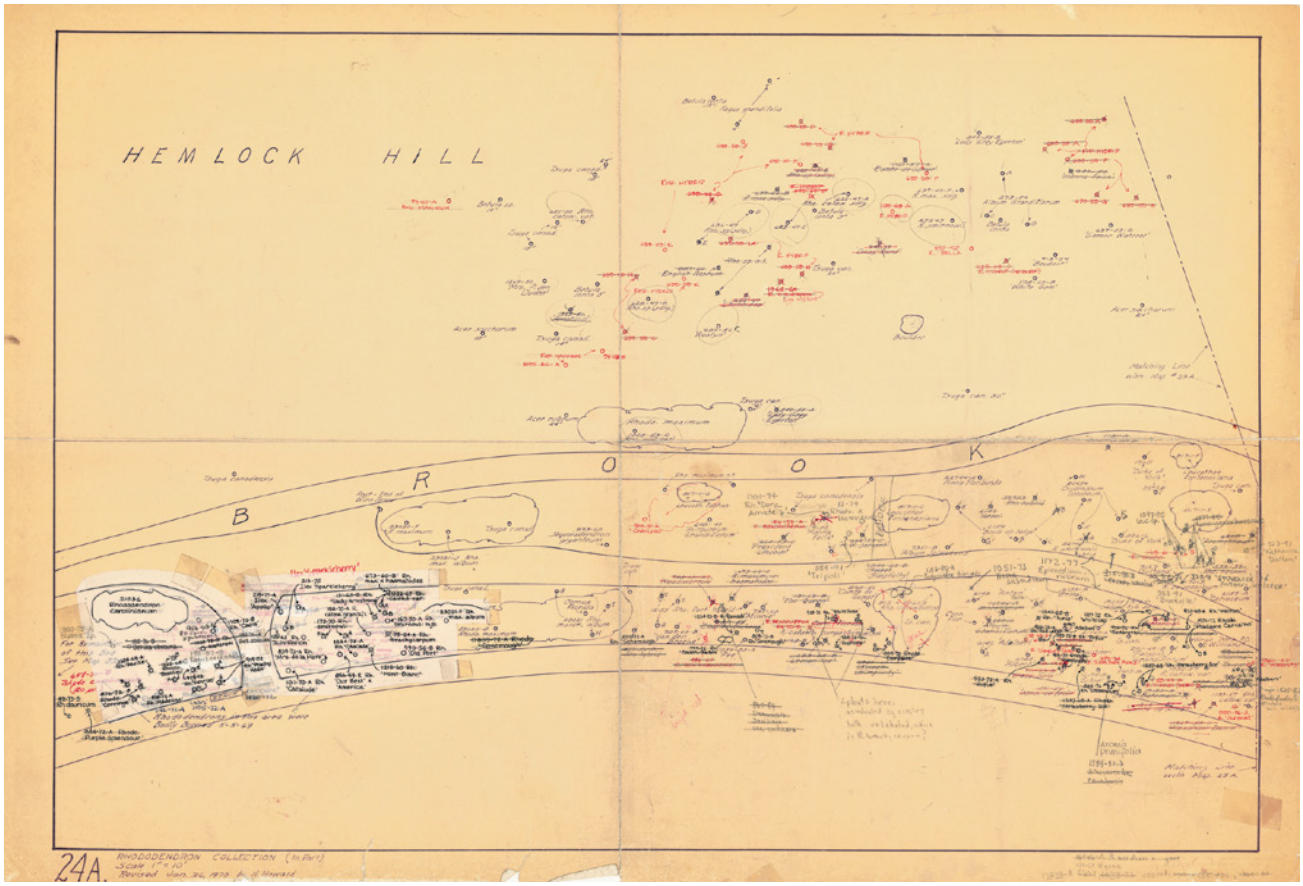
Archival maps and records

The first maps documenting the location of accessioned plants in the permanent collections were purportedly authored by Henry Sargent Codman in 1887. Plan views of the landscape

This specimen of *R.* 'Purpuream Elegans', accession 6135-B, came to the Arboretum in 1891 from the nursery of Anthony Waterer, who hybridized this and many other rhododendron cultivars.

from this era were copied from the Frederick Law Olmsted papers in 1987 but as yet do not reveal individual planting sites. Fortunately, the detailed cartography begun by León Croizat in the 1930s is well preserved in the Arboretum archives. Croizat, employing a triangulation survey method, made his cartographic representations of features (e.g., plants, hardscape) on 24- by 36-inch tracing cloth. Iterations of these drawings were annotated based on the field work of Heman Howard and a few others. The last notations on hand-drawn maps covering the two acre Rhododendron Dell area are from the 1980s and 1990s. A total of 90 maps at scales of 1 inch=10 feet and 1 inch=20 feet masterfully convey the scope of these collections over a roughly fifty year period. Since 1987, map edits have been accomplished digitally using AutoCAD (from 1987 to 2008) and ArcGIS (since 2009) software.

ARNOLD ARBORETUM



Hand-drawn and annotated paper maps like this one have been replaced with accessible digital files.

Rhododendron flower color is often lost in herbarium specimens; compare the 1936 specimen of 'Melton' (left) to a current digital image of its flowers (right).

In 2010, grant funds awarded through the Museums for America program of the Institute of Museum and Library Services (IMLS-MFA) allowed Jonathan Damery, then a curatorial assistant, to scan and georeference the collection of hand-drawn maps. Using ArcGIS software, these rasters can be layered with current representations of the Arboretum grounds. In addition, they can easily be printed on 11- by 17-inch paper for problem solving in the field. The IMLS-MFA grant also provided resources to enter the Arboretum's entire plant records card catalogue and review accession books (dating from 1872 to 1987). Spearheaded by curatorial assistant Kathryn Richardson, the entry of these data has improved all aspects of curatorial work.

Herbarium resources

A curatorial review would not be complete without a thorough review of specimens in the Arboretum's Cultivated Herbarium. In the case of hybrid rhododendron, these resources are limited for one major reason: flower color. Often lost in the drying process, flower color variations (including the blotch on the dorsal lobe) are critical identification characters of rhododendron hybrids. Other flower data such as truss height, width, shape, fragrance, and number of buds can be difficult to discern (or be entirely absent) from a two-dimensional dried specimen. Without question, examination of the whole plant at relevant phenophases provides a more accurate determination.

The importance of identifying rhododendron flower color accurately is well documented. Arboretum horticulturist Donald Wyman was a proponent of the Nickerson Color Fan published by the American Horticultural Society and used this resource to describe the flowers of Rhododendron Dell collections (Wyman 1969). Agents of the Royal Horticultural Society, United Kingdom, have also published a color chart, which many have used to describe rhododendron cultivars (Leslie 2004). These color designations have been saved to the Arboretum's plant records database and are easily retrieved.

A LOOK AHEAD

Collections development

The Arboretum's curatorial staff is analyzing the current inventory of evergreen hybrid rhododendrons and will determine which new cultivars will be acquired. In the meantime, anticipation grows around rhododendron hybrids already being raised by Dana Greenhouse staff. Of these, *R.* 'Robert Stuart' will likely be sited in Rhododendron Dell next year. Registered with the Royal Horticultural Society in 2006 by long-time Dana Greenhouse volunteer George Hibben in collaboration with the Massachusetts Chapter of the American Rhododendron Society, *R.* 'Robert Stuart' is an early flowering lepidote with *R. minus* and *R. concinnum* in its parentage. Hybridized by the late Robert Stuart of Stratham, New Hampshire, unrooted cuttings were obtained from Gus Mehlquist's garden by Arboretum propagator Jack Alexander in 1978. The resulting plants were sited in the permanent collections and propagated for distribution through the 1989 Arboretum Plant Sale. By 1991, the Arboretum's specimens had died but George Hibben's plant thrived. It is from Hibben's plant that repatriation by way of cuttings of this cultivar is made possible. Our detailed record keeping and relationships with like-minded plantspeople ensure important germplasm is conserved. *R.* 'Robert Stuart', with its purple hued flowers, fading to pink, has been missed in the permanent collection and its return will be welcomed.

This specimen of *R. fortunei* (accession 1-2008-A) with a lineage from west of Tien Mu Shan Reserve in China was planted in Rhododendron Dell this spring.

Beyond historical cultivars, the core collections of large-leaved *Rhododendron* species are under continuous development. In 2006, wild collected seeds of *R. catawbiense* and *R. maximum* were obtained from Mount Holyoke College Botanic Garden in South Hadley, Massachusetts. Cultivated under a lath house added to the Dana Greenhouse in 2007, these T. E. Clark collections from North Carolina were added to the permanent collections in 2012. More recently, a lineage of Peter Del Tredici's 1989 collection of *R. fortunei* from west of Tien Mu Shan Reserve, Zhejiang, China, was added to the collection this spring.

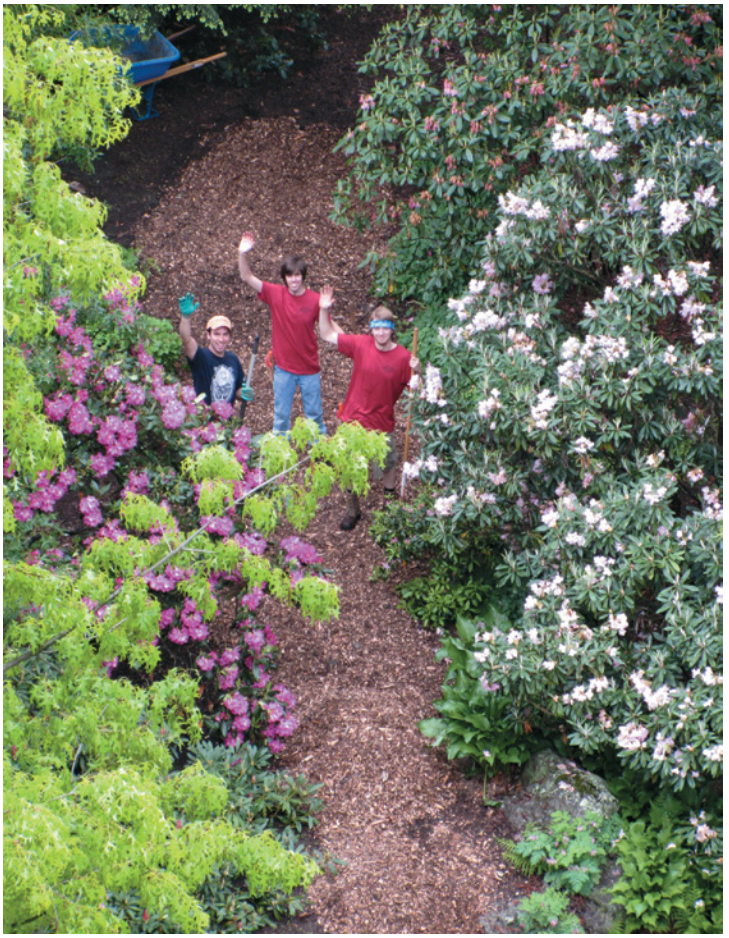
Infrastructure and horticultural care

In Rhododendron Dell, scouring by Bussey Brook has compromised the root zones of *R.* 'Purpureum Elegans', 'Coriaceum', 'Caroline', and 'Francesca'. Repropagation efforts to conserve these accessions are underway by Dana Greenhouse staff. At the same time, collections managers are considering options that would slow the flow of Bussey Brook upstream and shore up existing infrastructure installed to mitigate bank erosion through Rhododendron

Other Notable Rhododendron Dells

The Arnold Arboretum's Rhododendron Dell is modest when compared to the largest rhododendron collections of the same name found on earth.

- **Dunedin Botanic Garden is New Zealand's oldest botanic garden. Celebrating its 150th anniversary in 2013, its nearly 3,500 rhododendrons are displayed across 10 acres (4 hectares). Dunedin's Rhododendron Dell specimens flower during the month of October.**
- **Royal Botanic Gardens, Kew, United Kingdom, maintains a Rhododendron Dell dating to 1734. It contains more than 700 rhododendron specimens and reaches peak flowering in April and May.**
- **Conceived in 1942, Golden Gate Park's John McLaren Memorial Rhododendron Dell in San Francisco, California, has been under extensive renovation since 2001. Between April and May, an estimated 850 rhododendron hybrids flower.**



Arboretum horticulturist Brendan McCarthy and Hunnewell interns John Aloian and Ryan Plante at work in Rhododendron Dell, May 2012.

Dell. Previous efforts in this regard were completed for the western section (in 1990) and eastern sections (in 1995) of Bussey Brook. With some repairs over 20 years old, an undertaking of similar scope is needed.

Arboretum horticulturists put much effort into maintaining the Rhododendron Dell collections. Annual removal of bud blast, a fungal disease that ruins flower buds, has greatly reduced its incidence. Damage from root weevils (chewed leaves) and stem borers (dead branches) is being monitored and control methods are being investigated. Extensive deadwood removal by horticulturist Sue Pfeiffer in the fall of 2012 has encouraged new stems to regenerate from the base of many historical cultivars. This new growth is encouraging, since some of the finest specimens in the collections currently hold their flowers well above the heads of their admirers. In addition to maintenance pruning, the separation of abutting accessions by removing tangled layers is underway. This step is critical and will undoubtedly help prevent identity confusion going forward.

Attention has also turned to the overstory. The application of imidacloprid (insecticide) has saved some of the surrounding eastern hemlocks (*Tsuga*

canadensis) from the voracious appetites of hemlock woolly adelgid (HWA), but we continue to research which tree species should be planted to succeed old-growth hemlocks. To prevent excessive competition, it is likely that a number of oak (*Quercus*), mountain ash (*Sorbus*), beech (*Fagus*), and linden (*Tilia*) accessions will be removed or transplanted from Rhododendron Dell in the coming year.

HYBRIDIZATION

Hybridization in *Rhododendron* can occur naturally and frequently between sympatric species (Milne et al. 1999), but it takes the hands of plant hybridizers to bring together wild and cultivated *Rhododendron* from around the globe. When successful, these intentional unions result in exciting new crosses. The Rhododendron Dell collections reveal the masterful talents of many hybridizers through the years. The earliest and latest documented hybridization efforts in the Arboretum's collection are seen in *R.* 'Cunningham's White' (introduced by James Cunningham in 1830) and *R.* 'Landmark' (from Wayne Mezitt in1985).

The specimens in Rhododendron Dell come from over 65 sources, including nurseries, hobbyists, and other botanical institutions. The highest numbers of accessions were acquired from Waterer (Bagshot and Knap Hill), Van Veen Nursery, Westbury Rose Company, and agents of the American Rhododendron Society, Massachusetts Chapter. There are extensive personal and institutional legacies tied to each specimen in Rhododendron Dell.

Parentage

Tens of thousands of *Rhododendron* cultivars have been formally registered under the auspices of the Royal Horticultural Society. Of these, the Arnold Arboretum grows a mere fraction. At least one or all of the parent species of Rhododendron Dell cultivars are known. Eighteen cultivars (17% of total) are of unknown parentage or probable parentage is cited; these are excluded from Table 1.

***Rhododendron* 'Cunningham's White' was introduced around 1830 by James Cunningham of Edinburgh, Scotland, and has been widely used in hybridizing.**

A catawbiense hybrid from E. V. Mezitt, Weston Nurseries, *Rhododendron* 'Henry's Red' is a relatively young cultivar (selected around 1970, registered in 1987) noted for its deep red flowers and excellent cold hardiness.

Table 1. Arnold Arboretum: The Parent Species of Rhododendron Dell (RD) Cultivars as of January, 2013

SUBSECTION	SPECIES	TRAITS VALUED BY HYBRIDIZERS	NATIVITY	% of total (RD) cultivars (n = 103) with known parent (backcrosses not tallied)
Fortunea	*R. griffithianum*	Large flowers (some of the largest of the genus)	E. Nepal, Sikkim, Bhutan, N.E. India	3% (n = 4)
Fortunea	*R. fortunei*	Scented flowers; heat resistant	Most widely distributed Chinese species.	7% (n=8)
Pontica	*R. catawbiense*	Extreme hardiness; tolerant of exposed sunny sites	E. United States; South-eastern Appalachian Mountains	48% (n = 50)
Pontica	*R. caucasicum*	Tolerant of poor, dry soil	N.E. Turkey and parts of the Caucasus	2% (n = 3)
Pontica	*R. macrophyllum*	Flowers often with crinkled lobes, rachis fairly tall	W. North America	<1% (n = 1)
Pontica	*R. maximum*	Large, narrow, dark green leaves	E. North America	5% (n = 6)
Pontica	*R. ponticum*	Species commonly used as understock	Caucasus and N. Turkey	5% (n = 6)
Pontica	*R. smirnowii*	Hardiness; thick indumentum	N.E. Turkey and Caucasus	2% (n = 3)
Rhodorastra	*R. dauricum*	Hardiness; early flowering	E. Russia, Siberia, Mongolia, N. China, Japan	1% (n = 2)
Rhodorastra	*R. mucronulatum*	Hardiness; early flowering	E. Siberia, China, Mongolia, Korea, Japan	2% (n = 3)
Neriiflora	*R. haematodes*	Small stature; longevity of leaf retention	China: W. and N.W. Yunnan	<1% (n = 1)
Pentanthera	*R. prinophyllum*	Hardiness	E. North America	<1% (n = 1)
Scabrifolia	*R. racemosum*	Tolerant of dry soils	China	1% (n = 2)
Arborea	*R. arboreum* ssp. *arboreum*	Leaf, silvery indumentum; flower bright red to carmine, rarely pink or white	Himalayan foothills, Kashmir to Bhutan	2% (n = 3, two are R. arboreum)
Arborea	*R. arboreum* ssp. *cinnamomeum* var. *roseum* (Album Group)	Leaf, rusty brown indumentum; flower with purple spotting in throat	E. Nepal, N.E. India, Bhutan, S. Tibet	<1% (n = 1)
Maddenia	*R. ciliatum*	Hardiness (variable)	E. Nepal, Sikkim, Bhutan, S. Tibet	1% (n = 2)

Additional hybrids of interest grown in Rhododendron Dell include:
R. × *myrtifolium* (*R. hirsutum* × *R. minus*); *R. hirsutum* tolerates near-alkaline soils and is native to the European Alps
R. × *laetevirens* (*R. minus* × *R. ferrugineum*); *R. ferrugineum* does not flower in abundance but is hardy and late flowering.

***Rhododendron* 'Catawbiense Album' is a hardy hybrid introduced by Anthony Waterer in 1886.**

Native to the Caucasus Mountains, *R. smirnowii* is the hardiest indumented rhododendron species. Its distinctive indumentum and crinkled petal edges are traits favored by hybridizers.

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The World of Mosses

Stephanie Stuber

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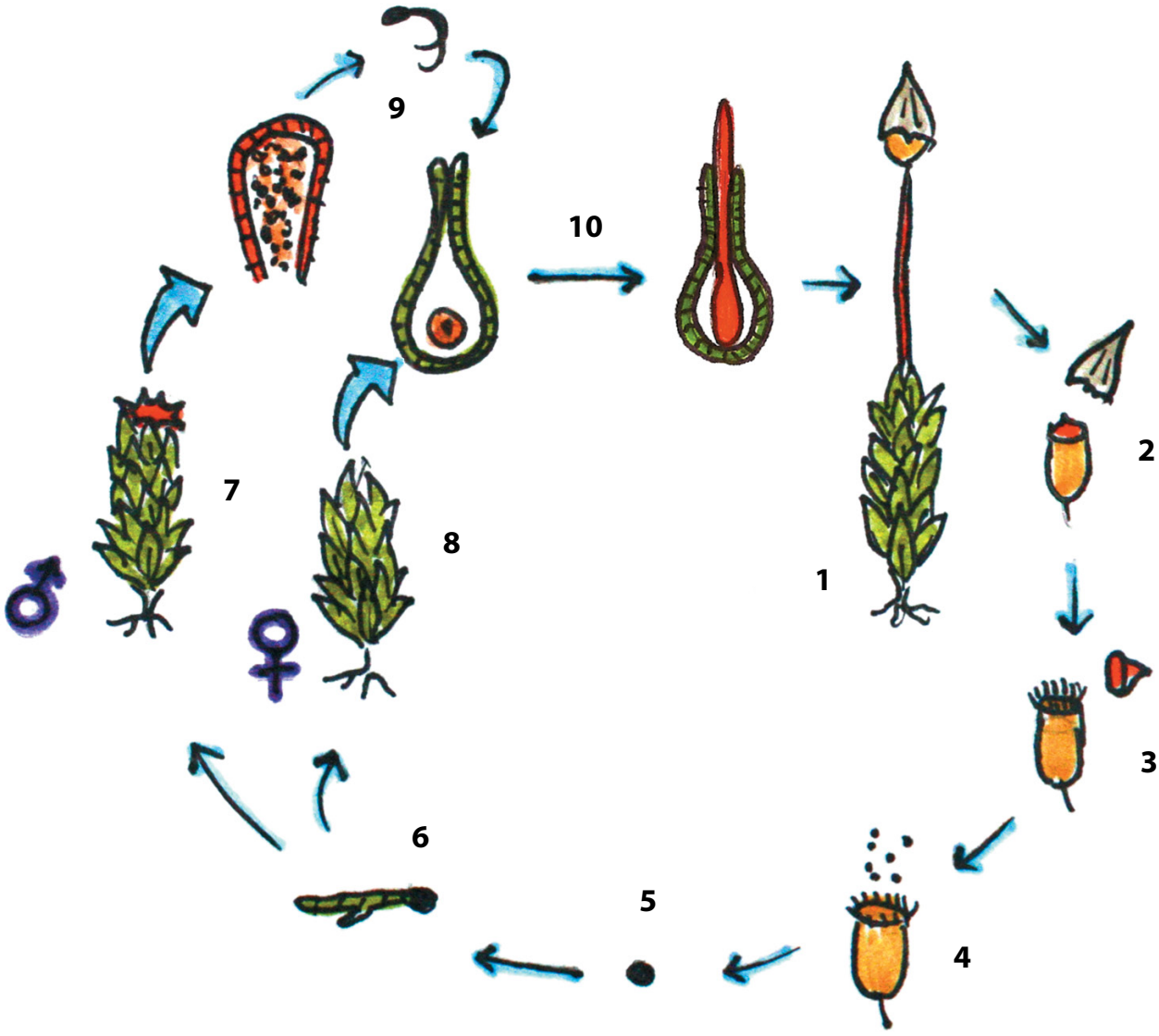
Mosses carpet the forest floor at the Coastal Maine Botanical Gardens.

While the more charismatic trees and flashy flowers initially catch our attention, mosses have an enchanting, charming presence. What is it about these tiny plants that intrigue us? Perhaps we are aware that there is so much more to their story, but their secrets remain intangible, concealed by their diminutive size.

Mosses differ from other plants largely in their life cycle. Mosses and tracheophytes (traditionally known as vascular plants) both alternate between two conditions throughout their lives, the gametophyte and sporophyte. The gametophyte is haploid (n), having 1 set of chromosomes, and the sporophyte, being the product of fertilization, is diploid ($2n$) with 2 sets of chromosomes. Tracheophytes conceal their gametophytes in reproductive structures, like flowers, never to be seen while they develop into the gametes (sperm and egg). For tracheophytes, the dominant condition is the sporophyte—the woody or herbaceous plant itself. The sporophyte produces spores that remain hidden when they develop into the gametophytes which then develop into the gametes. In essence, the gametophytes are dependent on the sporophyte.

But in mosses, the sporophyte is dependent on the gametophyte. The dominant condition is reversed; the conspicuous green leafy plant is the gametophyte, and the sporophyte is an ephemeral structure produced seasonally. The roles are the same, though—gametophytes produce gametes and the sporophyte produces spores. The spores, however, are released into the air before they develop into the gametophyte, rather than remaining hidden in reproductive structures.

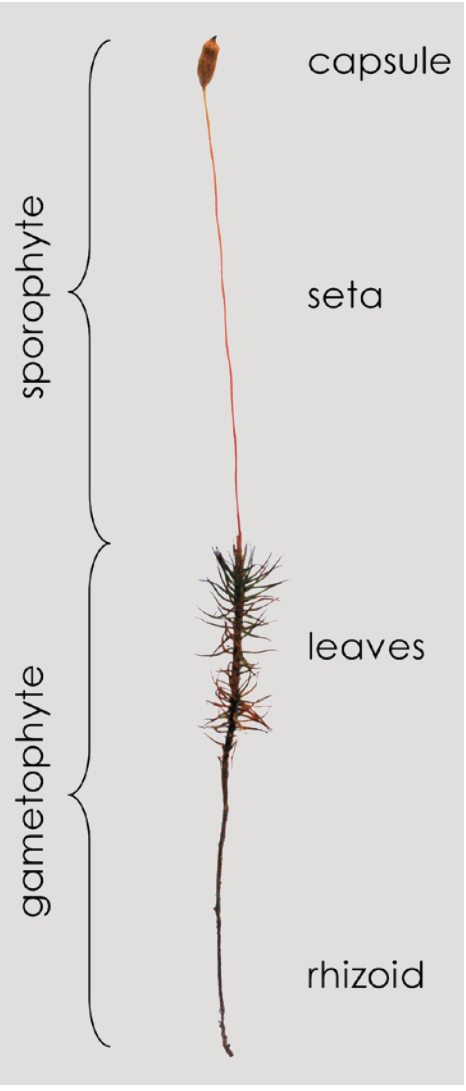


SEXUAL REPRODUCTION IN MOSSES

1. **A leafy female gametophyte (*n*) with attached terminal sporophyte (2*n*).**
2. **A papery protective covering, the calyptra (*n*), sheds off when the capsule (2*n*) fully develops; a remnant of the interior archegonial wall. Spores develop by meiosis inside the capsule.**
3. **A cap, the operculum (2*n*), pops off the capsule when spores are mature.**
4. **A row of tiny teeth, the peristome (2*n*), aids in spore dispersal.**
5. **A spore (*n*) settles on a place to germinate.**
6. **The protonema (*n*) emerges from the spore, reminiscent of filamentous algae, and develops into mature male and/or female plants depending on the species.**
7. **A cluster of antheridia (*n*) develop on the male.**
8. **A cluster of archegonia (*n*) develop on the female.**
9. **In the presence of water, flagellate sperm (*n*) are released from the antheridium and swim to the egg (*n*) in the archegonium to fertilize it.**
10. **The fertilized egg (2*n*, zygote) develops inside the archegonium and emerges as the sporophyte.**

Tetraphis pellucida **frequently produces terminal cups holding gemmae (clusters of undifferentiated photosynthetic tissue). With the splash of a raindrop, the gemmae are dispersed. One gemma will develop into a new moss plant. Orange sporophytes can also be seen in this photo. This species is very common on rotting stumps.**

Dicranum flagellare **is frequently found with filamentous brood branches. These tiny clusters of branchlets are borne in the leaf axils extending past the leaves, giving the moss a distinctive texture. These branches will easily break off when you rub a finger across the surface, as evidenced by the indented area with broken brood branches. This is a very common woodland species on soil.**



All mosses possess these basic anatomical parts (with few exceptions) as displayed by ***Polytrichum commune.***

When conditions do not favor sexual reproduction, mosses can always reproduce vegetatively from broken fragments of the plant. Moss cells are totipotent, which means that a single, differentiated cell has the ability to develop into an entire, fully functional plant. Some species produce propagules specifically designed to break off with the help of a passing animal or a raindrop. Above are two examples of these asexual structures.

A couple of studies were recently published which introduced the idea that mosses are not exempt from the animal pollinator association. The flagellate sperm were thought to require a film of water to swim to an egg. But this study has shown water is not necessarily a limiting factor in fertilization (Cronburg 2006). Apparently springtails and mites can play a significant role in moss fertilization, independent of sufficient water availability. A second study found that mosses produce pheromone-like chemicals that actively entice these tiny invertebrates to carry the sperm to an egg (Rosensteil 2012). This profound discovery gives credence to the theory that mosses may have instigated the plant-pollinator relationship so prevalent in

higher plants today. This model may also bridge the gap between their aquatic algal ancestors and the terrestrial tracheophytes.

MOSSES UP CLOSE

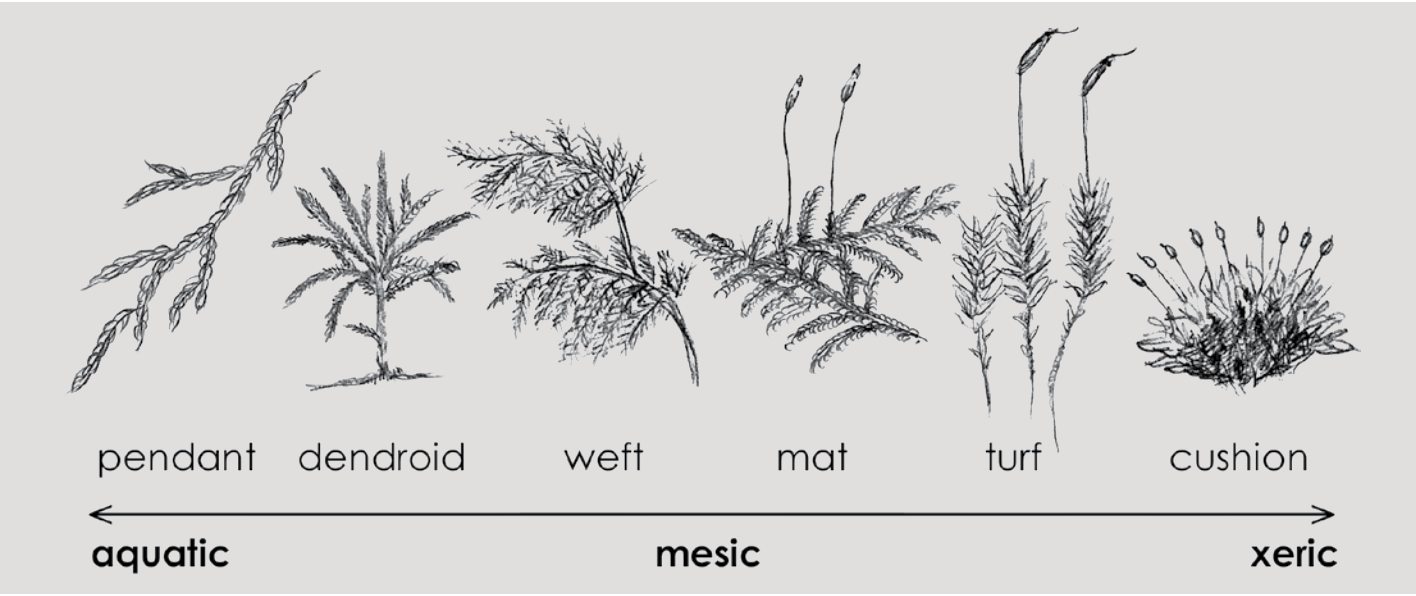
When you first take a look at a moss plant, with your naked eye or under a hand lens, often the first thing you notice are striking similarities to other plants. Mosses have stems, tiny leaves, and little rootlike structures. With the aid of a microscope you may see more parallels: a midrib, a serrated margin, conductive tissues, even tomentum. These structural analogs have similar purposes in both mosses and tracheophytes.

Mosses come in an enormous array of shapes, sizes, forms, colors, and textures, but most are made up of the same components. Members of the genus *Polytrichum* are commonly used to represent a typical moss species because of their relatively large size and distinct features. The gametophyte consists of parts similar to most other tracheophytes. The leaves of mosses are called phyllids to distinguish them from the true leaves of tracheophytes, which have lignified vascular tissues, but bryologists will call them leaves regardless, understanding their technical differences. These simple leaves are arranged spirally along the stem. This is a good distinguishing characteristic from liverworts, whose leaves are distichous (arranged in a two-ranked fashion on opposite sides of the stem). Instead of roots, mosses have similar structures called rhizoids. They do not make up an extensive subterranean network; rather, they are superficial and act more as a holdfast to anchor the moss to its substrate. The sporophyte consists of a stalk called a seta and the capsule, whose main parts are shown in the lifecycle image.

My undergraduate professor, Dr. Robin Kimmerer, described mosses as "time made visible," and mosses undoubtedly do lend a certain timeless aesthetic to the landscape. Intuitively we relate the amount of mosses in an area to the length of time it has remained undisturbed. What perpetuates their reputation for being slow growing? Mosses, unlike most life forms on this planet, are poikilohydric. This means that they cannot internally regulate water, so are subject to moisture fluctuations in their

The acrocarpous *Ulota hutchinsiae* has sporophytes that emerge terminally from the gametophyte.

The mat-forming pleurocarp *Hypnum imponens* sends out sporophytes laterally.



This drawing illustrates the shift in moss morphology based on habitat water availability.

immediate environment; when it is wet, they are wet, when it is dry, they are dry. Like other plants, mosses need to have access to water and light simultaneously to photosynthesize—only then can they actively grow. They are adept at capturing light at very low levels, but not at holding water, so their window of opportunity to grow is limited in many natural systems.

Moss leaves are usually only one cell layer thick. They lack an epidermis and mesophyll layer, and rarely have a waxy cuticle as found in true leaves. This is what makes mosses poikilohydric, but it also gives them great flexibility in where they can live. Water and nutrients are acquired primarily through the surface of their leaves. This also makes them especially sensitive to toxins and other pollutants, making them ideal environmental indicators. They do not necessarily depend on their substrate for their nutritional needs; their rhizoids provide minimal water and nutrient uptake. The combination of their rhizoids and their thin leaves allow them to grow superficially on impermeable surfaces like rocks and tree trunks.

With little to guard them against their environment, mosses are quite vulnerable. They are always open and receptive to what is offered to them, to their benefit or detriment. Amazingly, they can lose up to 98 percent of their water content and cease their metabolic functions for a time. Any other organism in this state would be considered dead, but mosses will revive once water returns.

Mosses can be divided into two growth forms—acrocarpous or pleurocarpous—based on the location of their sporophyte. Acrocarps bear theirs terminally, while pleurocarps bear theirs laterally. This is often the initial distinction used when identifying mosses. Typically the gametophytes of either form are distinctive enough, which helps in year-round identification if the sporophyte is not present. Acrocarps are generally upright, rarely branched, and form turfs and cushions, whereas pleurocarps are generally prostrate with pinnate, ferny forms.

FORM FOLLOWS FUNCTION

Within these two growth forms, mosses are segregated into many different life forms; six of the most common are shown here. One thing about these life forms that is especially fascinating is the link between morphology and habitat. In the diagram above, the forms are arranged along a water availability gradient ranging from aquatic to xeric habitats. Clearly morphology is a function of water availability. Those species that grow in fresh water are not limited by extended dry periods, so their gametophytes are

filamentous and essentially formless, offering much of their surface area to the open environment. As you move through mesic to drier habitats, the forms become more complex. The dendroid forms are still loose, but have rigid stems to support upright growth on saturated land. The pinnate forms with more intricate and rigid designs increase the amount of capillary spaces, helping to conserve water in mesic areas. Habitats with limited water tend to support turf and cushion forms best. Their tight, dense forms and specialized cellular structures and appendages facilitate water retention in drier environments.

Their desiccation tolerance is also directly related to their morphology; those species that live in wet areas will have less tolerance to desiccation than those species that are subjected to intermittent water availability. Because of their poikilohydric nature, mosses have had to develop ways to survive those dry periods in order to continue colonizing land further away from a water source.

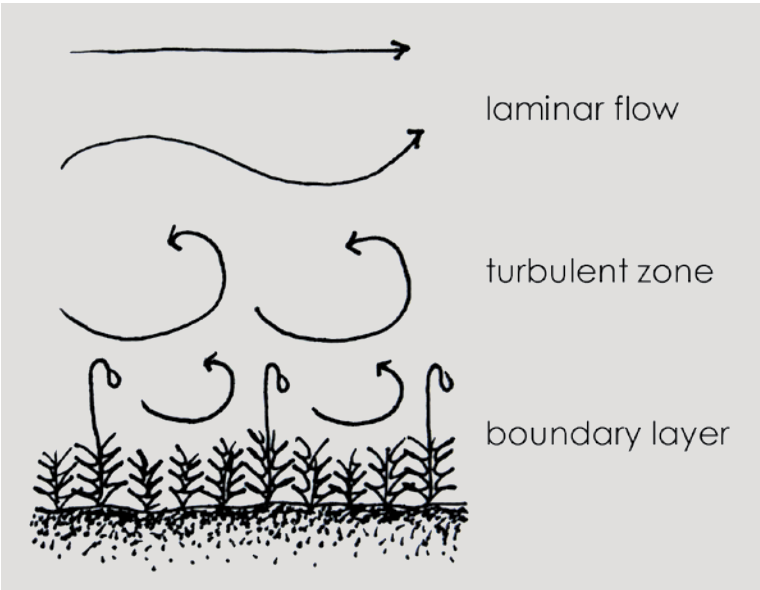
The length of time that some mosses can survive without water is remarkable. Aquatic mosses can remain desiccated for a few months to as much as a year, mesophytic species can wait several years without water, and xerophytic species are known to survive decades or centuries without water. Once water returns, they will begin repairing the cellular damage incurred by the desiccation process and then begin photosynthesizing once more. Of course, this is observed along a spectrum. The trend between form and desiccation tolerance, though positive, is dependent on the rate of the desiccation process; the slower the drying rate, the longer it can survive in that state.

A close-up view of sphagnum moss reveals its rich texture.

Mosses are able to tolerate colder temperatures than tracheophytes. Some species that live in harsh winter climates are nearly black when dry, allowing them to absorb as much light energy as possible to increase warmth. When the snow arrives, they lie protected underneath the icy blanket until it begins to melt. As water becomes available and even slight amounts of sunlight penetrate through the snow, the moss will begin photosynthesizing. Even the minor amount of nutrients dissolved in melted snow is enough to sustain them. Their incredible temperature tolerance and low-light-capturing ability gives them the upper hand at colonizing the harshest of climates. They are unique among plants in that they are found on all seven continents and every ecosystem except the ocean.

THE WIND IN THE MOSSES

The boundary layer exists as the interface between any surface and the surrounding air. At the surface, air is slowed by friction, while higher up the air is unimpeded. In between is turbulence. Mosses thrive close to their substrates, where, in the stillness, they can capture and retain heat, water, nutrients, and gases in their capillary spaces.



The movement of air across a bed of moss.

While moss gametophytes are content to grow within the boundary layer, the sporophytes depend on air movement for spore dispersal. Most sporophytes are designed to extend beyond the boundary layer into the turbulent zone, elevating the capsules with the seta so that spores can be released into the wind. The peristome that surrounds the opening of the capsule ensures that the spores are released at optimal times and in an effective way. Spores travel farther in dry conditions, so the peristome teeth reflex outward when it is dry, allowing spores to escape, and retract inward when it is wet. These teeth also act as a "salt shaker" by making sure the spores do not clump together as they are released.

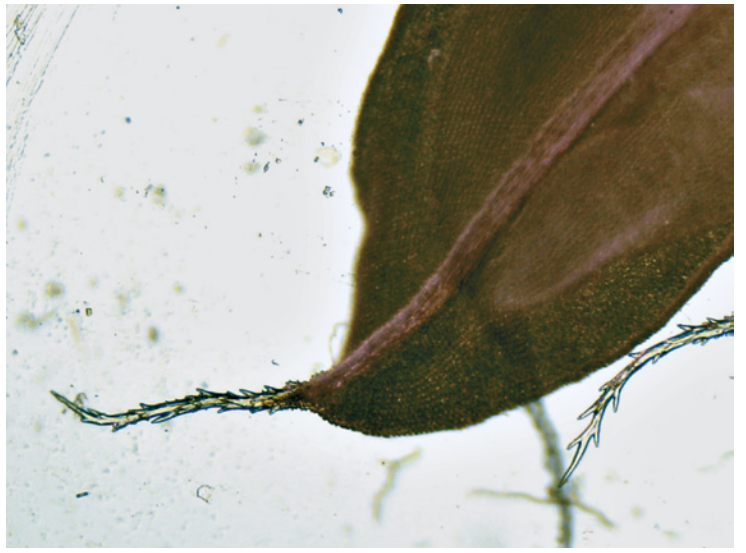
The effects of the boundary layer benefit not only the moss itself, but the whole ecosystem. In many respects mosses act like mulch by absorbing and releasing water slowly and maintaining humidity in the atmosphere and below ground. They also help reduce water runoff and control erosion. As water moves through a carpet of moss, most of the particulates and sediment is left behind, leaving clean, filtered water and keeping the top soil intact (Thieret 1956). Like all plants, mosses sequester carbon and other nutrients until they are released back into the environment from leaching or decay. Interestingly, this sediment retention is what gives some mosses the ability to literally build stone. Beds of moss can form the calcareous limestone known as travertine by providing a site that accelerates the evaporation of calcareous water, leaving the minerals underneath behind. The dissolution of this stone with acid can reveal tiny moss fragments as evidence (Thieret 1956).

The complex morphology of xerophytic mosses clearly illustrates the clever ways mosses have arranged themselves to conserve water. Many of these species can tolerate a good amount of sun exposure, so to counteract the subsequent water loss these species often possess filamentous apical structures called awns. The

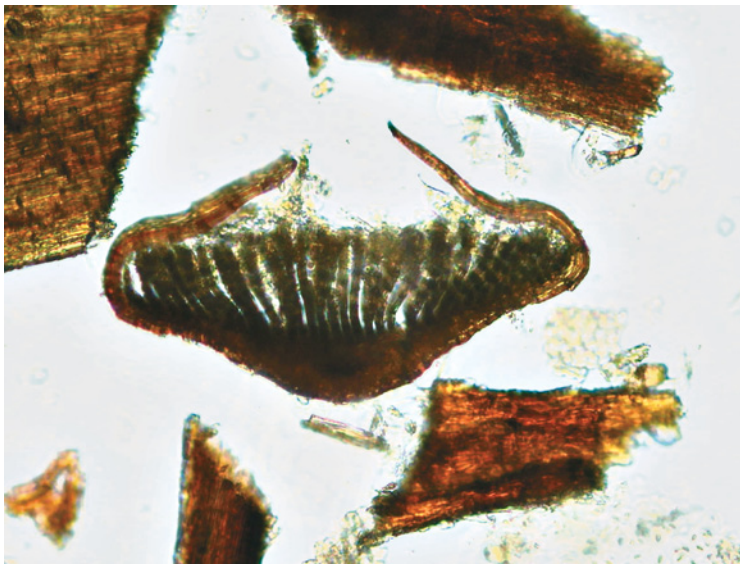
Polytrichum piliferum **gives off a silvery cast with its very long clear awns and thin waxy cuticle that covers the leaves.**

awns are often white or greyish, which is thought to aid in light reflection, thus cooling the plant and protecting it from damaging ultraviolet light. These awns extend beyond the leaf margins, increasing the boundary layer blocking desiccating air flow.

Some species have found ways to thicken their leaves to help retain water longer. Some can have short protrusions on the cell surface called papillae. Papillose species have a dull, matte appearance from a distance because of their roughly shaped cells, as opposed to the shiny appearance of species with smooth cells. Members of the Polytrichaceae have lamellae—multistratose plates of cells aligned perpendicularly over the leaf surface, effectively thickening the



The awn of ***Tortula ruralis*****.**



Transverse cross section of *Polytrichum juniperinum* showing the lamellae and the leaf margin folds over them (100x).

leaf. Those extra cells and the capillary spaces between the lamellae hold water as well as add more surface area for photosynthesis and gas exchange. Some species will even fold their leaf margins over the lamellae for added protection as seen in the image above.

Another way mosses counteract water loss is by altering their form as they dry out. For many species, their leaves begin to fold and curl when cells lose water. This reaction helps trap and hold any remaining water by creating more capillary spaces for water to adhere. The uneven surface created by the contorted leaves also increases the boundary layer. It is this action that makes some species look very different in a hydrated versus desiccated state. The rehydration process can take less than a minute and is amazing to watch. The thin leaves will readily absorb water, and as the cells expand, the tiny leaves unfurl gracefully.

MOSSES: A WORLDVIEW

A couple of years ago I took a trip to Denver. I have flown countless times, and I always enjoy viewing our planet from that altitude. It seemed during that trip, however, that my perception of plant life had crossed a new threshold. Over the years I had trained my eyes to focus on the patterns of mosses growing in their natural setting. So, at 32,000 feet, I could not help but draw the comparison between moss growth patterns and the patches of forest below. From that perspective I noted how trees formed turfs and tufts across the land, concentrating along waterways and protected areas. This is not unlike what we observe of mosses on the forest floor from our human perspective. The same natural, microclimatic forces apply in the colonization of a forest along land as it does for mosses along its substrate. I was reminded of the ancient hermetic axiom "As above, so below," which points to the irrelevance of scale; the same ecological patterns are apparent throughout all level of natural systems.

On your next encounter, I invite you to stop and pet the mosses (by doing so you will be breaking off tiny pieces, helping it grow vegetatively) and reflect on their significance, similarities, and strength. They hold a necessary place in the ecological function of their environments and, while tiny, they still share many traits with their tracheophyte relatives. They model themselves in patterns congruent with much larger plants to perform the same processes optimally—that is the reason why some mosses resemble little conifer seedlings! Mosses reflect that which we already see and know of our natural world and while they can help us reflect on the importance of being open and accepting and having patience and faith, they will continue to enrich us with their concealed secrets and attractive aesthetic.

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A moss microcosm composed of star-shaped *Polytrichum commune,* windswept *Dicranum scoparium,* and short, pale *Leucobryum glaucum.*

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Chamaecyparis obtusa 'Chabo-hiba' 877-37: A Venerable Survivor

Peter Del Tredici

When people ask "What's the oldest tree growing at the Arnold Arboretum?" they're usually surprised to learn that it's a 276-year-old compact hinoki cypress (*Chamaecyparis obtusa* 'Chabo-hiba', accession 877-37) that stands only four feet tall. It is one of seven 'Chabo-hiba' specimens in the Larz Anderson Bonsai Collection that were imported from Yokohama, Japan in 1913. This makes 2013 a milestone for the tree—the hundredth anniversary of its arrival (and survival) in North America. It makes my head spin to think that someone has been watering this plant pretty much every day since well before the American Revolution! While this 'Chabo-hiba' is not the oldest Japanese bonsai in the United States (there are older ones at the United States National Arboretum in Washington, D.C.) the Arboretum's plant has been under continuous cultivation longer than any other bonsai growing in North America.

Larz Anderson attended Harvard College (class of 1888) and later served as a diplomat in the Foreign Service. In 1912, near the end of the Taft administration, he was appointed "Ambassador extraordinary" to Japan, a post he held for only six months, until Woodrow Wilson moved into the White House. During his brief stay, Anderson was smitten by the "bonsai bug," and in early 1913, shortly before completing his posting, he purchased at least forty plants from the Yokohama Nursery Company to bring back to his estate in Brookline, Massachusetts. Many of the specimens offered for sale by the nursery were already hundreds of years old. Photographs from the time show that the 'Chabo-Hiba' plants were often trained into a conical shape—suggestive of a distant mountain—with regularly arranged, horizontal branches.

Anderson and his wife Isabel (Weld) left Japan on March 6, 1913, and it seems likely that the plants followed them across the ocean in a shipment that autumn. Once they arrived, the trees were displayed on the terraces of the Anderson home where they resided for nearly twenty-five years.

The collection was donated to the Arboretum in two batches, initially in 1937 following Larz's death, and later in 1948, following Isabel's death. 'Chabo-hiba' 877-37 came to the Arboretum in the first installment and was put on display along with the other plants in a lathhouse on the grounds of the former Bussey Institution. They remained there until 1962 when they moved into their current hexagonal home near the Dana Greenhouses.

In 1969 the Arboretum appointed Connie Derderian to take care of the plants. As honorary curator, Connie revitalized the collection after years of neglect and took care of the plants until 1984. Having worked as Connie's apprentice since 1979, I became the new curator the year she retired. In 1998, the noted English bonsai master, Colin Lewis, became involved with the collection.

The fact that seven large 'Chabo-hibas' have survived the ravages of both time and occasional neglect for the past hundred years is a testament to the incredible durability of the plants themselves. By virtue of their longevity, the plants provide a direct link not only to the early 1900s, when wealthy Americans were passionately collecting cultural artifacts from Asia, but also to the Tokugawa era in Japan (1600 to 1868) when shoguns ruled the land and the plants themselves occupied places of honor in temples throughout the country.

The hinoki cypress cultivar name *chabo-hiba* is not widely used in Japan today, and it took some effort to uncover its history and meaning. The word *hiba* is the common name for the arborvitae-like conifer *Thujopsis dolobrata* and means "hatchet-shaped," in reference to the scale-like foliage of the plant. *Chabo* means bantam or dwarf chicken, and when combined with *hiba* means "compact or dwarf cypress." In the landscape, *Chamaecyparis obtusa* 'Chabo-hiba' is a relatively slow-growing plant that develops a pyramidal shape when left unpruned. When grown in a container and intensively pruned, it produces congested, planar foliage and contorted horizontal branches, resulting in striking bonsai specimens like accession 877-37.

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Selected specimens from the Larz Anderson Bonsai Collection will be on display at the Isabella Stewart Gardner Museum in Boston from October 2nd to 13th, 2013.