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...
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.

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.

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

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.
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, Ceris 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
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.

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

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).
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 thelobes 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-

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.

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.
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 distal-most 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...
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.

References

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*.

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.


William (Ned) Friedman is Director of the Arnold Arboretum and Arnold Professor of Organismic and Evolutionary Biology, Harvard University.