On the Worldwide Distribution of Azaleas

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Any gardener who has been paying even a little attention to garden literature over the past two decades has seen the upheaval DNA testing has brought to the world of plant naming and classification. The same technology that allows crime scene investigators to identify a perp from an errant drop of blood or the folks at AncestryDNA® to trace your lineage back to the Old Country, has allowed plant taxonomists to assess the kinship of all living things. In some instances, this has led to major rewriting of the classification systems used by earlier generations of taxonomists who based their work primarily on recognizable features. But in the Rhododendron world, and our subset of it the azaleas, the changes have been more one of rearranging the furniture in the room, not knocking down walls and throwing everything in the dumpster.

If we are to assess the evolutionary history of azaleas, we must consider the over 1000 Rhododendron species that have been described and where and when they appeared on the world stage. The simplest and one of the most recent classification schemes was presented by Loretta Goetsch and her colleagues in 2005.[1] They divide the genus into five clades (a group of closely related plants that can trace their lineage back to a single ancestor) based on DNA analysis. The three clades concerning most gardeners are: A. Subgenus Rhododendron, B. Subgenus Hymenanthes, and C. Subgenus Azaleastrum.

The subgenus Rhododendron clade is characterized as small leafed, mostly evergreen species with scales on the underside of the leaves and consists of about 400 species plus the tropical Vireyas. These are the lepidote rhododendrons of classic taxonomic schemes.

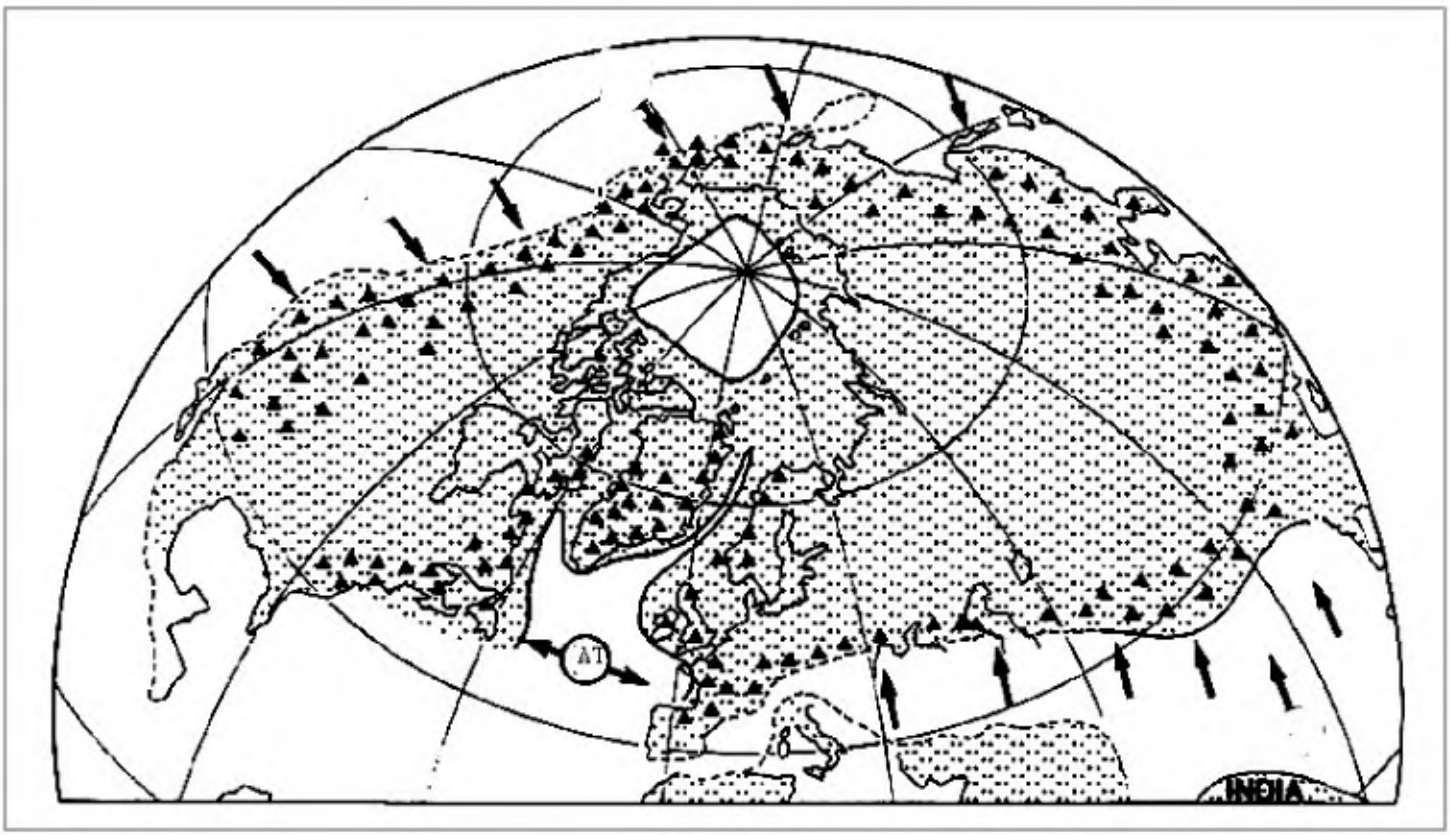
The subgenus Hymenanthes clade includes 225 species including the large, smooth-leafed evergreen rhododendrons most gardeners know as such, and most deciduous azaleas. The deciduous azaleas of North America are placed in subsection *Pentanthera* of the subgenus Hymenanthes. The Asian deciduous *R. mole* is alone in its own subsection Hymenanthes. These two subgenera are present in both Asia and North America, thus indicating their more ancient lineage than that of subgenus Azaleastrum, which includes the evergreen azaleas which grow in eastern China, Japan, and adjacent areas in Korea. Some shoehorning was done to get everything to nest into this simplified scheme, so one deciduous North American species (*R. vaseyi*) is included in the Azaleastrum group, while the other deciduous azaleas of this country are in the Hymenanthes subgenus. To make these subsections useful in classification, most are subdivided into subcategories that group likes together, further sharpening the focus of the classification scheme.

Gardeners primarily rely on visual reference when considering the plants we know as rhododendrons and azaleas. Most gardeners divide them into azaleas, deciduous azaleas, and rhododendrons. The most observant amongst us might divide the rhododendrons into two groups: those with little hairy leaves, and the large, smooth leafed types. From the above paragraph it becomes apparent that the evergreen azaleas are nicely segregated out as a group, but that deciduous azaleas are included under the umbrella with the large leafed rhododendrons.

As humans it is hard to think on a geological time scale, but to understand the worldwide distribution of Rhododendrons and how azaleas fit into this puzzle we must give it a go. The first recognizable pollen associated with the *Ericaceae* (the Rhododendron family) was discovered in rock deposits dating back to the late Cretaceous, about 68 million years before present (mybp). As a point of reference, the Appalachians and Ouachita Mountains formed from 250 to 300 mybp, when Africa and South America (respectively) collided with the North American plate. Continental collisions are slow moving train wrecks, with the plates moving only as fast as your fingernails grow–or about an inch a year. About this time the first seed bearing plants appeared at the end of the Carboniferous period. Ginkgo appeared about 190 mybp, pines about 140 mybp, while the first modern flowering plants (the angiosperms, to which Rhododendron belong) appeared about 120 mybp with the evolution of this group expanding rapidly by 100 mybp. Dinosaurs went extinct about 65 mybp and the world made its transition towards modern flowering plants, gradually leaving the conifers behind.

Two papers, separated by 25 years, do a good job of explaining the worldwide distribution of Rhododendrons. The first, by Irving and Hebda in 1993 and presented to the Annual Meeting of the American Rhododendron Society in Vancouver, relies on the older, pre-DNA scheme of classification and fills in gaps in knowledge by a series of well-reasoned hypotheses.[2] They report that fossil evidence is scarce, but specimens have been found that date back to the early to mid-Eocene about 55 mybp. At this time a land bridge connected Alaska and adjacent areas of Northern Asia (Siberia), while the northeastern parts of North America were only beginning to pull away from Greenland and Europe. The climate was warmer and wetter during this period and a more or less contiguous mixed forest of hardwood deciduous trees covered the land. Rhododendrons, almost exclusively associated with cooler, mountainous terrain, probably established themselves in these geographic niches across the range during this period.

As shown in Figure 1, during the early Tertiary period (about 55 mybp) the supercontinent Laurasia was still marginally intact but beginning the process of separating into its contemporary components of North America, Europe, and Asia. The arrows show the direction of tectonic plate compressional forces. Notice that India has not yet encountered Asia at this time. Continental boundaries



▲ Figure 1

are often associated with mountainous terrain, so it is hypothesized that ancestral Rhododendron species spread through these moderate regions during this time. During the next 20 million years, the Atlantic Ocean continues to widen, separating North America, and India collides with Asia and begins the period of rapid speciation in the Himalayan region. [Adapted from Irving and Hebda, 1993.[2]]

Most of their paper goes into considerable detail expounding on the effect of the Indian collision with the Chinese plate that began about 30 mybp and forced the Himalayan Mountains to rise. The authors explore the mountain building events that are still ongoing with the rapid speciation of rhododendrons–especially the Vireyas–that continues to the present time. They theorize that episodes of warming and cooling, on about a 50,000-year cycle, fueled the rate of Rhododendron speciation in the Himalayan region and adjacent areas of the Malayan archipelago. Warmer periods would allow Rhododendron species to ascend into new mountainous terrain, only to be chased back down when the climate cooled again. This retreat to warmer climes resulted in comingling of once-separated species, providing abundant opportunity for cross-species fertilization and the appearance of new species. Because the Himalayas are often separated by tropical valleys, selection pressures occurred in isolation on each mountain range, leading to the large number of species now recognized.

In 2018, Nawal and his colleagues in China use mega data analysis to model Rhododendron distribution and speciation patterns during the past 65 million years. Their data set establishes a predictive value of 63.5 mybp as the point when Rhododendrons separated from their nearest relative in the ericaceous family.[3] Crunching the numbers and looking backwards at the mutation rate of the DNA samples, they conclude the origin of the genus Rhododendron was somewhere in Northeast Asia, not in Southern Asia and the Malayan Archipelago, the current hotspot of biological activity.

About 45 mybp species begin to radiate out from Northeast Asia to Europe and North America, primarily via means of mountain ranges where they spread in the cooler, more northerly latitudes of the cool temperate forest. During this period new species development is progressing at a slow to moderate rate until the period from 30 to 25 mybp. Speciation, almost all of which is centered in Southern Asia and adjacent parts of the Malayan Archipelago, takes a rapid uptick in rate during this period, which coincides with the uplift of the Himalayan Mountains. The authors conclude that even as Rhododendrons progress into the tropical climes, mountains and cooler niches continue to be an important feature associated with species spread. I would guess that it is during this age that the first evergreen azaleas arose in the far southeast part of Asia, far removed from any connection with North America.

Nawal reports that the rate of new species formation in North America was slow after Asia, North America, and Europe split apart in the Eocene (55–34 mybp) and is a strong indicator of the relative climatic stability during this period. Because the major North American mountain ranges run north and south, even glacial epochs such as began 5 mybp and concluded about 15,000 years ago, did not cause undue extinction pressure on our native flora. As glaciers spread south across the continent, species migrated south

during cold periods. When warmer periods were at hand, species followed the retreating ice north.[3]

During the past 20 million years, the eastern parts of North America have been dominated by deciduous hardwood forests, a habitat not unlike that which has prevailed during most of the time Rhododendrons have inhabited North America. Of the 27 species of Rhododendrons described as native to North America (including the five species transferred from other genera in the 2005 reclassification scheme), only five of these are found in the western states. While the east has remained environmentally stable with plentiful rainfall during the past 20 million years, the west has undergone a steady march towards desertification. During that time span the western part of North America has gone from a mixed hardwood forest in the north and a broadleaf evergreen woodland in the south to mostly desert and semi-desert scrub across much of the region. Coniferous forests only persist in northern latitudes and higher elevations. Though no fossil evidence is available to support this statement, it seems likely that western parts of North America have lost species during the period of desert expansion while the eastern areas have remained stable.

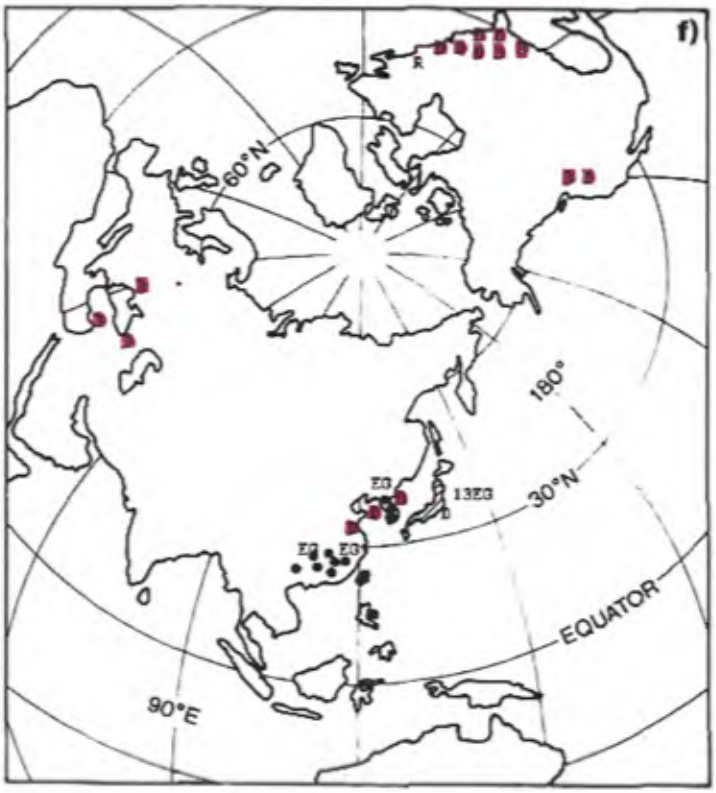
Figure 2 shows the generalized distribution of deciduous (D) and evergreen (EG and •) azalea species at the current time. Notice that the evergreen species are limited to East Asia, while the deciduous species are found in four regions: Southeast Europe, East Asia, Northwestern North America, and Eastern North America. (Modified from Irving and Hebda, 1993[2])

As mentioned above, *R. vaseyi* (Pinkshell Azalea) from the mountains of North and South Carolina is classified as belonging to the subgenus Azaleastrum. This deciduous species, along with *R. pentaphyllum* from Japan, is joined into a subsection that separates them from the eighty-plus evergreen azaleas that make up the majority of species in this subgenus. Apparently, these two deciduous azaleas are closely related, perhaps making up a long-separated disjunct (found in two widely separated locations) population. Because evergreen azaleas are confined to eastern parts of Asia, it seems likely the evergreen species evolved sometime after the middle tertiary time (say 35 - 25 mybp) after the continents separated.

The classic disjunct pattern of *R. vaseyi* and *R. pentaphyllum* closely resembles that highlighted in the 1850s by Harvard botanist Asa Gray who noted the similarity in flora between the southeastern United States and southeastern Asia. To date, over 80 species have been recognized, including many species with only two recognized species–one in Asia and one in the southeastern states–including sweetgums, tulip poplar, sassafras, pachysandra, and many others. Whether *R. pentaphyllum* is an ancestral progenitor of the evergreen azaleas classified in the subgenus Azaleastrum, a biological dead end, or an artifact of the classification scheme is beyond my ability to ascertain.

Development of Modern Azalea Groups

While geologic and environmental forces initially established the limits of rhododendron distribution, it was humankind that shaped the contemporary dispersal of these



▲ Figure 2

plants across the urban landscape. The selection of "new and improved" rhododendrons and azaleas are of recent vintage–playing out over the past 500 or so years. To even summarize modern development of garden hybrids is not possible here, but it might be interesting to look at a few of the deciduous and evergreen azaleas available in the nursery trade today and trace a bit of their lineage.

Before azaleas could be hybridized, they first had to be assembled into collections. As plants were introduced from the United States, south-central Europe, China, and later Japan into European (and later, American) collections, they arrived bearing the name in vogue at the time. Most of the deciduous species then recognized from the eastern states–primarily from Virginia to Georgia–had been collected by the early years of the 19th century and sent to wealthy collectors who in turn shared them with gardening friends and nurserymen throughout much of northern Europe. The deciduous Chinese azalea–now called *R. molle* but known at various times as *R. sinense* or *R. japonicum*–arrived in Europe during the first two decades of the 19th century. The yellow flowered deciduous azalea from the Caucasus-Black Sea region of Europe (known today as *R. luteum,* but then as either a form of *R. flavum* or *R. ponticum*) closely resembled the deciduous American species and was introduced into England by 1792. **(See Table 1)**

The first controlled breeding efforts appear to have been made in the 1820s in Ghent, Belgium, by a baker named P. Mortier who crossed the American Flame and Pinxterbloom azaleas. About the same time J. R. Gowen, an estate gardener in England, crossed the yellow European azalea *R. luteum* with the American Flame azalea (*R. calendulaceum*) and Swamp azalea (*R. viscosum*). Gowen and others also began

using the Chinese azalea (*R. molle*) with several American species. M. L. Verschaffelt, a nurseryman in Ghent, and Anthony Waterer, an English nurseryman, carried on extensive crossing programs and introduced hundreds of selections over the next several decades that were collectively known as the Ghent Hybrids.

The Mollis Azaleas began development in the 1860s after the gunboat diplomacy of Commodore Perry forced Japan to open to western trading in 1854. Peter von Siebold returned to Japan, after being exiled 30 years earlier by Japanese officialdom, and collected seeds of deciduous Japanese azaleas, and distributed them to Louis van Houtte in Ghent who incorporated them into the established breeding programs of the area.

In the 1860s the father and son nurseryman team in England–Anthony Waterer Senior (1822–1896) and Junior (1848–1921)–began a serious breeding program looking for late blooming, winter hardy types with good garden characteristics. The main genetic infusion to the hybrid stream by the Waterers was using the western American *R. occidentale*. These Knap Hill Azaleas relied on the genetic pool that preceded it but went forward with ruthless determination to save only the best of each new cross. Later in his life, Junior became a bit reclusive and overly protective of his plants, but fortunately in 1920 Rothschild managed to acquire a nucleus of Knap Hill Azaleas. Over the next two decades over a million rhododendron plants were grown at the Exbury estate in England, primarily from crossing and re-crossing the best of the best to achieve the array of orange, orange-red, yellow, pink, and white azaleas we see offered under the name "Exbury" today. The name Exbury has become a generic name for deciduous azaleas amongst nurserymen even though many other breeders have since added their touches to the plants being offered.

Table 1 shows the development of modern deciduous hybrid azaleas began about 200 years ago when collectors used the species available to them to make the first crosses. Over time new species were added to the gene flow, incorporating new traits. Though most of the initial hybrids were selected in regions with benign, maritime climates, the most exciting advances have come about by selecting in diverse climatological regions.

▼ Table 1—Development of Hybrid Deciduous Azaleas

Species Assembled in European Gardens - 1730 onward

R. arborescens	Sweet Azalea	US	<1818
R. calendulaceum	Flame Azalea	US	1806
R. luteum	Yellow Pontic A.	SE Europe	1792
R. periclymenoides	Pinxterbloom A.	US	1730
R. viscosum	Swamp Azalea	US	1734

Ghent Hybrids began about 1820 from above species

R. molle	Mollis Azalea	China	1820s
R. molle ssp. *japonicum*	Japanese Azalea	Japan	1861

Mollis Hybrids used east Asian species and began by van Houtte in 1860s

R. occidentale	Western Azalea	W US	1850

Knap Hill Hybrids began about 1870 by Anthony Waterer Sr. who added Western Azalea

Exbury Azaleas, Rothschild - beginning about 1920 recrossed the best **Knap Hill** hybrids

Ilam Azaleas (1930s) developed in New Zealand from **Exbury** hybrids

Northern Lights: (1950s) Minnesota program using **Knapp Hill** and **Exbury** with US species

R. austrinum	Florida Azalea	SE US

Aromi Azaleas: (1970s) Crossed **Exbury** hybrids with R. austrinum to achieve heat tolerance in Mobile, AL

Photo G. Klingaman

▲ Photo 1—Gable's 'Rosebud' has always been a personal favorite and illustrates how Gable's inclusion of hardy forms, including *R. yedoense* var. *poukhanense*, *R. kaempferi*, and 'Hexe,' which has some hardiness through *R. obtusum* var. *amoenum* and sizzle through the more tender *R. simsii* and *R. indicum*, came together to create a cold hardy, evergreen beauty. Upon closer reading, I find the plant I have long known as 'Rosebud' may in fact be Gable's 'Lorna', both sibs (fraternal seedlings) that appeared in his catalog just after WWII.

Photo G. Klingaman

▶ Photo 2—Buddy Lee, the father of the repeat blooming azaleas, is one of the long list of azalea breeders who have added new and useful traits to the genetic pool that makes up modern azaleas.

The scaffolding built by these early breeders has been added to and improved by many American breeders, each with their own breeding goals. A few of these include the Girard deciduous hybrids using Knap Hill Hybrids as basis but selecting for mildew resistance; the Northern Lights Series using Knap Hill and Exbury Hybrids with various native species to achieve bud hardiness in Minnesota; Aromi Hybrids developed in Mobile, AL using *R. austrinum* to incorporate heat tolerance into the Exbury types, and any number of other breeders who have added in small or large measure to the deciduous azaleas we now grow in our gardens.

Evergreen Azaleas

The evergreen azaleas in our gardens are a meld of Eastern and Western cultures. Two of our most popular azalea groups–the Kurume and Satsuki–were dropped into our gardens fully formed after centuries of breeding and selection in Japan. The Western additions–starting with the Belgian-Indian Hybrids of the middle years of the 19th century–were developed as flowering pot plants for wealthy estate gardens and the then-emerging middle class that developed as the industrial revolution caught hold. By the 1840s these Belgian-Indian Hybrids had crossed the Atlantic and found a home in South Carolina in Drake's Magnolia Gardens. A generation later a Belgian immigrant, P.J. Berckman, began improving on these early hybrids and produced many still popular Southern Indicas at his Fruitland Nursery in Augusta, GA.

While evergreen azaleas are all native to Asia, modern garden selections are a blending of Eastern and Western aesthetics. Of the over 80 recognized species, fewer than ten have been used to develop our modern hybrids. (See Photos 1 & 2)

Table 2 shows a condensed chronology of the development of the modern azaleas we grow today. I credit most of the progress to hybridizers working at nurseries or B. Y. Morrison's large government (USDA) supported program at Glenn Dale, MD. But after WWII, hobby breeders began adding their own touches to the flow of new introductions. Buddy Lee's introduction of the repeat-blooming azaleas less than three decades ago has led to at least a dozen new, competing fall blooming series that are profoundly reshaping the image of our beloved plants. Just as breeders such as Gable, Girard, and Morrison reworked old southern favorites for northern gardens, this same opportunity exists for the repeat bloomers.

Future Possibilities

The opportunity for developing new, more exciting and interesting azaleas is far from over. By perusing Tables 1 and 2, it is apparent how few species have been used to develop the garden forms of our deciduous and evergreen hybrids. About eight species have been used in the deciduous line;

▼ Table 2—Development of Hybrid Evergreen Azaleas—A Chronology

R. kaempferi	Kaempfer Azalea	Japan	1690
R. kiusianum		Japan	1918
R. sataense		Japan	
R. "hybrid swarms"		Japan	1915

Kurume Azaleas: Mentioned in *Kadan ko moku* in 1681; introduced here 1915

R. indicum	Indian Azalea	China / Jap	1680
R. eriocarpum (tamurae)	Dwarf Indian A.	Japan	
R. "hybrid swarms"		Japan	1938

Satsuki Azaleas: some perhaps date to 1500 in Japanese gardens; U.S. in 1938

R. simsii	Sims Azalea	China	1806
R. simsii (Fortune's collection)	"Indica Azaleas"	China	1851
R. ripense 'Mucronatum'	"Indica Alba"	China	1819
R. indicum 'Variegatum'		China	1833
R. 'Phoeniceum'		China	1824
R. indicum - various colors	Indian Azaleas	China	1830s

Belgian Indian Hybrids: Developed for forcing; introduced to Magnolia Gardens 1848

Southern Indian Hybrids (GA): started 1870s by P.J. Berckman's Fruitland Nursery

Rutherford Hybrids (NJ): ***s*** tarted in 1920s using Belgian Indian hybrids; later added Kurumes

R. kaempferi	Kaempfer Azalea	Japan	1892
R. yedoensis var. poukhanense	Korean Azalea	Korea	1905

Gable Hybrids (PA): start 1920s Joe Gable used above with Kurumes and other hardy forms

Glenn Dale Hybrids (MD): starting in 1935, B. Y. Morrison used most of what came before

Robin Hill Hybrids (NJ): **s**tart 1937, Robert Gartrell used Satsukis but selected for hardiness

Girard Hybrids (OH): starting late 1940s used Gables and backcrossed to his own seedlings

R. oldhamii 'Forth of July'	Oldham Azalea	Taiwan	1918

Encore Azaleas (LA): starting about 1980, Buddy Lee added summer and fall flowering genes

Photo G. Klingaman

▲ Photo 3—The Western Azalea (*R. occidentale*) is probably a relic of a once more-numerous group of rhododendrons that occupied space in western North America. The hard-to-grow and somewhat gangly plant seemingly had little to offer breeders, but Anthony Waterer, Sr. used it successfully to develop the Knap Hill Hybrids.

Photo G. Klingaman

▲ Photo 4—'Jacob Allen' is one of Eugene Aromi's hybrids that leaned heavily on southern native deciduous azaleas, especially the Florida Azalea (*R. austrinum*), for adaptability to the hot and humid South.

fewer than ten in the evergreen. Over 30 species of wild deciduous azaleas and over 80 evergreen species have been described. The merits of introducing a new species into a breeding line may not be apparent at first glance. Anthony Waterer's use of *R. occidentale*, even though it had been spurned by other breeders of his day, led to the development of most of the deciduous azaleas we grow today. Most azalea experts apparently did not recognize or had overlooked the merits of *R. oldhamii* before Buddy Lee picked it up about 1980 and started swapping pollen. Other possibilities remain to be discovered, and it will be interesting to see what comes next. (See Photos 3 & 4)

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Further Reading

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