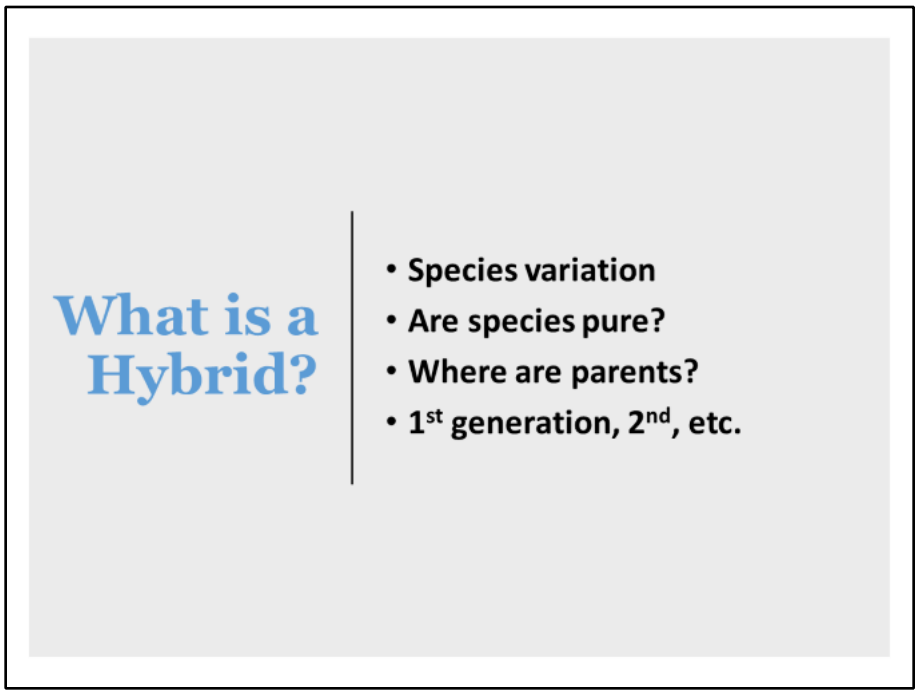
We are fortunate in this area of North America to have wonderful trilliums and stewartias. It is also near the epicenter of American deciduous azaleas. The commercial market does not begin to offer the spectacular beauty that is found naturally in our forests, balds, woods, hills, and swamps. You can close your eyes and go to sleep now, unless you want to learn more about American azalea natural hybrids.

Currently, taxonomists seem to have settled on 17 species of American azaleas. We have added and subtracted to the total since Linnaeus listed two Americans in 1753.

The correct number may never be possible to determine because foremost there is no and will never be a precise definition of what a species is.

Genus and species are fuzzy, vague concepts, theories, created by humans to satisfy our need to categorize plants and animals. But evolving living things, especially plants, do not always fit cleanly into precise boxes.

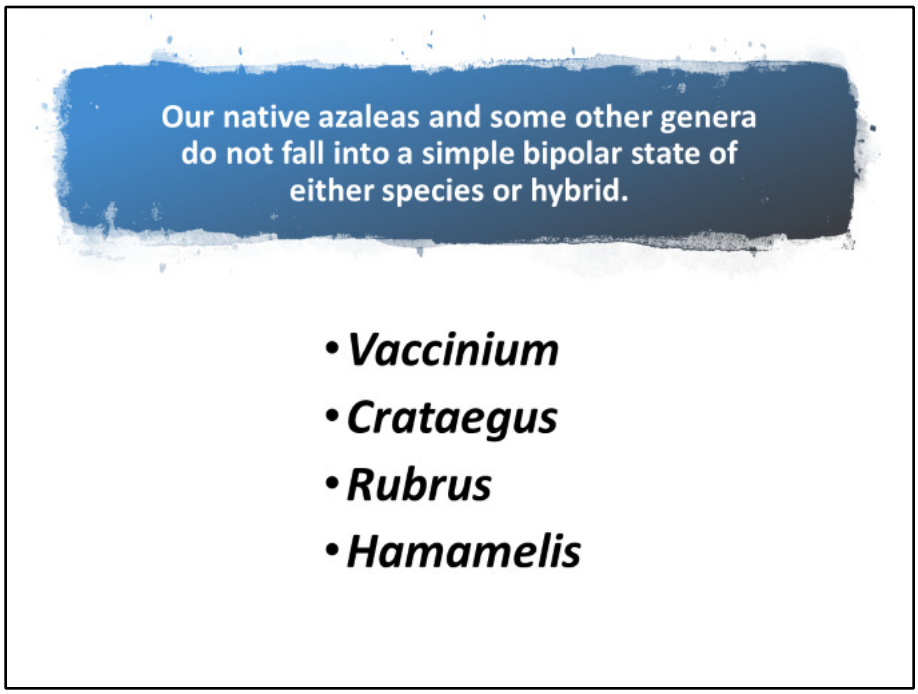
Taxonomy and classification are not exact sciences. They are more akin to the soft sciences of economics, social studies, and political science than to the hard sciences of math, physics, and chemistry.



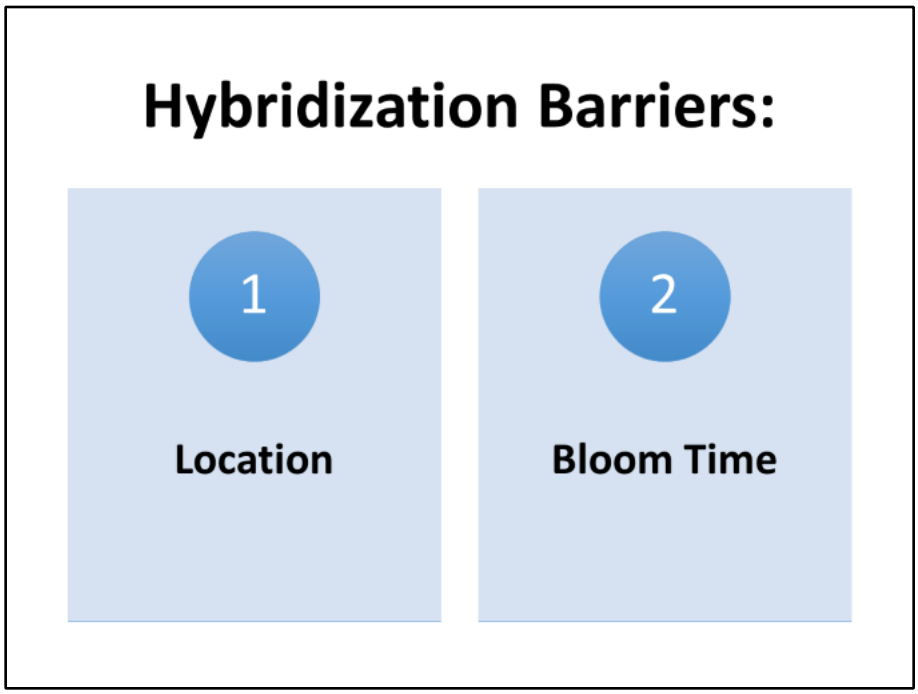
What is a hybrid? In theory, a first-generation hybrid is a cross where the seed parent and the pollen parent are different species. Second-generation seedlings could be back crosses to one of the original parents or to sister seedlings. And with subsequent generations things get murkier from there.

When we are out in the field, we tend to assume too much. We assume there are such exact things as species and hybrids, that the plant is one or the other. It could be that the supposed species is not “pure” and has a mixture of genes from past generations. After all, we haven’t met its ancestors. It could be the supposed hybrid is just further variation of a species or has formed a stabilized population and no parental species are nearby. We assume hybrids came from species, but didn’t species transition from hybrids that stabilized in a satisfactory niche? Is it a duck or not? It could be just mostly duck.

We do know that among our native azaleas, with the exceptions of *R. vaseyi* and *R. canadense*, the other named species will naturally hybridize if given a chance, some more than others.



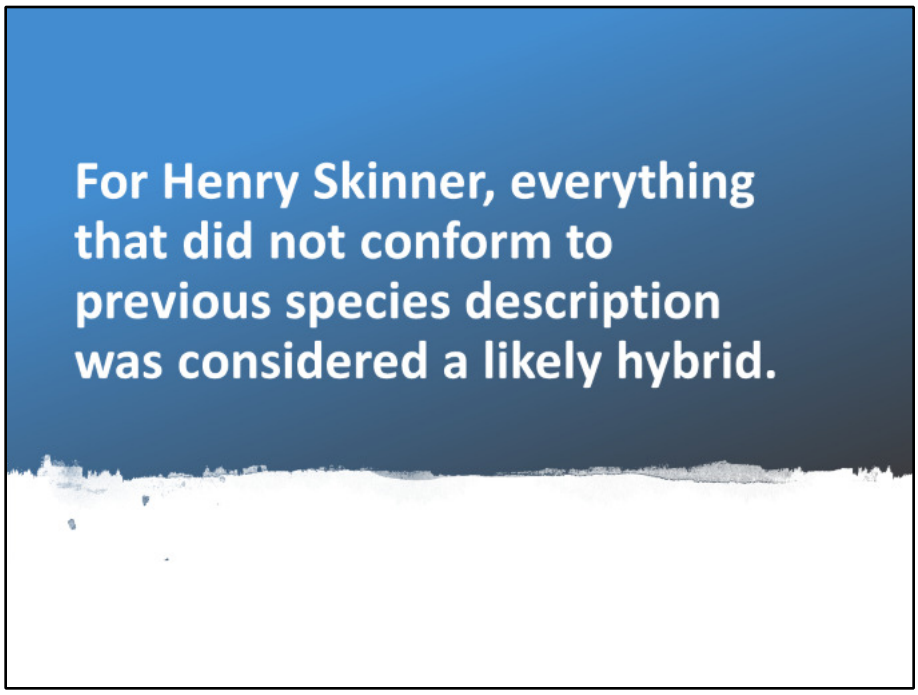
Field experience strongly suggests that our native azaleas, as *Vaccinium*, *Crataegus*, *Hamamelis*, and some other genera similarly, do not fall simply into a bipolar state of either species or hybrid.



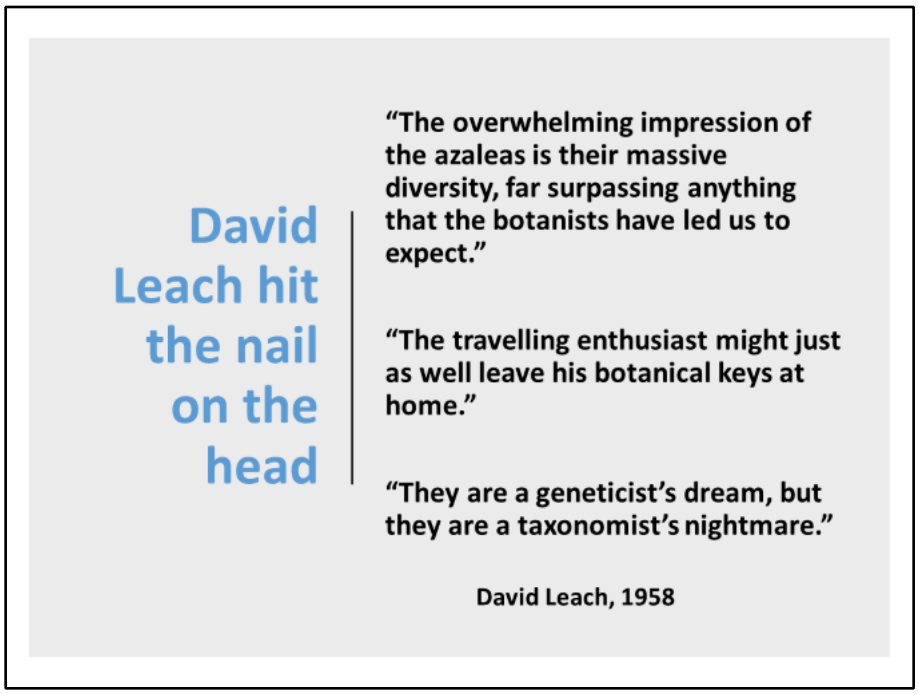
While there are factors that affect hybridization, there are no **significant** hybridization barriers other than location and bloom time.

And we know bloom times can be so erratic that bloom overlap can occur on rare occasions when the bloom ranges do not normally overlap.

Don Hyatt has a *R. prunifolium* that has bloomed in the spring after failing to bloom in the previous fall.

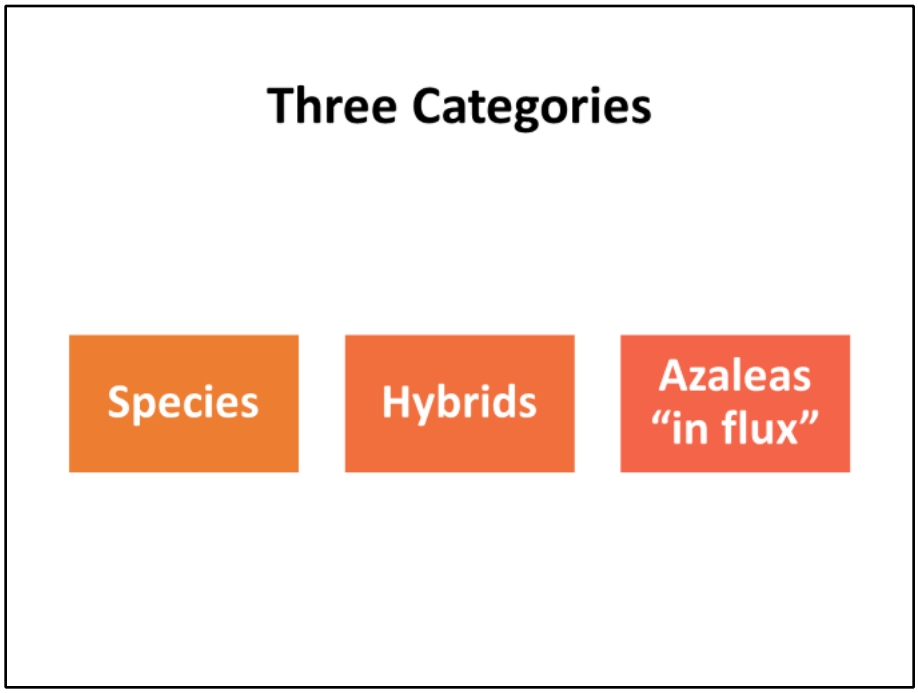


If you read Henry Skinner's 25,000-mile epic "In Search of Native Azaleas" and David Leach's "A New Look at the Azaleas and Rhododendrons of the Blue Ridge Mountains," and go see some of these populations for yourself, you will realize that there are many populations that are not species according to species descriptions and not hybrids in the definitional sense, for no species parents can be found.



Leach went on to say the evidence is indisputable that azaleas are in flux, and the species in typical form are often the exception in "vast seas of Azaleas undergoing introgressive hybridization." He recognized that our wild populations often refuse to fit into the classifications we call species. Instead they are intergrading hybrids constituting uninterrupted progressions of variations linking them to their ancestry.

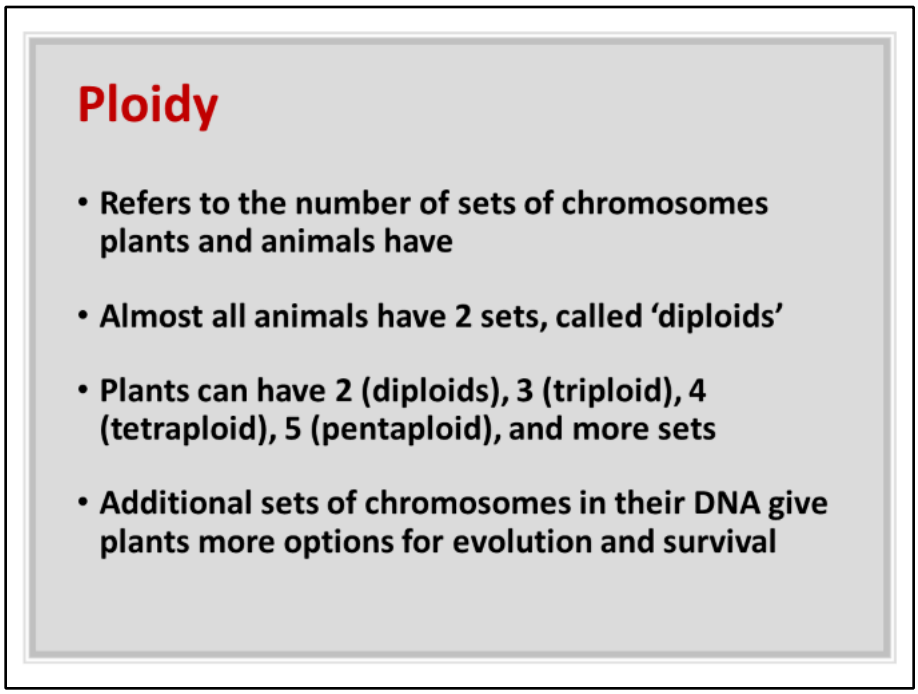
Leach did not think the so called hybrids had a genetic disadvantage. In some sites he saw them thriving more than their progenitors.



So with native azaleas in addition to natural hybrids and the declared 17 species there is really a third category that does not have a name. It is made up of the groups of plants that do not fit neatly within one of the 17 species but appear in isolation, apparently without potential parents nearby. This tells us our species concept has problems. We really need a better paradigm.

Of course, we are not going to throw out the species concept any time soon. But the interbreeding, dynamic entity (American azaleas) seems to be at a higher level than the current 17 vague species and groups of plants containing characteristics that cross those species boundaries. What we have is a continuous breeding system within which are transient groups that cannot in most cases be cleanly defined.

These groups fall roughly into three categories: (1) species that are not very well defined and described, (2) hybrids whose parent species are nearby, and (3) populations that do not fit in the other two groups.



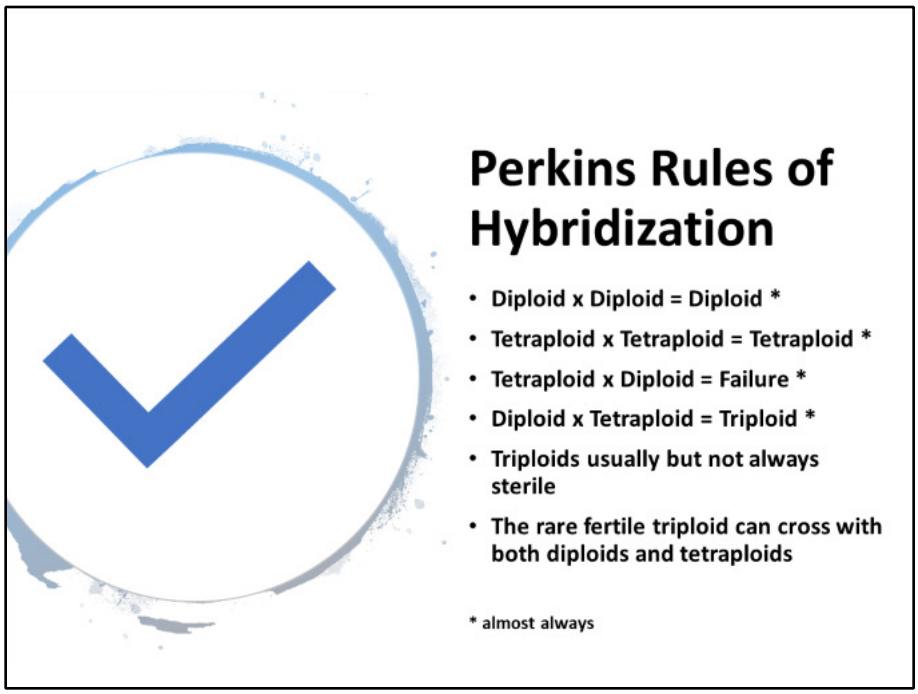
In addition to the ability and tendency of most of our named species to hybridize naturally if pollen meets stigma, we now know, thanks to the results of significant ploidy and hybridization research of John and Sally Perkins with the team under Dr. João Loureiro at the University of Coimbra in Portugal, that there are "rules" native azaleas tend to follow in hybridization.

Ploidy refers to the number of sets of chromosomes plants and animals have. Almost all animals have two sets and are called diploids. Plants can have two, three (triploid), four (tetraploid), five pentaploid), six (sexaploid), and more sets of chromosomes. Having additional sets in their DNA gives plants more options for reproductive evolution and survival.

Until recently, all American azaleas were thought to be diploid, except for *R. calendulaceum* and *R. canadense*, which were said to be tetraploid. Visually counting tiny microscopic *Rhododendron* genes, however, is difficult and fraught with error.

A modern technique called flow cytometry, essentially weighs the chromosomes rather than counting them and appears to be more reliable.

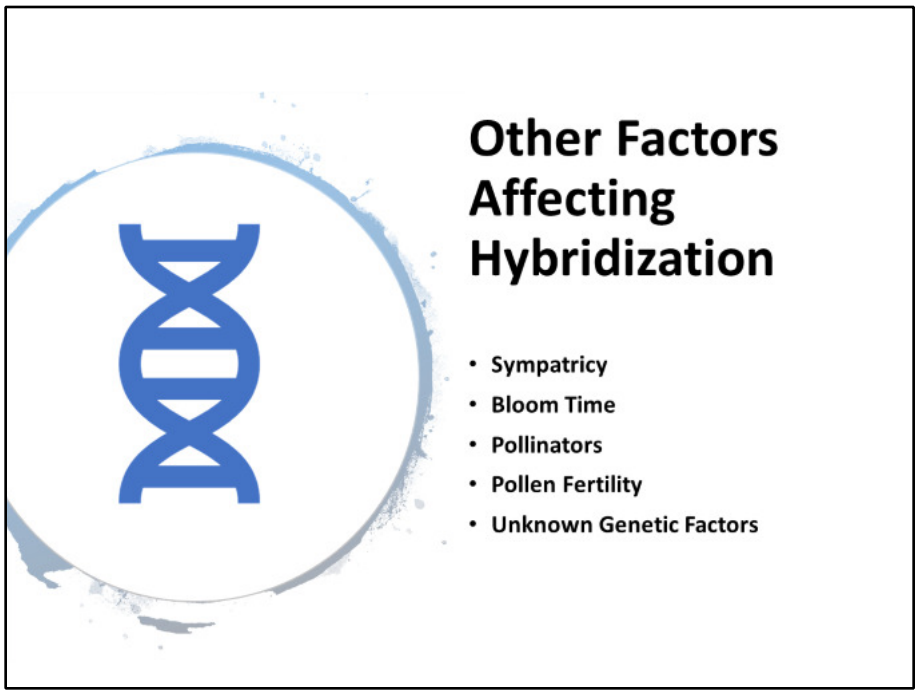
We now know with confidence that *R. atlanticum*, *R. austrinum*, *R. calendulaceum* and *R. colemanii* are tetraploid, while all the rest of the 17 American species are diploid.



The Perkins Rules explain why *R. periclymenoides* pollen (diploid) is almost never successful on a *R. calendulaceum* (tetraploid), while the pollen from *R. calendulaceum* is successful on the *R. periclymenoides*.

The diploid must be the seed parent in a diploid–tetraploid cross. Triploids are almost always sterile, but not always. The rare fertile triploid can cross with diploids or tetraploids, producing an array of ploidies: diploids, triploids, tetraploids, pentaploids, sexaploids, etc.

Thus, the rare fertile triploid is a two-way bridge that can transfer genetic material upward into tetraploids from diploids and downward from tetraploids into diploids.



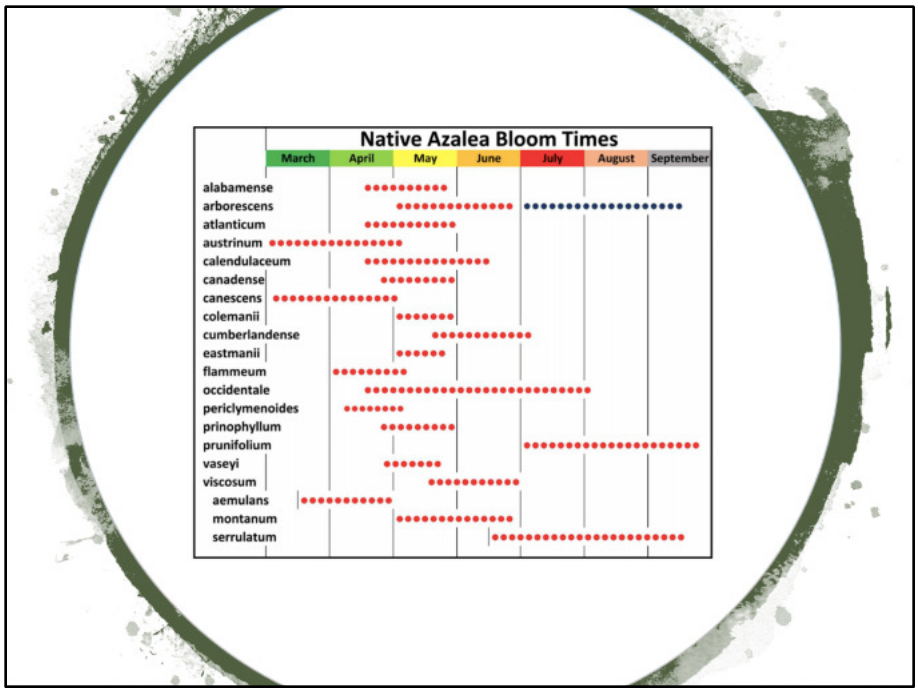
In addition to ploidy, there are other factors affecting successful hybridization

- Sympatricy
- Bloom Time
- Pollinators
- Pollen Fertility
- Unknown Genetic Factors

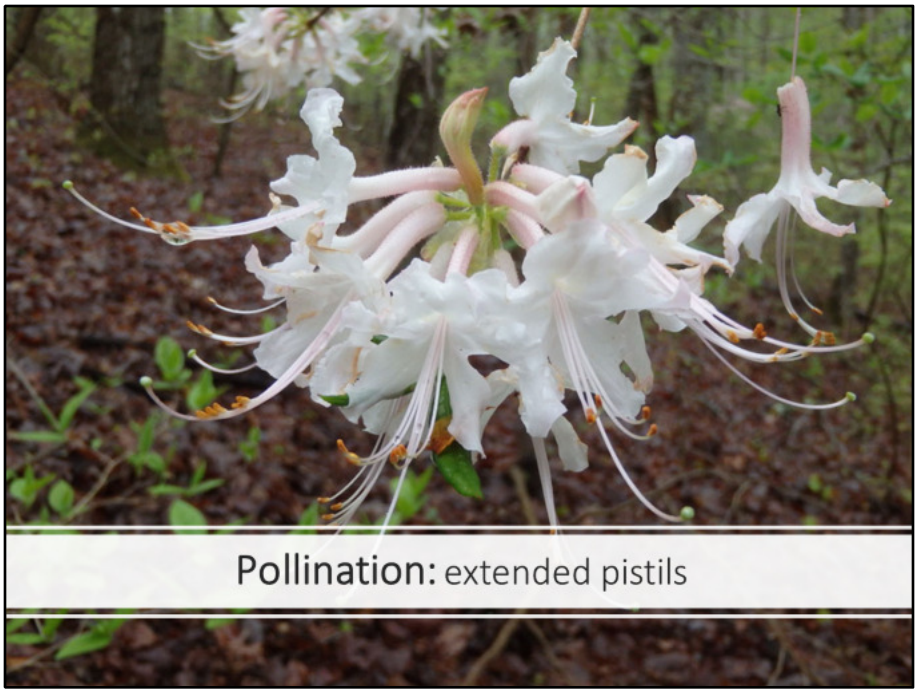
Sympatricy is a fancy word meaning occurring together in the same local area. The opposite of sympatric is allopatric. Many of our species overlap in distribution and can be found growing in close proximity to one another. *R. canescens* is the most common azalea in the Southeast and can be found in various places with *R. alabamense*, *R. atlanticum*, *R. austrinum*, *R. calendulaceum*, *R. cumberlandense*, *R. flammeum*, *R. periclymenoides*, and *R. viscosum*.

R. periclymenoides also overlaps in distribution with *R. prinophyllum*, *R. calendulaceum*, and *R. viscosum*. *R. calendulaceum* also has overlapping distribution with *R. cumberlandense*. and *R. arborescens*.

These are only examples of sympatricy. There are more. *R. occidentale* is the only native azalea west of the Rocky Mountains, thus there are no natural *occidentale* hybrids.



Obviously, for natural hybridization to take place the seed parent and pollen parent must be in bloom at the same time. **Monsieur Mortier** of Ghent, Belgium was able to create the first hybrid group, the Ghent Hybrids, by delaying the flowering of early-blooming species and speeding up the flowering of later-blooming species. Even within a single species, not all plants bloom at the same time. There is a **bloom range**, which can extend over a month or more. Some individual plants of the same species may be early bloomers, some later. On the same plant, **not all blossoms open at once**. Over how long a period a plant blooms **depends on the temperature**; the warmer the temperature, the shorter the bloom period. **Seasonal weather** affects the bloom cycle. A cool spring delays the start of early blooming. Cool weather followed by very warm weather can cause unusual situations where plants that do not normally overlap in bloom times to do so. Late-season blooming plants like *R. prunifolium* and *R. viscosum* var. *serrulatum* require the right conditions for their fall blooming. As referred to previously, Don Hyatt noticed a very late *R. prunifolium* that after a hot, dry summer failed to open its blossoms in the fall, but interestingly these "failed" blossoms opened in the following May. It **only takes an occasional overlap** in bloom time to create an opportunity for hybridization.



With two co-located species blooming at the same time, pollen has to be exchanged and not all species attract the same pollinators. Native azalea pollination has had limited research. On most species, the pistil extends beyond the pollen-producing stamens, discouraging self pollination. The anatomy of a native azalea flower suggests a small insect like an ant or beetle is unlikely to pollinate a plant. Further, hand-pollination experimentation indicates that some plants are reluctant to self pollinate and will not produce viable seed from pollen of the same plant.

Fragrance, color, and bloom time seem to play vital roles in attracting pollinators. Red and pink attracts hummingbirds. White attracts moths, which mostly feed at night.

The most common pollinators seen on native azaleas appear to be butterflies and various species of bumblebees. Honey bees and wasps play a minor role. Wind pollination can occur but appears to be negligible on native azaleas.

Large butterflies brush against the stamens, cover their lower wingtips and tails with pollen as they search for nectar with their proboscises.

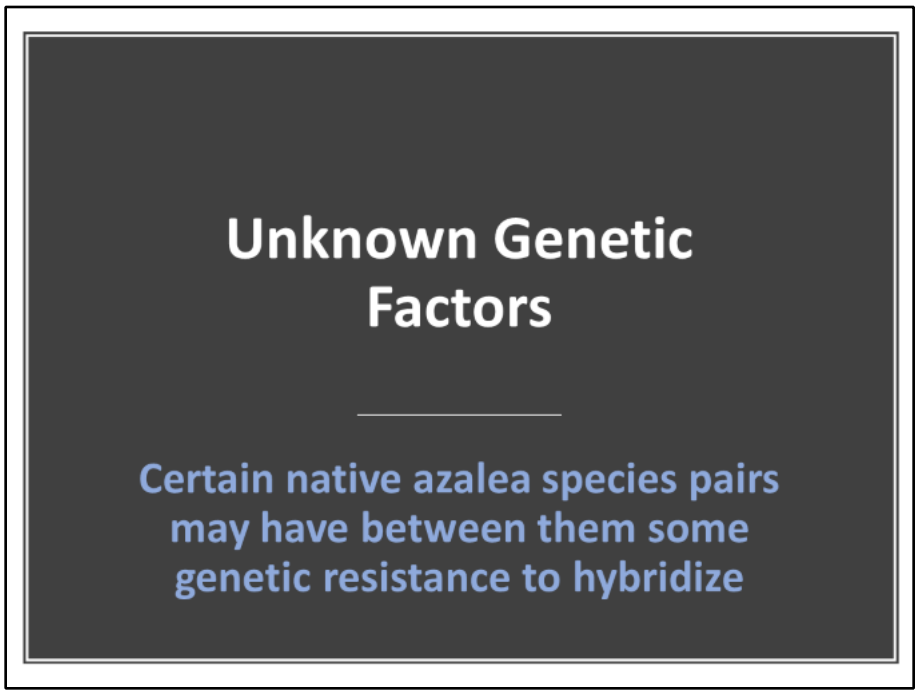
Butterflies need an open canopy immediately above them. If one observes where flowers are on a plant and where fertilized seed pods form, one will see very few seed pods on the inside of the shrub or lower-tier branches. The capsules will always be on those branches with extra air space above.

Some bumblebees use buzz pollination to vibrate the stamens and cover their whole bodies with pollen. Electrostatically charged pollen is then attracted to the oppositely charged hairs on the bumblebee. Covered in pollen, both butterflies and bumblebees then come in contact with the stigmas on nearby plants.

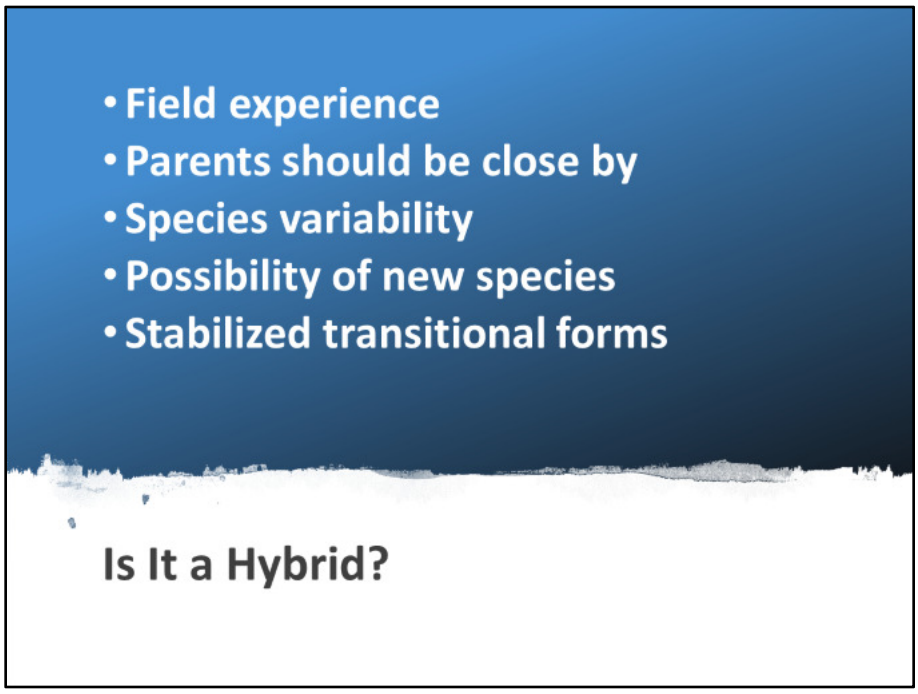
Bumblebees are not as efficient pollinators as large butterflies because they do not always touch the stigma.

Even if a stigma is anointed with pollen it may or may not result in much seed. In the 1970s, Frank Willingham studied *R. calendulaceum* and *R. bakeri* (*R. cumberlandense*) in the Nantahala Mountains of North Carolina. One finding was that pollen fertility was much lower in *R. cumberlandense* than in *R. calendulaceum*. No details in the published report disclosed how Willingham determined pollen fertility.

A study of pollinators on Gregory Bald found most seed pods contained significantly fewer seeds (up to 40) than typical *R. calendulaceum* (200-500). The primary species on Gregory Bald is *R. cumberlandense*, yet the primary pollinators are the less-efficient bumblebees. Still, a possibility exists that some species may be more pollen fertile than others, making certain crosses more likely than others.



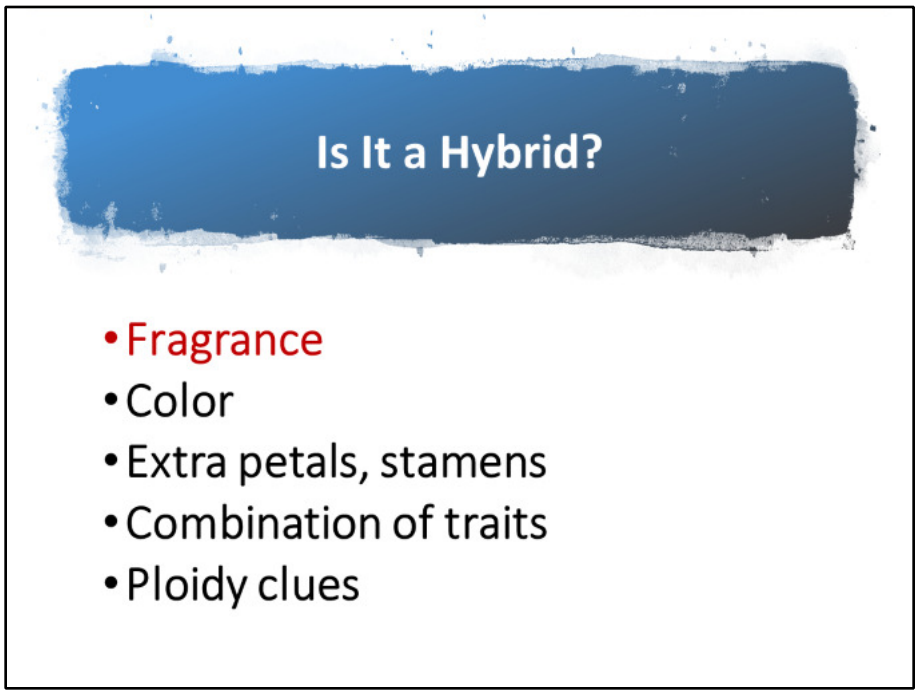
Other as yet unknown genetic factors may affect hybridization. Certain native azalea species pairs may have between them some genetic resistance to hybridize. Others may willingly and even aggressively hybridize. As far as I am aware, little to no research has been done in this area.



How does one tell if a wild plant is a hybrid? **It is at best an educated guess.** Field experience is the best partner in evaluating possible hybrids. The more plants one has seen in the field the better one can judge how a particular plant fits. One has to appreciate the variability, the habitats, and the expected distribution of the azaleas to be able to realize when something may be other than a recognized species. Unfortunately, identification keys often lead one astray because only one or two characters are used and the possibility of hybrids is almost always ignored.

Both parents of a hybrid should be close by. If they cannot be found, one should consider the possibility of the plant being variation within a species, even if it exceeds the expected boundaries. We learn more about these plants every day. There is also the possibility of as yet undeclared species or one of these groups with mixed characteristics.

For example, the literature has stated that new growth on *R. canescens* is hairy but eglandular. We have recently found pink-flowered diploid plants, primarily but not exclusively in the western portion of *R. canescens* distribution that has glandular new growth and several other distinctive characters. Is this a hybrid? Is it a new species? Is it merely a refinement of what the species *R. canescens* is?



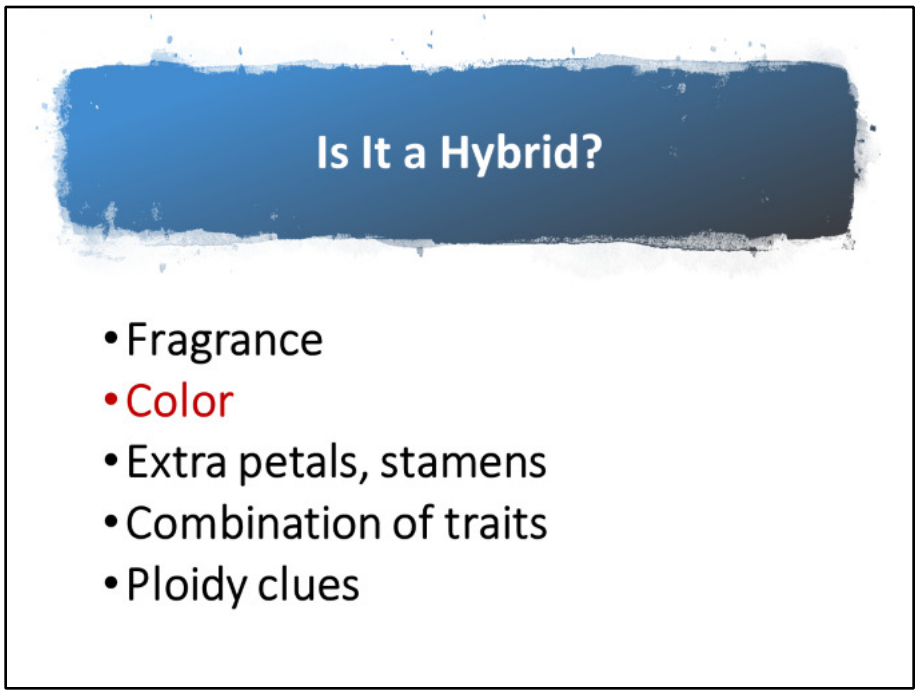
Here are some clues to evaluate possibility of hybridity.

Some of the fragrant azaleas have distinctive odors. A plant with some morphological characteristics of one species but the fragrance of another may be a hybrid.

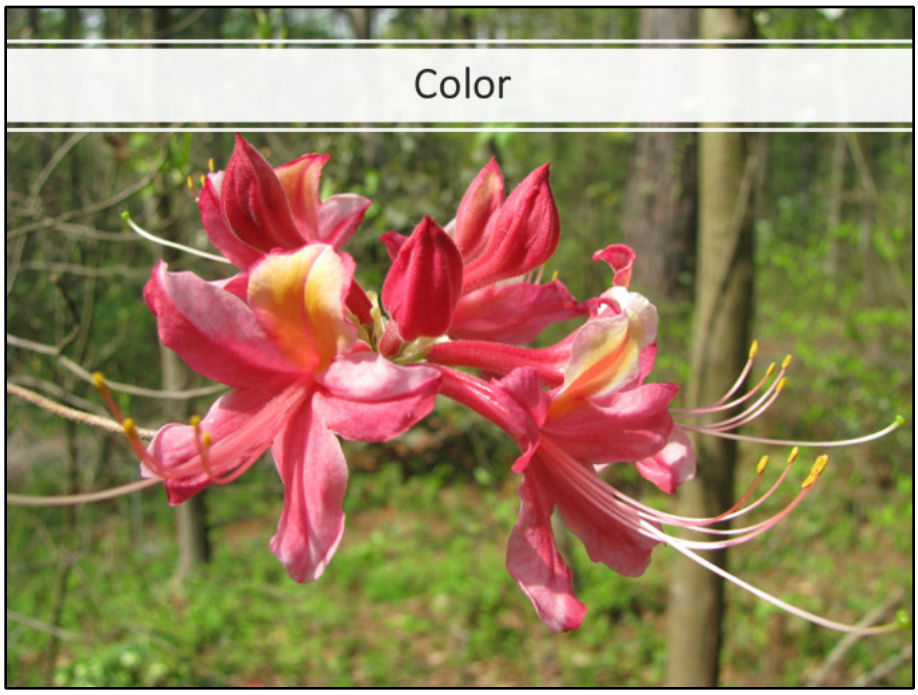
Fragrance

Sweet	Spicy	Non-fragrant
arborescens	alabamense	calendulaceum
atlanticum	colemanii	canadense
austrinum (variable)	prinophyllum	cumberlandense
canescens (variable)	viscosum	flammeum
eastmanii		prunifolium
occidentale		vaseyi
periclymenoides (slight to none)		

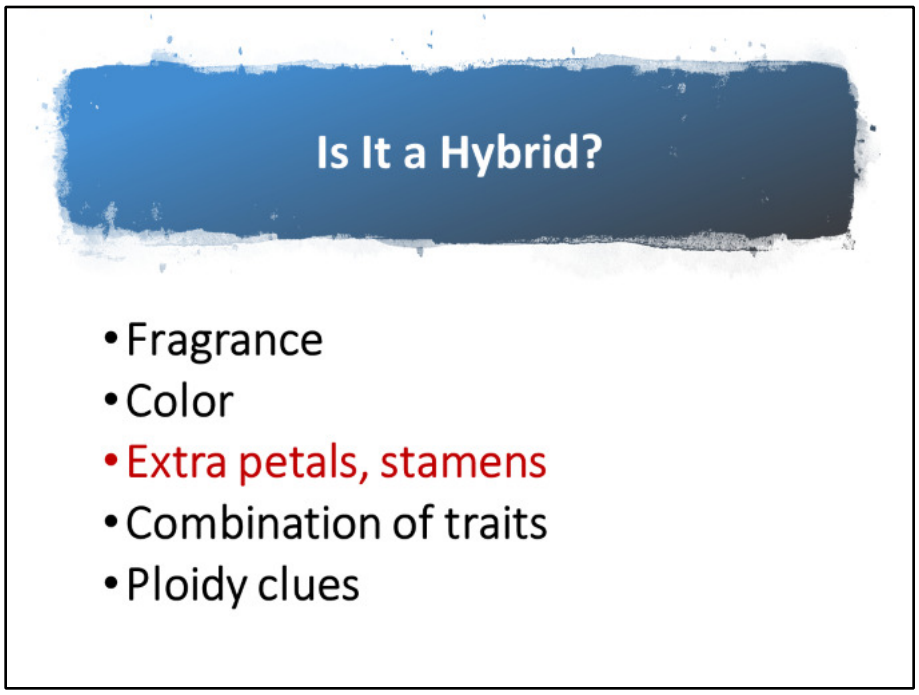
Unfortunately, fragrance descriptions are subjective, noses differ, individual plants differ, and even on individual plants fragrance varies during the day.



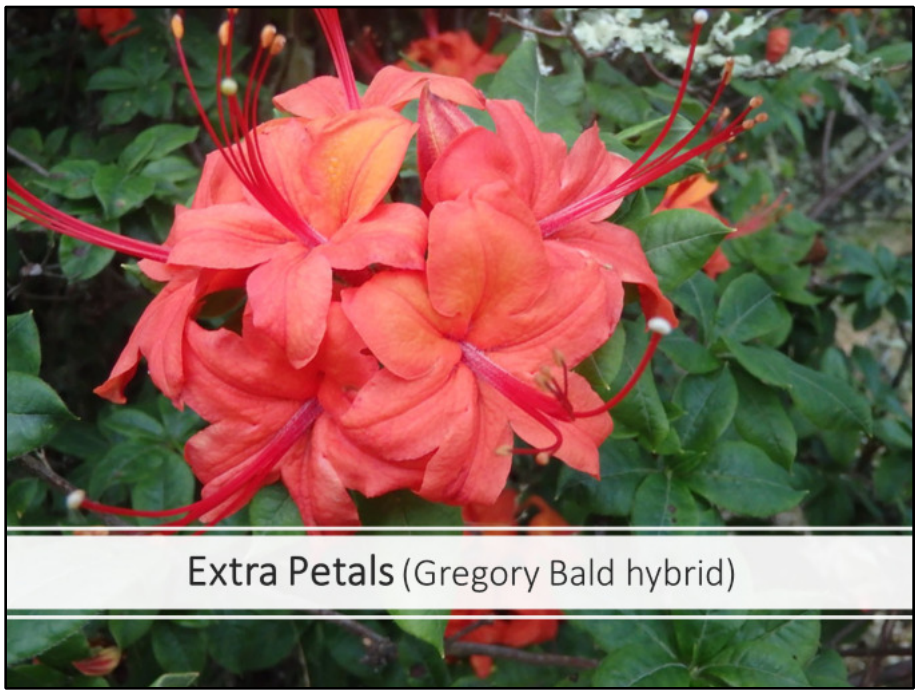
Color can give clues but can be deceiving. The early pink group of *R. prinophyllum*, *R. periclymenoides*, and *R. canescens* does not typically have a yellow or orange blotch unless it has been influenced by other species like *R. calendulaceum*, *R. flammeum*, or *R. alabamense*. Such hybrids often produce vivid pink colors.



This is what can happens when *flammeum* kisses *canescens*.

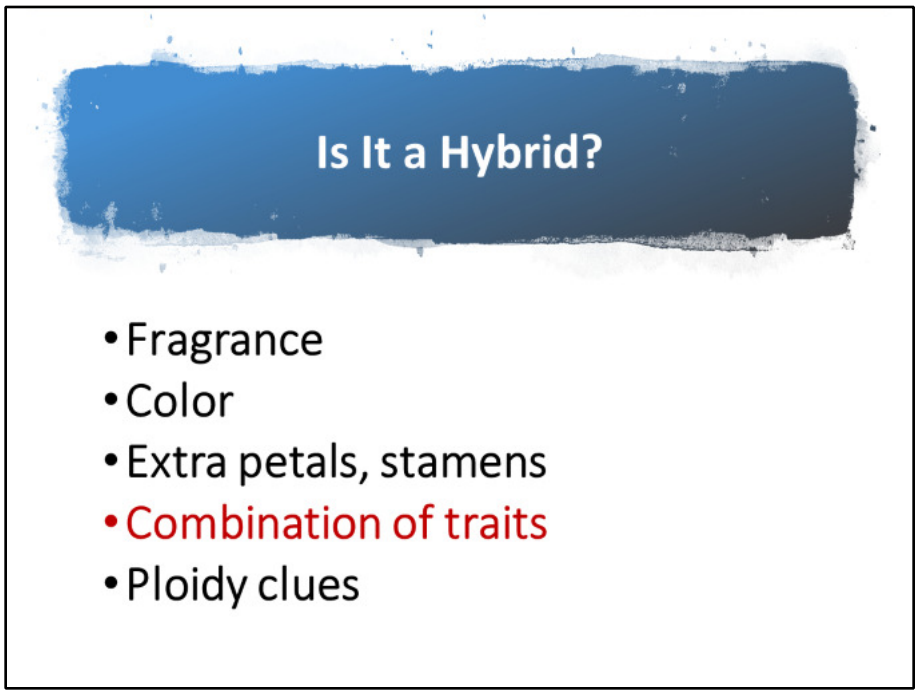


Genetic abnormalities such as 4 or 6 petals, rather than the typical 5, are not unusual in hybrid populations, suggesting such conditions may be a sign of hybridization.



Extra Petals (Gregory Bald hybrid)

Here we have 7 petals.



When one knows the detail morphological traits of individual species, a combination of traits is a sign of hybridization.

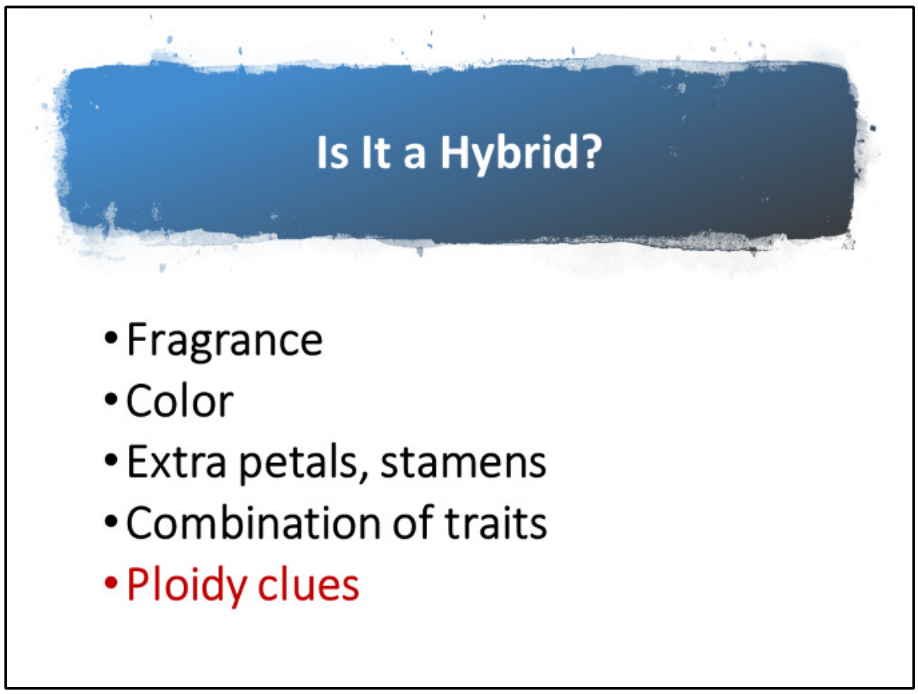
Color; fragrance; stoloniferousness; Winter buds; hair characteristics; and glands on flower tubes, new growth, and bud scales are examples of traits to inspect.

Typically tall *R. arborescens* has smooth stems and is not known to be stoloniferous.

The low-growing mountain form *R. viscosum* var. *montanum* is highly stoloniferous and has hirsute new growth.

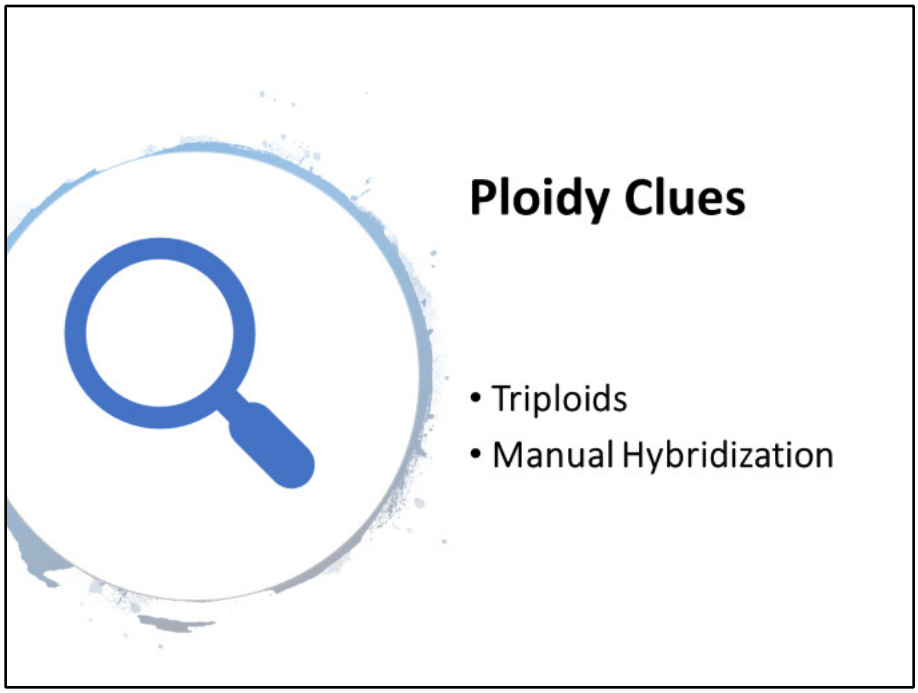
In the Southern Appalachians are both tall and low, smooth-stem, stoloniferous plants found among typical *R. arborescens* and *R. viscosum* var. *montanum*.

We call these running arbs. Here is Dale Berrong showing a highly stoloniferous, smooth-stem hybrid.



These educated guesses can be wrong. Testing to date says Polly Hill's Choptank Hybrids seem to be tetraploids, suggesting they are not hybrids but forms of *R. atlanticum* because if *atlanticum* crossed with *periclymenoides*, *canescens*, or *viscosum*, the resulting hybrid should be a triploid.

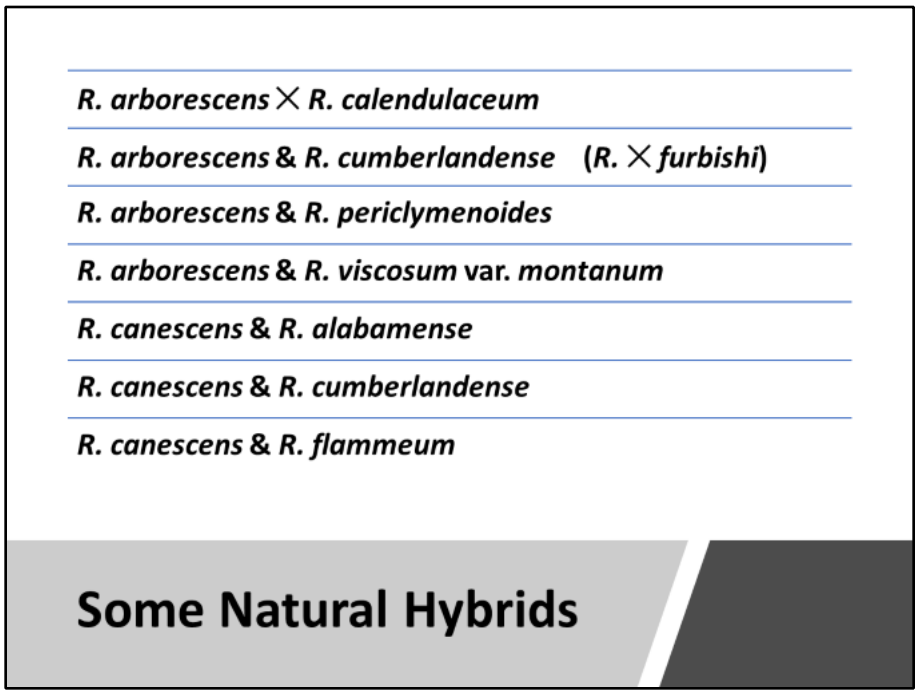
Callaway Gardens planted many May pinks that were labeled *R. alabamense* hybrids. These plants turned out to be the new tetraploid species, *R. colemanii*.



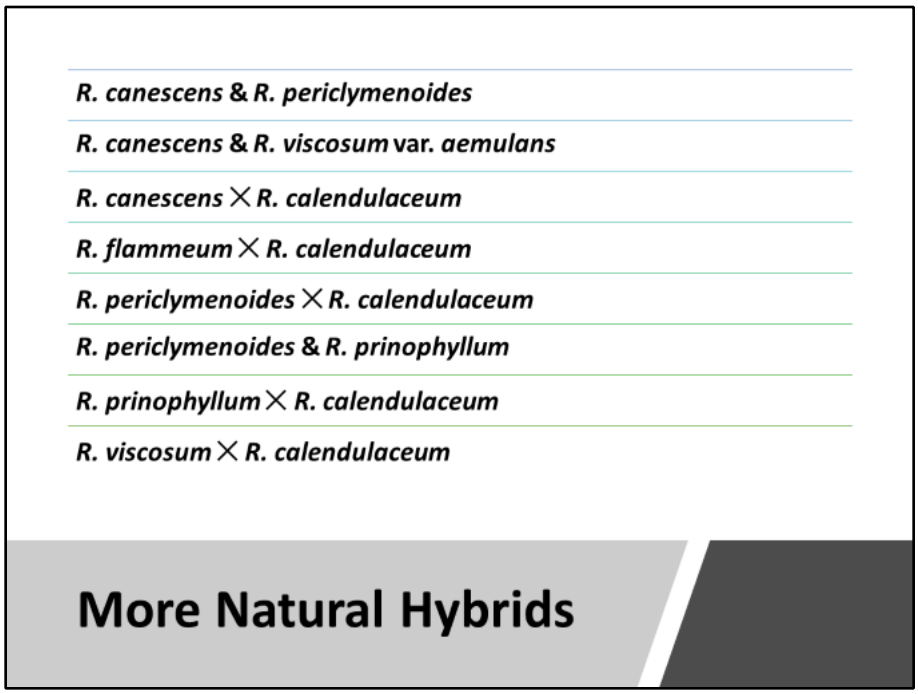
In the examples above, ploidy testing revealed plants that probably were not hybrids. Ploidy testing is useful when a tetraploid pollen parent may be involved in possible hybrids because the diploid x tetraploid cross almost always results in a triploid. Ploidy testing does not help in diploid x diploid crosses.

By using the Perkins Rules of Hybridization, one may be able to perform tests to suggest hybridity. A sterile azalea is probably a triploid hybrid. An azalea that accepts known tetraploid pollen but not known diploid pollen is probably a tetraploid. An azalea that accepts both known tetraploid pollen and known diploid pollen is probably a diploid.

These manual hybridization tests can sometimes help in deciding whether a plant is or is not a possible hybrid.

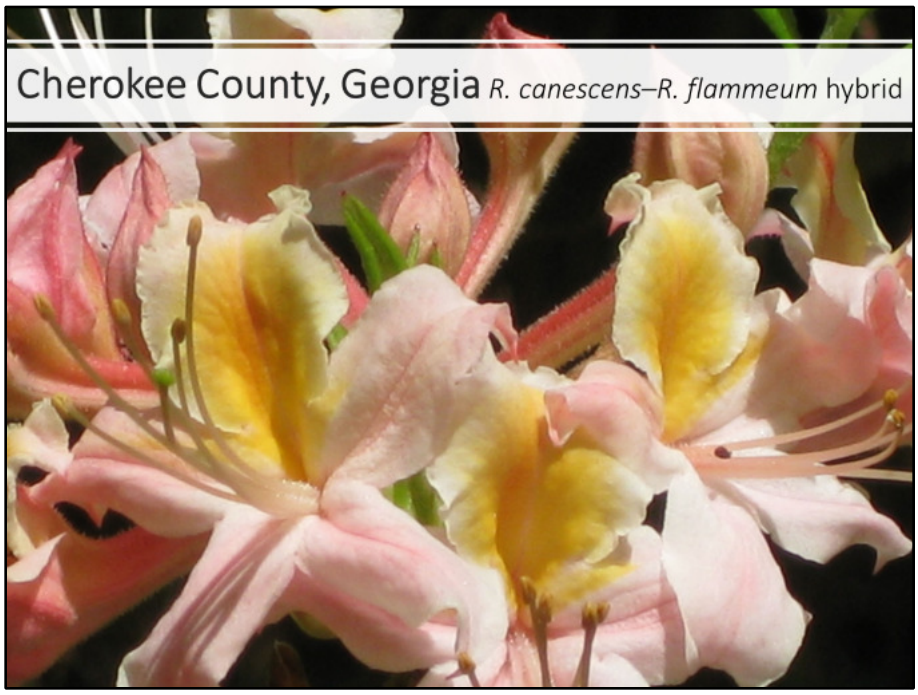


Here are some examples of known or almost certain natural hybrid combinations. When I use the X, it shows the species on the left is the seed parent. When I use the &, it shows either species could be the seed parent.

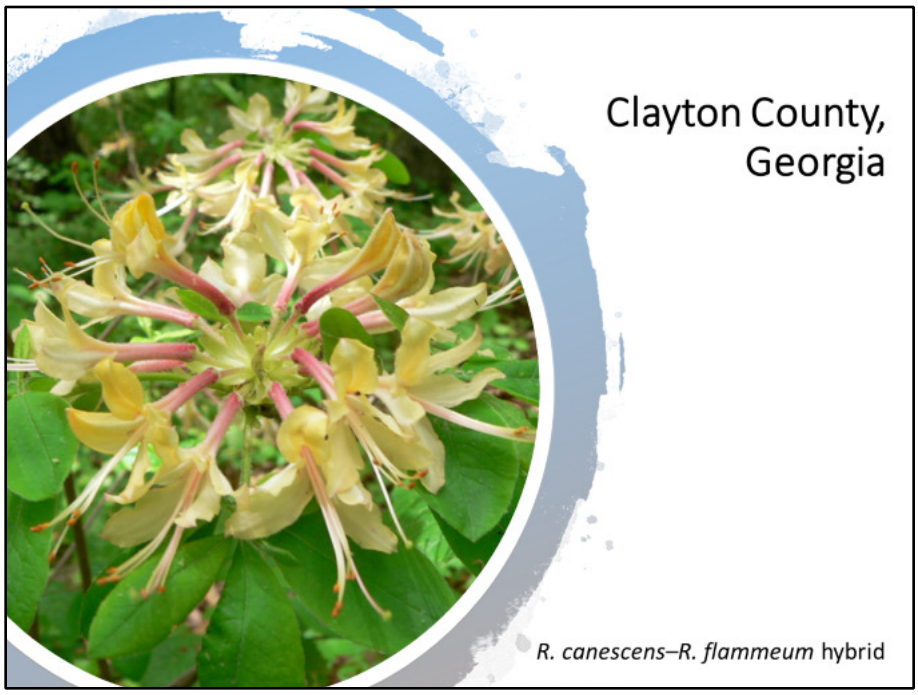


Here are some more combinations. Now let's look at some plants I think are hybrids.

R. viscosum var. *aemulans* is an early blooming, low-growing, highly stoloniferous, white-flowering plant that grows in sandy pine barrens in the transition between wet and dry. In areas like the Blackwater State Park, it has crossed with *R canescens*, creating a delightful, low-growing pink.



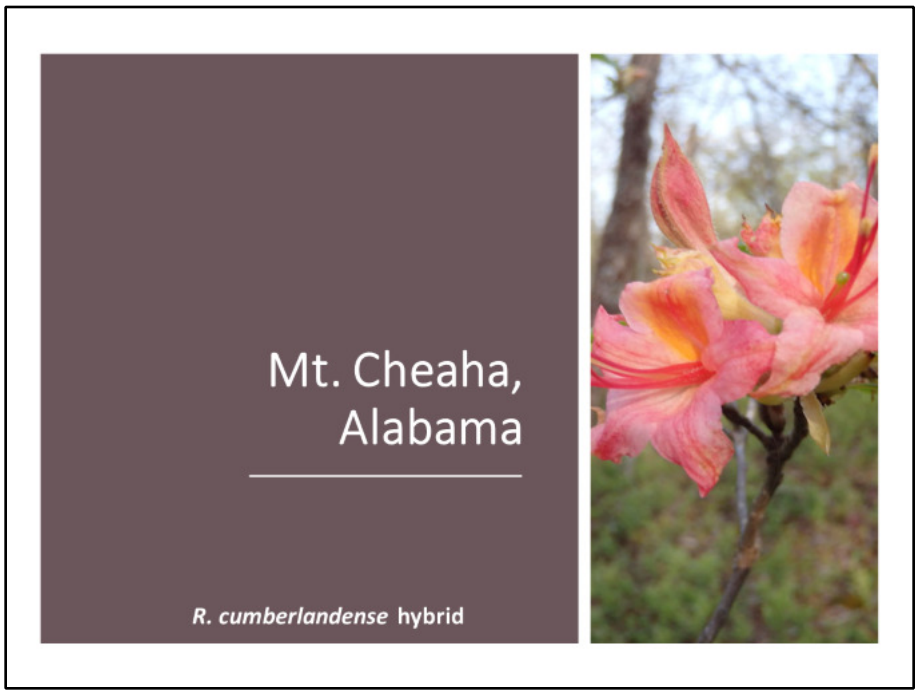
R. flammeum runs in a wide arc from the lower Savannah River up and over almost to the Chattahoochee River near LaGrange Georgia on the Alabama border. It is often found with *R. canescens*. Here is a tested diploid from Cherokee Co. Georgia.



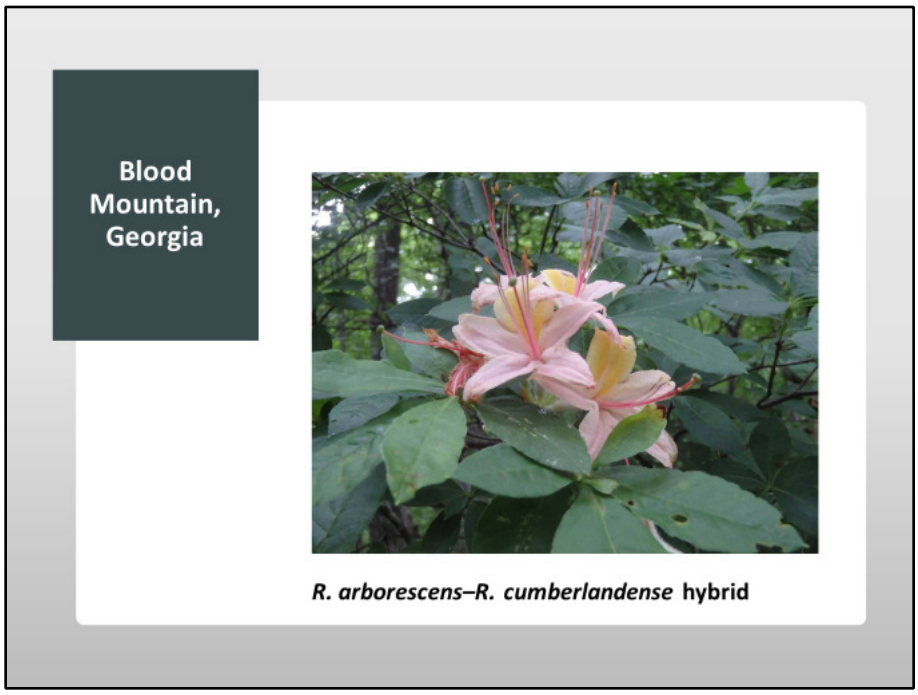
This plant is near Rex, Georgia in Clayton County.

Hot pinks are not uncommon when *flammeum* and *canescens* meet.

R. canescens, perhaps our most common azalea, bio-mass wise, will cross with practically anything. Here is a plant near Tuscumbia, Alabama, where *alabamense* and *canescens* grow side by side.



Mt. Cheaha, the highest elevation in Alabama, is known for its *R. cumberlandense*, but there are also early pinks and later *R. arborescens*. At times the Cumberland azalea there will bloom with both. This is a late-April hybrid, possibly with *R. canescens*.



Blood Mountain is near Vogel State Park where Walter Lemmon first found his *Azalea furbishii.*

David Leach suspected Lemmon's proposed new species *Azalea furbishii* was a hybrid. Leach proved his conjecture by producing man-made hybrids almost identical to Lemmon's species description and by crossing wild *furbishi* plants. Some of the *furbishi* x *furbishi* seedlings resembled *arborescens* and others *cumberlandense*. Gustav A. L. Mehlquist duplicated Leach's crosses with the same results.


Blood Mountain, Georgia
R. arborescens–R. cumberlandense hybrid


Springer Mountain, Georgia
R. arborescens–R. cumberlandense hybrid

And here is a May-blooming hybrid from Mt. Cheaha, probably crossed with *arborescens*.

The most well-known hybrid swarm is Gregory Bald on the North Carolina-Tennessee state line. Recent ploidy testing indicates the mix may be from *R. cumberlandense*, *R. arborescens*, and *R. viscosum*. No triploids have been found to date on the bald itself, eliminating *R. calendulaceum* from the mix.

Most of the plant on the bald look like typical *cumberlandense* as seen here. The spectacular hybrids compose about 10% of the plants on the bald but 95% of the photos seen in articles about Gregory.


Gregory Bald
R. cumberlandense hybrid


Gregory Bald R. cumberlandense hybrid

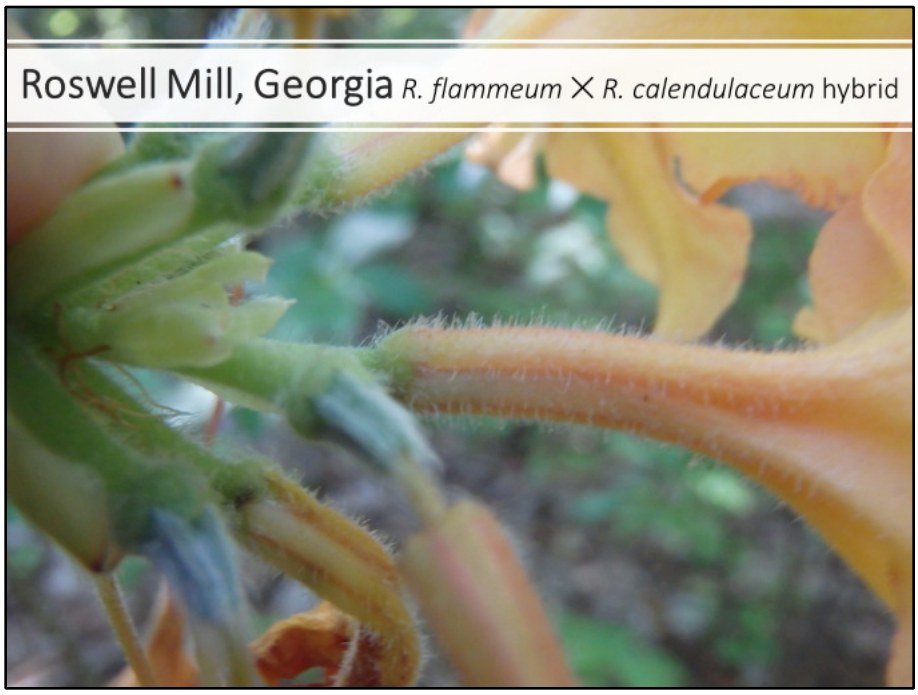

Gregory Bald
R. cumberlandense hybrid


Gregory Bald R. cumberlandense hybrids

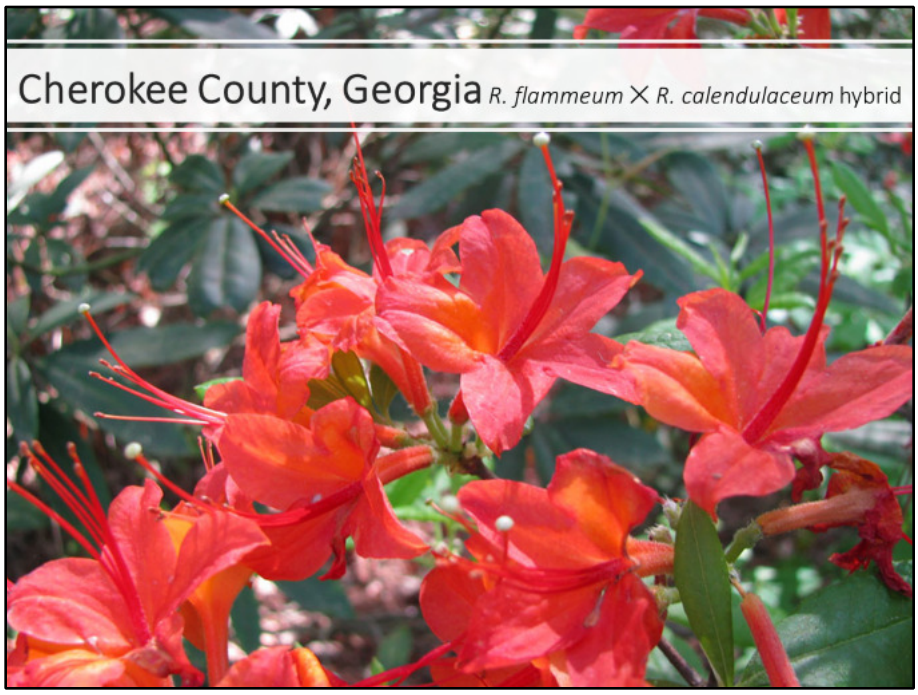
Where Vickery Creek meets the Chattahoochee River in Fulton County, Georgia is the site of the old Roswell Mill.

Here *R. canescens*, *R. flammeum*, and *R. calendulaceum* grow together along with some interesting *flammeum* X *calendulaceum* hybrids and well as *canescens* & *flammeum* hybrids.

Note the 6 petals on this *calendulaceum*-looking flower.



Some of the plants have glandular flower tubes and other eglandular, growing side by side. Glands are a characteristic of *calendulaceum*, while *flammeum* is known to be glandless.



This is a tested triploid from the foothills of Georgia where *flammeum* and *calendulaceum* overlap.

Another amazing hybrid swarm exists in North Georgia at a place I call Hurricane Creek. Here *R. canescens*, *R. calendulaceum*, and *R. arborescens* intermingle. To date, dozens of triploids have been identified.


Hurricane Creek, Georgia
R. canescens × *R. calendulaceum* hybrid

HC 055


Hurricane Creek, Georgia
R. canescens × R. calendulaceum hybrid

HC 116


Hurricane Creek,
Georgia
R. canescens × R. calendulaceum hybrid

HC 176.

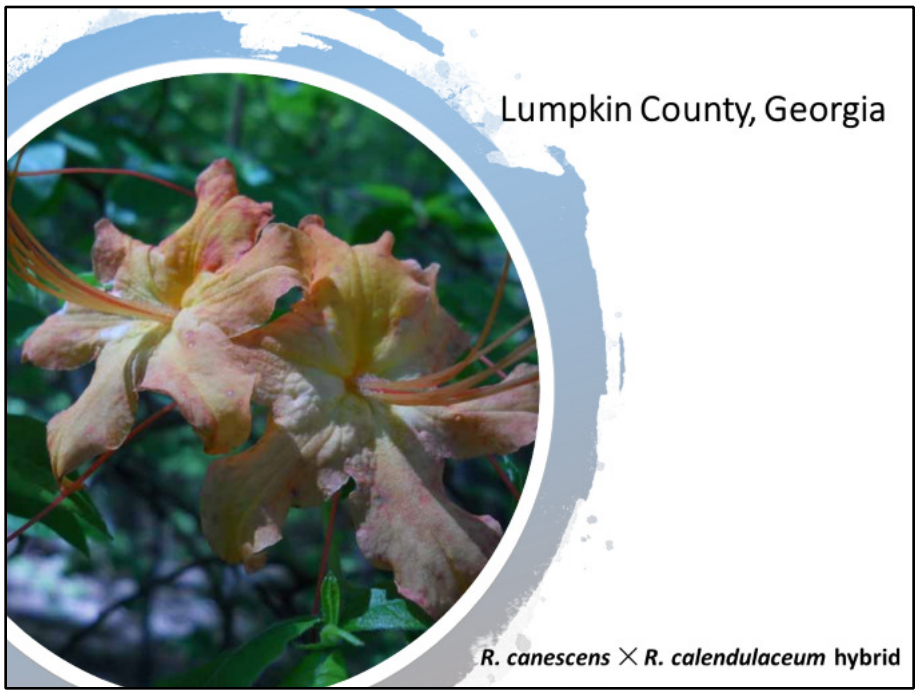
Hurricane Creek, Georgia

R. canescens × *R. calendulaceum* hybrids

Ron Miller examines some hybrids. These in the presentation are but a small taste. There are thousands of Hurricane Creek azaleas, all natural.

A tested triploid.

A suspected triploid.


Lumpkin County, Georgia
R. canescens × *R. calendulaceum* hybrid

A Clarence Towe find.

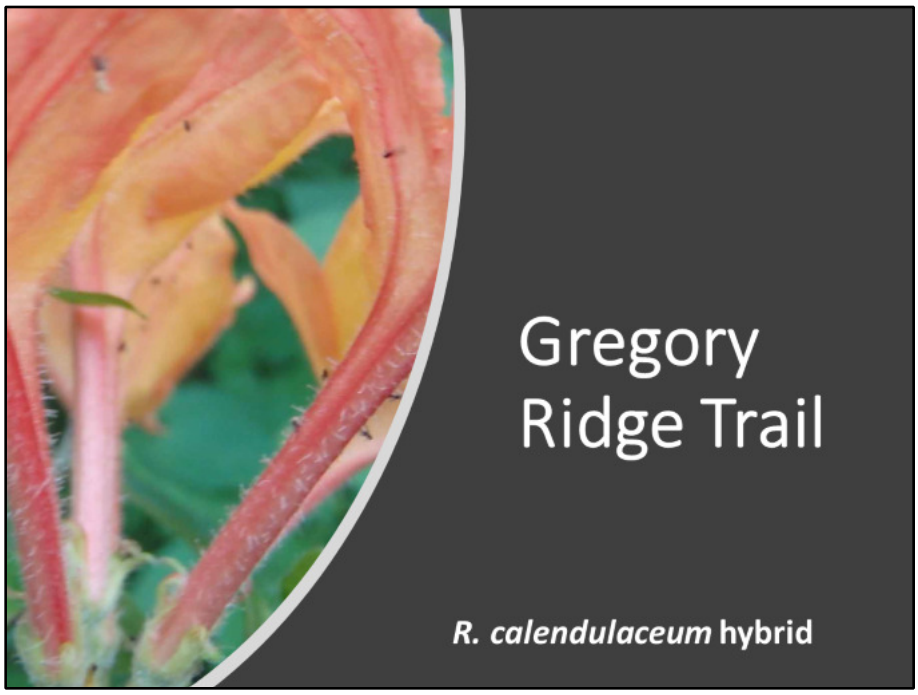
These Audra State Park plants are from Doug Jolly. At Audra on can find *R. periclymenoides*, *R. prinophyllum*, and *R. calendulaceum*. I do not know which of the diploids were involved in these plants.


Audra State Park, West Virginia
R. calendulaceum hybrid

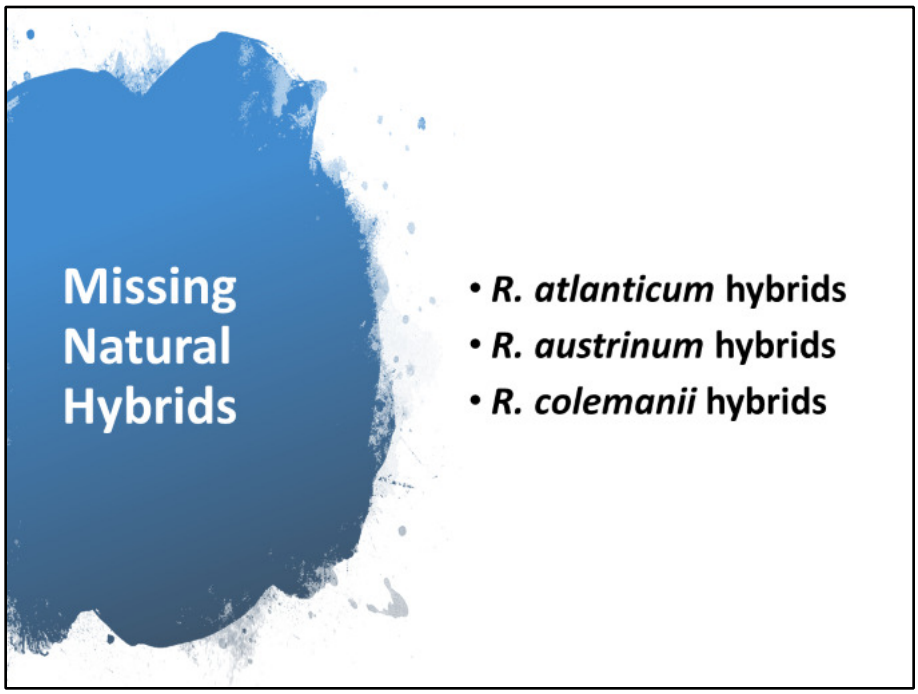

Audra State Park, West Virginia
R. calendulaceum hybrid


Audra State Park, West Virginia R. calendulaceum hybrid

One does find *R. calendulaceum* on the trail up to Gregory Bald and from Gregory out to Parsons Bald. Here is one that did not fit as “pure” *calendulaceum*.



Note it has eglandular hairs in the corolla tube, uncharacteristic for *calendulaceum*.



An interesting puzzle is why we have not found much evidence of hybridization with *R. atlanticum*, *R. austrinum*, and *R. colemanii*. So far, almost all suspected examples of *atlanticum* hybrids have turned out to be tetraploid, yet they are found with *viscosum*, *periclymenoides*, and *canescens*.

The tetraploid *austrinum* grows with diploid *canescens*, but where are the triploids? The pinks on the lower portion of the Yellow River in Florida are tetraploids, otherwise identical to the yellow *austrinum* farther up the river.

Colemanii is a relatively new species and has some overlap with *alabamense*, *canescens*, *prunifolium*, and perhaps *austrinum*. Theoretically there could be triploid and tetraploid *colemanii* hybrids.

We have look at some of the may hybrids. Let's conclude by considering that third category, what Leach called azaleas in flux.

We are finding so many plants that do not fit typical species descriptions but parents are not in the vicinity. This suggest they are not recent hybrids. Where do we put these plants with mixed characteristics? Let's look at some.

This is a tested tetraploid.

In the Appalachian Mountains a tetraploid azalea should be a flame azalea.

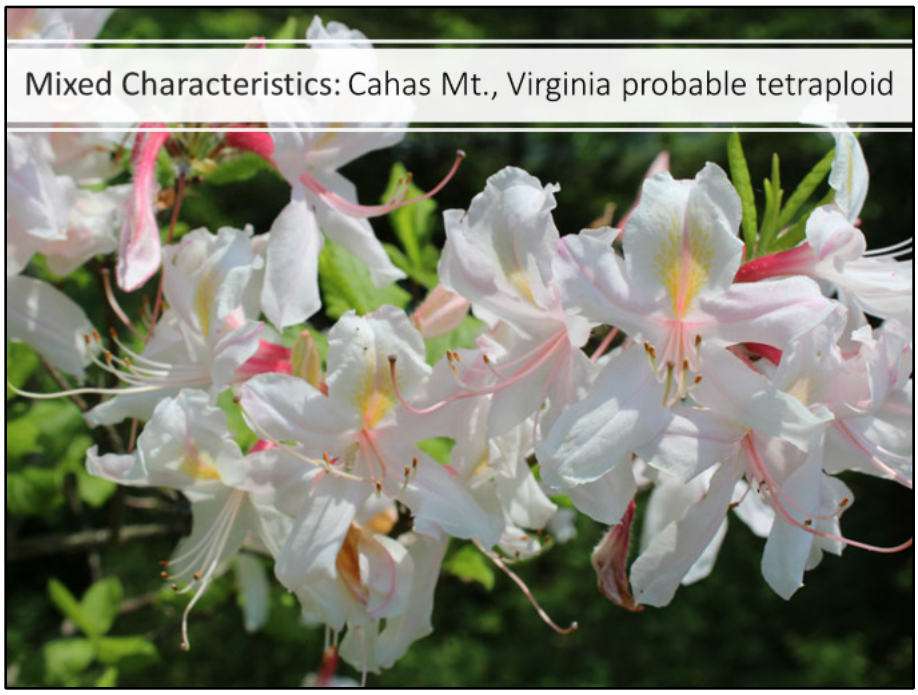
Another tested tetraploid. Does anyone want a dark pink *calendulaceum* with a large gold blotch?

Again

Mixed Characteristics

Hurricane Creek tetraploid

And again



Cahas Mountain is below Roanoke Virginia, elevation about 4,000 feet. Here is another swarm of *calendulaceum*-like plants with unusual colors for flame azaleas, often white. Some have fragrance. Limited tests have produced tetraploids.

The two species found on Cahas Mountain are *R. periclymenoides* and *R. calendulaceum*.

Now let's look at some pinks. The problem is when one sees a pink in the Southeast, one assumes *R. canescens*. Even the experts did. It turns out the pinks on the lower portion of the Yellow River in Florida are tetraploid, not diploid like *canescens*.

Except for the color, this plant is identical to our tetraploid *R. austrinum*. Is it an *austrinum*? Should it be a separate species?

It is hard enough to separate *R. canescens*, *R. periclymenoides*, and *R. prinophyllum*, especially in the zones where they overlap. We know they can hybridize with one another.

Yet even deep within *canescens* territory, we are now finding pinks that do not fit the traditional *canescens* description. First Ron Miller discovered a diploid form of early pink with glandular new growth and stoloniferous. Interestingly, glandular new growth is found on the tetraploid austrinum and those Yellow River pink tetraploids. Typical *canescens* has no glands on new growth.

Now we have discovered a third form of early pink, shown above.

In Jackson County Alabama up on the Cumberland Plateau, I kept thinking they had some resemblance of alabamense: so many whites in the populations, runnery, occasional yellow blotches or throats. The light to no fragrance, however, was not alabamense, they were often tall like canescens, and we had both apple-blossom pinks and raspberry pinks along with 15-20% whites. Yet, we covered much territory and found not a single typical alabamense. There were no parents available to claim hybrid. If we must use the ancient, faulty language of species and hybrid, these are a third category, the one David Leach calls azaleas in flux.

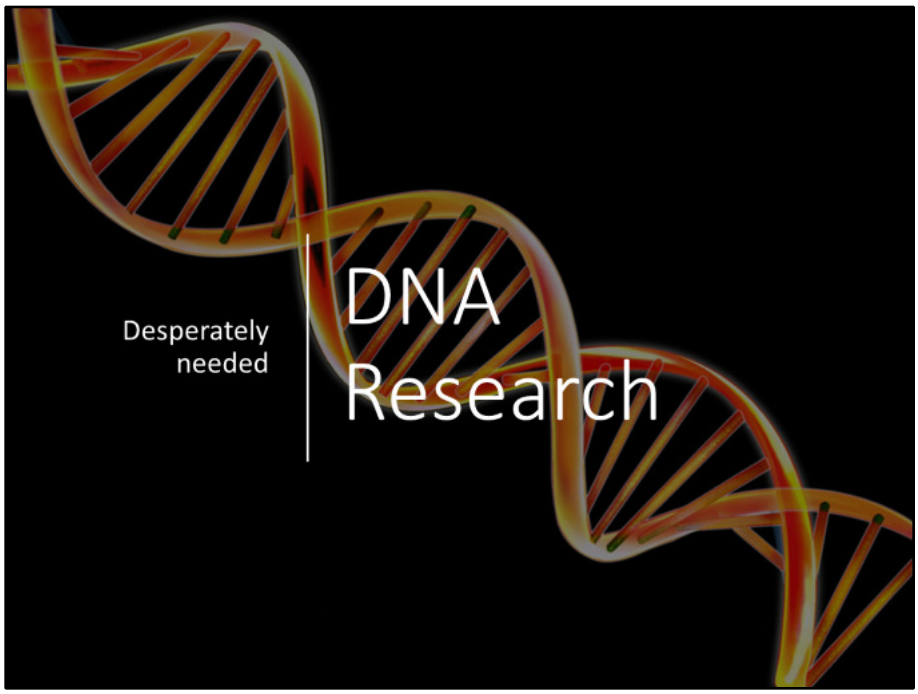

Mixed
Characteristics
Jackson County, Alabama pink probable diploid

Mixed Characteristics

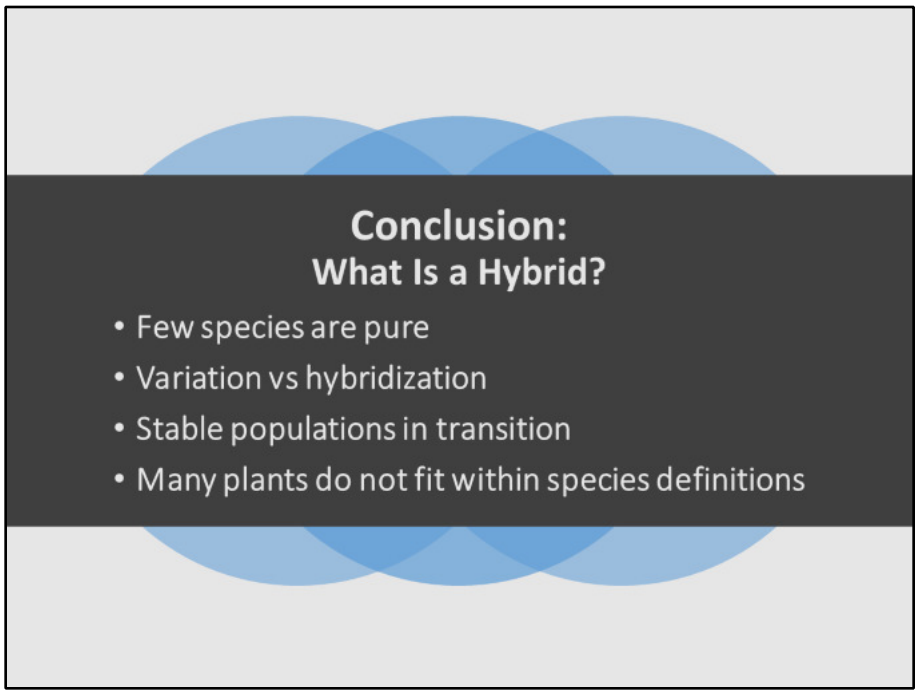
Jackson County, Alabama pink probable diploid

Where do all these yellow blotches come from? No other species in sight.

Once again, more blotches, which destroys an old belief that blotches on an early pink comes from hybridization with something like *alabamense* or *flammeum*. Multiple years of searches have turned up no *flammeum* here.



One area in great need of research is DNA analysis. Such a structured analysis with carefully selected specimens may be able to show the relationship among and within what I am calling the three categories: species, hybrids in the strict sense, and azaleas in flux.



I know you are all happy to see the title of this slide.

I hope I have shown that it is not so simple to think in terms of species and hybrids. We have a third category that is neither.

In fact we need to step back and look at this complex group called American azaleas and think of it a continuum rather than a collection of discrete units.

Thank you for your patience.