

Is *Rhododendron austrinum* Always Yellow?

A Case Study in Blindness

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Some time ago, the *Wall Street Journal* ran an op-ed arguing that accuracy in medical diagnosis actually diminishes in situations where personal records are available online. Once a person has been labeled as suffering from (say) chronic headaches, subsequent physicians tend to pigeon-hole their observations according to the inherited diagnosis. Though time and money are no doubt saved, what if the current problem is actually something more serious?

As I read the article, I reflected upon almost 40 years of springtime azalea touring—first by canoe and later by jon boat—on two local rivers near my home in Pensacola, Florida. One river, the murky, semi-alluvial Escambia, has a delta and upstream chock full of mixed pink and yellow deciduous azaleas—all very, very spectacular. The other river, the Yellow, is a sandier, almost tea-colored stream that displays only pink azaleas for the lowest 30 miles or more. Above that, mixed pinks and yellows take over, while on the upper reaches of the Yellow River in Alabama, yellows predominate. I naturally assumed that the pinks were *Rhododendron canescens* and the yellows were *R. austrinum* because my hero Henry Skinner encountered the bicolor middle of the Yellow River in bloom and called the pinks *R. canescens* and the yellows *R. austrinum*, providing an influential diagnosis of their interaction:

The flower [of *R. austrinum*] may be wholly a clear, golden yellow or, more often, the petals may be yellow and tubes a variable strawberry red, giving one the impression that this red tube belongs more properly with *R. canescens* and has perhaps been acquired by *R. austrinum* after



▲ Figure 1—Close-up comparison of seed capsules and pedicels from eglandular genuine *R. canescens* and from the glandular Yellow River pink

flowering at the same time along the same streamsidés and producing a proportion of those unmistakably anemic buff-colored hybrids for many years past. As the banks of the Yellow River grow luxuriant *R. canescens* so elsewhere they are appropriately covered with masses of the yellow “Florida” Azalea . . . (Skinner, 1955).

So, inheriting Skinner’s labels, I raved to family and friends about the mixing between the two species along the natural levees of the Escambia River, never observing that some of the yellow plants are, oddly enough for a reputedly non-rhizomatous upland species, spreading vigorously in spots where their root crowns are covered by brackish water during spring tides and strong south winds. Indeed, hurricanes put many feet of salt water over the lower parts of the colony. Even odder is that all the “canescens” in the swarm turn out to be as rhizomatous as the yellows and in addition are highly glandular on the lower edges of their flower bud scales and on the multicellular hairs on their vegetative parts. As for the lower Yellow River, I never bothered once to look closely at “just old canescens” while boating upstream to enjoy the yellows. For some reason, *R. austrinum* did not seem to like the sugary sand ridges and peat hummocks where the pinks prevailed. Recently, I have concluded that the yellows cannot compete in the highly acid, sterile, sometimes droughty conditions near the river’s mouth. A handy ecosystem distinction in my region separates white-sand from brown-sand communities. Yellow azaleas prefer darker sand with clay in it; the Yellow



Photo Ron Miller

▲ Figure 2 — Escambia River Tetraploid

▼ Figure 3 — Escambia River Tetraploid



Photo Ron Miller

River pinks thrive on white.

Thus, blinded by an authoritative, inherited diagnosis, I failed to observe that those Yellow River *R. canescens*:

- (1) often sport very uncharacteristic yellow petal blotches;
- (2) are radically rhizomatous;
- (3) have stiff leaves that are rough and rather grayish;
- (4) send down a deep, water-seeking root system rather than the shallow splay of *R. canescens*; and
- (5) bear flower bud scales edged with wavy glands and vegetative parts so copiously forested with stalked glands that the tips of winter stems seem covered in gray velvet.

For decades, my only observation was that the Escambia River pink-and-yellow swarm often starts blooming at the end of January but usually peaks a week or so into April, conveniently after the Yellow River pinks.

Then, a few years ago, Clarence Towe called my attention to the taxonomic utility of stalked and flower-bud-scale glands. Dusting off an old microscope, I stared at the glands on the local yellow azaleas in my yard. No such glands, however, could be found on my lone *R. canescens* cultivar. Months later, on a lazy float trip on the tidewater section of the Yellow River, I snatched a few budded branch tips for microscope practice. Under magnification, the pinks looked like the yellows in my yard. Glands everywhere, on the flower bud scales as well as on the vegetative parts.

Figure 1 provides close-up comparison of seed capsules and pedicels from eglandular genuine *R. canescens* and from the glandular Yellow River pink. If glands on multicellular hairs are present elsewhere than on the corolla tubes of an azalea, they can be found on the pedicels and on the sepal areas of the capsules. Azaleas on both my local rivers also bear glands on new growth shoots, on leaf petioles and bases, and on the underside veins of the leaves.

The next year, I read the seminal article which finally put azalea ploidy determination on firm ground by using flow cytometry (Jones et al., 2007). *R. austrinum* is a tetraploid! Skinner was therefore just flat-out wrong about that hybrid swarm on the Yellow River, as was I about the Escambia River. Diploids (*R. canescens*) almost always produce infertile triploid F₁s with tetraploids (*R. austrinum*). Everything out on the Escambia, however, was covered year in, year out with fat clusters of highly glandular seed capsules, from tagged pink plants to oranges and to yellows. Then I remembered that John Thornton had mentioned years before that he had crossed *R. canescens* and *R. austrinum* and that the hybrids were sterile and puny. Another friend, Tom Milner, had the same disappointment. The Escambia plants, on the other

hand, were fecund brutes, occasionally 15 and sometimes 20 feet tall.

Quickly I motored forth onto the Escambia delta with a jeweler's loupe in hand, seeking eglandular *R. canescens*. No luck. Though there are widely scattered colonies in my area, eglandular pinks seem to have been displaced entirely along the main river banks by more aggressive glandular azaleas. Then it hit me: there had to be another, this time pink, tetraploid in the region for *R. austrinum* to be canoodling with. Where is it? I already knew. Within 20 miles, on the Yellow River. Hauling my jon boat out again, I plucked a series of leaf samples from azaleas along a 10 or so mile run up and down the tidewater Yellow. Off in Ziplocs to Dr. Tom Ranney at North Carolina State. In a few days, Ranney, prompt and generous as always, emailed that they were tetraploids. Earlier, he had tested samples from totally pink, quite glandular plants that had been flagged and photographed on the other river, the Escambia River. They were tetraploids, too.

When is a hybrid not a hybrid?

In a tidier world, this would be the end of the story. Two reproductively compatible species occupy adjacent niches. They cross. Since the vast majority of hybrids are less competitive than their parents, the F_1 s will not develop on their own but die off, to be replaced by additional crosses from the parent species. If a hybrid happens to be truly competitive and can gain reproductive isolation, it might "speciate out" by finding a separate niche for which it, and not the parents, is maximally suited. Or it might even replace, though the chances are infinitesimally small, one of the parent species. Evolutionarily, hybrids and mutations seem identical in this regard: many are called but very, very few are chosen (Arnold, 1997).

Consider those wonderful hybrids on Gregory Bald. They are apparently byproducts (a) of the presence of three compatible diploid species on the bald itself or on nearby mountains and (b) of a transitory clearing now kept open by yearly governmental intervention. Such



▲ Figure 4—Lower Yellow River Tetraploid Pink

bailouts will inevitably fail, because the only way to halt the replacement of the hybrids in the vegetational sequence would be to burn the bald to re-create a mineral soil mountaintop where, briefly, nesting sites would be effectively unlimited and hybrid uncompetitiveness would not matter.

The Escambia River swarm, aided by nothing more than the intervention of our occasional tree-thinning hurricanes, violates this pattern. The azaleas seem to be a vigorous part of a climax association of riparian trees, palmettos, vines, and almost impenetrable evergreen brush. There is no evidence whatsoever that either unmixed *R. austrinum* or unmixed Yellow River pink can be found anywhere within or near the swarm, in spite of the hunch that first sent me scurrying out onto the Yellow River seeking a pink tetraploid. No doubt the swarm, for all its intergradation, tends to be bimodal in color, with the vast majority of plants falling about half and half into the basically-pink and the basically-yellow categories. Circumstantial evidence from proximate color distribution and from bloom time suggests that the pinks are as likely to produce yellow as pink seedlings, and vice versa.

In hybrid swarms known to me, one parent will inevitably bloom a tad earlier than the other, so the balance of the mix changes over the blooming season. One parent will occupy a site drier or rockier or shadier or chemically different from the other. Thus in northern Alabama where *R. canescens* and *R. alabamense* hybridize, later *R. alabamense* occupies the dry sandstone ridge tops; earlier *R. canescens*, the damp valley floors; and the intermediate hybrids, the slopes in between. However, no one boating on the Escambia River and coming around a bend can guess whether the next cluster will be mostly pink or mostly yellow, no matter whether the bank ahead is a dry sand ridge or a wet peaty swale. If one ventures out in late January or early February, the isolated earliest patches are about half pinks and half yellows. In the first weeks of May, when the very latest plants bloom, the same color balance obtains. Certain quite limited neighborhoods have very early plants and others have very late plants; no area holds exclusively yellow or pink plants.

The situation differs markedly with the swarm on the middle Yellow River. In the transitional areas, the color balance shifts as the season advances. At first, the river banks are almost pure pink, then shade into mixtures, then become pri-



▲ Figure 5— Lower Yellow River Tetraploid Pink

marily yellow. Scattered yellows prefer the drier sandy-clay bluffs. Dense pink swaths cover white sand slopes near water and peaty flats away from the river. Thus the very conventional swarm itself consists of both apparent hybrids and apparent parental types in their customary habitats and growth forms. If Skinner had arrived at his Yellow River bridge two weeks later, he would never have seen those massed “*canescens*” on the river slopes.

The Escambia population behaves as though the plants are not hybrids at all but are well on their way to speciating out toward a bicolor, rhizomatous, glandular, saltwater-immersion-tolerant, self-sustaining adaptation to the levee-and-bank ecosystem. More challenging is the pink tetraploid of the Yellow River. Is it a form of *R. austrinum*? Can *R. austrinum* sometimes be pink? Should this pink azalea be interpreted instead as a subspecies or even a separate species? This puzzle I bequeath to any taxonomist or evolutionary botanist willing to take it up. The numbered list on page 5 lays out ways in which the Yellow River azaleas are distinctive other than in corolla color. Most suggestive of the status of the pinks is their ability to sustain an apparently conventional hybrid system, and not to merge, with *R. austrinum* along the middle river. Habitat requirements seem to have driven what Darwin would call a “wedge” on the Yellow River between the closely related white-sand pinks and the darker-sand standard yellows.

Figures 2-6 and the cover photo show characteristic plants from both rivers. Note the two lower Yellow River plants without a trace of yellow (Figures 4 and 5) and the Escambia River pure pink (cover photo) that must be genetically indistinguishable from the preceding yellow (Figure 2) and from the following half-and-half (Figure 3).

Learning to See

Most of us assume that nowadays plant hunters can locate new taxa only in the wilds of Amazonia or New Guinea; yet these tetraploids have been hiding, like the purloined letter in Poe’s short story, in plain sight, passing for recognized plants because we amateurs defer too much to authority and spend too little time observing plants as a whole, roots and runners and glands and growth form and habitat and warts and all. Conversely, professionals are wed to that pre-industrial data-storage device, the herbarium sheet, wherein definitive behavioral hints as

well as fragile stalked glands get lost. Think how long it took to recognize *R. colemanii* in plain sight, not just in the woods but in our gardens, when there were probably nearly as many *R. colemanii* as *R. alabamense* sheets in herbariums. A sheet of *R. eastmanii* existed long before an alert birder chanced upon plants blooming in a well-visited South Carolina park. Such blindness is not accidental but structural. Basing azalea studies on herbarium sheets is like basing animal studies on roadkill.

Plant hunting epitomizes what engineers call a “feedback loop”: you look in order to learn, at last, what to look for. It helps, admittedly, to have high-tech ploidy determination available to adjust your vision. After my eyesight was trained by the plants along my two rivers, I boated up the Escambia River to see that the yellows became dominant, with true, eglandular, diploid *R. canescens* finally appearing above the Alabama line; yet the yellows were accompanied by scattered glandular pinks all the way north into the Red Hills region where *R. colemanii* thrives. Thus the range of uniform yellows is split right down the middle by a mixed-color tetraploid population. Just how many more not-all-yellow tetraploid swarms remain to the east or to the west, no one knows. Many *R. austrinum* variants in the trade, such as ‘Millie Mac’ and ‘Riefler’s White’ and ‘Apricot Austrinum’, resemble material found along my local rivers. White tetraploids, for instance, along with extra petals, seem symptomatic of hybrid dissonance on the stretch of the Yellow River where pinks from below first collide with the yellows from above. Picotees resembling ‘Millie Mac’ and ‘Calamity Junction’ are scattered along both streams.

So far, I have found another extensive pink and yellow patch in a sandy area in southern Covington County, Alabama, just east of the Yellow River drainage, and very rare pinks scattered among the yellows on the lower Choctawhatchee River in the middle Florida Panhandle. Nothing yet to the far east or west. Throughout, especially in Alabama, extensive populations abound where glandular *R. austrinum* and eg-

landular *R. canescens* intertwine with absolutely no hint of hybridizing. However, any group of “canescens” anywhere with yellow throats, with no red or yellow diploids about, merits a closer look with a magnifier and a search on hands and knees for rhizomes.

The westernmost colonies of *R. austrinum* in the Pascagoula watershed of Mississippi add a final surprise while underscoring that variations tend to be river-system specific. These verified tetraploids are, except in rare instances, totally eglandular save for their corolla tubes, yet their colors are rich, opaque “austrinum” yellows and oranges, not the paler, almost transparent yellows of *R. colemanii*. As one gets closer to the Pascagoula, *R. austrinum* becomes progressively less glandular. The popular cultivar ‘Escatawpa,’ found on the border of Alabama and Mississippi, is significantly less glandular than more easterly plants; and occasional yellows along the Escatawpa River itself are as eglandular as any yellow further west. No patch of yellow azaleas anywhere, on the other hand, seems to be as consistently, profusely glandular as those aggressively rhizomatous pinks along the lower Yellow River.

In sum, *R. austrinum* and its allies offer a rich, hitherto unnoticed puzzle that is not at all reflected in academic descriptions or in botanical keys. The evidence suggests that *R. austrinum* is not so much an inbreeding, genetically coherent species as an inhomogeneous stew derived from disparate populations of pink and yellow, rhizomatous and non-rhizomatous, glandular and eglandular tetraploids isolated within steep, protected coastal river valleys during the last glacial maximum, ~12,000 years ago, when the sea level was more than 350 feet lower than at present. The closer to the Gulf today, the more distinct the populations. Glands and rhizomes and pink coloration radiate outward from the lower Yellow River region, glandlessness from the Pascagoula, diminished rhizomes from the lower Choctawhatchee and from the Apalachicola. Yellow epicenters must have been scattered all along the now-submerged continental shelf. The pres-



▲ Figure 6—Middle Yellow River Hybrid Tetraploid

ent northern tier of the *R. austrinum* range in Alabama and Georgia seems to be most homogenized, i.e., closest to published norms.

As for the other American tetraploids, who knows? Perhaps locally varicolored *R. colemanii* and oddly variable *R. atlanticum* (remember the tetraploid Choptanks?) are also migrants-in-progress from epicenters on the shelf. The present range of *R. atlanticum*, except for its southernmost fringe below Savannah, was occupied until recently by spruce, fir, and jack pine (Graham, 1999). Research suggests that evolution can take place at bewildering speed in the wake of ecological catastrophes (Weiner, 1994), and what, this side on an asteroid collision, could be more catastrophic than the explosive post-Wisconsin warm-up in a region where boreal vegetation patterns have prevailed for ~90% of the last few million years? (Graham, 1999). Consider the non-coastal tetraploid, *R. calendulaceum*. In spite of the cliché, the southern Appalachians can scarcely have been its cradle. That cradle must be rocking, temporarily empty, much further down this way. At most, the mountains are the flame azalea’s brief summer retreat. Who knows what *R. calendulaceum* might have looked like, or whether it existed at all, before the ~18 (yes, 15-20!) slowly-cool-down/explosively-warm-up cycles of the Pleistocene? We do know that polyploids, with their geometrically enhanced genetic potential, can be far more opportunistic than diploids in adapting to radically altered conditions (Van de Peer et al., 2009). That is why many of our noxious invasive weeds are polyploids; and indeed, by colonizing huge areas abandoned by subarctic and tundra vegetation, *R. calendulaceum*, by far our most numerous azalea, might itself be seen as a highly variable, invasive polyploid weed. Recall the adaptive bag of tricks shown by the weedy Escambia River tetraploid, with its three-month-plus bloom time, its tolerance for immersion and for salt, its rhizomes, its heightened fertility, its color variety and odor.

Unfortunately, it took me almost 40 years to look at those plants though my own rather than through Skinner’s eyes. The horticultural world would be richer, and the chat groups would have more grist for their mills, if we azalea fanciers would occasionally forgo our pilgrimages to the same all-too-familiar spots

New Members

and practice de-familiarizing our visions by looking nearer at home for quirks and inconsistencies, examining more than the flowers, seeking details that Skinner or Frisbee or others missed on account of the very scope of their pioneering surveys. Easterners in particular need to avoid Skinner's great pitfall: an azalea that doesn't "key out" should not be chalked up as a hybrid unless the imagined parents are front-and-center visible for minute examination. This is not, mind you, a "splitter's" call to multiply taxa but quite the opposite, a hard-won recognition that the facile urge to pin labels and impose categories on polymorphous living things can blind us to nature's complexity. Stephen J. Gould's "punctuated equilibrium" can be an invaluable way to think about speciation (Gould, 2002), so long as you keep open to the possibility that sometimes, as with *R. austrinum*, you may find yourself looking very closely at a punctuation mark.

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Acknowledgements

The author would like to thank Clarence Towe for serving as his tutor and sounding board; Dr. Tom Ranney for directing him to technical publications and for running ploidy tests, both with unfailing generosity; and Dr. Ben Hall for sending him out in the field, looking, while fetching DNA lab samples. He would also like to tip his cap to Dr. Kathleen A. Kron, whose meticulous dissertation on the *Pentanthera* notes several anomalous herbarium specimens that gave him confidence, when he belatedly pored over her work, that he just might have stumbled onto something real.

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