

Evolution, Adaptive Radiation and Vireya Rhododendrons - Part II

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Part I of this article (*JARS* 66(4), Fall 2012); described the phylogenetic, or evolutionary relationships, discovered in a study of the DNA of vireyas (Goetsch et al. 2011). As described in Part I, the results of the study demonstrated how the studied group of over a hundred vireya species form a single clade, meaning all the studied species are genetically related to one common ancestor (with one exception), as shown in Fig. 1. And within *Schistanthe*, the study divided the section into several branching clades within the vireya clade. Several of these clades corresponded to existing subsection-level taxonomic groups of vireyas identified by botanists in the past (Sleumer 1966; Argent 2006). But the study also showed that many other vireyas, despite widely varying visible characteristics (morphology), are much more closely related than previously believed, reducing the number of subsections that group vireya species together. More will be discussed on this below.

Many other fascinating and exciting results were also obtained in this study. One interesting result involved *R. vanderbiltianum*, which while listed as a vireya by Chamberlain et al. (1996), had been suggested as an intermediate maddenian-vireya by George Argent (Argent 2006). Indeed, the DNA sequences uncovered in the Goetsch et al. (2011) study do place this species in an intermediate position between

maddenias and vireyas. By including *R. vanderbiltianum* in the vireya genetic relationship tree, statistical support for a monophyletic vireya clade was significantly improved, making it even more likely that all vireyas have just one common ancestor! But, to be clear, by analyzing living specimens, genetic studies do not identify ancestors, but rather similarities or differences in genes. Both *R. vanderbiltianum* and the vireya species studied are all derived organisms, today's forms based on what existed in the past. So what exactly are we studying here with this odd species?

While "missing link" is a misleading and non-scientific term, evolutionary biology has a concept of "transitional fossils" representing intermediate forms between earlier and later organisms. Indeed, many forms have been found in the fossil record that appear to share some characteristics of both earlier and later organisms. However, the old view of evolution as a consistent, linear onward march from one organism morphing into a subsequent form is not supported by our modern understanding of genetics. Today's cladistics, the classification of organisms into evolutionary clades, is based on measurable genetic characteristics, not their morphological (visual shape or configuration) similarities. Rather than a linear line of evolution, modern cladistics shows a complex, bush-like pattern of evolution with many branches and many dead ends. So instead of trying to identify organisms that are directly ancestral to other organisms, like a family tree, genetic-based cladistics classifies living species based on greater or lesser similarities between their DNA, the molecular blueprint of life.

Indeed, this could not be otherwise. Genetic changes, alterations of the DNA molecule, necessarily occur only

in individual organisms carrying the altered DNA and these individuals may, or may not, pass this alteration down to their offspring. Evolution is based on innumerable small variations within normal genetic variability. Since variations are random, if a positive change is possible within an existing genotype, one or more individuals may eventually come up with this improvement and pass it on to future generations. In addition, variations that give no particular advantage may be simply carried along within a surviving lineage. Unfortunately, genetic changes are more frequently detrimental than advantageous so in any evolutionary process, the actual lineage or "family tree" sufficient to produce a new species, must be the contributions of many individuals, common ancestors passing along and mixing traits over a very long time interval. So *R. vanderbiltianum*, while not a direct ancestor, shares sufficient genetic similarities to other vireyas that including it "fills out the family," and further strengthens the monophyletic vireya relationship.

One strange result is the "anomalous" (Goetsch et al. 2011) phylogenetic position of *R. santapau*, surprisingly close to both *R. ferrugineum* (section *Rhododendron*), the European "Alpenrose," and *R. micranthum* (China and Korea) (see Fig. 1) and outside the identified vireya monophyletic clade (Fig. 1). While being clearly identified as a vireya, *R. santapau*'s outlier genetic position is supported by its unusual geographical location in Eastern India (Arunachal Pradesh), a considerable distance from the typical vireya territory of eastern Mainland Asia and further to the west. Perhaps more importantly, *R. santapau* is also the least derived (i.e., more closely related to the *R. camtschatium* outgroup as noted in Fig. 1) of vireyas. During periods of rapid evolution separate

lineages may produce similar mutations. The result is that lineages may look similar in genetic makeup while being in fact separate. Also, perhaps the ancestors of *R. santapau* began their dispersal much sooner, possibly in the earlier stages of tectonic plate movement that eventually led to today's geographic locations of the Himalayas, Asia, Malesia and Australia. *R. santapau* may be a modern vireya that is genetically more similar, i.e., less changed, to the original progenitors of vireya at a time when geography, climate and/or dispersal patterns were different.

The status of *R. santapau*, i.e., its being outside the vireya clade and its location in eastern India, confirms its unique status. *R. santapau*'s situation contrasts with the various species within the least derived subclade (subsection) that was clearly identified as being within the larger monophyletic vireya clade (*Schistanthe*). This subclade, *Discovireya*, had been previously identified as a separate subsection within the section *Vireya* (now *Schistanthe*) (Sleumer, 1966; Argent, 2006). Unlike *R. santapau*, *Discovireya* is not geographically isolated at all. This subsection is widely, if not richly, found from Indonesia to the Philippines and even in New Guinea. Perhaps the implication is that *Discovireya* ancestors dispersed at a time after *R. santapau*'s isolation when these geographical regions were physically closer together, sea levels were lower or before tectonic movement enlarged the distances between the islands. But to add to the mystery, a more derived (i.e., with greater genetic differences from the *R. camtschatium* outgroup) subclade, *Pseudovireya*, whose members were also identified as a distinctive *Vireya* subsection in the past (Sleumer, 1966; Argent, 2006), is quite confined to the Asian Mainland. Perhaps their evolution took place after the Asian islands became inaccessible through seed dispersal. Another speculation is that the ancestor species of *Pseudovireya* had physical characteristics that particularly limited their seed dispersal.

Another major result of the study

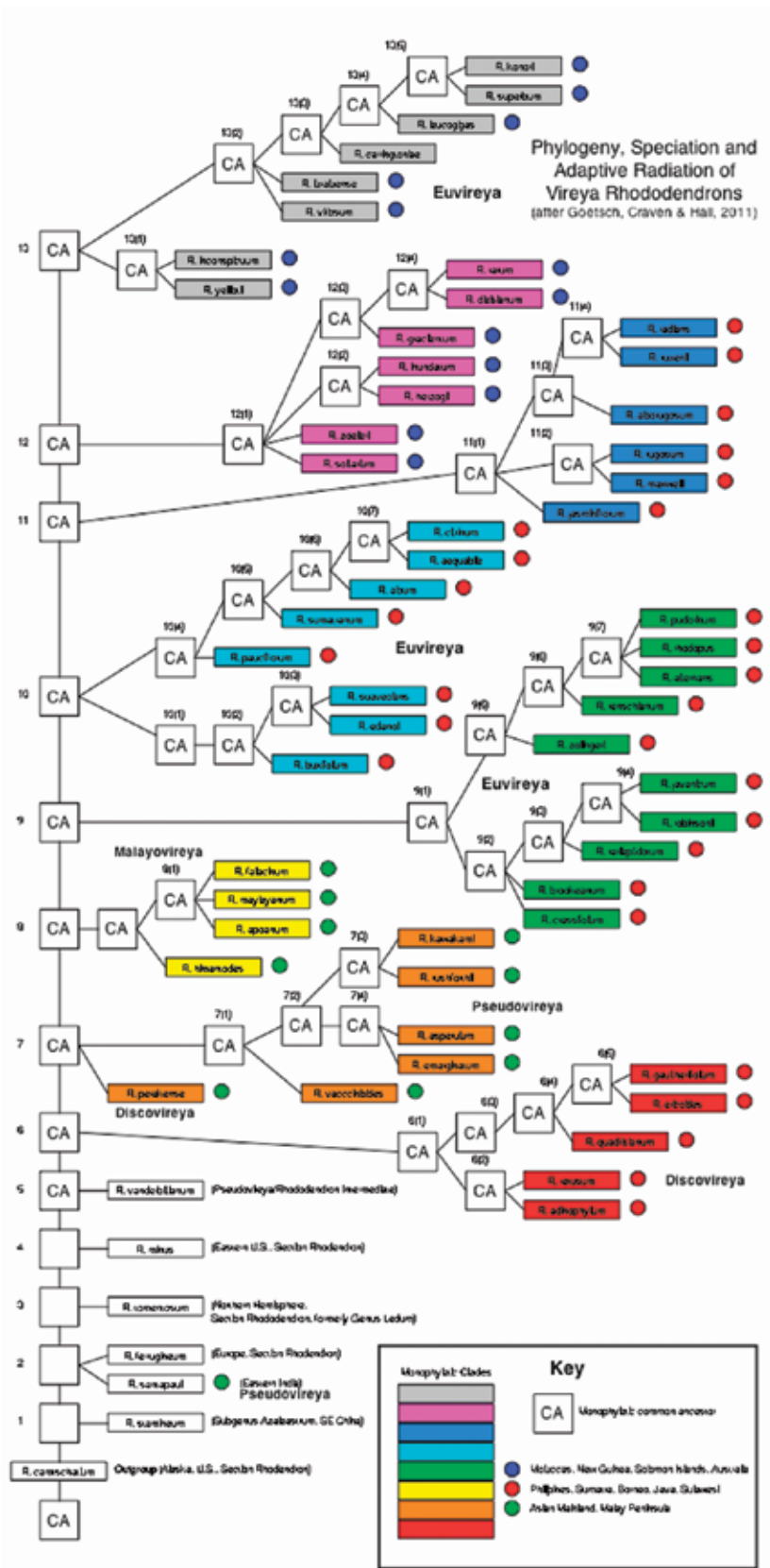


Figure 1.

is that the phylogenetic tree of vireyas, as determined by genetic analysis, maps very well to their overall geographic range dispersal, termed “adaptive radiation” in biology. As the article pointed out, the genetic analysis supports the conclusion “that evolutionary divergence of the various [vireya sub]clades accompanied a dispersal that was polarized in an eastward direction” (Goetsch et al. 2011). Looking at Fig. 1, one can see the radiation of more derived species moving eastward. From the *Pseudovireya* section with the green dots on the Asian Mainland and Malay Peninsula, to the broad mix of medium-derived species in the larger Malesian region indicated by orange dots and, finally, to the blue dots showing the most-derived species in the most eastern locations, the radiation indeed appears polarized to the east.

But wait! There’s more! As earlier noted, the phylogenetic analysis suggested that there were such close relationships between species that the existing subsection *Euvireya* had to be broadened much further than previously understood. In fact, the phylogenetic relationships are so close that the 150 species of *Euvireya* in New Guinea, Australia and the Solomon Islands had perhaps only one common ancestor! The article’s discussion of this point is worth quoting extensively, as it points up the physical basis for the diversity that we find so fascinating in *Rhododendron* and vireyas in particular (some definitions in brackets):

These *Euvireya* species are noteworthy for the wide range of appearances they present. Whether it be corolla [flower] architecture or color, pollination syndrome, leaf size, shape or texture, or preferred growth habit, the range of phenotypes [visible characteristics] within these plants is extraordinary among *Rhododendrons*. Yet, phylogenetic analysis of the DNA sequences show that all *Euvireya* species native to New Guinea, Australia and the Solomon Islands share a unique common ancestor.

Two probable factors contributing to this radiation are based on tectonism, namely the recent juxtaposition of New Guinea with Asia, which was a source of *Rhododendron* germplasm, and the creation of new habitat by accretion of volcanic terranes [fault-bounded regions with a distinct geological history] (Hall, 1996) and the mountain building that followed the collision of Australian plate with the Pacific plate. Following the colonization of New Guinea by one or a few founding *Euvireyas*, the evolving mountainous landscape, with consequent interactions between aspect, slope, altitude, vegetation, and soil produced many unique ecological niches wherein each newly evolved morph [gradual transformation from one form to another] could speciate. The variation in corolla color and shape in *Euvireya* species...provides ample opportunity for the development of flowers attractive to major pollinator phyla, i.e., birds, ants, nocturnal moths, diurnal butterflies, bees, etc. (Stevens, 1976) and it seems this has been an important driver of the radiation. (Goetsch et al. 2011).

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