Mongrels and Hybrids: The Problem of "Race" in the Botanical World

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My difficulty probably is that I do not know the exact meaning of words like species, speciation, populations, reproductive isolation, allopatric and sympatric speciation, geographic and ecological isolation as applied in your paper. If I am wrong in my interpretation of them would you therefore kindly correct me. I must confess that I always have difficulties in reading papers discussing terminology, for I have in mind that the living world does not lend itself too well in our rigid classifications. I feel therefore that all kinds of transitions exist between sympatric and allopatric distribution as well as between different kinds of species. Scientific progress has often been delayed by a premature freezing of our concepts into a terminology that hinders our clear thinking.

—Jens Clausen, botanist, writing to Ernst Mayr, zoologist[1]

The problem of race hasn't figured prominently in the entire biological world. In the plant world, for example, it rarely figures at all. What does figure, especially since Darwin first noticed it, is the deeper problem of variation. What it is, its origin, its maintenance and preservation (or its heritability), its pattern (continuous or discontinuous), and ultimately what biological purpose or function it serves does matter greatly. Common sense would tell us that if organisms were in fact adapted to suit their environments, then we would expect to find perfectly adopted forms, not all kinds and manners of endless variability.

The fact of the matter is that the problem of variation has been at the heart of evolutionary thinking, yet few historians of evolution have directly studied it. We know, for example, that Darwin drew the distinction between variation under nature and variation under domestication in much the same way that he drew the distinction between natural and artificial selection.[2] We also know that he recognized its importance to his theory of descent with modification because he devoted an entire two volumes to the subject titled *Variation of Animals and Plants Under Domestication*. We also know that it was at the heart of the celebrated debate between his later intellectual supporters, the biometricians, and his detractors, the Mendelians, at the turn of the century, as well as the source of Hugo de Vries's popular mutation theory at the turn of the century.[3]

Simply understood, the problem of variation was a central concern for evolutionists after 1859.[4] Questions posed included the following: What was its origin? How was it maintained? What purpose did it all appear to serve? Why, if adaptation were the case, did not one perfect, ideal form exist and occupy each particular zone? That question, of course, undergirded much of Darwin's thinking while he explored the natural history of the world during his five-year voyage aboard the HMS *Beagle*. Answering it took more than twenty years and more than four hundred pages of text organized by the familiar title *On the Origin of Species by Means of Natural Selection*, with the less familiar subtitle *Or the Preservation of Favoured Races in the Struggle for Life*.

If Darwin's famous title is an accurate indication, *race* was intended to be a category that applied to all living organisms, which in the nineteenth century mostly included plants and animals. Throughout the book, Darwin drew generously on examples from both the animal and the plant world, yet strangely enough, he did not in any systematic sense apply the term *race* to plants and mentioned it only rarely in the case of animals. Like others before and after him, terms like *variety* and *subspecies* or *species* were used instead when reference was made to the stages in plant evolution and even more generally to the discernable stages of evolution. Chapter 2 of *Origin of Species*, titled "Variation under Nature," which outlines the stages in the origin of species, notes the grade from individual differences to lesser varieties to well-marked varieties to subspecies to species. Differences between these groups "blended" into each other in an "insensible" series. Darwin wrote, "No clear line of demarcation has as yet been drawn between species and sub-species . . . or, again between subspecies and well marked varieties, or between lesser varieties and individual differences."[5] Defining *species* proved to be difficult, however, and Darwin famously skirted any attempt at a rigorous definition.[6] He wrote, "It will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms."[7] (This is ironic indeed, given the book's title.)

It is a small wonder, then, that when Theodosius Dobzhansky turned to the subject in the late 1930s, he titled his book *Genetics and the Origin of Species*.[8] It was his intention to remedy the fact that Darwin didn't properly discuss the origin of species, nor did he actually attempt to provide a true definition. The problem of defining species remained difficult, of course, and indeed intractable until the 1930s. Darwin understood that it remained one of the weakest parts of his theory and noted that his understanding of species was problematic and that evolution from the plant world made that understanding even more difficult. To Darwin, plants had made splendid examples, but at times they made his project even more complicated because they appeared to demonstrate so many special cases and anomalies.[9] As an example, Darwin was acutely aware of the problem of hybridization and how it could challenge the tidy branching patterns he tried to discern for his picture of general evolution. This much was stated in a special chapter—chapter 8—he devoted specifically to the subject of hybrids, which drew mostly on examples from plants. For Darwin, *hybrid* was a term that denoted a cross between species, while the term *mongrel* was used to denote any cross between varieties. Darwin never properly resolved the issue of hybridization in his book, nor did many of his successors. At the turn of the century, for example, as knowledge of genetics drew attention to the origin of variation on a physiological level, botanists turned seriously to hybridization as explaining the origin of variation and, thenceforth, the origin of new species. Explored by individuals like J. P. Lotsy in the years 1910–1919 and 1920s or so in books like *Evolution by Means of Hybridization*, hybridization was thought to be the specific source of raw material that generated variation.[10] If selection acted, it was to cull out the less adapted forms. Lotsy wrote, "Crossing therefore is the cause of the origin of new types, heredity perpetuates them, selection is the cause—not of their origin as was formerly supposed—but of their extinction."[11] Because crossing and hybridization were central evolutionary processes, any attempt at creating a natural or phylogenetic method in taxonomy was therefore futile. Lotsy wrote, "Phylogeny e.g. reconstruction of what has happened in the past is no science but a product of phantastical speculations which can be held but little in check by the geological record, on account of the incompleteness of the latter."[12]

Lotsy himself is now regarded as a marginal and obscure figure, but at the turn of the century he was part of a large community of "planty" people (I hesitate to call them all "botanists" since many only used plants for utilitarian ends) who rejected strict notions of Darwinian evolution in favor of an alternative number of theories to account for the origin of species. Not only did plant evolutionists espouse evolution by means of hybridization and embrace theories like de Vriesian *Mutationstheorie*, but a large number also remained ardent neo-Lamarckians, accepting the direct modification of characters by the environment, well into the 1930s. Individuals like Frederic Clements, the celebrated ecologist, and others studying the variation patterns of plants in nature saw what appeared to be the direct modification of the environment on plant characters.

The Biological Attributes of Plants

What was it that made plant evolution so intractable? While they were the preferred study or model organism (to use a modern term) for a number of evolutionists and especially geneticists in the early years of the twentieth century, plants also displayed phenomena unusual and quite different from animals. According to contemporary biological understanding, there are at least six notable differences between plants and animals:[13]

1. Plants tend to be developmentally simpler than animals. Animal systems are generally considered more complex because they require close integration between the various organs and organ systems required for functions not apparent in animals (e.g., behavior, motility, sense perception, and the coordination and balance of such complex functions). Plant hybrids are therefore easier to attain because animal hybrids require great coordination between complex parts.

2. Plants cross-pollinate "promiscuously" (in botanical terms), making reproductive isolation more difficult. This is in contrast to animals, which are able to establish barriers to species interbreeding more readily because of phenomena such as behavior motility and sense perception. These phenomena provide opportunities for preserving species boundaries or creating new species through reproductive isolation.

3. Plants also have an open or indeterminate system of growth and development. This is because they bear meristematic tissues (a kind of embryonic stem cell at both the root and shoot and sometimes in axillary buds). Indeterminate development allows plants to amplify the number of body parts they have and their overall size, and it can make possible greater individual longevity as well as asexual or vegetative reproduction. In plants, it is possible to establish a large clonal population from one individual mutant or a hybrid since sexual reproduction is not required. The establishment of a clonal population is also enabled by the fact that in plant species, low sexual fecundity does not necessarily impair the establishment of a plant population. The same open system also provides the opportunity for genetic mosaics through random mutations in the meristematic tissues. Unlike animals, one individual plant could therefore potentially generate a population of genetically different descendants.

4. Plants demonstrate much greater phenotypic plasticity than animals do. Plants vary more widely and respond rapidly to

environmental shifts. (Good examples of this include the variation between sun and shade leaves on trees and the difference in the leaf shape of plants submerged and those not submerged in aqueous environments or exposed to air).

5. Though it is not unique or exclusive to the plant world, plants demonstrate the phenomenon known as polyploidy, or the doubling or multiplication of chromosome sets. Through this mechanism, it is possible to have a sterile hybrid give rise to fertile progeny, which may in turn serve as founding members of a new species.

6. Finally, many plant species are capable of self-fertilization. They may be considered biological "hermaphrodites," for which uniparental reproduction is the typical method of sexual reproduction.

For all these "biological" reasons, as we now understand them, gaining a good understanding of the basics of plant evolution was thus especially difficult for geneticists, ecologists, and taxonomists after Darwin. Determining what counted as species and discriminating between phenotypic and genotypic responses to the environment were problematic in plants; but even the general pattern of variation in evolution, which in plants could be reticulating or networklike rather than dendritic or treelike, because of hybridization or the phenomenon of introgression, posed a number of complications in deriving a general theory of evolution.[14] (See figure 1.) Yet the need to create such a general theory was acute, since plants were ideal study organisms for biologists. As researchers relied more and more on plants as study or model organisms, plants' peculiarities or anomalies in comparison to organisms like birds and mammals became apparent.

It isn't surprising, therefore, that it took nearly one hundred years after Darwin first addressed the problem of variation for a general theory of variation and evolution in plants to be addressed. This appeared in 1950, under the unsurprising title *Variation and Evolution in Plants*.[15] The book was written by George Ledyard Stebbins, Jr., on the occasion of the invitation to deliver the Jesup Lectures at Columbia at the request of mammalian geneticist L. C. Dunn and Dobzhansky, Stebbins's lifelong friend and colleague. The book appeared at the tail-end of the interval of time between approximately 1930 and 1950 that saw a number of texts written that contributed to the overall synthesis of evolution, which historians have designated as the "Evolutionary Synthesis," or the synthesis between Darwinian selection theory and Mendelian genetics, in the hope of explaining the origin of biological diversity.[16]

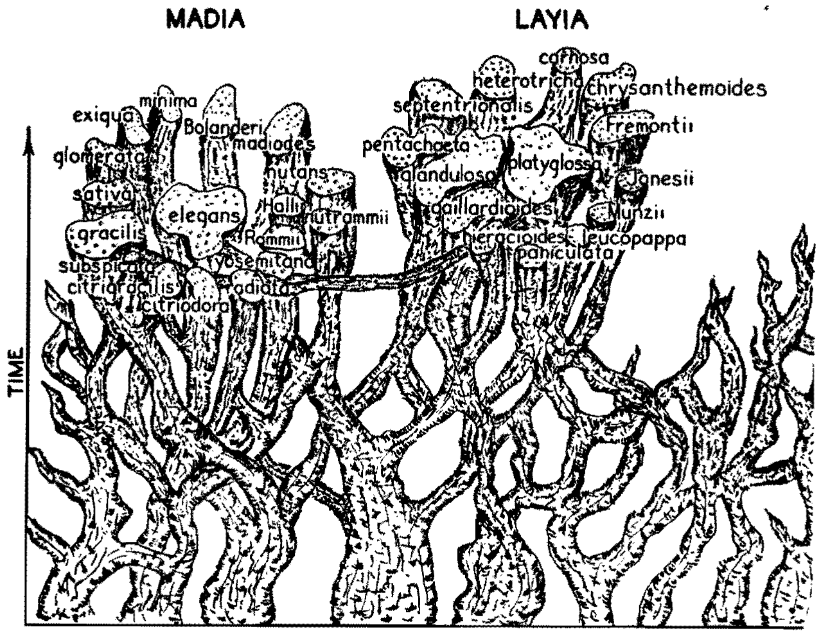

Figure 1. Hypothetical diagram of reticulating evolution and the relationships between the species of two genera of *Madia* and *Layia* at the present and projected back in time. (Jens Clausen, *Stages in the Evolution of Plant Species* [New York: Hafner Publishing, 1951], 179.)

Stebbins's book was the last in a number of such important texts, establishing what would be called "the synthetic theory of evolution" (which is sometimes referred to as neo-Darwinism or the new or modern synthesis of evolution). It was the only book on evolution that was taxon defined—meaning it was the only one organized around a specific biological group, namely plants. It was also the longest of all the books (at nearly 643 pages, which included nearly 1,250 references to a disparate body of literature on the subject). The first four chapters were organized around the general subject of variation patterns in plants, and the account of variation understood at the genetic level formed the remainder of the book. The subject of species and speciation was the subject of some three chapters, and the problem of defining a species was discussed explicitly a number of times in the book. The final set of chapters included a discussion of the big picture of evolution, namely the fossil history of plants with an eye to explaining macroevolution, in terms of the microevolutionary theory developed in earlier chapters.

Stebbins was closely following the work of Dobzhansky, the key architect of the evolutionary synthesis.[17] Stebbins's book in 1950 closely followed the arguments and organization Dobzhansky followed in his 1937 *Genetics and the Origin of Species*. It was in fact a kind of consistency argument—bringing into line (either by agreement or elimination) an understanding of plant evolution within a larger understanding of animal evolution. Dobzhansky and Stebbins had been friends and had been drawn together because of shared interests in formulating a general evolutionary theory and because their own organismic systems showed evolutionary compatibility. Dobzhansky's own research organism had been the famous *Drosophila pseudoobscura* while Stebbins had worked on a number of plant genera, including the genus *Crepis*. But while Stebbins followed Dobzhansky closely in a number of ways, he did not follow Dobzhansky explicitly on the importance of race as a meaningful category for understanding variation. Dobzhansky used race explicitly in reference to biological and especially geographic races in a number of organisms, including his *Drosophila*. Stebbins did not bring up the category in any formal way in his work. A quick glance at even the index to both volumes reveals Dobzhansky's singling it out prominently while Stebbins did not appear to single it out at all. Instead, in the chapter titled "Variation Patterns," the one chapter that would have demanded such a consideration, Stebbins wrote a familiar refrain for plant systematists:

> *The experience of most plant systematists, as well as their zoological colleagues, has been that the recognition of infraspecific units of several degrees or rank, such as subspecies, variety, subvariety, and form, produces more confusion than order. Units of one rank, termed subspecies by all zoologists and many contemporary botanists, are enough to express the great majority of the biologically significant infraspecific variation that can be comprehended by anyone not a specialist in the group.*[18]

Dobzhansky's book echoed his own research program into the geographic races of *Drosophila pseudoobscura*. Dobzhansky had selected this organism because its evolutionary history, as revealed by adaptations to local environments, could easily be determined by mapping of the giant salivary chromosome.[19] But Dobzhansky didn't stop there. He actively discussed and endorsed the existence of geographic and biological races in other insects and "lower" forms of life like snails, drawing on the work of Alfred Kinsey's studies of variation in the Cynipedae, or the gall wasps, as well as John Thomas Gulick and Henry Edward Crampton's work on geographic variation in *Partula*, a complex genus of snails. Examples of racial variation also abounded in the dominant areas of zoology, like that dealing with birds and mammals, but Dobzhansky skirted the issue of race existing in plants (as we would expect), and what examples of plants he did include mostly referred to the conventions botanists used to group plants into varieties or subspecies. Microbes were, for the most part, absent from examples he drew on, which is also as we would expect, since little was known about their taxonomy in the 1930s.

Where *race* did gain some usage was in ecology, or more precisely in genecology, the study of plants under a variety of environmental conditions that was popular in the early decades of the twentieth century. Race here was usually used to denote different groups that seemed to be correlated with climate, geography, or edaphic conditions. As noted by D. Briggs and S. M. Walters in their comprehensive, popular book *Plant Variation and Evolution*, one person who used the term *petites especes*, which translated into "local races," in a paper of 1901 was F. Ludwig.[20] Until Ludwig, the term *local race* had been used "rather loosely for plants from particular areas used for biometrical study or experiments." Ludwig, however, sought to make these entities of local races "real" by using biometrical evidence based on the number of floral parts in *Ranunculus ficaria*. In the early issues of the journal *Biometrika*, Briggs and Walters pointed out that the "reality" of local races had been an important topic for discussion, though the reality of races was challenged by an editorial in 1902 that disputed the sampling of polymorphisms, which were deemed spurious; questions could be raised about what counted as a "locale" by collectors. The use of the term *race* continued, however, but in that "loose" sense of the term and was usually associated with climatic, edaphic or geographic parameters.[21]

In the mid-1930s, the term *race* was used, though loosely again, by the celebrated interdisciplinary team of Jens Clausen, William Hiesey, and David Keck, though more than any other contemporaries, they challenged any strict definitions even of terms like *species*.[22] Plants seemed to have a more complex pattern of variation and evolution, and they defied any simple or rigid categorization that might work for birds or mammals. The opening epigraph, a private exchange between Clausen and avian systematist Ernst Mayr, is a nice demonstration of the differences between many botanists and zoologists in the middle decades of the twentieth century, though to be sure, some of the distinctions or differences were glossed over by the drive to create a coherent view of evolution. In one celebrated instance, Mayr, reviewing the latest monograph by the Carnegie Institution of Washington at Stanford team of Clausen, Hiesey, and Keck, showed how nicely birds, mammals, and even insects and plants could be integrated together, all recognizing the notion of race. He wrote:

> *It is evident from these studies that there is no fundamental difference between plants and animals in the evolution of populations and races that have become adapted to local environments. The difference is one of degree, with insects and plants having much more localized races than birds or mammals. That some of the insect races are as localized as the plant races is indicated by the work of Dobzhansky on Drosophila pseudoobscura. None of the insect material, however, can compare with some plant species in the abundance of conspicuous morphological characters in addition to the physiological ones.*[23]

Similarly, the contrast between Dobzhansky and Stebbins and their reliance on notions of race is telling. For most botanists, the word *race* held little meaning or utility, in part because the patterns of variability were more complex and the underlying mechanisms more complex and unlike those seen in animals. To be sure, some botanists had occasion to resort to the concept, but even then it was in a limited and questionable capacity.

The other instance where *race* was employed heavily was in designating the varied forms of an important crop plant: corn, or maize, as in *Zea mays*. Maize, a heavily modified (meaning "domesticated") plant, had a complex evolutionary history that could not in fact be easily separated from humans. Corn had been so heavily altered by human use that its own evolutionary history—and its taxonomy—remained obscure until the early to mid decades of the twentieth century. Its history was unraveled by methods involving both cytogenetics and anthropology (ethnography, to be more precise) as they came together in the area defining itself as ethnobotany. The efforts of maize historians like Paul Manglesdorf (probably the best known of the maize workers) and researchers like Edgar Anderson helped unravel corn's evolutionary history.

In 1942, in a paper published in the *Annals of the Missouri Botanical Garden* titled "Races of *Zea Mays*: Their Recognition and Classification," Anderson, along with Hugh Cutler, set out one of the first "natural" taxonomic schemes for corn that would reflect this evolutionary history. Up to that point, geneticists like E. Lewis Sturtevant had used an artificial system that had held to human patterns of use of corn types such as pop, flint, dent, flour, and sweet. To create what was a "true" and natural scheme based on corn's complex evolutionary history, Anderson and Cutler looked to the science of anthropology and the concept of race, substantively using the work of E. A. Hooton and his method of racial analysis, and one of its celebrated applications by Carleton Coon in his book *The Races of Europe*, published in 1939.[24] There were a number of parallels: both had been "domesticated" and both had a complex history. "The problem of races and their recognition," they noted, "is indeed almost the same in *Zea Mays* as in mankind. In both cases it is not easy to work out the racial composition of the whole, and it is difficult to give a precise definition of the term 'race.'"[25] Since Coon had discussed this "latter problem" in 1939, Anderson and Cutler directly referred to Coon in one long direct citation in their own paper.[26] The link to currents of thought in anthropology was not surprising; corn had been racialized by human practices, and drawing on some of the prevailing racial schemes like that of Coon's appeared to make sense for a plant whose racial qualities appeared obvious to anyone in the 1930s and 1940s wishing to create a classification scheme. Both were, after all, "domesticated," and old in their histories. Anderson and Cutler, therefore, adopted Coon's somewhat vague but popular definition of race to define the word "race as loosely as possible, and say that race is a group of related individuals with enough characteristics in common to permit their recognition as a group."[27] Despite its initial popularity, the term *race* and Coon's use of it began to gain some notoriety after 1963 when Coon published his book *Origin of the Races*. In it, Coon continued to draw on his initial formulation of race and suggested that five races of humans were in fact subspecies dating back to *Homo erectus*. Interestingly enough, Dobzhansky challenged Coon on his understanding of speciation and "race."[28] Anderson and Cutler's responses are unknown.

There is at least one other use of the term *race* in the plant world, and that is in mycology, the study of fungi, but this may not be all that surprising. The history of mycology has been dominated by the history of plant disease, and the history of plant disease is closely linked to agriculture and thence to human history. As in the case of corn, this is an instance where plants are either domesticated or seen through the lenses of human social practice. To the extent that it can be seen at all independently of humans, the biological world in general, and the botanical world in particular does not require the use of the category of race, and has in fact relied very little on it, especially given that plant taxonomy is a heavily worked field. Perhaps it is because of the staggering assortment of variation that exists in the plant world that makes all categories (and not just race) especially provisional, or perhaps because plants are so alien to humans, that categories like race, which are loaded with human meaning, are less easily transported; but there is little doubt that the use of *race* has had much less importance or meaning in the botanical sciences. To state this further, though variation is especially abundant and problematic in the plant world, plant evolutionary biologists have, for the most part, not relied on racial categories, preferring instead to speak of varieties, subspecies, cultivars, or "lines," and even then these terms are held provisionally (certainly more so than by some zoologists). The word *race* has been used but oftentimes in situations closest to human history.

If I were to try to conclude this paper with only one closing thought, it would be to echo the well-known sentiments of evolutionists and historians like Stephen J. Gould and to point out that race is not a biological category that has much meaning outside of human history.[29] To be sure, all categories are human inventions—attempts to order the world on our terms—but it is clear from the history of botany and my attempt here to understand the problem of race in plants—and its absence—that this is one explicitly nonbiological and cultural category that makes little sense apart from human or cultural history. I close with the thoughts of yet another forgotten plant taxonomist, the Harvard botanist Charles Weatherby. In a response to a questionnaire asking about the species problem in 1937, he spoke for many plant taxonomists who recognized the provisional nature of their work:

> *It looks to me as you were trying to generalize on the assumption that there is a basic uniformity in taxonomic groups. There is nothing of the sort. Taxonomy is only a glorified guess—an attempt to construct a cross-section of lines of descent in a form intelligible to the human mind. It always contains two variable quantities—the plasticity of animate nature and the differing points of view of the people who work at it. You can generalize successfully, if at all, only by keeping these facts constantly in mind. I suspect that the situation is best expressed by the old aphorism; the only general rule is that there is no general rule.*
>
> *Therein lies the fascination of taxonomy for those who like it. It is not a matter of mechanically applying a universal set of categories to given groups of facts. Each group has to work out anew the method by which he may best achieve that transforming of confusion into order which is the greatest satisfaction of pure taxonomy.*[30]