

CHAPTER 3

DOUGLAS ALLCHIN

DISSOLVING DOMINANCE

1. INTRODUCTION

The time has come to dissolve the concept of dominance in genetics. The concept is a vestige of history, a frozen accident that may have aided Mendel's important discovery but is hardly essential as a basic principle of genetics (section 2). Moreover, the concept of dominance is ill-framed and often misleading in terms of heredity, natural selection, and molecular and cellular processes (section 3). More direct language is available to refer to the key relevant principles in inheritance and the phenotypic expression of genetic states (section 4).

At first, the concept of dominance seems simple enough: when two different traits are inherited, only one will be expressed—that trait is *dominant*, the other is recessive. But even this simple formulation hides a wealth of implicit assumptions about genotype-phenotype interaction, numbers of available alleles, the typical effects of combining two alleles in diploid organisms, interaction of allelic pairs, definitions of 'similar' alleles, and more. This paper aims to tease apart these conceptual issues and clarify genetics by discussing how to proceed without the concept of dominance and the confusions it frequently generates.

2. WHENCE DOMINANCE?

Today's term 'dominance' originated, of course, in Gregor Mendel's now classic 1865 paper on "Experiments Concerning Plant Hybrids" (1966a). Those who read the original paper over a century later are often impressed with its clarity and modern style, accessible even to high school students. But the conceptual context has changed dramatically since Mendel's time, and contemporary readers often miss

differences in meaning obscured by the use of familiar terms. These differences offer important clues, however, to understanding how the modern concept of dominance emerged, evolved, and has continued to shape our thinking about genetics.

2.1 Mendel's "Discovery"

Mendel introduced the term *dominirende* (translated variously as 'dominating' or 'dominant') to refer to characters "which are transmitted entire, or almost unchanged in the hybridization" of two contrasting parental types (1966a, §4; see also §11). The other traits, of course, he termed *recessive*. While today's popular accounts tend to portray this as a significant and novel claim, Mendel and his contemporaries who conducted breeding experiments would have readily acknowledged that some parental forms are more likely to be found in offspring—a phenomenon they called *prepotency*. Theories at the time, however, often attributed the prepotency to the sex of the parent (i.e., whether the trait was transmitted by the male or female gamete). By doing reciprocal crosses, Mendel was able to underscore the "interesting fact" that "it is immaterial whether the dominant character belongs to the seed plant or to the pollen plant" (§4). He was not wholly novel in this claim or approach. Mendel himself cites work by Carl Friedrich von Gärtner, and there were others earlier in the century (Orel, 1996). In this respect, Mendel's concept of dominant traits would have been important, but hardly revolutionary (and hence not especially noteworthy to his contemporaries). Dominance embodied a familiar notion—familiar even to non-scientists then as much as now—that some specific traits resemble one parent and not the other. By itself, the concept of dominance explained nothing new.

In discussing dominant traits as he did, Mendel thus addressed an existing misconception about parental influence in inheritance. At the same time, however, he provided a foundation for another misconception. That is, he primed a tradition of attributing the appearance of certain traits to the traits themselves. For later interpreters of Mendel, certain traits appeared *because* they were dominant, rather than because of, say, some feature of inheritance, development, or the coupling of traits. The term 'dominant,' originally introduced as a mere descriptive label, became widely regarded as a causal property (precipitating some unexpected consequences and confusions, discussed more fully in section 3 below).

While noting that some traits are dominant, Mendel also noted that other, complementary traits—which he called 'recessive'—"withdraw or entirely disappear in the hybrids, but nevertheless reappear unchanged in their progeny" (§4). The non-dominant traits were not lost by crossbreeding. Rather, they were 'latent.' Later, they reappeared wholly intact. In this case, too, Mendel's results merely illustrated another familiar hereditary phenomenon: the reappearance of ancestral forms, known at the time as *reversion*. By calling such traits 'recessive,' Mendel hardly did more than redescribe a widely-known feature of inheritance in new terms.

Mendel's work was indeed exceptional—though not always in the ways or for reasons most frequently attributed to him. For example, among most biologists now,

Mendel's legacy falls squarely in the abstract principles of inheritance, or genetics. Yet as much as people cite Mendel's original paper, they often overlook the title that reveals Mendel's primary focus: "Experiments Concerning Plant Hybrids." Hybridization was an important field at the time, both for practical breeding purposes and for addressing questions about evolution and the origin of new species. Could hybrids ever breed true, for example? If so, under what conditions? Could they create new species or stable domestic varieties? For those studying hybridization, reversion had been relatively unpredictable and puzzling. Not so for Mendel.

Mendel highlighted the fact that recessive traits not only reappeared (or reverted) in a hybrid's offspring, but reappeared "unchanged," "fully developed," "without any essential alteration," and thus "remain constant in their offspring" (§§4, 5). As if pure, they could once again breed true, even if their hybrid parents did not. Indeed, a dominant trait could also emerge from a hybrid in true-breeding form. The dominant character could have a "*double signification*" (§5), some plants being mixed (hybrids again) and others breeding true (like the original parents). For Mendel, this reappearance from hybrids of true-breeding forms—sometimes recessive, sometimes dominant—was as important as any 'reversion' of the recessive trait. Something allowed both types of traits to be transmitted "unchanged," and for them to reunite on occasions.

But only some offspring were true-breeding. Others behaved like the hybrid parents. Mendel quantified this pattern in the now familiar 1:2:1 (or 2:1:1) ratio, and showed that the pattern repeated itself in successive generations of hybrids (§§5-7). He thereby revealed an unexpected regularity to or 'law' in the development of hybrids (also see Olby, 1997, §III). Several times during his original paper, Mendel repeated his thematic claim in virtually identical phrasing (see Hartl and Orel, 1992):

...it is now clear that the hybrids form seeds having one or the other of the two differentiating characters, and of these one-half develop again the hybrid form, while the other half yield plants which remain constant and receive the dominant or the recessive characters in equal numbers. (Mendel, 1966a, §6, original italicized; also see §§7, 8, 9)

That is, hybrids produced equal numbers of hybrid and true-breeding offspring; of the true-breeding forms, half showed the dominant trait and half the recessive. Mendel further elaborated the ratios mathematically in terms of a "developmental series" (based on the binomial expansion). Most important, the "foundation and explanation" of this pattern was the formation of *different* gametes, each representing one of the two "pure" characters originally brought together in the hybrid (hence, $Aa \times Aa \implies A + 2Aa + a$). Genes, we say now, segregate and recombine without losing their integrity. That was Mendel's significant insight, not dominance.

Mendel's conception of the 'laws' or mathematical rules of the development of hybrids relied very much on thinking about pairs of different gametes (egg and pollen) and pairs of distinct traits. He thought "in twos" and in combinations of

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