

The Construction of Mendel's Laws

JONATHAN MARKS

While “Mendel's Laws” are generally taught as natural facts, they are actually pedagogical constructions, which originated in a series of lectures at Princeton in 1916. What accounts for their popularity?

Any modern textbook of genetics, or even of general biology or biological anthropology, presents the fundamentals of heredity in a stereotypical fashion, beginning with the two laws of heredity derived from the work on peas by the monk of Brunn, Gregor Johann Mendel. These two laws are “segregation” and “independent assortment,” to wit:

These observations of discrete inheritance and the segregation of alleles are collectively known as “Mendel's first law” or the “Law of Segregation”...

This phenomenon, known as “Mendel's second law” or the “Law of independent assortment,” means that the alleles of different genes get shuffled between parents to form offspring with many different combinations.¹

This formalization into two general laws about segregation and independent assortment is not explicit in

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Mendel's work, although he drew the familiar conclusions from the famous data. But at the dawn of the Mendelian era 35 years later, William Bateson² began his “Defence” of “Mendel's principles of heredity” with “the rediscovery and confirmation of Mendel's Law...”(p. 104). Note the odd-sounding singular in place of the now-familiar plural.

Bateson described this law quite simply, stating “that there are three dominants to one recessive” in a mating of two hybrids (p. 10). What Bateson proposed is actually an explicit alternative to Galton's *Law of Ancestral Heredity*, which divided a person's heredity equally among the lineal ancestors in any generation.

Punnett's³ 1905 textbook *Mendelism* self-interestedly declared, “As our knowledge of heredity clears, and the mists of superstition are dispelled, there grows upon us with ever-increasing and relentless force the conviction that the creature is not made but born” (p. 54). But even this early expression of what has come to be known as geno-hype⁴ didn't mention Mendel's Two Laws. Neither did other genetics textbooks of that first Mendelian generation.^{5,6} Rather, they all spoke vaguely about “Mendel's Law”: nothing more than general recognition of the segregation of unit characters into the germ cells and their subsequent statistical union with other germ cells, producing offspring in predictable genetic proportions.

William Bateson,⁷ who by now had named his youngest son Gregory in

Mendel's honor, conspicuously avoided the term “law” in his 1909 *Mendel's Principles of Heredity* (and no longer a “defence” against W. F. R. Weldon). Indeed, Bateson retained the explicit denial that (as Weldon had said) Mendel enunciated a “Law of Dominance” (p. 13). Bateson in fact took pains to contrast, once again, Galton's Law of Ancestral Heredity against the proper Mendelian “scheme,” “principles,” “phenomena,” “methods,” “analysis,” and “facts.”

Whatever he considered “Mendel's law” actually to be in 1911, the Harvard geneticist William E. Castle⁸ condensed it into “three principles: (1) the existence of unit characters; (2) dominance, in cases where the parents differ in a unit character; and (3) segregation of the units contributed by the respective parents, this segregation being found among the gametes formed by the offspring” (p. 37). This is repeated in Castle's⁹ 1916 textbook, in which he also referred to Hugo de Vries' “law of the splitting of hybrids” and observed that “the same law had been discovered and clearly stated many years previously by ... Gregor Mendel, and we have now come to call this law by his name, Mendel's law” (p. 82).

By now, the modern Mendelian lexicon was nearly fully established, with Bateson's “homozygous,” “heterozygous,” and “allelomorphs” alongside Wilhelm Johannsen's “phenotype,” “genotype,” and “gene.” And yet, there still were no laws of segregation and independent assortment.

That formalization would only arise with the research program of the geneticist who was most interested in the transmission of genes on different chromosomes, distinguishing pairs of genes that assort independently of one another from those

that are on the same chromosome, or "linked." That was the Columbia University geneticist Thomas Hunt Morgan. He invented Mendel's Laws in 1916.

In 1915, Morgan and his students¹⁰ published *The Mechanism of Mendelian Heredity*, in which they presented a synthesis of their work, unifying the genetic research of cytologists and breeders. The Mendelian unit characters of the breeders existed as discrete points on the chromosomes of the cytologists. The genes could travel into the next generation separately, as Mendel had described, if they lay on different chromosomes; or together, if they lay on the same chromosome, although they might still be transmitted separately due to crossing-over, the group's own crucial discovery. Indeed, this work introduced the famous metaphor of "chromosomes . . . as a linear series of beads" (p. 131–132).

Mendel's Law, however, is presented in the singular. The book opens forthrightly: "Mendel's law was announced in 1865. Its fundamental principle is very simple. The units contributed by two parents separate in the germ cells of the offspring without having had any influence on each other." (p. 1). The preface mentions "the Mendelian laws" but with no greater subsequent specificity. And the phrase "independent assortment" makes its first pedagogical appearance on p. 26.

Morgan's next book, however, presented a heuristic change (one is tempted to say "mutation") for Mendelian genetics. Based on a series of lectures he gave at Princeton in early 1916, Morgan¹¹ published *A Critique of the Theory of Evolution* later that year. In the second lecture, from a presentation given on 1 March, 1916, Morgan tells us "what Mendel's law did for heredity" and then sets out for the first time "his first law—the law of segregation".¹¹ A few pages later, Morgan writes, "The second law of Mendel may be called the law of independent assortment of different character pairs." (p. 53).

It need hardly be mentioned that this pedagogical separation and enunciation of a "second law" implicitly privileged Morgan's own work and

research program, which was focused on the relationship between genes and chromosomes. Further, at the time, Morgan's Columbia group was involved in a dispute with William E. Castle's Harvard group over whether genes always passed across generations intact or could be contaminated by the presence of other genes. In that context, the Law of Independent Assortment might also have had the rhetorical effect of de-legitimizing the contamination argument. The Morgan

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group's explanation for Castle's data on coat coloration in hooded rats was in terms of independently assorting modifier genes, rather than contamination of a single gene, a point of sufficient gravity to constitute the closing argument of the book. In Morgan's¹² *The Physical Basis of Heredity* (1919), he devoted separate chapters to "Mendel's First Law—Segregation of the Genes" and "Mendel's Second Law—The Independent Assortment of the Genes."

THE "DOMINANCE" OF MORGAN'S APPROACH

The next generation of trade books and textbooks dealt with the Men-

delian Law/s in three ways. Some presented it as it had always been presented, as a singular "Law." Thus, the 1932 fourth edition of Castle's¹³ *Genetics and Eugenics* retained the structure of its earlier editions, dating to 1916, the year Morgan first presented Mendel's two laws. To Castle, there was still just "Mendel's Law," including "three principles" in the same words as quoted earlier, from the first edition of his text. And while the principle we now call "independent assortment" is discussed, Castle does not use the phrase. Indeed, genetics textbooks into the 1940s could readily discuss the phenomenon of independent assortment without acknowledging its status as Mendel's Second Law.^{14–16}

Others wrote of Mendel's (singular) Law or (multiple) principles, but conceded that there were indeed some who presented them in the form of two laws. Herbert Walter¹⁷ in 1922 continued to write of Mendel's Law: "The essential feature of Mendel's law is briefly this: *hereditary characters are usually independent units which segregate out upon crossing, regardless of temporary dominance*" (p. 100), but went on to mention, "This *law of segregation*, or 'independent assortment' as Morgan prefers to call it. . . ." (p. 103). In this passage, he thus manages to conflate the two "laws" of Mendel/Morgan in precisely the same fashion that would continue to vex introductory biology students for decades to come.

As late as 1939, two former protégés of Morgan, Sturtevant and Beadle,¹⁸ discussed independent assortment with a parenthetical phrase, "... (sometimes known as 'Mendel's second law,' segregation being considered the 'first law'). . . ." (p. 52).

Still others, however, adopted a third pedagogical strategy: presenting it more or less Morgan's way. The enormously successful *Principles of Genetics* by Sinnott and Dunn¹⁹ went through four editions in a quarter of a century, the last, in 1950, with Theodosius Dobzhansky as third author. In the first (1925) edition, they explicitly presented students with the statement that "Mendel's Laws of Inheritance . . .

include several distinct principles” (p. 40). Those principles included dominance and unit characters, but also a “Principle of Segregation” in one chapter, called “Mendel’s Laws of Inheritance. I” and a “Principle of Independent Assortment” in the next chapter, called “Mendel’s Laws of Inheritance. II.”

For their 1932 second edition, which notably involved jettisoning the entire chapter that had formerly extolled eugenics,²⁰ Sinnott and Dunn rewrote the particular sentence introducing the laws, to agree more fully with Morgan: “Mendel’s Laws of Inheritance ... include two major principles of Segregation and Independent Assortment, together with a number of less fundamental generalizations”²¹ (p. 41). That sentence remained unchanged in subsequent editions. Dunn had wanted to do his doctorate with Morgan in 1914, but Morgan’s facilities were overcrowded, so Dunn did his work at Harvard and eventually replaced Morgan at Columbia.²²

Similarly, Shull’s²³ 1926 textbook *Heredity* referred to “Mendel’s law,” stating that its “essential features ... are (1) the segregation of the genes ..., and (2) the assortment of the genes of different pairs into the germ cells wholly independently of one another” (p. 134). He noted ambivalence about including other features of the Mendelian corpus as “diagnostic of Mendelian heredity.” (p. 134). In the second edition, however, not only did the indexed citations of Morgan grow from one to nine, but Shull²⁴ now presented Morgan’s laws without ambiguity or accurate attribution: “Mendel’s laws, as derived from his own experiments, involved, (1) segregation of the genes of the same pair; and (2) independent assortment of genes of different pairs” (p. 206). The phrase “Mendel’s law” remained only in two end-of-chapter problems for students.

Colin’s²⁵ *Elements of Genetics* (1941) presented Mendel’s work explicitly in Morgan’s fashion, as two named laws. Across the Atlantic, an influential 1938 textbook by Waddington,²⁶ who had spent some time visiting Morgan’s fruitfly laboratory

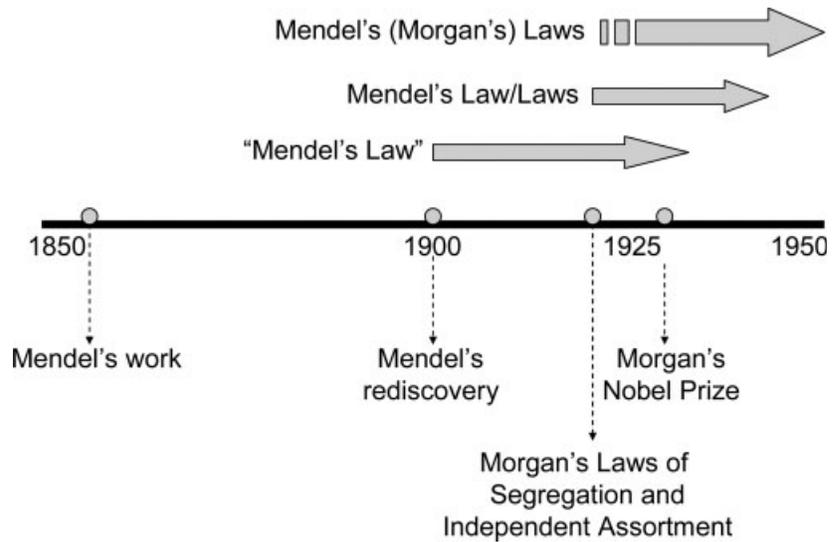


Figure 1. A “memic” depiction of the origin and spread of Mendel’s Laws. Mendel’s work was published in 1866, but did not affect the field of heredity. The work was rediscovered in 1900 and precipitated the wide-scale presentation of Mendel’s Law. Thomas Hunt Morgan divided and named the Two Laws in 1916, and won the Nobel Prize in 1933. By mid-century, all textbooks on the subject were presenting Mendel’s results in Morgan’s fashion.

at Cal Tech, also now presented Mendel’s laws Morgan’s way.

CONCLUSION

While I generally do not feel as though “memes” have much value in understanding or analyzing cultural evolution, there may be some value in depicting the origin and spread (i.e., the history) of Mendel’s Laws “memically” (Fig. 1). Mendel’s Two Laws of Segregation and Independent Assortment were invented in 1916 and diffused gradually across the field of genetics over the next two decades, so that by mid-century they constituted the normative, official version of the science of heredity. With the timeline imposed, one can identify the formerly invisible question: What factors might account for the success, in the latter half of the twentieth century, of Mendel’s Two Laws of Segregation and Independent Assortment, in spite of having been formulated as such neither by Mendel nor by the first generation of Mendelians?

Obviously, it is difficult to demonstrate an answer with any degree of rigor, but it seems possible that three social factors were acting in parallel. First, Thomas Hunt Morgan was

awarded the Nobel Prize in 1933, which greatly increased his stature and may well have given his heuristic presentations of Mendel greater weight. Another factor might have been the perceived value for genetics to formalize its generalizations into laws, in accordance with the normative contemporary philosophy of science. Perhaps, then, “Mendel’s Two Laws” sounded a bit more “sciencey” than do Mendel’s Principles, Mendel’s Generalizations, or even Mendel’s (vague) Law.

And third, perhaps the operation of Planck’s Principle.²⁷ A new generation of geneticists was writing the textbooks. When Morgan first coined “the two laws” in 1916, L. C. Dunn was 21 years old and a first-year graduate student; C. H. Waddington was but 11 years old. Morgan’s contemporaries from the dawn of Mendelism in 1900 were thinning out and a new generation had been weaned on Morgan’s prestige and research program. Moreover, Morgan was, with the exception of William Bateson, who died in 1926, the least tainted of his generation by the eugenics movement. The wholesale embrace of that movement by the

Nazis cast the entire field of genetics in an ugly light.

In short, Morgan was an excellent role model. His Mendelian heuristic might have been unfamiliar either to Mendel himself or to the first wave of his followers, but it was, and remains, a good way to present things and consequently has been universally memorized by students of genetics since at least mid-century. Mendel's Two Laws, however, are not so much facts of nature as facts of nature/culture.²⁸

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