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About Our Cover

The red fox kit on the cover was photographed in a wooded area in North Hero, Vermont, along the shores of Lake Champlain. North Hero is one of the many islands found in Lake Champlain, which is 120 miles in length and separates Upstate New York from Vermont.

Red foxes (*Vulpes vulpes*) can live in diverse habitats, including forests, farmland, grasslands, suburban areas, mountains, and deserts. They are lone hunters, and their diet comprises a wide range of foods, including rabbits, rodents, birds, fishes, frogs, fruits, and vegetables.

Red foxes mate during winter, and a female can produce a litter of two to 12 kits. The kit that is pictured on the cover was part of a litter of seven. At birth, the kits are brown or gray; within four weeks they typically grow a new red coat. The den for this litter of kits was dug at the base of a tree on the slope that went from the wooded area to the lakeshore. Both parents take care of their kits from spring until fall, as was the case for this family of kits. The photographer had the pleasure of watching this family (from a distance) on her property.

The average life span in the wild for the red fox is two to four years. They can weigh 6–24 pounds.

This photo was taken using a Nikon D3200 with an F stop of f/5.6, ISO of 3200, and focal length of 300 mm.

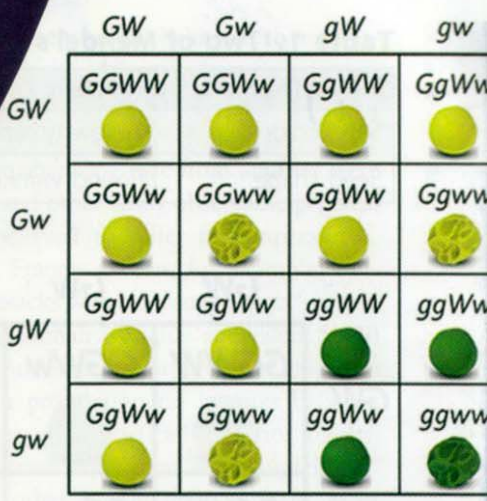
The photographer is Nancy L. Elwess, a Distinguished Teaching Professor in the Department of Biological Sciences at the State University of New York at Plattsburgh. She lives in North Hero, Vermont.

Contents

FEATURE ARTICLE

The Misuse of Genetics: The Dihybrid Cross & the Threat of "Race Crossing"

MARK SHOTWELL



Abstract

Biology teachers consider basic Mendelian genetics to be value-free, objective science, immune to misinterpretation and misuse. It may thus come as a surprise to learn that in the early days of genetics a cornerstone of genetics education, the dihybrid cross, was employed to support claims of the racial superiority of whites over blacks and to provide a "scientific" rationale for laws prohibiting interracial marriages. In 1917 the prominent eugenicist Charles B. Davenport warned of the danger of "disharmonious combinations" of physical and behavioral traits in the second generation of "wide race crosses," equivalent to the F_2 generation of a dihybrid cross. He tried and failed to find data to support his arguments in a study of the mixed-race inhabitants of Jamaica. Davenport's analysis was deeply flawed, especially by the racist assumptions underlying this work. Although these events occurred a century ago, biology teachers may still be able to use this regrettable episode as an example of how even the most basic science may be misapplied by those with a social or political agenda.

Key Words: *Mendelian genetics; eugenics; race; history of biology.*

○ Introduction

In genetics, a dihybrid cross is one in which the two parents differ in two characteristics. Gregor Mendel described such a cross in his 1866 paper "Experiments on Plant Hybrids" (Corcos & Monaghan, 1993), and it has been a staple of genetics education ever since. In 1905 R. C. Punnett, the originator of the familiar Punnett square, described the dihybrid cross in his book *Mendelism* (Punnett, 1905), which was published a year before the study of inheritance was even referred to as genetics (Gayon, 2016). The dihybrid cross was initially valuable as an experimental test of Mendelian principles, showing that traits may be inherited independently, with each obeying Mendel's rules. Later, it was a key tool in the mapping of genes to chromosomes and the elucidation of how genes may interact to determine a phenotype. The dihybrid cross has been described in an early chapter of practically every genetics textbook published since Punnett's.

"Heeding the lessons of the eugenics movement may help us navigate the treacherous waters of the new genetic age we are about to enter."

Today, few students of genetics – or their teachers – would suspect that the dihybrid cross was once employed to support claims of genetic differences between races and to provide a "scientific" rationale for prohibiting interracial marriages. This occurred a century ago during the heyday of the so-called eugenics era when social reformers believed they could use recent scientific advances, namely Mendelian genetics, to solve difficult social problems. From our vantage point, we can see that the eugenicists misapplied genetics to justify their notions of racial superiority. Present-day students of genetics, or of any science for that matter, could learn important lessons from this regrettable episode: first, that apparently "value-free" science has been used in the past to discriminate against entire groups of people, and second, that we should be cautious in the future not to employ science to justify social inequality and repeat the mistakes of the eugenicists. Before examining this long-forgotten example of the misuse of genetics, let's review the dihybrid cross.

○ The Dihybrid Cross

Gregor Mendel examined the inheritance of his seven traits in peas not only one at a time but also in combination. One such cross involved the two independent traits seed color and seed shape, with one gene controlling each trait as shown in Table 1.

One of the parental plants will be homozygous dominant for both traits and the other parental plant homozygous recessive for both. The P_1 cross will thus be

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Table 1. Two of Mendel's traits in peas.

Trait	Allelic Forms	Genotypes
Seed color	Yellow green	*G–gg*
Seed shape	Round wrinkled	*W–ww*

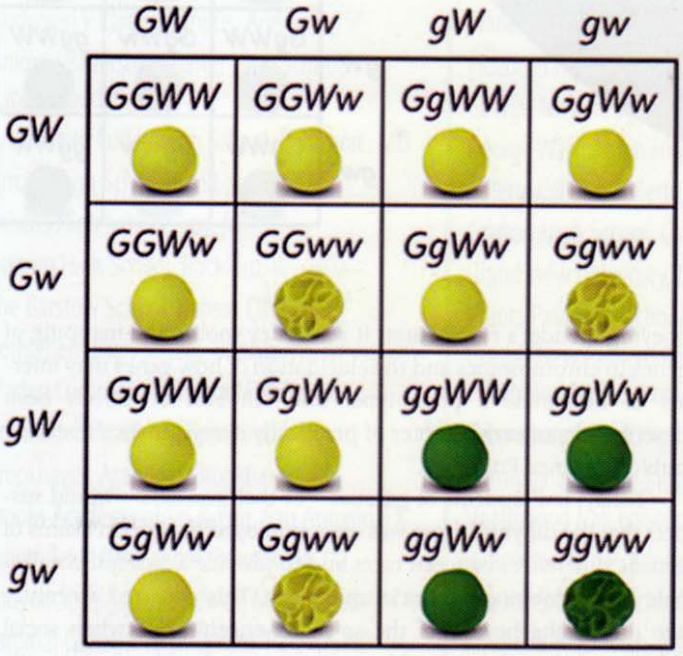

Figure 1. Punnett square for the F_2 generation of a dihybrid cross showing the independent inheritance of seed color and seed shape.

$$\underset{\text{Yellow \& Round}}{GGWW} \times \underset{\text{green \& wrinkled}}{ggww}$$

When the parental plants undergo meiosis, each will produce only one gamete type:

$$\underset{\text{Yellow \& Round}}{GGWW} \times \underset{\text{green \& wrinkled}}{ggww}$$
$$\downarrow \qquad\qquad \downarrow$$
$$GW \qquad\qquad gw$$

All the F_1 plants will therefore receive *GW* from one parent and *gw* from the other, so all of the F_1 seeds will have the genotype *GgWw* and be Yellow and Round. These are dihybrid seeds, heterozygous for two genes and showing the two dominant phenotypes.

The doubly heterozygous F_1 plants will self-fertilize (or be intercrossed) to produce the F_2 generation. The F_1 plants make four gamete types in equal proportions:

$$^1/_4\,GW \quad ^1/_4\,Gw \quad ^1/_4\,gW \quad ^1/_4\,gw$$

The Punnett square for the F_2 generation will therefore have four columns in the square and four rows, and a total of 16 possible combinations after random fertilization (Figure 1).

$$P_1 \quad \underset{\text{DomDom}}{AABB} \times \underset{\text{recrec}}{aabb}$$

$$F_1 \quad \underset{\text{DomDom}}{AaBb} \otimes$$

$$F_2 \quad 9/16\ A–B–\ \text{DomDom}$$
$$3/16\ A–bb\ \text{Domrec}$$
$$3/16\ aaB–\ \text{recDom}$$
$$1/16\ aabb\ \text{recrec}$$

Figure 2. Diagram of a generic dihybrid cross showing the inheritance of genes *A* and *B*. (Note that the symbol ⊗ indicates self-fertilization.)

Both genes show complete dominance, which is to say the seeds must be either Yellow (dominant) or green (recessive) and either Round (dominant) or wrinkled (recessive). Because of this, there will be only four combinations of phenotypes in the F_2 generation:

$^9/_{16}$ *G–W–* Yellow, Round

$^3/_{16}$ *G–ww* Yellow, wrinkled

$^3/_{16}$ *gg W–* green, Round

$^1/_{16}$ *gg ww* green, wrinkled

This 9 to 3 to 3 to 1 ratio is Mendel's dihybrid ratio of phenotypes in the F_2 generation.

After carrying out this cross, Mendel counted the following phenotypes in the F_2 seeds: 315 Yellow and Round, 101 Yellow and wrinkled, 108 green and Round, and 32 green and wrinkled (Mendel, 1866). This was a ratio of 9.1 to 2.9 to 3.1 to 0.92, almost identical to the expected ratio.

The dihybrid cross may be summarized using *A* and *B* for the two segregating genes and Dom and rec for the two phenotypes as shown in Figure 2.

○ The Threat of "Race Crossing"

Eugenics was a pseudoscientific movement that originated with the late 19th-century writings of the English polymath Francis Galton (Darwin's half-cousin) and flourished in the first three decades of the 20th century. Its goal was to improve the hereditary quality of the human race by controlling breeding (Kevles, 1998).

Eugenicists hoped to eliminate inherited disease and to solve a host of social problems, including poverty, crime, alcoholism, mental illness, and sexual immorality. They believed this would be achievable by keeping the "unfit" from having children, thereby preventing the passing on of harmful genes and eventually removing them from the population altogether. They also held that it would be possible to raise the average intelligence of the population by eliminating the reproduction of "feebleminded" people.[1] The original eugenicists in England, including Galton, were concerned with what they perceived to be hereditary

differences between socioeconomic classes. They feared that the lower classes were out-reproducing the "eminent" in society and predicted that the intellectual ability of the country would decline unless steps were taken.

In contrast to the socioeconomic focus of those early eugenicists, many American eugenicists came to be preoccupied with race. Race is an elusive concept in human biology. At one time or another, it has meant everything from a family to a tribe to a nation to an entire species. To most adherents of eugenics, however, it was not mysterious at all. It was an article of faith that the human species could be exactly divided into separate races that differed from each other in inherited characteristics. Here, for example, is the definition of a race proposed by the prominent American eugenicist Charles B. Davenport (Figure 3):

> A race is a more or less pure bred "group" of individuals that differs from other groups by at least one character, or, strictly, a genetically connected group whose germ plasm is characterized by a difference, in one or more genes, from other groups. (Davenport, 1917)

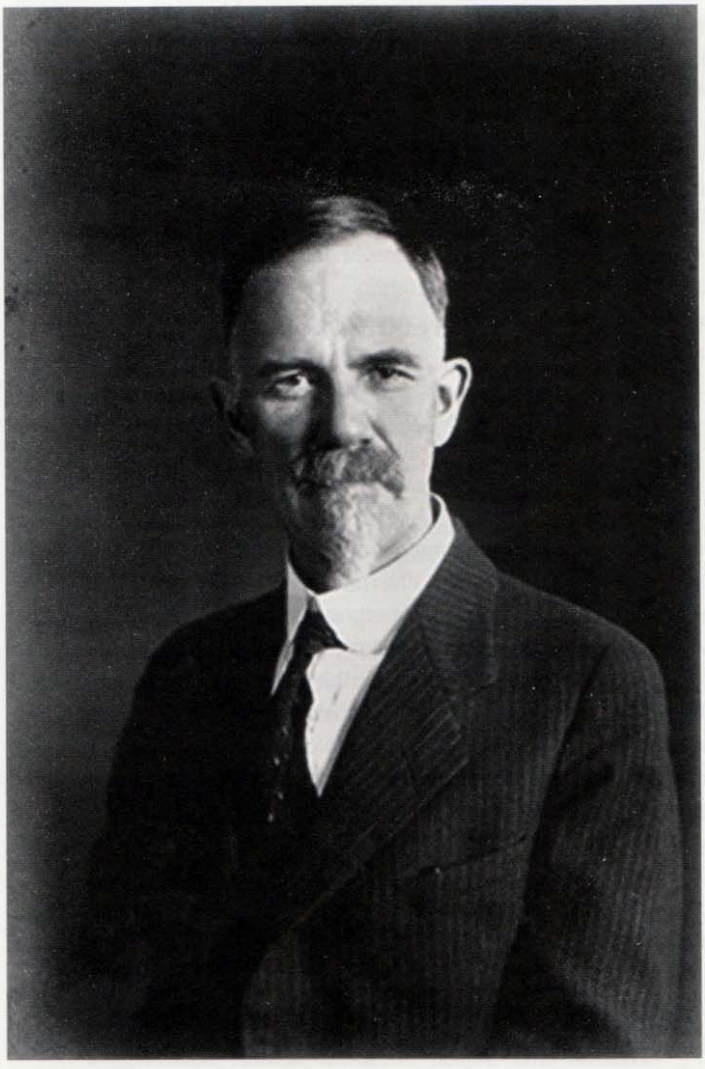

Figure 3. Charles B. Davenport (1866–1944). https://upload.wikimedia.org/wikipedia/commons/e/e1/Charles_Benedict_Davenport.jpg

To Davenport, a "blue-eyed Scotchman" belonged to a different race from "the dark Scotch," and by a strict genetic criterion could even be considered members of different "elemental species" (Davenport, 1917).

The attributes that distinguished one race from another were not merely skin pigmentation and other easily observable physical traits. The races were also believed to differ in temperament, behavior, and mental ability. Francis Galton, for example, estimated that the intelligence of blacks was, on average, two "grades" below that of the average Englishman (roughly equivalent to 20 IQ points; Provine, 1973). An effective program of eugenics would thus seem to require a prohibition on matings between the genetically superior whites and genetically inferior blacks. Such interbreeding was considered equivalent to "mongrelizing" in thoroughbred horses and other highly bred animals. Most eugenicists therefore strongly warned of the dangers of "race crossing." One of the first was Davenport.

Davenport's rather haphazard investigations persuaded him that physical features like eye color, skin color, and hair color were inherited separately as simple Mendelian characters (Provine, 1973). In other words, he believed that each trait was controlled by one or two genes, and that each gene had two alleles, one dominant and the other recessive. He proposed, for example, that skin color was determined by two genes working together (Davenport, 1913). After analyzing data collected by fieldworkers from the Eugenics Record Office, he concluded further that these physical features were inherited independently of each other. For example, he assumed that it was possible to inherit a short torso from one parent and long legs from the other parent (Davenport, 1917).

○ "Race Crossing" & the Dihybrid Cross

Like most other eugenicists, Davenport believed the races to be genetically distinct. This, he maintained, was due to thousands of years of natural selection adapting each race to its environment. He thought that matings between people of two widely divergent races, who differed in several Mendelian characters, would produce "disharmonious" genetic combinations in subsequent generations. By way of analogy, he gave the example of two breeds of chicken, Leghorn and Brahma. The Leghorn hen (Figure 4) is an indeterminate egg-layer; it will keep laying new eggs to replace those removed from the nest. It lacks the brooding instinct, however, and will rarely sit on a clutch of eggs. In contrast, the Brahma hen (Figure 5) is only a fair egg-layer and becomes broody two or three times a year, staying on the nest day and night for up to three weeks without laying new eggs. Moreover, it excels at mothering its chicks.

Davenport crossed the two breeds and found that the hybrid hens laid an intermediate number of eggs, but just a day or two after hatching they stopped mothering the chicks, leaving them to die, and resumed laying a few days later. The hybrid hens thus failed both in egg laying and in mothering their chicks. In Davenport's words, "the instincts and functions of the hybrids were not harmoniously adjusted to each other" (Davenport, 1917).

With this unsatisfactory cross as an illustrative case, Davenport turned his attention to "wide race crosses" in humans, with the dihybrid cross as his primary explanatory tool. He cited the example of

Figure 4. Leghorn White hen. www.downthelane.net/img-new/chicken-breeds/leghorn-white-330.jpg

Figure 5. Brahma hen. www.henleechickens.co.uk/chickens-for-sale#Red Pyle

matings between people of a large, tall race and people of a small, short race.[2] In the second generation, "disharmonious" combinations would appear, such as "large frames and inadequate viscera" or "children of short stature with too large circulatory apparatus" (Davenport, 1917). Consider a mating between two people of different "races," one with a large body and correspondingly large internal organs, and the other with a small body and appropriately small organs. Assuming that body size and organ size are separate

	AB	*Ab*	*aB*	*ab*
AB	*AABB* large body, large organs	*AABb* large body, large organs	*AaBB* large body, large organs	*AaBb* large body, large organs
Ab	*AABb* large body, large organs	*AAbb* large body, small organs	*AaBb* large body, large organs	*Aabb* large body, small organs
aB	*AaBB* large body, large organs	*AaBb* large body, large organs	*aaBB* small body, large organs	*aaBb* small body, large organs
ab	*AaBb* large body, large organs	*Aabb* large body, small organs	*aaBb* small body, large organs	*aabb* small body, small organs

Figure 6. Punnett square for the F_2 generation of the dihybrid cross showing the independent inheritance of hypothetical genes for body size and organ size.

Mendelian traits, each controlled by one gene with two alleles, the mating would be as follows:

AABB		*aabb*
	×	
large body, large organs		small body, small organs

All the children would be doubly heterozygous, genotype *AaBb*, and would show the dominant phenotypes, large body and large internal organs. So far, so good; in Davenport's words, the "internal organs are well adapted to care for the large frames" of the children. But what would happen when two double heterozygotes had children together? The outcome would be equivalent to the F_2 generation of a dihybrid cross, as illustrated in Figure 6. Summing up the expected genotypes and phenotypes, we get the ratio of phenotypic combinations shown in Table 2.

The genotype *A–bb* results in large bodies with small internal organs, a clear example of what Davenport called a "disharmonious combination." In this case, the circulatory system would be too small to supply blood to the large body, leading to poor health and early death. The genotype *aaB–*, on the other hand, produces children of small stature whose circulatory systems are simply too large to fit, another bad hereditary arrangement.

Another example suggested by Davenport involved tooth size and jaw size, two traits he considered to be independent of one another. The original mating:

AABB		*aabb*
	×	
large teeth, large jaw		small teeth, small jaw

As before, the children of this mating would be doubly heterozygous and have the harmonious combination of large teeth in a

Table 2. Phenotypes in the F_2 generation of the hypothetical dihybrid cross involving body size and organ size.

Proportion	Genotype	Body Size	Organ Size
9/16	*A–B–*	large	large
3/16	*A–bb*	large	small
3/16	*aaB–*	small	large
1/16	*aabb*	small	small

large jaw. But 3/16 of grandchildren would be expected to be genotype *A–bb* and have large teeth crowded into a jaw too small to accommodate them, and another 3/16 would be *aaB–* and have small teeth widely spaced in a large jaw. Davenport believed that these disharmonious combinations accounted for the higher incidence of irregular teeth in the "tremendously hybridized" United States (Davenport, 1917).[3]

It was thus on strictly genetic grounds that so-called "wide race crosses" could be opposed. And it was not the prospect of Scots-Italian marriages that concerned Davenport, and certainly not matings between the large-jawed and the small-jawed. No, it was the widest "race cross" of all that was of primary concern: that between whites and blacks.

Davenport wrote, "What is true of physical traits is no less true of mental" (Davenport, 1917). Like most eugenicists of the day, he believed that not only were physical characteristics separate Mendelian traits, but so too were intelligence, temperament, and personality, along with such traits as criminality, immorality, and even "nomadism" (Provine, 1973). Inasmuch as blacks were held to be both less intelligent and less ambitious than whites, an interracial mating could be depicted as follows:[4]

white		black
AABB	×	*aabb*
high IQ, high ambition		low IQ, low ambition

Once again, the problem was not in the children of this mating (the "hybrids," equivalent to the F_1 generation), but in the grandchildren (the "F_2 generation"). Three-sixteenths of the grandchildren would have been expected to have genotype *aaB–* and be social strivers without the intelligence to be successful at it. In Davenport's words, such a person would be an "unhappy hybrid dissatisfied with his lot and a nuisance to others" (Davenport, 1917). The dihybrid cross had thus, he thought, provided solid scientific support for his contention that "miscegenation commonly spells disharmony" (Davenport, 1917). (*Miscegenation*, literally "mixing of kinds," is an outmoded term referring to sexual relations, cohabitation, or marriage between people of different races.) Davenport's warning against race crossing was clear:

> A hybridized people are a badly put together people and a dissatisfied, restless, ineffective people. One wonders how much of the exceptionally high death rate in middle life in this country is due to such bodily maladjustments; and how much of our crime and insanity is due to mental and temperamental friction.[5]

Marriages between whites of different ethnicities were acceptable, but "wide race crosses" between whites and blacks were a genetic time bomb set to go off in two generations' time.

○ Race Crossing in Jamaica

To support his claim that "wide race crosses" were a danger that should be blocked on genetic grounds, Davenport needed better evidence. So he went looking for "disharmonies" in the only place he knew where interracial matings had been sufficiently common over a long enough time to provide abundant research subjects. That place was Jamaica.

With the assistance of several governmental agencies, Davenport's assistant Morris Steggerda managed to examine 370 Jamaicans, including college students, farmers, police officers, seamen, office workers, and prisoners, whom he classified as black, white, or "brown" (mixed race). He amassed 8000 pages of raw data, everything from head width and cranial capacity to ankle girth and foot length. His psychological tests included such things as the discrimination of musical pitch and rhythm, the ability to draw a circle in 30 seconds, and skill in assembling a wooden figure of a human from a torso, two arms, two legs, and a head (the "manikin test"; see Figure 7). The results of this study appeared in a 500-page book entitled *Race Crossing in Jamaica* (Davenport & Steggerda, 1929).

Davenport had hoped to find hard data showing "disharmonious combinations" of traits in "browns" – in the children and especially the grandchildren of interracial marriages. He did, in fact, find physical differences between Jamaican blacks and whites: both the arms and legs of blacks were, on average, 0.5 cm (0.2 inches) longer than those of whites.[6] So what about the "disharmonious combination" of long legs and short arms in the grandchildren of a black-white mating? According to Davenport, this combination would "put them at a disadvantage in picking things up from the ground" (Jennings, 1930), although this would have only required these people to reach 1 cm (0.4 inches) farther to reach the ground.

Having unexpectedly documented few examples of physical disharmonies among the "browns" living on the island, Davenport and Steggerda fell back on their contention that mental traits segregated among the "browns," yielding a certain percentage of mental incompetents. This, to them, was sufficient evidence to recommend against black-white crosses. Despite all this, Davenport was more moderate in his racial views than many other eugenicists. He never claimed that entire races were genetically inferior to others and was a staunch supporter of civil liberties for all Americans regardless of race (Provine, 1973).

○ Further Opposition to Race Crossing

Many eugenicists went beyond Davenport in their opposition to race crossing, as it was abundantly clear to them that blacks were subordinate to whites both physically and mentally. The eugenic philosophy on race crossing may have been most clearly articulated in the widely used textbook *Applied Eugenics* by Paul Popenoe and Roswell Hill Johnson, published in 1918 (Popenoe & Johnson, 1918). In a chapter entitled "The Color Line," Popenoe and Johnson considered whether social discrimination against blacks was, in their words, "justified by eugenics." They concluded that it was.

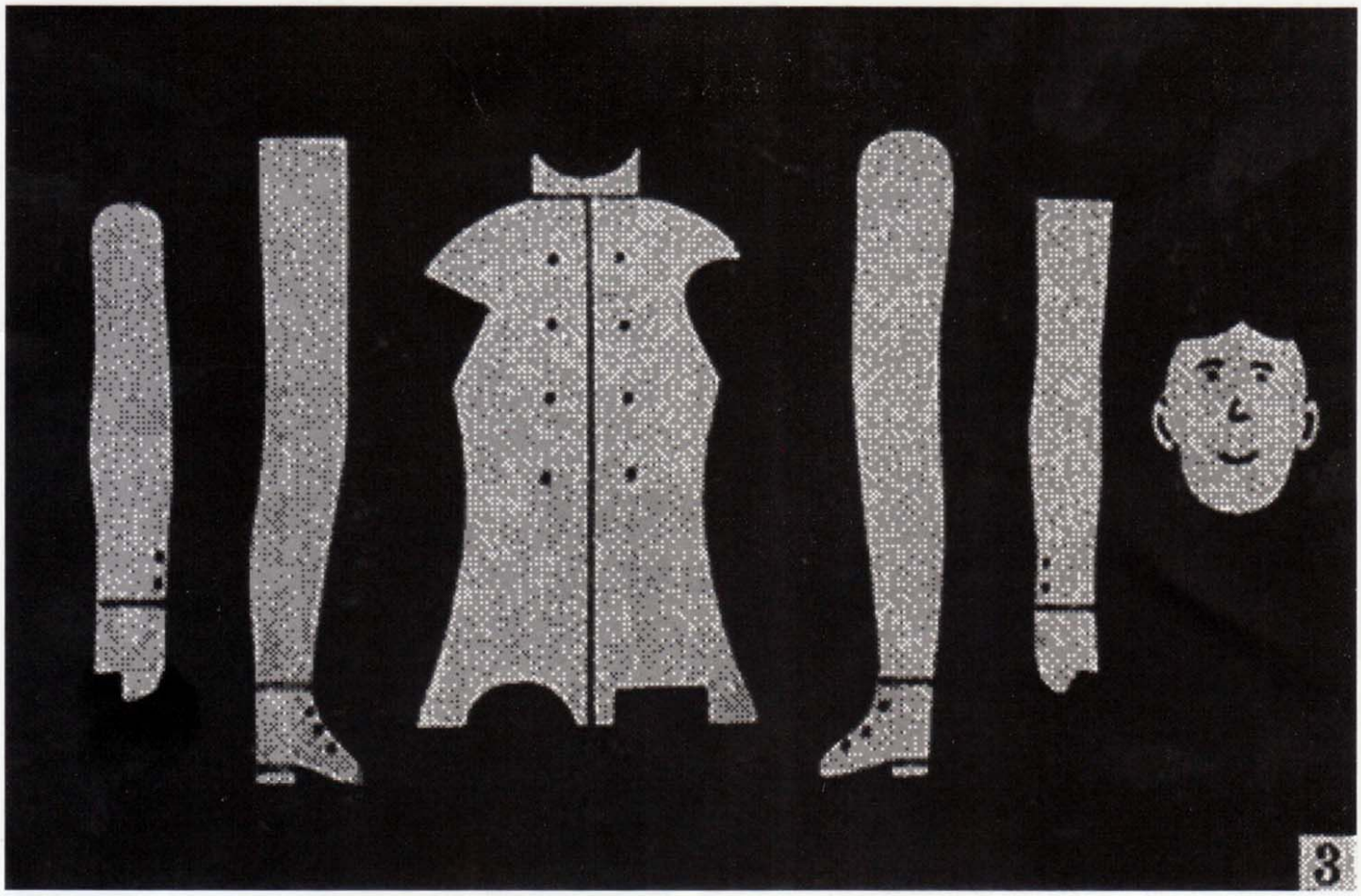

Figure 7. The manikin test used by Davenport and Steggerda in Jamaica (Davenport & Steggerda, 1929, p. 503).

They began by stating that blacks had made no original contributions to the world's civilization and cited historical "considerations" reflecting the intellectual deficiency of blacks. This evidence led Johnson and Popenoe to conclude that blacks were genetically inferior to whites. They went on to discount results of studies that inconveniently revealed little difference between blacks and whites in mental abilities, including one that showed no difference between "full-blood Negroes and mulattoes" (persons of mixed black and white ancestry).

The difference, they maintained, was in "higher" mental functions, which could only be measured using newly developed intelligence tests. The evidence here seemed to clearly indicate that blacks were inferior to whites. One study they referred to revealed a direct correlation between performance on an intelligence test and percentage of "white blood," from "full-blood Negro" to "quadroon" (a person one-quarter black by descent). "Pure Negroes," it was concluded, possess only 60% of the intellectual capacity of whites (Popenoe & Johnson, 1918).

But it wasn't just in brainpower that blacks came up short. Based on little evidence, Popenoe and Johnson also concluded they were deficient in foresight, initiative, persistence, impulse control, and sexual inhibition. These deficits were held to be largely hereditary as they persisted in all environments, whether in Africa, Jamaica, or the United States. As if that weren't enough, American blacks also seemed to lack resistance to tuberculosis and typhoid fever, diseases to which their African forebears had never been exposed. Their lower life expectancy (fully 16 years less than whites) was taken as proof of their lower Darwinian fitness. This was more than enough evidence for Popenoe and Johnson to conclude that blacks are genetically inferior to whites, at least in the modern civilization of North America. The implications with respect to intermarriage were clear. Here's how Popenoe and Johnson put it: "Without going into detail, we feel perfectly safe in drawing this conclusion: that in general the white race loses and the Negro gains from miscegenation." Intermarriage must therefore be opposed, as it would bring a halt to "racial and social progress" and produce a "race of mediocrities" lacking in leadership and genius. That, Popenoe and Johnson believed, would in the long run hurt even blacks, since they benefited from the continued progress of white civilization (Popenoe & Johnson, 1918).

Popenoe and Johnson noted with approval that intermarriage between blacks and whites was illegal in 28 states. But this was not enough; they called for laws in every state banning not merely interracial marriages, but all sexual relations between the two races (i.e., miscegenation). Their position on this could not be clearer: "Miscegenation can only lead to unhappiness under present social conditions and must, we believe, under *any* social conditions be biologically wrong" (Popenoe & Johnson, 1918).

○ Criticisms of Race Crossing Theory

As with other major tenets of eugenics, the danger of race crossing was eventually debunked by geneticists who did not let their prejudices stand in the way of clear analysis. One such geneticist was William E. Castle, who challenged the idea that physical traits were inherited as separate Mendelian characters, as Davenport and others had claimed. From his crosses between purebred large and small rabbits, Castle concluded that rather than separate factors controlling individual physical traits, the effect of genes on stature was more general. Hence, long legs and large internal organs would tend to be inherited together, not independently. The "disharmonies" that Davenport had cautioned against would not, therefore, be expected to occur. Castle argued instead for the apparent blending of characters in the offspring of race crosses, with intermediate values of traits to be expected in the offspring of "wide crosses." Castle wrote in 1930:

> We like to think of the Negro as inferior. We like to think of Negro-white crosses as a degradation of the white race. We look for evidence in support of the idea and try to persuade ourselves that we have found it even when the resemblance is very slight. The honestly made records of Davenport and Steggerda tell a very different story about hybrid Jamaicans from that which Davenport and Jennings tell about them in sweeping statements. The former will never reach the ears of eugenics propagandists and Congressional committees; the latter will be with us as the bogey men of pure-race enthusiasts for the next hundred years. (Castle, 1930)

○ Concluding Thoughts

Charles Davenport's paper warning of the threat of race crossing was published a century ago, and from this vantage point we can easily identify Davenport's mistakes and the flaws in the entire eugenics program (Allen, 2000).

First of all, Davenport, along with every other prominent eugenicist, assumed that because a particular trait appeared in consecutive generations (i.e., was familial), the trait must be genetically determined. In almost every case, they ignored all possible social and environmental influences on the trait. Second, the eugenicists naively assumed that even those traits that were clearly inherited were simple Mendelian characters. In other words, they believed that each trait was determined by a single gene with two alleles, one dominant and the other recessive. They ignored the possibility that the trait could be influenced by multiple genes acting together, with each making a small contribution to the trait. (Davenport himself had concluded that skin color and height were polygenic, controlled by two or more genes.)

Additionally, Davenport and other American eugenicists allowed their prejudices to affect the interpretation of their honestly made research findings. Because they assumed blacks to be inferior to whites, they were unable to evaluate their data without bias. Even when the evidence failed to support their racist assumptions, they refused to abandon those assumptions.

This episode may serve as a cautionary tale even for 21st-century biologists. In the study of human genetics, simple answers must be viewed with extreme caution, as they can often lead us astray. Data must be interpreted without bias so that conclusions don't simply reinforce existing social prejudices. Finally, it should be clear that using the latest findings in genetics – or any other branch of biology – to solve social problems is fraught with danger. The eugenicists thought they were wise enough to take control over human reproduction, based on their understanding of Mendelian genetics. We might ask ourselves whether we as a society are about to display the same hubris in the application of gene editing and other new genetic technologies. Heeding the lessons of the eugenics movement may help us navigate the treacherous waters of the new genetic age we are about to enter.

○ Acknowledgment

I would like to express my appreciation to Dr. Randy Moore at the University of Minnesota for his encouragement.

NOTES

1. "Feeblemindedness" was an ill-defined category that encompassed a wide range of mental deficiencies and socially deviant behaviors. See Kevles (1998, pp. 77–79).
2. Davenport's examples were "the Scotch" and "the South Italian," respectively (Davenport, 1917, p. 366).
3. Davenport wrote: "Again it seems probable, as dentists with whom I have spoken on the subject agree, that many cases of overcrowding or wide separation of teeth are due to a lack of harmony between size of jaw and size of teeth . . . " (Davenport, 1971, p. 366).
4. Note that Davenport did not diagram such a cross, but it is clear that this is what he was referring to on pages 366 and 377 of his 1917 article.
5. Davenport (1917, p. 367).
6. 0.46 cm for arm length (Davenport & Steggerda, 1929, p. 88) and 0.52 cm for leg length (Davenport & Steggerda, 1929, p. 119).

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