Syntheses That Weren't: W.F.R. Weldon on Chromosomes

ISHPSSB 2017, University of São Paulo, 2017/06/18

Charles H. Pence
@pencechp

Department of Philosophy
LSU Institute for Ethics

LOUISIANA STATE UNIVERSITY

Outline

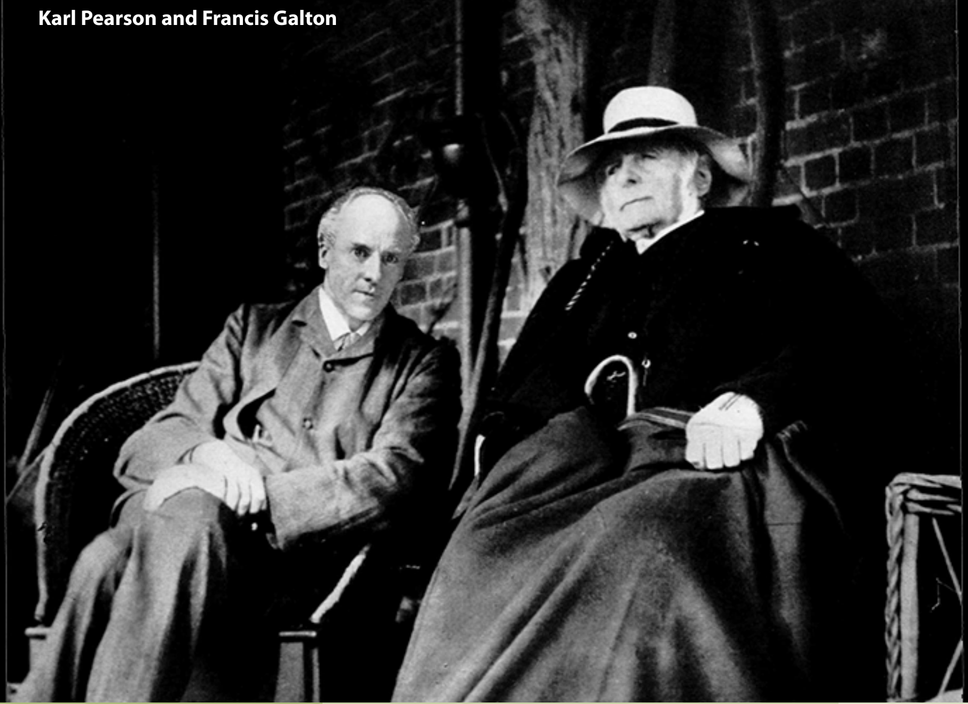
1. Introduction and Background
2. Weldon on Mendel
3. Hereditary Transmission and Chromosomes
4. The Problem
5. From Chromosomes to Somatic Characters
6. The Moral

The take-home: Weldon worked toward, but never completed, a combination of Galtonian inheritance, Mendel's data, and a statistical view of the chromosomes

Introduction and Background

Weldon's bust, Oxford Museum

Karl Pearson and Francis Galton



W.F.R. (Raphael) Weldon (1860–1906)

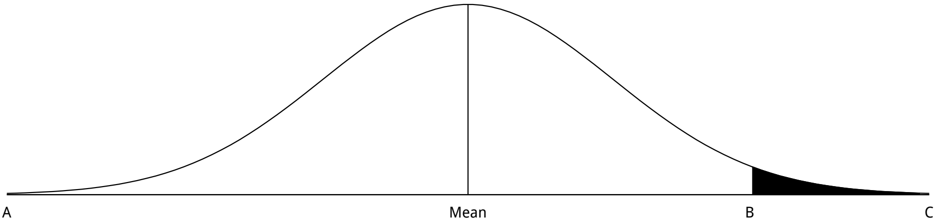
- Appointments: Cambridge (1882–1889); University College London (1889–1899); Oxford (1899–1906)
- Early statistical work with Francis Galton, 1889–1890
- Collaboration with Karl Pearson begins, 1890s
- Dispute with Bateson begins, 1894, escalates to open warfare by early 1900s
- "Rediscovery" of Mendel's work, 1900
- Dies of acute pneumonia aged 46, 1906

Weldon on Mendel

About pleasanter things, I have heard of and read a paper by one Mendel on the results of crossing peas, which I think you would like to read. It is in the Abhandlungen des Naturforschenden Vereines in *Brünn* for 1865 – I have the R.S. [Royal Society] copy here, but I will send it to you if you want it.

The point seems to me to be that the results indicate an exclusive inheritance with a very high parental correlation. (PEARSON 11/1/22/40.4.2, 1900-10-16)

I think there must be an element in each gamete corresponding to every quality transmitted by it; some of these may blend with the corresponding elements of the other, some may exclude corresponding elements of the other, some may make a patch work resulting in a particulate inheritance. (PEARSON 11/1/22/40.4.3, 1900-12-12)

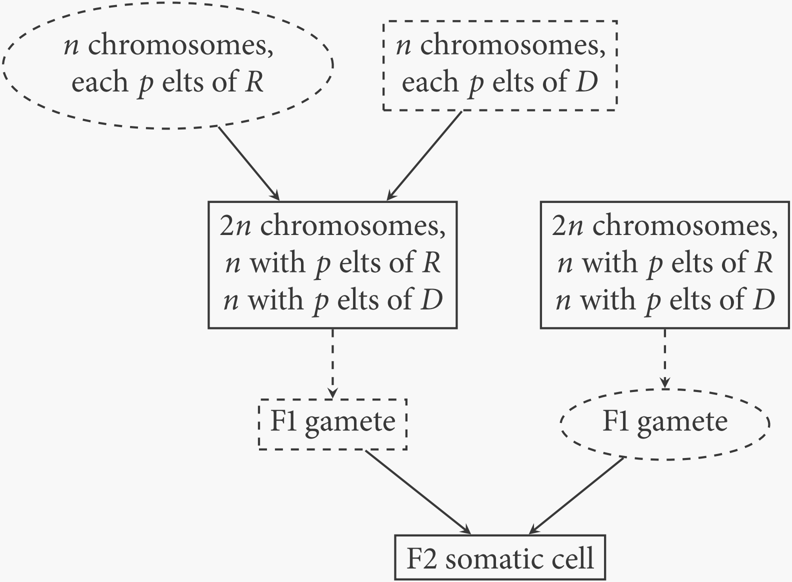

A
Mean
B
C

There must be a simple relation between AB, BC, and the S.D. [standard deviation] of the original system, which would make the chance that a grandchild falls within BC = 1/4?

[A] more important point would be this: that since some races of the same species are said to obey these laws, while others do not, one has a chance of predicting in a given case, from a knowledge of parental variability, what will happen, and so smashing the "pure gamete" once for all. (PEARSON 11/1/22/40.7.3, 1902-06-23)

Hereditary Transmission and Chromosomes

Don't worry over my attempts to understand inheritance formulae — They will do me good, but otherwise they are of no importance, and you have plenty of better things to do. (WFRW to KP, PEARSON 11/1/22/40.6.4, 1901-12-31)



n chromosomes, each p elts of R

n chromosomes, each p elts of D

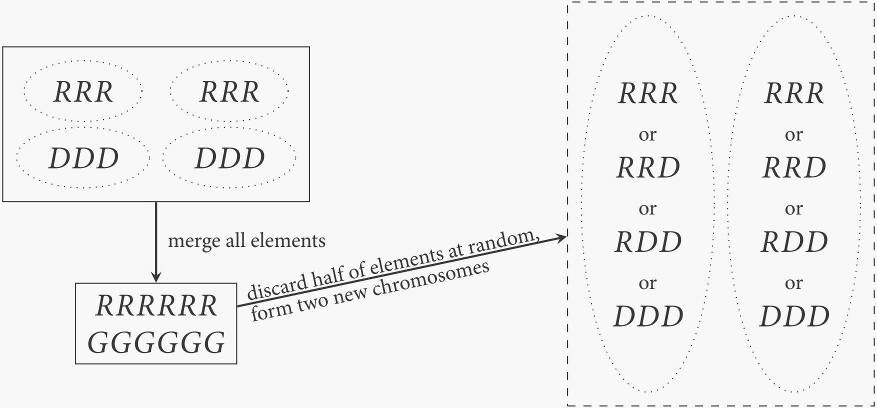
$2n$ chromosomes, n with p elts of R n with p elts of D

$2n$ chromosomes, n with p elts of R n with p elts of D

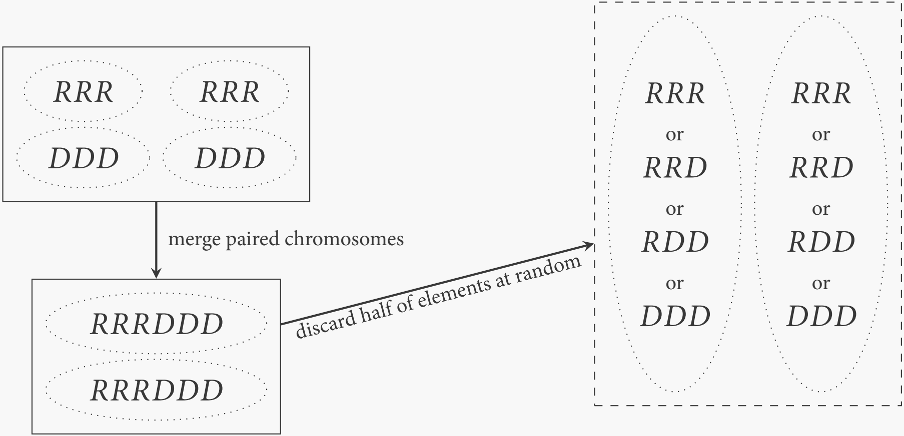
F1 gamete

F1 gamete

F2 somatic cell

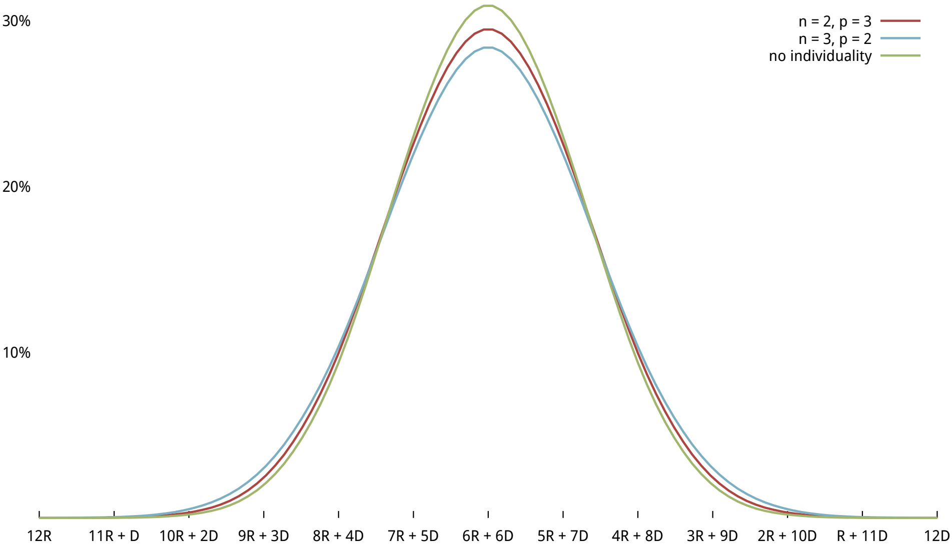


First Hypothesis: No individuality of the chromosomes



Second Hypothesis: Individuality of the chromosomes

The Problem


30%
20%
10%
n = 2, p = 3
n = 3, p = 2
no individuality
12R
11R + D
10R + 2D
9R + 3D
8R + 4D
7R + 5D
6R + 6D
5R + 7D
4R + 8D
3R + 9D
2R + 10D
R + 11D
12D

They're all the same graph!

Almost *none* of these will breed true.

I have laboriously worried through the effect of supposing the chromosomes to retain their individual constitution right on from the moment of fertilisation to the formation of new germ-cells; and it does not give anything like a proper segregation: there are very few “pure” individuals, among either dominants or “recessives.” (PEARSON 11/1/22/40.11.1, 1904-01-11)

Chromosomes and Somatic Characters

Of course, the thing really wants more than this. It wants segregation of elements, but what I have not and cannot put into it is the view of each element as a "stirp." — Dominance of yellow seed-colour in a Pea is not merely prevalence of the effect, due to one set of elements, over that due to the other set in the hybrid: it is also an excitation of the ancestral yellow-seededness of the race of green peas used in making the cross. (PEARSON 11/1/22/40.11.1, 1904-01-11)

Here is the true gospel, or a sort of approximation to it, at last! When a stirp goes into a zygote, it carries a lot of properties, but those which are manifested by the body into which the zygote develops are transmitted with increased intensity to the gametes of that body, thus establishing that correlation between character of a parent and character of its reproductive cells, which I had foolishly been unable to put in.

But if a stirp, having become active in this way, be introduced into a zygote in which the majority of stirps are so active in other directions that its own properties become latent in the body to which the zygote gives rise, then that stirp transmits its properties in a weakened condition to the next generation. (PEARSON 11/1/22/40.11.1, 1904-01-12)

I think this is good enough, at last! But I want to get the segregation generations into the proper $1/4 + 1/2 + 1/4$. To do that, I must assume that the "valency" of a yellow stirp which has grown up in a hybrid body is $(n/2 - x)$ yellow $= (n/2 + x)$ green where n is the whole number of *stirps* in a somatic element, = 2× whole number in a germ cell, and x is the *probable error* of the series representing the zygotes. [...] You see, I can't even find the S. D. [standard deviation], and if I could, I could certainly not find the relation between it and the probable error! (PEARSON 11/1/22/40.11.1, 1904-01-12)

I have been writing up a long account of the 'stirp,' because I think it worth doing, in answer to Bateson's statement that the Law of Ancestral Heredity is incomplete, because it does not give a theory of the constitution of gametes. (PEARSON 11/1/22/40.11.2, 1904-04-17)

We shall see in a future chapter how far the suggestion made [by Galton] can be brought into harmony with the facts of germinal structure which have been discovered during the last thirty years. (PEARSON 5/2/10/4, ch. 2, p. 2, f67r)

The Moral

Weldon had hoped that unaided statistical considerations of the assortment of chromosomal elements would allow him to duplicate the Mendelian segregation patterns, *along with* the non-Mendelian patterns the biometricians saw in their data.

They couldn't.

That meant that Weldon was forced to find a way to unite Galton's conception of patent and latent, active and inactive chromosomal elements with his statistical reasoning.

He never did.

But! We still learn several important things about biometry:

For Weldon, at least, this is *why* he wanted more data on plants, mice, horses, snails, and on and on. These hypotheses are *hard to separate!*

And the crucial next step for Weldon, at his death, was to determine the *physiological, biological details* that supported Galton's view of heredity. This is *not* data collection for its own sake.

Lastly, and perhaps most importantly, Weldon's view of heredity unites several apparently incompatible ways of understanding inheritance. We need *all* of Galton's picture, Mendel's data, and contemporary cellular biology.

Questions?

charles@charlespence.net
http://charlespence.net
@pencechp

It seems clear that such forms of segregation as I have assumed (see Book MCMV) during nuclear division will not lead to a separation of zygotes into classes sufficiently sharp for Mendelian purposes, unless some persistence of effect from one mitosis to another be assumed. Therefore, consider the other extreme hypothesis [the individuality of the chromosomes]. (PEARSON 5/2/10/6, f17r)

$$\frac{\left(\underline{\lvert p}\,\right)^2}{\underline{\lvert 2p}}\left\{1+p^2+\left(\frac{p\cdot\overline{p-1}}{1\cdot 2}\right)^2+\left(\frac{p\cdot\overline{p-1}\cdot\overline{p-2}}{1\cdot 2\cdot 3}\right)^2+\cdots+\text{etc.}\right\}$$

$$=\frac{\binom{p}{x}\binom{p}{p-x}}{\binom{2p}{p}}=\frac{\binom{p}{x}^2}{\binom{2p}{p}}$$

Somatic Cell Composition	Outcomes	Rel. Frequency (/160,000)
$12R$	$(6R) + (6R)$	1
$11R + D$	$(6R) + (5R + D)$	36
$10R + 2D$	$(6R) + (4R + 2D)$	198
	$(5R + D) + (5R + D)$	324
	sum	522
$9R + 3D$	$(6R) + (3R + 3D)$	328
	$(5R + D) + (4R + 2D)$	3564
	sum	3892
$8R + 4D$	$(6R) + (2R + 4D)$	198
	$(5R + D) + (3R + 3D)$	5904
	$(4R + 2D) + (4R + 2D)$	9801
	sum	15903
$7R + 5D$	$(6R) + (R + 5D)$	36
	$(5R + D) + (2R + 4D)$	3564
	$(4R + 2D) + (3R + 3D)$	32472
	sum	36072
$6R + 6D$	$(6R) + (6D)$	2
	$(5R + D) + (R + 5D)$	648
	$(4R + 2D) + (2R + 4D)$	19602
	$(3R + 3D) + (3R + 3D)$	26896
	sum	47148
$5R + 7D$	$(5R + D) + (6D)$	36
	$(4R + 2D) + (R + 5D)$	3564
	$(3R + 3D) + (2R + 4D)$	32472
	sum	36072