Of Stirps and Chromosomes: Abstraction through Detail

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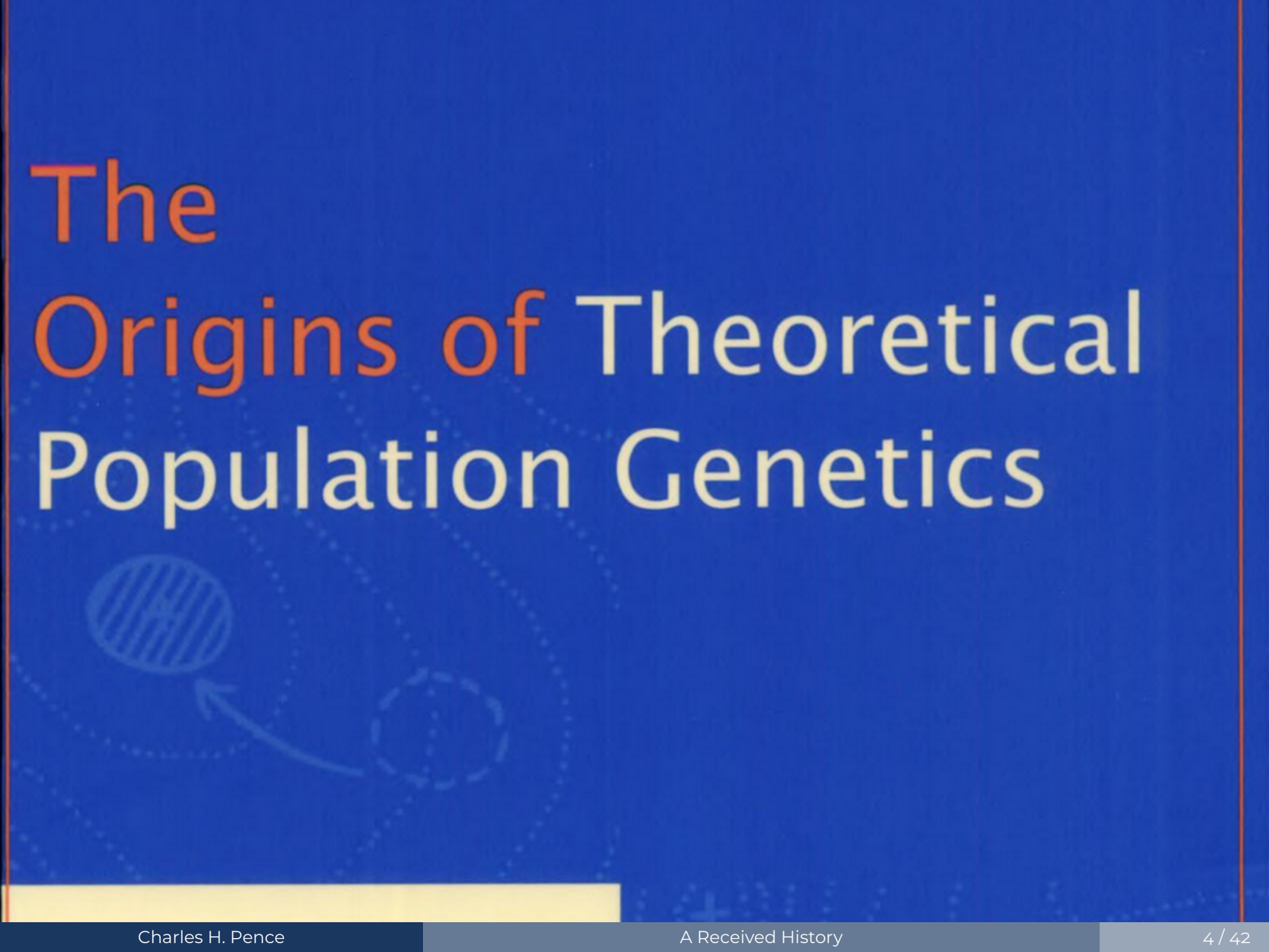
Outline

1. A Received History
2. Francis Galton on Stirps
3. W.F.R. Weldon on Chromosomes
4. From Detail to Abstraction

The take-home: The biometricians' work on the material basis of heredity is extensive, well-informed, and crucial to understanding their theoretical commitments.

A Received History

The Origins of Theoretical Population Genetics



Bateson “could have devastated Pearson’s theory” in 1900 using Mendelian insights about germ-cell composition, but himself failed to do so as a result of his skepticism about chromosome theory. (Provine 1971, p. 61)

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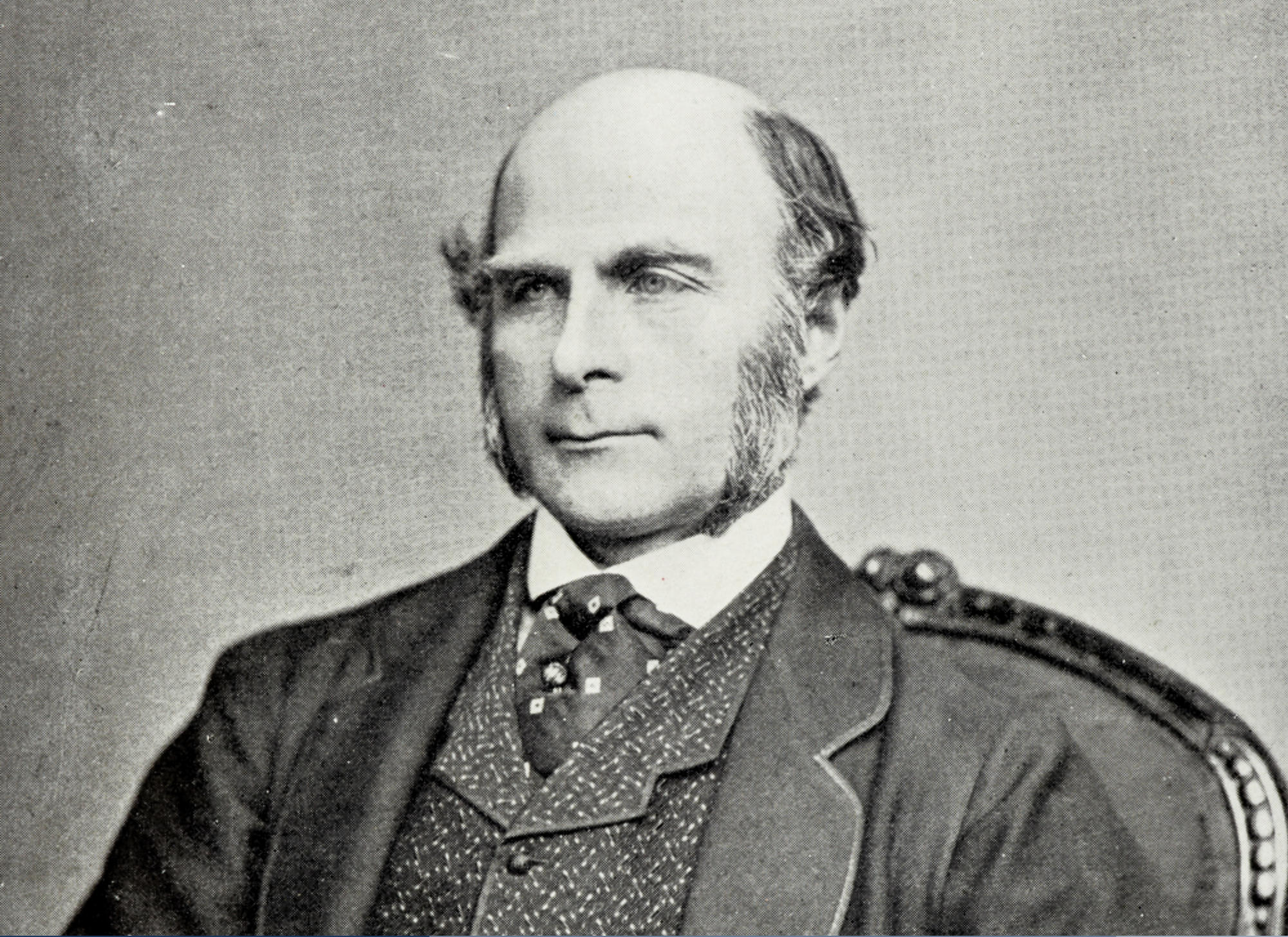
Rather, the biometricians were engaged in detailed work on the material basis of heredity, in dialogue with contemporary cellular biological work.

Galton on Stirps



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

[Pangenesis] gives a key that unlocks every one of the hitherto unopened barriers to our comprehension of its nature [heredity]; it binds within the compass of a singularly simple law, the multifarious forms of reproduction, witnessed in the wide range of organic life, and it brings all these forms of reproduction under the same conditions as govern the ordinary growth of each individual. (Galton 1869, p. 364)

- distinction between **patent** and **latent** elements
- ability to support **saltationism**
- explanation of **reversion**
- “appropriate for the **grasp of mathematical analysis**”

It becomes an interesting inquiry to **determine how much of a person's constitution is due, on average, to the unchanged gifts of a remote ancestry, and how much to the accumulation of individual variations.** The doctrine of Pangenesis gives excellent materials for mathematical formulæ, the constants of which might be supplied through averages of facts, like those contained in my tables, if they were prepared for the purpose. My own data are too lax to go upon; the averages ought to refer to some simple physical characteristic, unmistakeable in its quality, and not subject to the doubts which attend the appraisement of ability. (Galton 1869, p. 371)

[Elements must] **diverge from a common group and converge to a common contribution,** because they were both evolved out of elements contained in a structureless ovum, and they, jointly, contribute the elements which form the structureless ova of their offspring… (Galton 1872, p. 394)

I beg permission to use, in a special sense, the short word "stirp," derived from the Latin *stirpes*, a root, to express **the sum-total of the germs, gemmules, or whatever they may be called, which are to be found, according to every theory of organic units, in the newly fertilized ovum** – that is, in the earliest pre-embryonic stage – from which time it receives nothing further from its parents, not even from its mother, than mere nutriment. (Galton 1876, p. 330)

Since for each place there have been many unsuccessful but qualified competitors, it **must have been on some principle whose effects may be described as those of "*Class Representation*"** … avoiding any hypothesis or affirmation on points of detail, about most, if not all, of which we are profoundly ignorant. (Galton 1872, p. 395)

. . . it says nothing about the **number of electors,** their qualifications, or the motives by which they are influenced; it gives no information as to the **number of seats;** it does not tell us **how many candidates** there are usually for each seat, nor whether the same person is eligible for, or may represent at the same time, **more than one place,** nor whether the result of the elections at one place may or may not influence those at another (on the principle of correlation). (Galton 1872, p. 395)

The conditions under which each element in the sample became selected are, of course, unknown, but it is reasonable to expect they would fall under one or the other of the following agencies: first, self-selection, where **each element selects its most suitable neighbour,** as in the theory of pangenesis; secondly, general co-ordination, or the **influence exerted on each element by many or all of the remaining ones,** whether in its immediate neighbourhood or not...

...finally, a group of diverse agencies, alike only in the fact that they are **not uniformly helpful or harmful,** that they influence with no constant purpose – in philosophical language, that they are not teleological; in popular language, that they are **accidents or chances.** Their inclusion renders it impossible to predict the peculiarities of individual children, though it does not prevent the prediction of average results. (Galton 1885, p. 1213)

The **incalculable number of petty accidents** that concur to produce variability among brothers, make it impossible to predict the exact qualities of any individual from hereditary data. But we may predict average results with great certainty.… [This chapter's] intention has been to show the large part that is always played by chance in the course of hereditary transmission, and to establish the importance of **an intelligent use of the laws of chance and of the statistical methods that are based upon them,** in expressing the conditions under which heredity acts.

(Galton 1889, pp. 16–17)

Weldon on Chromosomes

The majority of writers consider, with you [Galton] and Weismann, that the assumption of a **sorting of determinants during development** makes an explanation of heredity easier; and so justify their assumption. But *first*, no one has attempted any mechanical explanation of ***how* a chromosome or determinant can "determine" the structure of a mass of protplasm** some thoudsands of times as big as itself; and *secondly* I want to tell you of some experiments which seem to me to upset the whole theory of the government of cells by any kind of substance. (Weldon to Galton, 1896-06-06, f. 4–5)

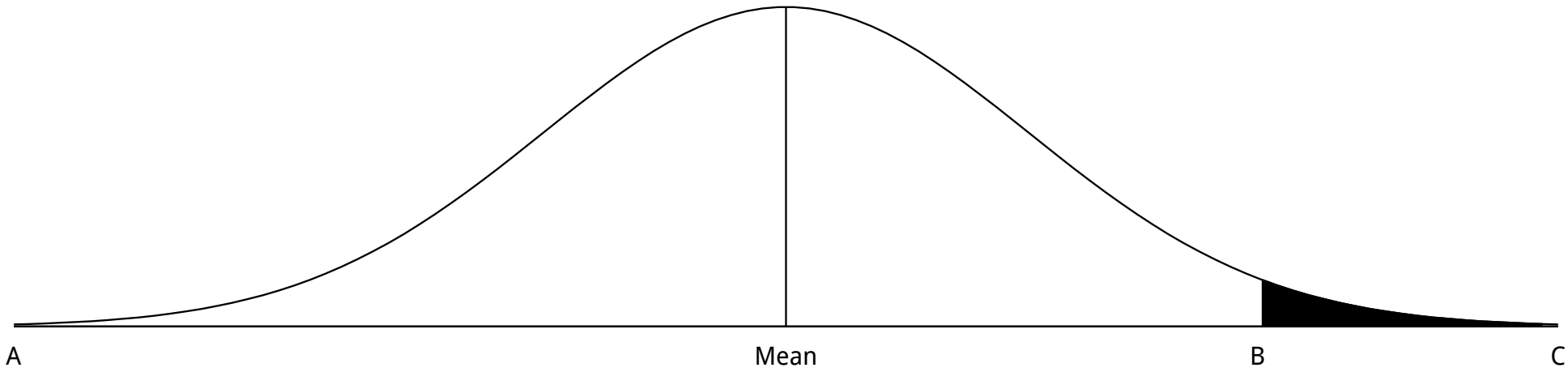
About pleasanter things, I have heard of and read a paper by one Mendel on the results of crossing peas, which I think you would like to read. It is in the Abhandlungen [*sic*] des Naturforschenden Vereines in *Brünn* for 1865 — I have the R.S. copy here, but I will send it to you if you want it. (Weldon to Pearson, 1900-10-16)

Our knowledge of *particulate* or mosaic inheritance, and of *alternative* inheritance, is however still rudimentary, and there is so much contradiction between the results obtained by different observers, that the evidence available is difficult to appreciate. (Weldon 1902, p. 228)

If I understand what you mean by gemmules, I certainly think they are necessary.

I think that 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 patchwork resulting in a particulate inheritance. (Weldon to Pearson, 1900-12-12)

What Bateson does, and what all Mendelians do, is to take the diagram of frequency and to call a range AB one "character," and the range BC another "character" of a Mendelian pair.


A
Mean
B
C

There must be a simple relation between AB, BC, and the [standard deviation] of the original system, which would make the chance that a grandchild falls within BC = $\frac{1}{4}$?
(Weldon to Pearson, 1902-06-23)

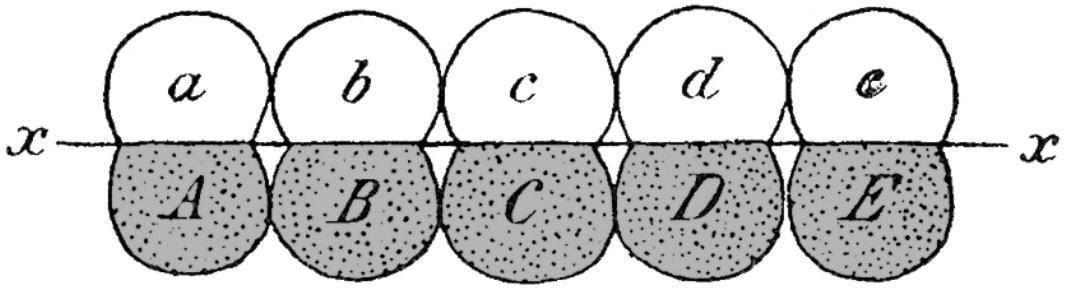


Fig. 1.

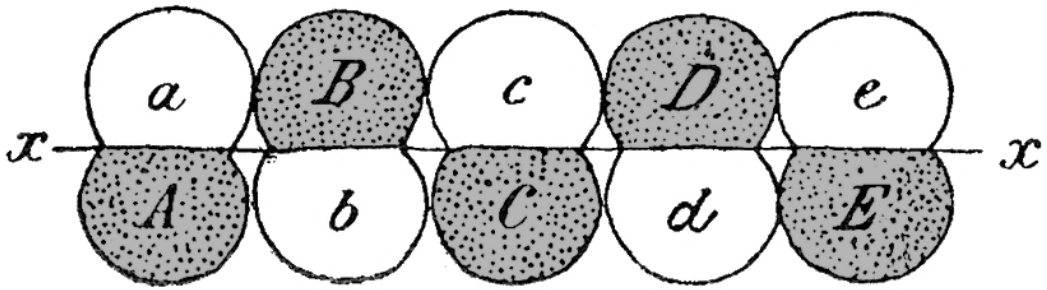


Fig. 2.

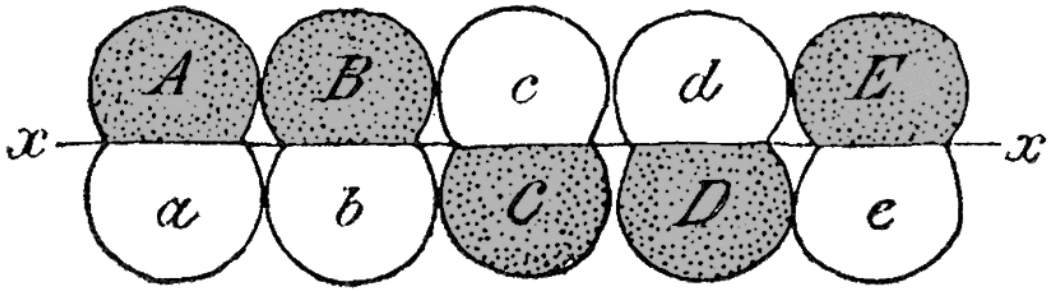


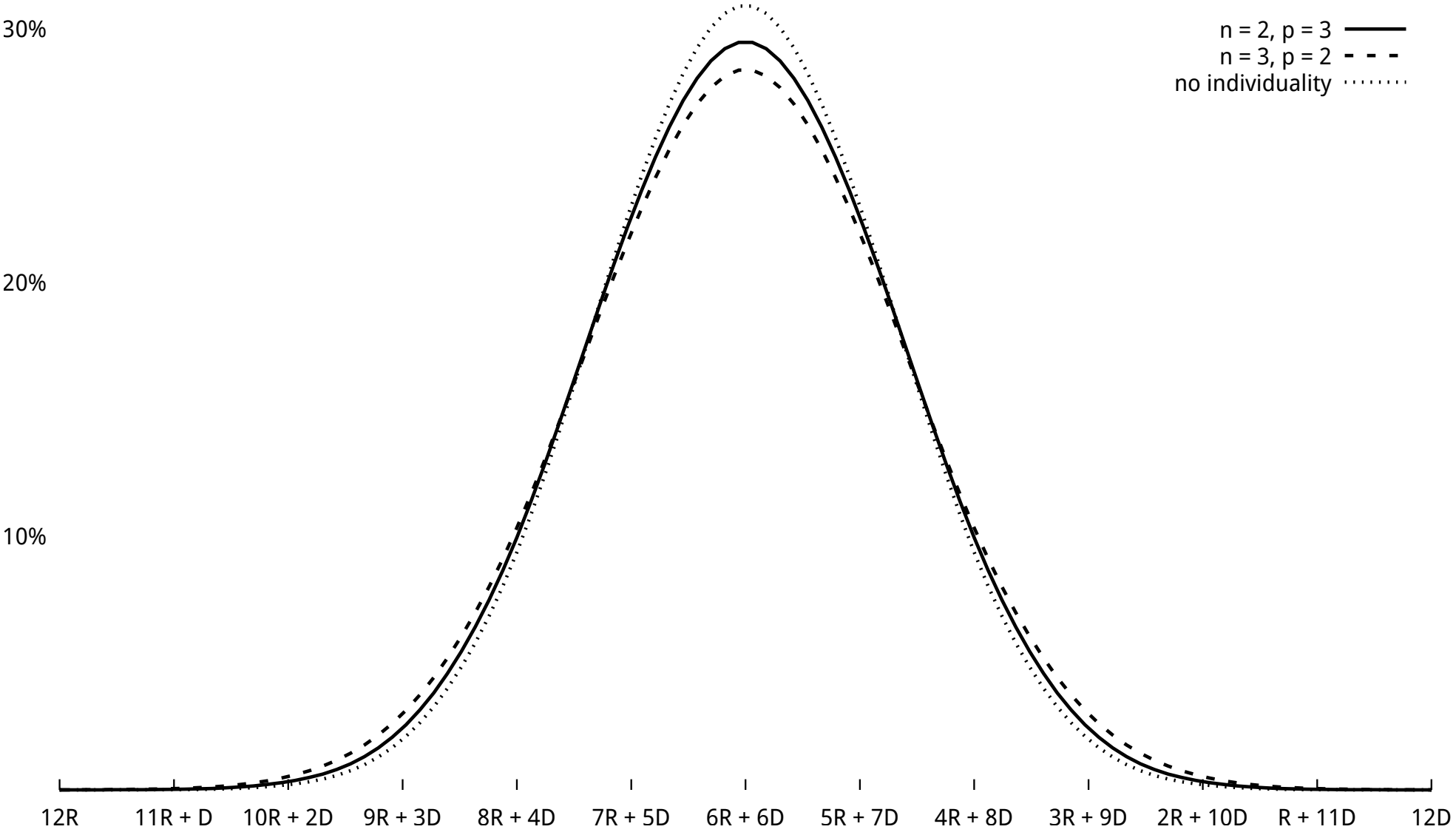
Fig. 3.

2. — The above facts do not invalidate [the] conception of nuclear elements as a series of *stirps*, in Galton's sense, each containing something capable of exciting the development of *any* of the somatic characters, according to its position in the organism.

3. — It seems necessary to regard a *stirp* as capable of exciting, not only somatic characters like those of its parents, but characters like those of its more remote ancestors, under certain circumstances.

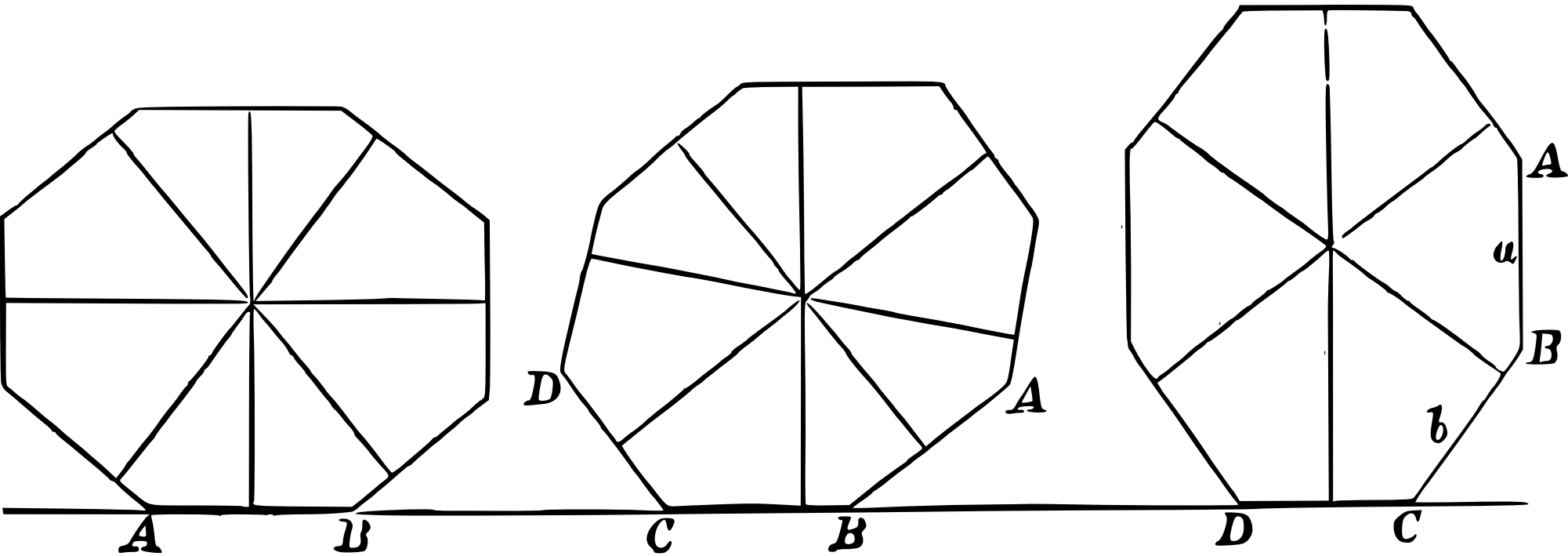
4. — It is evident, from the facts of growth and regeneration, that the characters of any one stirp which become active in any one generation are determined by the position of that stirp with reference to the rest – i.e., by a process of the same nature as Mendelian "dominance." (Weldon 1905)

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." (Weldon to Pearson, 1905-01-11)


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

From Detail to Abstraction

[A]lthough characteristics of plants and animals conform to the law, **the reason of their doing so is as yet totally unexplained.** The essence of the law is that differences should be wholly due to the collective actions of a host of independent *petty* influences in various combinations.… **Now the processes of heredity … are not petty influences, but very important ones.** (Galton 1877, p. 512)


A
B
D
C
C
B
D
A
A
a
B
b
D
C

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 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.**

If you apply this luminous principle to Peas, **you get Mendel pat.** (Weldon to Pearson, 1905-01-12)

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

Questions?

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The Pence Lab

This loosening enables a change of position of *A* with *a*, *B* with *b*, etc., independently in each pair from its neighbors and in its outcome dependent on chance. If we stick to our picture, we can assume that **the five pairs of elements are rotatable around the axis *xx* … each receiving an arbitrarily strong (variable) impulse, which sets it into rotation, independently of its neighbors.** Then, when calm has returned, 32 different positions will be possible, each of which has the same chances, i.e., will occur the same number of times [e.g., 'Fig. 2' and 'Fig. 3']. (Correns 1902, 304)