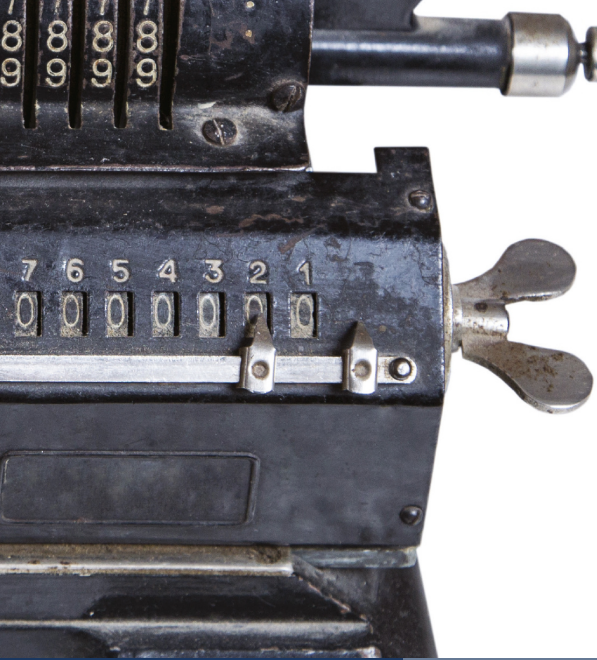

The Rise of Chance in Evolutionary Theory

A Pompous Parade of Arithmetic

IILP, Universitat de València, 25/5/2022

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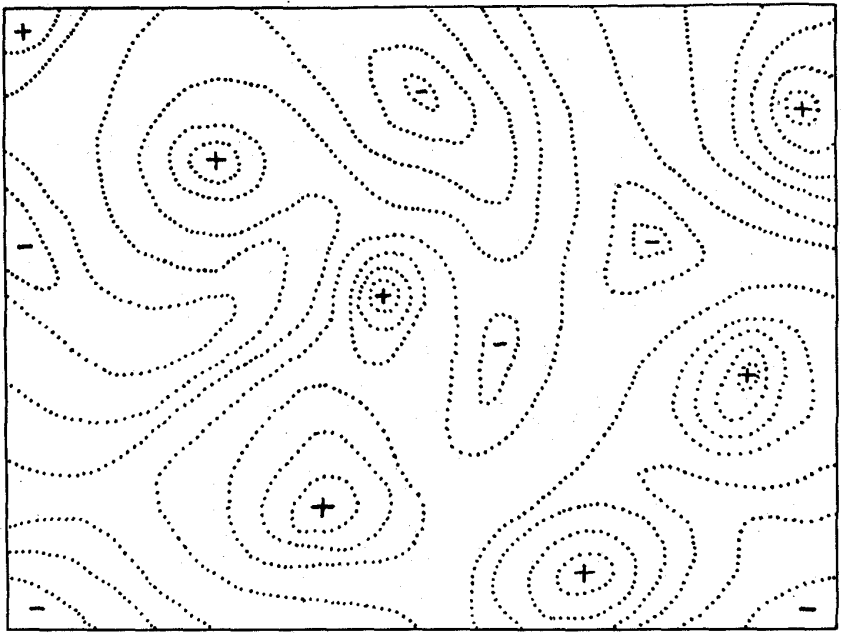
Institut supérieur de philosophie (ISP)

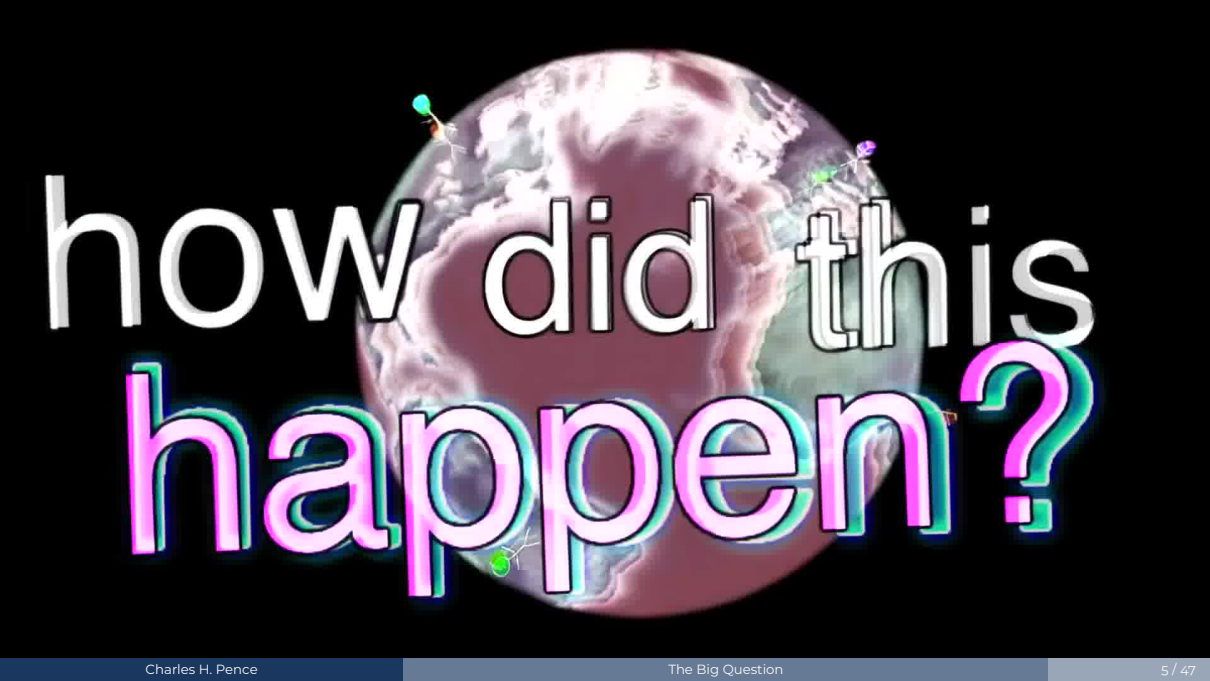
THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.



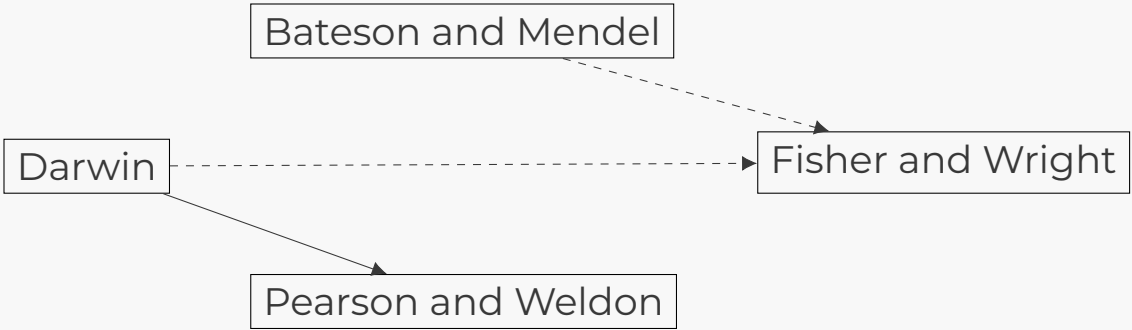

how did this
happen?

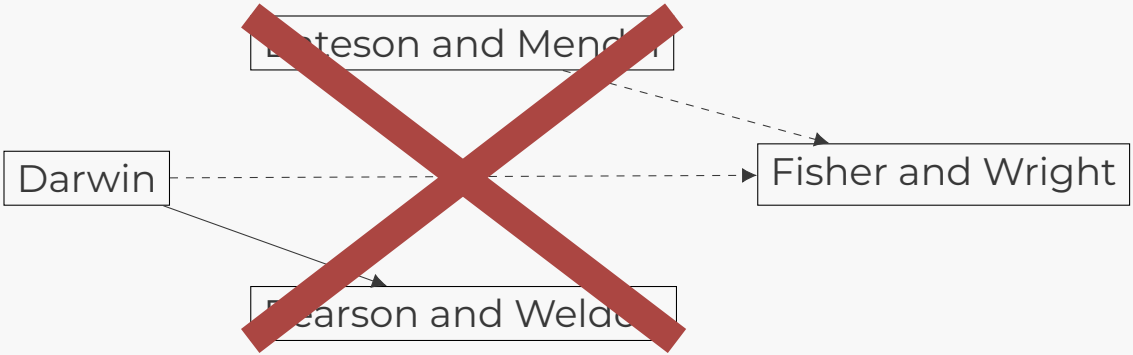
A shift to a **statistical** theory of evolution, which could let us understand the action of **natural selection** across generations, at the **population level,** which could be harmonized with **Mendelian transmission**

The Classic Story

William B. Provine

The Origins of Theoretical Population Genetics


Bateson and Mendel
Darwin
Fisher and Wright
Pearson and Weldon

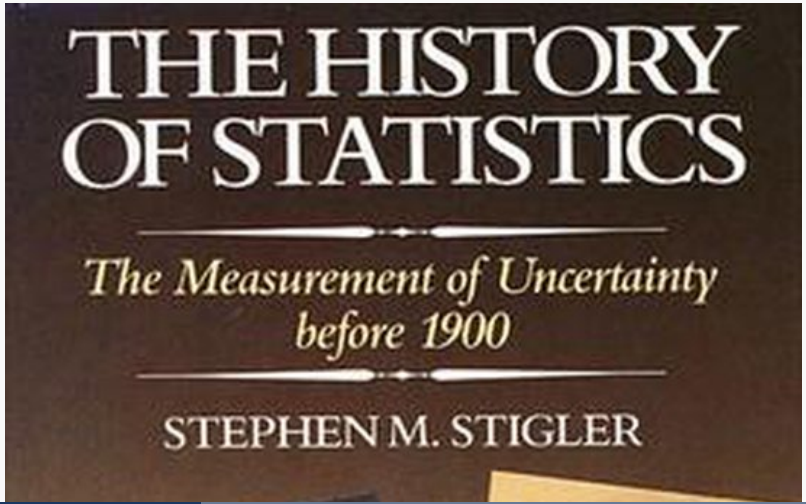

Darwin
Fisher and Wright

While G. Udny Yule followed “the approach of population genetics,” nonetheless “conflicts among his contemporaries prevented its development at this time.” (Provine)

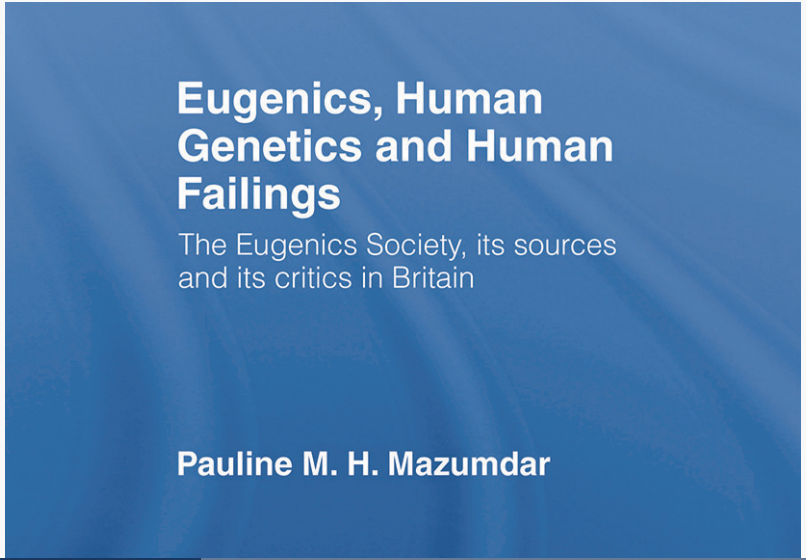
The “personal quarrel” between Bateson and Weldon “certainly delayed the utilization of the powerful methods of statistics in much of genetics.” (Sturtevant)

Two Caveats

First caveat: Not a history of statistical method or mathematical techniques.



Second caveat: Not a history of eugenics.

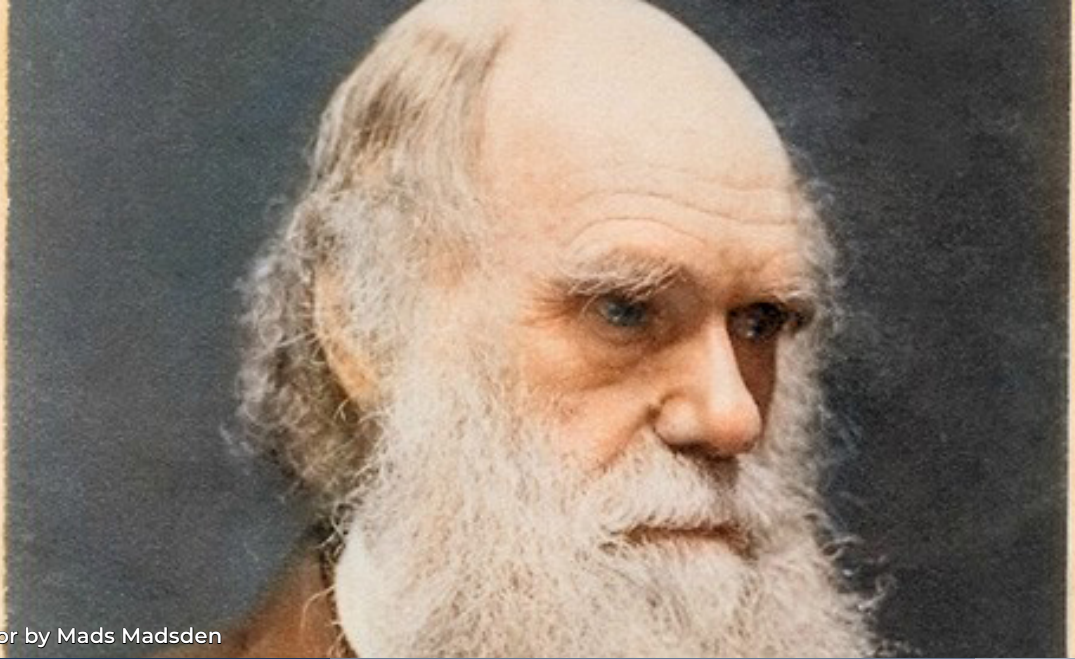


The Big Theses

The biologists involved in this shift – including, at least, Darwin, Galton, Weldon, Yule, and Fisher – were **self-conscious** about their relationship with probabilistic and statistical reasoning, and developed **surprisingly rich philosophies of science** to justify their work.

A story of **continuity** is better supported than one of **revolution,** at least with respect to these questions of chance and probability.

The Story in Outline



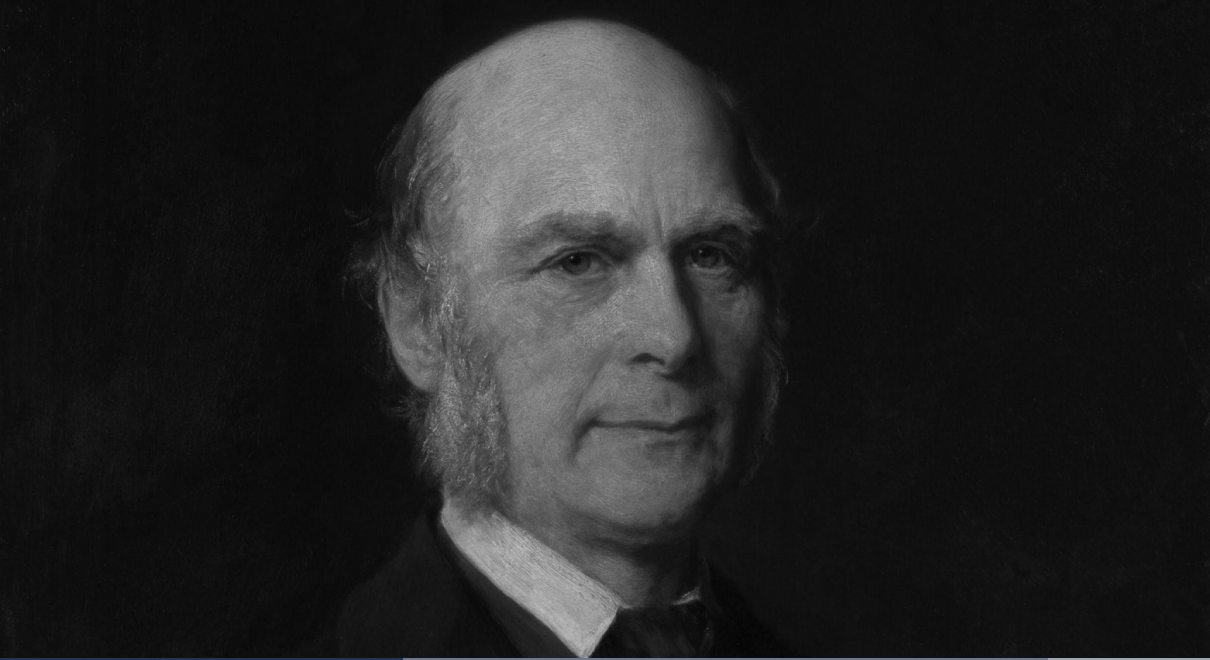
color by Mads Madsden

Darwin deploys a number of notions of “chance” (and friends):

- **accident** (as opposed to design)
- **the law of large numbers**
- natural selection’s action **as a tendency** rather than an exceptionless law
- our **ignorance of the precise causes** of variation

But they are always **contained** by the non-chancy action of natural selection's pursuit of adaptation.

The flowers of Orchids, in their strange and endless diversity of shape, may be compared with the great vertebrate class of Fish, or still more appropriately with tropical Homopterous insects, which **seem to us in our ignorance as if** modelled by the wildest caprice.
(Darwin, 1862, p. 285)



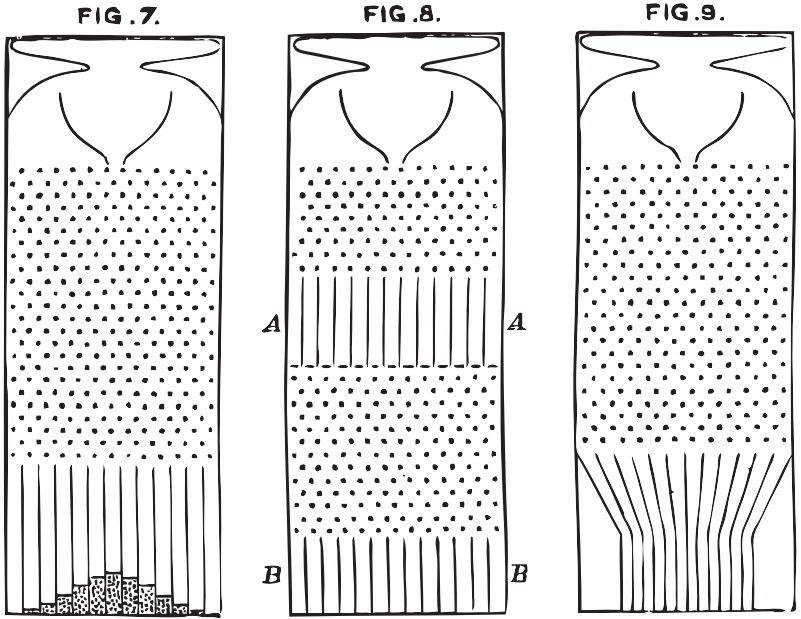
> The argumentation concerning this concept [natural ability] was, as frequently with Galton, very bad, but the concept was powerful if vague… (B. Norton, 1978, p. 43)

> He claimed that his law, which applied to unimportant characteristics like stature and colour, could not account for evolution. His argument is quite extraordinarily bad. (Swinburne, 1965, p. 28)

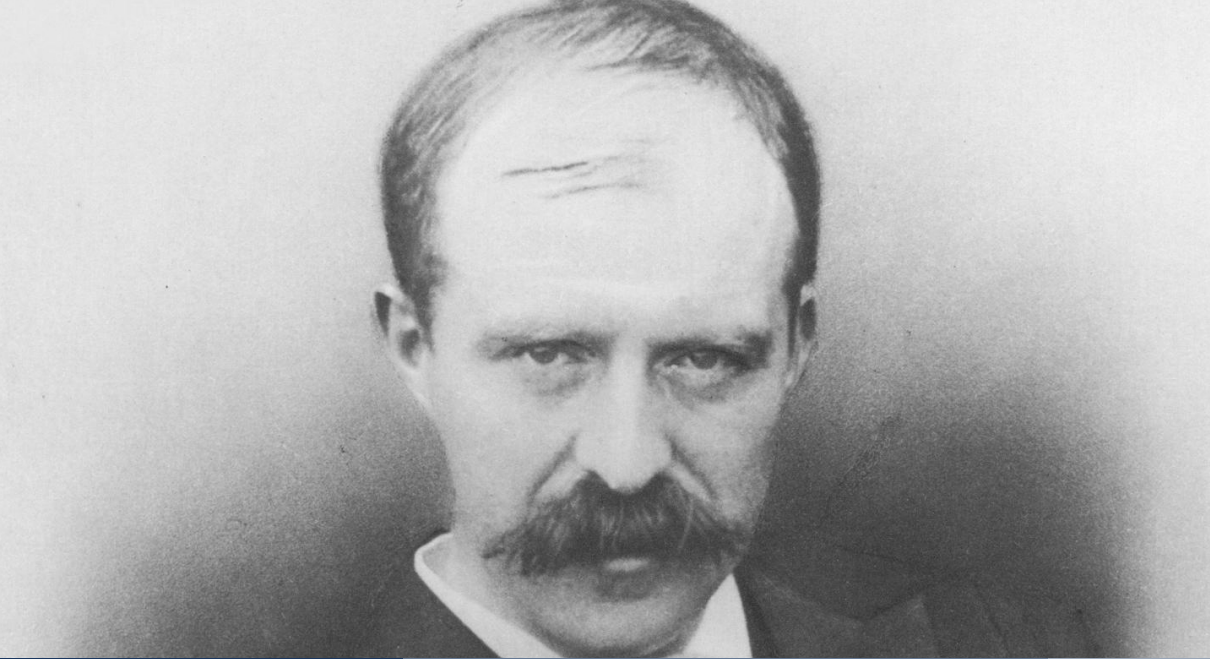
…no one who studied it on its appearance and had a receptive and sufficiently trained mathematical mind could deny its great suggestiveness, or be other than grateful for all the new ideas and possible problems which it provided. The methods of *Natural Inheritance* may be antiquated now, but in the history of science it will be ever memorable as marking a new epoch… (Pearson, 1930, pp. 57–58)

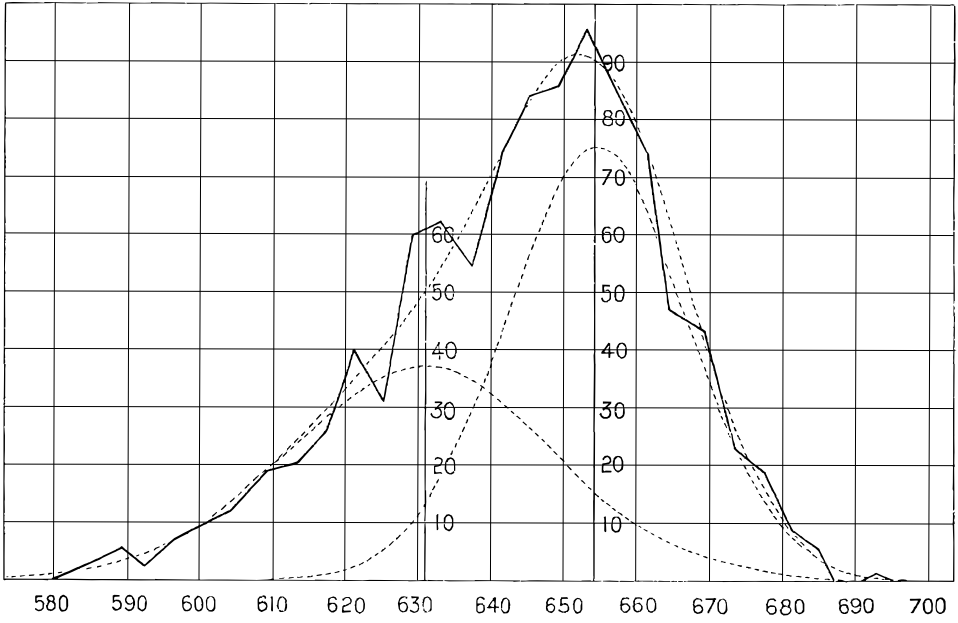
Galton's importance lies in his having pinpointed the **two open questions** in Darwin's theory that have to be filled in to create a statistical theory of evolution.

1. How is statistical evolution connected with the **transmission of characters** from parents to offspring?
2. How can we recover **evolutionary dynamics** from a theory of static normal distributions of characters?



Galton (1889)

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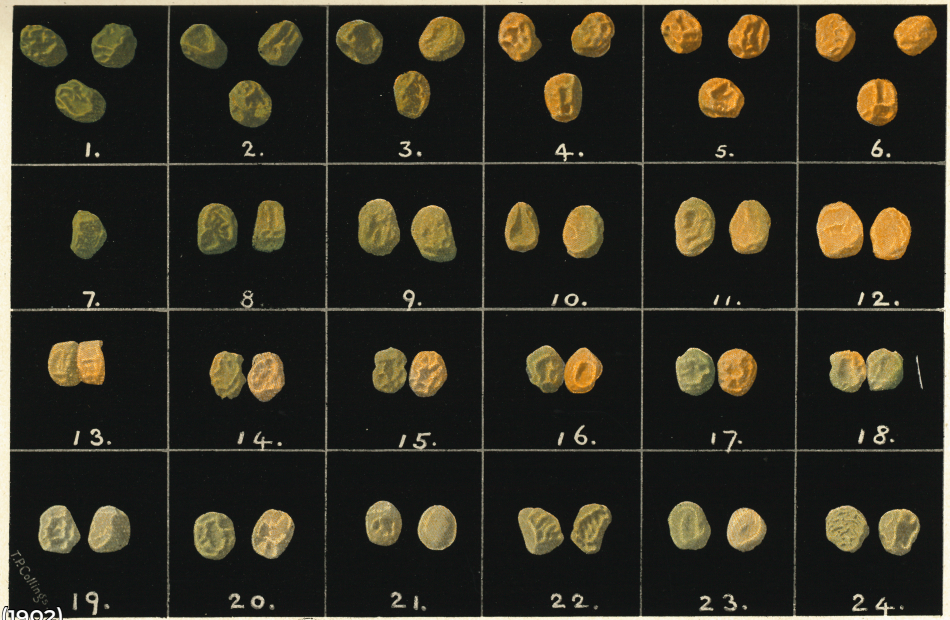
[Weldon's colleague] finds that in crabs of the same carapace length the frontal ratio is always from 1.5 to 2 units less in the 1895 stock than in the others: so that there is a possibility that the ♂ crabs are slowly diminishing their frontal breadth,—i.e., that their mean is being pushed in the direction indicated by the above hypothesis of selection. (Weldon, 1896)

> Plymouth Sound is everywhere, and especially near here, becoming yearly muddier, so that the number of dredgers necessary becomes yearly greater, the fauna yearly more scanty… (Weldon, 1896)


Crab!



Weldon (1902)

Good old Galton's stirp, in which some of the ancestral characters are latent, is still the only "machine" which will work: and the proper line of research is an enquiry into those embryonic stimuli which make a given character evident or latent. That is my fixed belief. (Weldon, 1904)

It seems possible on this assumption to [develop] a theory of nuclear division, which may give Mendel's results without eliminating ancestral influence—i.e., without a theory of "pure" gametes. Such a theory would start **by taking "chromomeres" as units.** (Weldon, 1905)

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

A shift to a **statistical** theory of evolution, which could let us understand the action of **natural selection** across generations, at the **population level,** which could be harmonized with **Mendelian transmission**

Three stories of intellectual continuity:

1. Well-known works that advance **parts of this program** without advancing the whole thing
2. George Udny Yule (1902)
3. The **textbooks of evolution** from this period

don't have time to cover the first two points here…

RECENT PROGRESS IN THE STUDY OF VARIATION, HEREDITY, AND EVOLUTION

By ROBERT HEATH LOCK, M.A.
FELLOW OF GONVILLE AND CAIUS COLLEGE, CAMBRIDGE

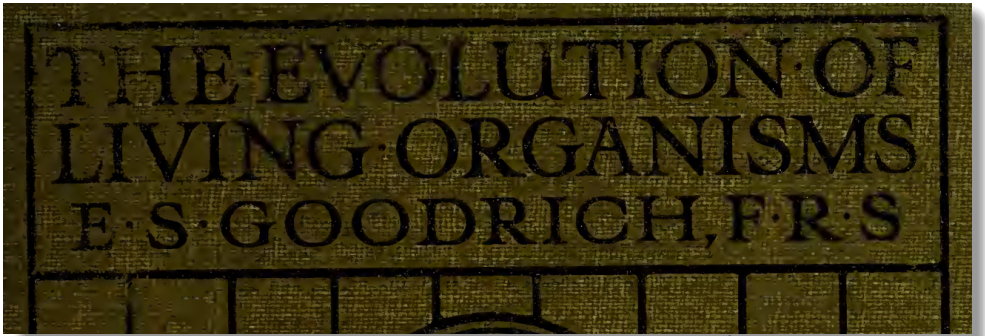
HEREDITY

By J. ARTHUR THOMSON, M.A.

Regius Professor of Natural History in the University of Aberdeen

AUTHOR OF "THE STUDY OF ANIMAL LIFE," "THE SCIENCE OF LIFE," "OUTLINES OF ZOOLOGY," "THE PROGRESS OF SCIENCE," "HERBERT SPENCER," ETC.; JOINT-AUTHOR OF "THE EVOLUTION OF SEX"

HEREDITY


THE EVOLUTION OF
LIVING ORGANISMS
E. S. GOODRICH, F.R.S
JOINT-AUTHOR OF "THE EVOLUTION OF SEX"

What's There?

- Careful, reasonable presentations of **both biometry and Mendelism**
- **No indication** of a hefty conflict between them
- A **genuine desire** to unify biology, along broadly the lines we've already seen

A complex (and perhaps unstable?) mixture of:

- eugenics
- Anglican Christianity
- indeterministic causation
- refined statistical method, including the distinction between *statistics* taken on *samples* and the *parameters* of *hypothetical populations* that they are intended to estimate

Fisher is trained in **this very textbook tradition,**
and he extensively reads **the biometrical literature**

THE GENETICAL THEORY OF NATURAL SELECTION

BY

R. A. FISHER, Sc.D., F.R.S.

rich philosophies of science

continuity over revolution

Questions?

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Darwin: Accident vs. Design

> The shape of the fragments of stone at the base of our precipice may be called accidental, but this is not strictly correct; for the shape of each depends on a long sequence of events, all obeying natural laws; on the nature of the rock, on the lines of deposition or cleavage, on the form of the mountain, which depends on its upheaval and subsequent denudation, and lastly on the storm or earthquake which throws down the fragments. But in regard to the use to which the fragments may be put, their shape may strictly be said to be accidental. (Darwin, 1875, p. 2:427)

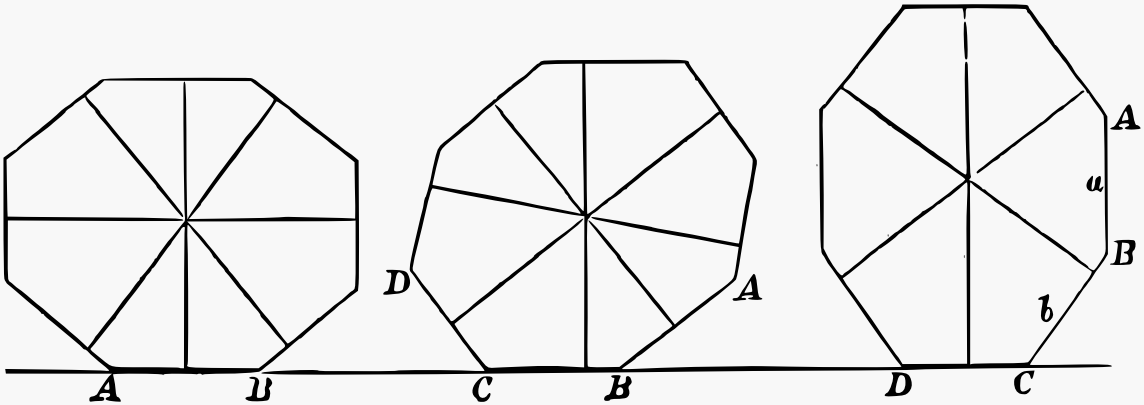
Darwin: Ignorance of Causes

> I have hitherto sometimes spoken as if the variations – so common and so multiform in organic beings under domestication, and in a lesser degree in those in a state of nature – had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation. (Darwin, 1859, p. 131)

Galton: Particulate Inheritance

> It would seem that while the embryo is developing itself, the particles more or less qualified for each new post wait as it were in competition, to obtain it. Also that the particle that succeeds, must owe its success partly to accident of position and partly to being better qualified than any equally well placed competitor to gain a lodgement. (Galton, 1889, p. 9)

Galton: Natural Selection



Weldon: Early Statistics

It cannot be too strongly urged that the problem of animal evolution is essentially a statistical problem: that before we can properly estimate the changes at present going on in a race or species we must know accurately (a) the percentage of animals which exhibit a given amount of abnormality with regard to a particular character; (b) the degree of abnormality of other organs which accompanies a given abnormality of one; (c) the difference between the death rate per cent. in animals of different degrees of abnormality with respect to any organ; (d) the abnormality of offspring in terms of the abnormality of parents, and *vice versâ*. (Weldon, 1893, p. 329)

Weldon: Early Selection

> For by purely statistical methods, without making any assumption as to the functional importance of the frontal breath, the time of life at which natural selection must be assumed to act, if it acts at all, has been determined, and the selective death-rate has been exhibited as a function of the abnormality… (Weldon, 1895a, p. 371)

Weldon: Shift

> The whole difficulty of the theory of Natural Selection is a quantitative difficulty. It is a difficulty of believing that in any given case a small deviation from the mean character will be sufficiently useful or sufficiently harmful to matter. [...] For numerical knowledge of this kind is the only ultimate test of the theory of Natural Selection, or of any other theory of any natural process whatever. (Weldon, 1898, p. 902)

Piecemeal Advances

- Statistical methods without a statistical theory of inheritance (merely for data analysis): William Castle (MacCurdy and Castle, 1907); Wilhelm Johannsen (1909)
- Mathematical inheritance without statistical methods (recurrence equations): Herbert Spencer Jennings (1912–6), Robbins (1917–8), Howard C. Warren (1917)
- Estimations of the speed of selection: Harry Norton and R.C. Punnett (1915)
- Statistical inheritance without natural selection: Herman Nilsson-Ehle (1908), Edward Murray East (1910–3)

Yule on Mendelism

> The value of the work of Mendel and his successors lies not in discovering a phenomenon inconsistent with that law [of ancestral heredity], but in shewing that a process, consistent with it, though neither suggested nor postulated by it, might actually occur. (Yule, 1902, p. 227)

Yule on Biometry

> What is required from a physical theory of heredity is that it should assign a meaning to the variations in the constants that do occur, enabling one, given the law of ancestral heredity for an organ, to state the relative influences thereon of the different agencies concerned—selection, in all forms, circumstance, and so forth. (Yule, 1902, p. 237)

Fisher: Causal Processes

> Generalized description should, however, never be regarded as an aim in itself. It is at best a means towards apprehending the causal processes which have given rise to the phenomena observed. Beyond a certain point it can only be pursued at the cost of omitting or ignoring real discrepancies of detail, which, if the causes were understood, might be details of great consequence. (Fisher, 1930, p. 178)

Fisher: Indeterminism

> [Indeterminism] does not in the least imply an anarchy of causelessness…natural law is none the less real if, when precisely stated, it turns out to be a statement of probability: causation is none the less recognizable, and an action is just as much an effective cause of subsequent events, if it influences their respective probabilities, as if it predetermines some one of them to the exclusion of the others. (Fisher, 1934, pp. 105–106)

Contra Gayon

- Too centered on the "eclipse of Darwinism" framework – following Largent, it's really not clear that there *was* an eclipse
- For my purposes, too centered on the concept of *heredity* – I simply have a different focus
- A bit Whiggish in looking for the history of "Darwinism" – of a kind that I'm not sure is recognizable to the historical authors

Contra Depew & Weber

- Too committed to the “biometry-Mendelism debate” frame, and the distinction between continuous variation and saltationism
- Too much emphasis on the novelty of Fisher and his contributions arising from the perspective of statistical physics