



## 2 Evolution & natural selection

# Natural Selection

Can it, then, be thought improbable . . . that . . . **variations useful** in some way to each being in the great and complex battle of life, should sometimes occur **in the course of thousands of generations**? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any **advantage**, however slight, over others, would have **the best chance of surviving and of procreating their kind**? On the other hand, we may feel sure that any variation in the least degree **injurious** would be rigidly **destroyed**.

**This preservation of favorable variations and the rejection of injurious variations, I call Natural Selection.**

(1859, 80–81)

# Natural Selection

LETTER 79. TO ASA GRAY. Down, November 29th [1859].

What you hint at generally is very, very true: that my work will be **grievously hypothetical**, and large parts **by no means worthy** of being called **induction**, my commonest error being probably induction **from too few facts**.

I had not thought of your objection of my using the term "**natural selection**" as an agent. I use it much as a geologist does the word denudation—for an agent, expressing the result of several combined actions.

# Natural Selection

LETTER 79. TO ASA GRAY. Down, November 29th [1859].

I will take care to explain, not merely by inference, what I mean by the term; for I must use it, otherwise I should incessantly have to expand it into some such (here miserably expressed) formula as the following:

“The **tendency to the preservation** (owing to the severe **struggle for life** to which all organic beings at some time or generation are exposed) of any, the slightest, **variation** in any part, which is of the **slightest use or favourable** to the life of the individual which has thus varied; together with the **tendency to its inheritance.**” Any variation, which was of **no use** whatever to the individual, would **not be preserved** by this process of “**natural selection.**”

...I will only add one other sentence: several varieties of sheep have been turned out together on the Cumberland mountains, and one particular breed is found to succeed so much better than all the others that it fairly starves the others to death. **I should here say that natural selection picks out this breed, and would tend to improve it, or aboriginally to have formed it...**

## Origin:

But the **chief cause** of our **natural unwillingness** to admit that one species has given birth to other and distinct species, is that **we are always slow in admitting any great change of which we do not see the intermediate steps.**

The difficulty is the same as that felt by so many **geologists**, when **Lyell** first insisted that long lines of inland cliffs had been formed, and great valleys excavated, by the slow action of the coast-waves. **The mind cannot possibly grasp the full meaning of the term of a hundred million years; it cannot add up and perceive the full effects of many slight variations, accumulated during an almost infinite number of generations.**

Although I am fully convinced of the truth of the views given in this volume under the form of an abstract, **I by no means expect to convince experienced naturalists whose minds are stocked with a multitude of facts all viewed, during a long course of years, from a point of view directly opposite to mine.** ... Any one whose disposition leads him to **attach more weight to unexplained difficulties than to the explanation of a certain number of facts** will certainly **reject** my theory. A few naturalists, **endowed with much flexibility of mind**, and who **have already begun to doubt on the immutability of species**, may be **influenced** by this volume; but I look with confidence to the future, to young and rising naturalists, who will be able to view both sides of the question with **impartiality**.

# Darwin on Struggle for Existence (Origin)

I SHOULD premise that I use this term in a **large and metaphorical sense** including dependence of one being on another, and including (which is more important) not only the life of the individual, but **success in leaving progeny.**

Two canine animals, in a time of dearth may be truly said to struggle with each other which shall get food and live. **But a plant on the edge of a desert is said to struggle for life against the drought,** though more properly it should be said to be dependent on the moisture. **A plant which annually produces a thousand seeds, of which only one of an average comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground.**

# Darwin on Struggle for Existence (Origin)

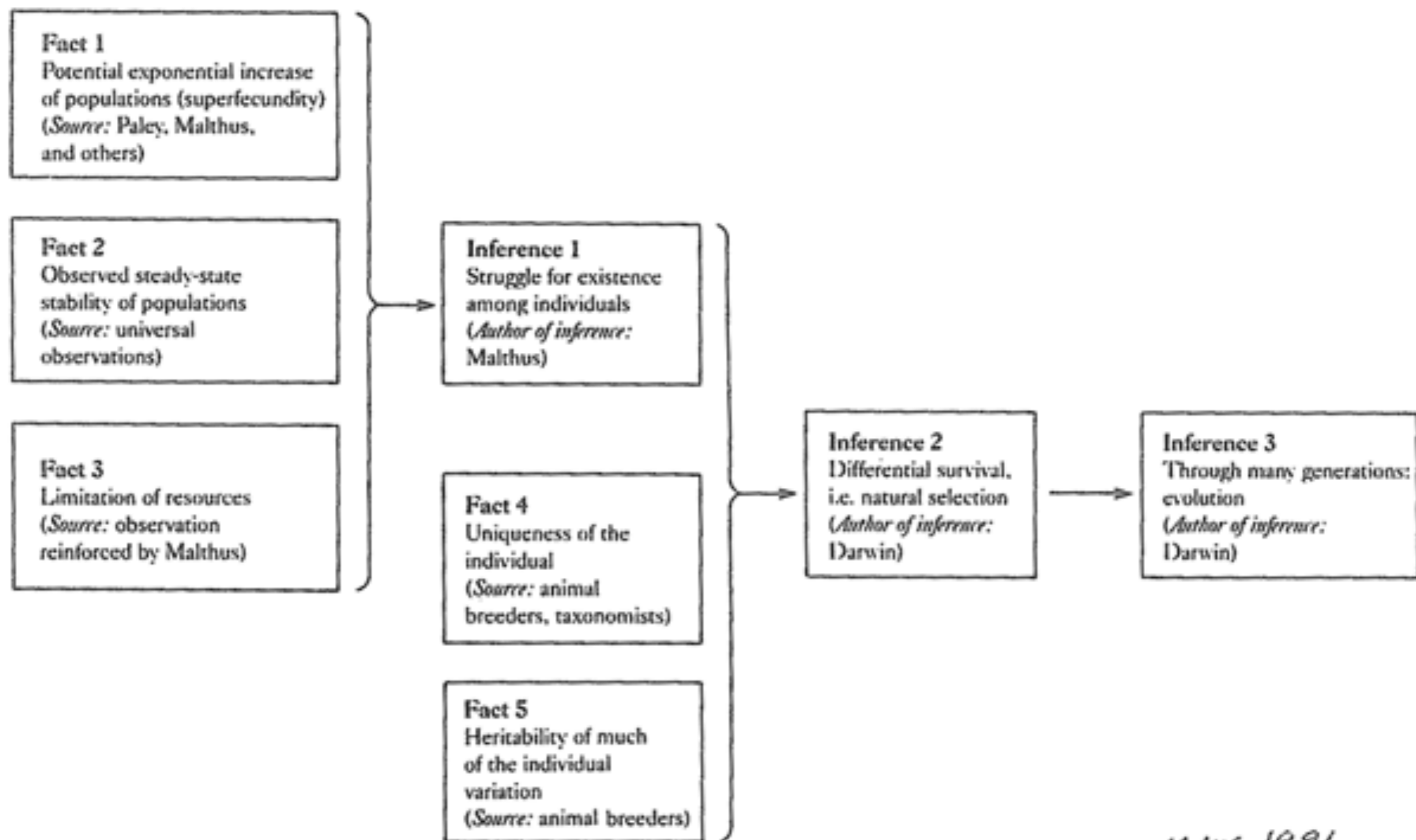
The mistletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said **to struggle with these trees**, for, if too many of these parasites grow on the same tree, it languishes and dies. But several seedling mistletoes, growing close together on the same branch, may more truly be said to **struggle with each other**. As the mistletoe is disseminated by birds, its existence depends on them; and it may methodically be said to **struggle with other fruit-bearing plants**, in tempting the birds to devour and thus disseminate its seeds. In these several senses, which pass into each other, I use for convenience' sake the general term of Struggle for Existence.





FIGURE 1

Darwin's Explanatory Model of Evolution through Natural Selection



Mayr, 1991

# Natural Selection

1. **natural vs artificial** selection -> NS does not have a **mind**  
(‘the survival of the fittest’ -> Origin, 5th ed)
2. evolution of populations through NS depends on **contingent features of the environment**
  - > difference with **Lamarck**
  - > not an **intrinsic** disposition towards **complexity**
  - > due to the **initial conditions**, complexity is expected to **increase**
3. NS acts on **random** variation





**The Archangel**



**French Mondain**



**Jacobin**



**English Pouter**



**German Modena**



**Helmet Crested**



**Mookie**



**Saxon Fairy Swallow**



**Saxon Blue Spangle**



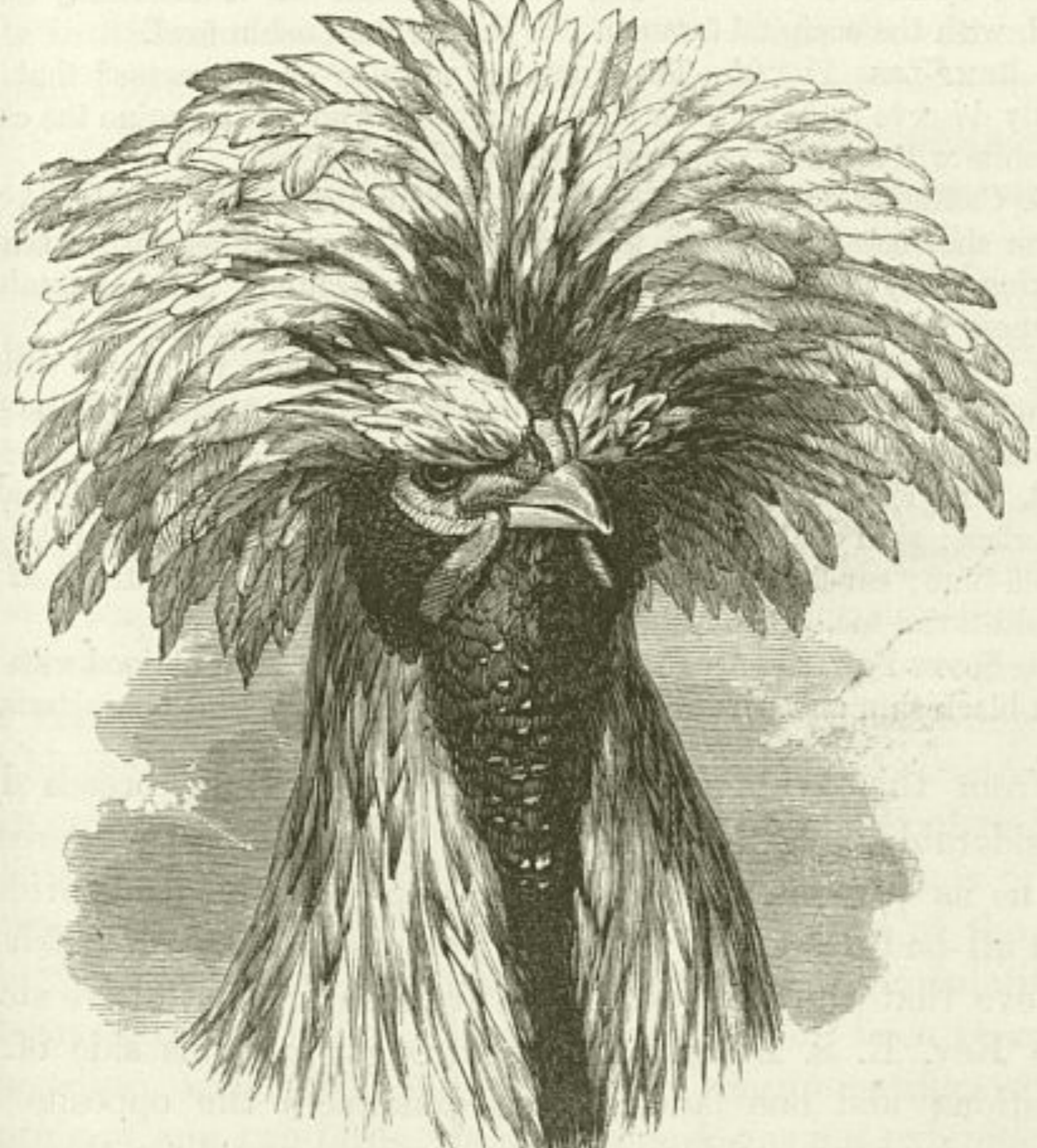
**South German Whitetail**

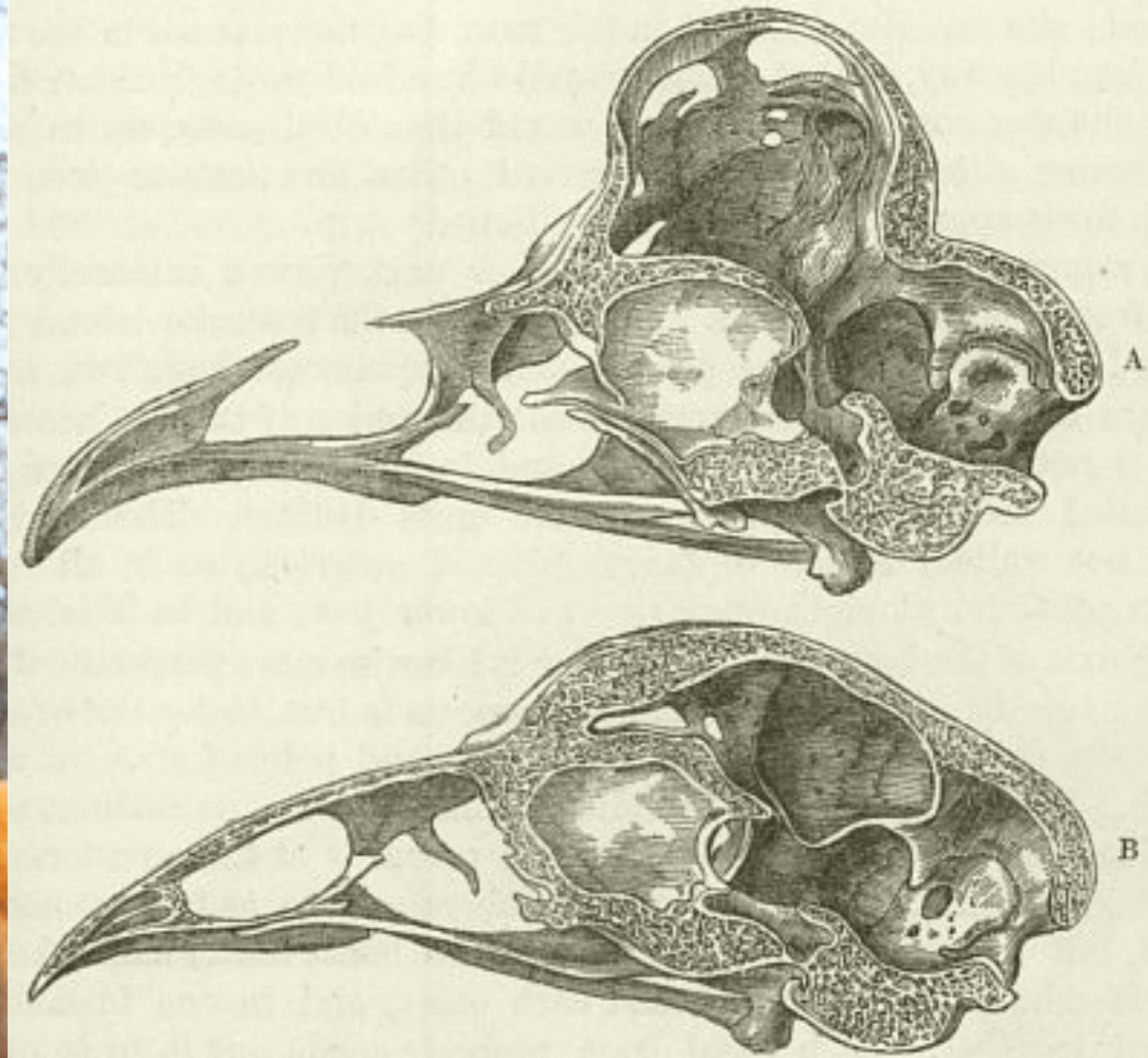


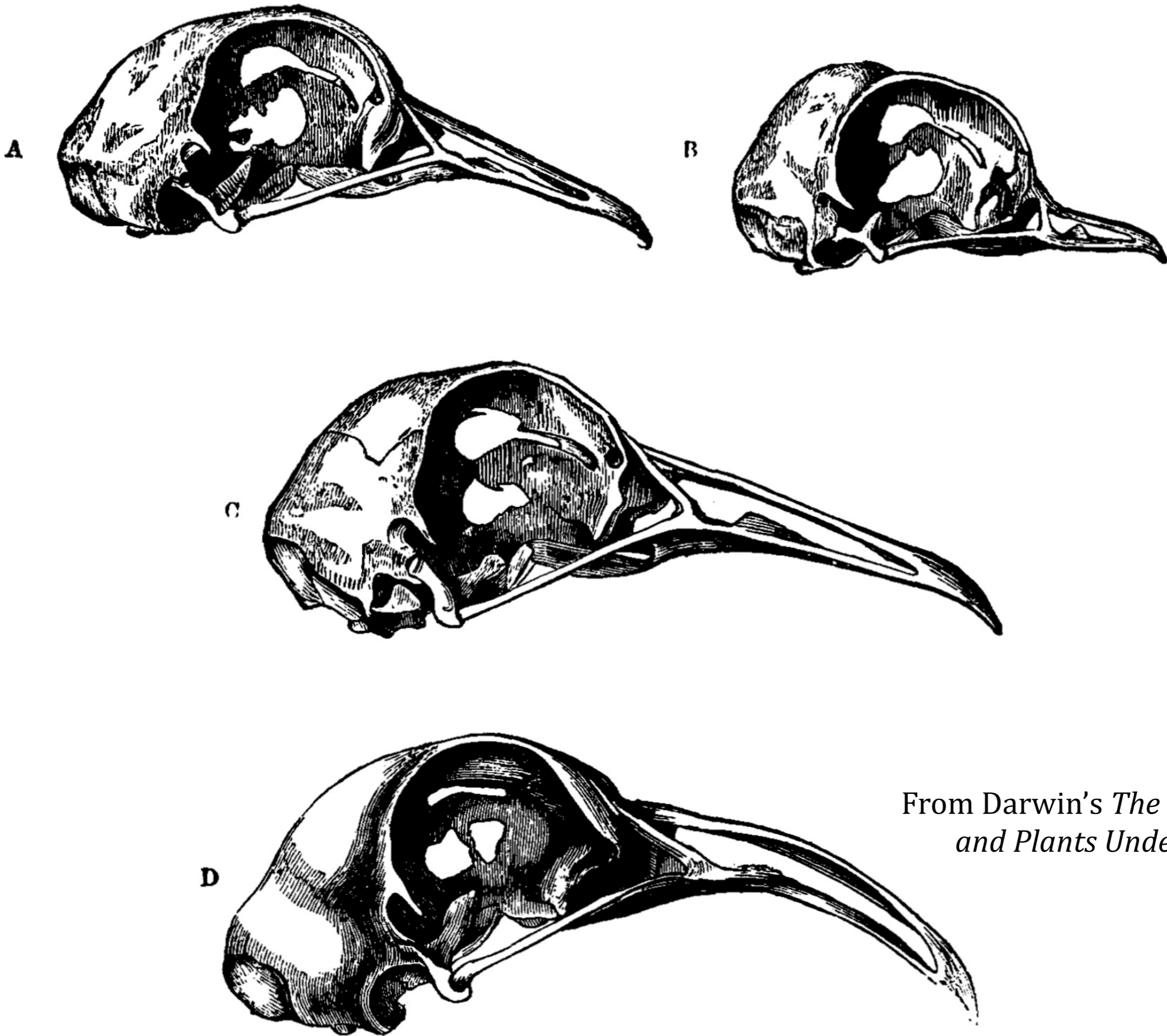
**Scandaroon**



**West of England Tumbler**

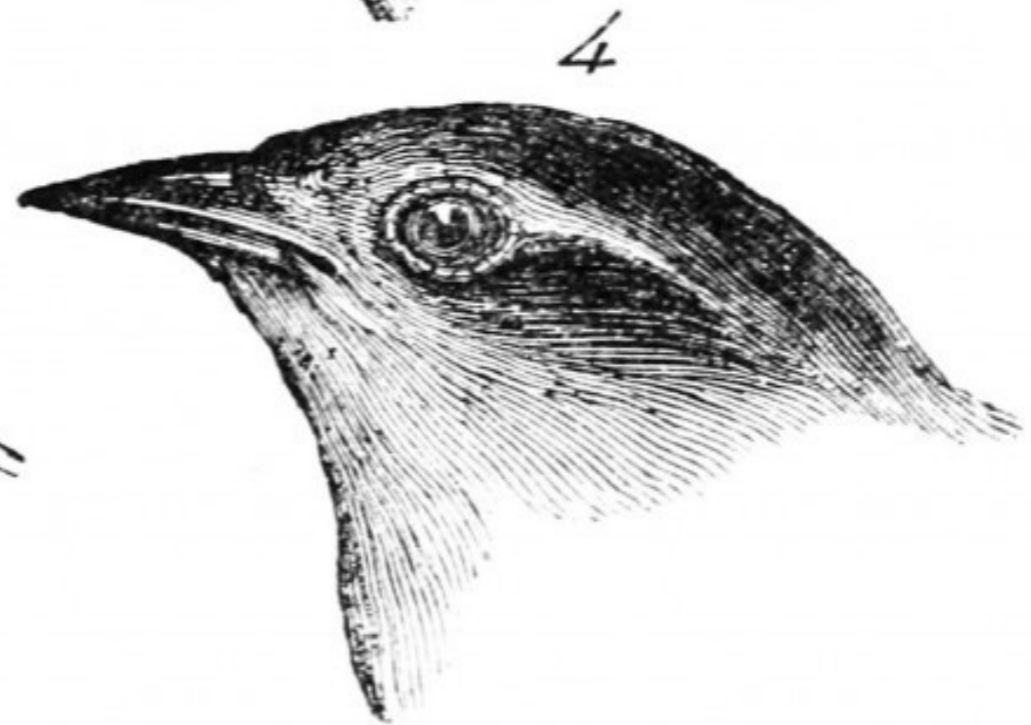
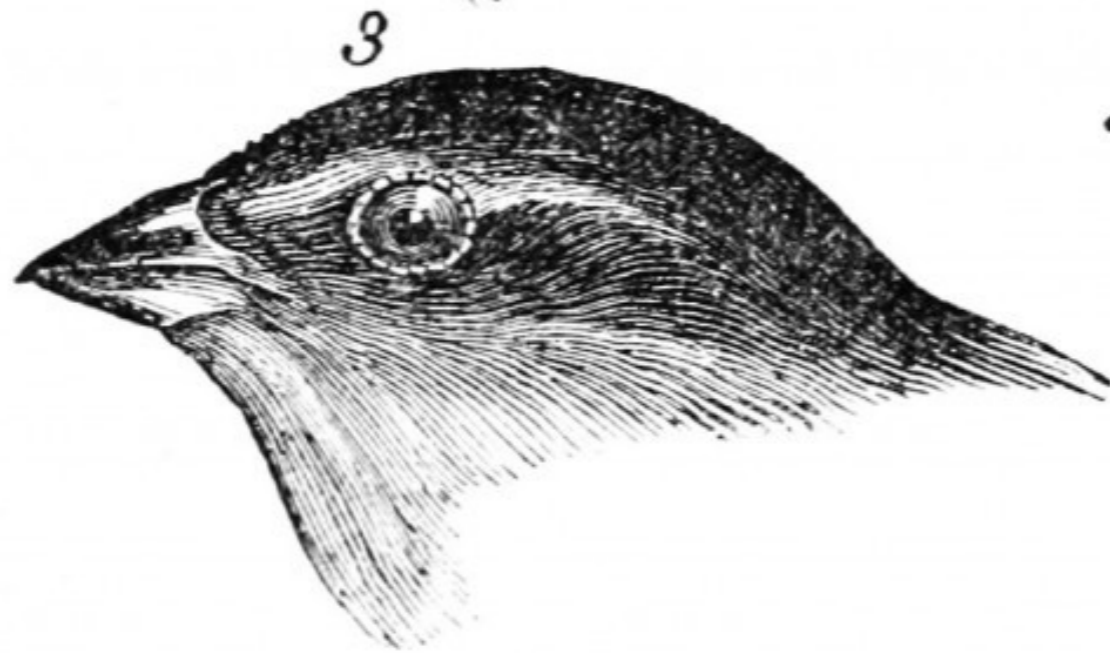
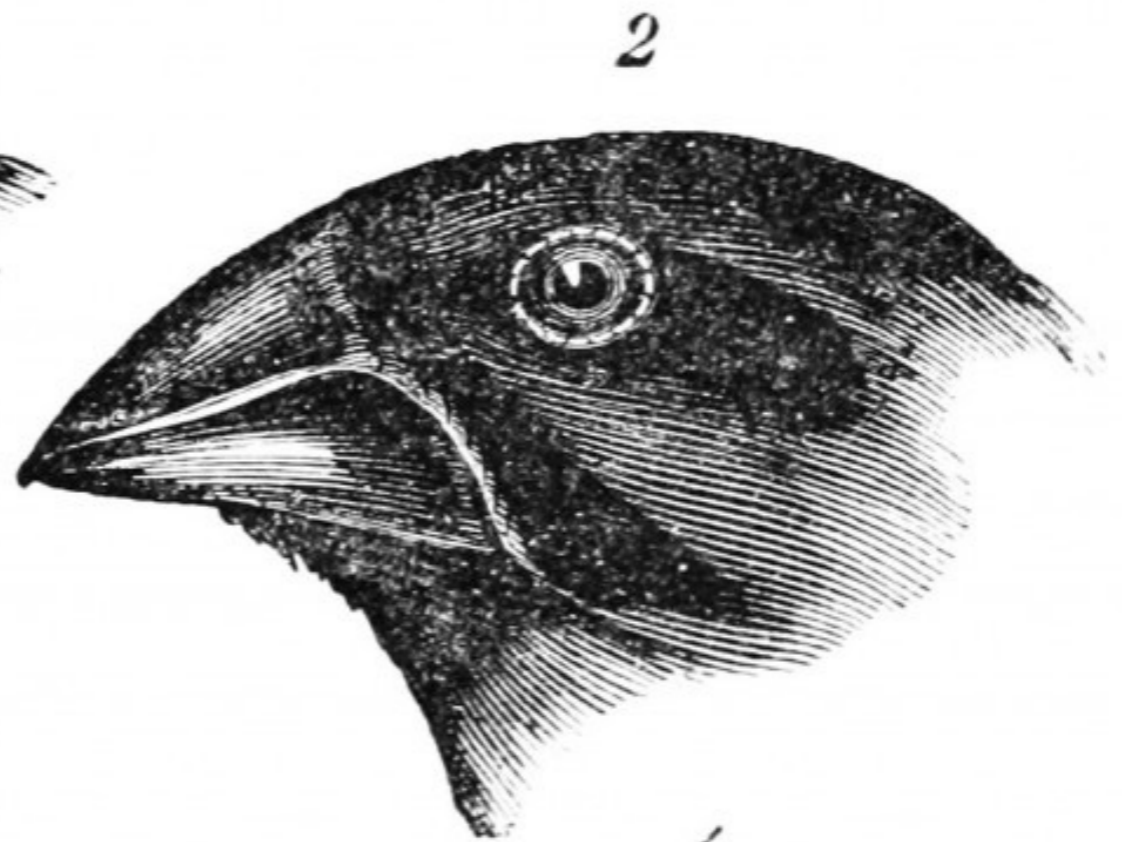
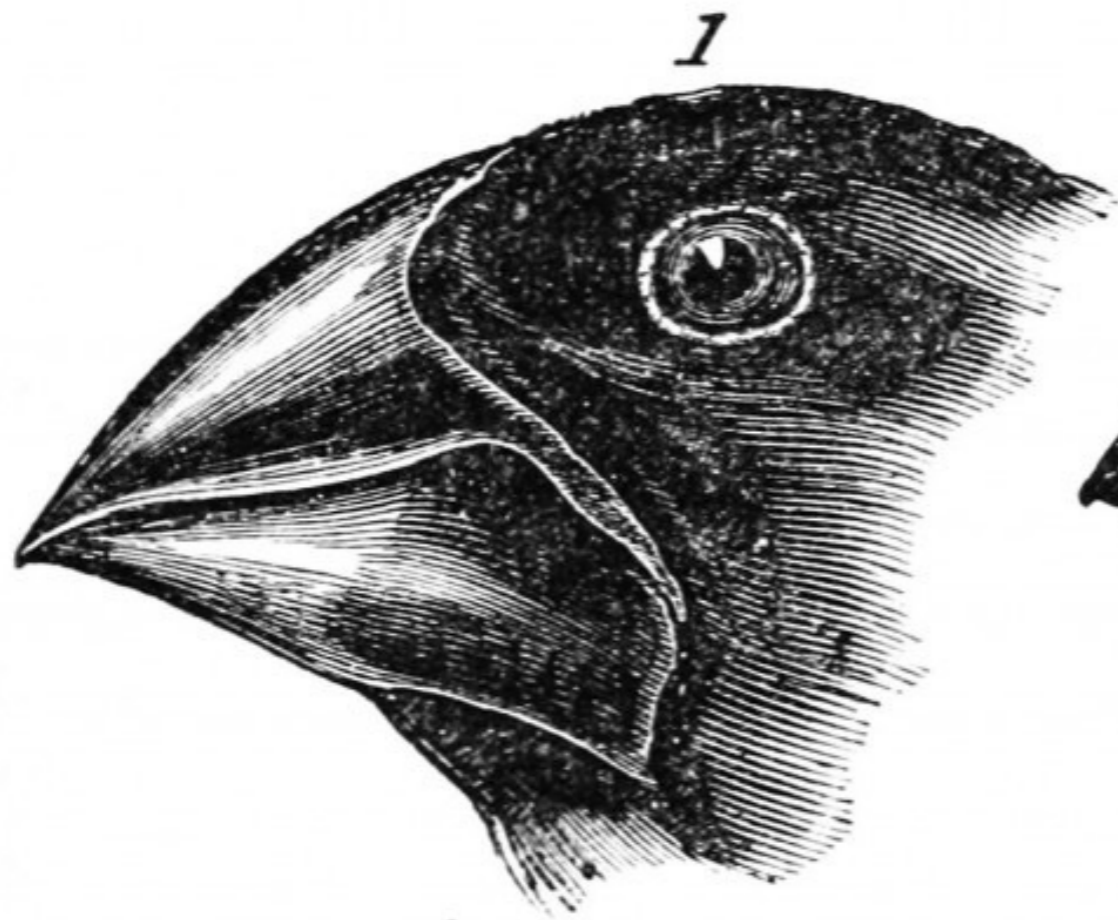






From Darwin's *The Variation of Animals and Plants Under Domestication*

Fig. 24.—Skulls of Pigeons viewed laterally, of natural size. A. Wild Rock-pigeon, *Columba livia*. B. Short-faced Tumbler. C. English Carrier. D. Bagadotten Carrier.



1. *Geospiza magnirostris*.  
3. *Geospiza parvula*.

2. *Geospiza fortis*.  
4. *Certhidea olivacea*.

Σπίνοι των Γκαλαπάγκος - από το βιβλίο του Δαρβίνου *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N.* (1845).



Let an **architect** be compelled to build an edifice with **uncut stones, fallen from a precipice**. The **shape** of each fragment may be called **accidental**; yet the shape of each has been determined by the force of **gravity**, the **nature** of the **rock**, and the **slope** of the precipice,—events and circumstances all of which depend on **natural laws**; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are **determined by fixed and immutable laws**; but these bear no relation to the living structure which is slowly built up through the power of natural selection, whether this be natural or artificial selection.

(Darwin 1868, 236)

# Natural Selection

4. NS acts on **individuals** (individual selection)

-> traits are 'selected' because they help the organisms that possess them to survive and reproduce

-> does not act **for the good of the species**, the ecosystem, etc

-> BUT: **group selection** in order to explain altruism



# Natural Selection

## 5. gradualism

6. NS as the “the main but not the sole cause” of evolution (e.g. use and disuse, ancestral influence, correlation of characters other causes for **Darwin**)

# Natural Selection

1. **natural vs artificial** selection -> NS does not have a mind
2. evolution of populations through NS depends on **contingent features of the environment**
3. NS acts on 'random' variation
4. NS acts on **individuals**
5. **gradualism**
6. NS as the “the main but not the sole cause” of evolution

# Lewontin's criteria

heritable variation in fitness

1. There is **variation** in morphological, physiological, and behavioural traits among members of a species

-> variation

2. The variation is in part **heritable**, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, **offspring resemble their parents**

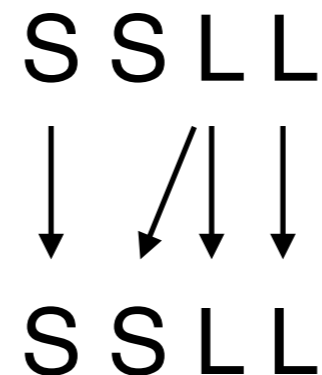
-> heritability

3. Different variants **leave different numbers of offspring** either in immediate or remote generations

-> differential fitness

All three conditions are **necessary as well as sufficient conditions** for evolution by natural selection. . . . Any trait for which the three principles apply may be expected to evolve.

-> counterexample



(1985, p. 76)

# Natural Selection

**In every species on earth**, variation **continually arises**. Some of these new traits tend to be **inherited** across generations, and some inherited traits are **beneficial** to survival and reproduction while others are not. **In many cases**, the traits beneficial to survival and reproduction become **more common**, while less useful traits are lost. **This leads to ongoing change in the features of organisms in all species.**

VS

**If** there is **variation** in a population, **reproduction** is **asexual** and offspring are **exact copies** of their mothers, everyone lives for the same length of time and reproduces at once, no one enters the population from outside or leaves, and individuals with some traits **reproduce more than others**, **then** the population will change.

(PB 33)

-> idealised model: **replicator dynamics**

# Fitness

natural selection vs **genetic drift**

-> genetic drift as an explanation of evolutionary change

*Principle of Natural Selection:* For all reproducing entities x and y, all environments E, and all generations n: if x is **fitter** than y in environment E at generation n, then **probably** there is some future generation n', after which x has more descendants than y.

(Rosenberg & Kaplan 2005)

-> realised fitness vs fitness as propensity

[ **propensity**: a tendency or disposition that can be described in terms of probabilities ]

-> fitness (as propensity): **expected** number of offspring

# Origin explanations vs Distribution explanations

in order to be **selected**, a change must first have been **produced**

(de Vries 1909)

[Natural selection] is **only a sieve**, and **not a force of nature**, not a direct **cause** of improvement. . . . [W]ith the **single steps** of evolution it has **nothing to do**. Only after the step has been taken, the sieve acts, **eliminating the unfit**.

(1906, pp. 6–7)

-> however, NS can have a **creative role** too (i.e. it can explain the origin of **complex organs**, such as the eye)



- Ernst Mayr
- population thinking vs typological thinking
- major evolutionary transitions -Maynard-Smith