CLASS 4 - 17 March: EVOLUTION

1. History of the concept
2. Centrality of evolution in biology
3. The causes of evolution

<u>Bibliography: slides at the end</u>

1.1 History of the concept

In all previous classes (life, organism, development) the concept of evolution was implicit:

1. Life originates somehow and then evolves by exhibiting a huge variety of forms.

2. New composite forms of organismality evolve from prokaryotic unicellular organisms.

3. Organisms develop and self-maintain during ontogeny, but they also form lineages through reproduction, whereby these lineages diversify genomically and phenotypically.

In brief, life evolves. But until Lamarck and Darwin, the idea of evolution or transmutation was uncommon. Why?

1.2 History of the concept

Because, in pre-evolutionary times, “naturalists” endorsed a static view of nature based on four interrelated theses:

1. Creationism: God produced all the existing biodiversity at the moment of creation;
2. Essentialism: biological forms are endowed with immutable and unchangeable essences;
3. Continuity: all life forms grade into each other with no jumps;
4. Fixism: no new biodiversity could be originated by transmutation because biological forms are fixed, immutable and unchangeable.

1.3 History of the concept

The static view finds its sophisticated rationale in Plato's Timaeus.

His argument is based on the endorsement of the principle of plenitude, i.e., the idea that the universe contains all possible forms of existence, that is, all mathematical, geometrical, physical, chemical, biological etc. ones.

Applied to the biological case, Plato argues that the creator of the cosmos (i.e., "demiurge") must have created all life forms from the start, otherwise the appearance of new forms after creation would render the cosmos' original plan incomplete and hence imperfect: given that all potential forms of life are essential to a perfect creation, all must become actual at the moment of creation.

Plato thus defended a static idea of the natural world: all biological forms have originated at once at creation in a fixed and immutable form.

1.4 History of the concept

How to explain the observable variation in life forms of the same type then?

Plato thought that, notwithstanding the observable appearance, all things could be classified as belonging to a natural type characterised by a constant and invariable essence.

Think of Aristotle's natural state model (class 3): there is a natural phenotypic state of development; when variation exceeds a certain threshold, the "monster" will not be able to reproduce. Unity of type and constancy of species is preserved.

Ernst Mayr (1982, p. 304) called Plato "the great antihero of evolutionism".

How to represent the variety of forms or the extant biodiversity pattern? (cf. Ragan 2009)

1.5 History of the concept

Principle of continuity: linear and progressive order of the relationships between all life forms from less to more complex:

"…proceeding little by little from things lifeless to animal life in such a way that it is impossible to determine the exact line of demarcation, nor on which side thereof an intermediate form should lie. Thus, next after lifeless things in the upward scale comes the plant, and of plants one will differ from another as to its amount of apparent vitality; and, in a word, the whole genus of plants, whilst it is devoid of life as compared with an animal, is endowed with life as compared with other corporeal entities. Indeed, as we have just remarked, there is observed in plants a continuous scale of ascent toward the animal."

Aristotle 1910, 588b:4

1.6 History of the concept

"There were two principles… that guided natural history in the eighteenth century: plenitude and continuity. The principle of plenitude says that all forms possible are exemplified in nature, while the principle of continuity says that all forms in nature insensibly grade into one another. Consequently, the *scala naturae*, the Great Chain of Being, is the adequate representation of order in nature, one that reflects the Plan of Creation (Lovejoy 1936)." Rieppel 2010

Plato's influence: nature is perfection.

Aristotle's influence: *Natura non facit saltus*.

1.7 History of the concept

Bonnet: "‘‘The polyp links the plant with the animal. The flying squirrel unites the bird with the mammal. The monkey touches the mammal and the human’’ (Bonnet 1764 p. 29)."

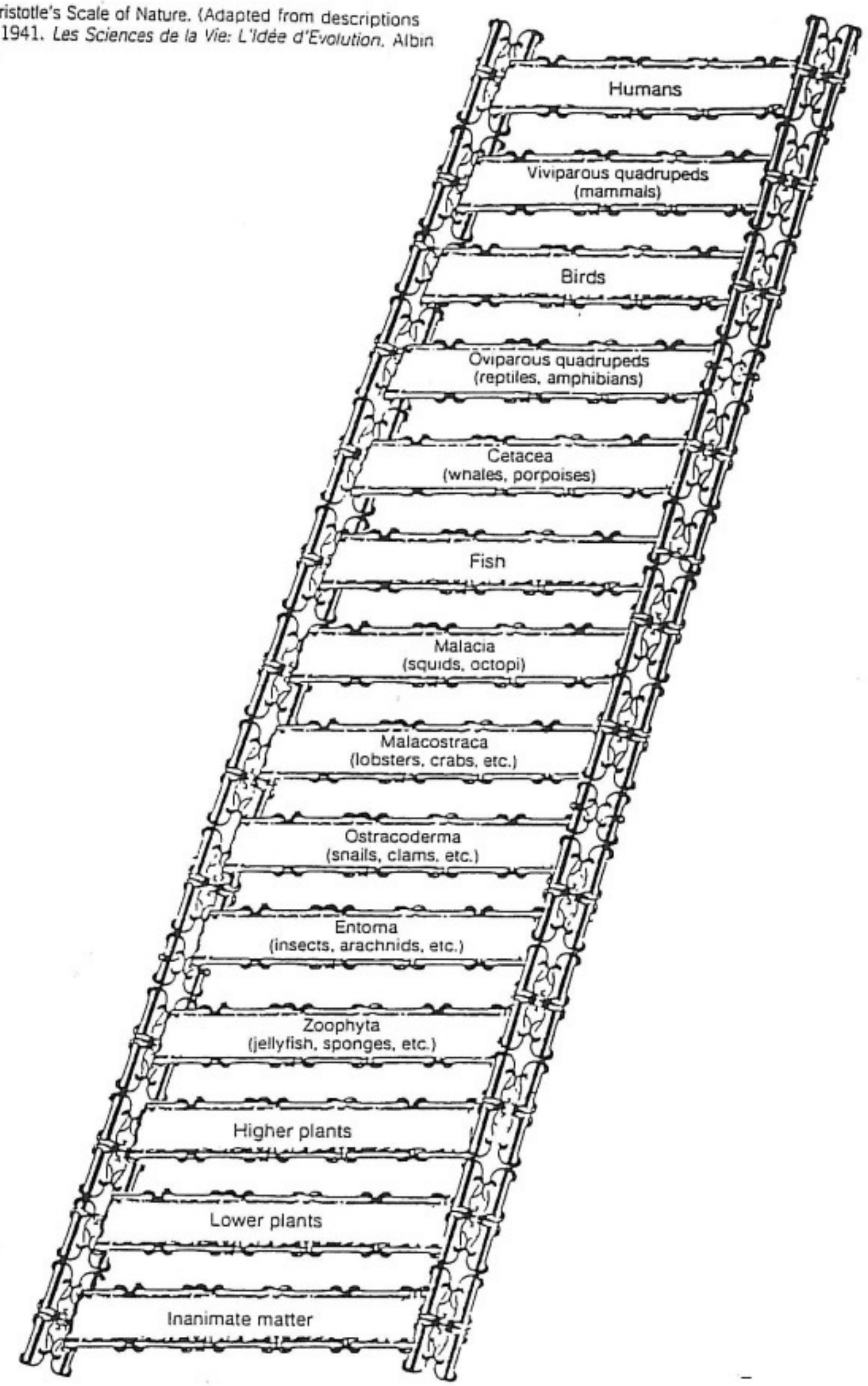
Remember Trembley’s *Hydra* (class 3), which has plant and animal features: respectively capacity to propagate by budding and predatory habits. It is an organism unifying two realms.

‘‘Intelligent minds will recognize in the ladder of our world as many rungs as there are individual beings’’ (Bonnet 1764, p. 29).

Discontinuity reflects ignorance: ‘‘Let us not pronounce that there exists a jump, a break here: such a gap is nowhere but in our current knowledge’’ (Bonnet 1768 p. 191).

1.8 History of the concept

FIGURE 1-2 Aristotle's Scale of Nature. (Adapted from descriptions in E. Guyénot, 1941. *Les Sciences de la Vie: L'Idée d'Evolution*. Albin Michel, Paris.)



From Ragan 2009

1.9 History of the concept

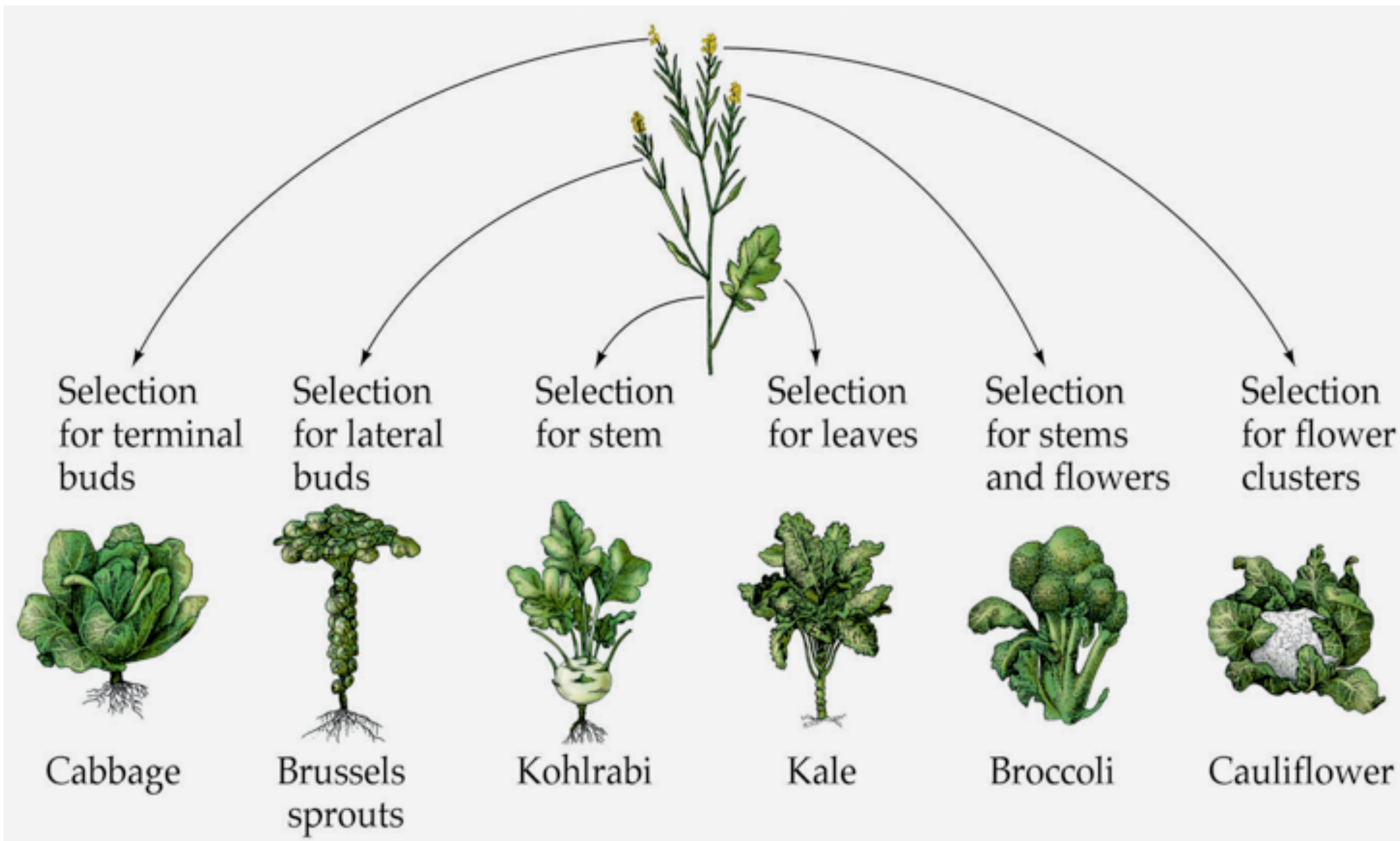
How many naturalists believed in creationism, essentialism, continuity and fixism? Interesting and complex historical question.

Essentialism faced the problem of variation: organisms of the same species vary in all observable respects and the postulation of an immutable natural type became increasingly difficult to defend in the light of growing naturalistic evidence.

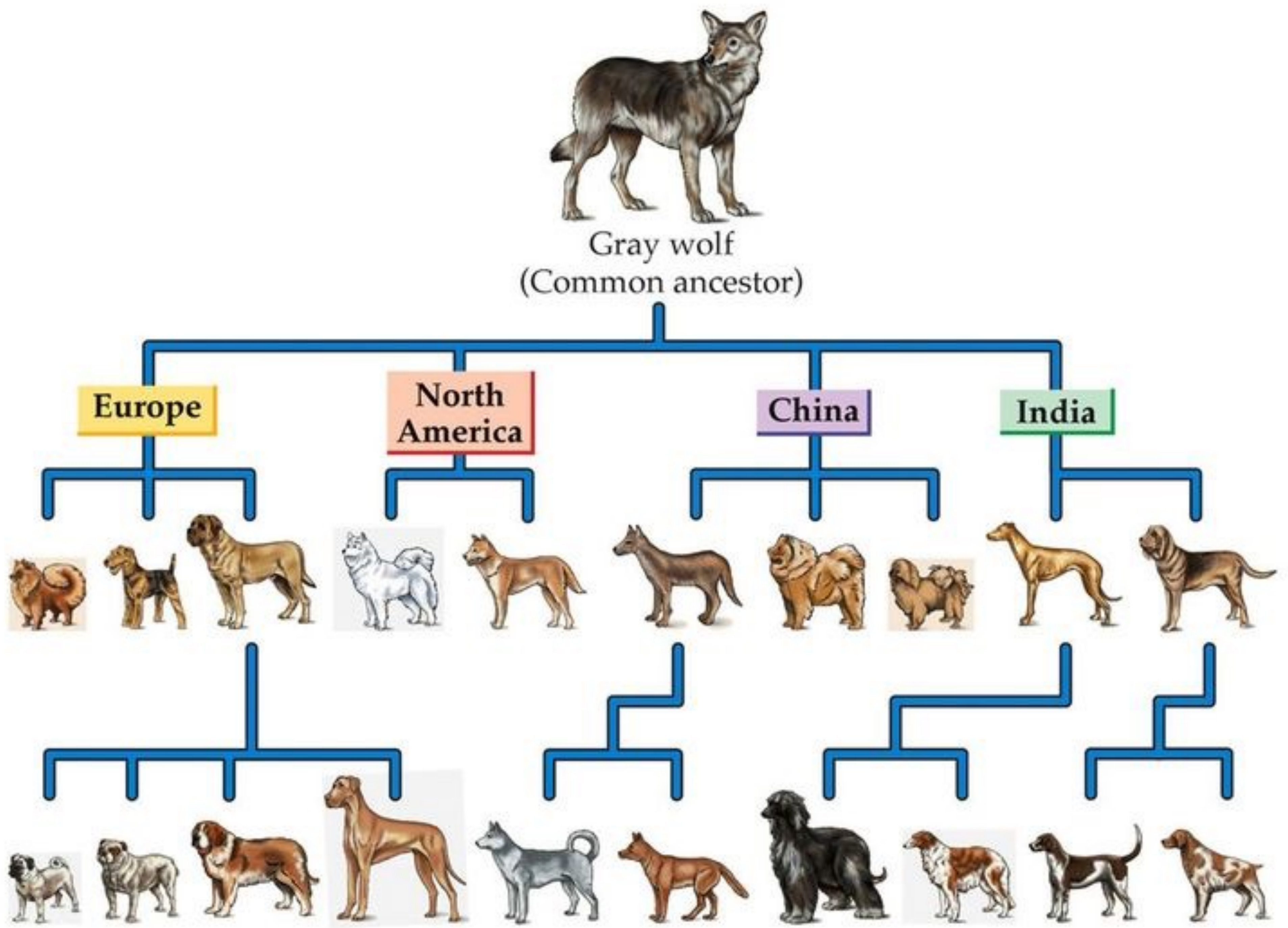
Artificial selection performed by breeders has created a variety of “unnatural” types sometimes vaguely similar to the original.

1.10 History of the concept

Brassica



1.11 History of the concept



DISCOVER BIOLOGY, **Second Edition, Chapter 21 Box** © 2002 Sinauer Associates, Inc., and W. W. Norton and Company

1.12 History of the concept

How many naturalists believed in creationism, essentialism, continuity and fixism? Interesting historical question.

Continuity faced the problem of gaps in classification. Evidence of transitional forms not always found in the fossil record.

Darwin reported that most of his contemporary animal and plant breeders did not believe in creationism but were fixists, they simply did not believe in common ancestry and often were essentialists.

Their argument was often that some ancient species had existed in the wild but were now extinct. So, new species could not be generated, but they could die.

But the idea that nature might make jumps of some sort became more popular.

1.13 History of the concept

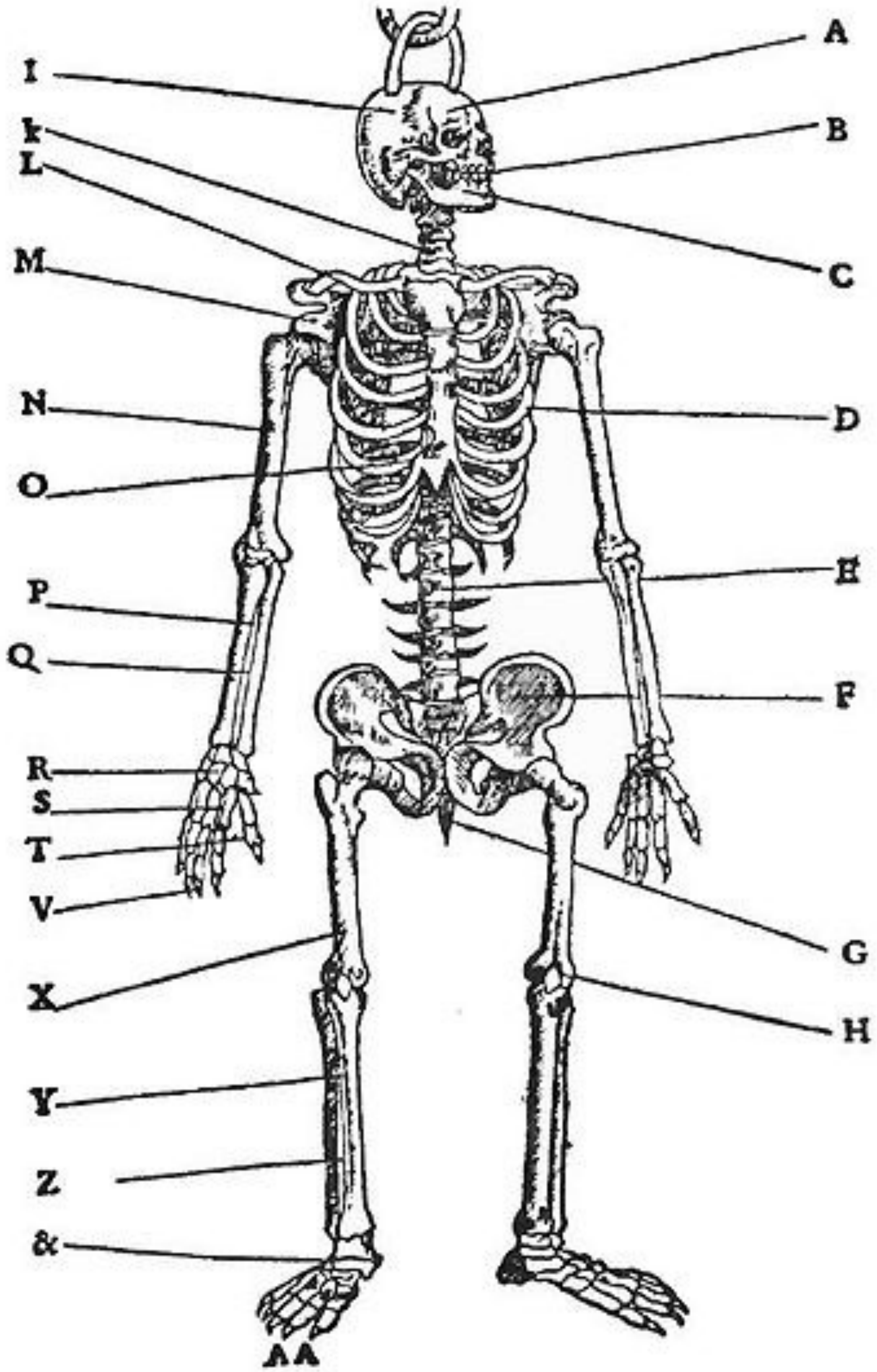
How many naturalists believed in creationism, essentialism, continuity and fixism? Interesting historical question.

Fixity faced the problem concerning the growing evidence of homology coming from embryology and comparative anatomy.

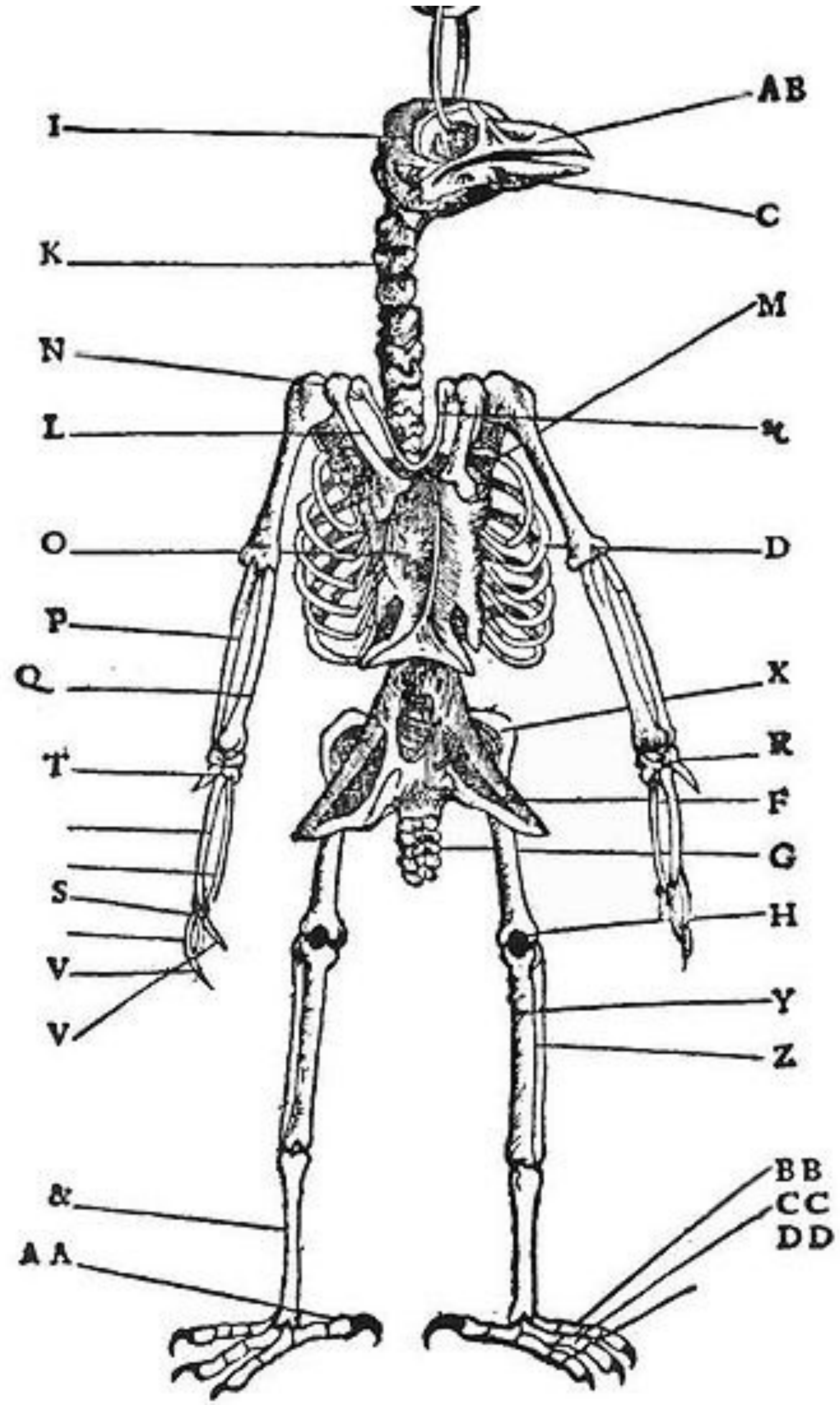
Life forms - even those classified as distant within the *scale naturae* - seem to share structural features both when anatomically analysed and even when their developmental patterns are considered.

The idea of a common ancestor gained traction.

1.14 History of the concept



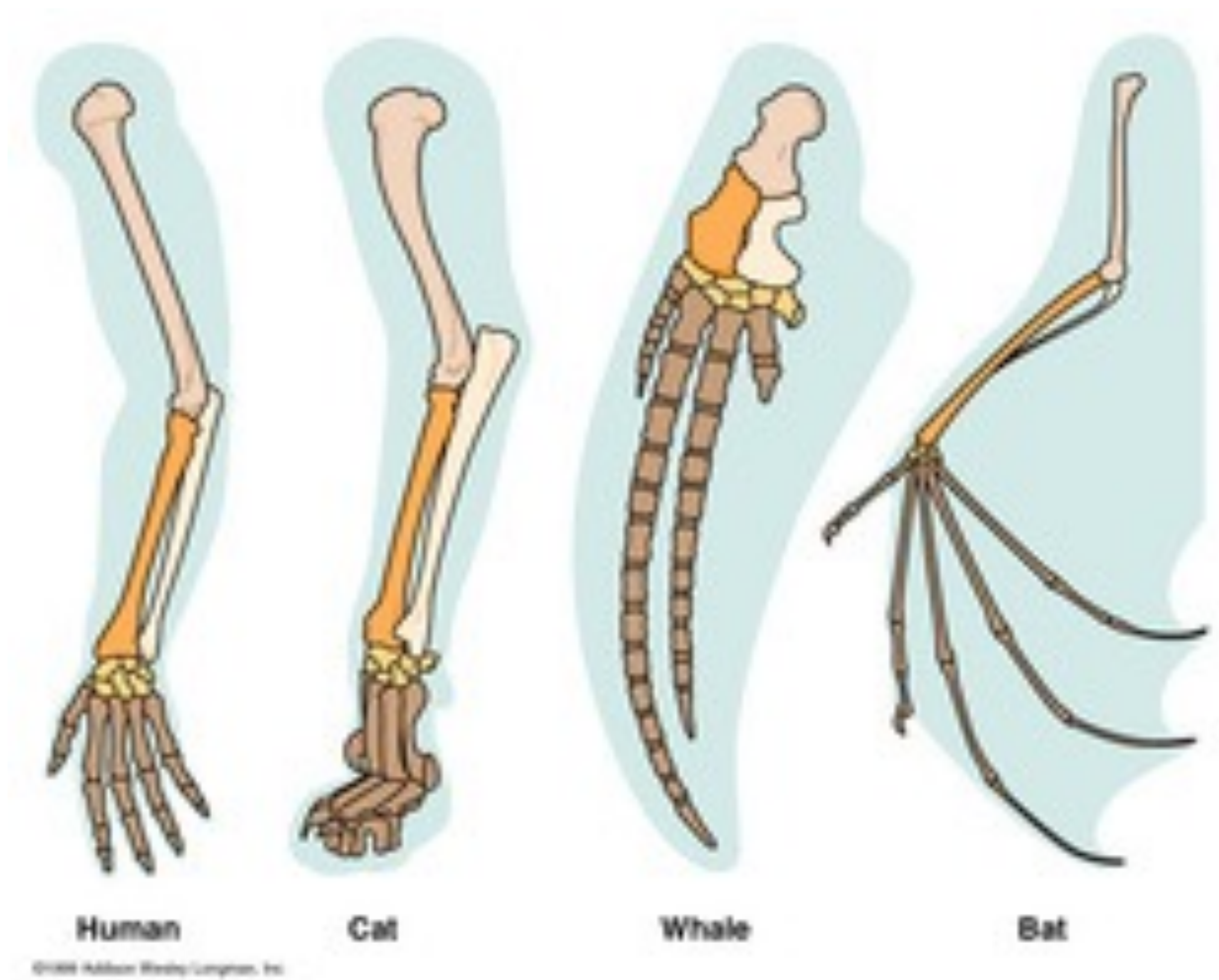
HUMAN SKELETON.



BIRD'S SKELETON.

From Belon's *Book of Birds*, 1555.

1.15 History of the concept



Homology of mammal limbs: pentadactyly

1.16 History of the concept

These challenges to the static view rendered the idea of transmutation of life forms increasingly more appealing.

Nature seems to have the means to create forms different from the postulated immutable types.

Nature seems to proceed by some sorts of jumps sometimes.

Nature’s life forms might be linked by common ancestry.

Overall, from an evolutionary perspective centred on transmutation, creationism either becomes useless or the creative role of God has to be rethought.

1.17 History of the concept

Evolutionary thinking was probably always present. But in which form?

Historically, the most prominent pre-Darwinian model for understanding evolutionary phenomena was taken from embryology (Lewontin 1982). In fact, before Darwin, the term “evolution” was synonymous with development.

The embryological model is based on the assumption that the system of reference (be it an organism, a species, a society) “evolves” by following pre-determined stages that are immanent or endogenous.

1.18 History of the concept

Examples of this model come from many theories of history (e.g. Comte, Hegel).

Auguste Comte (1798-1857) suggested to see societies as developing from a pre-scientific to a scientific age (theological —> metaphysical —> positive stages).

Evolution is a finalistic and progressive developmental process governed by the unfolding of immanent and necessary stages.

Change in this model comes from the “inside” rather than being exogenous.

But then, cutting a complex story short, came Lamarck.

1.19 History of the concept

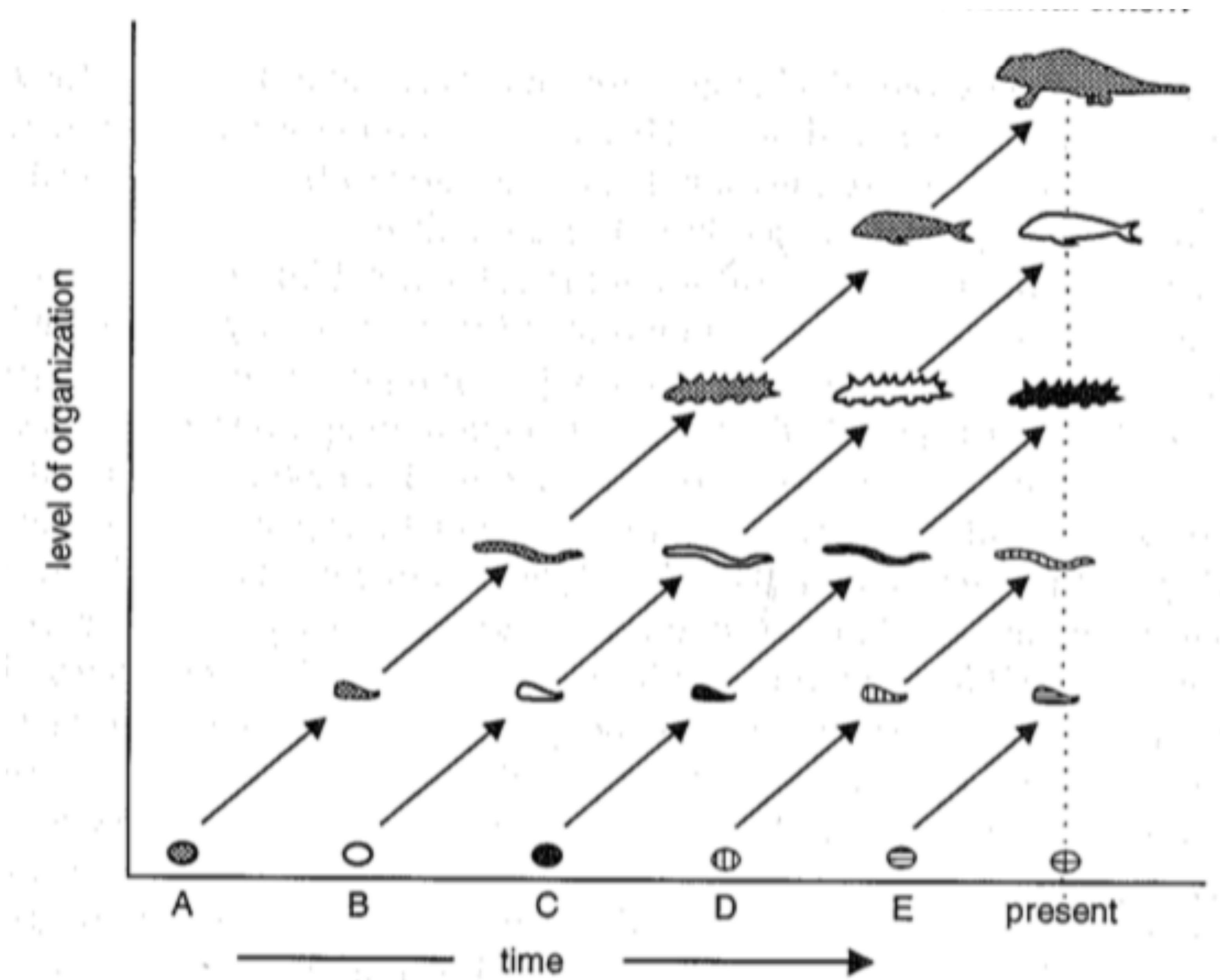
Lamarck is the first genuine evolutionist (*Philosophie Zoologique* dates 1809):

1. life comes from non-living matter opportunely reorganised; spontaneous generation is a common and ongoing process;

2. spontaneously generated simple life forms change in two ways: there is an inherent tendency to complexify (a materialistic teleological drive) and also the ability of organisms to react to environmental changes and produce adaptive modifications; these two forces account for the divergent and complex patterns of biological evolution;

3. simpler forms are the newest, more complex the older;

1.20 History of the concept



Phylogeny according to Lamarck: no common ancestry and continuous spontaneous generation.

1.21 History of the concept

4. use and disuse of organs is at the basis of the process of adaptation to the environment; the environment does not determine adaptation but it is the active organism that mediates environmental stimuli through behaviour or their internal activities;

5 . the adaptive changes acquired through use and disuse are inherited by the offspring; if environmental inputs of the same kind persist, the lineage will evolve in a specific adaptive direction; physiological adaptations are evolutionary adaptations;

6. new environments elicit new adaptive and heritable variations in many organisms simultaneously.

1.21b History of the concept

I think Maurizio Esposito will talk about Lamarck.

In any case, take a look at these books:

1. Jablonka, E. & Lamb, M. 1995. Epigenetic Inheritance and Evolution. Oxford University Press. (One chapter is in the materials I'm sending)
2. Jablonka, E. & Lamb, M. 2005. Evolution in Four Dimensions. MIT Press.
3. Gissis, S., Jablonka, E. (Editors). Transformations of Lamarckism. The MIT Press.

In the third book you will also find a chapter by Pietro Corsi, a historian specialised on Lamarck:

Corsi, P. 2011. A reappraisal of Lamarckism - its historical impact and contemporary significance. Gissis, S., Jablonka, E. (Editors). Transformations of Lamarckism. The MIT Press, pp. 12 - 28

1.22 History of the concept

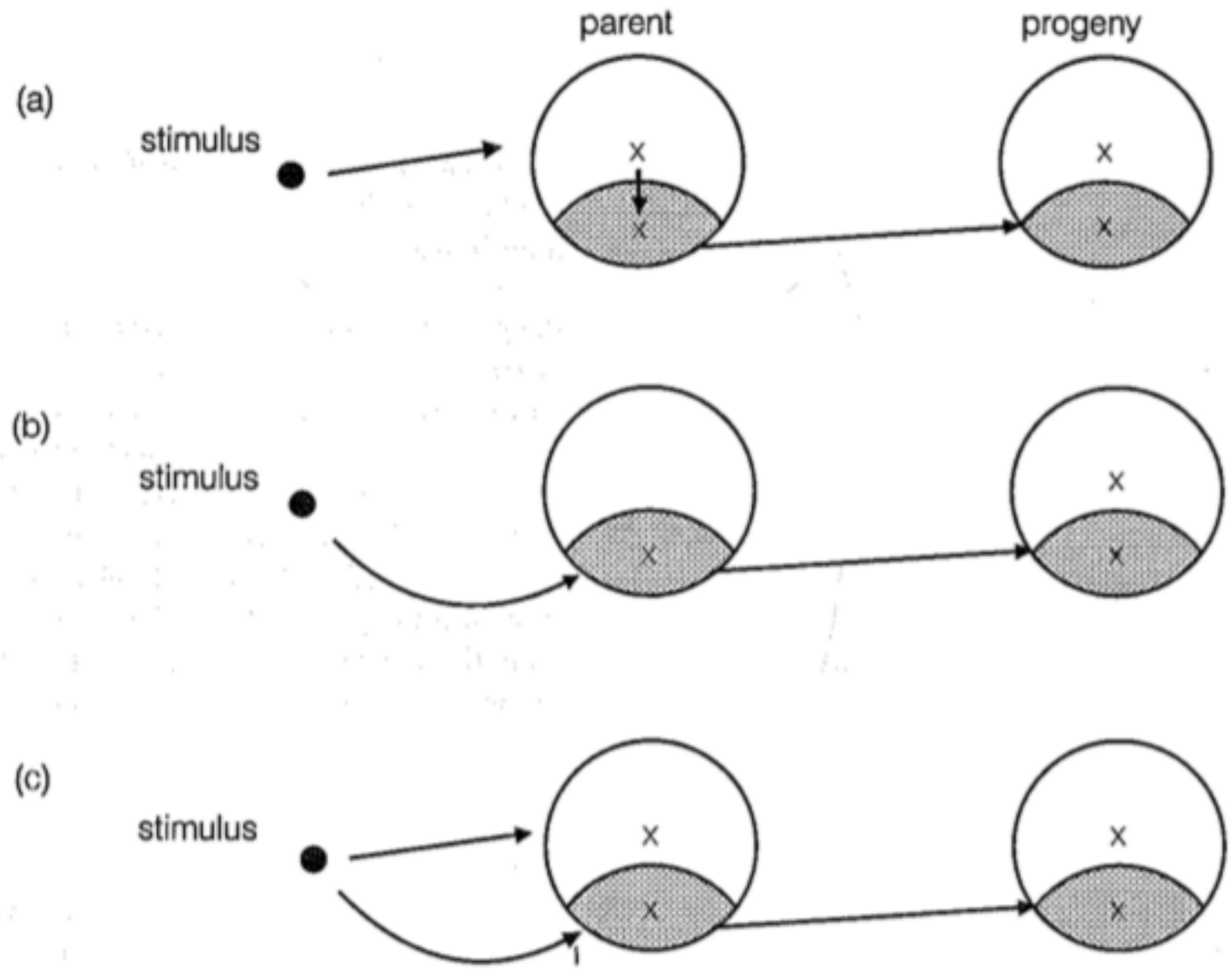
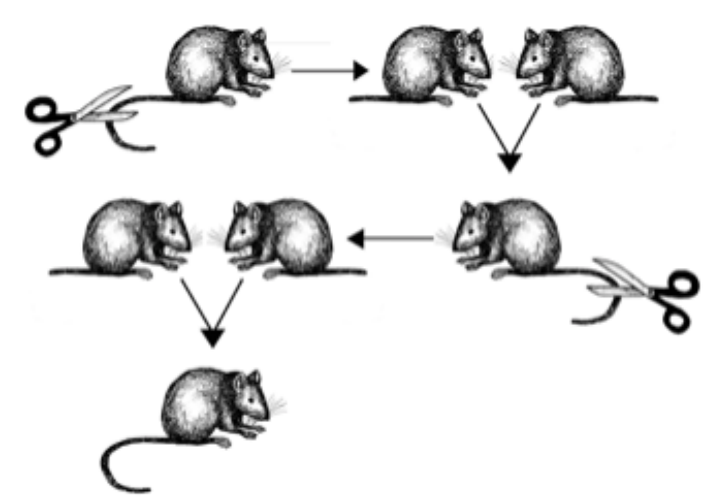


Fig. 1.4 Inherited environmental effects. Circles represent organisms with a soma (unshaded) and germ line (shaded); **X** is the effect of the environmental stimulus. (a) Somatic induction (a 'Lamarckian' mechanism): the stimulus produces an effect in the parental soma, which is transferred to the germ line and thence to the progeny. (b) Random or directed germ line variations (Weismann's mechanism): the germ line is affected directly, so the effect is passed to progeny. (c) Parallel induction: the stimulus acts on both the germ line and soma, so the effect is passed to the progeny. (Based on Fothergill 1952, p. 158.)

Inheritance according to Lamarck: process of type (a) in particular.

Weismann's experiments with rats' tails (below) refutes Lamarckism of type (a).



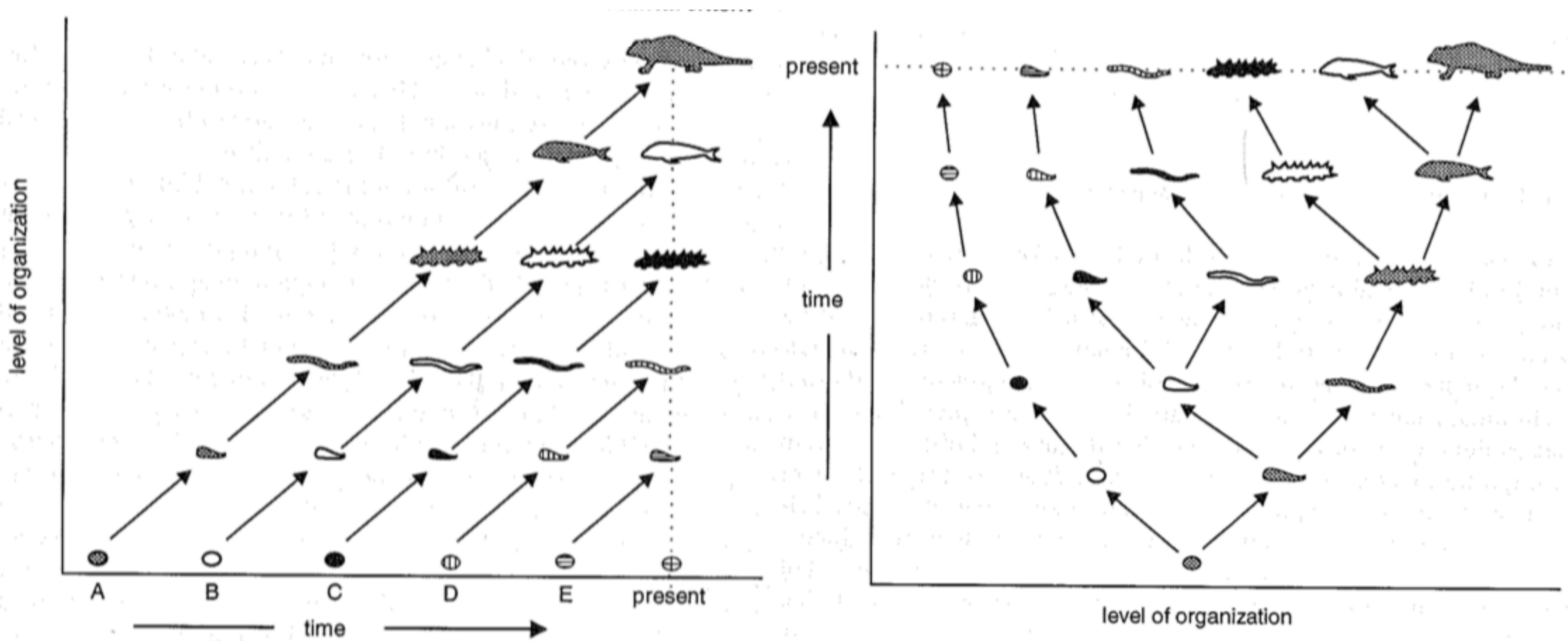
Jablonka & Lamb1995. Chapter 1.

1.23 History of the concept

“Darwin's theory of evolution contains two big ideas, neither of them totally original with him. What was original was their combination and application. The first ingredient is the idea of a tree of life.” Sober 1993 p. 7

Life = specific pattern representable as a single tree with a single root (vs. Lamarck and great chain of being).

1.24 History of the concept



Phylogeny according to Lamarck and Darwin:
common ancestry is the difference + spontaneous generation

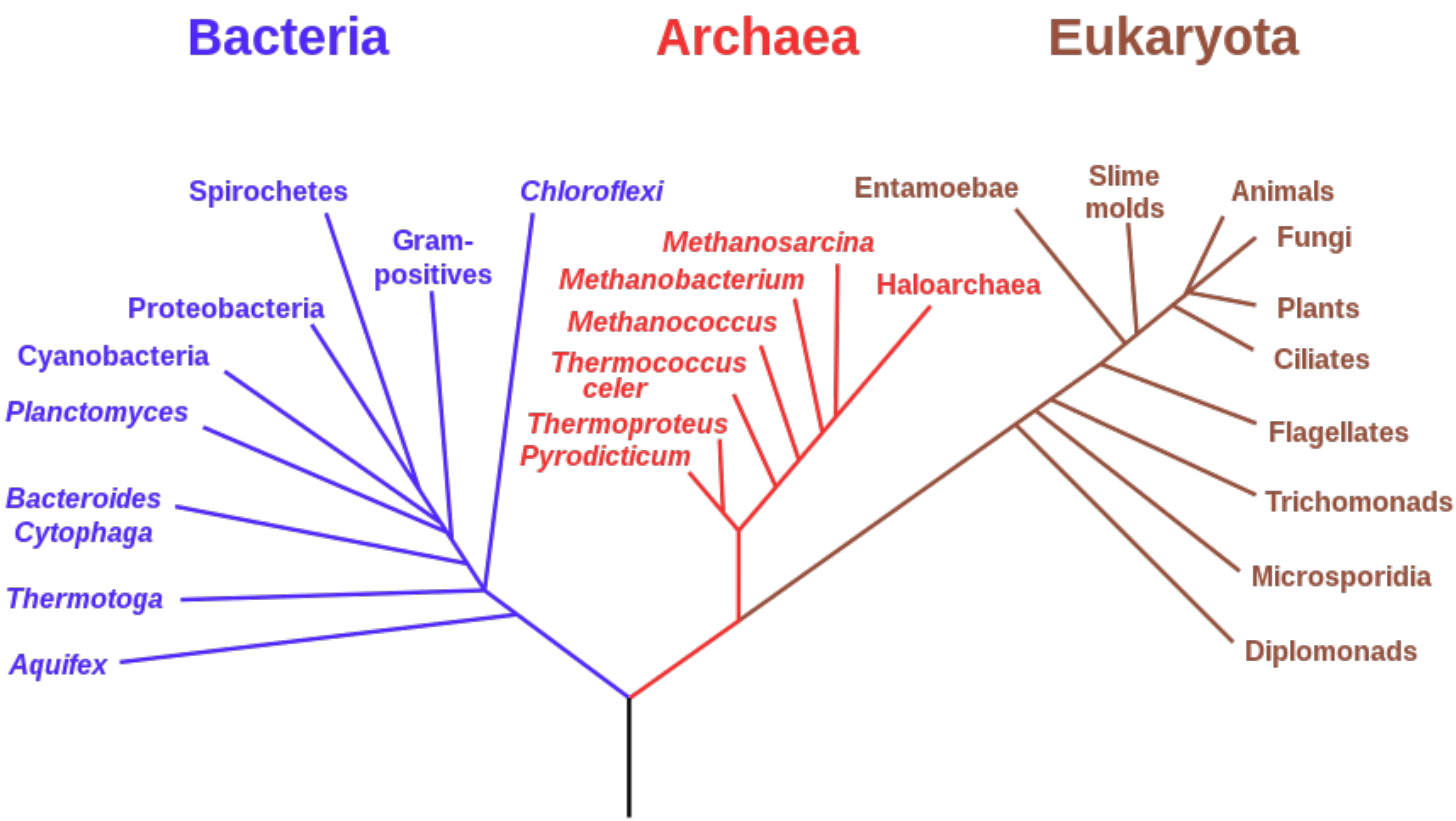
1.25 History of the concept

Contemporary evolutionism merges the idea of transmutation with the idea of common ancestry. Transmutation is the antithesis of fixism.

But what is common ancestry? The idea that extant life forms are variations on older ones and that they are all related. Darwin in "The Origin of Species" hypothesized that all life forms originated from one or few common ancestors.

Contemporary evolutionism is Darwinian. It is compatible with the hypothesis of abiogenesis (i.e., the origin of life from non-living matter), namely that spontaneous generation happened at some point in the history of our planet (see class 1). But, differently from Lamarck, contemporary evolutionism considers spontaneous generation not as a continuous process, but as a process confined to the origin of life.

1.26 History of the concept



Last universal common ancestor

1.27 History of the concept

“If we described the tree of life in some detail, we would say which species are descended from which others and when new characteristics originated and old ones disappeared. What is left for evolutionary theory to do, once these facts about life's pattern are described? One task that remains is to address the question of why. If a new characteristic evolved in a lineage, why did it do so? And if a new species comes into existence or an old one exits from the scene, again the question is why that event occurred. Answers to such questions involve theories about the process of evolution. … Darwin’s answer to this question about process constituted the second ingredient in his theory of evolution. This is the idea of natural selection.” Sober 1993 p. 9

1.28 History of the concept

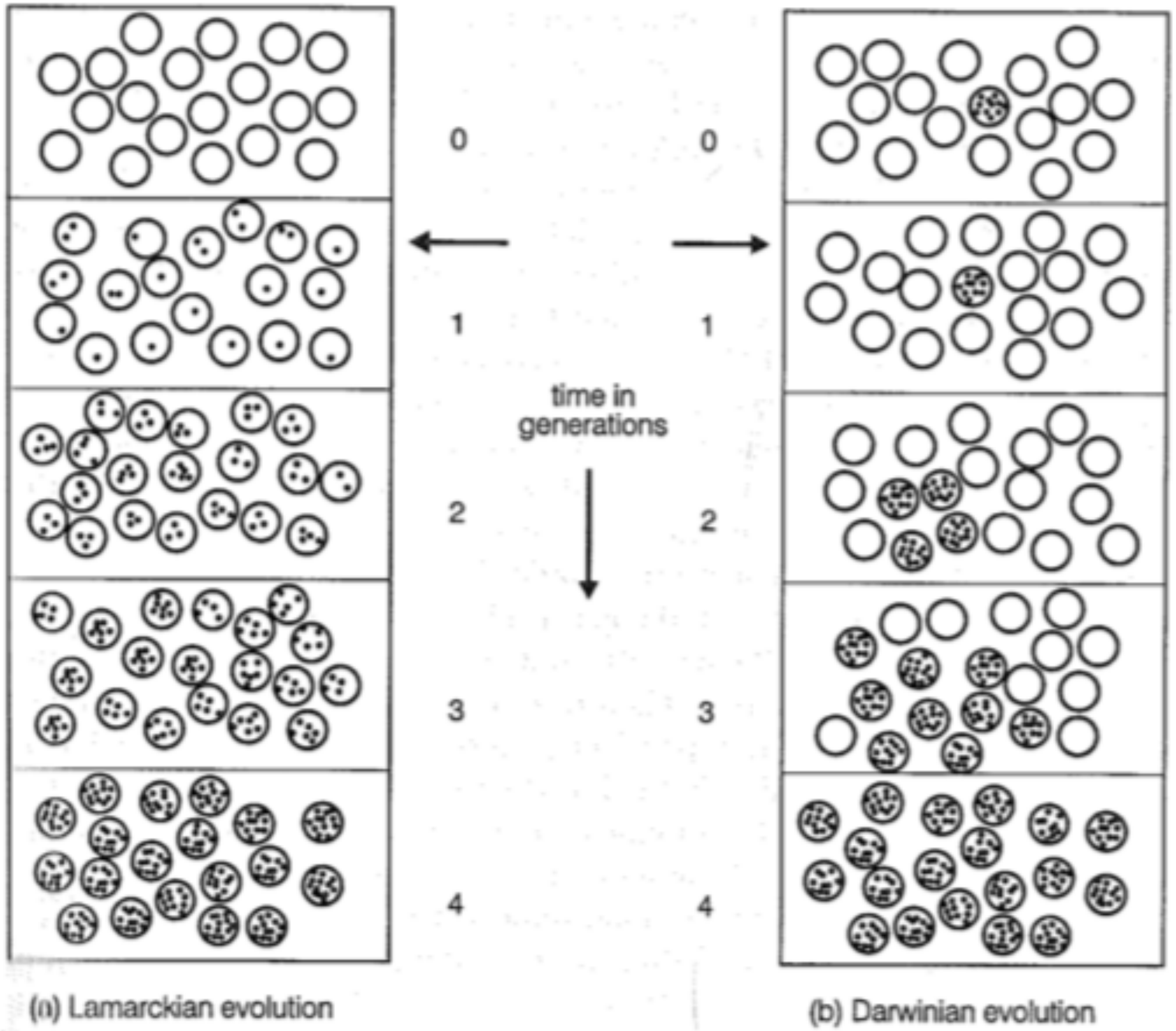


Fig. 1.3 The evolution of an adaptation to a new environment by (a) Lamarckian evolution and (b) Darwinian evolution. Individuals with the adaptation are represented by shaded circles, the intensity of shading indicating the degree of adaptation. At the time indicated by the horizontal arrows, the environment changes, and this change persists through subsequent generations. In Lamarckian evolution, all individuals acquire the adaptation, and it is gradually enhanced as individuals in subsequent generations continue to respond to the environment. In Darwinian evolution, by chance an individual has an appropriate adaptation that enables it to contribute proportionally more progeny to subsequent generations. (Loosely based on Medawar 1957, pp. 80–81.)

On the left a selection process that relies on the emergence of a new phenotype. This is not necessary. In 1.28a/b you will find a selection dynamic that relies on existing variation, without the emergence of a new phenotype. The first kind of selection might be called "positive". The second "negative". There are many kinds of selection, but we didn't talk about that.

Jablonka & Lamb 1995. Chapter 1.

1.28a History of the concept

1. **There is variation in traits.**
   For example, some beetles are green and some are brown.

2. **There is differential reproduction.**
   Since the environment can't support unlimited population growth, not all individuals get to reproduce to their full potential. In this example, green beetles tend to get eaten by birds and survive to reproduce less often than brown beetles do.

https://evolution.berkeley.edu/evolibrary/article/evo_25

1.28b History of the concept

3. **There is heredity.**
The surviving brown beetles have brown baby beetles because this trait has a genetic basis.

4. **End result:**
The more advantageous trait, brown coloration, which allows the beetle to have more offspring, becomes more common in the population. If this process continues, eventually, all individuals in the population will be brown.

Download this series of graphics from the Image library.

If you have variation, differential reproduction, and heredity, you will have evolution by natural selection as an outcome. It is as simple as that.

https://evolution.berkeley.edu/evolibrary/article/evo_25

1.29 History of the concept

Darwinism	Lamarckism
Spontaneous generation possibly only once	Continuous spontaneous generation
Tree of life and no progress	More complex life forms are the oldest
Natural selection	Progressive adaptation to environment through use and disuse
Population effect of germ-line inheritance	Individual change and inheritance of acquired characters
Random mutation *	Directed mutation *

* "Mutation" today refers to processes of genomic change. The better term should be "variation". The distinction between Darwinism and Lamarckism is that in the first case the process of variation generation (either genetic or phenotypic) is considered to be "random" in the sense that beneficial variation is not more probable than non-beneficial variation. In the Lamarckian case, it is instead biased or directed. If you are interested, take a look at this: https://onlinelibrary.wiley.com/doi/10.1111/brv.12249

1.30 History of the concept

"In summary, Darwin advanced a claim about pattern and a claim about process. The pattern claim was that all terrestrial organisms are related genealogically; life forms a tree in which all contemporary species have a common ancestor if we go back far enough in time. The process claim was that natural selection is the principal cause of the diversity we observe among life forms." Sober p. 14

The pattern claim is considered a "fact" (see slides in section 2). The process claim is not: is natural selection the most important explanation of adaptation, diversity and complexity? We'll move back to this issue in section 3.

2.1 Centrality of evolution in biology

Theodosius Dobzhansky (1973) argued that "nothing in biology makes sense except in the light of evolution." But much of biology does not strictly have to do with evolutionary issues. (However, as we also saw when discussing about origin of life and origin of organismality, evolution is always in the background).

“Dobzhansky's remark about the centrality of evolutionary theory to the rest of biology is a special case of a more general idea. Nothing can be understood ahistorically. Of course, what this really means is that nothing can be understood completely without attending to its history …. Evolution matters because history matters.” Sober 1993 p. 7

2.2 Centrality of evolution in biology

Nothing in biology can be fully understood ahistorically.

What could be the alternative to evolution? A form of creationism whereby God actually deceives believers:

"…. what a senseless operation it would have been, on God's part, to fabricate a multitude of species *ex nihilo* and then let most of them die out!" Dobzhansky pp. 126-7

2.3 Centrality of evolution in biology

What is the epistemological role played by an evolutionary way of thinking within biology at large? **Unificatory** of a series of otherwise disconnected observations concerning biodiversity and the unity of life:

"Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts - some of them interesting or curious but making no meaningful picture as a whole." Dobzhansky p. 129

2.4 Centrality of evolution in biology

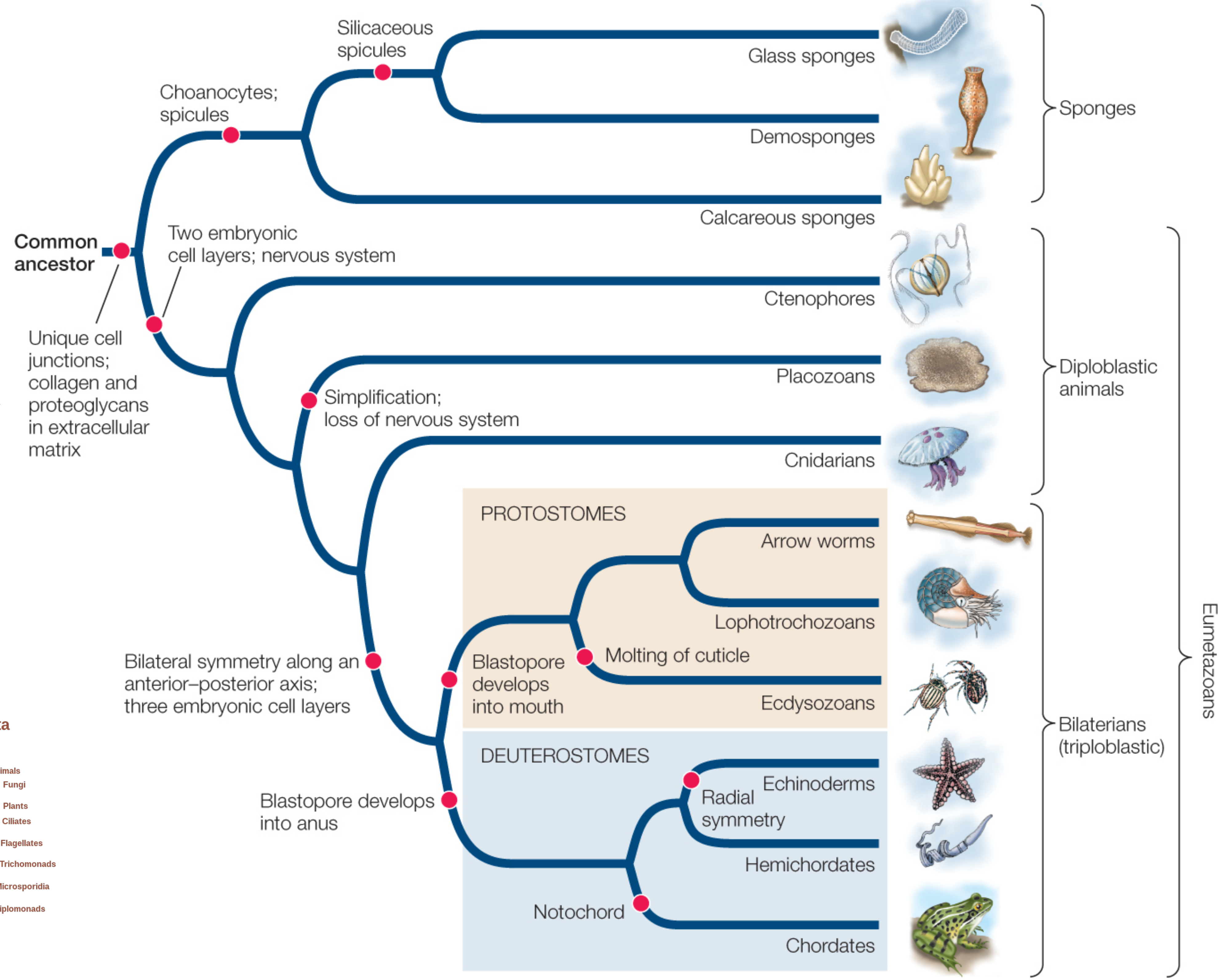
Unificatory role concerning biodiversity pattern:

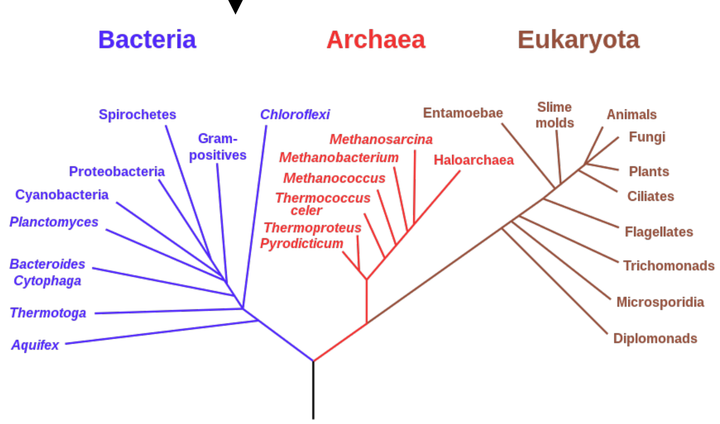
"The only explanation that makes sense is that the organic diversity has evolved in response to the diversity of environment on the planet earth…..the environment presents challenges to living species, to which the latter may respond by adaptive genetic changes …. Natural selection may cause a living species to respond to the challenge by adaptive genetic changes" Dobzhansky p. 126

2.5 Centrality of evolution in biology

Natural selection explains biodiversity.

Phenotypic tree vs genomic tree (rRNA).





2.6 Centrality of evolution in biology

Unificatory role concerning the unity of life:

“The unity of life is no less remarkable than its diversity. Most forms of life are similar in many respects. The universal biologic similarities are particularly striking in the biochemical dimension …. What do these biochemical or biologic universals mean? They suggest that life arose from inanimate matter only once and that all organisms, no matter how diverse in other respects, conserve the basic features of the primordial life.” Dobzhansky p.127

2.7 Centrality of evolution in biology

Unificatory role concerning the unity of life:

"Cytochrome C is an enzyme that plays an important role in the metabolism of aerobic cells. It is found in the most diverse organisms, from man to molds." Dobzhansky p. 128

Additionally, differences between human Cytochrome C protein variant and other species correlate with phylogenetic distance.

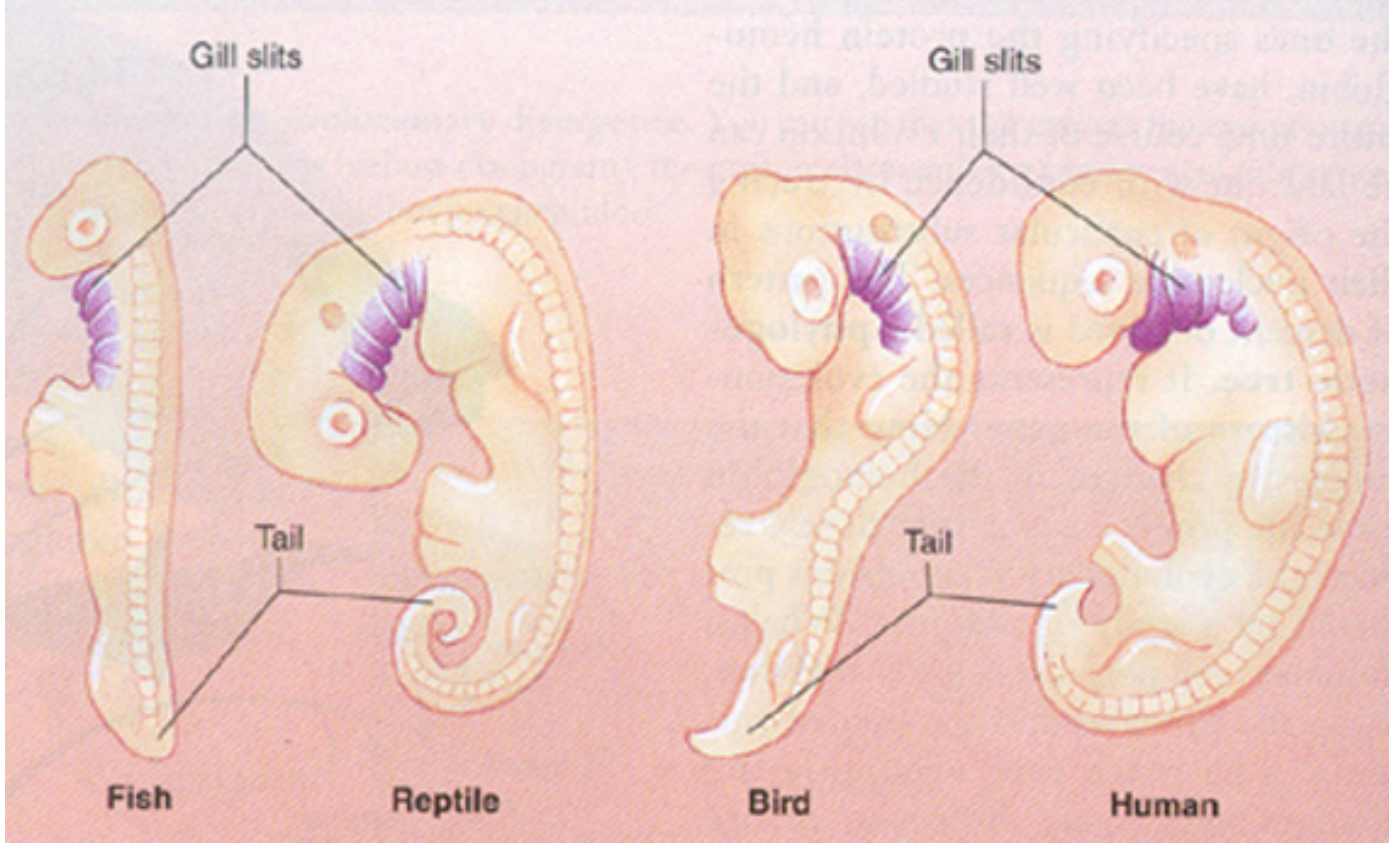
Monkey	1	Chicken	18
Dog	13	Penguin	18
Horse	17	Turtle	19
Donkey	16	Rattlesnake	20
Pig	13	Fish (tuna)	31
Rabbit	12	Fly	33
Kangaroo	12	Moth	36
Duck	17	Mold	63
Pigeon	16	Yeast	56

2.8 Centrality of evolution in biology

Unificatory role concerning the unity of life:

“The biochemical universals are … not the only vestiges of creation by means of evolution. Comparative anatomy and embryology proclaim the evolutionary origins of the present inhabitants of the world. The presence of gill slits in human embryos and in embryos of other terrestrial vertebrates is another famous example. Of course, at no stage of its development is a human embryo a fish, nor does it ever have functioning gills. But why should it have unmistakable gill slits unless its remote ancestors did respire with the aid of gills? Is the Creator again playing practical jokes?” Dobzhansky p. 128

2.9 Centrality of evolution in biology



Developmental homologies between various classes of organisms

2.10 Centrality of evolution in biology

Let us know take a brief look at Mayr's famous 1961 article "Cause and effect in Biology" (Science 134 (3489):1501–6).

Mayr asks what kind of notion of causality is used in biology. Is it the same notion used in physics (e.g., classical mechanics)? If this were the case, could biology be reduced to physics and chemistry? This is indeed what Descartes aimed at (remember the Cartesian programme, class 1).

2.11 Centrality of evolution in biology

In order to answer the previous question, Mayr distinguishes between two kinds of biology:

1. Functional biology: how does a biological system operate or function? To answer this question, experiments are needed, as in physics and chemistry. (Decoding of the genome is its focus).
2. Evolutionary biology: how did this sub-structure or entire biological system evolve? To answer this historical question, functional analysis is needed. (How a particular genome came about is its focus).

2.12 Centrality of evolution in biology

Mayr then asks: is *cause* the same thing in functional and evolutionary biology?

In order to answer this question, Mayr considers one specific example: “Why did the warbler on my summer place in New Hampshire start his south- ward migration on the night of the 25th of August?”

2.13 Centrality of evolution in biology

Mayr gives 4 possible causes:

1. Ecological cause: being an insect eater, the bird must migrate otherwise it would starve to death;
2. Genetic cause: the bird's genetic constitution induces the migratory behavioural response;
3. Intrinsic physiological cause: photoperiodicity (i.e., number of hours of daylight) induces migration to south;
4. Extrinsic physiological cause: a cold air mass arrived on 25th August and temperature dropped.

2.14 Centrality of evolution in biology

Mayr then argues that:

A. The immediate set of causes of migration affect the physiology of the individual bird (i.e., the intrinsic and extrinsic physiological causes). These he names *proximate causes*. Concern of the functional biologist.

B. The other two causes (i.e., ecological and genetic) have a history. They do not concern individual organisms, but the evolution of the species genome. These he calls *ultimate causes*. Concern of the evolutionary biologist.

2.15 Centrality of evolution in biology

This distinction allows Mayr to argue that ultimate causation is primary in biology (and that biology cannot be reduced to physics).

Ultimate causation refers to natural selection, the causal process acting on phylogenetic time scales.

Mayr’s distinction was part of a general argument to the amount that evolution should be studied by focusing on selection rather than variation.

After all, selection is the cause of the developmental mechanisms proximately causing (i.e., on an ontogenetic time scale) variation. Indeed, it “makes” the genetic programmes “decoded” in development (Mayr 1994).

2.16 Centrality of evolution in biology

The causal primacy of ultimate causation is grounded on the adaptationist working hypothesis that the evolution of complex traits is the result of cumulative, multi-generational natural selection.

The corollary of this view is that the "reductionist" sciences studying proximate causes (e.g., biochemistry, molecular and developmental biology) can only, in principle, identify the small, often phenotypically insignificant steps of the long series of ontogenetic changes accumulated by "creative" selection.

What is creative selection then?

2.17 Centrality of evolution in biology

Peppered moths have light pigment to camouflage on trees with light-coloured lichens from predators. Industrial pollution kills the light-coloured lichens off the trees, exposing their dark bark and making the light-coloured moths more vulnerable to predation. This slowly alters the balance of the population from the majority being light-coloured moths to the majority being dark-coloured moths. Melanic phenotype of the *Biston betularia* is fitter in polluted environments.

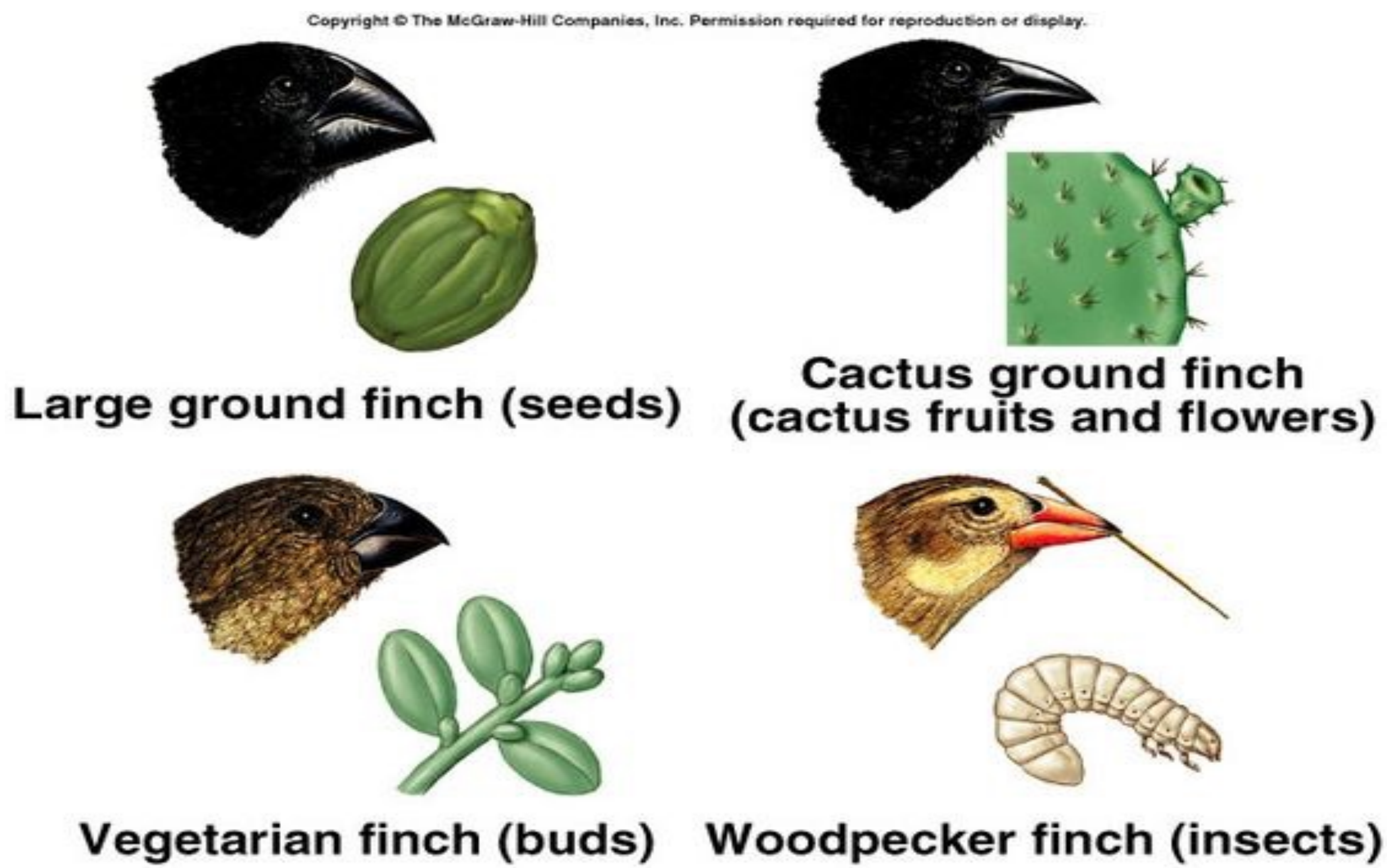
The increase in frequency of a trait is not, however, the formation of new species.

2.18 Centrality of evolution in biology

Take a second famous example: the evolution of beak morphology in Galapagos finches.

Selection for beak morphology dependent on the nature of food: example of origin of new species.

But changes in beak morphology are evolutionarily uninteresting compared to more complex traits (e.g., flagellum, feather, eye).



3.1 The causes of evolution

We finished section 1 by showing that Darwin's pattern claim (concerning common ancestry) is generally accepted (see also slides in section 2). Evolution is a fact in this sense.

The process claim (that natural selection is the most important evolutionary causal process and the fundamental source of biotic adaptation, biodiversity and complexity) is, on the other hand, an hypothesis.

In section 2, we saw that Dobzhansky and Mayr defend this hypothesis, called adaptationism. Whether they are right is still under dispute.

3.2 The causes of evolution

What is evolution?

"The concept of evolution is not restricted to biology. In fact, it is an ontological concept, for it applies to various natural processes: we speak, for instance, of cosmic, stellar, chemical, biotic, and cultural evolution … What is common to all these specific notions of evolution is, first of all, the ontological concept of change. Change, however, can be quantitative or qualitative, whereby every qualitative change is accompanied by some quantitative change, but not conversely. Admitting quantitative change renders one's ontology dynamicist as opposed to static, but it does not make it evolutionary. For an ontology to be evolutionary, we must posit in addition that there is also *qualitative change*. But the latter, though necessary, is still not sufficient for evolutionary change proper. For example, a developing organism undergoes qualitative changes, but we do not regard them as evolutionary." Mahner & Bunge 1997, p. 311

3.3 The causes of evolution

What is evolution?

"For a qualitative change to be considered *evolutionary*, we must finally assume that it consists in the *emergence of things of a new kind* or (ontological) species. In other words, a proper concept of evolution involves the concept of speciation in its ontological sense of the coming into being of a thing of a new kind." Mahner & Bunge 1997, p. 311

"… evolutionary theory is and should indeed be about the origin of species or, more precisely, about the origin of biotic entities belonging to a new species. Yet which are those evolutionarily changing, i.e., speciating, entities? In other words, which are the units of evolution: organisms, biopopulations, communities, ecosystems, or perhaps the entire biosphere or ecosphere, as some authors have suggested (e.g., Dunbar 1972; Walker 1985)? Mahner & Bunge 1997, p. 313

3.4 The causes of evolution

Typical definition: evolution = change in the gene frequencies found in a population.

What about: evolution = change in the genetic or phenotypic frequencies found in a population.

1. What is the biological entity that by changing qualitatively, engenders a new kid of biotic entity?

2. What processes cause such evolutionarily significant qualitative changes and their increase in frequency in the population?

3.5 The causes of evolution

Causes of evolutionary change

Outcome as evolutionary change

Origin of variants: developmental processes happening at the organismal level; e.g., mutation+altered development; origin of evolutionary novelty.

Sorting of variants: selection or drift of variants by inter-generational rounds of reproduction and inheritance.

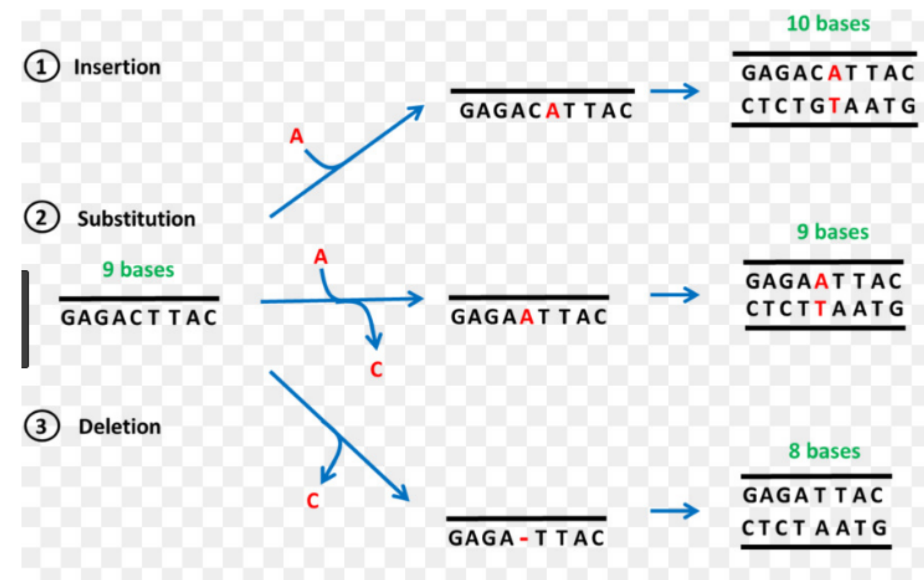
Change in variants' frequency in the lineage of reference; genomic and phenotypic variants might go to fixation in the lineage; basis of biological speciation.

3.6 The causes of evolution

Origin of variants = genomic change and developmental origin of new phenotypes.

Genomic variation is a product of genomic change. A variety of processes of genomic change exist that are generally referred in the literature under the umbrella term “mutation”.

Genomic variation has “developmental potential”, but the potential can only be actualised in an appropriate organismal and environmental context (“mutation-and-altered-development”, Stoltzfus 2006).



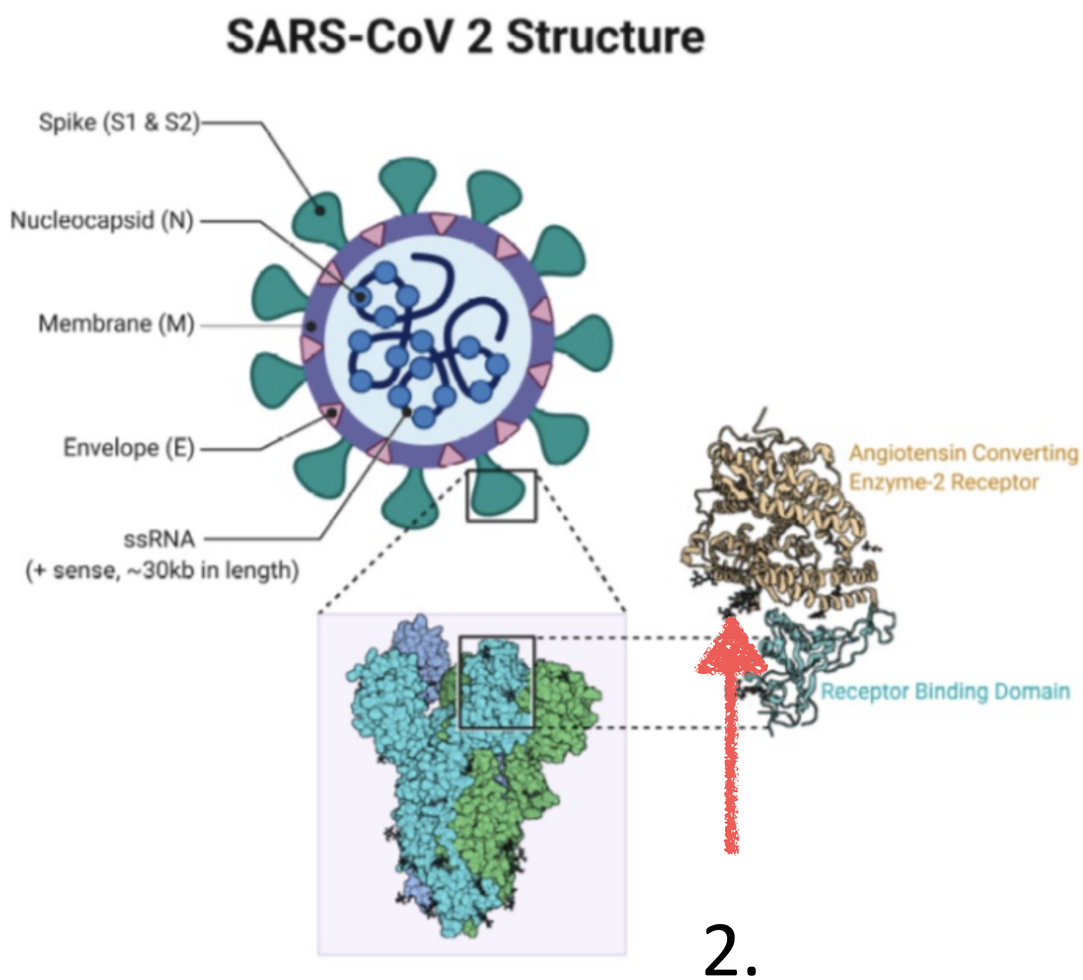
…. and then inversion, duplication etc.

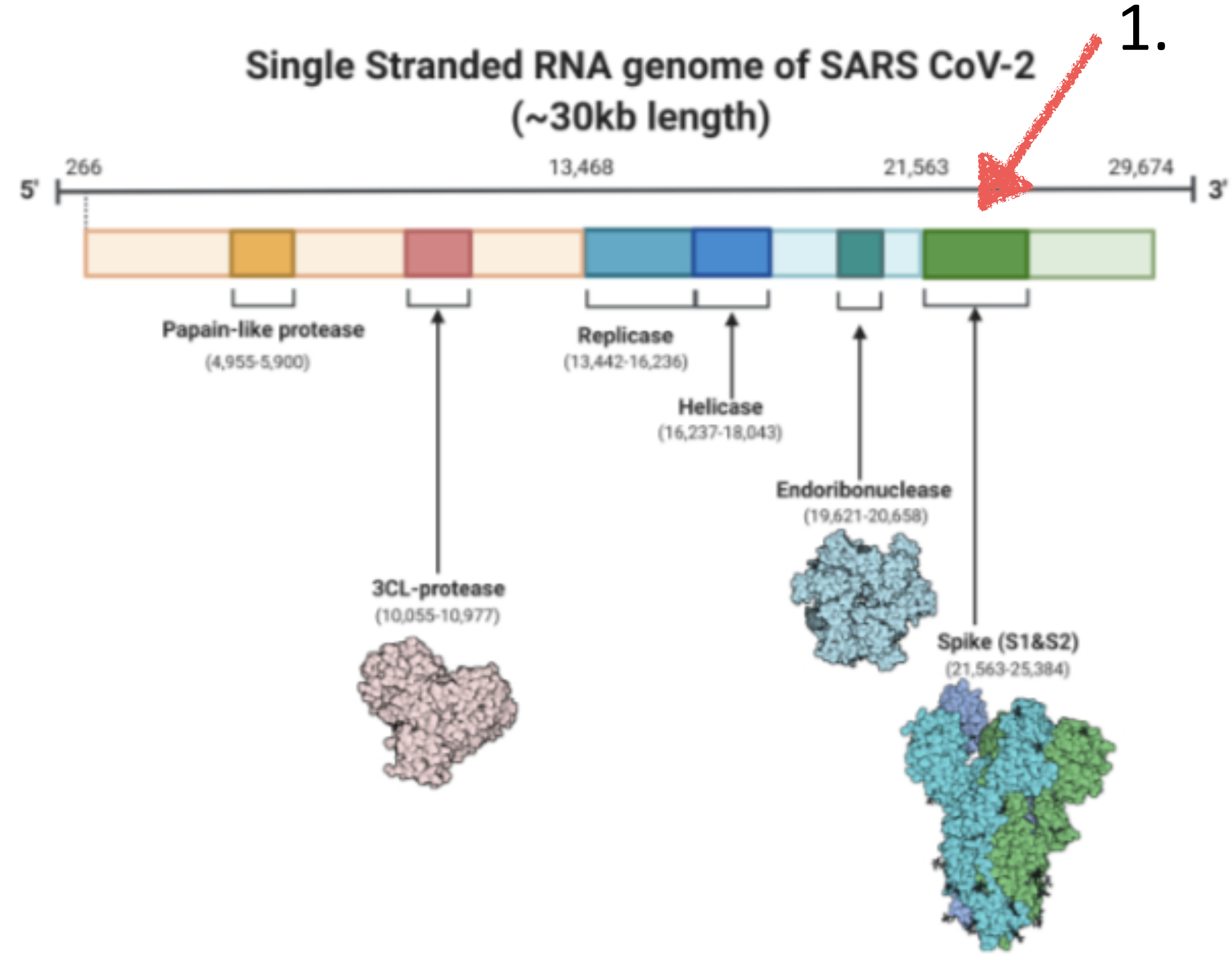
3.7 The causes of evolution

The sorting of developmentally produced variants can be by natural selection (when the ancestral and new variant confer a different reproductive advantage to the organism) or by drift (when the ancestral and new variant have same fitness):

“Random genetic drift also can modify gene frequencies …. If a fair coin is tossed, heads has the same chance of landing face up as tails does. But that does not mean that in a run of 100 tosses, there must be exactly 50 heads and 50 tails. By the same token, genes in a population may be selectively equivalent and still change their frequencies because of chance.” Sober p.. 19

3.8 The causes of evolution





1. Virus variant B: mutation M occurs in portion of genome coding for spike protein; 2. mutation M engenders a phenotypic change P (e.g., amino acid substitution) in the spike protein of the virus B; 3. phenotypic change P makes variant B fitter than most common variant A (without P) to infect host, in terms of transmissibility or in terms of resistance to vaccination-induced antibodies; 4. variant B will increase in frequency = evolution by natural selection.

3.9 The causes of evolution

1. What is the biological entity that by changing qualitatively, engenders a new kid of biotic entity?

Viruses and organismal entities that can replicate and reproduce.

Viruses replicate and construct lineages.

The changes they undergo are qualitative and a new kind of viral entity ensues.

The same goes for organismal entities.

3.10 The causes of evolution

Concerning the origin of variants: how does genomic change translate into a phenotypic change?

The simplest case is a point mutation such as the substitution of a nucleotide in a DNA molecule engendering an amino acid change in a polypeptide chain that, in its turn, changes the structure and/or function of the associated protein in a novel way (vis-à-vis the history of the lineage).

Note that the point mutation, *per se*, is ineffectual if it does not produce a change in the composition, structure or function of the phenotype (e.g., protein). Mutations could be "neutral".

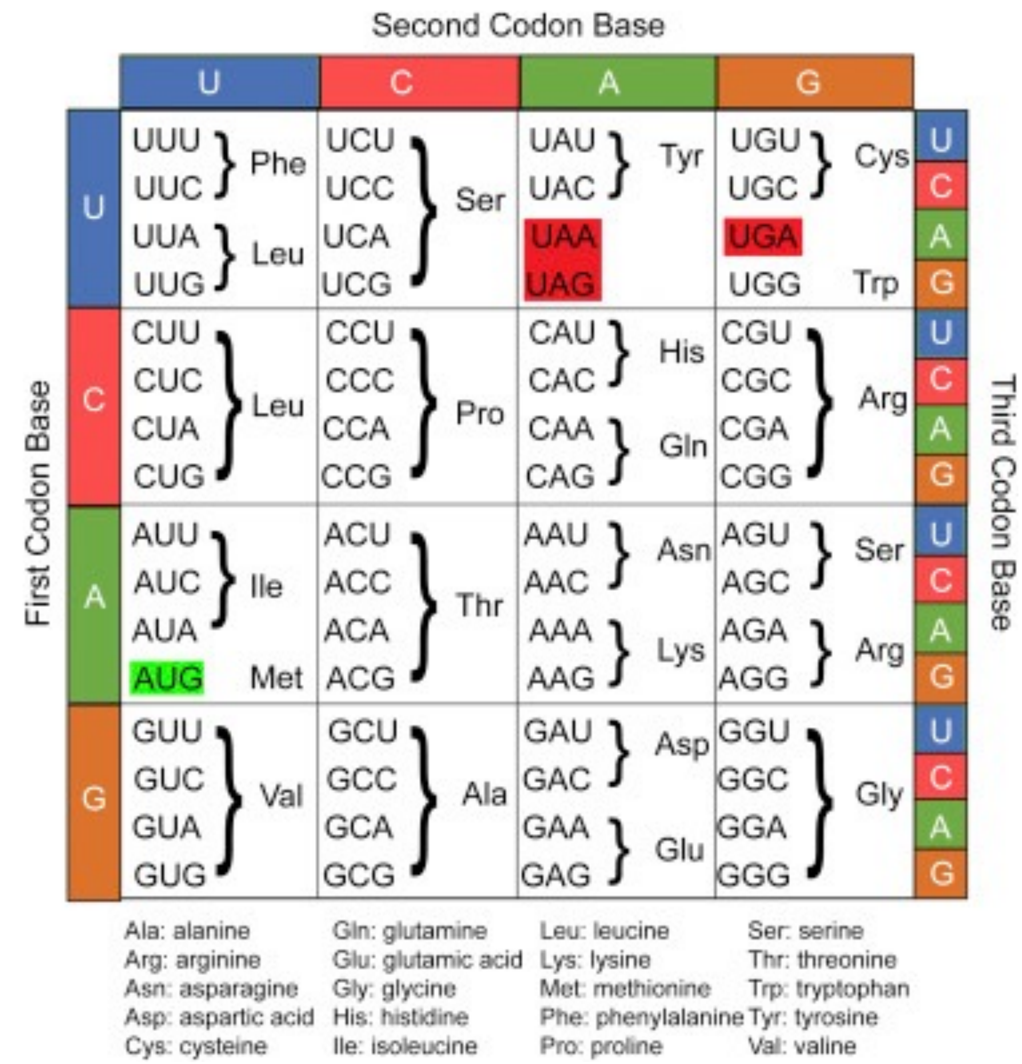
To engender such change, a developmental process is required (what Mahner and Bunge call an event of "ontological speciation" and Stoltzfus calls "mutation-and-altered-development).

3.11 The causes of evolution

Do neutral mutations exist in the first place?

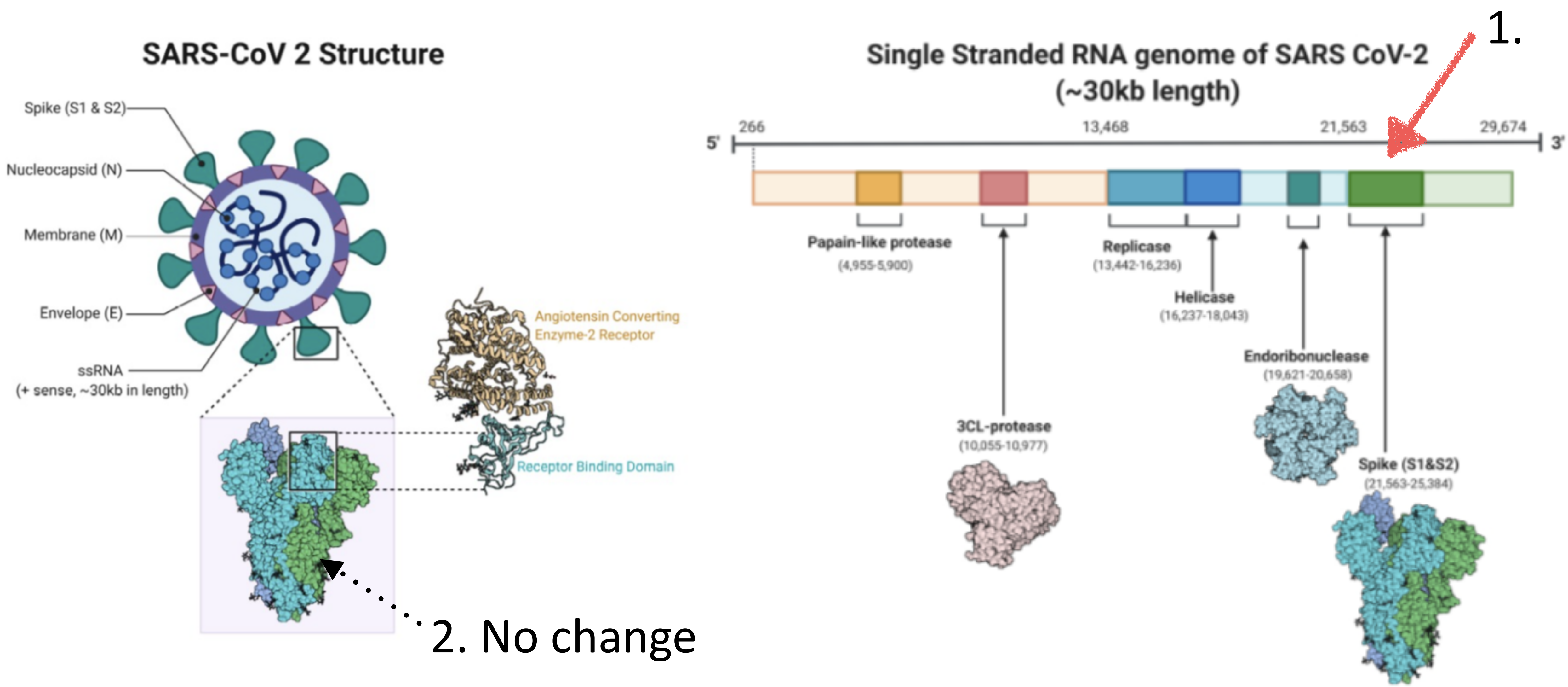
First of all, 25% of point mutations are clearly neutral because of the degeneracy of the genetic code.

If genomic changes are invisible to selection, they can only be sorted by drift (King and Jukes 1969).



Leucine is coded by six codons, among them CUU, CUC, CUA and CUG: changing the third nucleotide, in such case, would produce a neutral mutation.

3.12 The causes of evolution



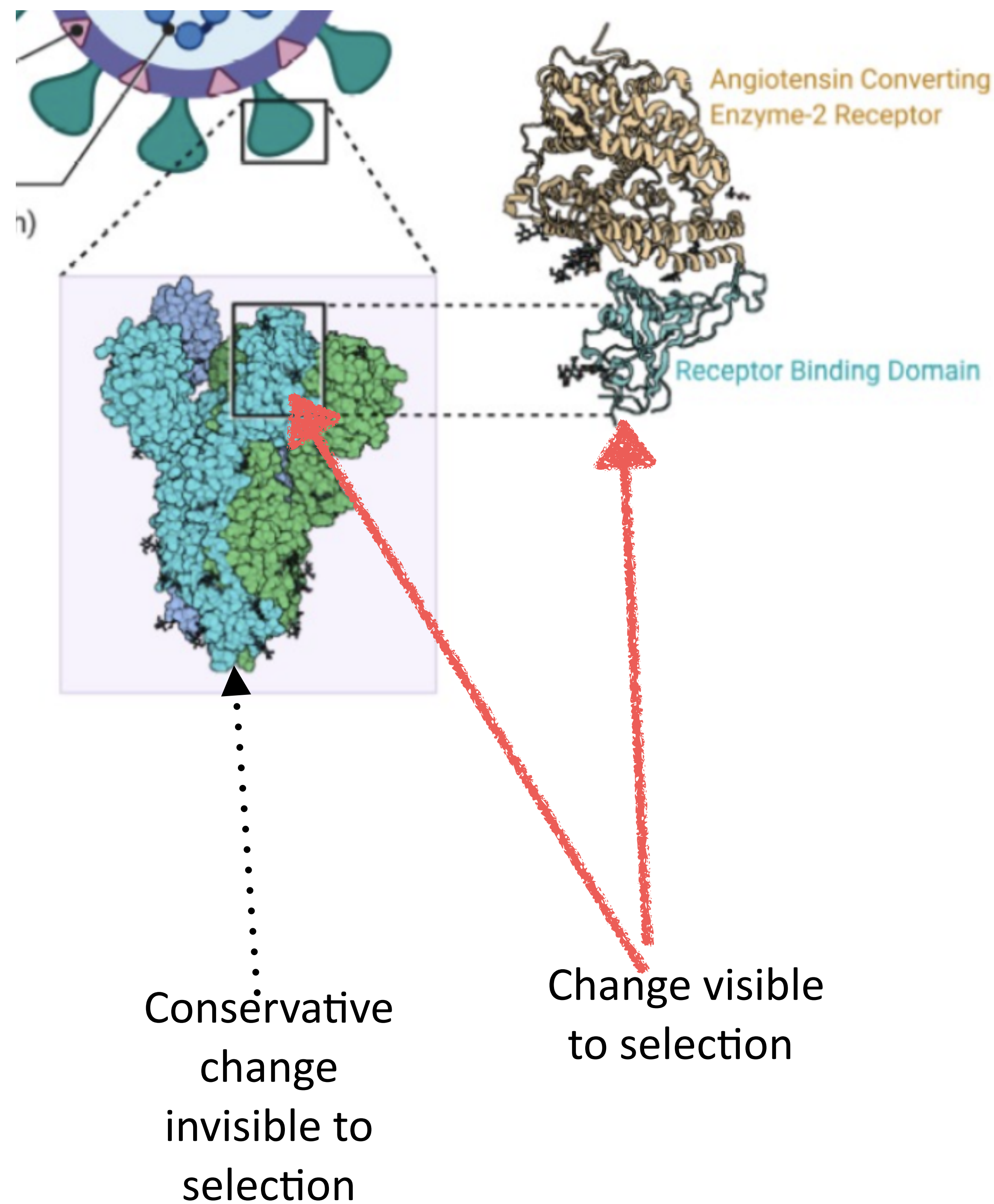
If the mutation M occurring in portion of genome coding for spike protein (1) does not engender a phenotypic change P (e.g., an amino acid substitution) in the spike protein (2), it is not an event of ontological speciation. This means that P evolves by drift because it is “invisible” to selection.

3.13 The causes of evolution

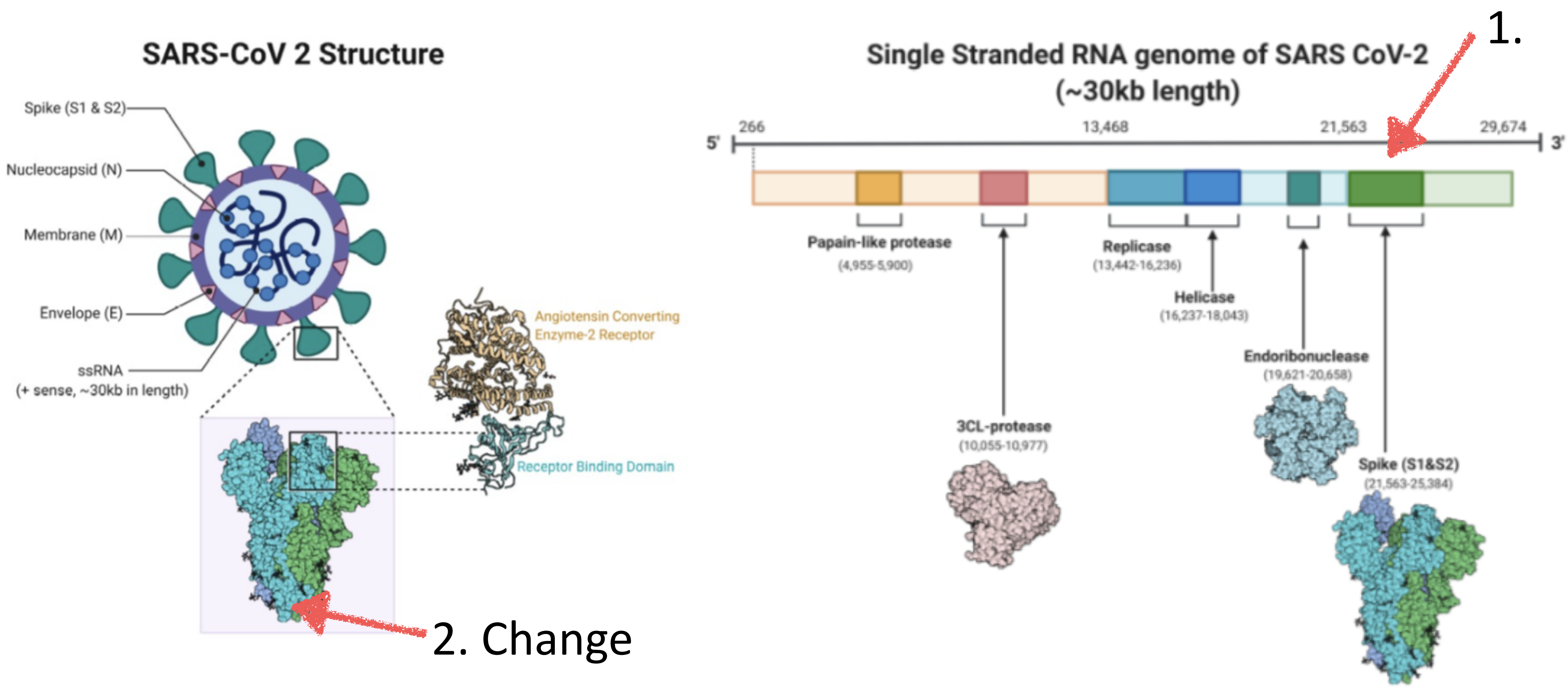
Secondly, many point mutations will be "conservative":

1. the replaced amino acid has the same chemical properties of the ancestral one (leucine, isoleucine and valine equivalence, King & Jukes 1969 p. 791) so that an amino acid change does neither cause a major structural or functional change;

2. the replaced amino acid has different chemical properties to the ancestral one but it is located in a functionally irrelevant site of the protein.



3.14 The causes of evolution

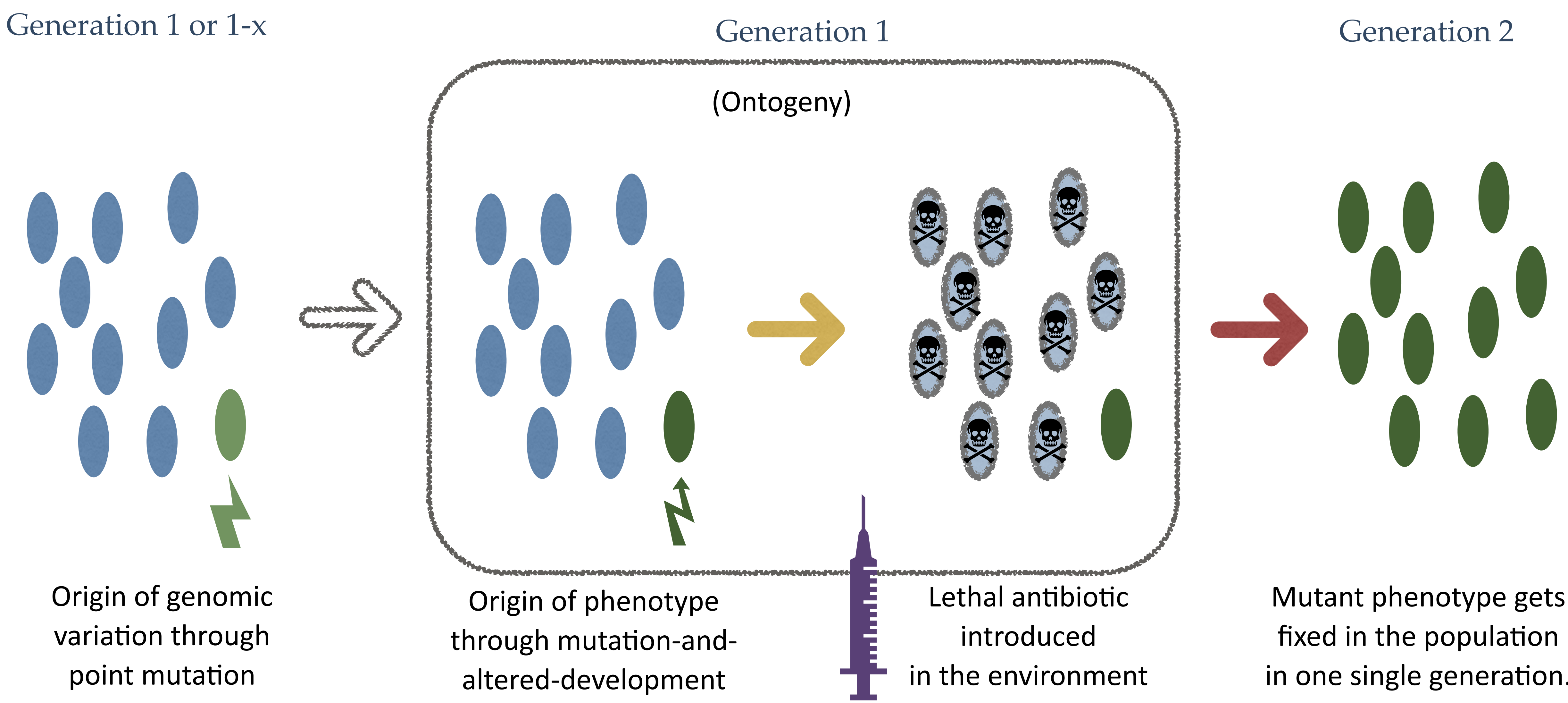


If the mutation M occurring in portion of genome coding for spike protein (1) engenders a phenotypic change P (e.g., an amino acid substitution) in the spike protein (2), but the spike protein is not functionally affected, it has no major fitness effect. This means that P might evolve by drift.

3.15 The causes of evolution

Evolution of antibiotic resistance.
Mutational and developmental events are distinguished. The mutant trait contributes hugely to organismal fitness.

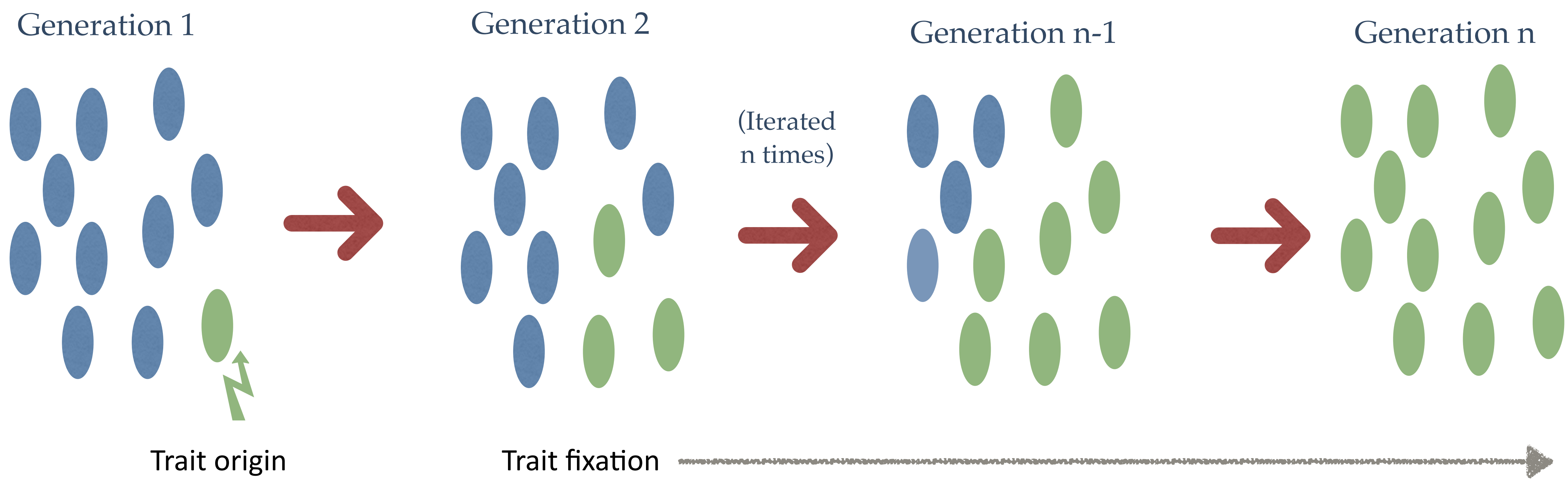
Example of selection for the mutant phenotypic trait.



3.16 The causes of evolution

<u>Evolution of vitamin C metabolic deficiency.</u> Here the mutational and developmental event coincide. The lost gene "codes" for a protein involved in the metabolism of vitamin C.

Mutant increases in frequency. Why? Selection or drift? Perhaps the mutant is "energetically" fitter? **<u>Likely example of drift</u>** (King & Jukes 1969, p. 792)**<u>: the phenotypic effect of gene loss is compensated by assimilation of vitamin C from the environment.</u>**



3.17 The causes of evolution

1. What is the biological entity that by changing qualitatively, engenders a new kid of biotic entity?

Viruses and organismal entities that can replicate and reproduce.

2. What processes cause such evolutionarily significant qualitative changes and their increase in frequency in the population?

Genomic change or mutation, mutation-and-altered-development, drift and natural selection.

Why advocating adaptationism then?

Summing up

Pre-evolutionism was characterised by stasis and fixity of species.

Darwin mixed a claim about common ancestry and the hypothesis that natural selection is the cause of biodiversity, biological complexity and adaptation.

Evolution is a unificatory framework for biology (Dobzhansky). Evolutionary biology is the fundamental biological science as it studies ultimate causes (Mayr).

Evolution is a process of qualitative change that leads to the emergence of new kinds of biotic entities. Many processes participate in such process. Emphasis on natural selection might thus not be justified.

Indeed, evolution might happen by genomic change, mutation-and-altered-development and drift. Evolution might be non-Darwinian (King and Jukes 1969).

Summing up

Another pending issue is whether evolution is ultimately gene-based.

Are there any non-genetic inheritance systems?

Does “evolutionary potential” have merely a genetic basis:

“… the opportunities for phenotypic evolution must ultimately be constrained by the physical resources existing at the genomic level ….” Lynch 2007, p. 8601

It’s not a very different view from Muller’s (last slide class 3).

Again, whether it’s correct, we’ll see.

Thanks again for participating to the classes. Anything else you need, feel free to contact me: dvecchi@fc.ul.pt (gabinete 4.3.16 FCUL).

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