CLASS 2 - 2 March: ORGANISM

1. Life = organismality
2. Autopoiesis
3. Organismal autonomy
4. Organismality is a continuum

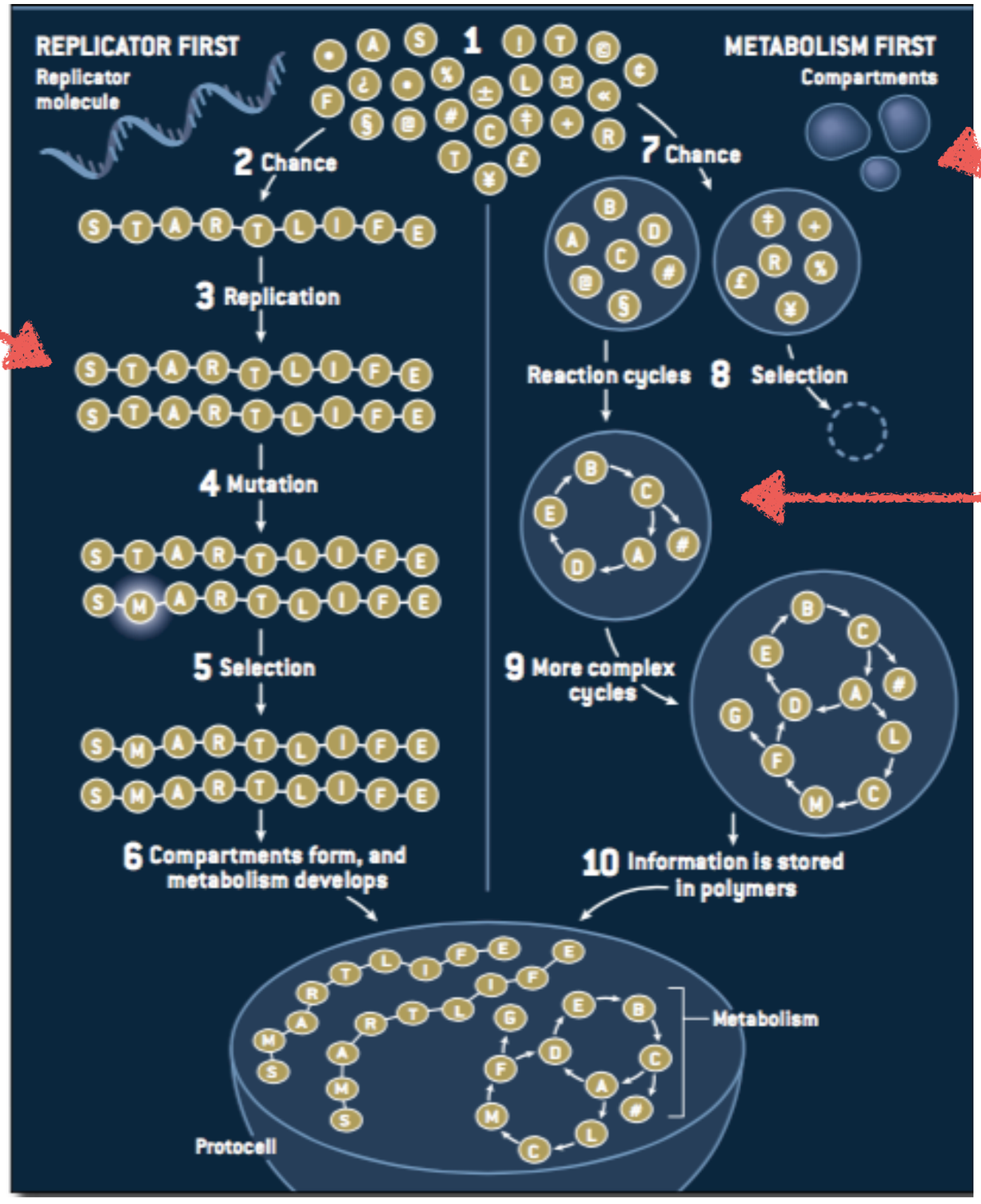
Bibliography: at the end

dvecchi@fc.ul.pt

0.1 Life = organismality

origin of replication

origin of compartments



origin of metabolism

QUESTION 1 - Replication, metabolism or compartments first?

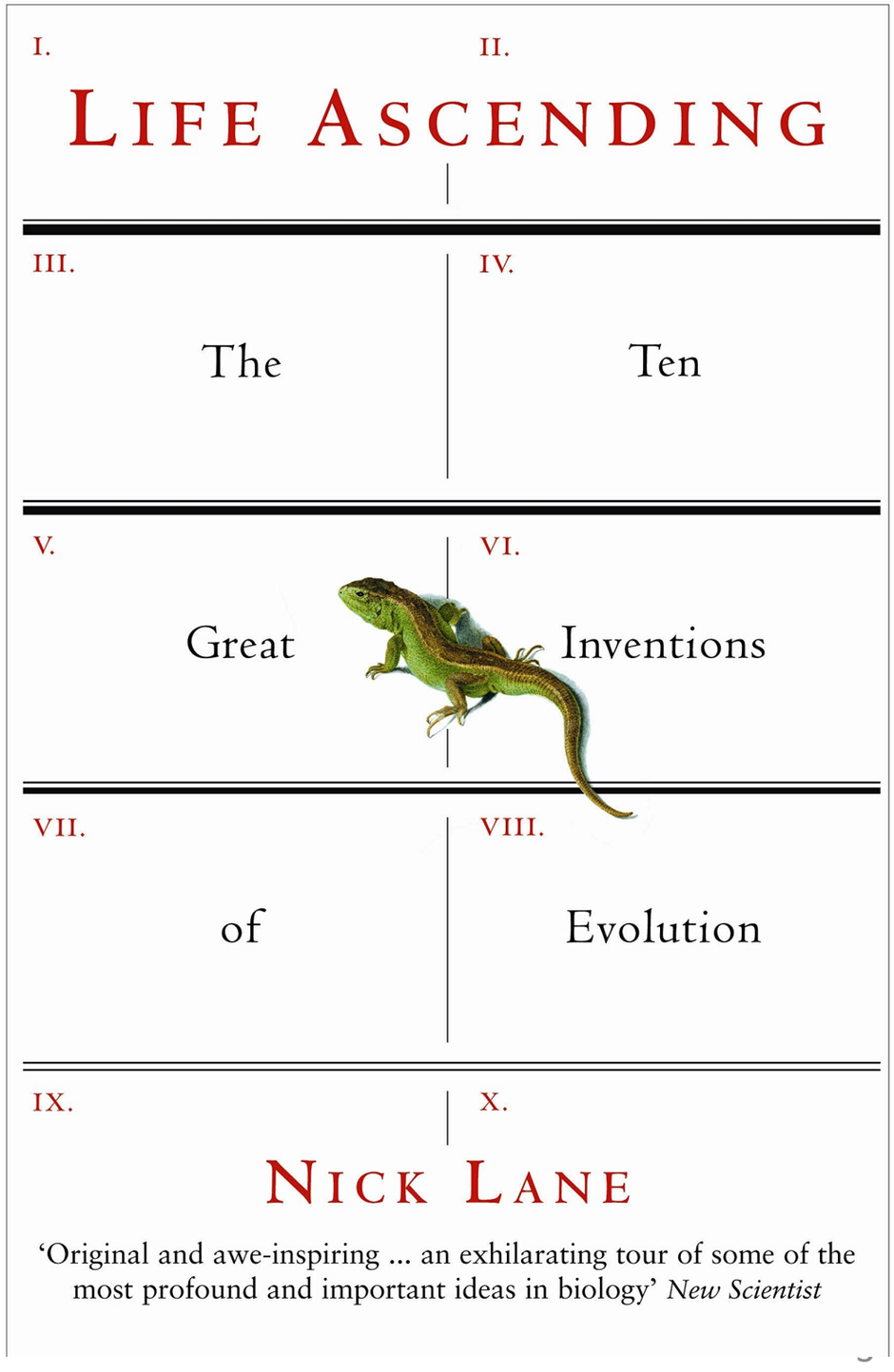
QUESTION 2 - What kind of biological system can be ascribed the property of living?

0.2 Life = organismality

QUESTION 1 - Replication, metabolism or compartments first?

Replication-first scenario as conceptually unsatisfying: “The idea that replicators like RNA were the first figments of life, predating any thermodynamic driving force, is, in Mike Russell’s words, ‘*like removing the engine from an automobile and expecting the regulating computer to do the driving*’.” Lane 2010, p. 14

We have seen in last class that the “thermodynamic force” might have been the Wood–Ljungdahl metabolic pathway according to Martin & Russell.

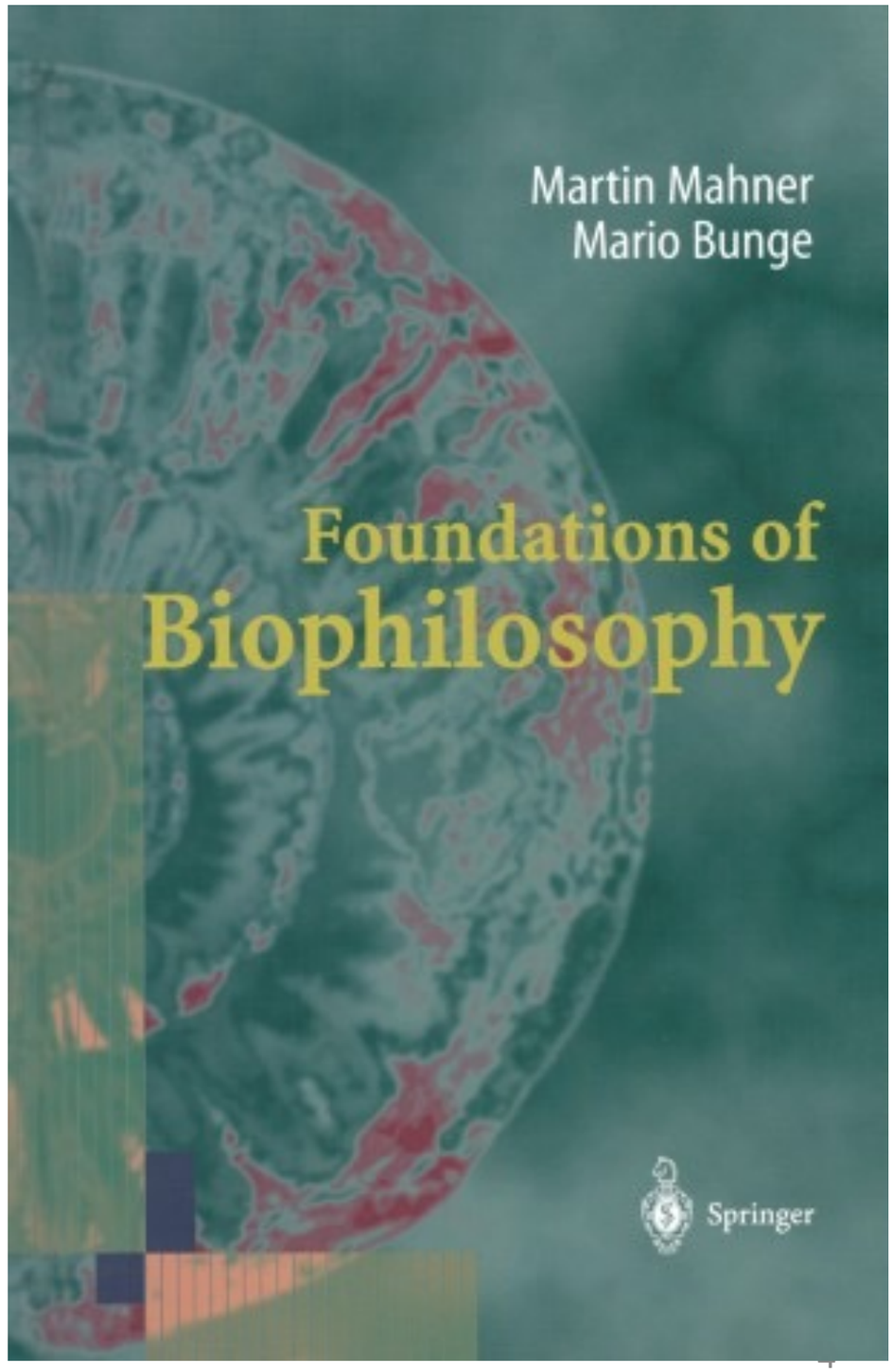


0.3 Life = organismality

QUESTION 1 - Replication, metabolism or compartments first?

<u>One alternative is to assume (by fiat, not argument) that life requires replication and compartmentalised metabolism:</u>

"… only the combination of nucleic acid molecules with metabolizing systems marks the '*beginning of life*' ….. Thus, the question of whether replicating molecules evolved first and metabolizing cells second, or whether the two originated the other way round, is irrelevant to the problem of life." Mahner & Bunge 1997 p. 145



0.4 Life = organismality

The simultaneous emergence of replication and compartmentalised metabolism potentially provides an answer to the second question:

QUESTION 2 - What kind of biological system can be ascribed the property of living? The evolutionary descendants of **protocells**.

Thus, **life = cell-based structure**.

0.5 Life = organismality

Life ≠ cell-based structure?

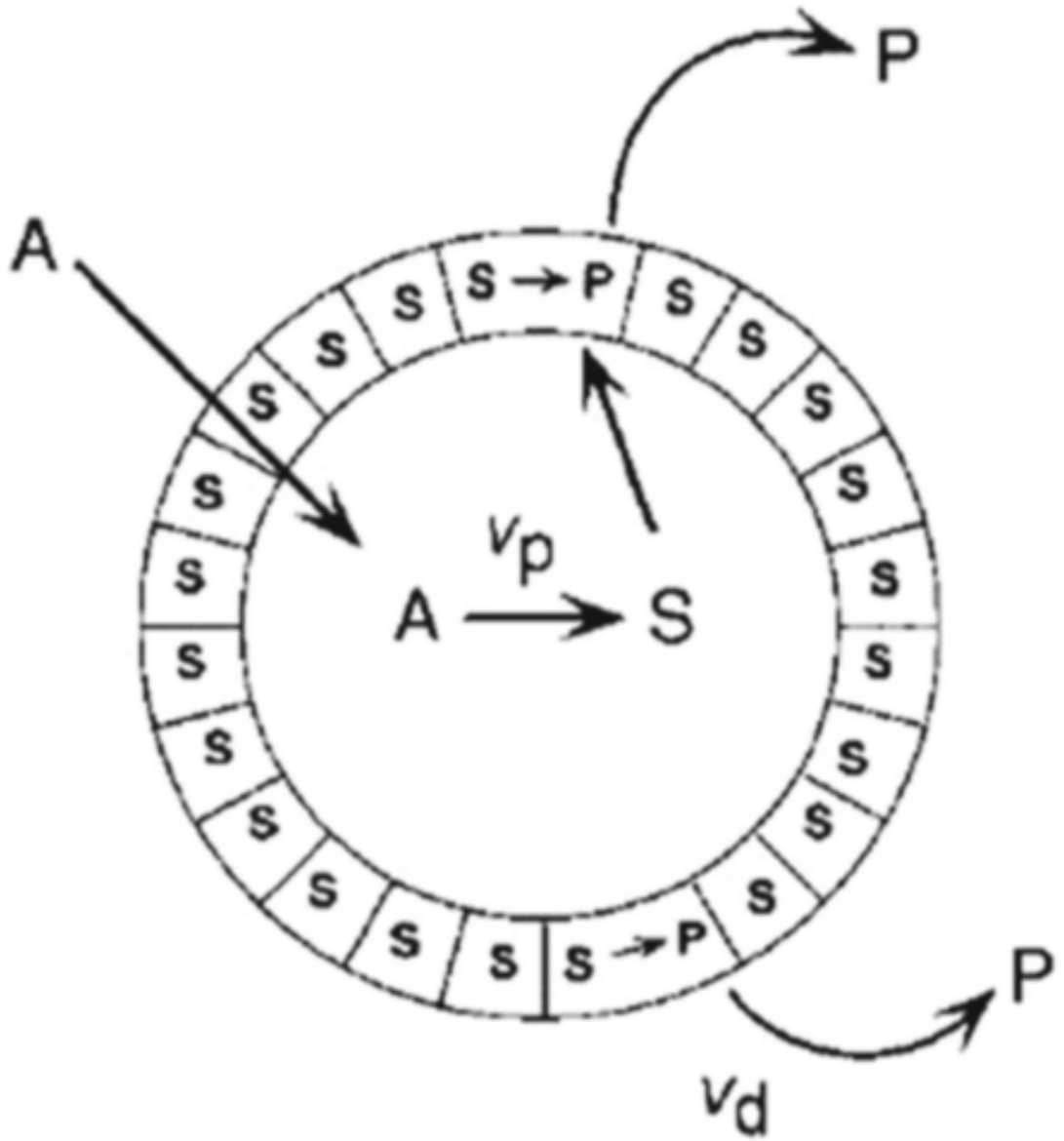
"Given the acceptance that life has evolved from a chemical context, ruling out self-replicating complexes of chemicals and molecules on the grounds that they are not cells seems misguided. **A commitment to life as exclusively cellular and monogenomically organismal would mean that the origins of life must involve a single leap from fully non-living to fully living, something that is conceptually difficult to accept** and, for that matter, provides a natural target for creationists to insist on the need for supernatural intervention." Dupré & O'Malley 2009 p. 15

0.6 Life = organismality

A commitment to life as cellular is implicit metabolic definitions (class 1): **life = cell = cellular organisation = organism = physiological autonomy**.

"A **living system** is spatially defined by **a semipermeable compartment of its own making** and which is self-sustaining by transforming external energy/nutrients by **its own process of component production**." Luisi, P. L. (1998). About various definitions of life. Origins of Life and Evolution of the Biosphere, 28, 613–622. p. 619

0.7 Life = organismality



$$v_p = \frac{d[S]}{dt} \quad ; \quad v_d = -\frac{d[S]}{dt}$$

if $v_p = v_d$ homoestasis

if $v_p > v_d$ self-reproduction

Zepik, H. H., Blöchliger, E., & Luisi, P. L. (2001). A chemical model of homeostasis. Angewandte Chemie, 113, 205–208.

0.8 Life = organismality

Metabolic definitions: emphasis on self-maintenance and physiological autonomy.

1. Thermodynamic openness and possibility to make a living out of environmental acquisition of precursors of molecular components and energy.

2. Self-maintenance is achieved through self-production of cellular components, including the cellular boundary.

How to characterise self-production or “autopoiesis” is the topic on section 2 and 3.

0.9 Life = organismality

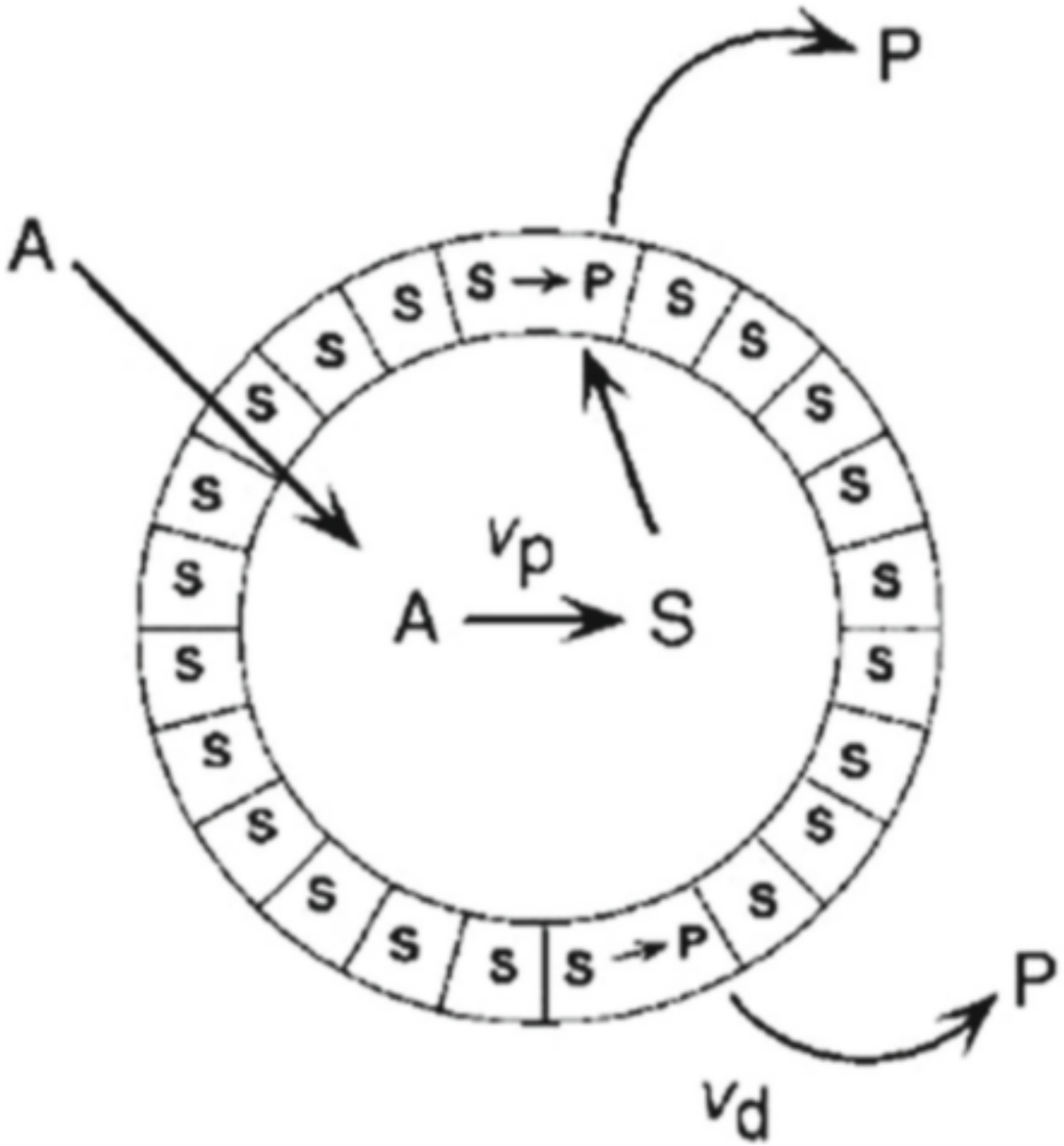
How do reproduction and evolution fit in this context?

In slide 2.10 of class 1, I claimed that the theory of evolution logically requires a beginning of life (by abiogenesis).

So, is life essentially replicative, i.e., is it essentially based on some form of reproduction and lineage-formation?

The metabolic definition we've considered denies this (see slide 4.15): "We have not forgotten evolution and reproduction, but …. we regard them as consequences of life, not prerequisites. A self-organizing …[if it grows by metabolism] …. will inevitably reach a size where it needs to divide …. In summary, staying alive is the fundamental necessity. Reproduction is not …" CBC p. 29

0.10 Life = organismality



$$v_p = \frac{d[S]}{dt} \quad ; \quad v_d = -\frac{d[S]}{dt}$$

if $v_p = v_d$ homoestasis

if $v_p > v_d$ self-reproduction

Zepik, H. H., Blöchliger, E., & Luisi, P. L. (2001). A chemical model of homeostasis. Angewandte Chemie, 113, 205–208.

0.11 Life = organismality

On the other hand, the origin scenarios taken into consideration clash only on whether replication is **causally primary**, not in the sense of denying that life is also about lineage-formation.

This poses two puzzling questions:

1. Are lineage-forming entities alive even though they have no independent metabolism (e.g., prions, viruses)?

2. Conversely, are entities with metabolism alive even though they do not form lineages or reproduce (e.g., somatic cells of multicellular organisms)?

0.12 Life = organismality

Prions: propagate without DNA involvement as templates for other prions; does the “self- propagational” status of prions gives them the status of being alive?

Viruses: 1. they exhibit “developmental stages” (from inert virions or dormant provirus to active state, whether lytic or lysogenic); 2. their evolutionary origin is unknown (primeval pre-cellular entities constituting a distinct super-domain vs. cellular parasites evolved after emergence of cellular life?); 3. they exhibit some form of autonomy; for instance, the mimivirus (Dupré & O’Malley 2009 p. 7) carries genes for translation and DNA repair, thus seemingly representing “ …. entities in transition from viruses to free-living organisms …”; 4. some viruses are “infected” by virophages. Are they alive?

0.13 Life = organismality

“Life, according to our analysis, occurs at the intersection of lineage formation and (typically collaborative) involvement in metabolism. Entities that are problem cases, such as viruses, can be understood as alive when actively collaborating. When not collaborating, they have at most a potential for life.” Dupré & O’Malley 2009 pp. 14-15

By accepting this claim, we avoid the question of whether prions, viruses etc. are alive or not (by fiat, not argument).

0.14 Life = organismality

2. Conversely, are entities with metabolism alive even though they do not form lineages or reproduce (e.g., somatic cells of multicellular organisms)?

Some entities might have the “potential” to reproduce but have relinquished their reproductive “rights”. E.g., in certain contexts, somatic cells might replicate and generate lineages.

Most importantly, all entities with an appropriate metabolism (captured by metabolic definitions such as autopoiesis, see part 3) seem intuitively alive even though they are not reproducing. **This shows, to me at least, that metabolism is an essential property of life.**

0.15 Life = organismality

We started from a metabolic definition of life in cellular terms, avoiding the question of whether non-cellular forms can be considered alive: life = cell-based structure = organism = physiological autonomy.

But we shall also consider another dimension of autonomy as potentially crucial: reproductive.

Let us thus take a more ecumenical stance and assume that: **life = cell-based structure = organism = physiological + reproductive autonomy**.

Characterising these two dimensions of autonomy is the topic of this class.

Let us first take a look at the history of the organism concept.

2.1 Autopoiesis

Let us take a deeper look at one metabolic-based view of the organism: Varela's and Maturana's autopoiesis.

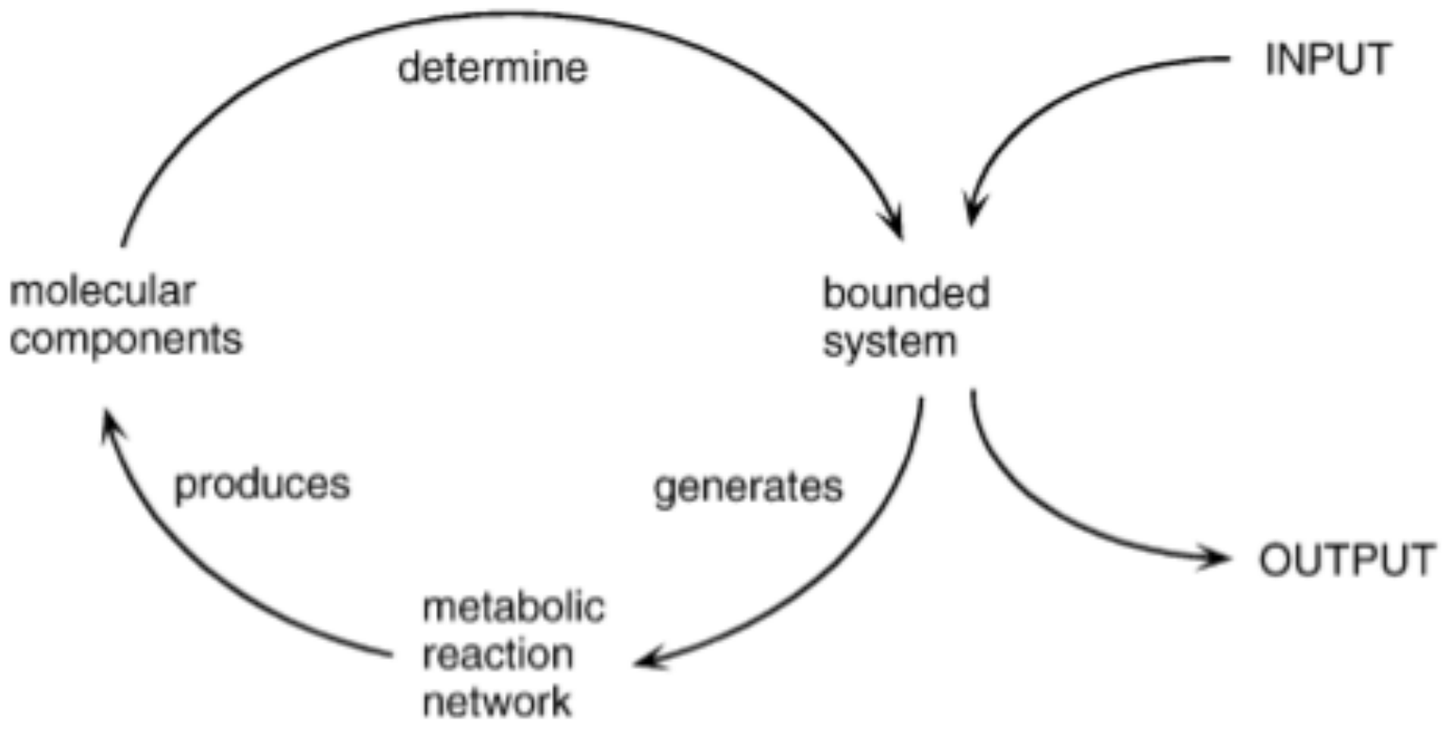
Autopoietic unit = minimal life form = most elementary organism = cell.

Autopoiesis = life as emergent property = essence of the living.

Autopoietic unit is capable of preserving its identity: "… system that is capable of self-sustaining owing to an inner network of reactions that re-generate all the system's components …. The living is a factory that makes itself from within. " Luisi 2003 p. 51-52

2.2 Autopoiesis

Life obeys a circular logic without an identified beginning and/or end. In order to ascertain whether an entity is living we need to verify: "…. (1) whether the system has a semipermeable boundary that (2) is produced from within the system and (3) that encompasses reactions that re-generate the components of the system." Luisi 2003, p. 51



2.3 Autopoiesis

Table 1 The game of the two lists

List of the living	List of the non living
The fly	The radio
The tree	The automobile
The mule	The virus
The baby	The crystal
The mushroom	The moon
The amoeba	The computer

What discriminates the living from the non-living?

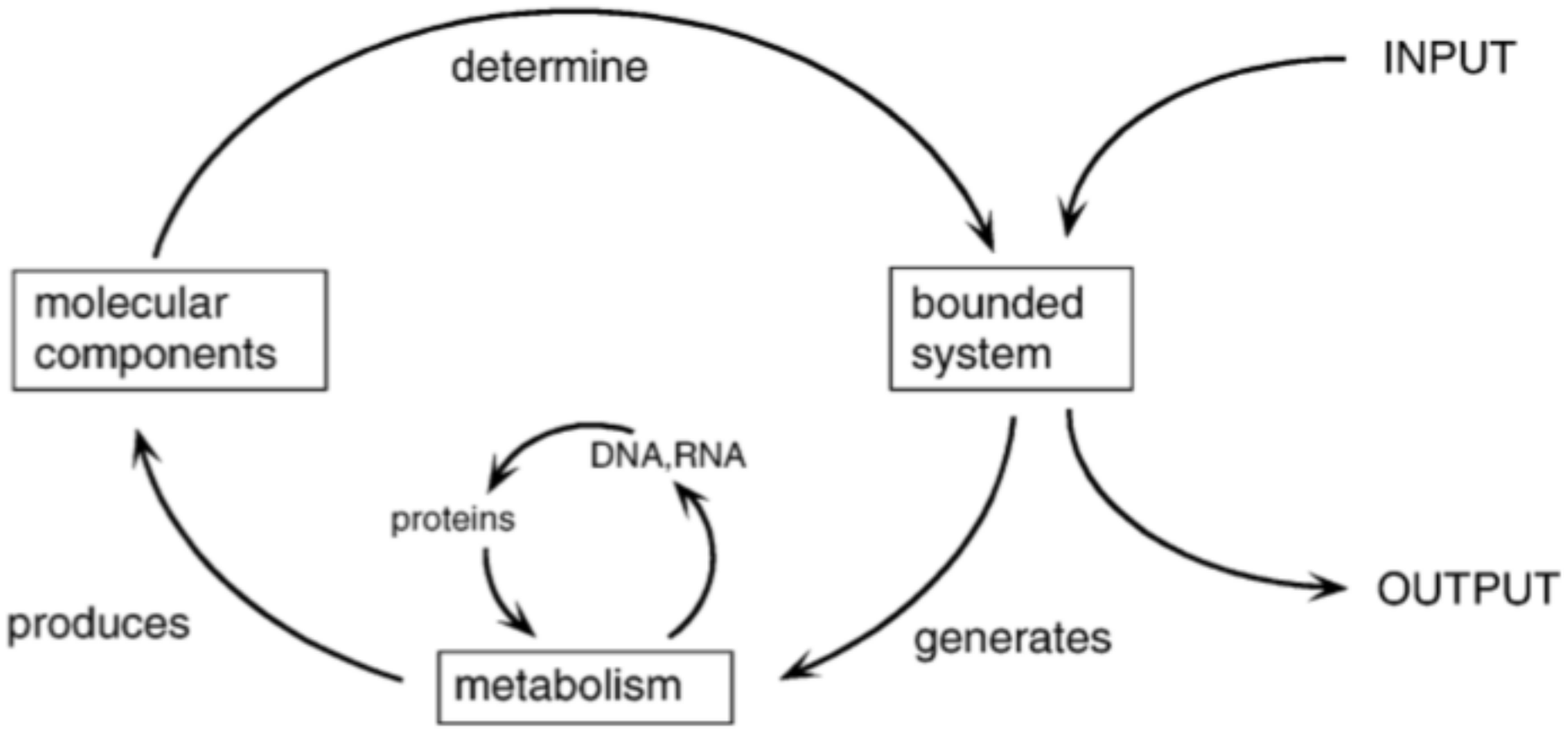
What is the quality (or qualities) which is present in all members of the "living list" and which is not and cannot be present in any of the elements of the "non-living" list?

(Luisi 2003, p. 51)

2.4 Autopoiesis

Characterisation does not take into account:

1. DNA (even though it is consistent with it, cf. Luisi 2003, p. 53);

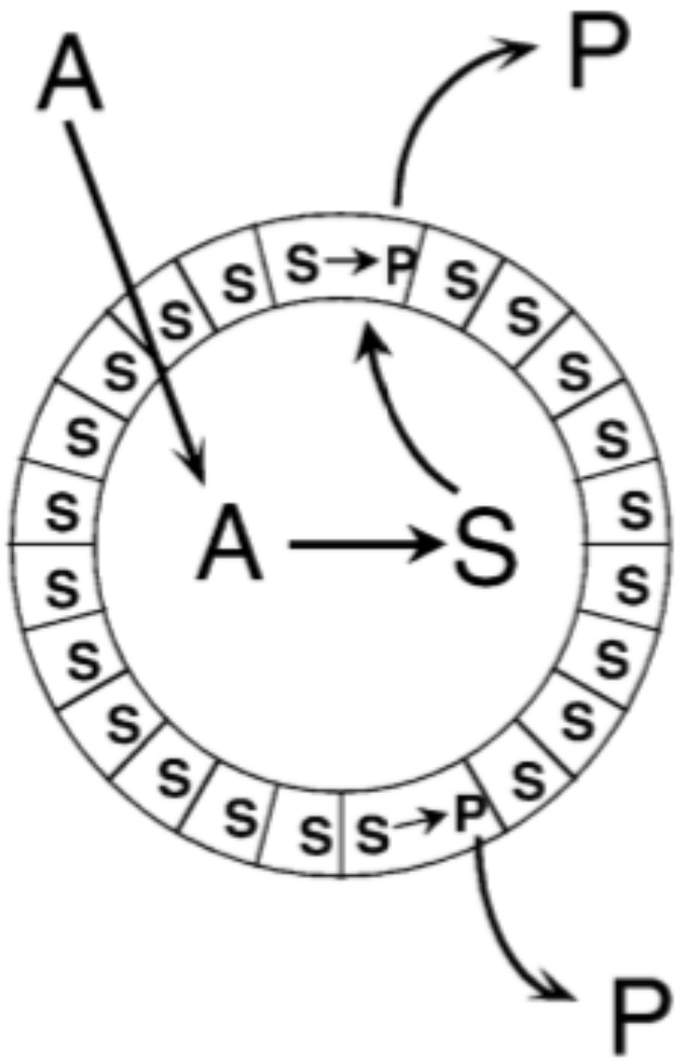


2.5 Autopoiesis

Characterisation does not take into account:
2. evolution and inheritance:

“Varela states that to include reproduction in the definition of the living would be ontologically wrong (Varela 2000), as “reproduction is a ...consequence of the existence of individuals. The difficult thing is to create an organism that is capable to self-reproduce with its own boundary. To divide it up in two is easy...”. And again (Varela and Maturana 1998), “In order to reproduce something, the unit must first be constituted as a unit, with an organization that defines this unit itself. This is simple common sense logic.” Luisi 2003, p. 53

2.6 Autopoiesis



$$v_{gen} = \frac{d[S]}{dt} \quad ; \quad v_{dec} = \frac{-d[S]}{dt}$$

if $v_{gen} = v_{dec}$ **homoestasis**

if $v_{gen} > v_{dec}$ **growth**

Growth —> reproduction (Luisi 2003, p. 53) …. equivalent to slide 0.11

2.7 Autopoiesis

Autopoiesis has an important implication, i.e., the emergence of autonomy:

"… with life, an autopoietic unit acquires the singular property of becoming a **biologically autonomous system**, namely one that is capable of specifying its own rules of behavior …. **autopoiesis is the mechanism that imparts autonomy to the living**." Luisi 2003, p. 52

How is an organism autonomous? Physiologically and reproductively.

Organism = **physiological and reproductive autonomy**.

2.8 Autopoiesis

Autopoiesis is a metabolic definition of life: emphasis on self-maintenance and physiological autonomy:

1. Thermodynamic openness and possibility to make a living out of environmental acquisition of precursors of molecular components and energy.
2. Self-maintenance is achieved through self-production of cellular components, including the cellular boundary.

2.9 Autopoiesis

Must the boundary be self-produced? “Martin and Russell (2007)… argue strongly against such theories [making a self-produced boundary a prerequisite] on various grounds ….. We find their arguments persuasive, and accordingly do not regard the lack of membranes fabricated internally …. as long as alternative natural compartments are available.” CBC p. 32

Must all cellular components be self-produced? How should cellular physiological autonomy be characterised?

2.10 Autopoiesis

How is self-production compatible with thermodynamic openness?

What kind of self-production is needed for autopoiesis?

1. All parts of the organism?
2. A subset of the parts? If so, which subset?

What organismal components are self-produced? It crucially depends on the nature of the organism-environment interface.

Organisms constantly, opportunistically and contingently assimilate and functionally integrate components from the environment. This process has been called “entrenchment".

3.1 Organismal autonomy

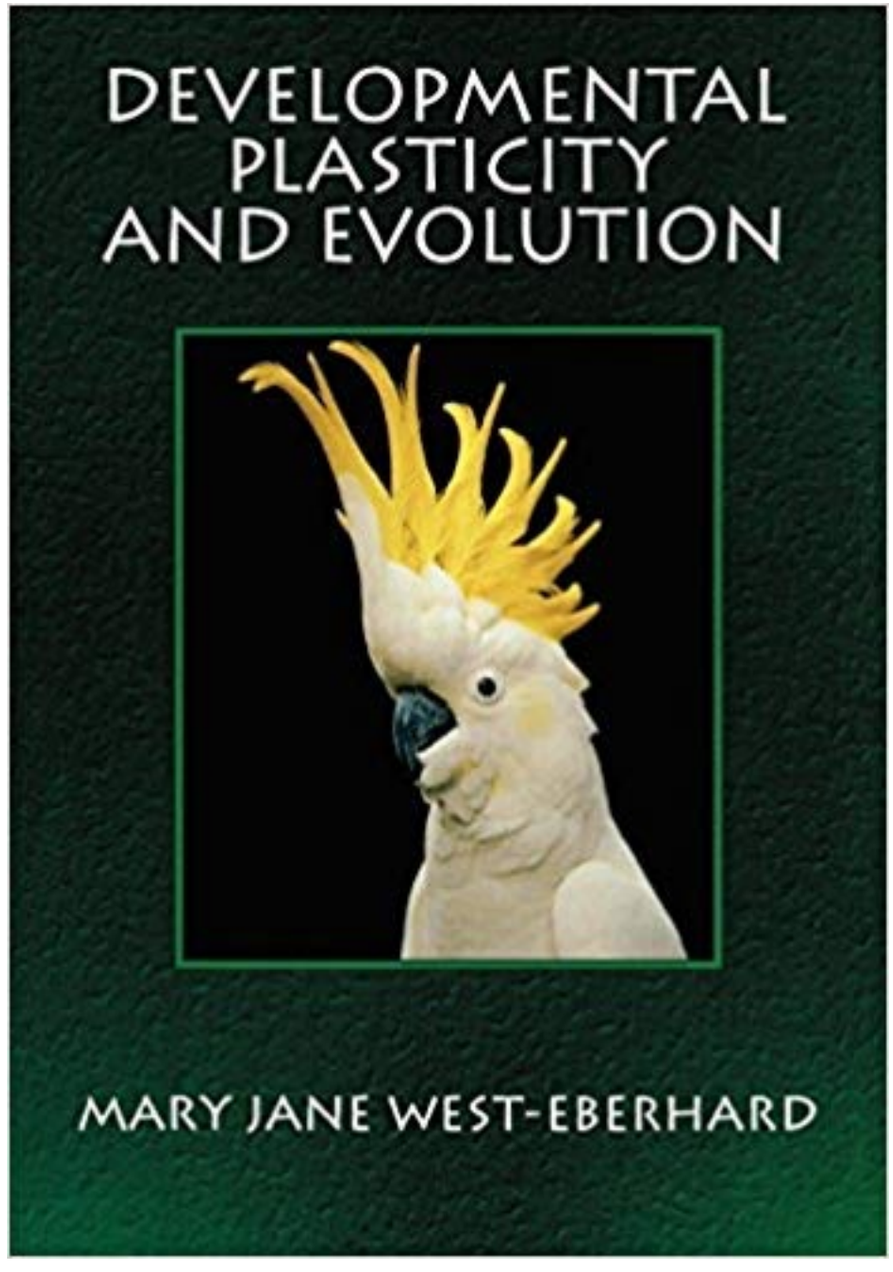
Entrenchment refers to the causal role of the environment:

a. in the regulation of development (as developmental signals);

b. in the production of the phenotype (as building blocks in phenotype construction or formation).

Focus on phenotype production.

“Entrenchment of some environmental elements is so thorough and widespread that we forget they were once evolutionary innovations.” West-Eberhard 2003, p. 500.



3.2 Organismal autonomy

Entrenchment refers to the causal role of the environment:

a. in the regulation of development (as developmental signals);

b. we shall focus on the assimilation of building blocks in phenotype construction.

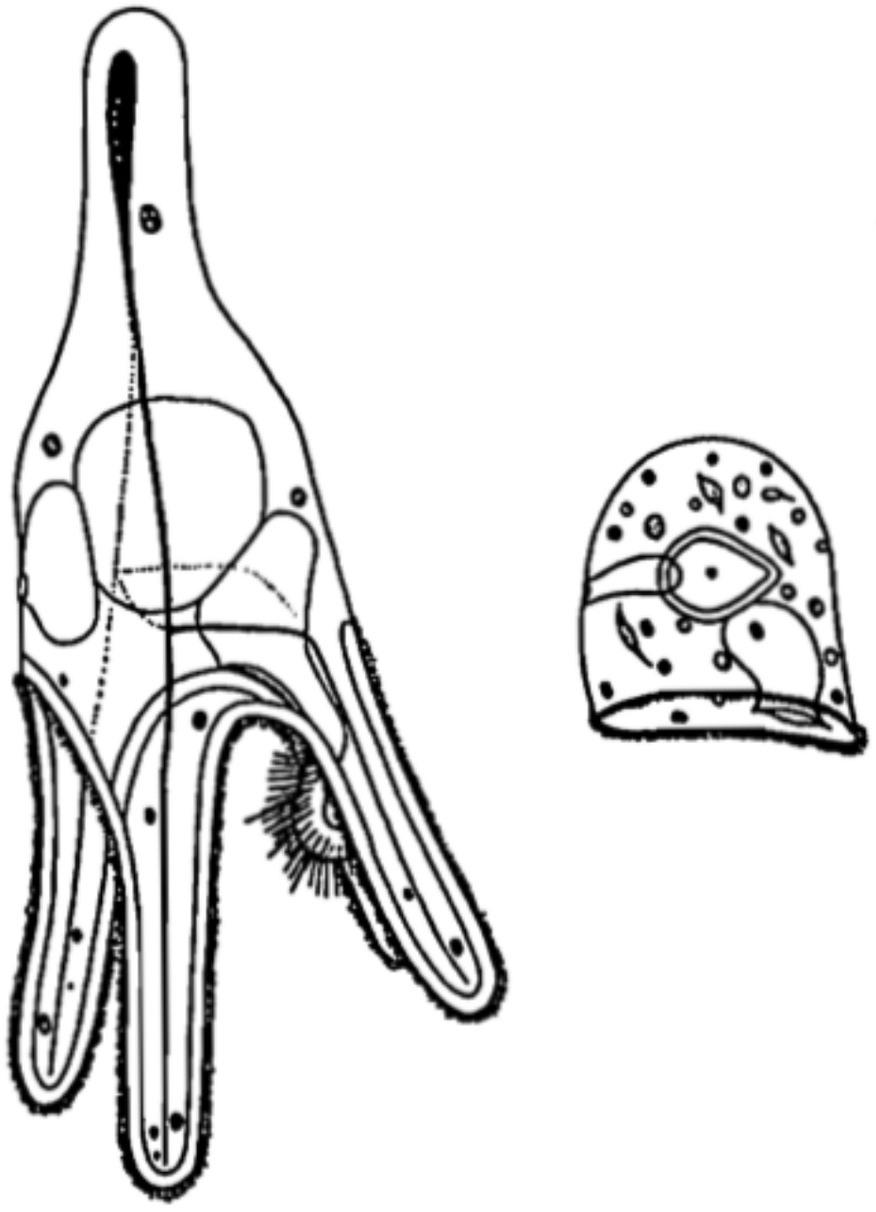


Fig. 26.2. Classical demonstration of environmental influence on larval development in a sea urchin:

3.3 Organismal autonomy

Varieties of material entrenchment:

1. abiotic: physical and chemical precursors of abiotic origin deployed for maintenance of metabolic capacities;

2. biotic:

2.1. of materials produced by other organisms (e.g., DNA, nutrition, proteins);

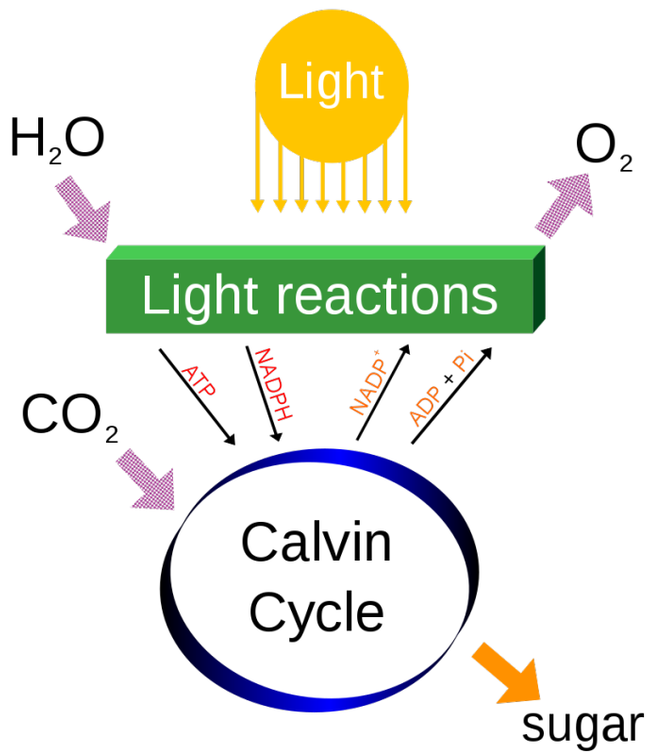
2.2 of entire organisms (e.g., symbionts).

3.4 Organismal autonomy

<u>1. abiotic entrenchment:</u>
physical and chemical precursors of abiotic origin deployed for maintenance of metabolic capacities.

Photosynthesis based on assimilation of photons.

Nucleotide synthesis (e.g., purines) based on assimilation of chemical precursors including carbon dioxide.

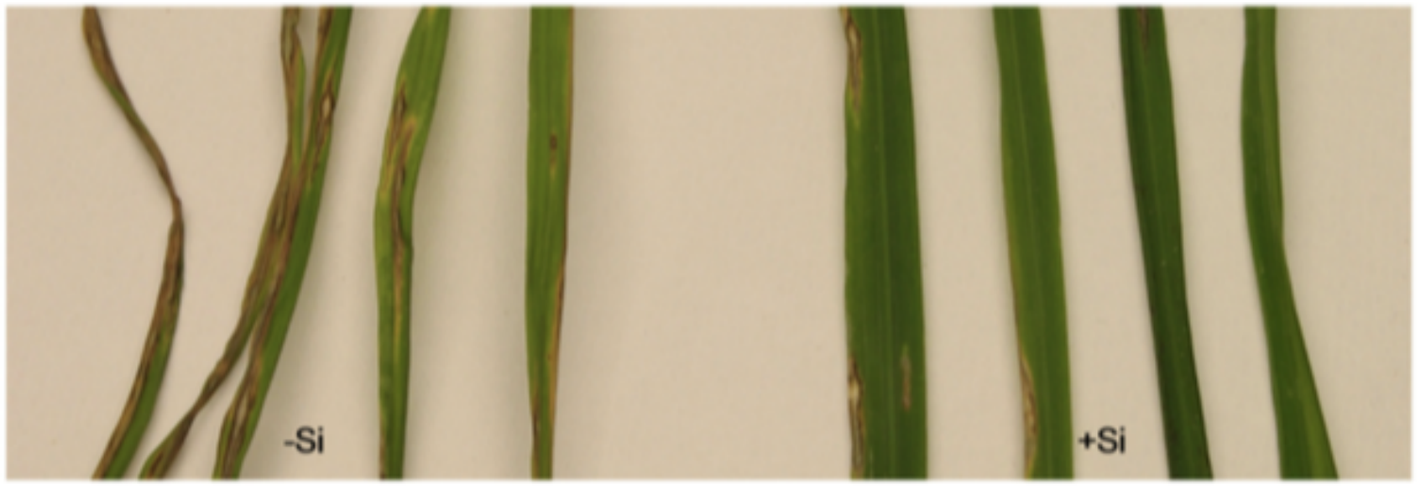


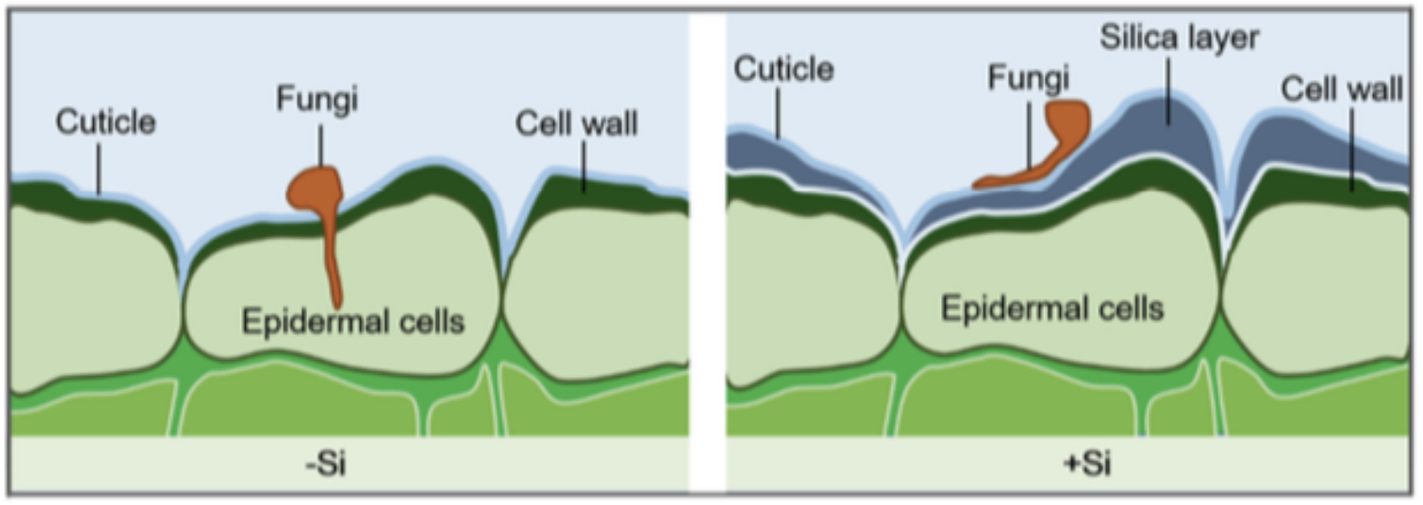
3.5 Organismal autonomy

<u>1. abiotic entrenchment:</u>
chemical precursors of abiotic origin deployed for phenotype construction.

Silicon was not considered a physiologically essential element (necessary to complete the plant's life cycle, cf. Epstein 1994).

But it plays a significant physiological role in rice plants (e.g., in cell walls for fungal resistance, cf. Wang et al. 2017).

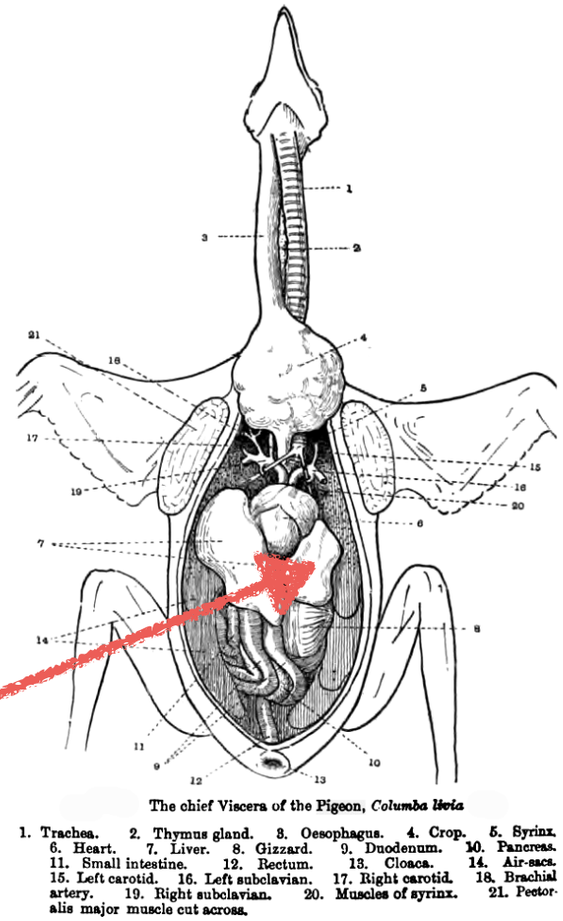




3.6 Organismal autonomy

<u>1. abiotic entrenchment:</u>
physical and chemical precursors of abiotic origin deployed for maintenance of metabolic capacities.

Turkeys assimilate stones, which are functionally integrated as gastroliths: gastroliths located in the <u>gizzard</u> perform a function in digestion.



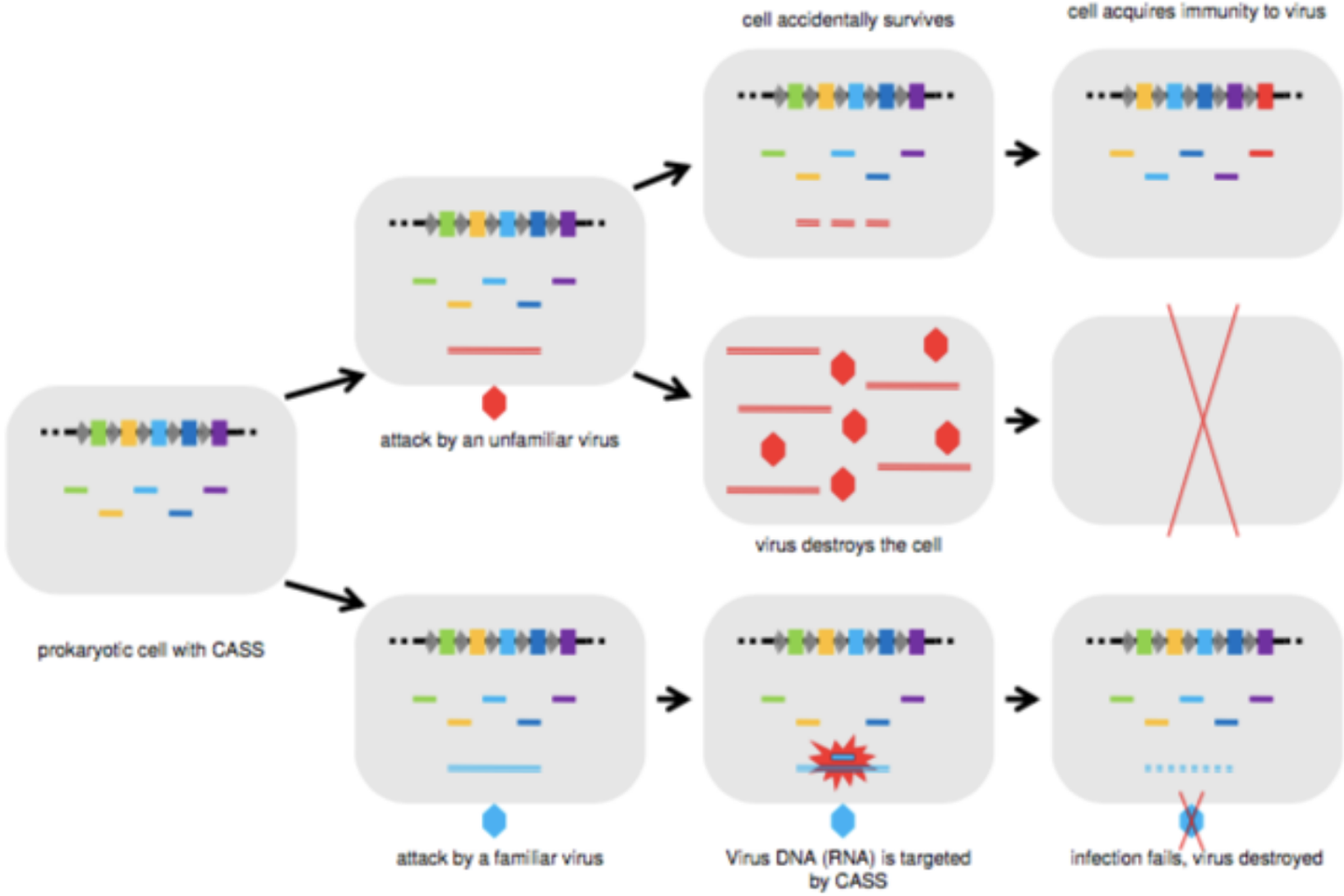
The chief Viscera of the Pigeon, *Columba livia*

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

3.7 Organismal autonomy

2.1. Biotic entrenchment:

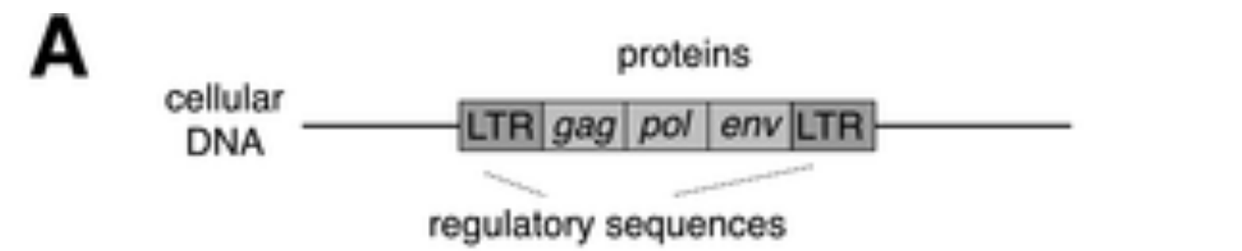
Lateral DNA transfer: e.g., bacteria incorporate viral DNA sequences in their genomes as CRISPR cassettes which are then redeployed to destroy phage mRNAs (Koonin and Wolf 2009).

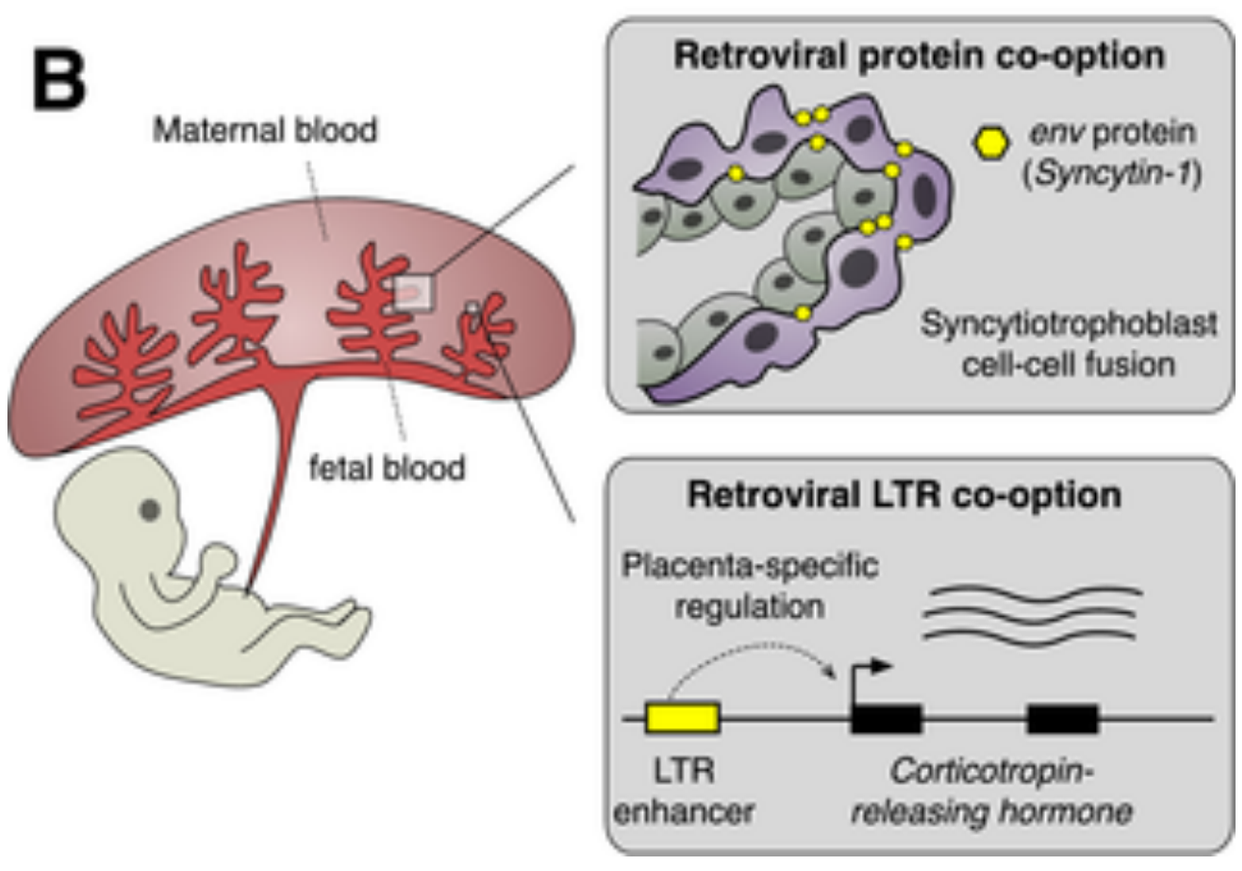


3.8 Organismal autonomy

2.1. Biotic entrenchment:

Lateral DNA transfer: origin of placental mammals likely due to the incorporation of retroviruses from other organisms (they allow the rewiring of cell circuitry to produce the progesterone-responsive uterine decidual cell as well as the syncytin fusion proteins of the mammalian placenta, (cf. Gilbert 2015 p. 616).



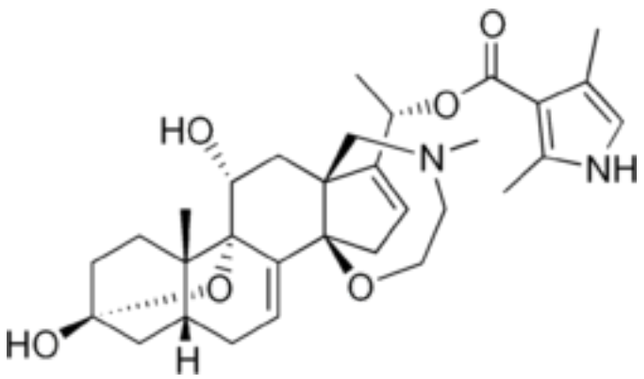


3.9 Organismal autonomy

<u>2.1. Biotic entrenchment:</u>

Nutrition: e.g., batrachotoxin - found, for instance, on the skin of several Colombian frogs (e.g., golden poison frog *Phyllobates terribilis*)
-cannot be extracted from them when reared in captivity or in the laboratory.

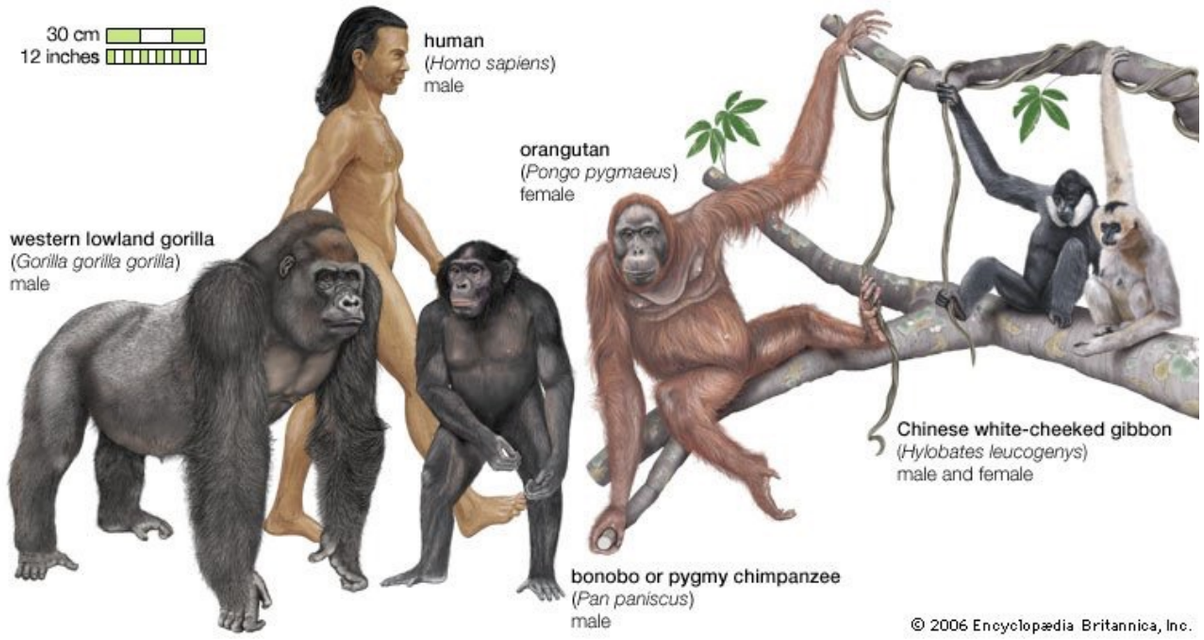
These frogs assimilate it by eating batrachotoxin-containing insects (Dumbacher et al. 2004).



3.10 Organismal autonomy

2.1. Biotic entrenchment:

Nutrition: the incapacity to convert 2-keto-L-gulonolactone to ascorbic acid (vitamin C) in primates and guinea pigs (King & Jukes 1969, p. 792). Assimilation from environment is generally simple.



3.11 Organismal autonomy

2.1. Biotic entrenchment. Nutrition -Microbiota (*Bacteroidess thetaiotamicron*) promotes angiogenesis (blood vessel formation) in mammals. Interaction between microbiota and organismal cells by induction in the expression of the Angiogenin-4 gene in mouse intestinal cells.

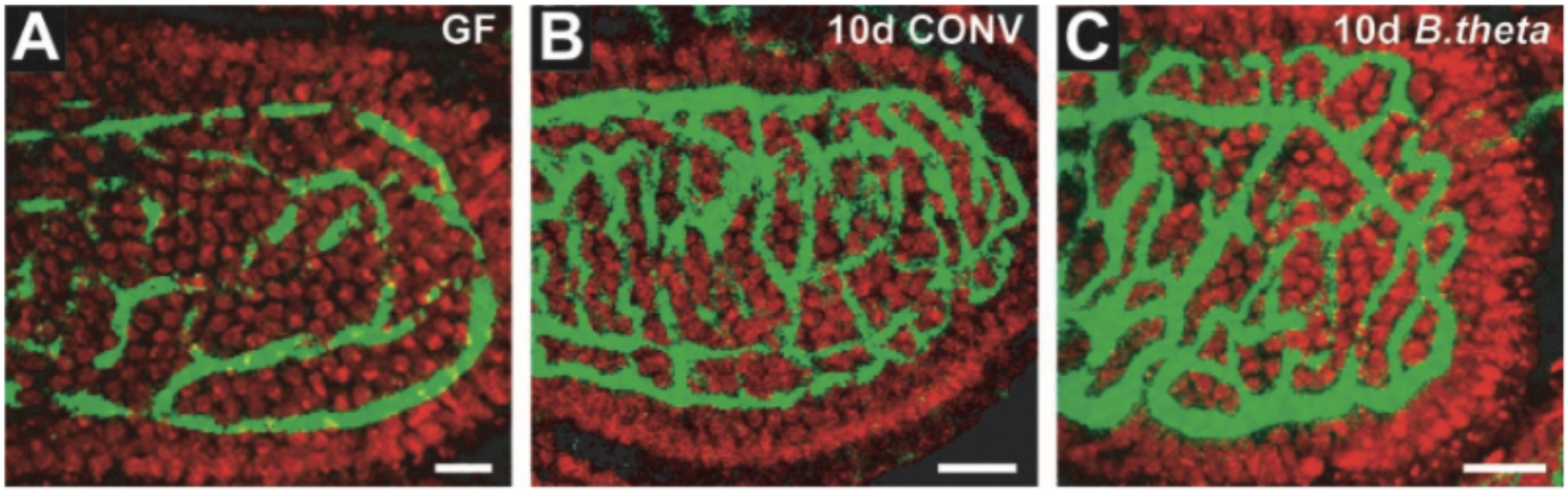


Fig. 2. Rapid microbial induction of angiogenesis in small intestinal villi of adult ex-germ-free mice. (*A–C*) Confocal scans of the capillary network present in the upper third of small intestinal villi. Whole mounts are from the junction between the middle and distal thirds of the small intestines of 6-week-old NMRI mice (capillaries, green; nuclei, red). (*A*) Germ-free (GF) mouse. (*B*) Age-matched ex-germ-free conventionalized (CONV) mouse killed 10 days after colonization with an unfractionated microbiota harvested from a conventionally raised "donor." (*C*) Ex-germ-free mouse 10 days after colonization with *B. thetaiotaomicron* (*B. theta*) alone. To view three-dimensional rotating images of the capillary networks shown in *A–C*, see Movies 3–5, which are published as supporting

Stappenbeck T.S. et al. 2002. Developmental regulation of intestinal angiogenesis by indigenous microbes via Paneth cells. PNAS 99(24):15451-5. doi: 10.1073/pnas.202604299.

3.12 Organismal autonomy

Entrenchment affects all organismal functions of all organisms.

3.4-3.6 compatible with self-production (the idea behind is thermodynamic opens); but 3.7-3.11 challenge directly self-production.

Thus, **self-production is conditional on what is available in the environment**. Organisms relinquish self-production capacities by assimilating the products of the self-production capacities of other organisms. Entrenchment compensates lack of self-production capacities.

3.13 Organismal autonomy

Hence, no self-produced physiological autonomy in the strict sense.

What kind of self-production is needed for autopoietic organismality (slide 2.10)?

~~1. All parts of the organism?~~

2. A subset of the parts? If so, which subset?

Cornish-Bowden & Cardénas (2020, p. 31, section 3.1.4): **all catalysts must be products of the system itself**.

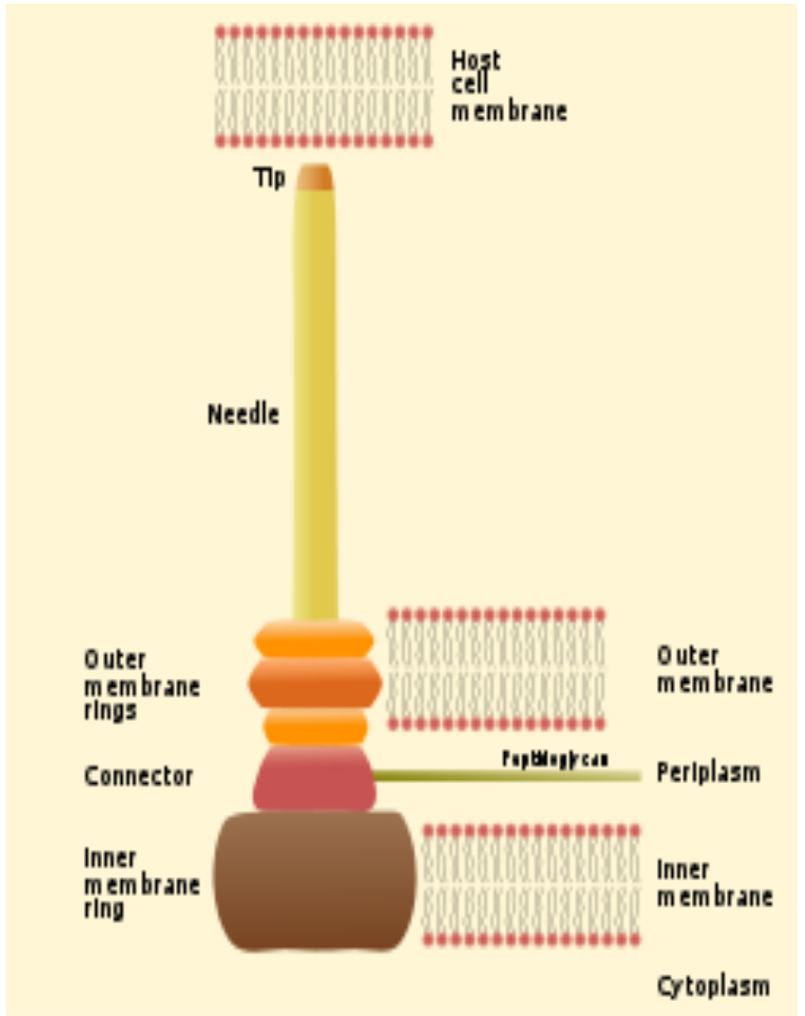
Are all catalysts (e.g., enzymatic proteins) needed for host metabolism synthesised internally?

3.14 Organismal autonomy

2.1. Biotic entrenchment: protein transfer:

“Many enteric pathogens have developed a specialized secretion system, called type III secretion, to mediate the direct transfer of proteins into the host cell membrane. Through this mechanism, extracellular bacteria that are in close contact with eukaryotic cells can deliver bacterial proteins into the cytosol of these cells.”

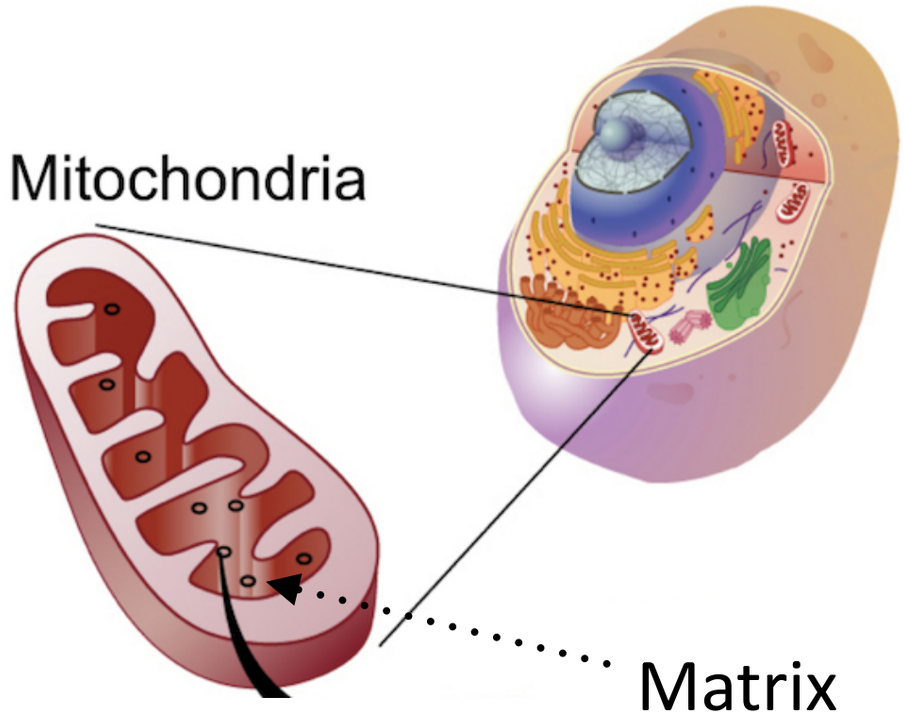
Lu et al. 2001 p. 1125S

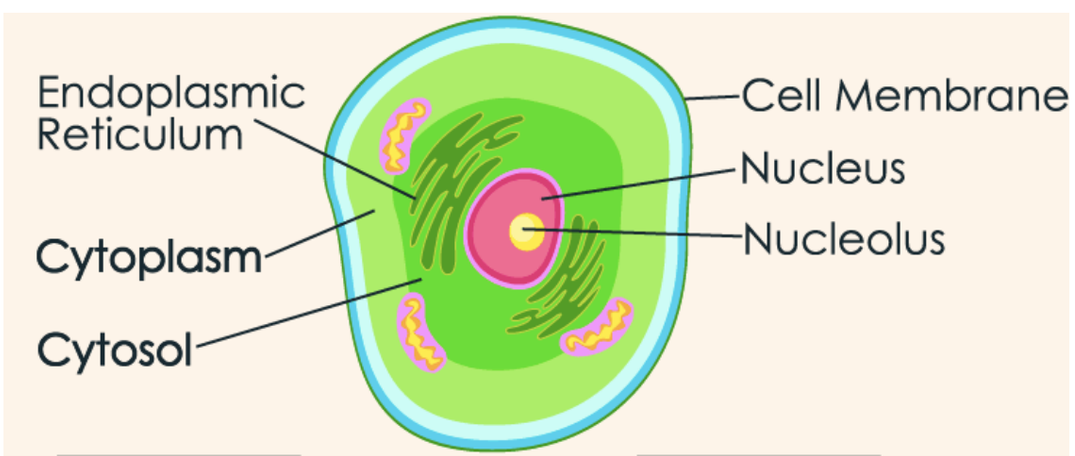


3.15 Organismal autonomy

2.1. Biotic entrenchment: protein transfer.

Assembly of a functional mitochondrion requires import of proteins from the cytosol (of the cell) and export of proteins from the matrix (of the mitochondrion) ….. it is now clear that proteins encoded in the nucleus as well as those encoded in the mitochondrion also move from the matrix into and across the inner membrane, a process defined here as export. (Poyton et al. 1992).





3.16 Organismal autonomy

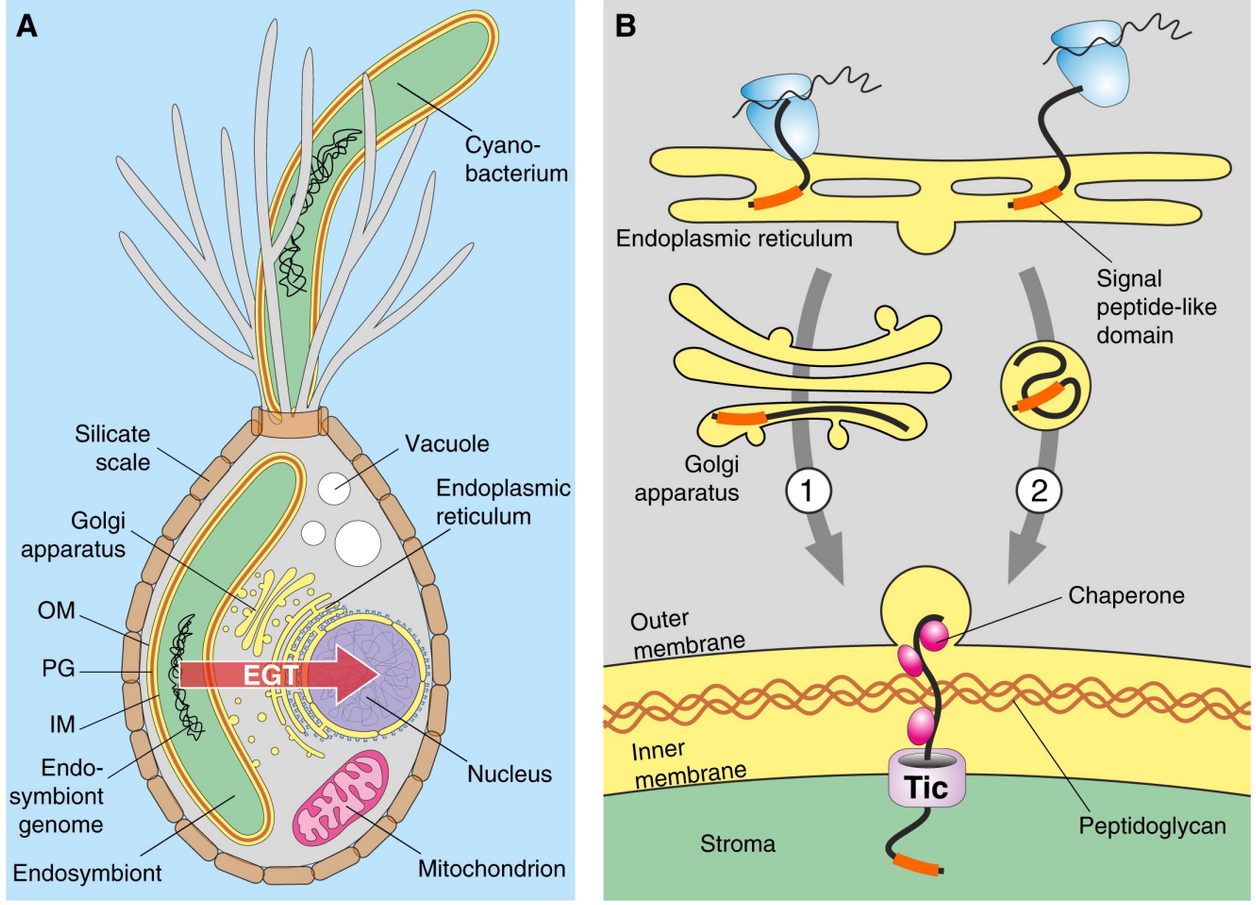
There is no biological defensible general sense of self-production (see 3-7-3.11) or even a more specific sense of enzymatic or catalytic self-production (see 3.14-3.15) that can be defended.

All organisms are not only thermodynamically open, but also open to entrenchment of environmental materials.

When biotic entrenchment of other organismal entities is involved, the same point is reinforced.

3.17 Organismal autonomy

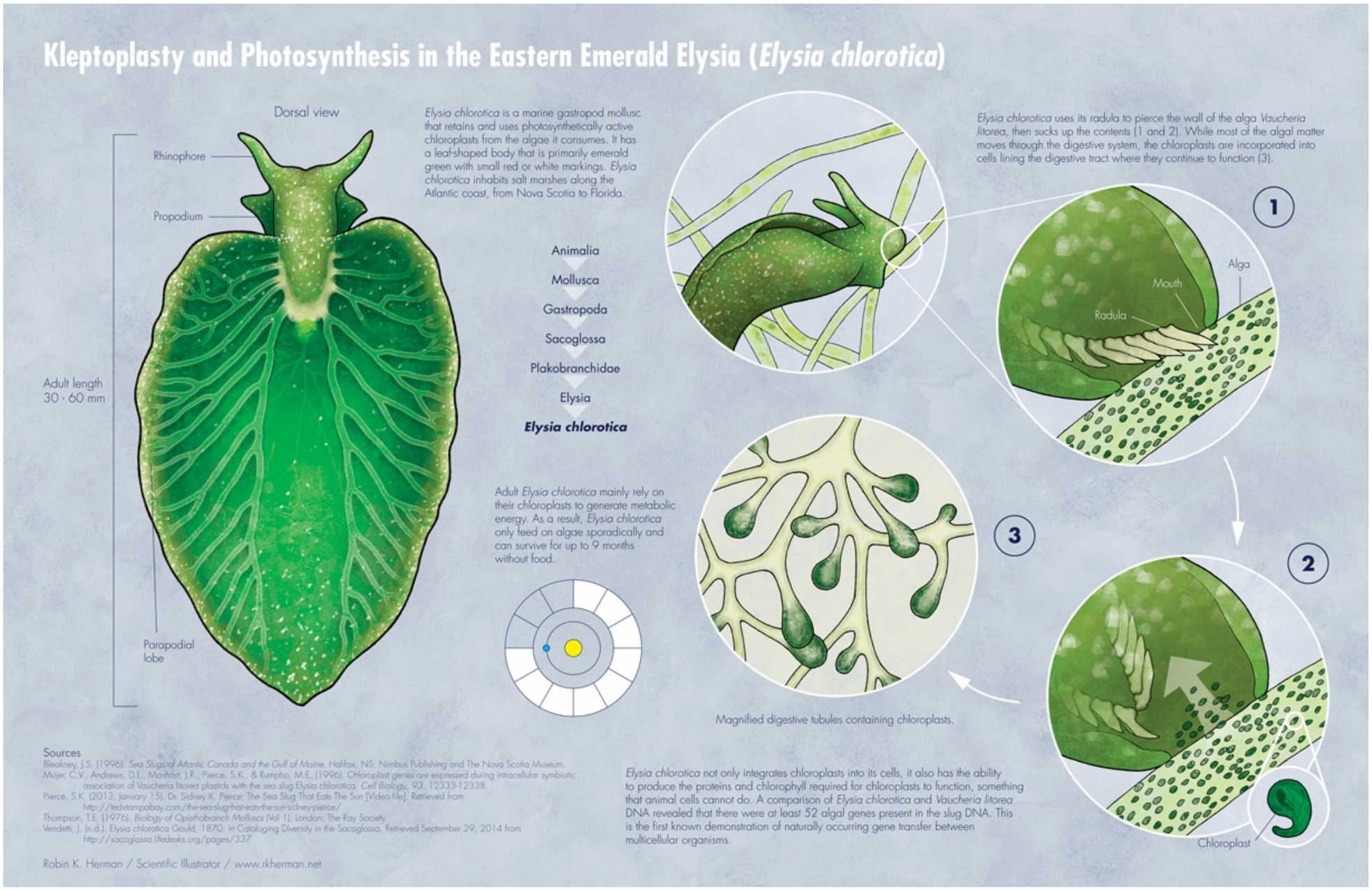
<u>2.2. Biotic entrenchment:</u> The amoeba *Paulinella chromatophora* has 2 chromatophore endosymbionts (unable to reproduce independently). Transfer of chromatophore genes coding for proteins involved in photosynthesis to host. Furthermore, cytosol-synthesized proteins are imported back into chromatophores (Bodył et al. 2012).



Current Biology

3.18 Organismal autonomy

2.2. Biotic entrenchment: *Elysia Chlorotica*.



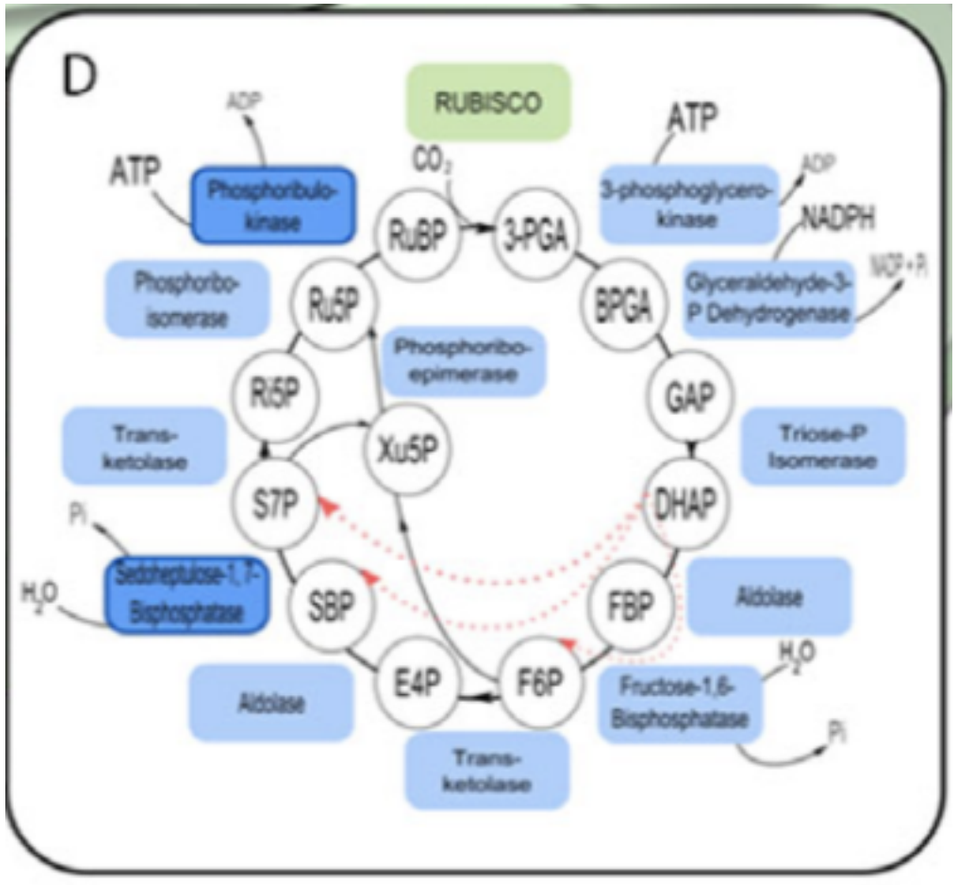
3.19 Organismal autonomy

<u>2.2. Biotic entrenchment:</u>

Slug-plastid relationship:

1. protein exchange from slug to plastid involves the simplification of the plastid membrane;
2. recruitment in plastid photosynthetic pathways of enzymes biosynthesised by slug.

Elysia chlorotica becomes a photosynthetic animal by the increasing mutual dependence (genomic, metabolic, cellular and reproductive) between slug and plastids.



In green plastid encoded enzymes. In dark blue nuclear encoded ones unique to phototrophs. All others are nuclear encoded and have homologues in animals (Rumpho et al. 2011).

3.20 Organismal autonomy

The biotic entrenchment of materials from the environment or produced by other organisms (e.g., DNA, nutrition, vitamins, proteins) or of entire organisms (e.g., symbionts) implies the structural re-organisation of the supposedly stable autopoietic structure of the organism, which is supposed to ground its identity (CBC pp. 31-2).

In the end, autopoiesis provides a drastic conceptualisation of physiological autonomy in terms of self-production that does not apply to many organismal entities.

Autopoiesis is primarily a characterisation of cellular life and organismality, not of life and organismality in general.

This is not surprising, because many kinds of organismal entities exist, i.e., the descendants of the ancestral porto-cell.

4.1 Organismality is a continuum

The most organismal - i.e., the paradigmatic organism – is the planktonic prokaryotic cell.

Prokaryotes possess the maximal level of reproductive and physiological autonomy: they can reproduce independently and, physiologically, they can biosynthesise most of the required organismal components by assimilating environmental resources (approaching the autopoietic idea of self-production).

This is an evolutionary-based view somehow consistent with the idea captured by autopoiesis.

4.2 Organismality is a continuum

Maximal physiological autonomy is approached by the planktonic bacterium not relying on, for instance, the lateral DNA transfer characteristic of a social lifestyle within a biofilm.

But the same planktonic bacterium assimilating genomic resources from a virus and integrating them in its genome, for instance through the Crispr-cas system, is not relying on self-production (3.7).

Thus, even prokaryotic organisms might merely approach the ideal of maximal physiological autonomy.

Autopoiesis captures the autonomy of the (idealised) planktonic prokaryotetic cell.

4.3 Organismality is a continuum

Prokaryotes also approach maximal reproductive autonomy.

Cell division is different from fertilisation because the latter requires two gametes. In this sense, asexual reproduction is more reproductively autonomous than sexual reproduction.

“…. the so-called sexually reproducing organisms are not really self-reproducing: it is not the individual but the mating-pair that produces offspring; and, in so doing, it does not really self-reproduce - it does not produce another mating-pair- but merely produces one or more organisms of the same species.” Mahner and Bunge 1997 p. 144

4.4 Organismality is a continuum

Some unicellular organisms have - in evolutionary time - lost their reproductive autonomy.

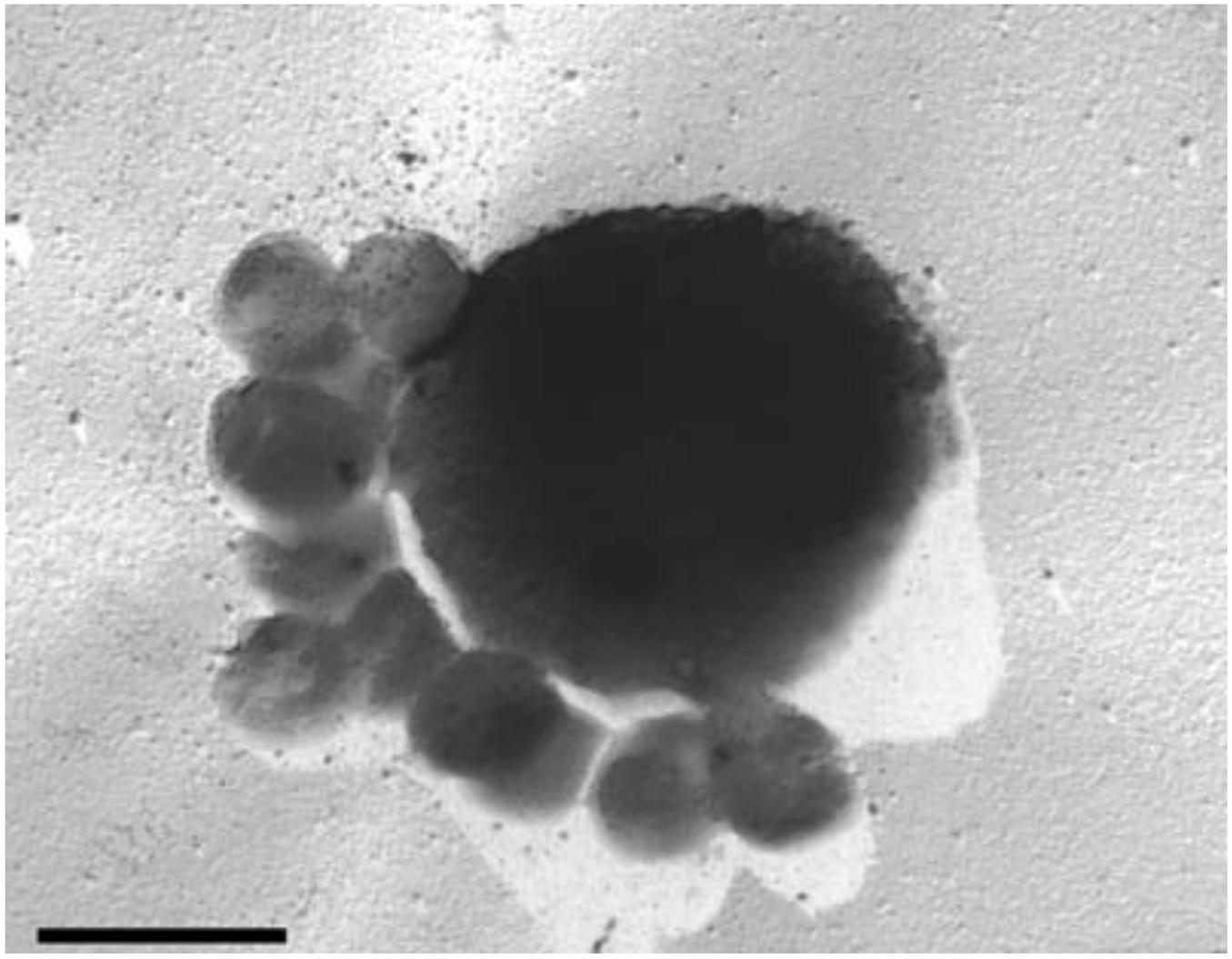
Organelles (e.g., mitochondria and plastids): preserve partial control of reproductive process (e.g., their membranes are generally inherited from pre-existing membranes, thus organelles are templated from pre-existing organelles) + their DNA is organelle-specific; but, the control of the reproduction cycle requires developmental resources (e.g., genes and proteins) from the host; hence, no total reproductive autonomy.

4.5 Organismality is a continuum

Some unicellular organisms (neither organelles nor endosymbionts) have lost their reproductive autonomy.

Nanoarchaeum equitans unable to metabolize, grow and reproduce independently of the other archaeon *Ignicoccus hospitalis*.

Whenever reproduction is dependent on other autopoietic units, reproductive independence is partial.



4.6 Organismality is a continuum

What to make of the life = collaboration and life ≠ autonomy conception (Dupré & O'Malley, slide 0.14)? Are physiological and reproductive autonomy biological myths? **They are idealisations.**

"…. of all the organisms on Earth today, only prokaryotes (bacteria) are individuals.* All other live beings ('organisms'—such as animals, plants, and fungi) are metabolically complex communities of a multitude of tightly organized beings . . . collection[s] of various numbers and kinds of autopoietic entities that, functioning together, form an emergent entity." (Margulis 1997, p. 273).

* Only the planktonic prokaryote approximates this autonomous, fully organismal state.

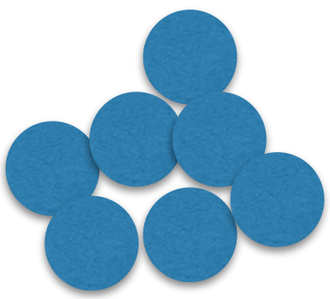
4.7 Organismality is a continuum

What does Margulis mean when she says that:

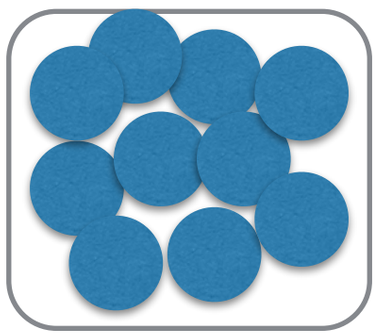
"All other live beings ('organisms'—such as animals, plants, and fungi) are metabolically complex communities …. collection[s] of various numbers and kinds of autopoietic entities that, functioning together, form an emergent entity." (Margulis 1997, p. 273).

Let us take a look at the kinds of extant organismal entities.

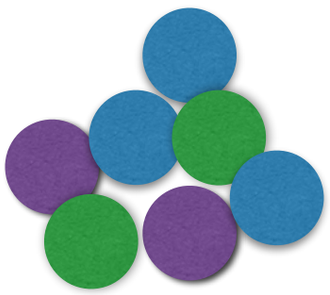
1. **Elementary organism** = prokaryotic cell (i.e., bacterium or archaeum).



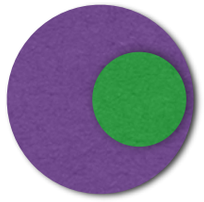
2. **Multi-cellular and mono-lineage composite organism without boundar**y = 2 or more elementary organisms of the same species (e.g., mono-species bacterial biofilm).



3. **Multi-cellular and mono-lineage composite organism with boundary** = 2 or more elementary organisms of the same species (e.g., mono-species bacterial biofilm living in a self-synthesised extra-cellular matrix).

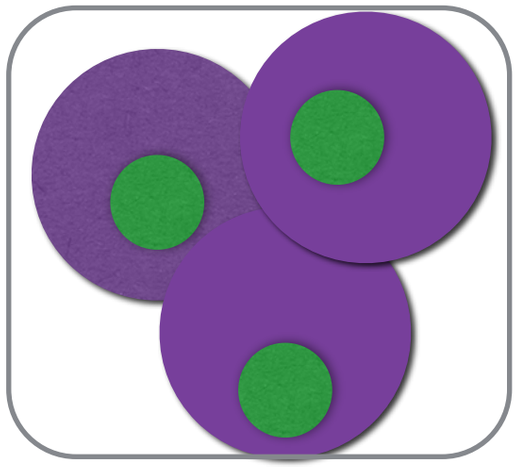


4. **Multi-cellular and multi-lineage composite organism without boundary** = 2 or more elementary organisms of different species (e.g., multi-species bacterial biofilm).

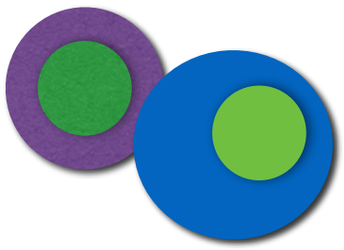


5. **Bi-cellular and multi-lineage composite organism with boundary and incorporation** = eukaryotic cell (e.g., host cell + mitochondrion) = 2 elementary organisms (if mitochondrion is only 1 as, probably, in the ancestral eukaryote).

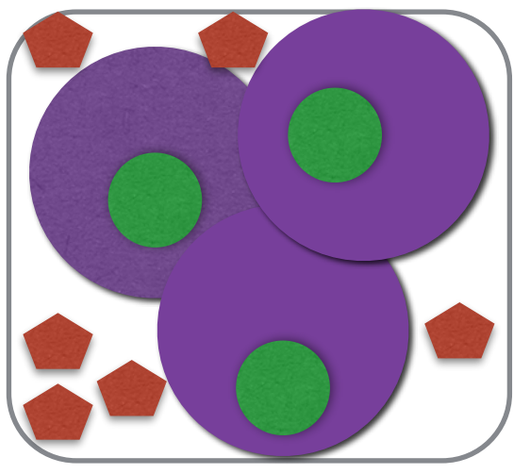
This classification is not exhaustive (e.g., [4] might come with a kind of boundary). Furthermore, also consider that [2], [4] & [7} might not be considered organismal enough if a boundary is essential for organismality ascription. But I argue that organismality is a continuum (slide 5.1).



6. **Multi-cellular and bi-lineage composite organism with boundary and two types of incorporation** = multicellular organism as set of eukaryotic cells surrounded by a boundary (epidermis) without microbiota.



7. **Multi-cellular and multi-lineage composite organism without boundary and only one kind of incorporation** = symbiotic association (e.g., lichen) of 2 or more composite organisms of different lineages.



8. **Multi-cellular and multi-lineage composite organism with boundary and two types of incorporation** = multicellular organism as set of eukaryotic cells surrounded by a boundary (epidermis) with incorporated (i.e., within epidermis) resident microbiota = 2 or more composite organisms + huge set of viruses and elementary organisms (many times called “holobiont”).

9. Then there are supra-organismal biosystems (i.e., whose level of physiological + reproductive integration is increasingly lower): e.g., populations of [8] or geographically dispersed species of [8], ecosystems made of different species of [1, 5 and 8] …. up to the entire biosphere.

4.8 Organismality is a continuum

If we consider the entire spectrum of cellular life forms, we need to make a distinction between two types of organisms: **elementary and composite** (Mahner & Bunge 1997 section 4.3).

All elementary organisms are prokaryotic cells (hence life begins at the cell level, slide 0.3). **Prokaryote = smaller unit of life**.

All the other biological systems are made out of elementary organisms and other composites (i.e., eukaryotic cells).

Given this diversity, instead of autopoiesis, it's better to call composite organisms "symbiopoietic" (Gilbert et al. 2015).

4.9 Organismality is a continuum

Autopoietic vs. symbiopoietic characterizations of life: the first focuses on preservation of bounded identity while changing chemical components and applies to elementary organisms; the second on the collaboration between organismal and semi-organismal biological systems, applying to composite organisms. Margulis was a proponent of both autopoiesis and symbiopoiesis. She pushed the autopoietic theory to its extreme consequences:

“The simplest, smallest known autopoietic entity is a single bacterial cell. The largest is probably Gaia—life and its environment-regulating behavior at the Earth’s surface” (Margulis 1998, 119).

4.10 Organismality is a continuum

Composite organisms (2 to 8 in slides 4.6-4.7) are generally less autonomous than elementary organisms.

The fundamental reason is that they rely on the *assimilation and functional integration of other organismal entities* and their self-produced products (i.e., what has been called entrenchment in section 3).

This implies that autonomy can be more properly thought of as a ***continuum*** along two dimensions: physiological and reproductive.

The autonomy continuum implies that *organismality ascription is also a question of degree*.

4.11 Organismality is a continuum

Biological systems can be more or less reproductively autonomous depending on how much they require resources from other organisms to reproduce.

Biological systems can be more or less physiologically autonomous depending on how much they rely on self-production rather than biotic entrenchment.

The interesting point about composite organisms is that the physiological and reproductive autonomy of the sub-units is often relinquished.

The crux of the problem of conceptualising composite organisms is to think in terms of the physiological and reproductive integration of the sub-units.

4.12 Organismality is a continuum

Should organismality be ascribed to parts, to whole or to both?

An intuitive metaphysical principle states that if a structurally complex object A has property x, then no part of A has also property x. Translated to our case: if an object is an organism, then no part of it is also an organism.

In the case of composite organisms, the metaphysical principle does not seem to hold.

The alternative is to give up the principle and *ascribe some degree of organismality to both parts and whole*.

After all, organismality is not a categorical property but a question of degree.

4.13 Organismality is a continuum

Sometimes, the organismality of the parts is higher than that of the whole (e.g., a holobiont) and vice versa (e.g., an eukaryotic cell).

When the organismality of the whole is higher than the organismality of the parts, **a new organismal form emerges**.

- maximal autonomy of the parts
- parts only are organisms
- whole not organismal

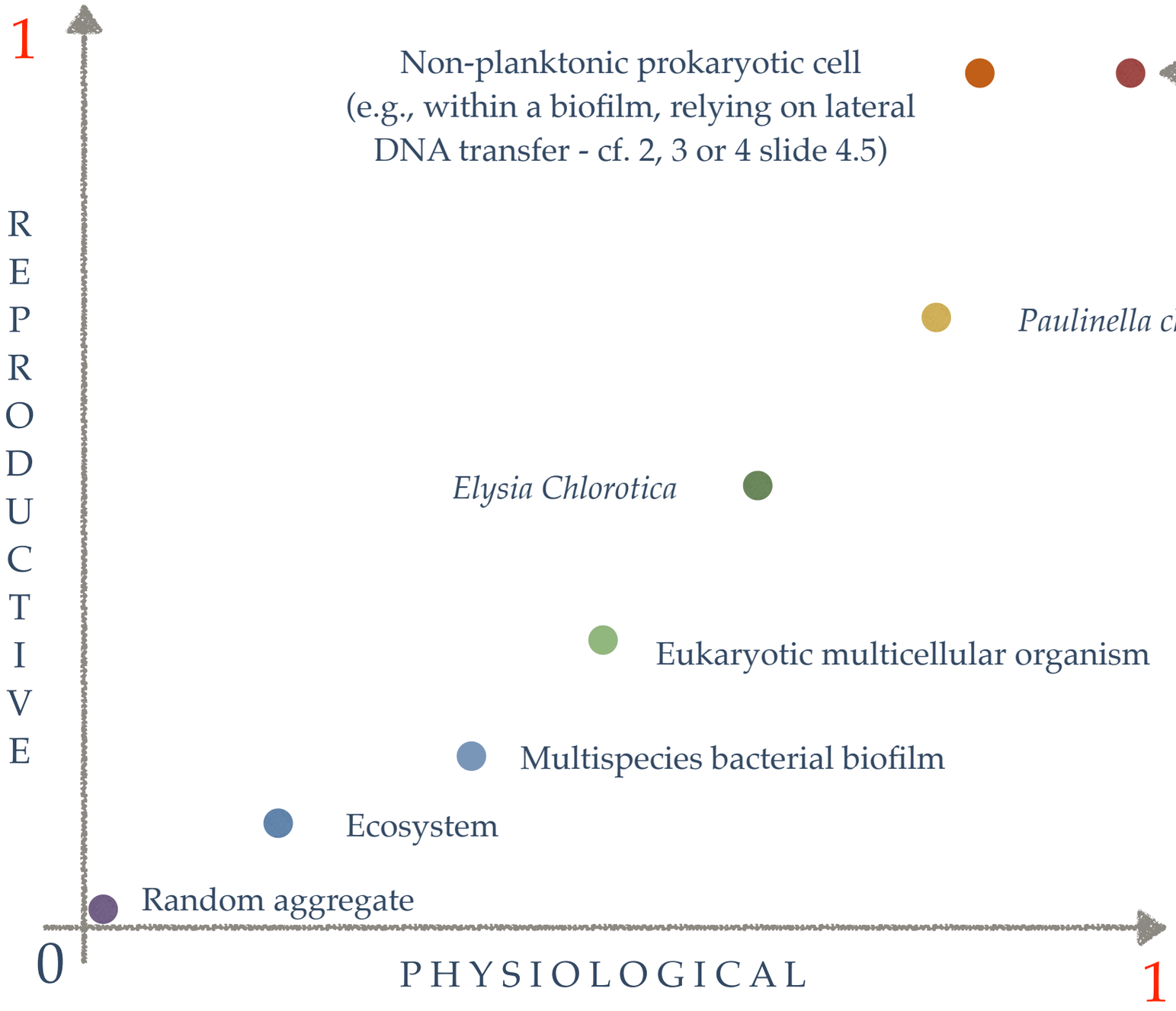
- maximal dependence of the parts
- parts less organismal
- whole organismal

Low

Organismality continuum

High

4.14 Organismality is a continuum



What levels of physiological and reproductive integration justify organismality ascriptions to composite organisms?

There's no obvious answer to this question.

Summing up

We started from a definition of life in cellular terms, dismissed (by fiat) the possibility that non-cellular forms can be alive, assumed on this basis that: life = cell-based structure = organism = physiological + reproductive autonomy.

We then considered the theory of autopoiesis, according to which to be an organism is to be physiologically autonomous through self-production.

We found that self-production applies chiefly to elementary organisms, that is, prokaryotic cells (especially when living planktonically).

Summing up

We also considered the other aspect of autonomy, i.e., the reproductive dimension. We found that elementary organisms approximate this ideal as well.

However, evolution has created many different kinds of composite organisms to which autopoiesis is not straightforwardly applicable.

For composite organisms, a better characterisation is that life is collaborative and symbiopoietic.

Indeed, all organisms, and particularly composite organisms, exhibit a more or less pronounced degree of organismality.

Organismality is a continuum.

CLASS 3 - 10 March: Development

Organism = unit of development

What is development: growth, differentiation and morphogenesis.
How to conceptualise development: epigenesis and preformation.
Causal role of DNA and environment in development.

Bibliography

1. Mahner, M. & Bunge, M. Foundations of Biophilosophy. Springer. 1997
Chapter 8, pp. 271-287
2. https://plato.stanford.edu/entries/epigenesis/

FOR MATERIAL, SEND EMAIL TO:
dvecchi@fc.ul.pt

Primary references

Cornish-Bowden, A. & Cárdenas, M.L. 2020. Contrasting theories of life: Historical context, current theories. In search of an ideal theory. (CBC)Biosystems, 188.https://doi.org/10.1016/j.biosystems.2019.104063.

Dupré, J. & O'Malley, M. 2009. Varieties of Living Things: Life at the Intersection of Lineage and Metabolism. Philos Theor Biol (2009) 1:e003

Secondary references

Luisi, P. 2003. Autopoiesis: A review and a reappraisal. Naturwissenschaften 90:49–59.

Mahner, M. & Bunge, M. A. 1997. Foundations of Biophilosophy. Berlin: Springer.

Other references

Bodył, A., Mackiewicz, P., Gagat, P. 2012. Organelle Evolution: Paulinella Breaks a Paradigm. Current Biology 22:R304–R306.

Dumbacher, J. P. et al. 2004. Melyrid beetles (Choresine): A putative source for the Batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. PNAS 101(45):15857–15860.

Epstein, E. 1994. The anomaly of silicon in plant biology. PNAS 91(1):11-7.

Gilbert, S.F. et al. Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents, Nature Reviews Genetics, 2015

Hehnemann et al. 2010 Transfer of carbohydrate-active enzymes from marine bacteria to Japanese gut microbiota. Nature Letters 464

King, J. L. and Jukes, T. H. . 1969. Non-Darwinian Evolution: Most Evolutionary Change in Proteins May Be due to Neutral Mutations and Genetic Drift. Science, 164:88–98.

Koonin, E. V. & Wolf, Y. I. 2009. Is evolution Darwinian or/and Lamarckian? Biology Direct 4, 42.

Lu, L. et al. Pathologic and physiologic interactions of bacteria with the gastrointestinal epithelium. American Journal of Clinical Nutrition 2001; 73(suppl):1124S–30S

Maturana, H. and Varela, F. 1980. Autopoiesis and Cognition: The Realization of the Living. Boston: D. Reidel.

Margulis, L. 1991. Symbiogenesis and symbionticism. In: Margulis L, Fester R (eds) Symbiosis as a source of evolutionary innovation. MIT Press, Cambridge, pp 1–14.

Margulis, L. 1997. Big trouble in biology: Physiological autopoiesis versus mechanistic neo-darwinism. In L. Margulis and D. Sagan, Slanted Truths: Essays on Gaia, Symbiosis, and Evolution. New York: Springer. 265-82.

Margulis, L. 1998. Symbiotic Planet: A New Look at Evolution. New York: Basic Books.

Meyer-Abich, A.1950. Beiträge zur theorie der evolution der organismen: typensynthese durch holobiose. E.J. Brill, Leiden

Poyton, R.O. et al. 1992. Protein export from the mitochondrial matrix. Trends in Cell Biology 2(12):369–375

Rumpho, M. E., Pelletreau, K. N., Moustafa, A., and Bhattacharya, D. 2011. The making of a photosynthetic animal. Journal of Experimental Biology 214:303–311.

Wang, M. et al. 2017. Role of Silicon on Plant–Pathogen Interactions. Frontiers in Plant Science 8:701. doi: 10.3389/fpls.2017.00701

Watkins, E. and Marius S. Kant's Philosophy of Science. The Stanford Encyclopedia of Philosophy (Fall 2014 Edition), Edward N. Zalta (ed.), URL = <https://plato.stanford.edu/archives/fall2014/entries/kant-science/>.