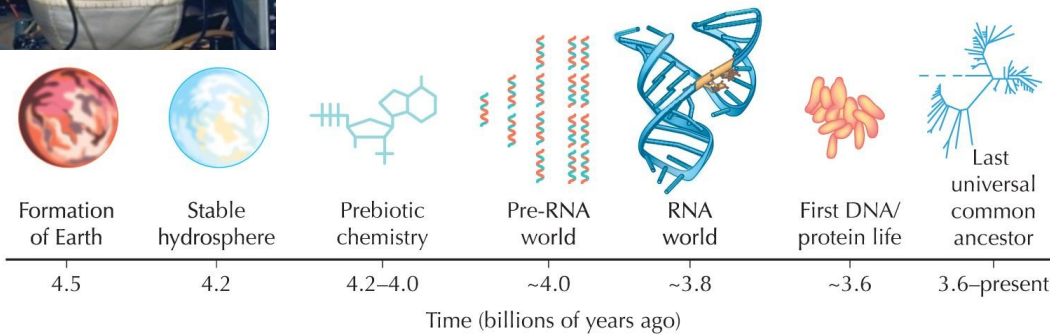
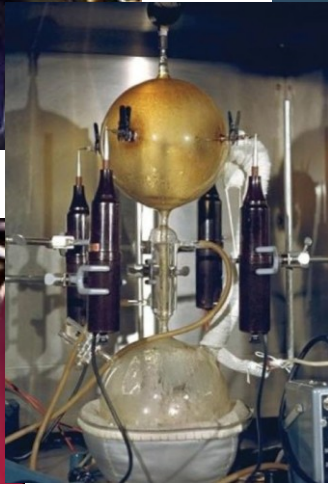
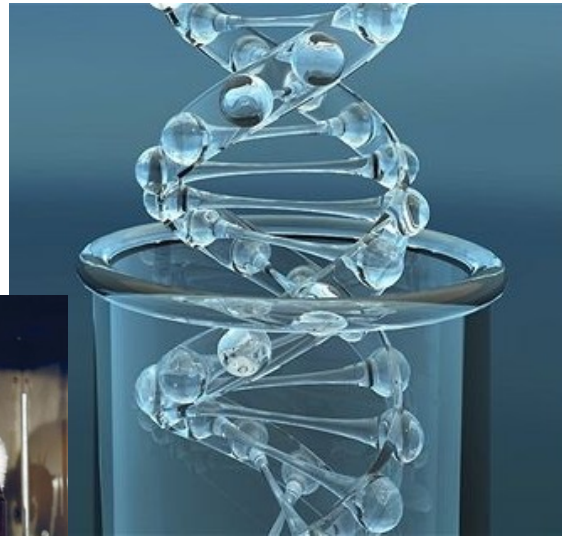
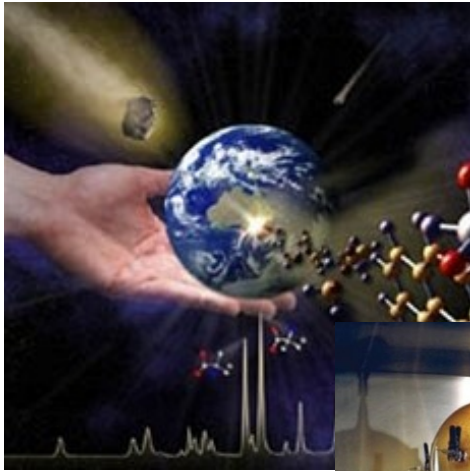


ORIGIN OF LIFE



Origin of life is to large extent outside evolutionary biology

→ in essence, it is interdisciplinary study: chemistry (nature of substances composing organisms), geology, study of atmosphere (nature of environment in which life has emerged) etc.

Actually, what is life?



What is life?

definitions: phenotypic evolutionary

Muller (1966): autoreproduction
variability
inheritance

prerequisite: ability to accumulate substances and their organization in more complex structures

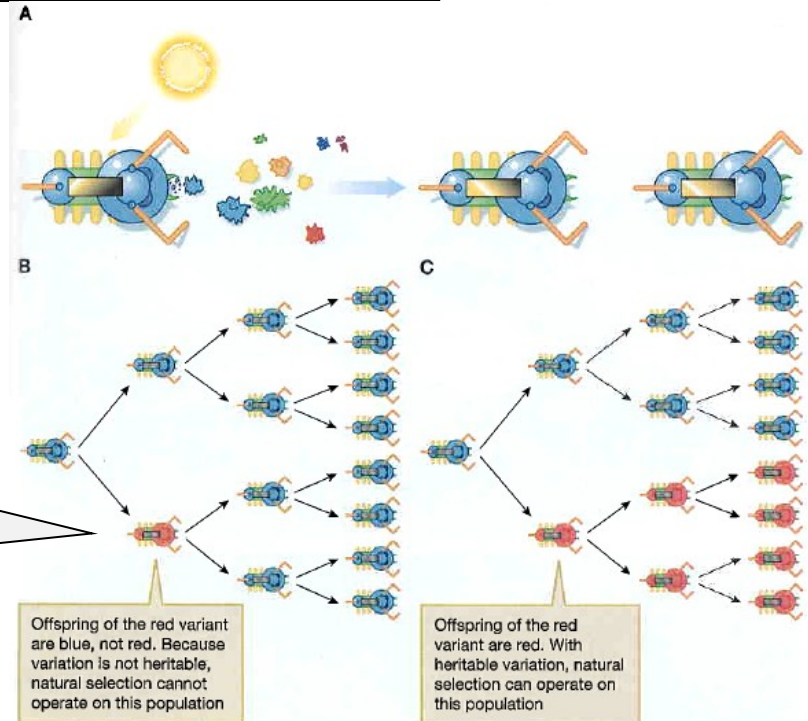
prerequisite: metabolism

prerequisite: memory of the system

Barton et al. (2007):
autoreproduction and natural selection

J. Maynard Smith & Eörs Szathmáry (1999):

prerequisite: heritable variation



Problem of study of the origin of life:

J. Monod: evolutionary tinkering, always short-term advantage or coincidence, never long-term perspective × assessment of evolution from backward view, with respect to long-term consequences

⇒ present-day life cannot help with solving

criticisms from creationists: nobody has succeeded to create life in the tube



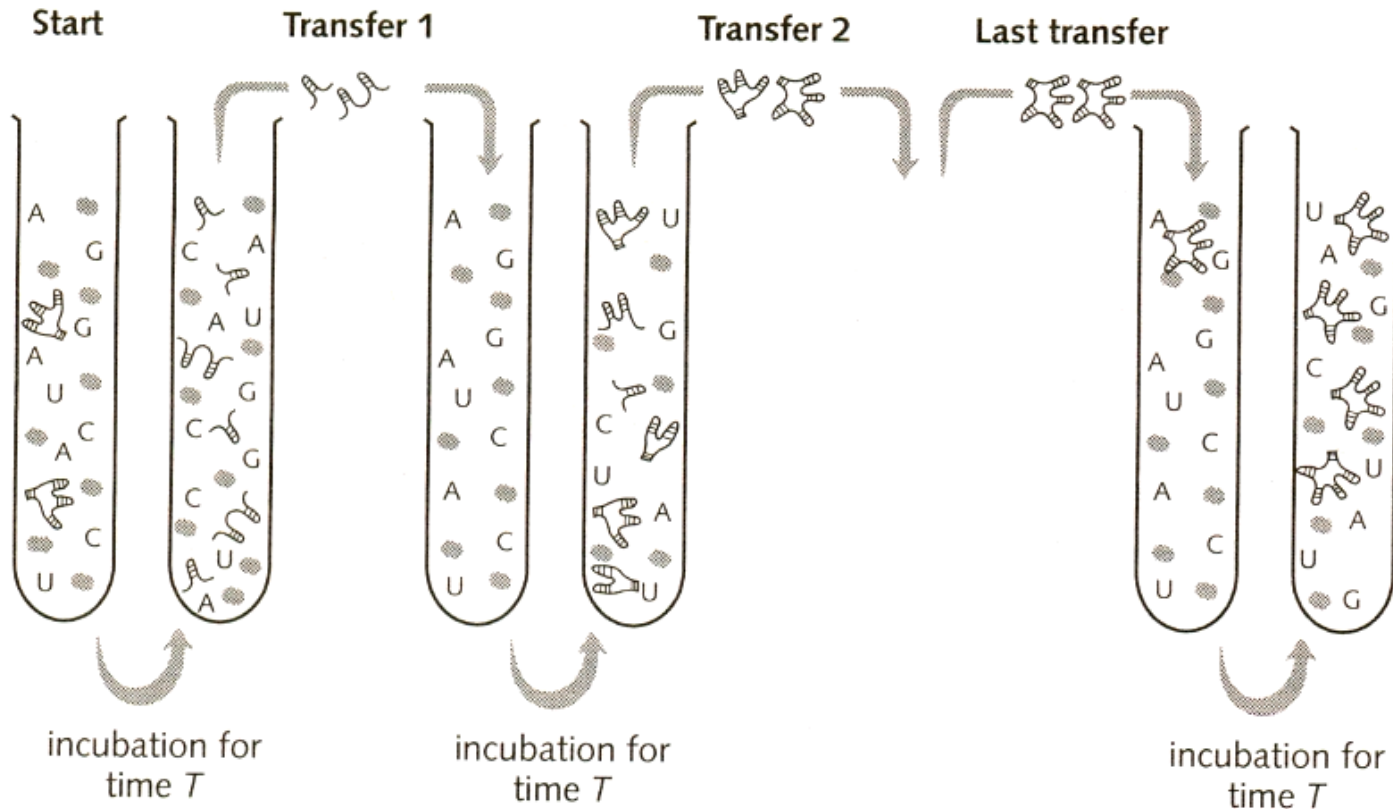
Evolution in the tube:

Sol Spiegelman et al. (1970):

RNA (template ~ 4500 bp) and bacteriophage Q β replicase,
+ nucleotides



Sol Spiegelman



⇒ evolution → „Spiegelman´s monster“:

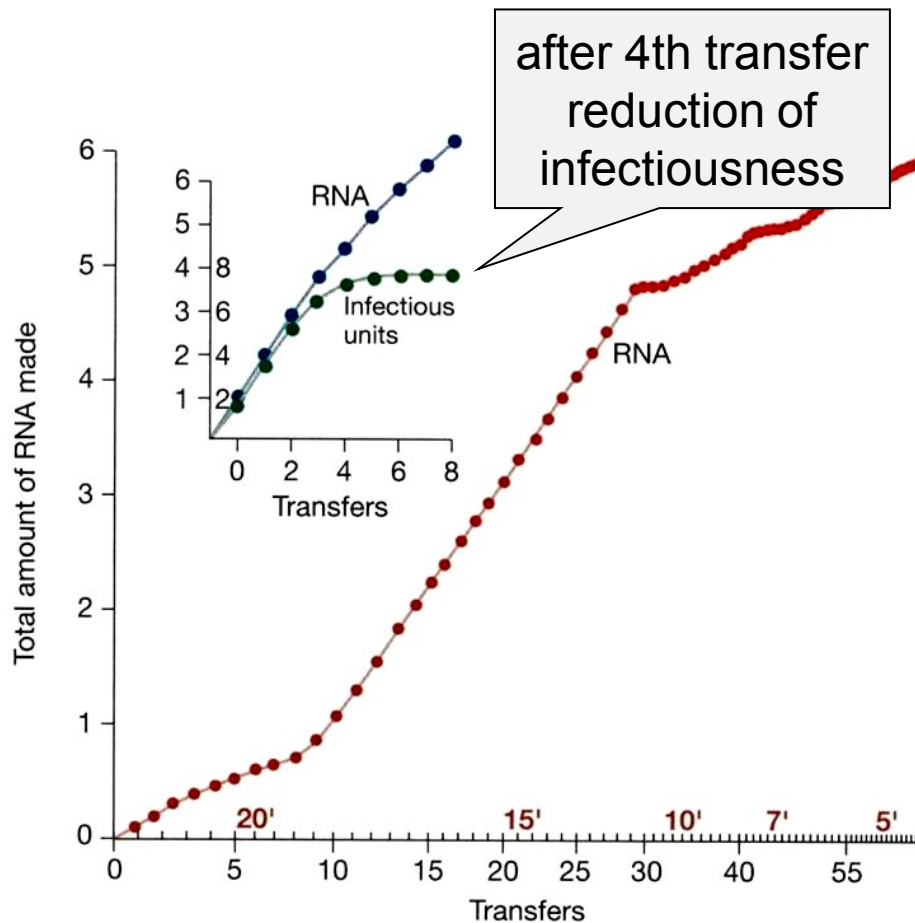
→ reduction of size after 74th transfer to 218 bp \approx 5% size of the original RNA*) ⇒ increase of replication rate

→ decrease of the ability to infect *E. coli*

*) Oehlenschläger a Eigen (1997):
finally only 48-54 bp (\sim binding site for RNA replicase)

Sumper a Luce (1975):

origin of the „Spiegelman´s monster“
even without template (only RNA bases and Q β replicase)



But these experiments don't explain origin of life (enzyme supplied)

ORIGIN OF LIFE

According to radiometric measurements age of Earth $\sim 4,54 \pm 0,04$ GYA

(but according to some theories Earth has been created secondarily and so it is younger)

lower limit: oldest rocks

gneiss in Great Slave Lake (Canada) – 4 GY

zircon crystals (Australia) – 4,3 GY

some meteorites – 4,5 GY

end of bombarding of Earth – ~ 4 GY

upper limit: microfossils, chemical fossils

chert in Warrawoona Group (Z Australia)

3,45 GY: resemblance to present stromatolites

... now questioned



Precambrian stromatolites
Siyeh Formation, Glacier Natl. Park



present-day stromatolites
Shark Bay, W Australia

chemical fossils – **kerogen** = organic matter created by decay and transformation of living organisms

Greenland glacier: 3,85 GY, confirmed by C^{12}/C^{13} ratio

Conclusion: life has probably emerged during 200 MY between 4 and 3,8 GY

Emmanuelle Javaux et al. (2010):

„*acritarchs*“ - 3,2 GYA

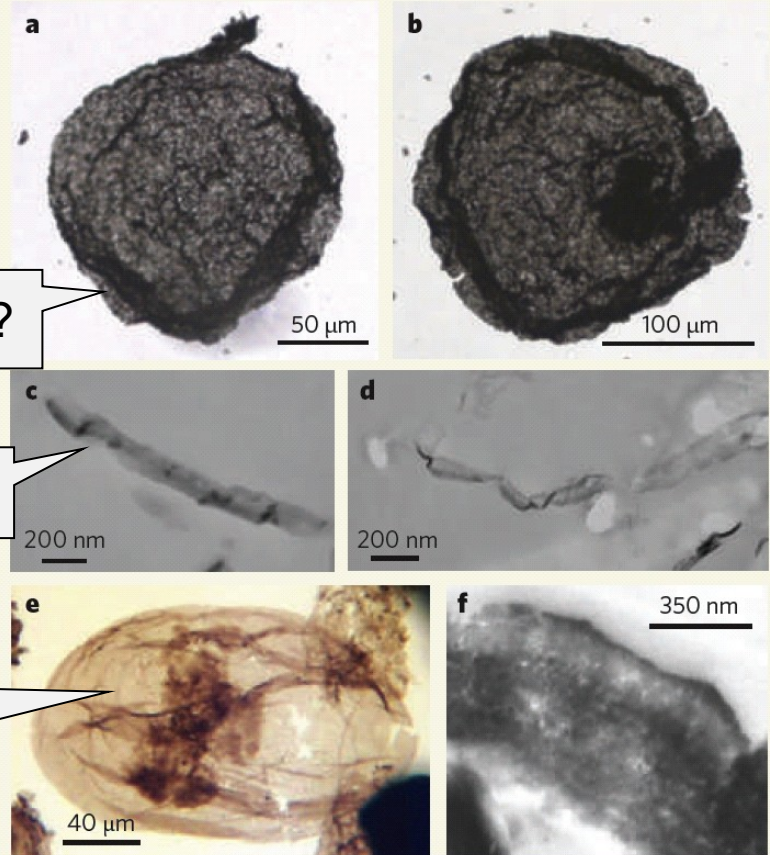
(Agnes gold mine, Moodies Group, S Africa) before – 1,8 GYA

není jisté, zda jde o eukaryota

nucleus?

cell wall

more complex cell structures
1,4 GYA



How has life arisen?

origin of simple organic molecules → chemical evolution,
primitive metabolism

origin of autoreplication, compartmentation and origin of cells, ...

First chemical experiments:

1828: ammonium chloride + silver cyanate + heat → urea
(= Wöhler synthesis)

1850s: formamide + H₂O + UV, electricity → alanine

formaldehyde + NaOH → saccharides

⇒ evidence against vitalism (claims that chemistry in living systems is fundamentally different from non-living, ie. organic ≠ inorganic)

Chemical evolution

Alexandr Ivanovich Oparin (1924)

J. B. S. Haldane (1928)

reducing atmosphere:

hydrogen, water, methane, ammonia

Stanley L. Miller, Harold C. Urey (1953):

methane + ammonia + H_2 + H_2O

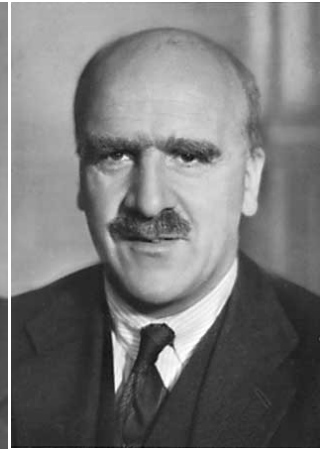
→ 10-15 % carbon in organic compounds

2 % carbon → amino acids, lipids, carbohydrates

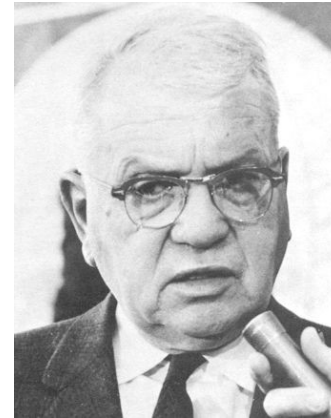
building components of nucleic acids



A.I. Oparin



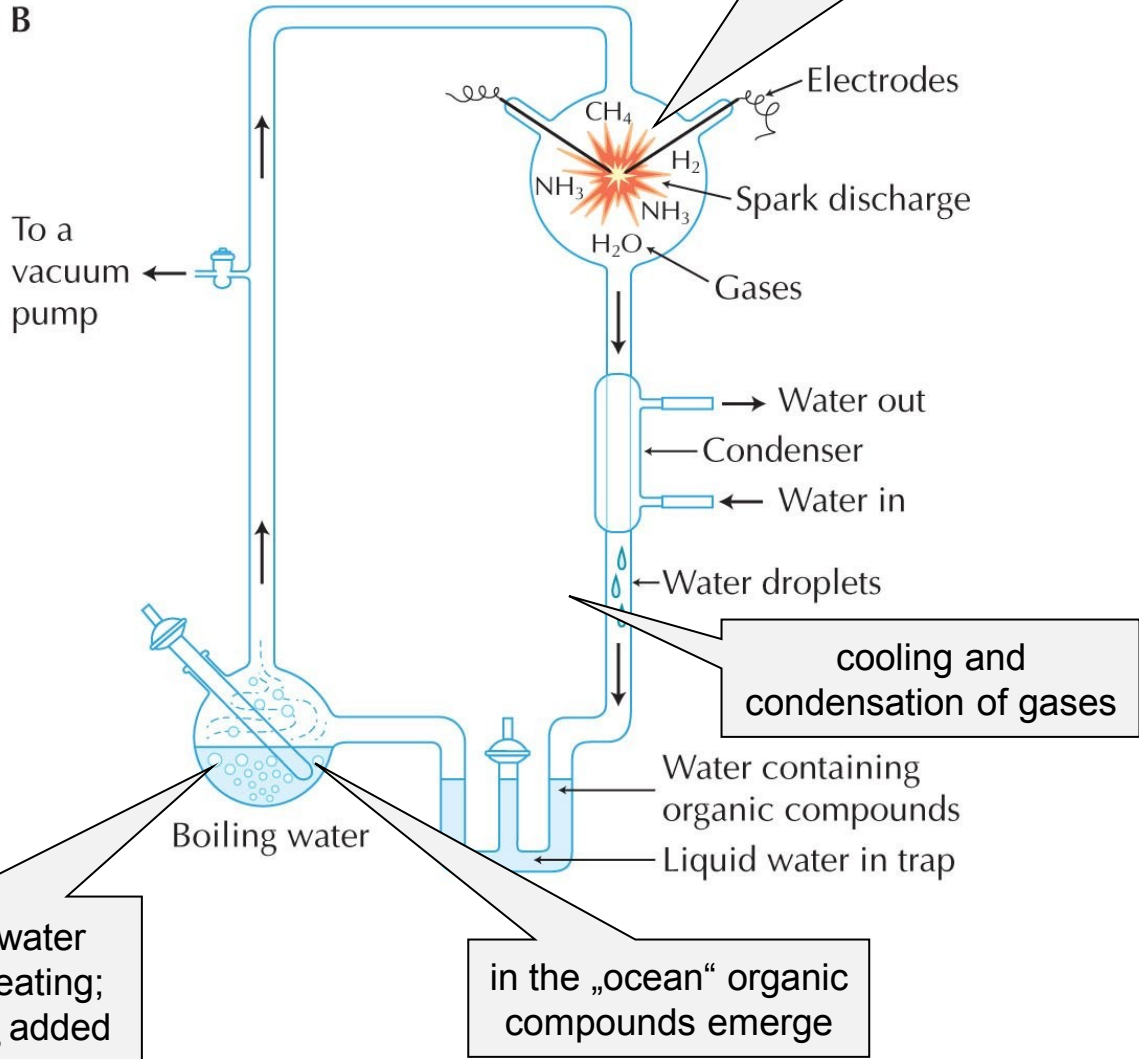
J.B.S. Haldane



H.C. Urey



S.L. Miller



Problems:

according to current knowledge the atmosphere then less reducing:

CO_2 , N_2 , H_2O and others \Rightarrow consequently much less molecules arising

not all nucleotides synthesized

phosphorus in nature rare

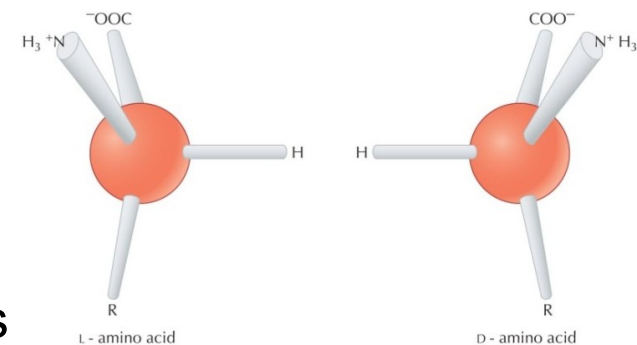
some compounds in minimal amounts

some products highly unstable (eg. along with ribose also other carbohydrates inhibiting ribose synthesis are produced)

limited production of long polymers

origin of both D and L AA and NA stereoisomers

spontaneous origin of ramose, not linear, lipids



Where has life originated?

Darwin: „hot little pond“, prebiotic soup

alternatives:

extraterrestrial origin:

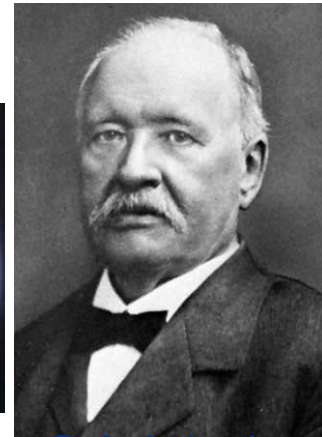
panspermia: [Svante August Arrhenius](#)

existence of organic compounds in universe (comets, meteorites):

eg. Murchison meteorite (1969, Australia): 4,6 GYA; many compounds as in the Miller-Urey experiment

bubbles: clouds, sea spume

[Thomas Gold](#) (1970): life deep under beneath the surface – existence of extremophilic archaeobacteria up to 5 km beneath surface



[S. A. Arrhenius](#)

hydrothermal vents = “black smokers“

Günter Wächtershäuser

thermal energy rather than Sun

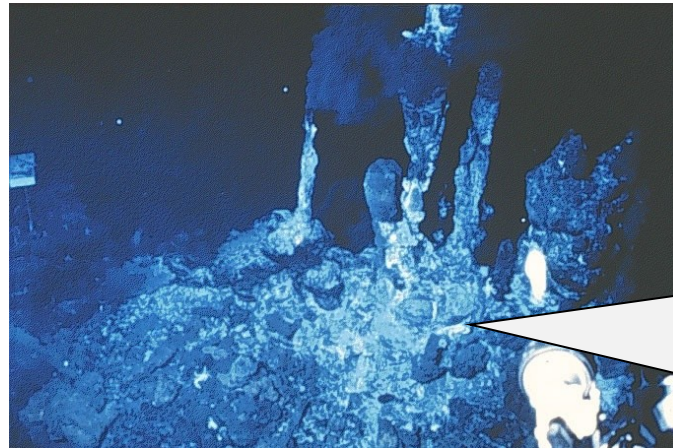
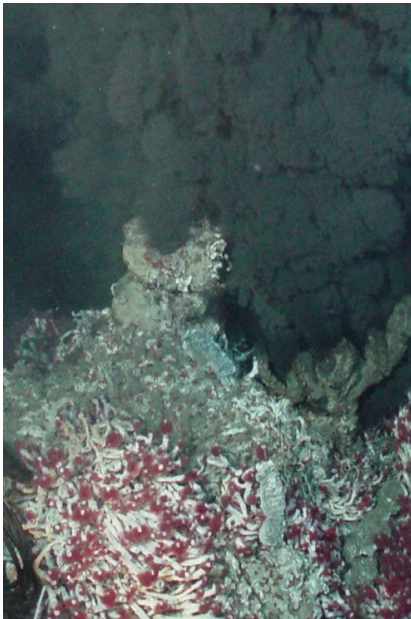
chemical synthesis: carbon fixation by chemical energy

protection against UV radiation and meteorite impacts

fixation of unstable molecules by cold water around
the vents



G. Wächtershäuser



1977: thermophilic bacteria
and archaeobacteria, three-
meter tube worms, bivalves,
starfish, barnacles, limpets,
crabs, annelids, shrimps

G. Wächtershäuser:

life on the pyrite surface = the Fe-S world hypothesis

„prebiotic pizza“

on the pyrite surface molecule clusters $[2\text{Fe}-2\text{S}]$ or $[4\text{Fe}-4\text{S}]$ → potential precursors of ferredoxins, pyridoxalphosphates, folates, and cofactors (NAD)

central role of acetyl-CoA

chemoautotrophy

Advantages of flat surface:

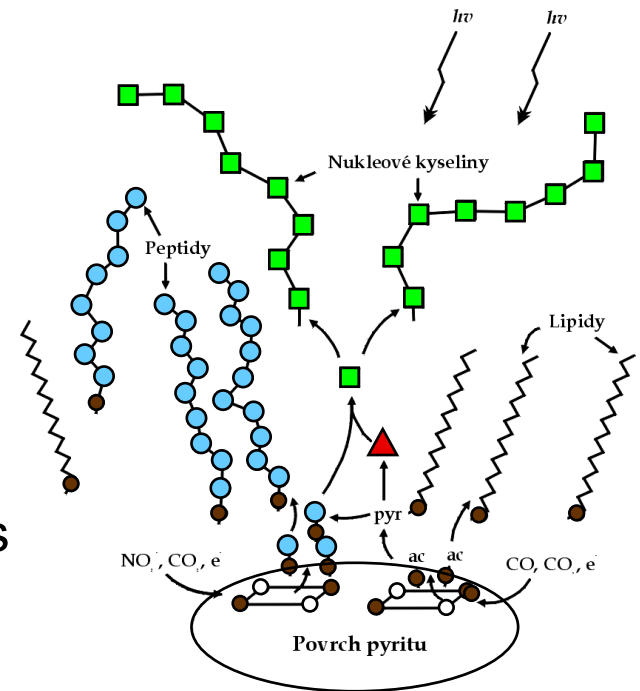
thermodynamics: lower entropy

kinetics: higher probability of molecule collisions

supply of ions to reactions (not clay!)

production of linear lipids

easier removing of water molecules



Origin of replicators – RNA world

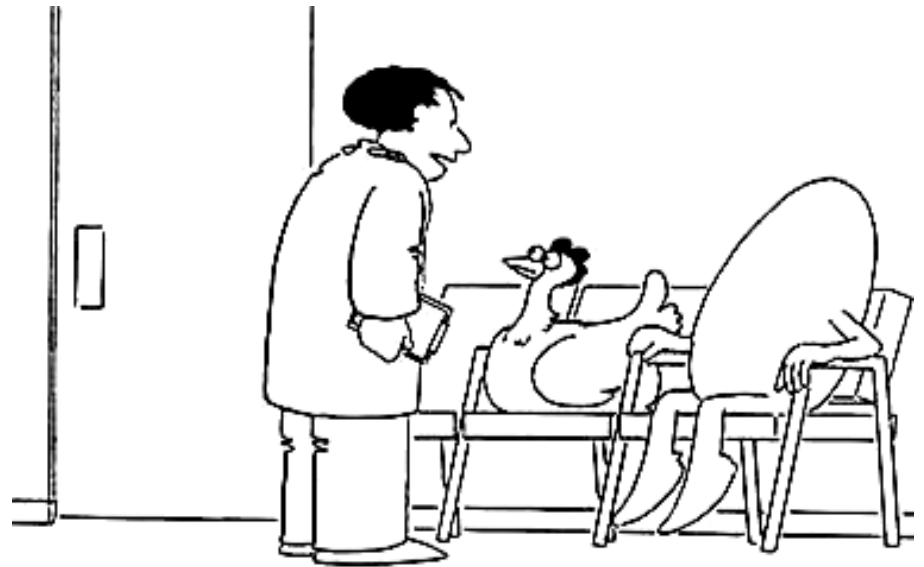
Experiments of Spiegelman, Sumper and others have shown that on the replicator level there is not only heredity and mutation but also selection but WHAT was replicated?

proteins

DNA

RNA

something else



"Who was first?"

Chemical structure of DNA

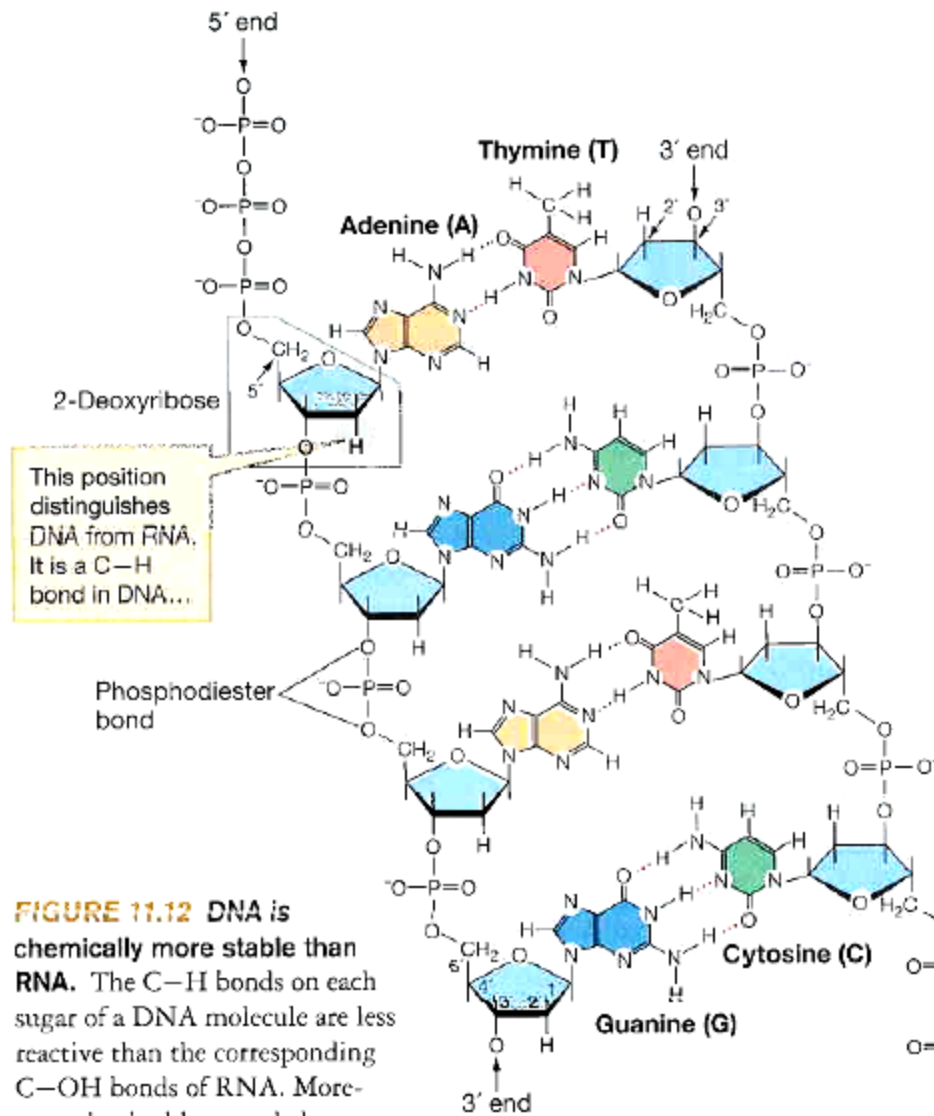
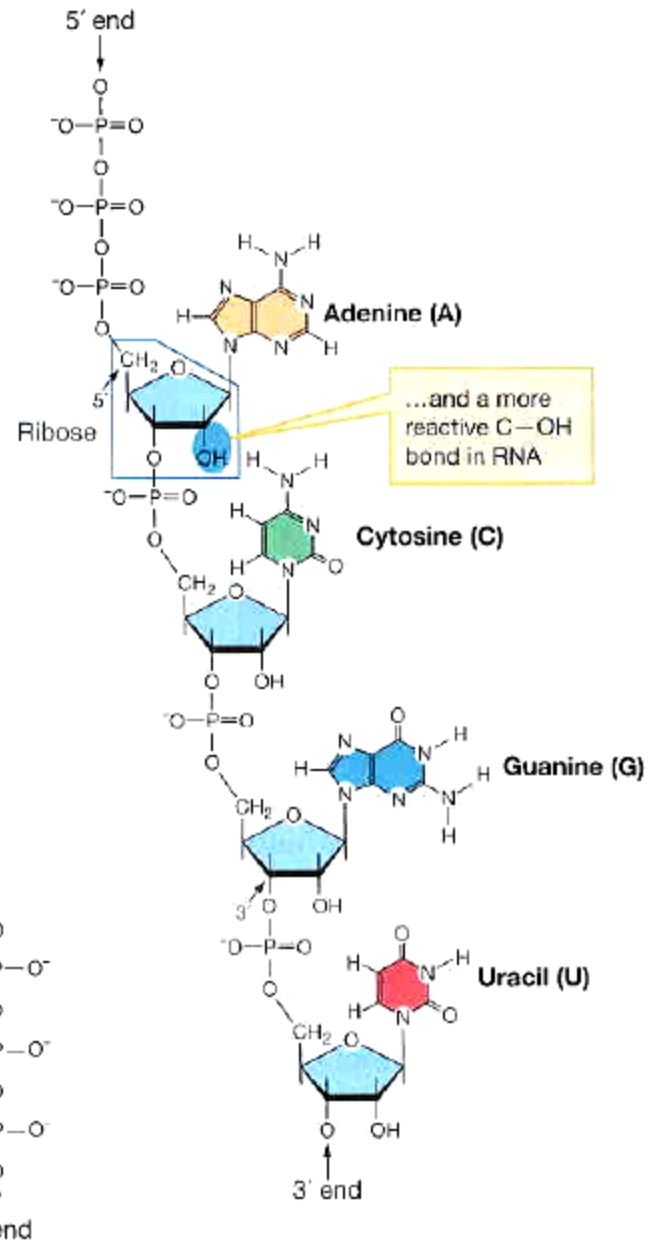


FIGURE 11.12 DNA is chemically more stable than RNA. The C—H bonds on each sugar of a DNA molecule are less reactive than the corresponding C—OH bonds of RNA. Moreover, the double-stranded structure of DNA protects the nucleic acid bases from chemical interactions with other molecules.

Chemical structure of RNA



Origin of replicators – RNA world

Experiments of Spiegelman, Sumper and others have shown that on the replicator level there is not only heredity and mutation but also selection but WHAT was replicated?

proteins

DNA

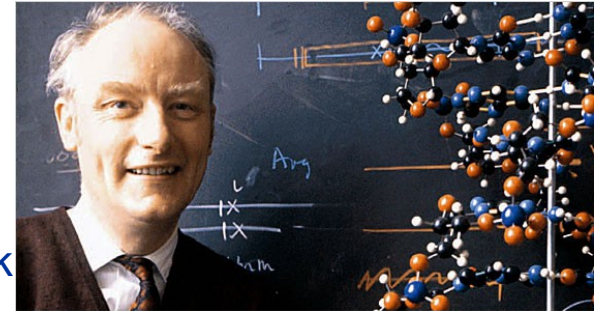
RNA

something else

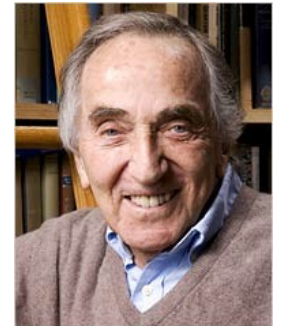
Francis Crick, Carl Woese, Leslie Orgel
(1967):

dual role of RNA: heredity + enzyme
= **ribozyme**

F. Crick



C. Woese



L. Orgel

RNA characteristics:

simpler than DNA

absence of complex repair mechanisms

ability to build multiple 3D conformations

more reactive than DNA (OH-group on 2' carbon)

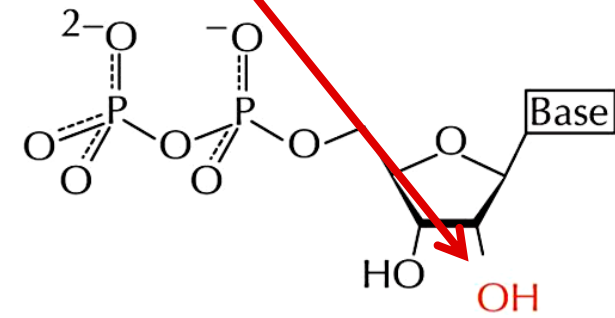
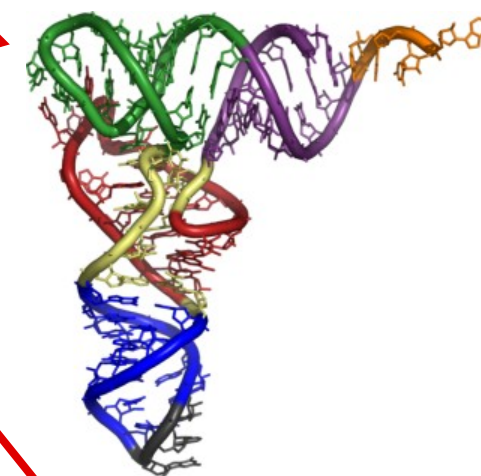
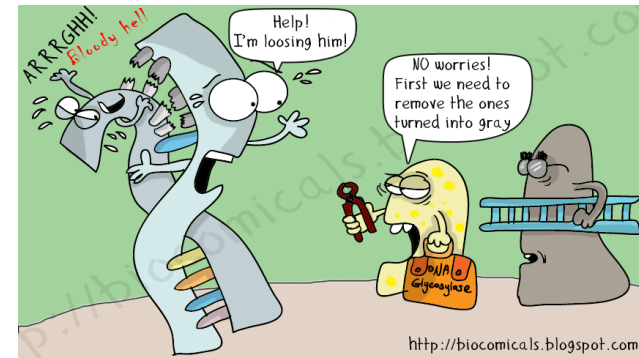


TABLE 4.3. Examples of modern RNA roles

Function	Type of RNA	Role of RNA
Translation	mRNA	Product of DNA transcription
	tRNA	Involved in translation of the genetic code
	rRNA	Serves as part of a ribosomal subunit
DNA replication	RNA primers	Replication of the lagging DNA strand initiates with an RNA primer
	Telomerase RNA	Needed at the ends of linear chromosomes
Splicing and RNA processing	Small nuclear RNA (snRNA)	Involved in splicing
	Small nucleolar RNA (snoRNA)	Required for posttranscriptional processing of rRNA
	RNase P	Essential for tRNA processing
Translation quality control	tmRNA	Targeting aberrant protein products for degradation in bacteria
Protein translocation	Signal recognition particle (srpRNA)	A component of the signal recognition particle (SRP)
RNA interference (RNAi)	Many types	Involved in regulating RNA stability and translation in eukaryotes
Transcription regulation	6S	Regulates the function of bacterial RNA polymerase

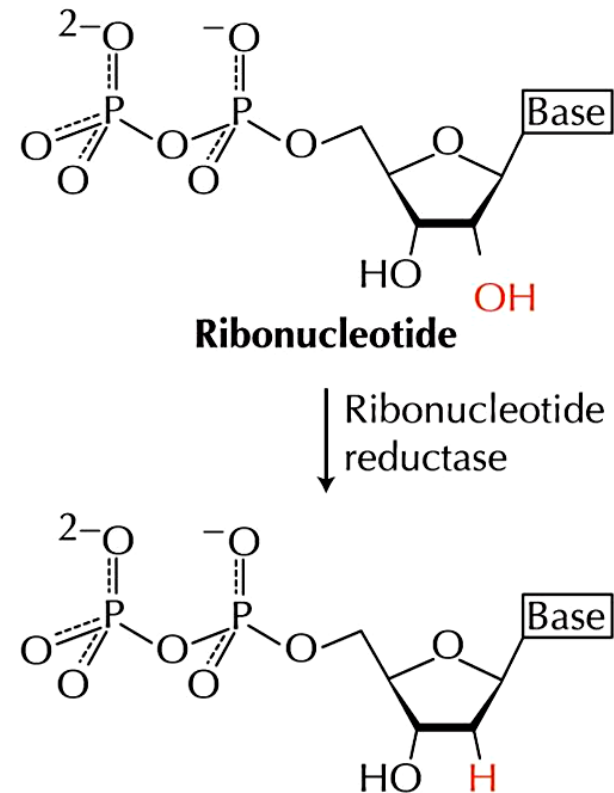
many functions have arisen long ago
RNA as „molecular fossils“

many essential coenzymes, eg. NAD⁺, flavin adenin dinucleotide (FAD)
= ribonucleotide derivatives

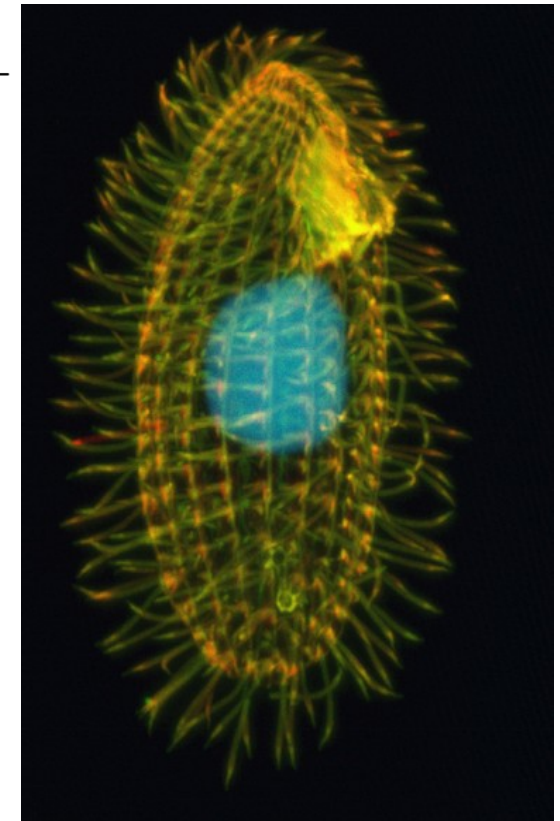
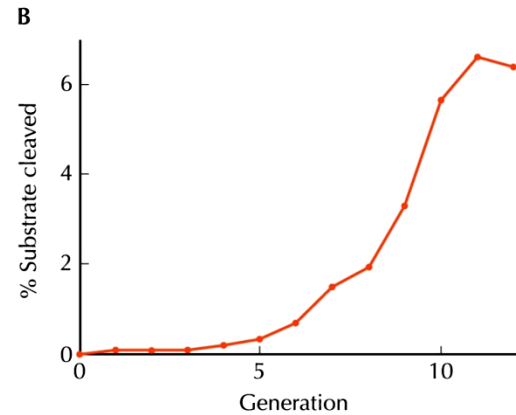
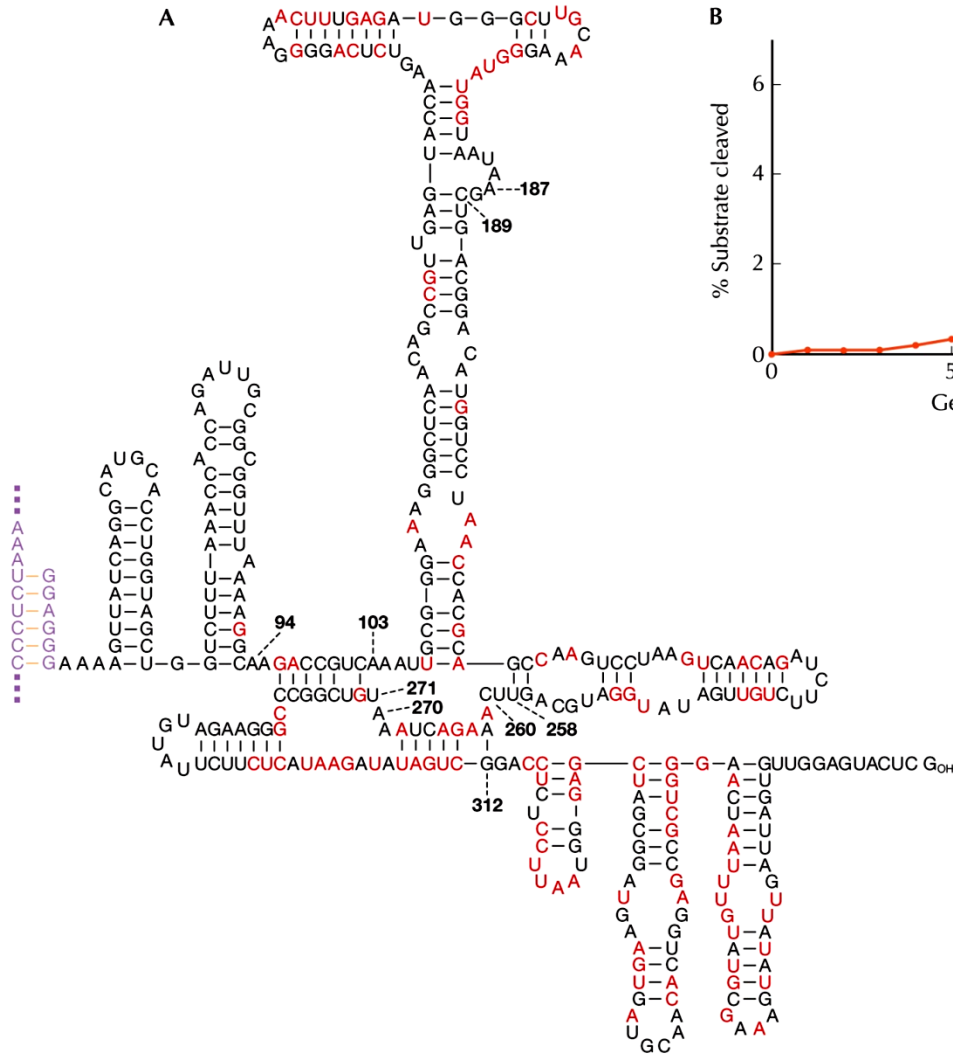
deoxyribonucleotides arise from ribonucleotides

RNA primer is used during DNA replication

ATP = ribonucleotide

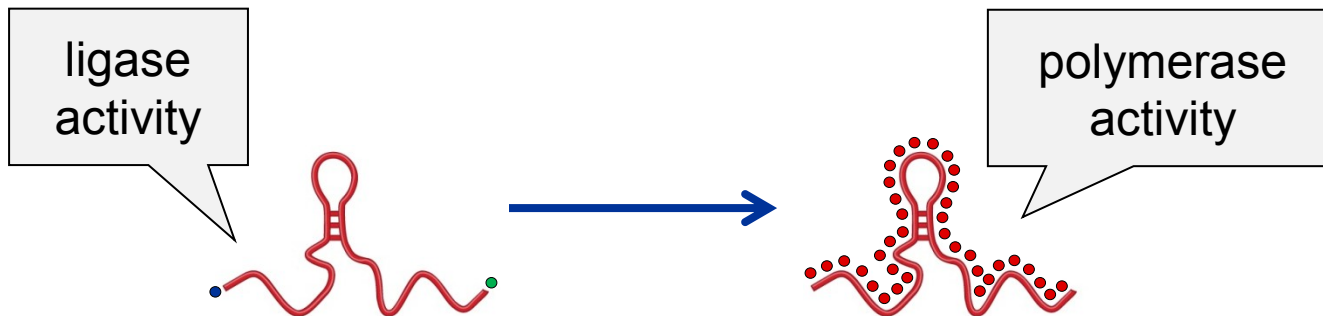
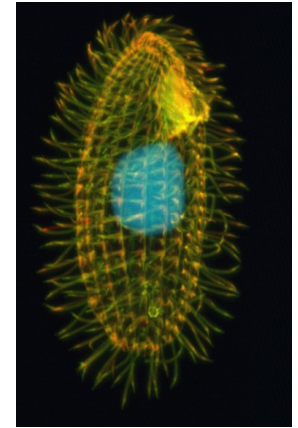
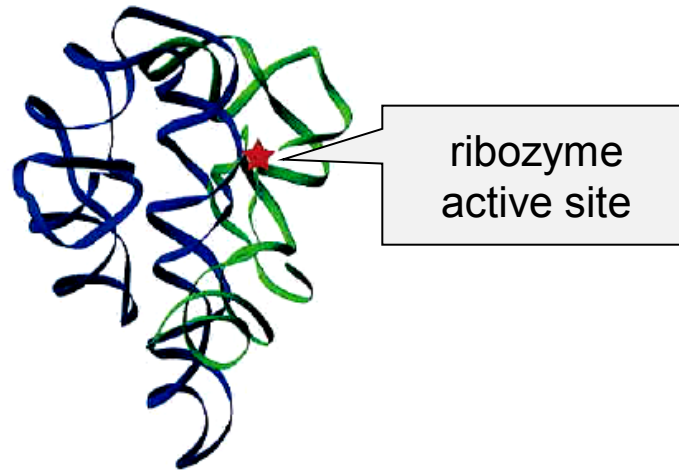


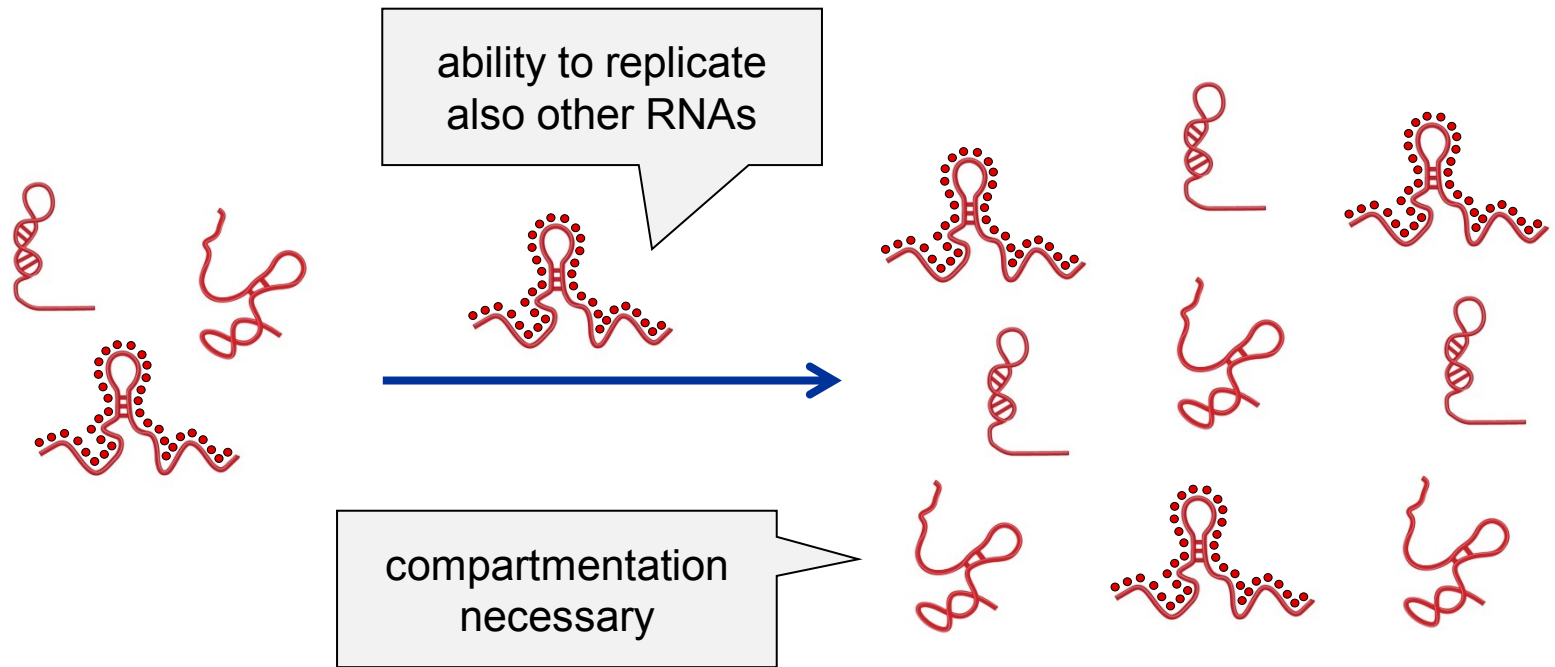
Kruger et al. (1982): self-cleaving of intron in pre-mRNA of *Tetrahymena*



Kruger et al. (1982): self-cleaving of intron in pre-mRNA of *Tetrahymena*

Zaug a Cech (1986): IVS (intervening sequence) → ribozyme





Doudna a Szostak (1989): modification of IVS → catalysis of synthesis of complementary strand according to external template – max. 40 nucleotides, only 1% complete

Doudna (1991):

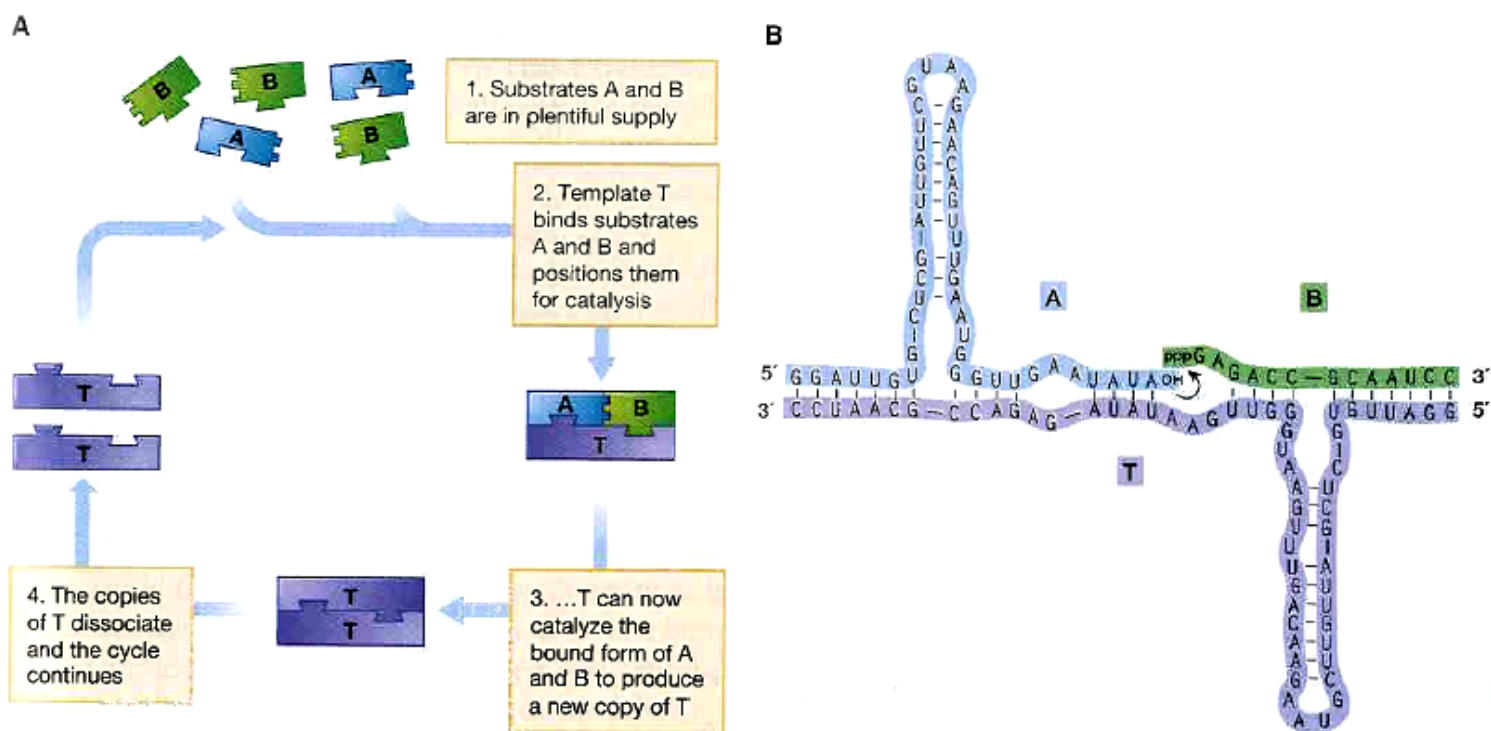
three-subunit ribozyme from sequence of *sunY* of T4 bacteriophage

Paul & Joyce (2002):

R3C ribozyme – ligation of two RNA molecules

R3C modified so that the ligation product is identical to R3C → catalysis of own replication

× only two rounds of replication and absence of selection (no variation)
→ these problems later solved (Lincoln & Jozce 2009)



Some known natural ribozymes:

peptidyl transferase 23S rRNA

introns of groups I and II

hairpin ribozyme

GIR branching ribozyme

leadzyme

hammerhead ribozyme

HDV ribozyme

mammal CPEB3 ribozyme

VS ribozyme

glmS ribozyme

CoTC ribozyme

TABLE 4.4. Ribozymes

Ribozyme	Description
Self-splicing introns	Some introns splice themselves by an autocatalytic process. There is also growing evidence that the splicing pathway of GU-AG introns includes at least some steps that are catalyzed by snRNAs.
Ribonuclease P	This enzyme creates the 5' ends of bacterial tRNAs. It consists of an RNA subunit and a protein subunit, with the catalytic activity residing in the RNA.
Ribosomal RNA	The peptidyl transferase activity required for peptide bond formation during protein synthesis is associated with the 23S rRNA of the large subunit of the ribosome.
Virus genomes	Replication of the RNA genomes of some viruses involves self-catalyzed cleavage of chains of newly synthesized genomes linked head to tail. Examples are the plant viroids and virusoids and the animal hepatitis delta virus. These viruses form a diverse group with the self-cleaving activity specified by a variety of different base-paired structures, including a well-studied one that resembles a hammerhead.
Telomeres	In some species, replication of DNA ends is catalyzed by an RNA subunit of its telomerases.

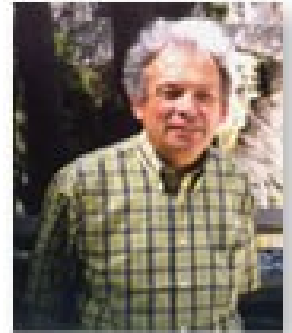
From Brown T.A. 2002. *Genomes*, 2nd ed., Table 10.4, BIOS Scientific Publishers Ltd., Oxford.
snRNA, small nuclear RNA; tRNA, transfer RNA.

Alternatives to nucleic acids:

Alexander Graham Cairns-Smith: crystalline clay as „urgene“
– initially anorganic replication, a kind of „scaffold“

Julius Rebek: autoreplication using AATE
(amino adenosin triacid ester)

Ronald Breaker (2004): DNA can behave
as ribozymes



A.G. Cairns-Smith



J. Rebek

Problem of ribozyme-aided replication:

Manfred Eigen (1971):

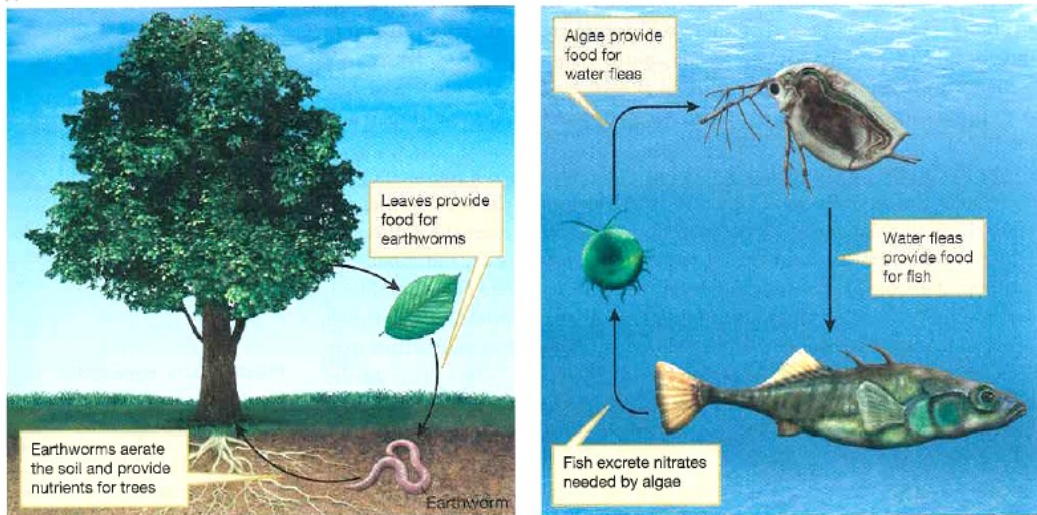
individual genes will compete

without repair mechanisms maximum size of replicating molecules ≈ 100 bp

length of DNA segment encoding functional enzyme much exceeds 100 bp

= **Eigen paradox**

hypercycles = stable coexistence of two or more cooperating replicators



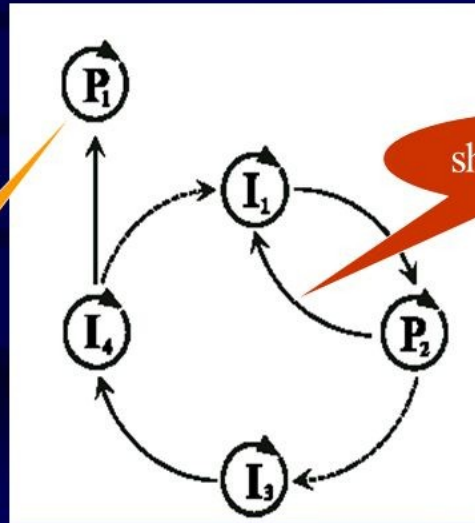
hypercycles:

molecular mutualism: reciprocal altruism (win-win relationship)

competition of the whole system with other cycles

risk of system „parasitism“ \Rightarrow need for compartmentation

Parasites in the hypercycle (JMS)

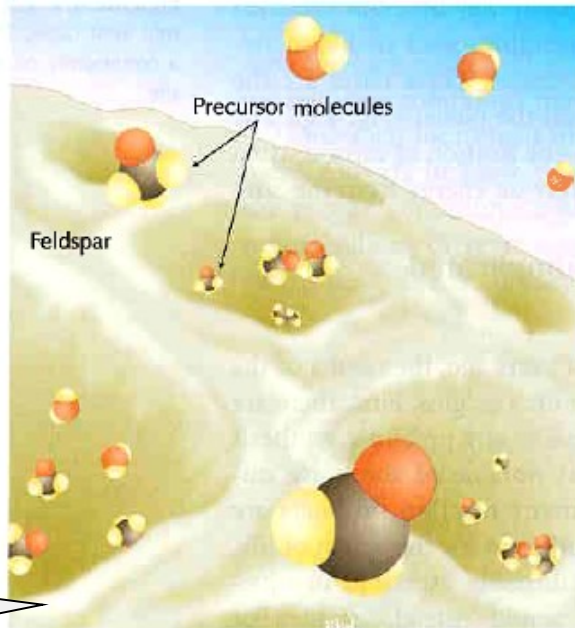


parasite

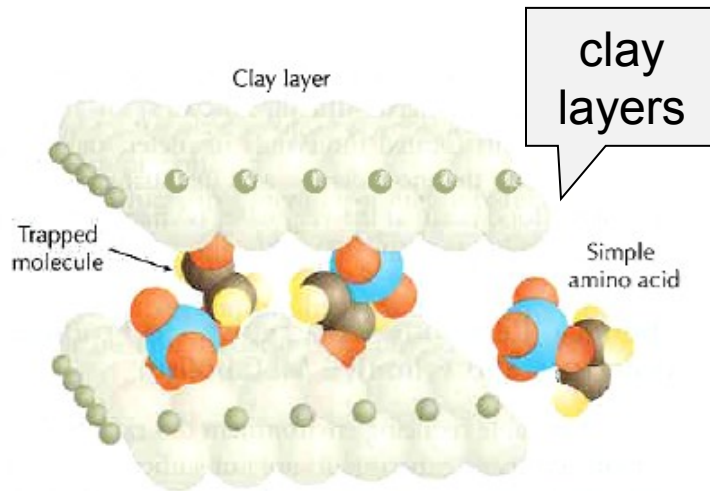
short circuit

Compartmentation and origin of cells

role of tiny crevices and unevenness of the mineral surface



felspar



protection, increase of concentration

Compartmentation and origin of cells

role of tiny crevices and unevenness of the mineral surface

proteins: microspheres (Sidney W. Fox)

lipids: spontaneous production of liposomes

spontaneous production of lipidic membranes: „oil on water“ → „water on oil“

semi-cell → proto-cell → cell

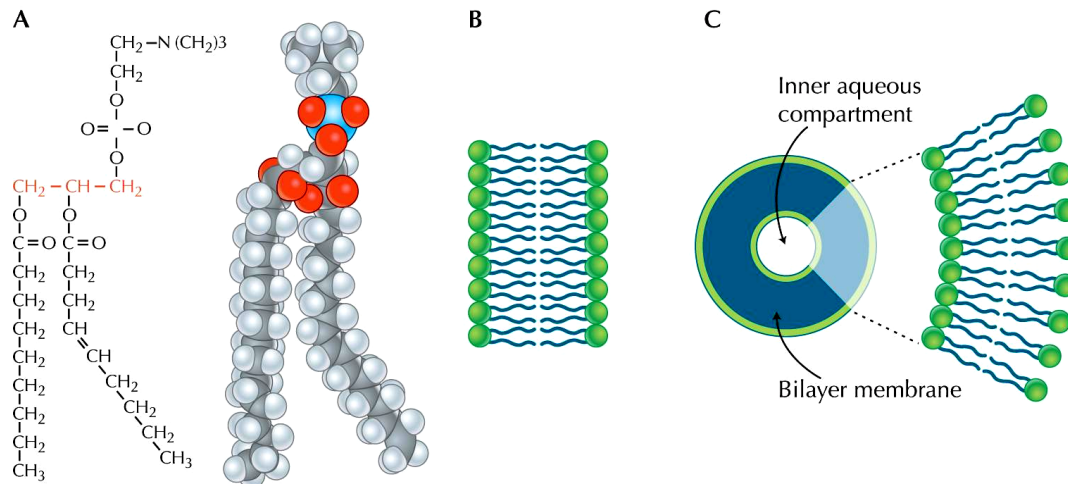


FIGURE 4.14. Lipids. (A) General structure of phospholipids. Phospholipids are made up of fatty acids, glycerol, and a phosphate group. They are amphipathic, with one hydrophobic end and one hydrophilic end. (B) Bilayers form when phospholipids spontaneously aggregate in water. The hydrophobic ends attract each other in the center of the layer and the hydrophilic ends are surrounded by water. (C) Liposomes are formed when a lipid bilayer folds over itself.



Origin of chromosomes and genetic code

fusion of replicators \Rightarrow longer replication \Rightarrow selective disadvantage

possible benefits:

1. reduction of competition between functionally connected replicators
2. products of functionally connected replicators at the same place

genetic code: redundant, redundancy random (Ser, Arg, Leu: 6 codons \times Met, Trp: 1 codon)

		Second Letter							
		T	C	A	G				
First Letter	T	TTT } Phe TTC } TTA } Leu TTG }	TCT } Ser TCC } TCA } TCG }	TAT } Tyr TAC } TAA Stop TAG Stop	TGT } Cys TGC } TGA Stop TGG Trp	T	C	A	G
	C	CTT } Leu CTC } CTA } CTG }	CCT } Pro CCC } CCA } CCG }	CAT } His CAC } CAA } Gln CAG }	CGT } Arg CGC } CGA } CGG }	T	C	A	G
	A	ATT } Ile ATC } ATA } ATG Met	ACT } Thr ACC } ACA } ACG }	AAT } Asn AAC } AAA } Lys AAG }	AGT } Ser AGC } AGA } Arg AGG }	T	C	A	G
	G	GTT } Val GTC } GTA } GTG }	GCT } Ala GCC } GCA } GCG }	GAT } Asp GAC } GAA } Glu GAG }	GGT } Gly GGC } GGA } GGG }	T	C	A	G

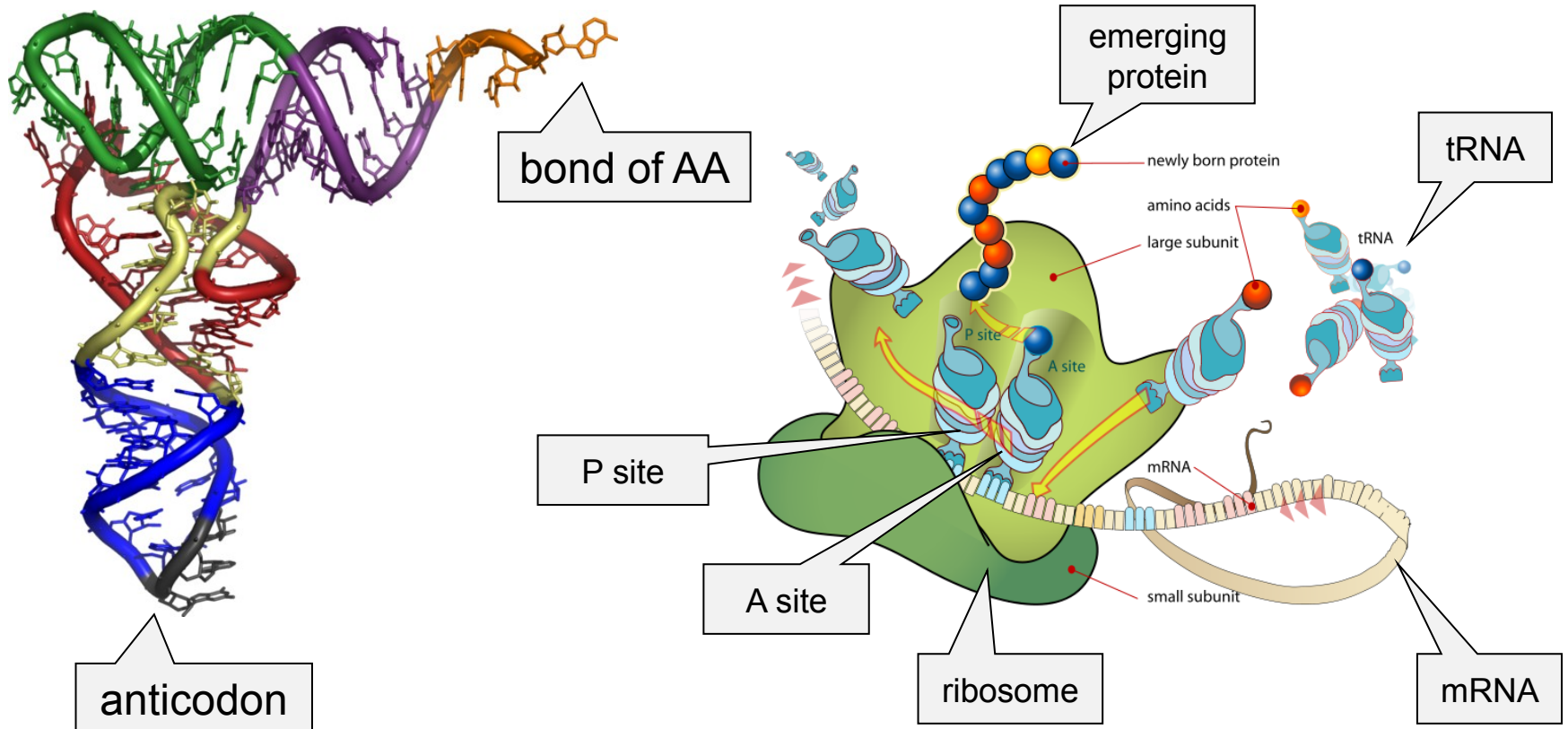
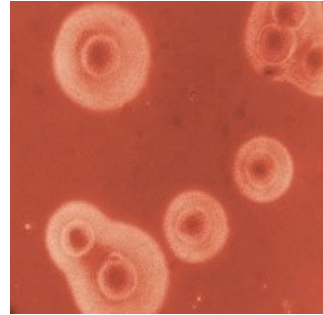
chemically related AAs → similar code

genetic code is not by far „universal“ – exceptions in some organisms
(eg. *Mycoplasma*) or organelles (mitochondria)

AAs perhaps initially helped to stabilize RNAs or

as enzymatic co-factors enhancing RNA activity

→ step by step emergence of function in translation system



Association AAs and RNAs:

synthesis of proteins governed by RNA

mapping of RNA sequence onto AA

origin of tRNA

„frozen accident“ – [F. Crick](#) (1968)

some RNA molecules evolved ability to transfer AA to other RNA
selection gradually favours one or more RNAs for each AA
association between AA and RNA random

stereochemical theory: [Carl Woese](#)

different RNAs tend to preferentially bind particular AAs

→ some experiments show that RNA molecules may be selected according to their preferential bond to particular AAs

Transition RNA → DNA

RNA world: RNA = both genotype and phenotype

with translation proteins adopt most catalytic RNA functions
(they can create broader range of polymers) \Rightarrow much more diverse
catalytic activities \rightarrow eg. no RNA molecule can catalyze redox
reactions or break C–C bonds

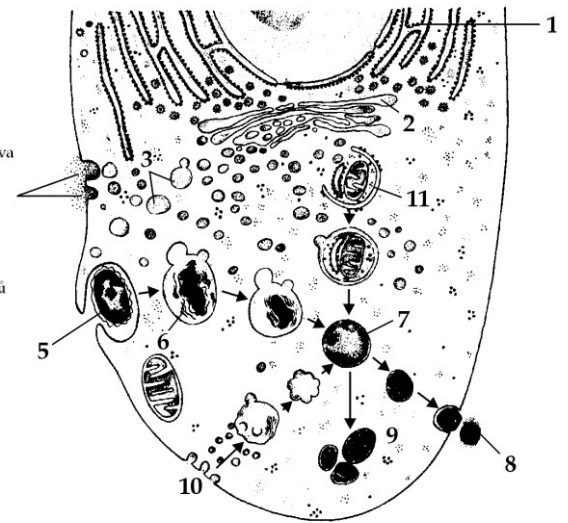
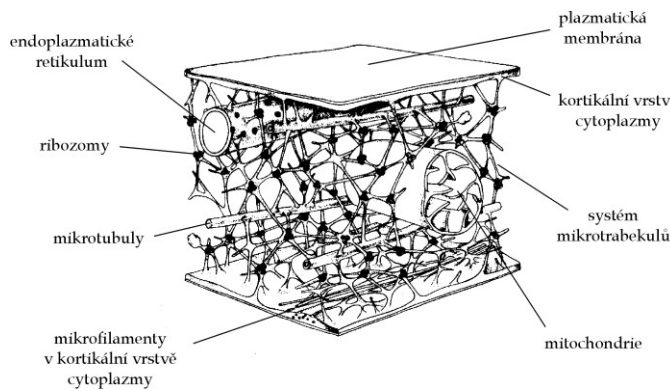
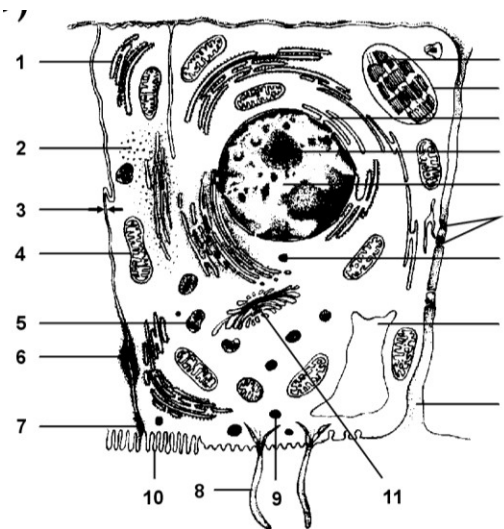
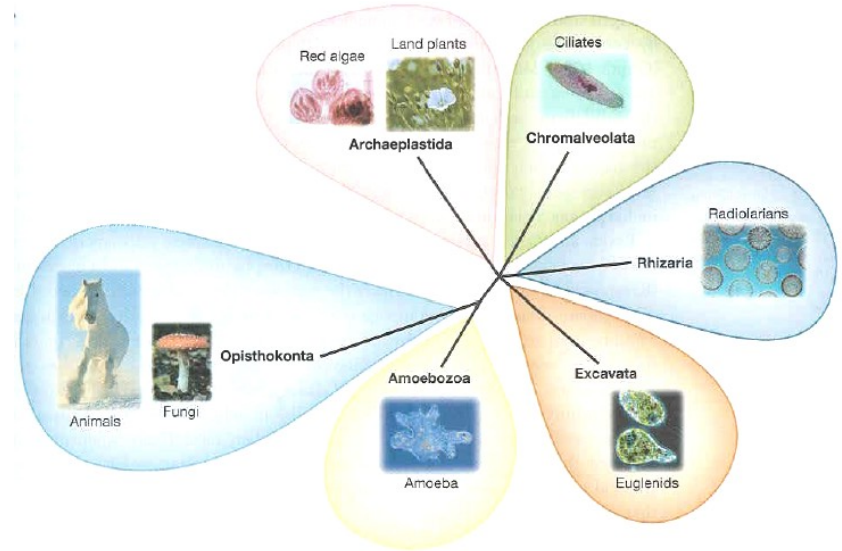
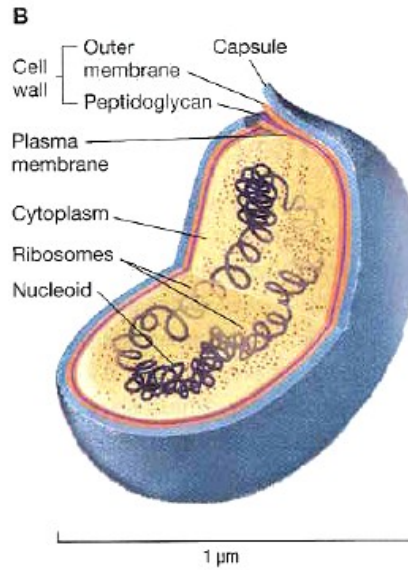
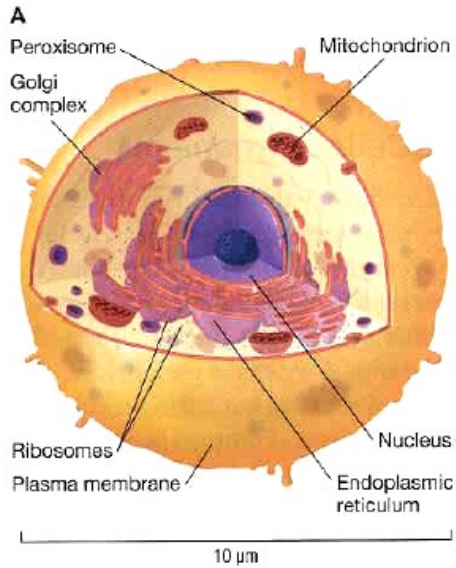
DNA advantages:

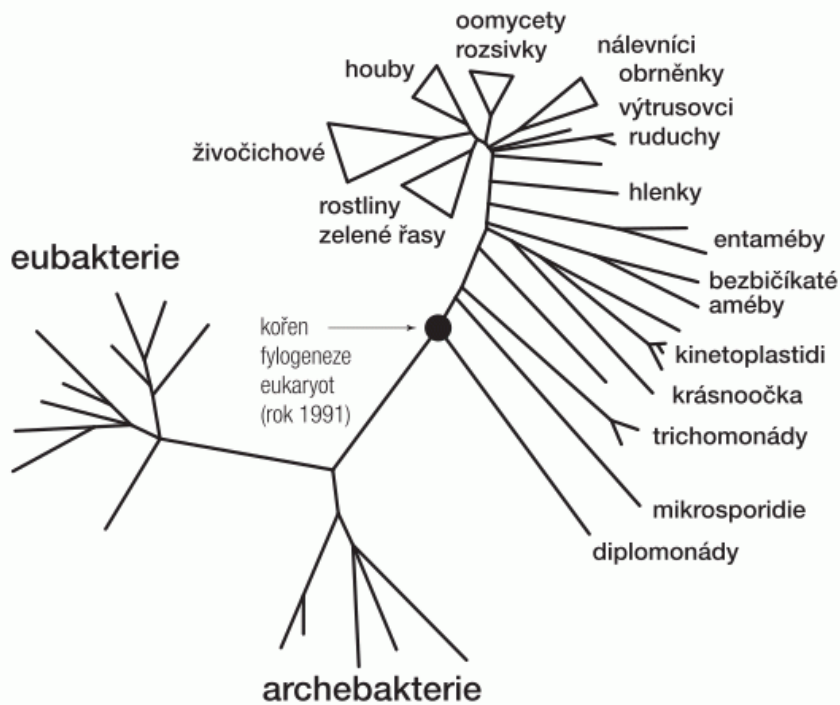
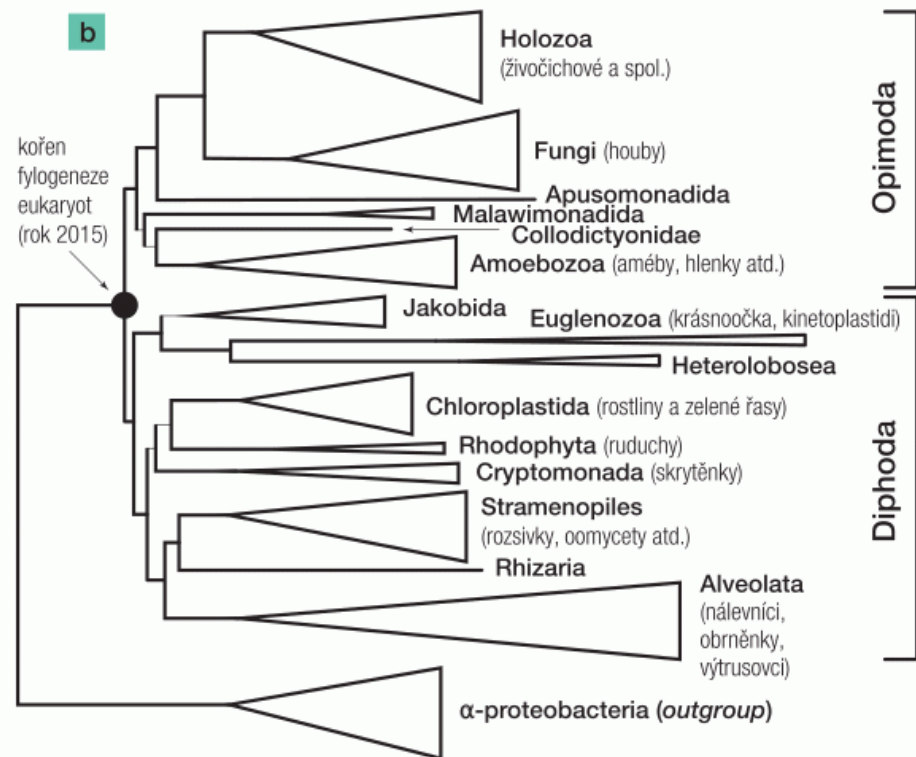
lower reactivity \Rightarrow higher stability \Rightarrow longer genes

division of labour between RNA and DNA

with loss of genetic function RNA could have carry out catalytic and
structural functions with smaller restrictions

Origin of eukaryotic cell



a**b**

Thomas Cavalier-Smith:

loss of cell wall \Rightarrow necessity to create endoskeleton \Rightarrow flexibility,
movement, fagocytosis

invagination of membrane \rightarrow ER

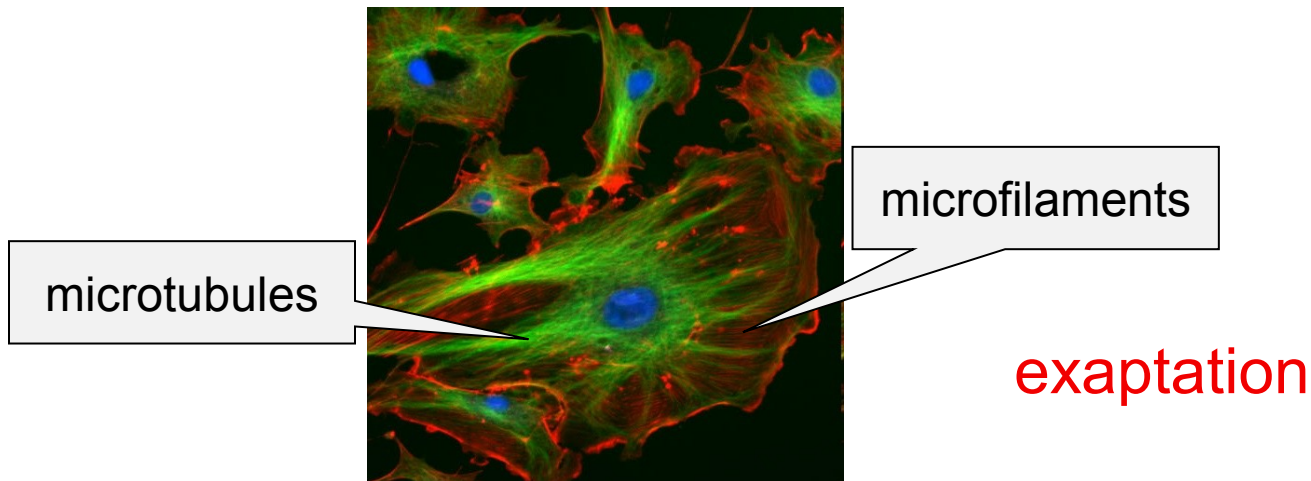
Prokaryotic cytoskeleton:

FtsZ: tubuline analogue, function in cell division

MreB: actin analogue, rod-shaped cell shape

Crescentin: analogue of intermediary microfilaments, helix creation

MinD, ParA: no analogue, cell division, separation of plasmids



Origin of cell organelles:

Konstantin Sergejevich Merezhkovsky (1905, 1909):

term **symbiogenesis**

chloroplasts = originally alien organisms

(Andreas Schimper, 1883: similarity between chloroplasts and cyanobacteria;

Richard Altmann, 1890: mitochondria [bioblasts] = originally bacteria)

first animal cell: anucleate amoeba + bacterium (nucleus)



K.S. Merežkovskij

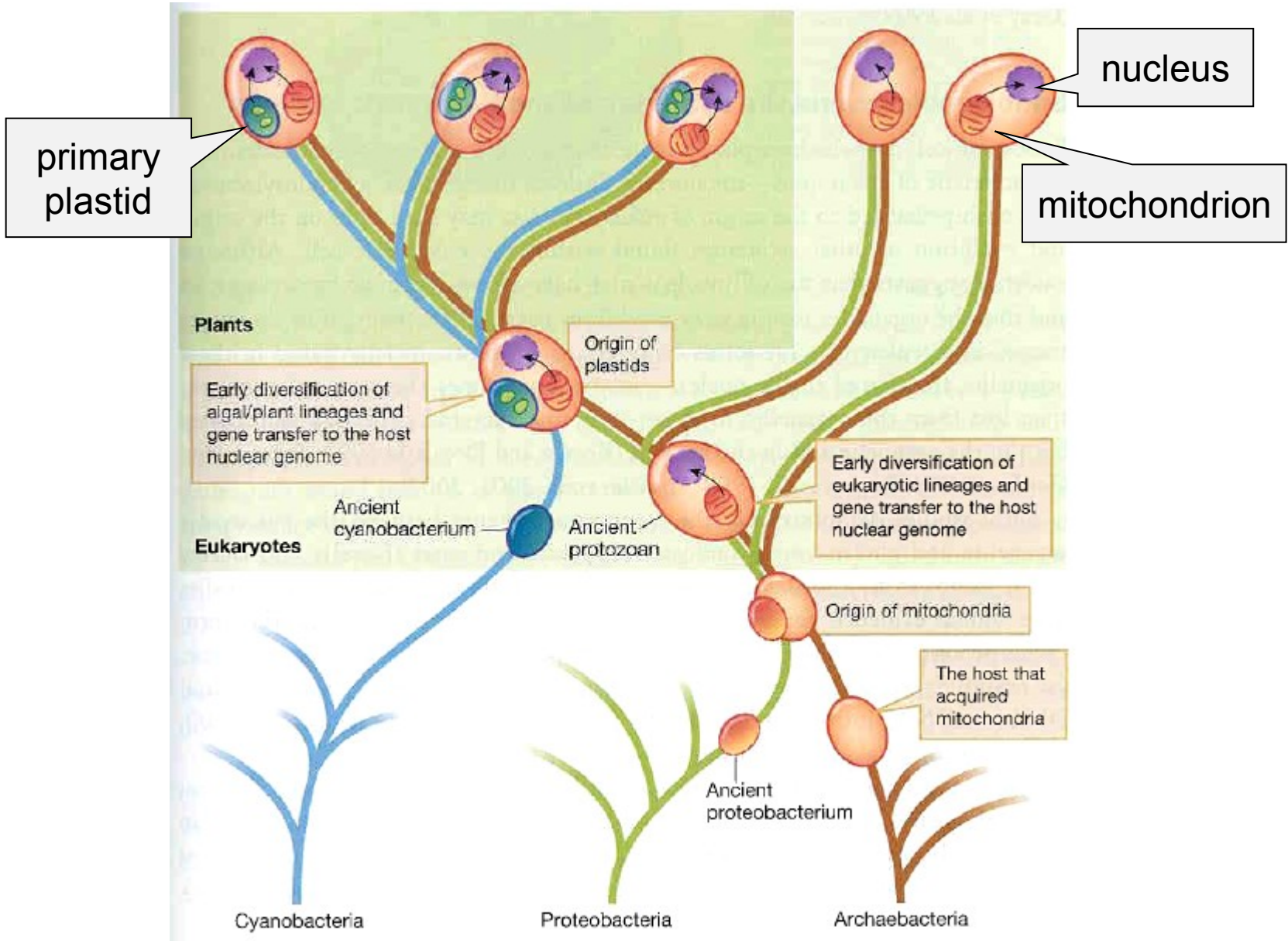
Lynn Margulis (1966, 1970): **endosymbiosis**

mitochondria: bacteria related to rickettsias or other α -proteobacteria (eg. *Rhodospirillum*),
gradually loss of photosynthesis

chloroplasts: cyanobacteria, loss of respiration



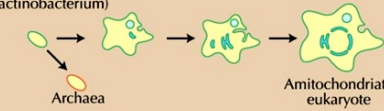
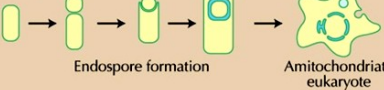
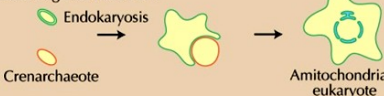
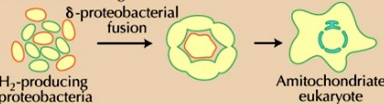
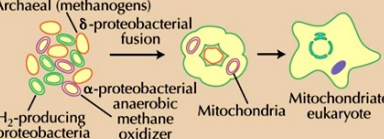
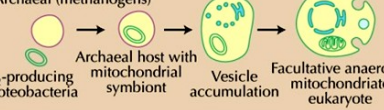

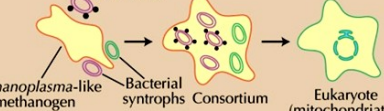
Lynn Margulisová



Theories of the origin of nuclear membrane:

1. fusion of vesicles of cytoplasmatic membrane
2. fusion of eubacterium and archaebacterium (archaebacterial membrane = nuclear, bacterial membrane = cellular)
3. viral origin (several alternatives) ... controversial
4. first origin of the 2nd cytoplasmatic membrane, from the inner eventually nuclear membrane

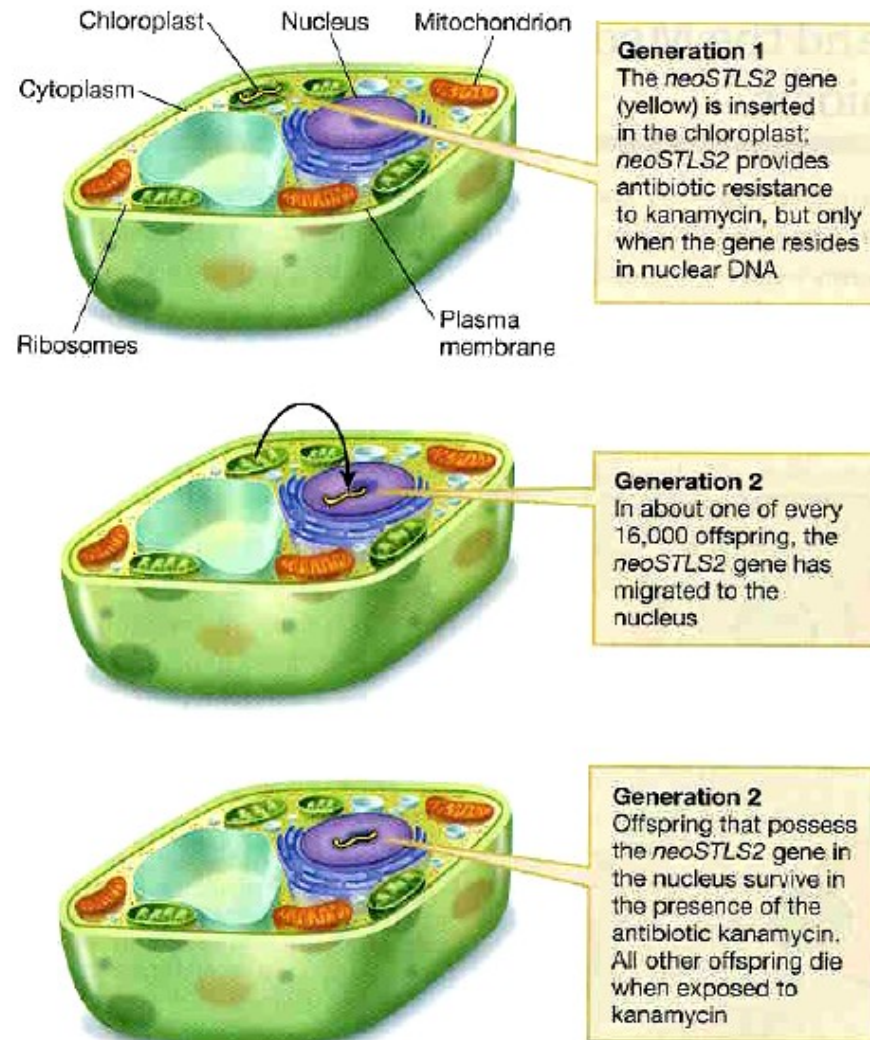
TABLE 8.2. Schematic summary of various models for the origin of the nucleus

Schematic Model	Membrane That Nuclear Membrane Is Derived from and Is Homologous to	Compartment That the Nuclear Compartment Is Derived from and Is Homologous to
<p>A Gram-positive bacterium (actinobacterium)</p>  <p>Archaea</p> <p>Amitochondriate eukaryote</p>	Plasma membrane of a bacterium	Bacterial cytoplasm
<p>B Gram-positive bacterium</p>  <p>Endospore formation</p> <p>Amitochondriate eukaryote</p>	Plasma membrane of a bacterium	Bacterial endospore
<p>C Gram-negative bacterium</p>  <p>Endokaryosis</p> <p>Crenarchaeote</p> <p>Amitochondriate eukaryote</p>	Plasma membranes of a bacterium and an archaea	Archaeal cytoplasm
<p>D Archaeal (methanogens)</p>  <p>δ-proteobacterial fusion</p> <p>H₂-producing δ-proteobacteria</p> <p>Amitochondriate eukaryote</p>	Plasma membranes of several bacteria	Archaeal cytoplasm
<p>E Archaeal (methanogens)</p>  <p>δ-proteobacterial fusion</p> <p>H₂-producing δ-proteobacteria</p> <p>α-proteobacterial anaerobic methane oxidizer</p> <p>Mitochondria</p> <p>Mitochondriate eukaryote</p>	Plasma membranes of several bacteria	Archaeal cytoplasm
<p>F Archaeal (methanogens)</p>  <p>Archaeal host with mitochondrial symbiont</p> <p>H₂-producing α-proteobacteria</p> <p>Vesicle accumulation</p> <p>Facultative anaerobic mitochondriate eukaryote</p>	Vesicles of bacterial lipids synthesized in an archaea cytoplasm	Archaeal cytoplasm around the chromosome
<p>G <i>Thermoplasma</i></p>  <p>Spirochaete</p> <p>Amitochondriate eukaryote</p>	Plasma membranes of a bacterium and an archaea	Spirochaete cytoplasm
<p>H</p>  <p>Complex-enveloped DNA virus</p> <p>Methanoplasma-like methanogen</p> <p>Bacterial syntrophs Consortium</p> <p>Eukaryote (mitochondriate?)</p>	Viral coat	Viral lumen

Reproduced from Martin W. 2005. *Curr. Opin. Microbiol.* 8: 630–637 (Table 1, p. 632) (© Elsevier).

Transfer of genes to nucleus:

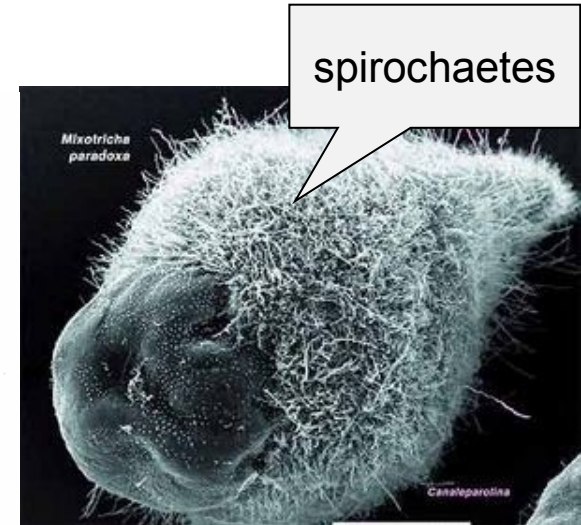
eg. *neoSTLS2* gene, tobacco chloroplast → in 16 of 250 000 ($\approx 1/16\ 000$) daughter cells transfer of the gene to nucleus ⇒ kanamycin resistance



peroxisomes: G+ bacteria

microtubules: spirochaetes

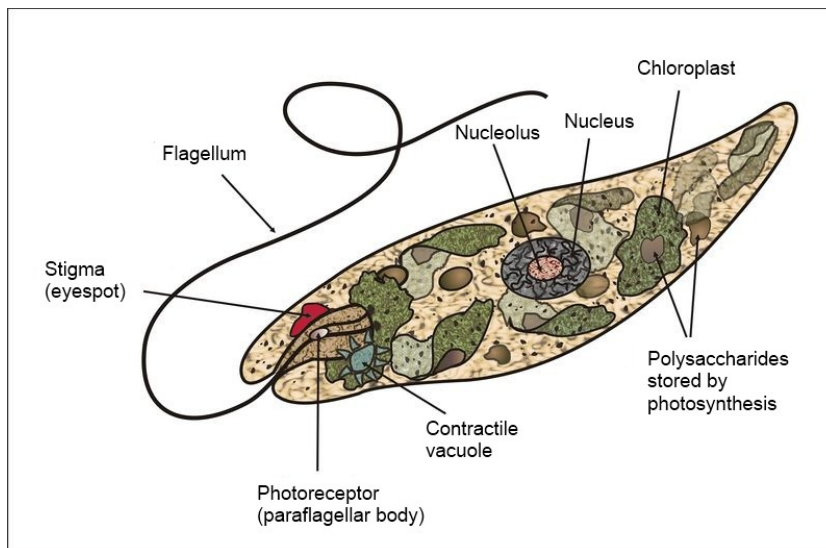
× současné poznatky nepotvrzují



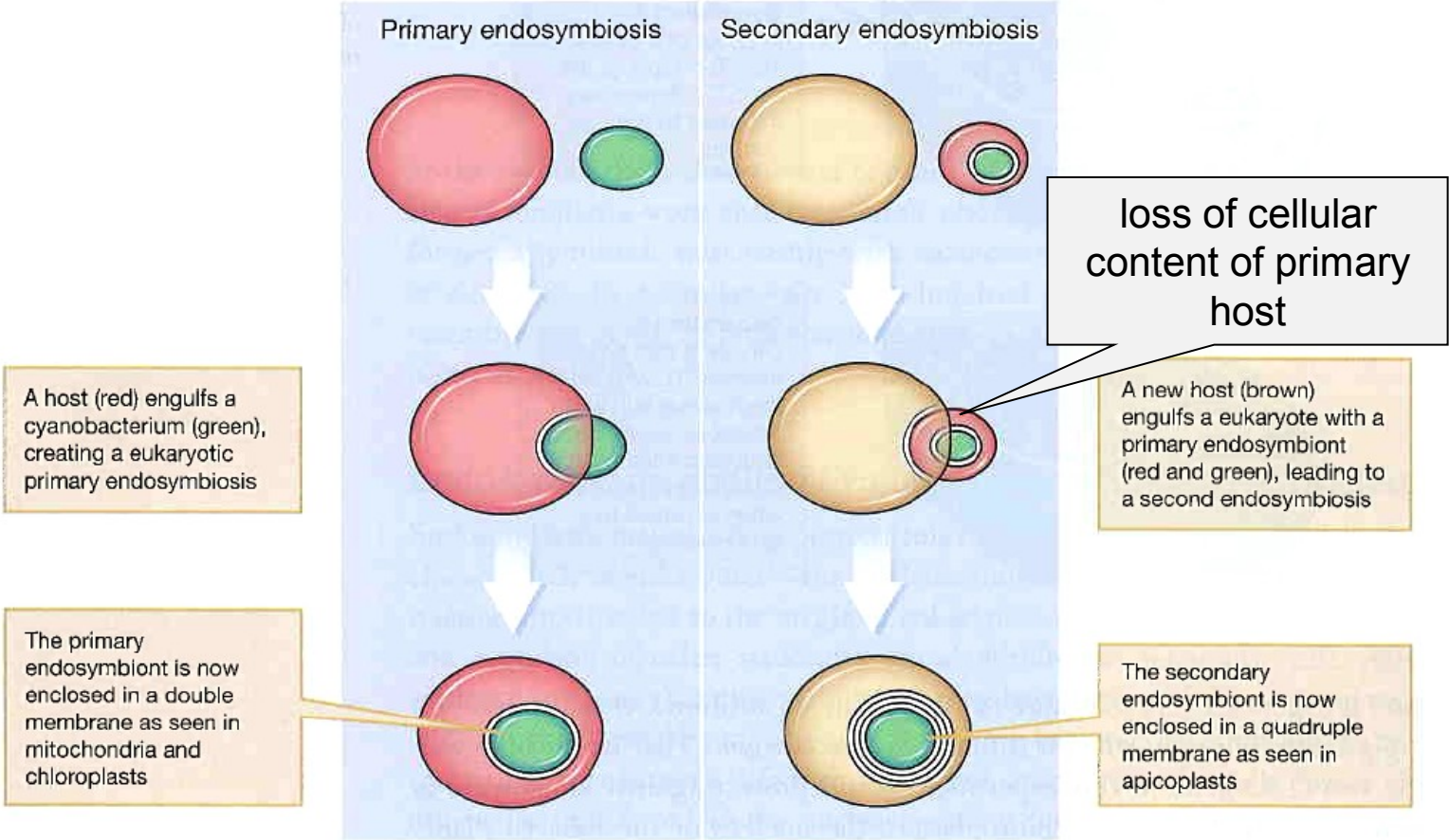
Mixotricha paradoxa

secondary and tertiary endosymbiosis

→ complex plastids: eg. euglena + green alga

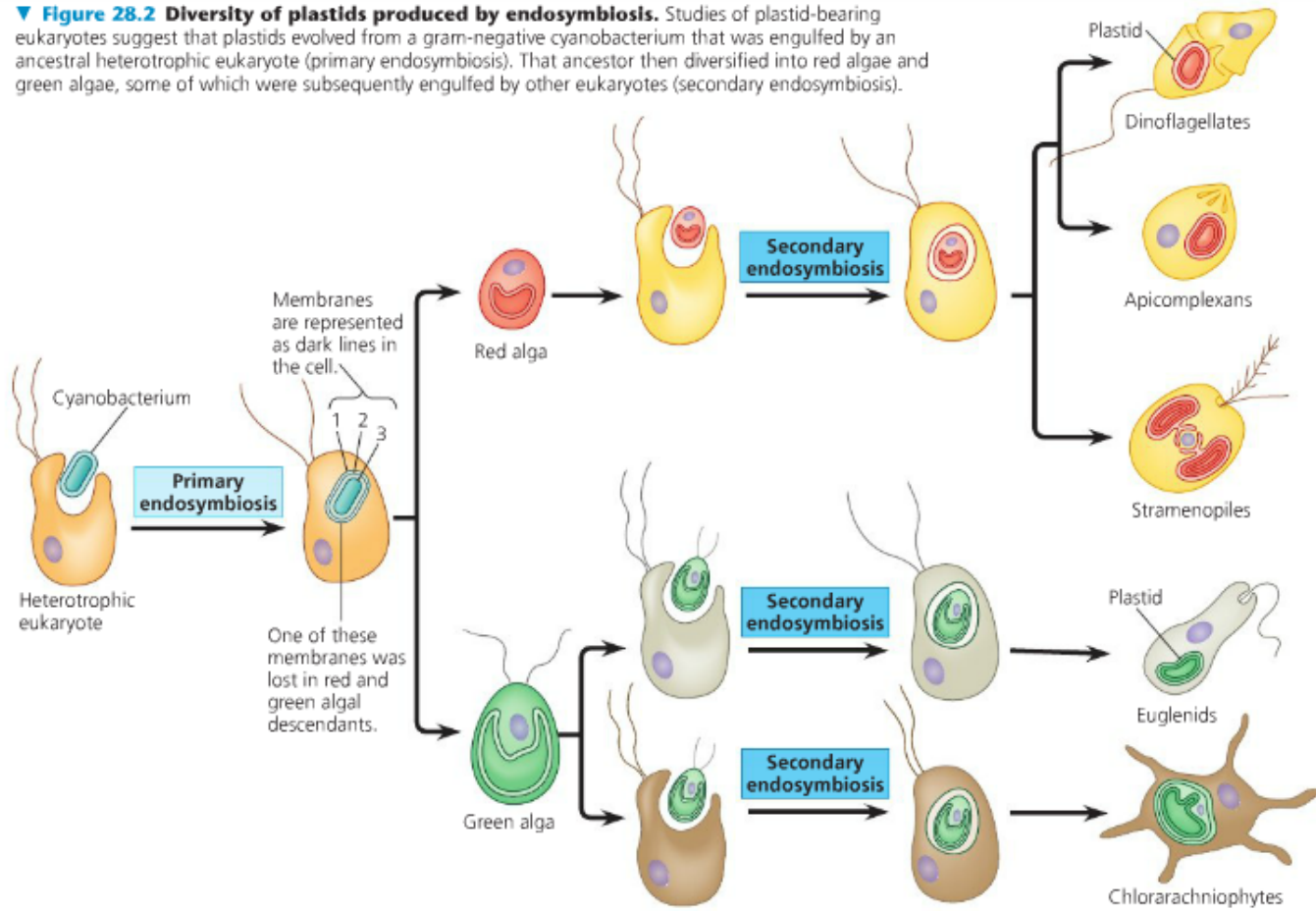


Secondary endosymbiosis:

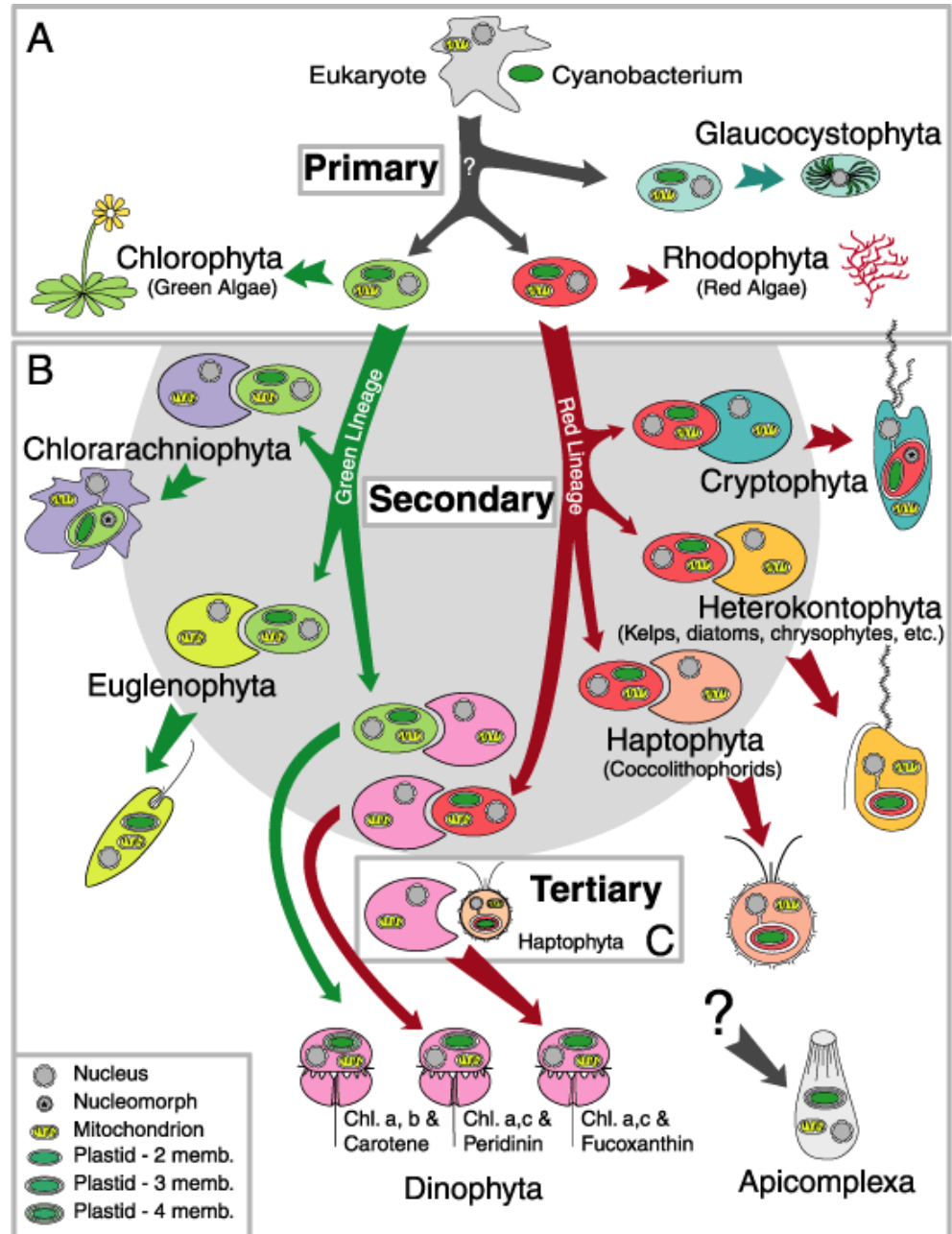
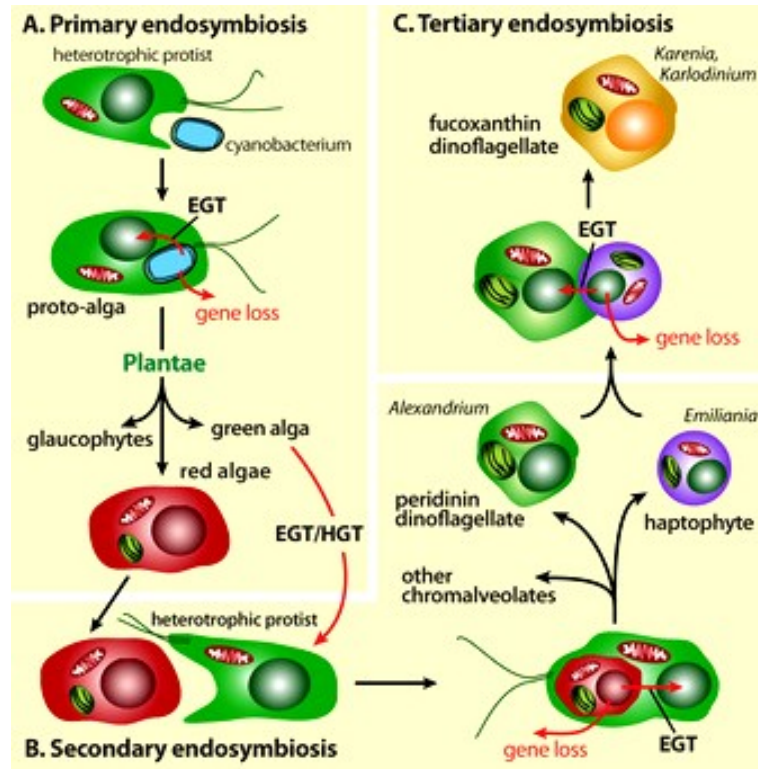


Secondary endosymbiosis:

▼ **Figure 28.2 Diversity of plastids produced by endosymbiosis.** Studies of plastid-bearing eukaryotes suggest that plastids evolved from a gram-negative cyanobacterium that was engulfed by an ancestral heterotrophic eukaryote (primary endosymbiosis). That ancestor then diversified into red algae and green algae, some of which were subsequently engulfed by other eukaryotes (secondary endosymbiosis).

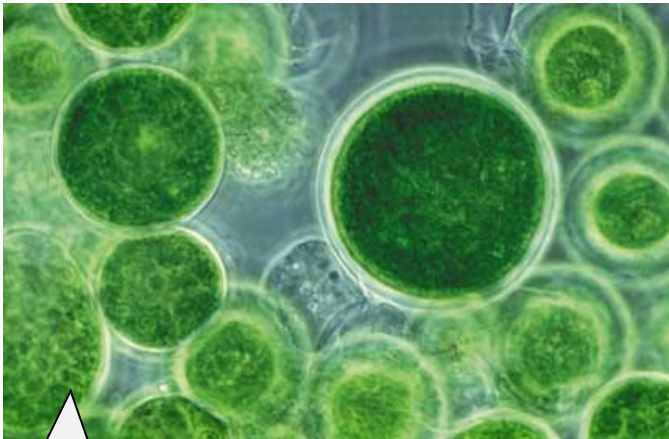


Tertiary endosymbiosis:



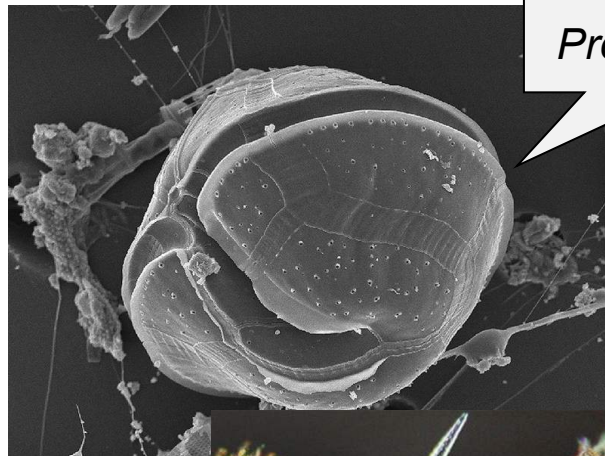
sometimes the existence of a secondary endosymbiont can be revealed only according to presence of its DNA (eg. chlamydia genes in plant plastids and primary algae)

in other cases endosymbionts still able of independent life, eg. photosynthetic algae (chlorellas, dinoflagellates, haptophytes) in cells of corals, foraminiferans, radiolarians, and some ciliates

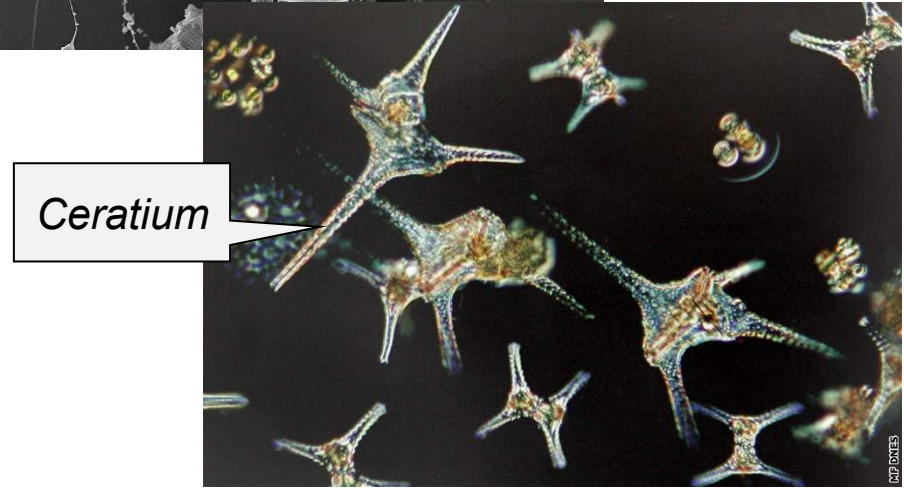


Chlorella

haptophyte
Gephyrocapsa



Protoperidinium

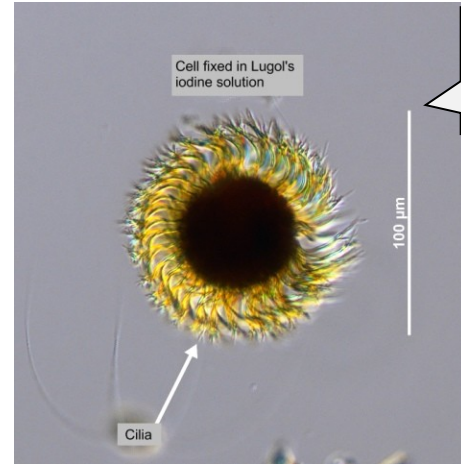


Ceratium

„kleptoplastids“ (eg. ciliate *Myrionecta rubra*, dinoflagellate of the genus *Dinophysis*, marine gastropod *Elysia viridis*)

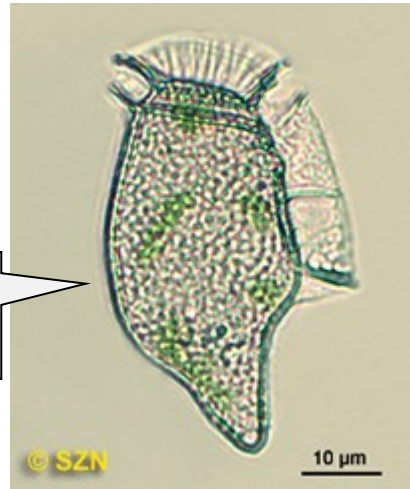


Elysia viridis

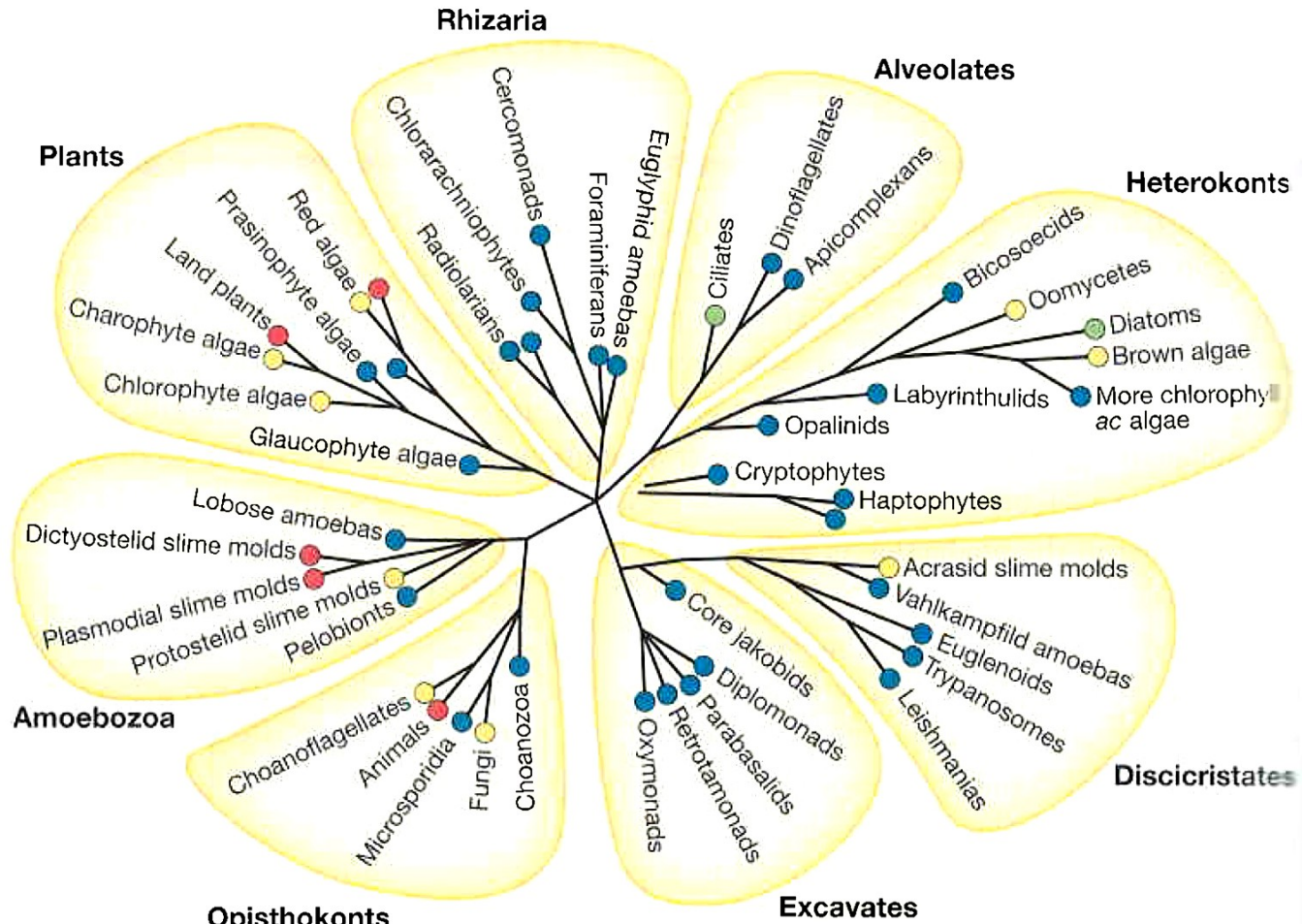


Myrionecta rubra

Dinophysis caudata

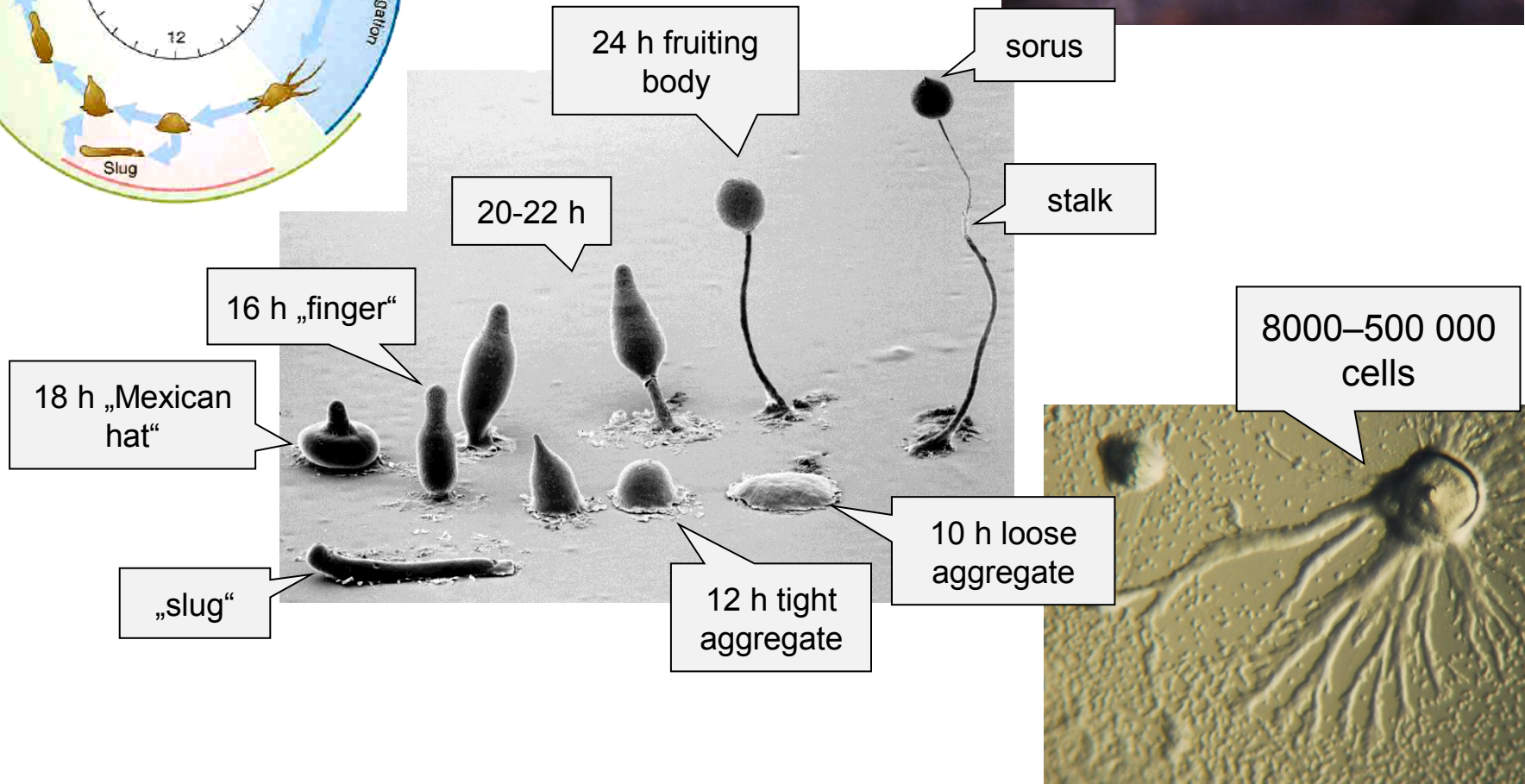
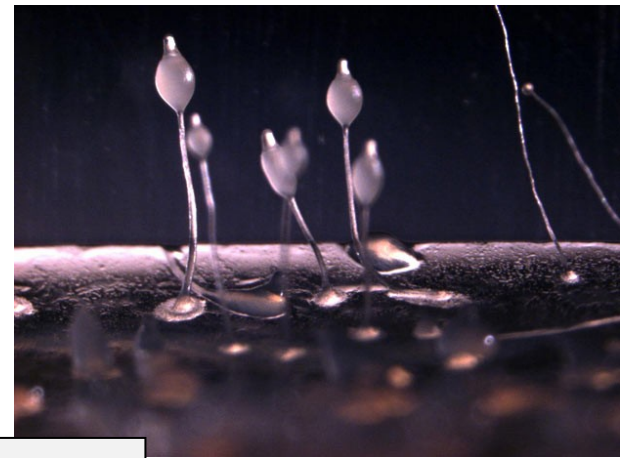
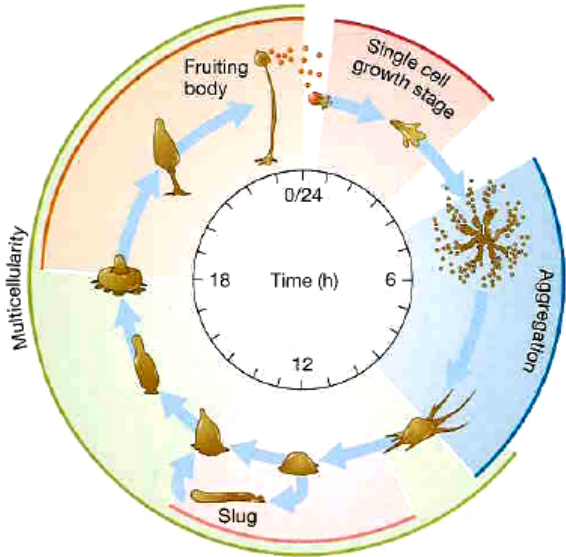


Origin of multicellular organisms



- All members are multicellular
- Clade contains unicellular and colonial/multicellular species
- Unicellular with rare multicellular forms
- All members are single celled

slime molds, eg. *Dictyostelium discoideum*

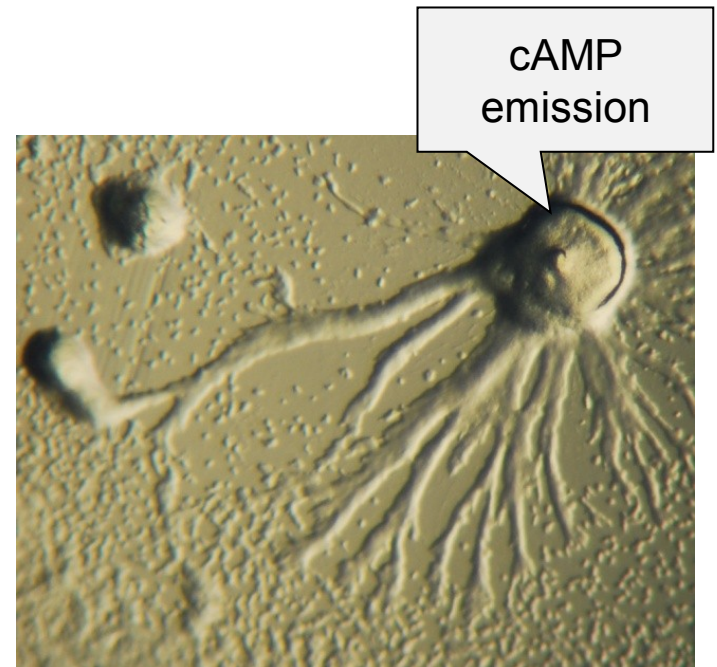
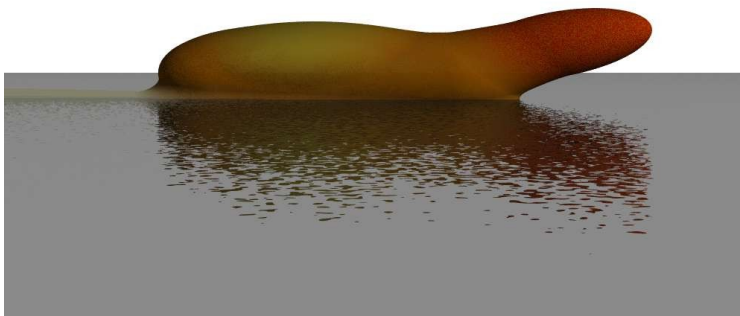
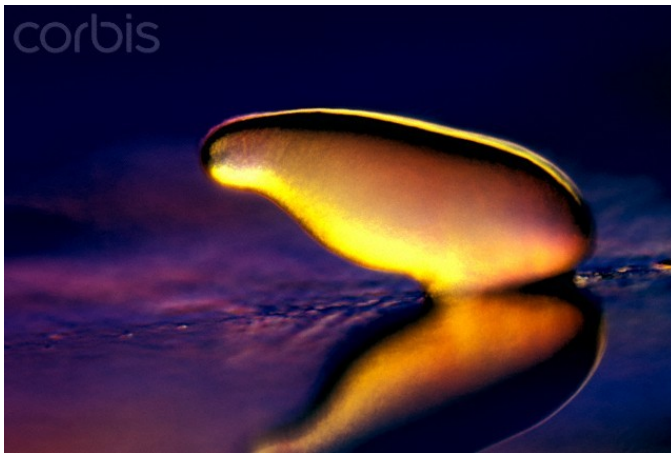


How can „slug“, composed of independent amoebas, orient itself in its environment?

cAMP (cyclic adenosine monophosphate): emission in area of the densest aggregation → signal for „downstream“ cells → gradual aggregation

production of protein enabling mutual attachment of amoebas

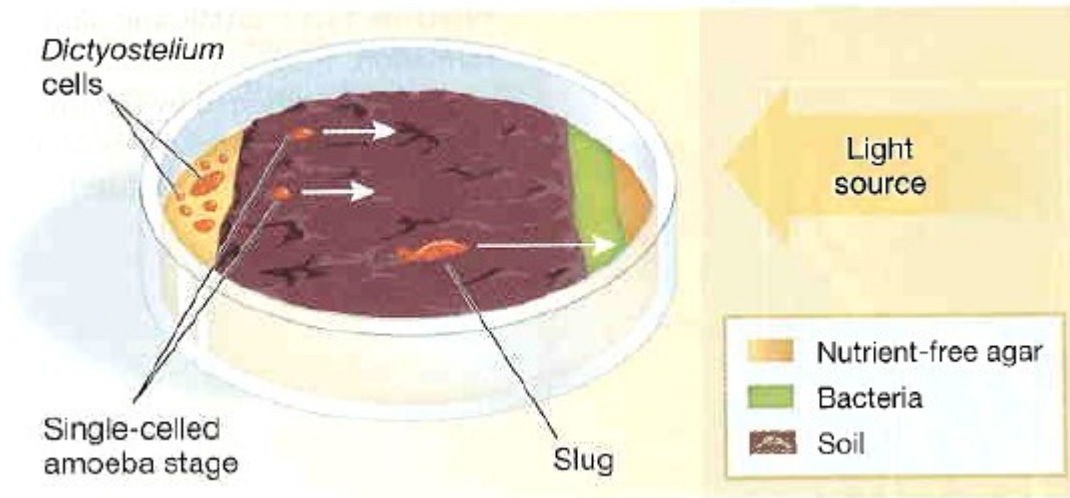
reaction to external stimuli: light, temperature, oxygen and ammonium in the soil



Advantages of *D. discoideum* aggregation?

production of coat made of cellulose and substances rich of proteins → protection against nematodes – only on the “slug” surface

faster movement



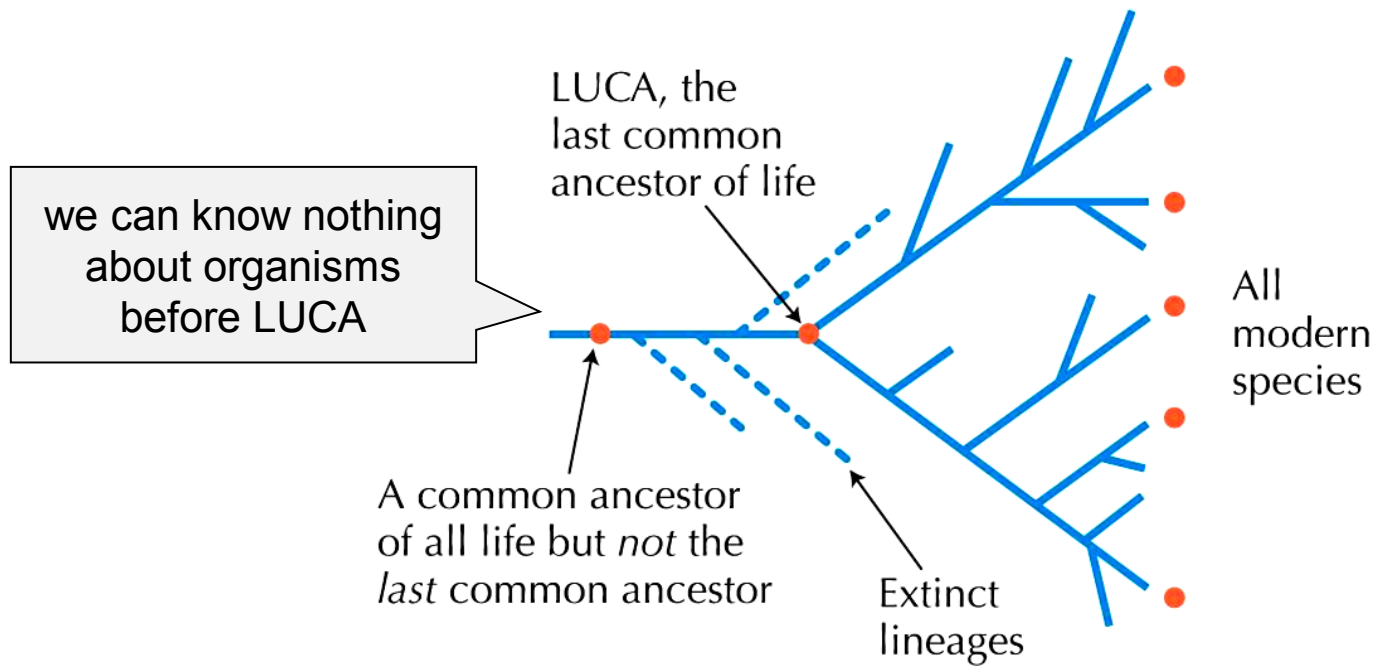
nematode

direction of „slug“ movement

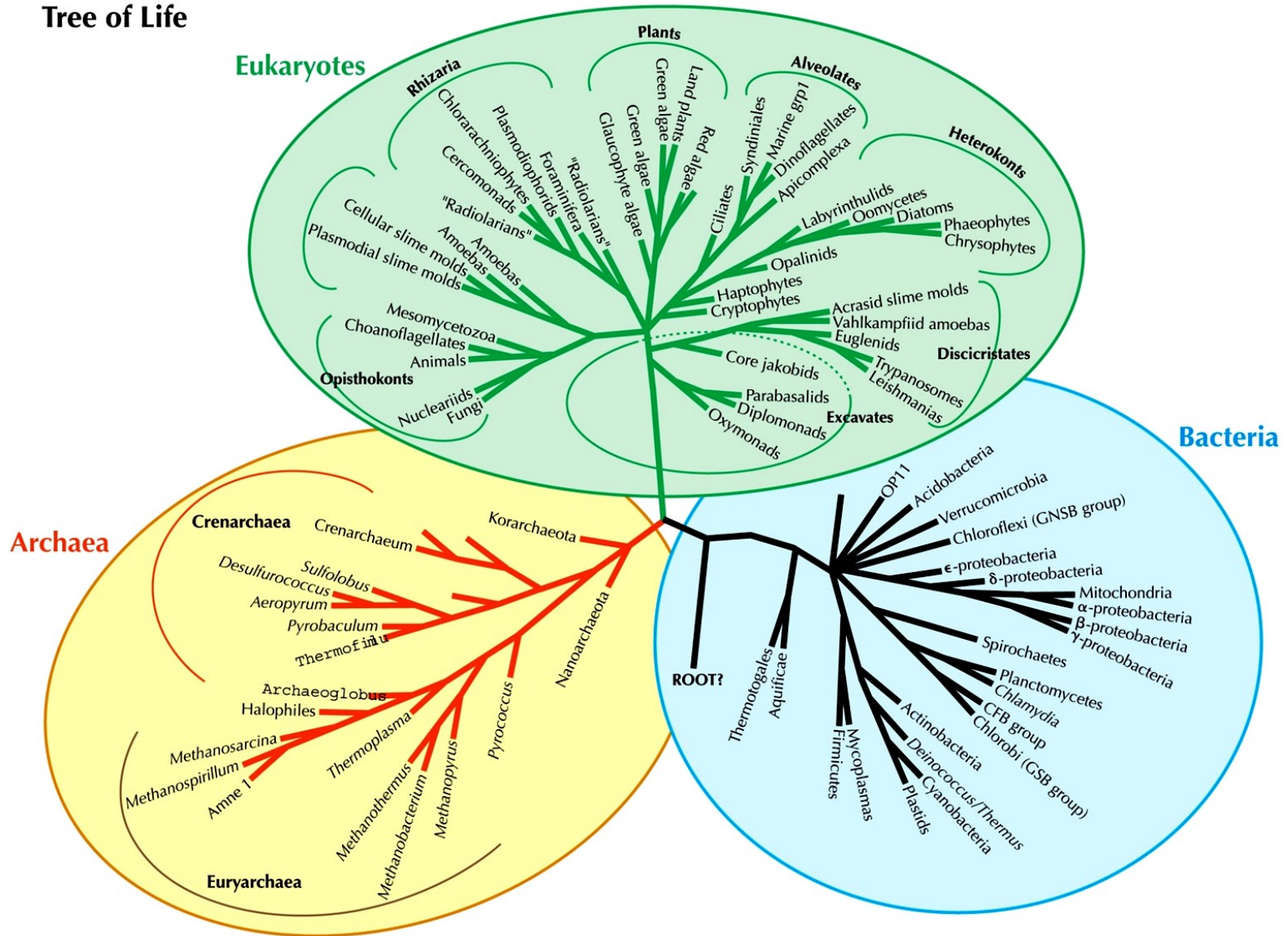
„slug“ protected by coat and size

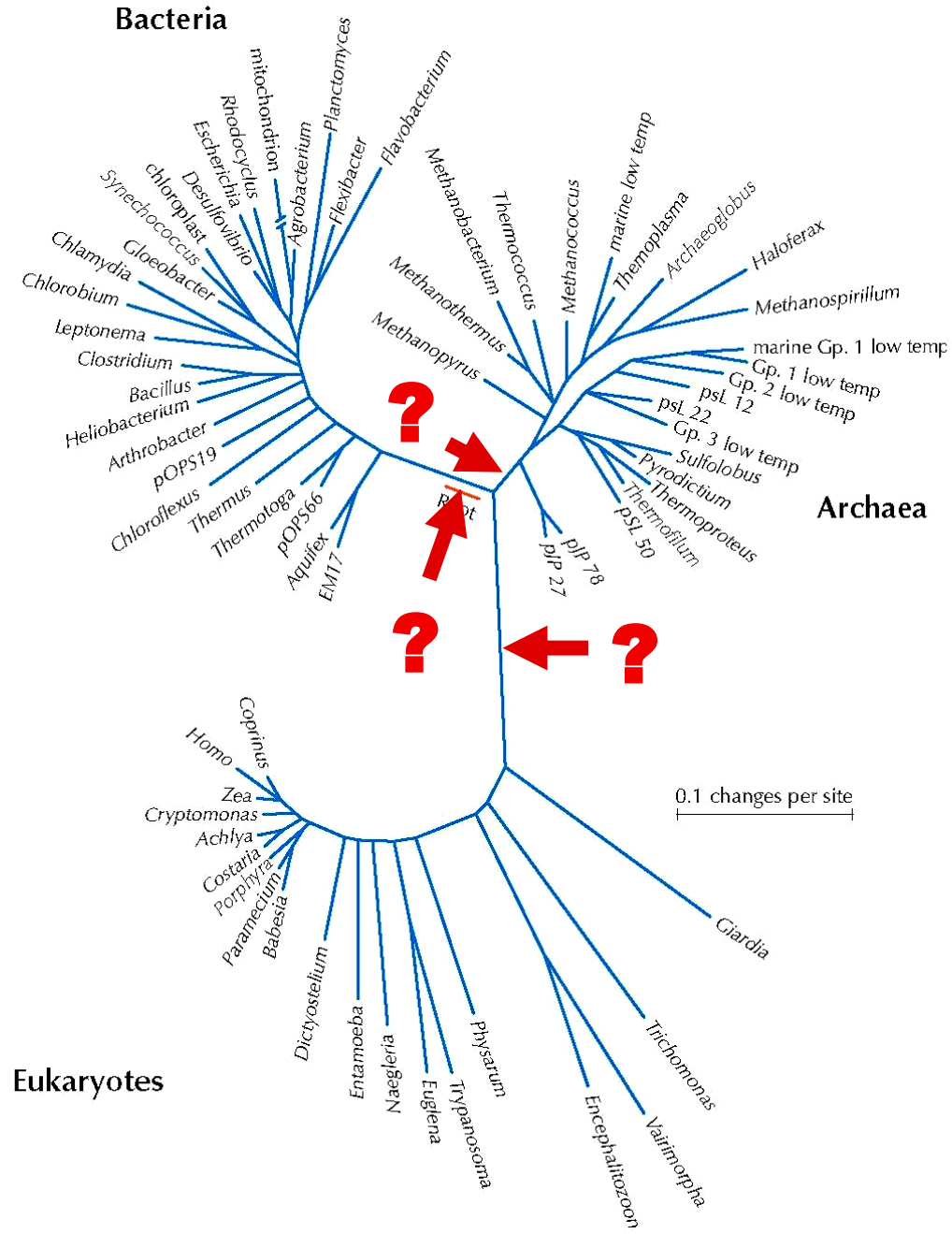
Tree of life:

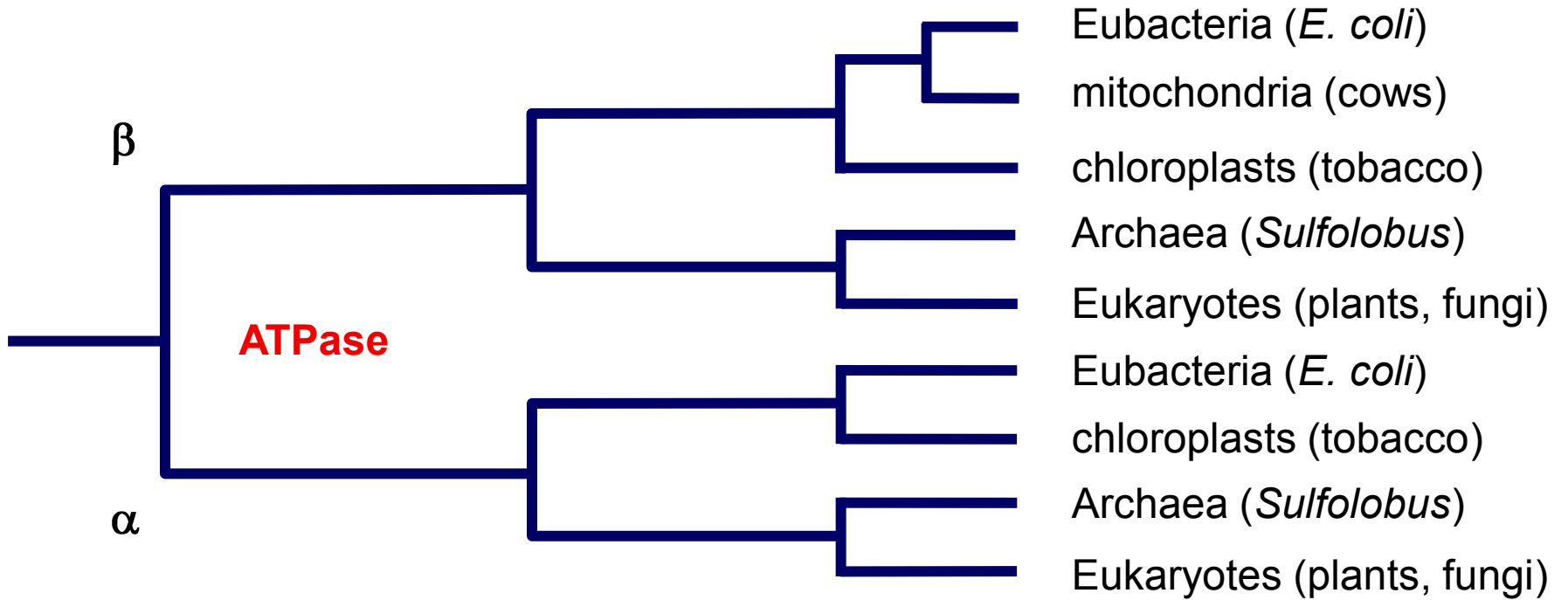
Last Universal Common Ancestor (LUCA)



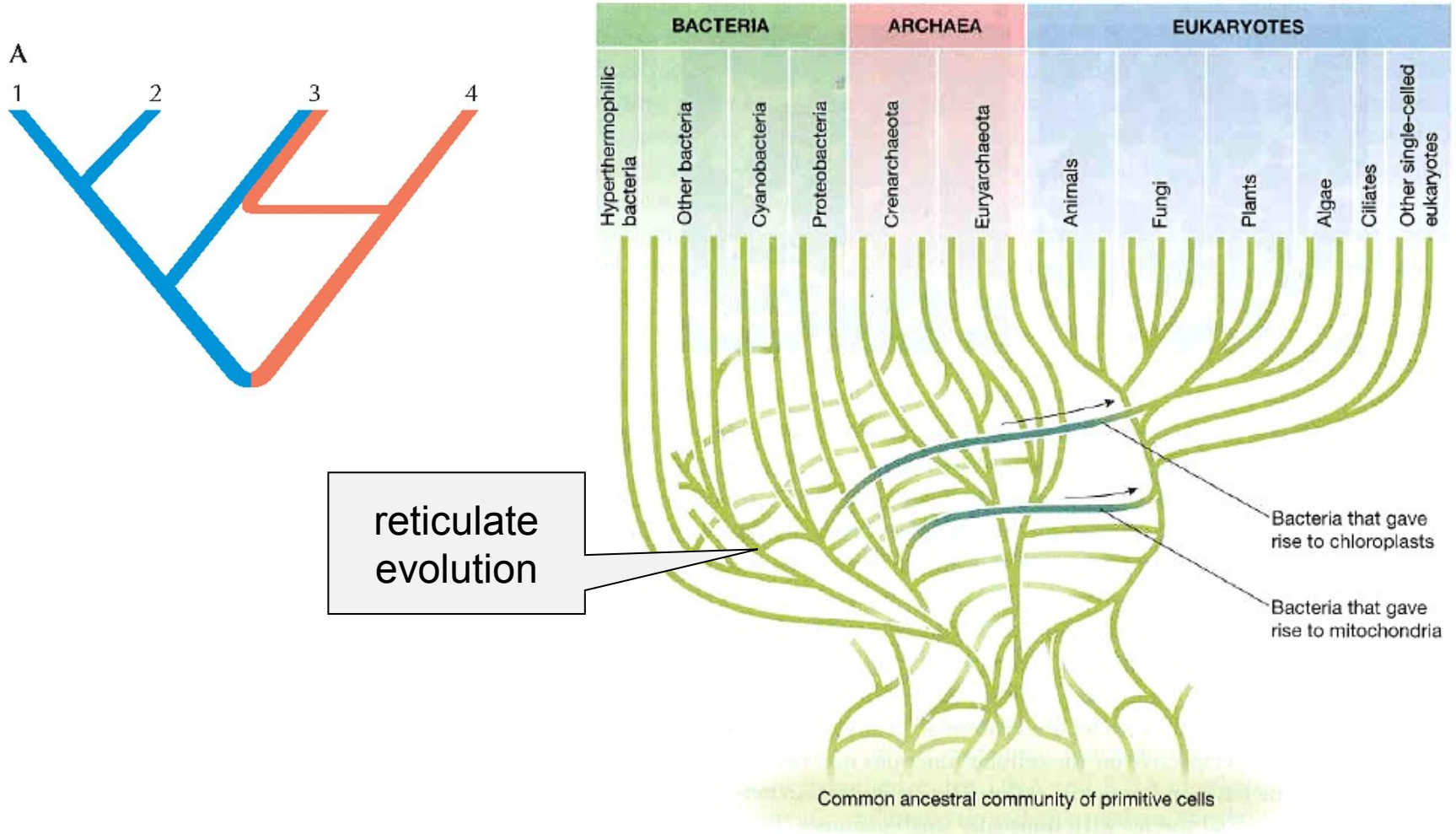
Tree of Life







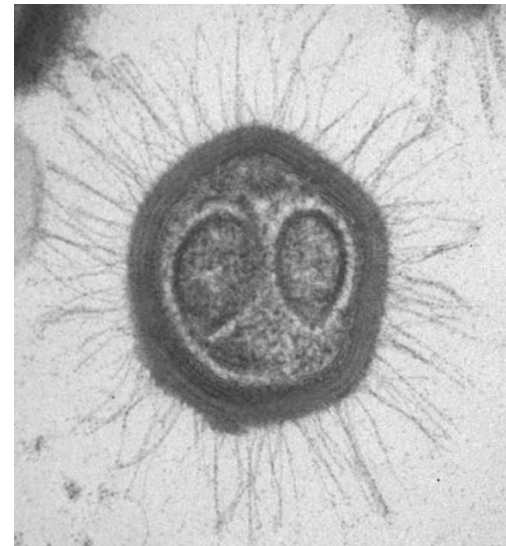
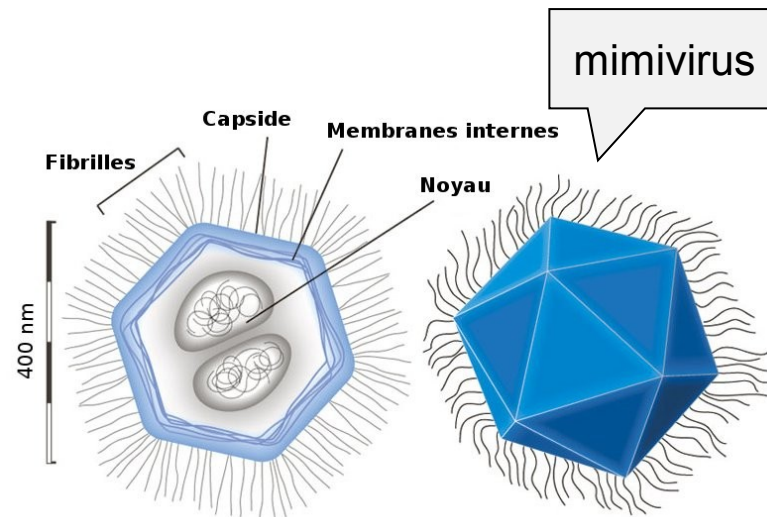
Horizontal transfer of genes



⇒ no LUCA of recent organisms × trees for individual genes can have LUCA

Where to place viruses on the Tree of Life?

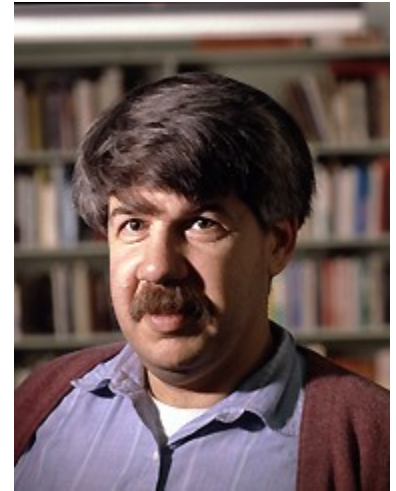
1. relics of pre-cellular world: some processes and genes ancient
many genes only very distantly related to their cellular counterparts
× how could they independently exist in pre-cellular world?
2. similarity with transposons → „escaped“ parts of cellular organisms
– (eg. RNA or DNA elements, plasmids)
3. originally free-living organisms
eg. mimivirus: genome size = 1,2 Mb, > 900 proteins, ie. more than some bacteria and archaeobacteria!



Increase of complexity:

Stephen Jay Gould:

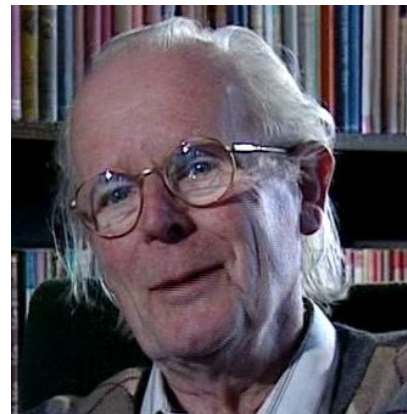
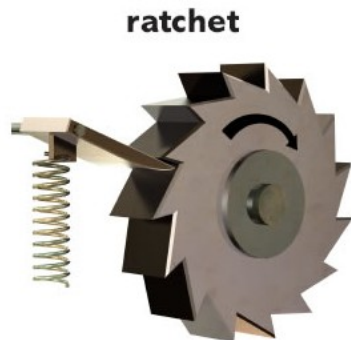
evolution moves as a drunk person which cannot return to the starting point however he wants even at present most organisms prokaryotic secondary simplification (eg. parasites)



×

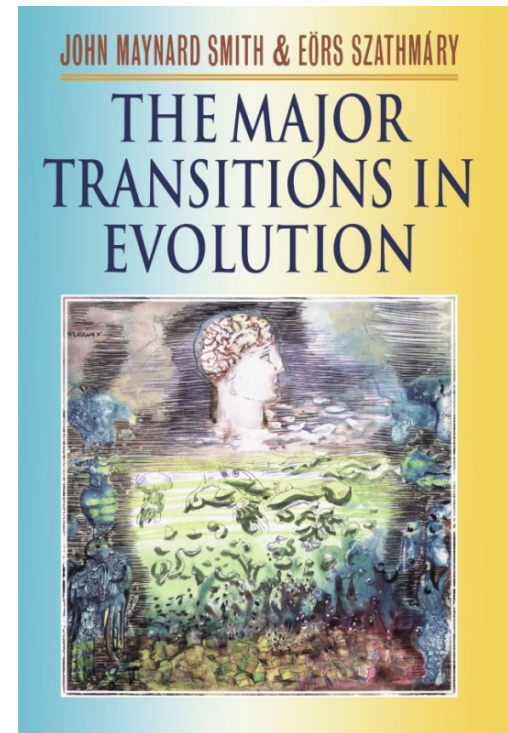
John Maynard Smith a Eörs Szathmáry:

the contingent irreversibility theory): steady tendency to increase of complexity major transitions complexity emerges without selection



Major transitions in evolution:

origin of replicators
compartmentation, origin of cell
origin of chromosomes
origin of genetic code, DNA
origin of Eukaryotes
origin of sex
multicellularity
societies
origin of language



Individuals cease to reproduce independently

Bigger size → bigger prey, specialization, division of labour

Origin of more effective ways of acquiring, processing, transmission, and saving of informations

But advantages of a transition to a „higher level“
do not imply group selection!

conflict of selections at different levels:

replication control × B chromosomes, transposition

fair meiosis × meiotic drive

differentiation of somatic cells × oncogenic growth

non-reproducing castes × egg-laying workers