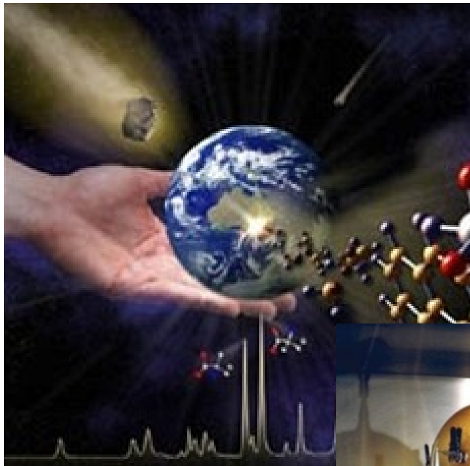
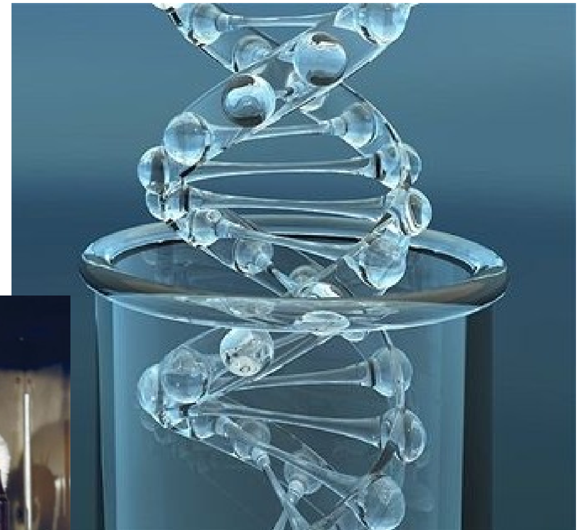
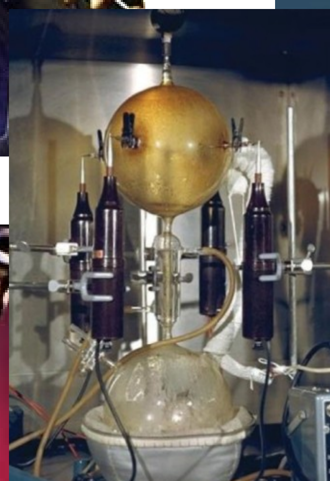
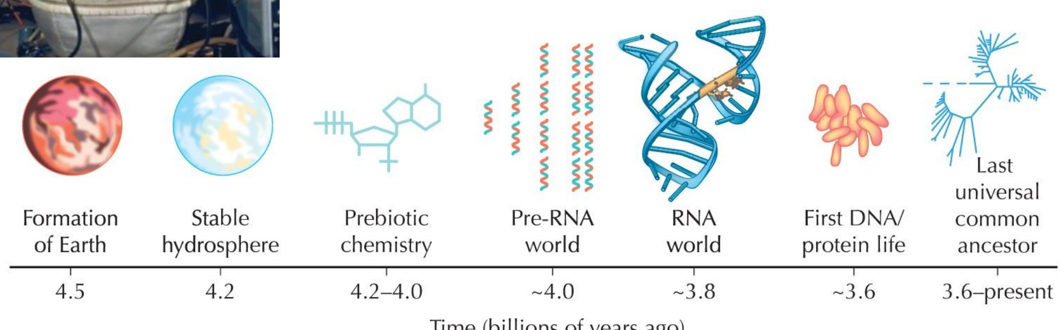
ORIGIN OF LIFE





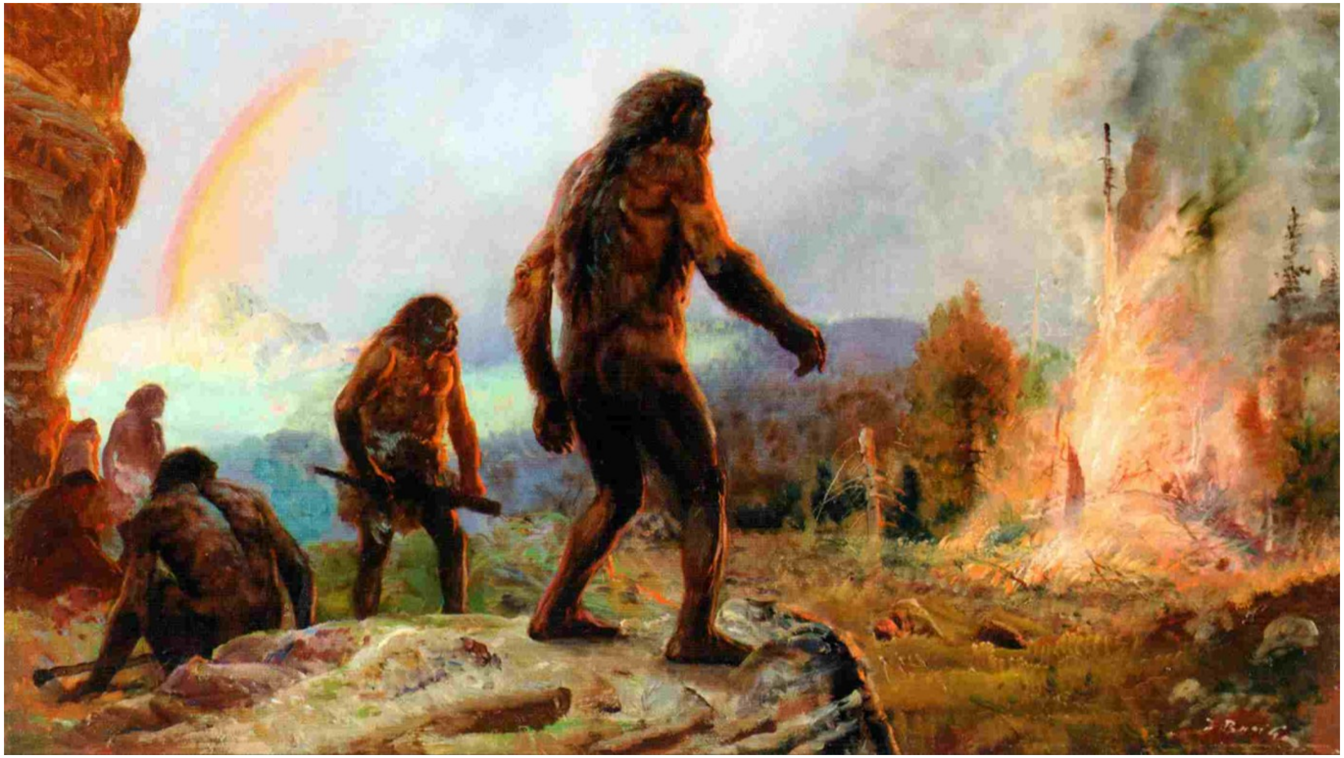




Origin of life is to large extent outside evolutionary biology

→ 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?

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

definitions: phenotypic
evolutionary

prerequisite: metabolism

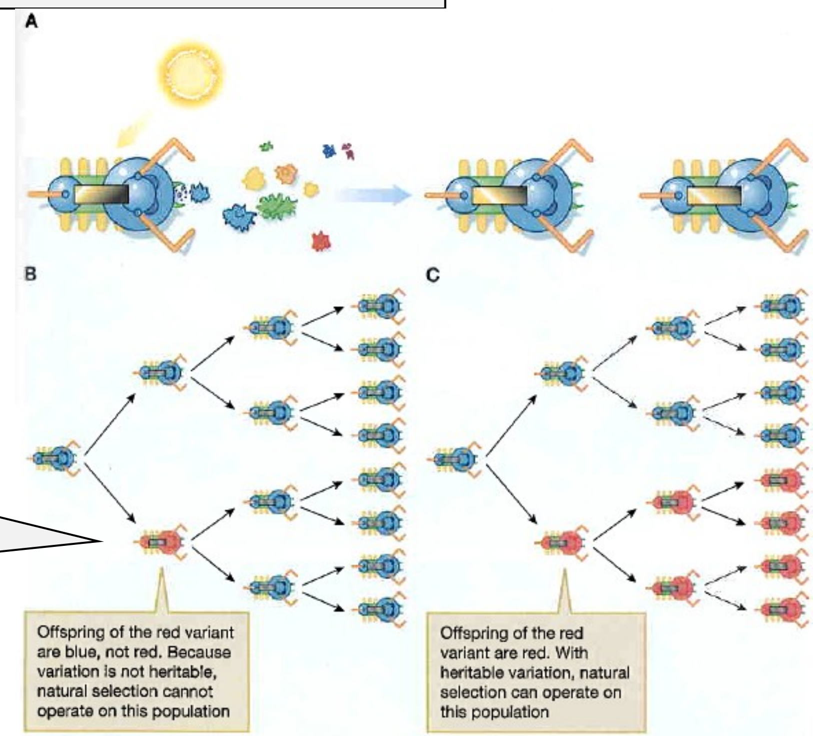
Muller (1966): autoreproduction
variability
inheritance

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 $\times$ assessment of evolution from backward view, with respect to long-term consequences

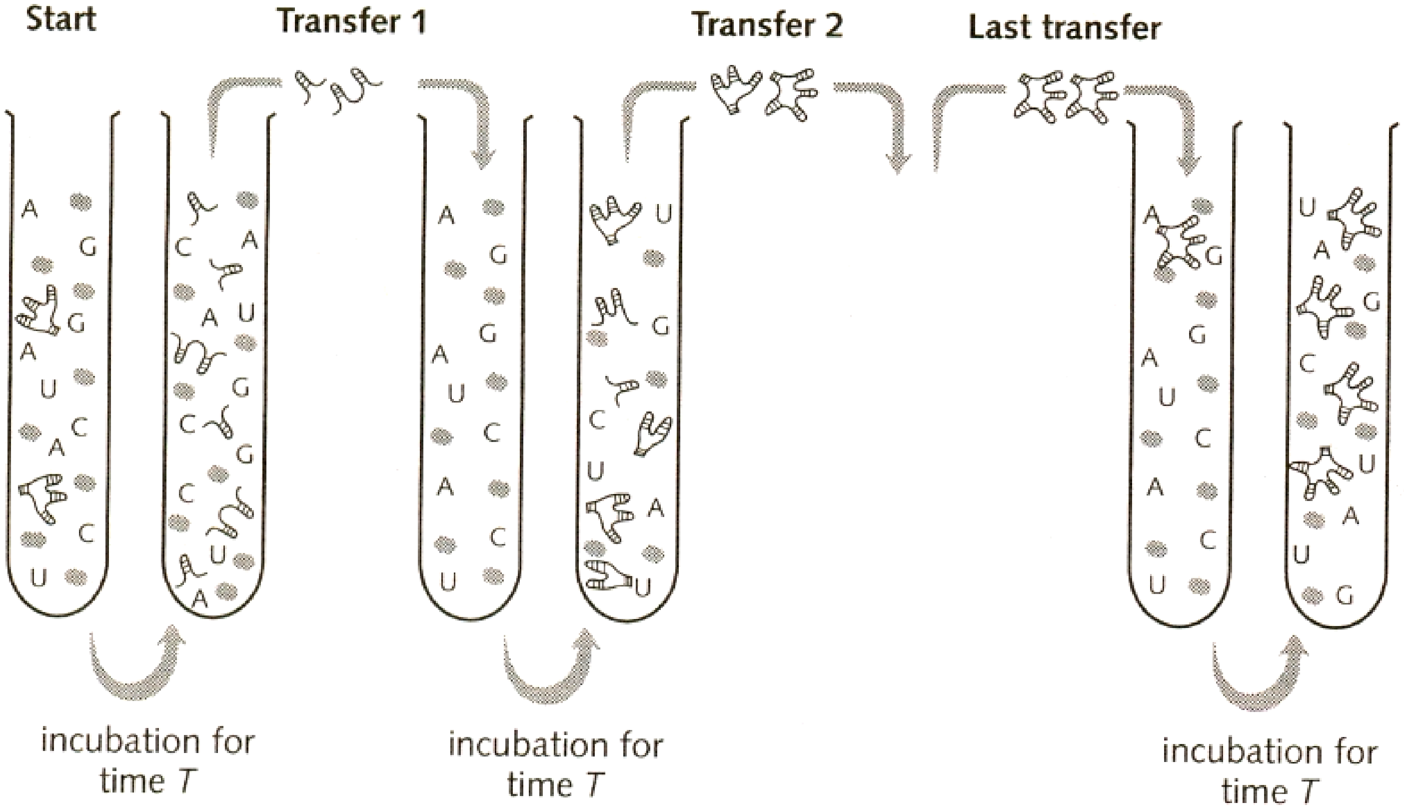
$\Rightarrow$ present-day life cannot help with solving

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 Qβ replicase,
+ nucleotides



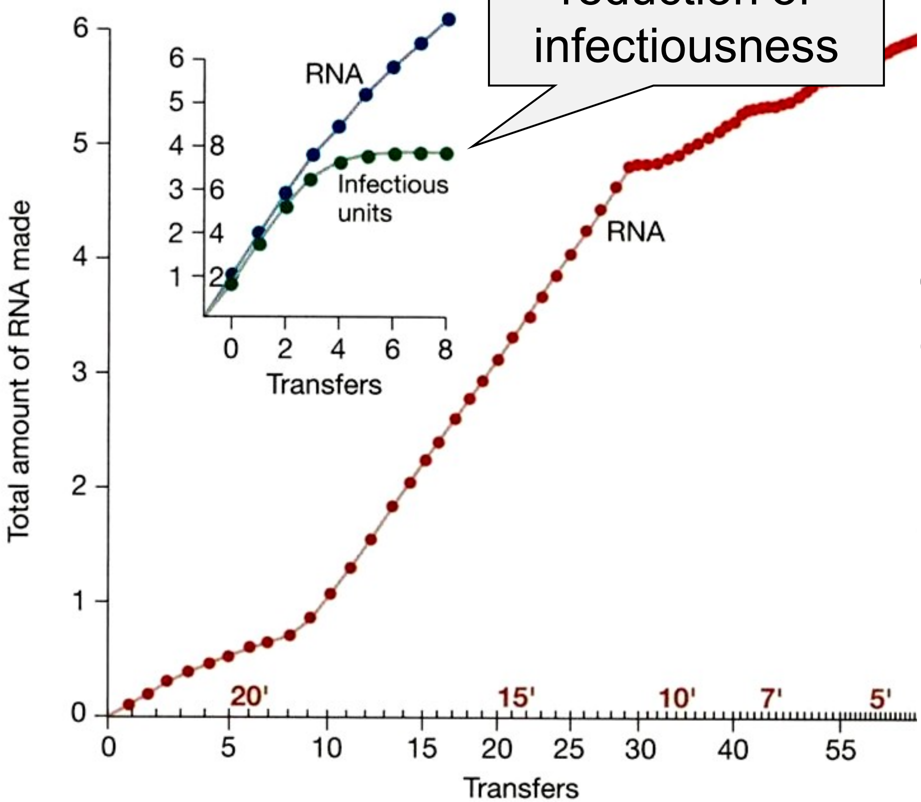
Sol Spiegelman

⇒ evolution → „Spiegelman´s monster“:

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

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

after 4th transfer reduction of infectiousness



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

Sumper a Luce (1975):

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

But these experiments don´t explain <u>origin</u> of life (enzyme supplied)

ORIGIN OF LIFE

According to radiometric measurements age of Earth ~ 4,54 ± 0,04 GYA

(but according to some theories Earth has been created secondarilly 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

Precambrian stromatolites
Siyeh Formation, Glacier Natl. Park

upper limit: microfossils, chemical fossils

chert in Warrawoona Group (Z Australia)
3,45 GY: resemblance to present stromatolites

... now questioned

present-day stromatolites
Shark Bay, W Australia

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

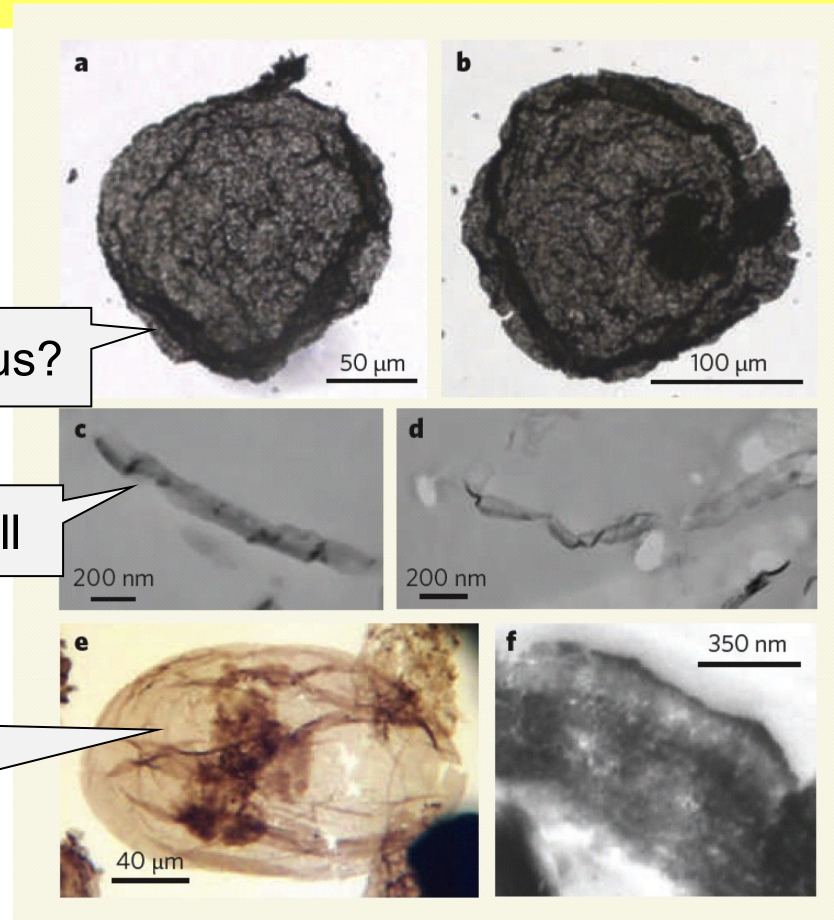
Greenland glacier: 3,85 GY, confirmed by C^{12}/C^{13} ratio

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 $\rightarrow$ chemical evolution, primitive metabolism

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

First chemical experiments:

1828: ammonium chloride + silver cyanate + heat $\rightarrow$ urine (= Wöhler synthesis)

1850s: formamide + H_2O + UV, electricity$\rightarrow$ alanine

formaldehyde + NaOH $\rightarrow$ saccharides

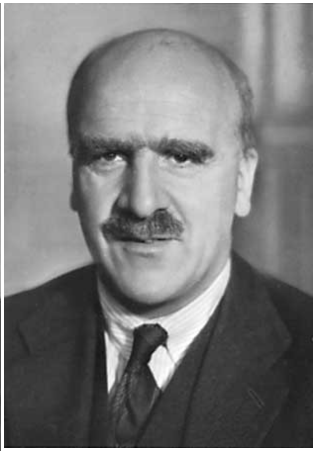
$\Rightarrow$ evidence against vitalism (claims that chemistry in living systems is fundamentally different from non-living, ie. organic $\neq$ inorganic)

Chemical evolution

Alexandr Ivanovich Oparin (1924)

J. B. S. Haldane (1928)

A.I. Oparin



J.B.S. Haldane

reducing atmosphere:

hydrogen, water, methane, ammonia

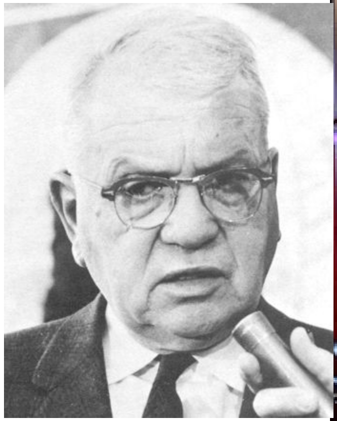
Stanley L. Miller, Harold C. Urey (1953):

methane + ammonia + H_2 + H_2O

$\rightarrow$ 10-15 % carbon in organic compounds

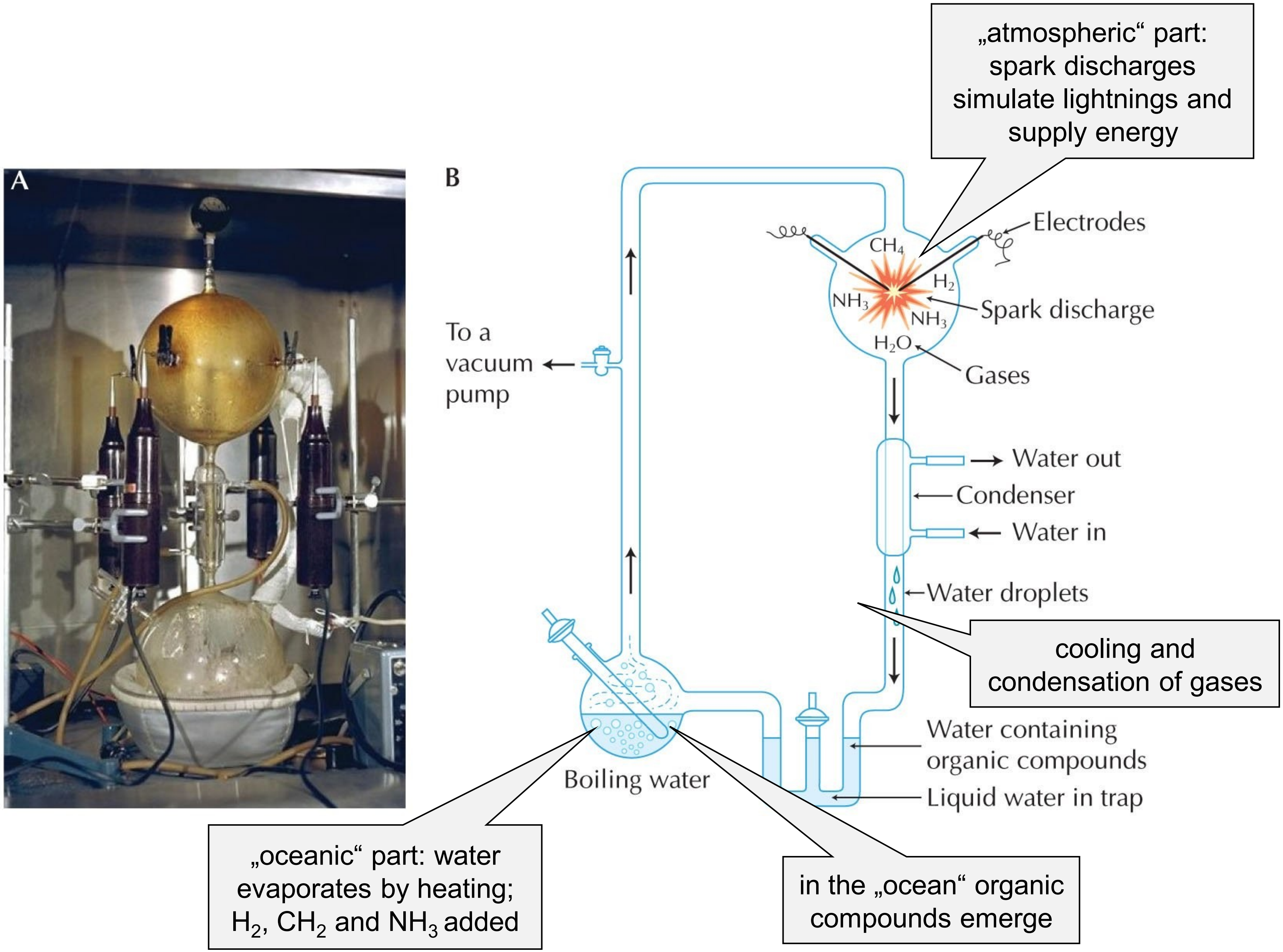
2 % carbon $\rightarrow$ amino acids, lipids, carbohydrates

building components of nucleic acids



H.C. Urey

S.L. Miller



A
B
„atmospheric“ part: spark discharges simulate lightnings and supply energy
Electrodes
CH_4
H_2
NH_3
NH_3
Spark discharge
H_2O
Gases
To a vacuum pump
Water out
Condenser
Water in
Water droplets
cooling and condensation of gases
Boiling water
Water containing organic compounds
Liquid water in trap
„oceanic“ part: water evaporates by heating; H_2, CH_2 and NH_3 added
in the „ocean“ organic compounds emerge

Problems:

according to current knowledge the atmosphere then less reducing: CO_2, N_2, H_2O and others ⇒ consequently much less molecules arising

not all nucleotides synthesized

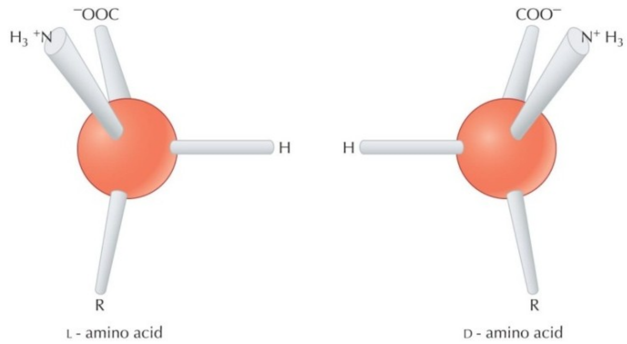
phosphorus in nature rare

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

S. A. Arrhenius

alternatives:

extraterrestric 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

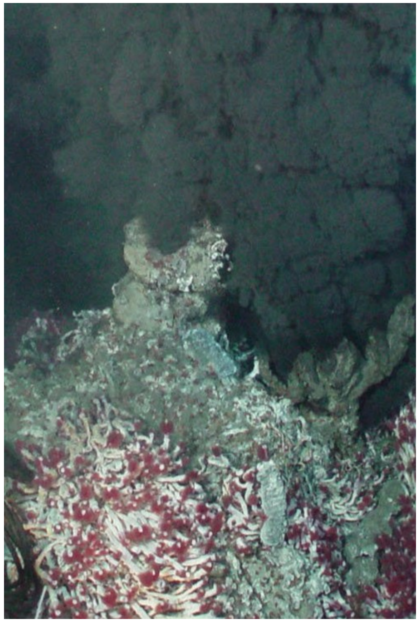
bubbles: clouds, sea spume

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

hydrotermal 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 archaebacteria, three-meter tube worms, bivalves, starfish, barnacles, limpets, crabs, annelids, shrimps

G. Wächtershäuser:

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

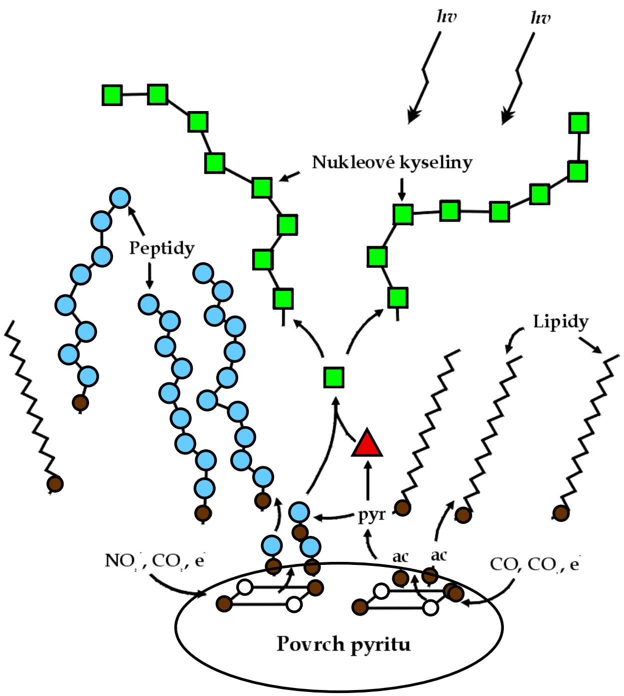
„prebiotic pizza“

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

central role of acetyl-CoA

chemoautotrophy

Advantages of flat surface:



<u>thermodynamics</u>: lower entropy

<u>kinetics</u>: higher probability of molecule colisions

supply of <u>ions</u> to reactions (not clay!)

production of <u>linear</u> lipids

easier removing of water molecules

Origin of replicators – RNA world

Experiments of Spiegelman, Sumper and others have shown that on the

replicátor level there is not only heredity and mutation but also selection

but WHAT was replicated?

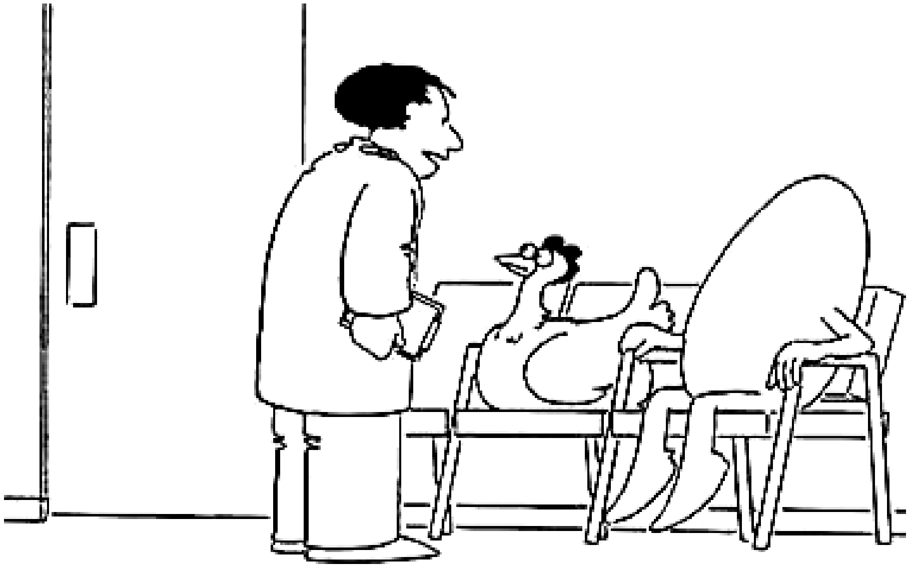
proteins

DNA

RNA

something else

?



"Who was first?"

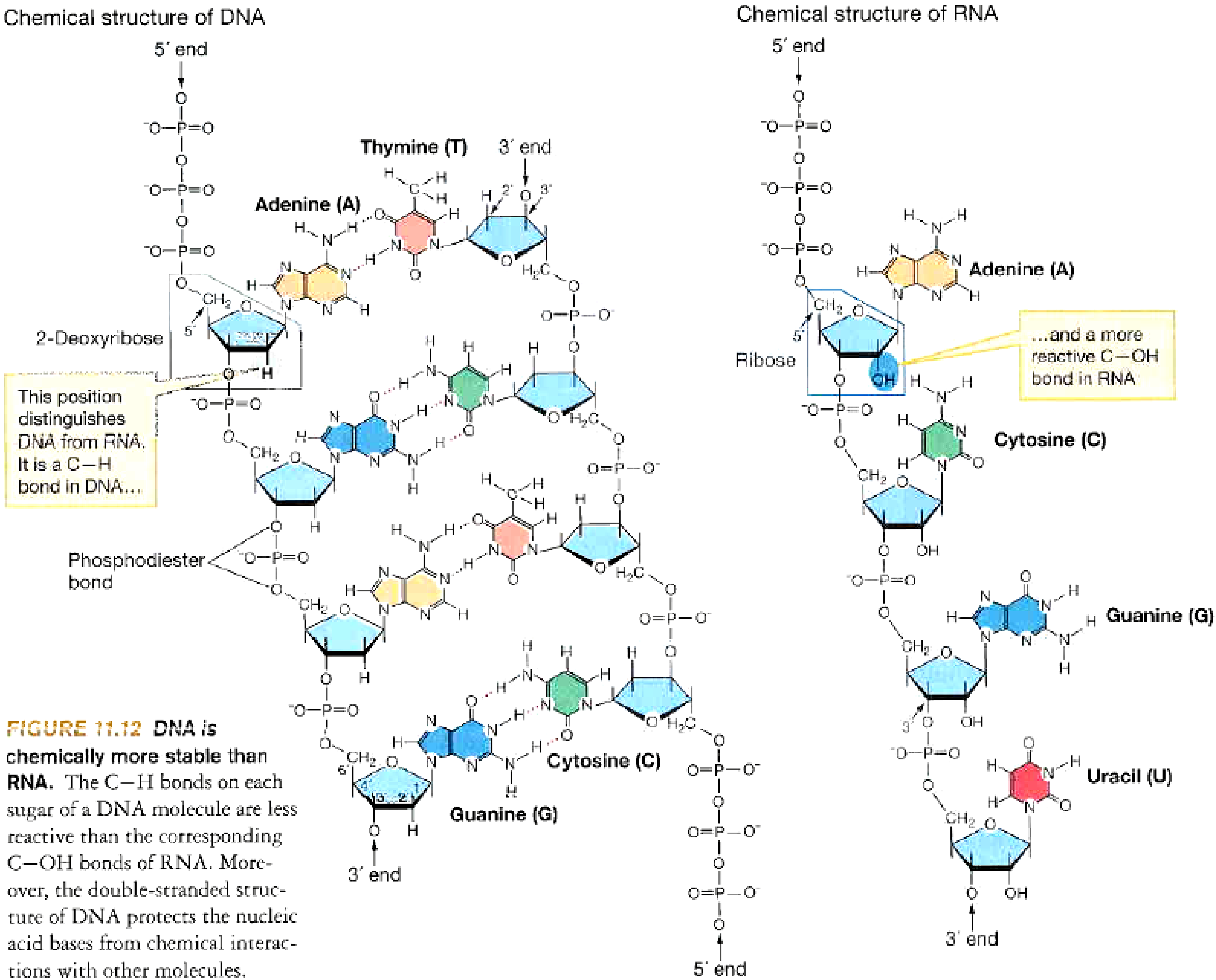


FIGURE 11.12 ***DNA is chemically more stable than RNA.*** The C—H bonds on each sugar of a DNA molecule are less reactive than the corresponding C—OH bonds of RNA. Moreover, the double-stranded structure of DNA protects the nucleic acid bases from chemical interactions with other molecules.

Origin of replicators – RNA world

Experiments of Spiegelman, Sumper and others have shown that on the replicátor level there is not only heredity and mutation but also <u>selection</u>

but WHAT was replicated?

proteins

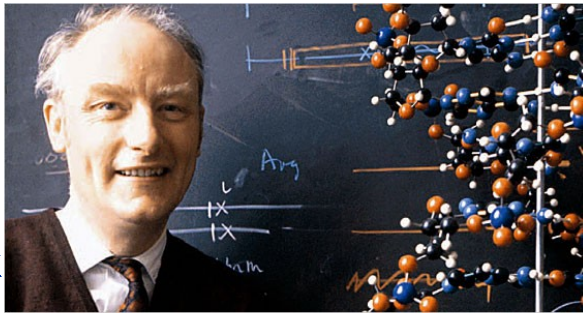
DNA

<u>RNA</u>

something else

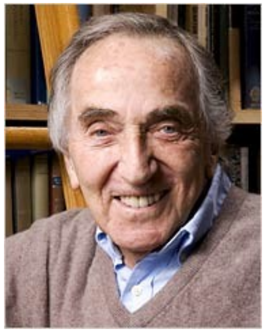
Francis Crick, Carl Woese, Leslie Orgel (1967):

dual role of RNA: heredity + enzyme = ribozyme



F. Crick

C. Woese



L. Orgel

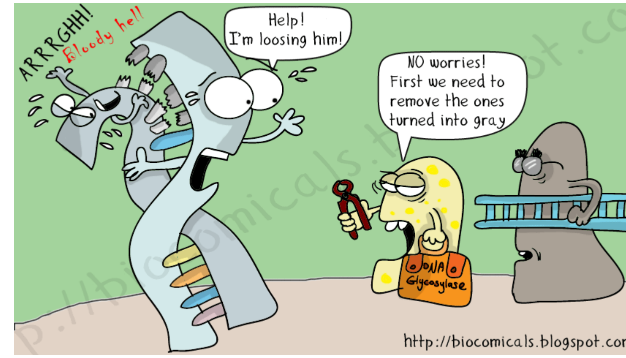
RNA characteristics:

simpler than DNA

absence of complex repair mechanisms

ability to build multiple 3D conformations

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



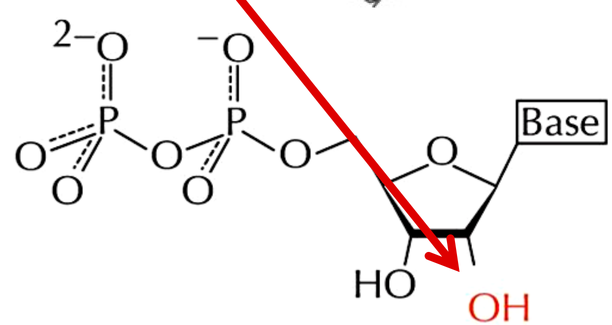


TABLE 4.3. Examples of modern RNA roles

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 euykaryotes
Transcription regulation	6S	Regulates the function of bacterial RNA polymerase

many functions have arisen long ago

RNA as „molecular fossils“

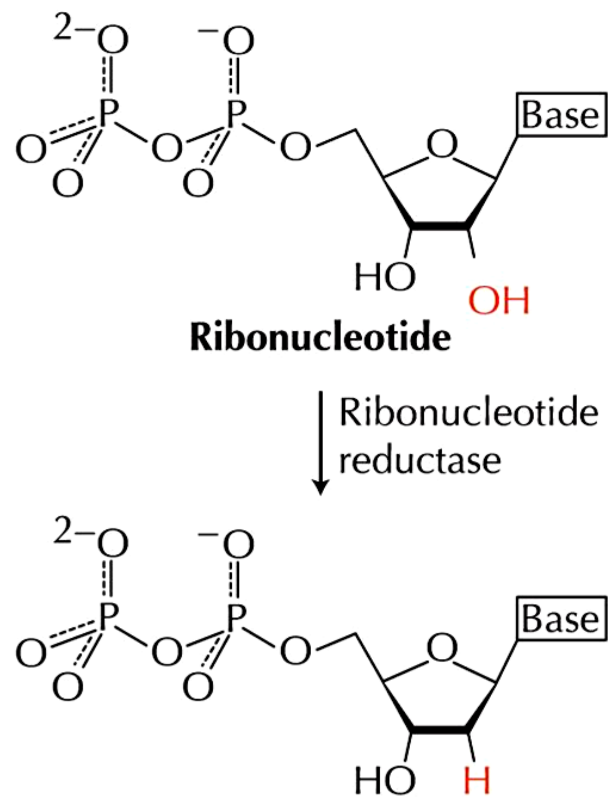
many essential coenzymes, eg. NAD^+, flavin adenin dinucleotide (FAD)

= ribonucleotide derivates

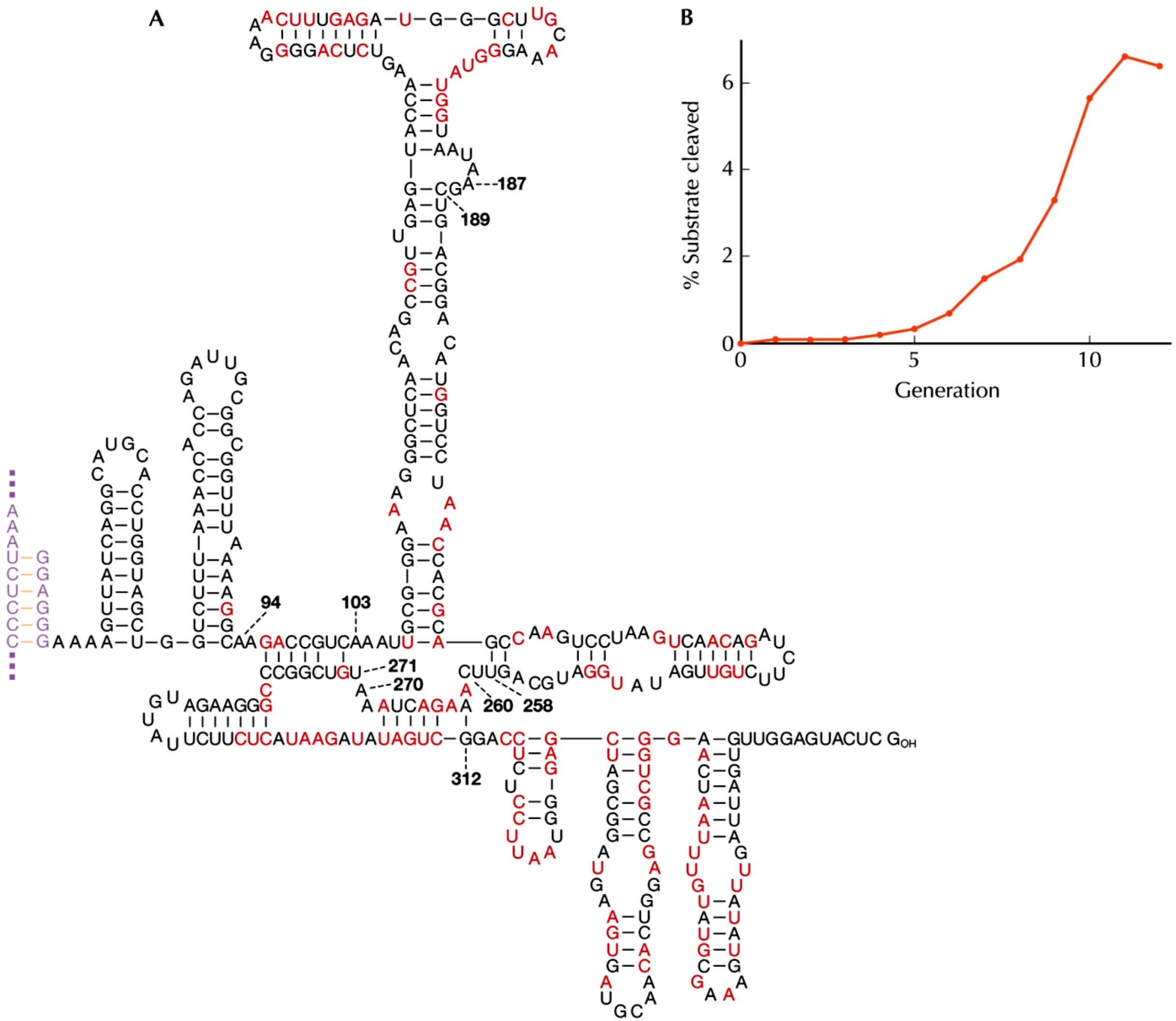
deoxyribonucleotides arise from ribonucleotides

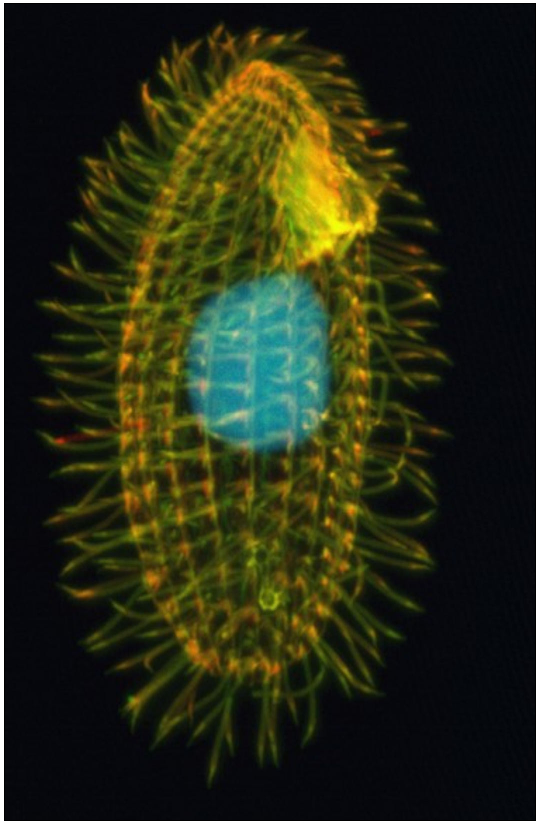
RNA primer is used during DNA replication

ATP = ribonucleotide



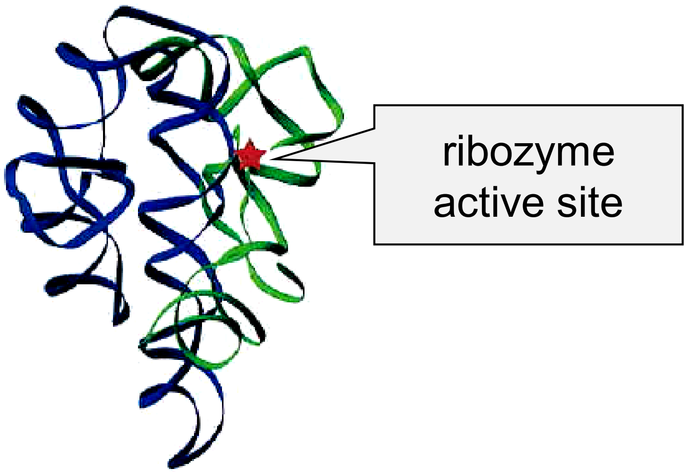
Kruger et al. (1982): self-cleaving of intron in pre-mRNA of *Tetrahymena*

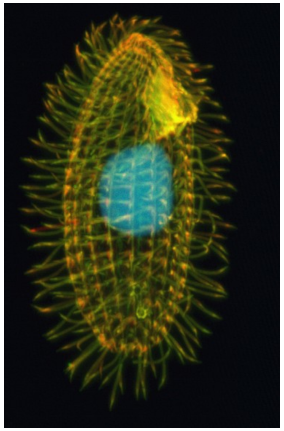


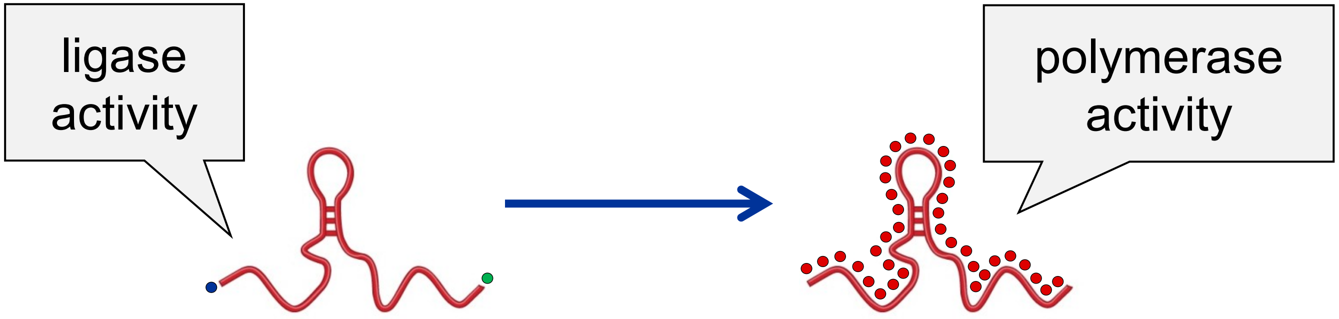


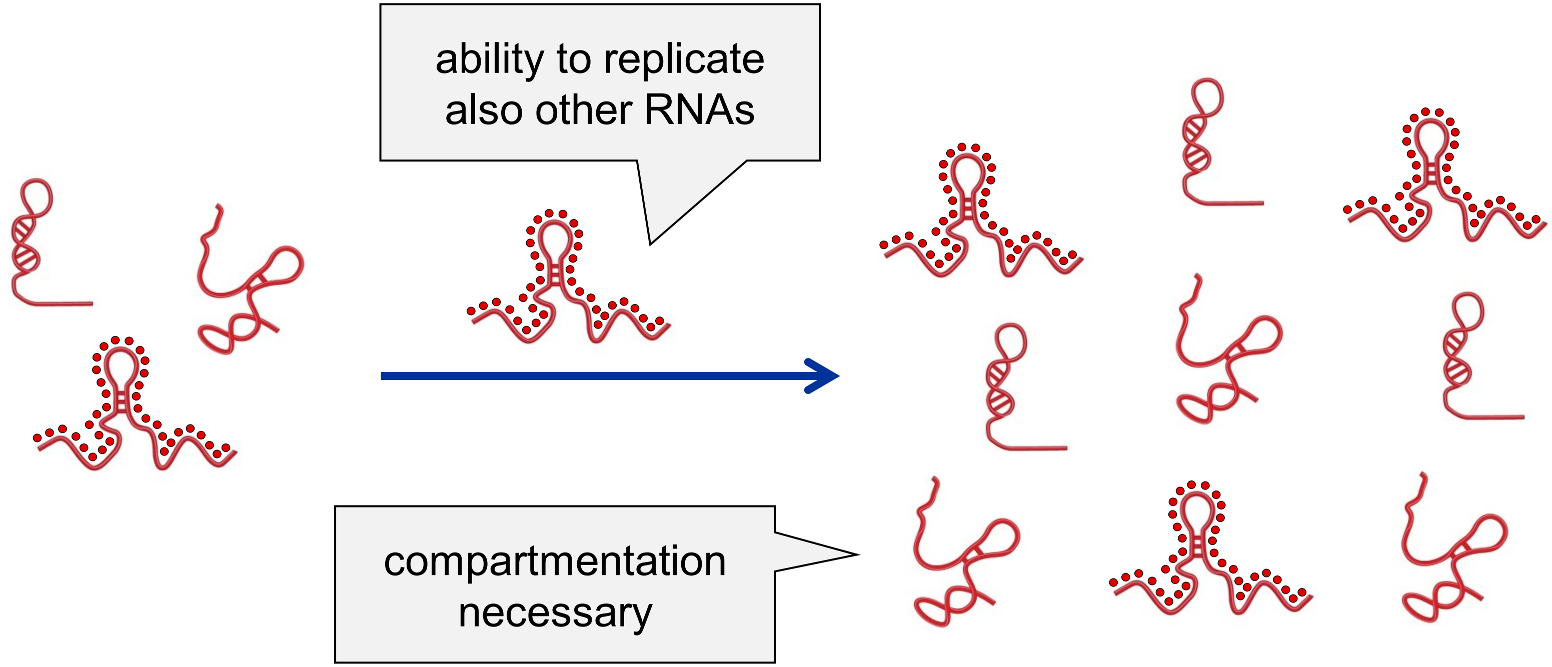
Kruger et al. (1982): self-cleaving of intron in pre-mRNA of *Tetrahymena*

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

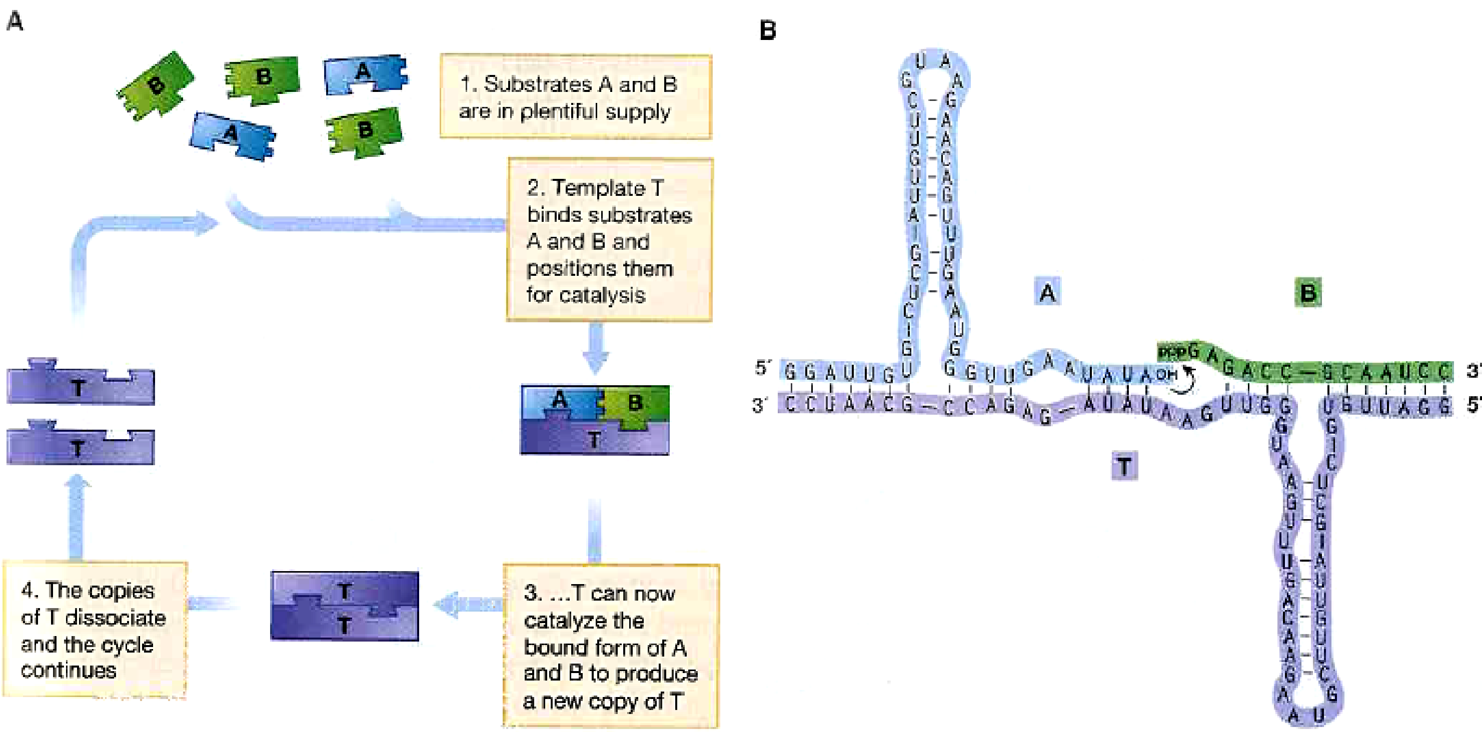
Doudna (1991):
three-subunit ribozyme from sequence of *sunY* of T4 bacteriophage

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 rRNARNase P
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.

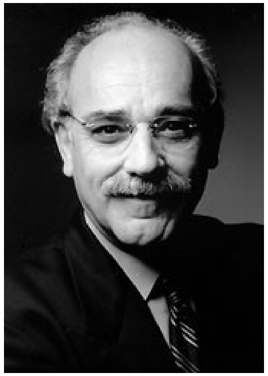
From Brown T.A. 2002. *Genomes,* 2nd ed., Table 10.4, BIOS Scientific Publishers Ltd., Oxford.
snRNA, small nuclear RNA; tRNA, transfer RNA.

Alternatives to nucleic acids:

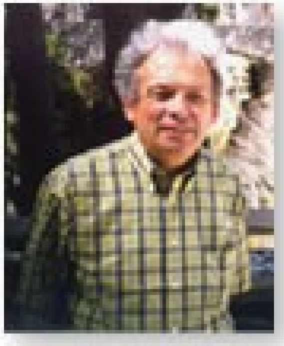
Alexander Graham Cairns-Smith: crystalic clay as „urgene“ – initially anorganic replication, a kind of „scaffold“

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

Ronald Breaker (2004): DNA can bahave as ribozymes



J. Rebek



A.G. Cairns-Smith

Problem of ribozyme-aided replication:

Manfred Eigen (1971):

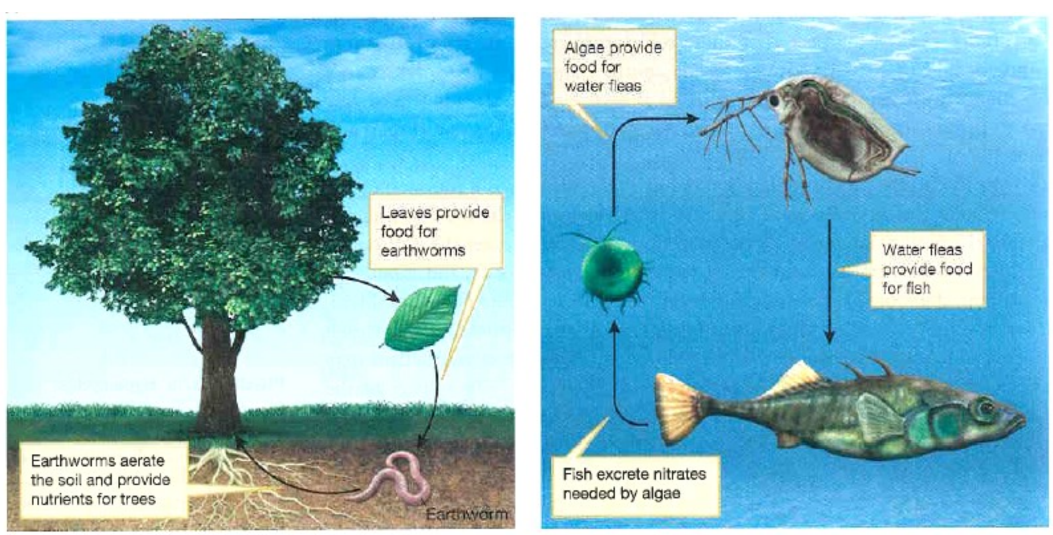
individual genes will compete

without repair mechanisms maximum size of replicating molecules $\approx$ 100 bp

length of DNA segment encoding functional enzyme much exceeds 100 bp

= Eigen paradox

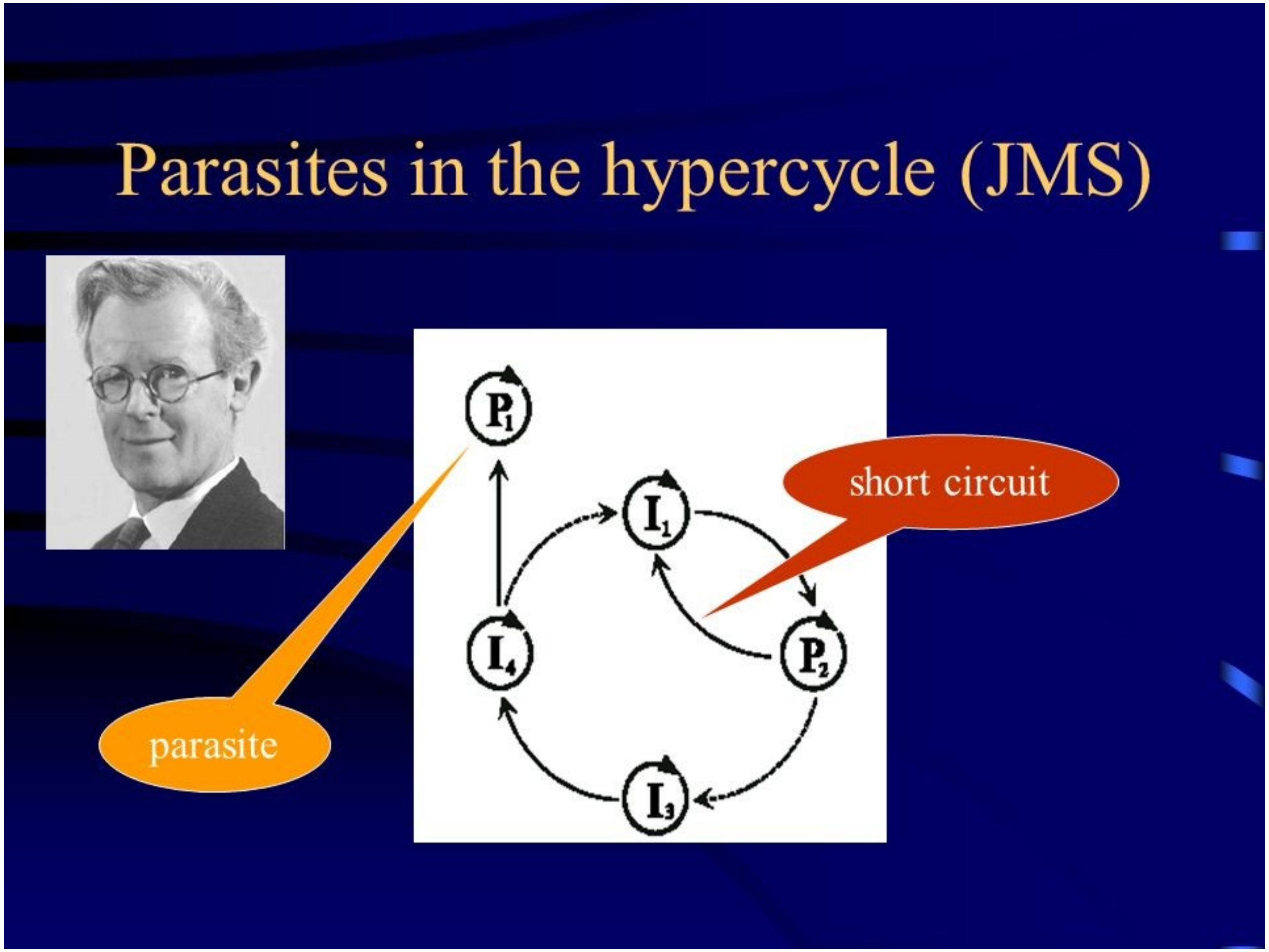
hypercycles = stable coexistence of two or more cooperating replicators



hypercycles:

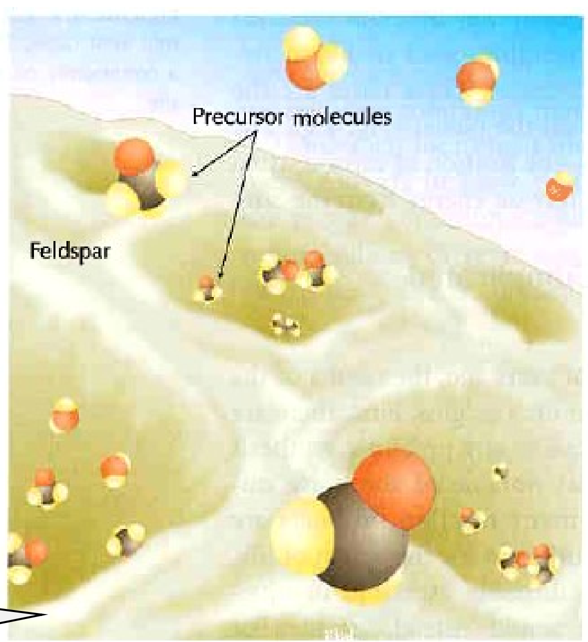
molecular mutualism: reciprocal altruism (win-win relationship)

competition of the whole systém with other cycles
risk of systém „parasitation“ ⇒ need for compartmentation

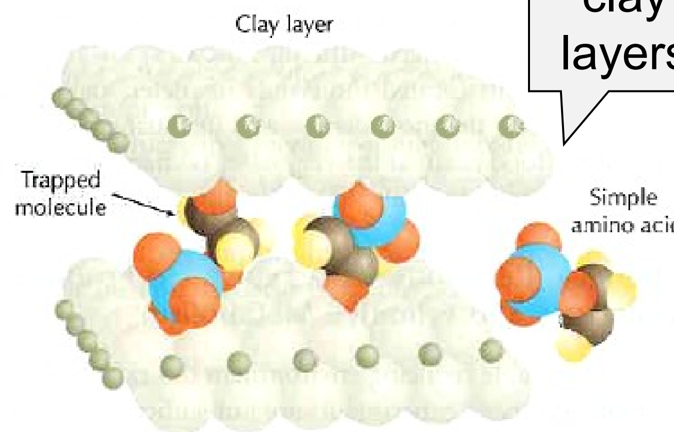


Compartmentation and origin of cells

role of tiny crevices and unevenness of the mineral surface



felspar



clay layers

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

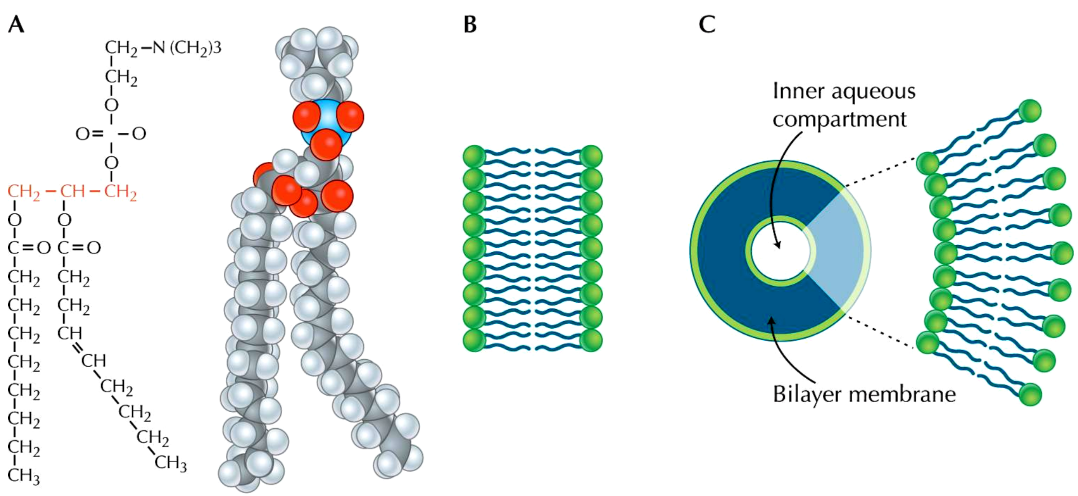
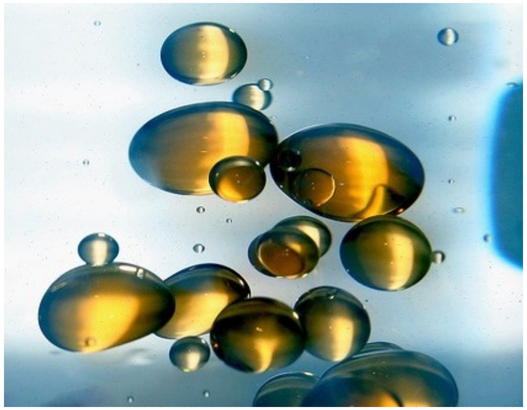


FIGURE 4.14. Lipids. (*A*) General structure of phospholipids. Phospholipids are made up of fatty acids, glycerol, and a phosphate group. They are amphipathic, with one hydrophobic end and one hydrophilic end. (*B*) Bilayers form when phospholipids spontaneously aggregate in water. The hydrophobic ends 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.



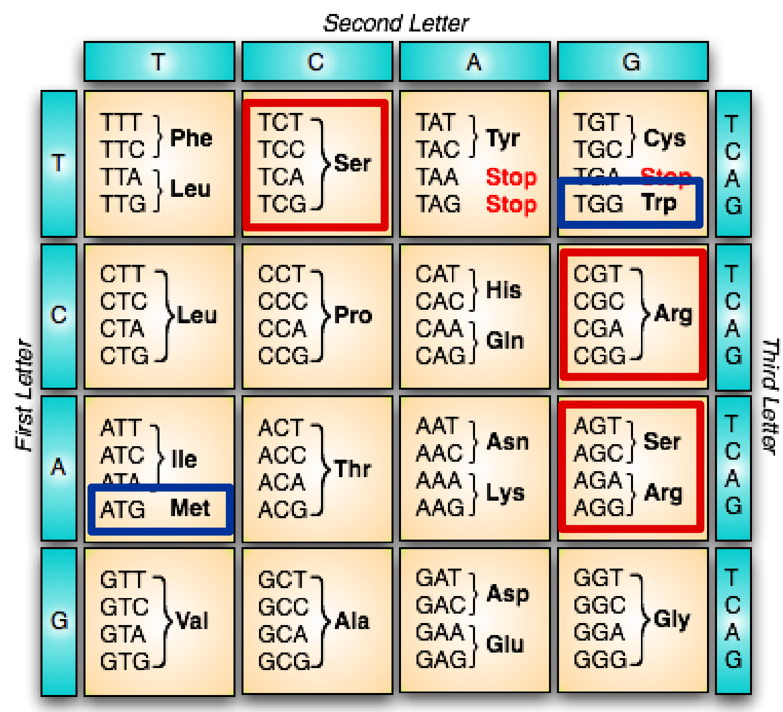
Origin of chromosomes and genetic code

fusion of replicators ⇒ longer replication ⇒ selective disadvantage

possible benefits:

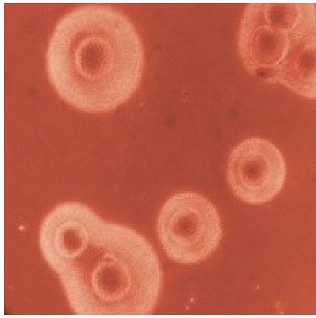
1. reduction of competition between functionally connected replicators
2. products of functionally connected replicators at the same place

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



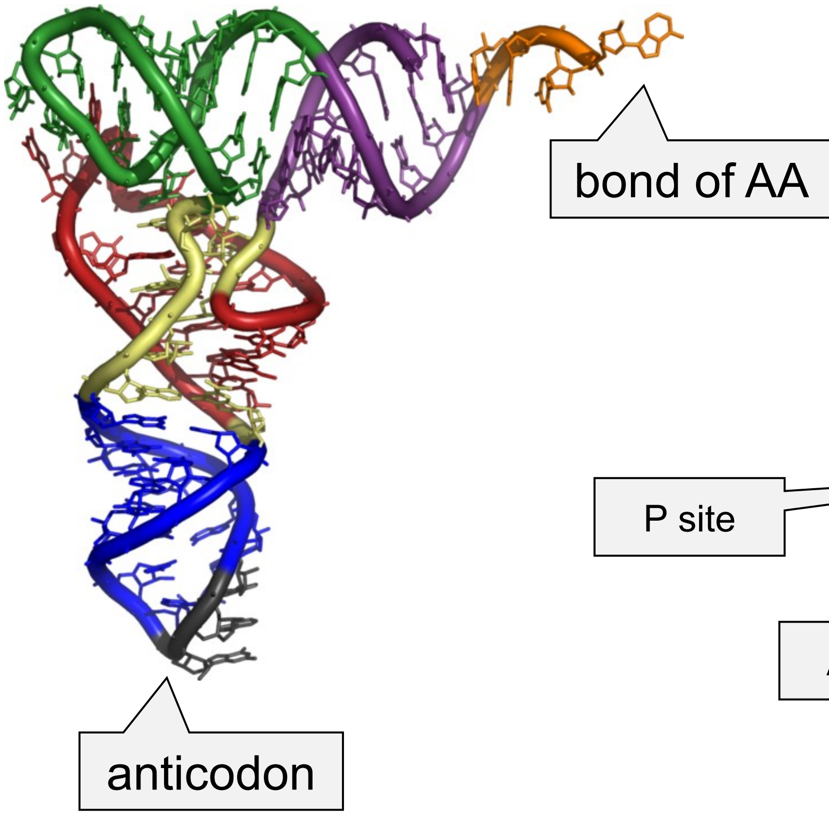
chemically related AAs → similar code

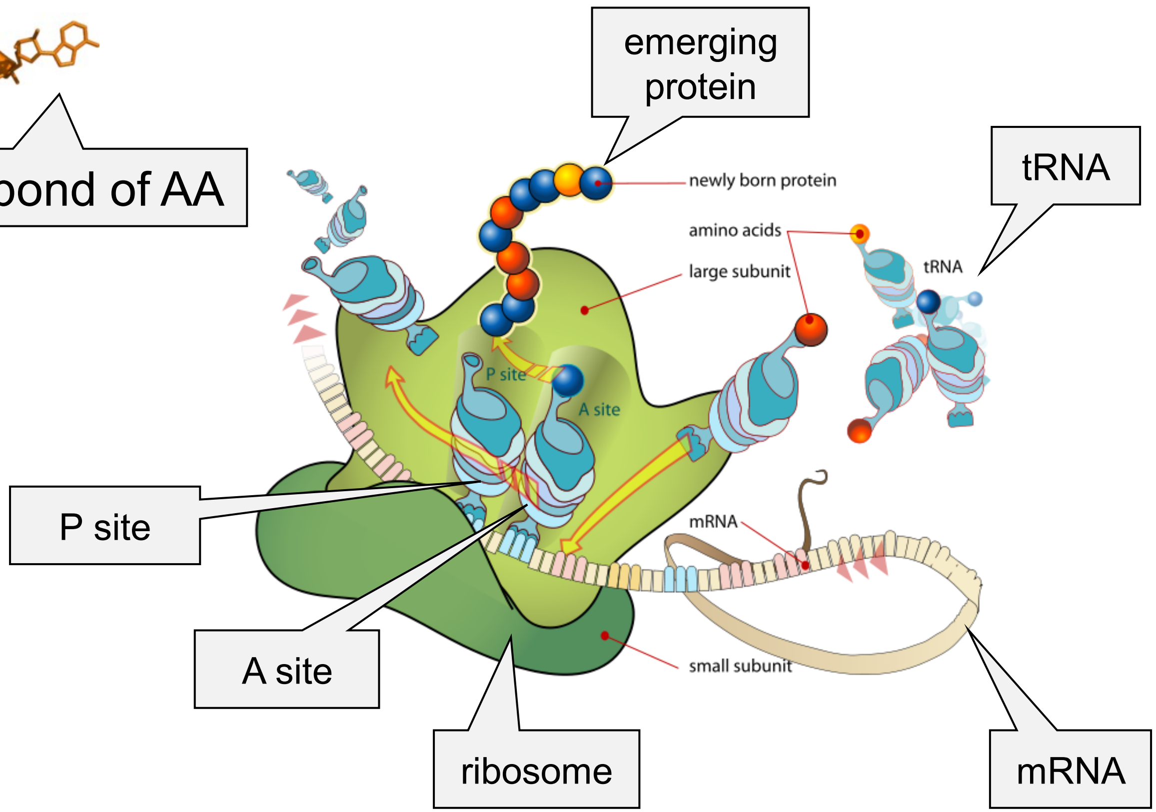
genetic code is not by far „universal“ – exceptions in some organisms (eg. *Mycoplasma*) or organelles (mitochondria)



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 <u>random</u>

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) ⇒ much more diverse catalytic activities → eg. no RNA molecule can catalyze redox reactions or break C–C bonds

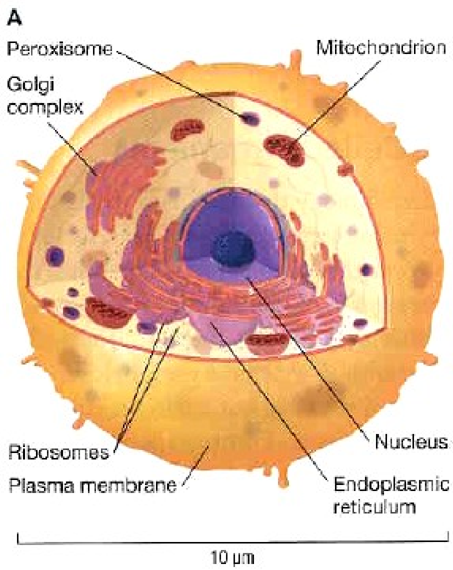
DNA advantages:

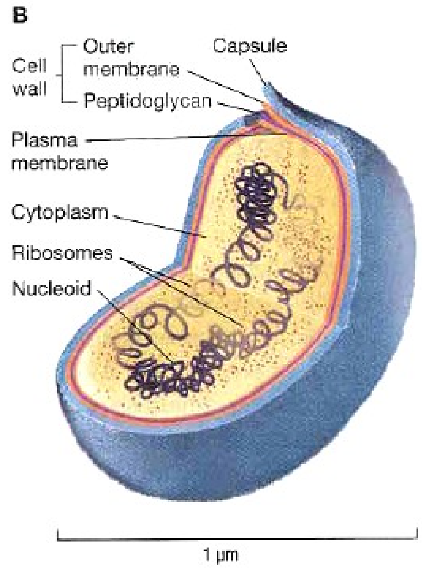
lower reactivity ⇒ higher stability ⇒ longer genes

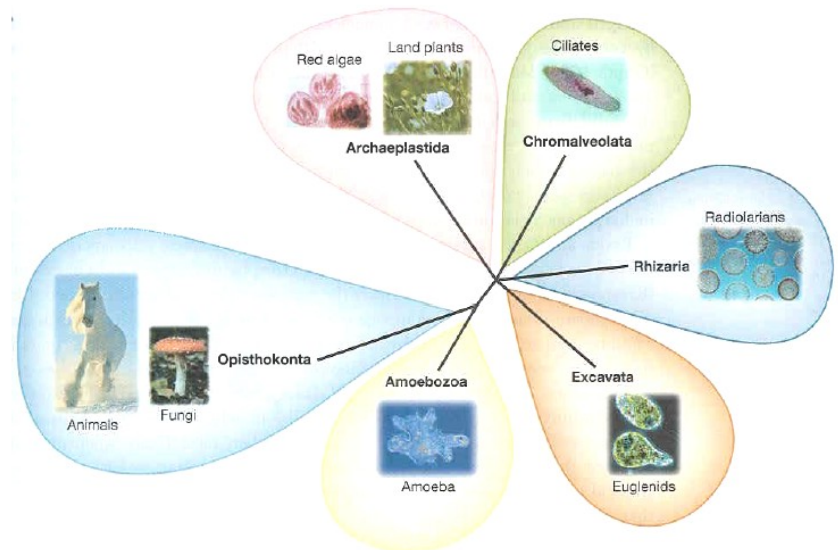
division of labour between RNA and DNA

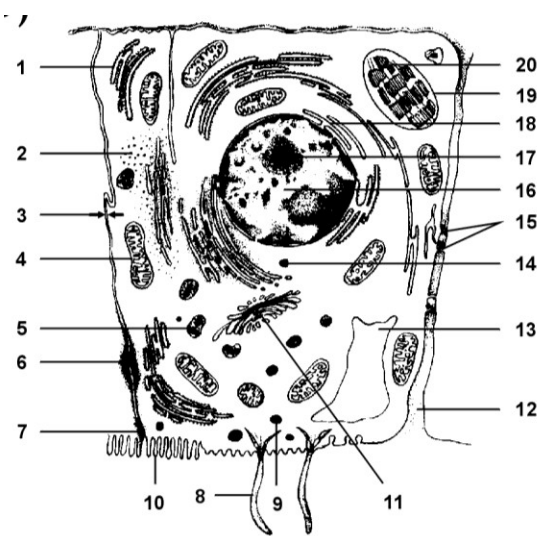
with loss of genetic function RNA could have carry out catalytic and structural functions with smaller restrictions

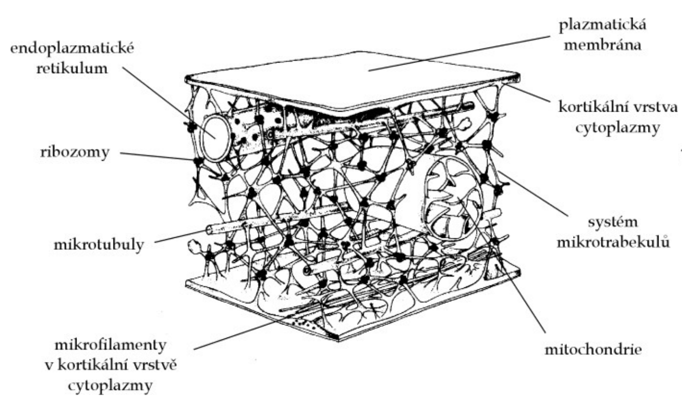
Origin of eukaryotic cell

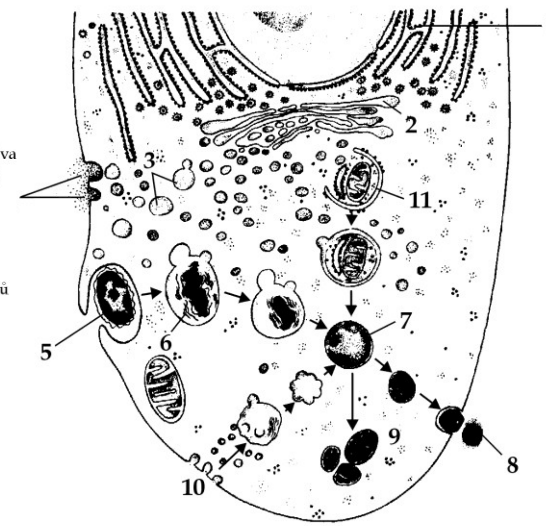


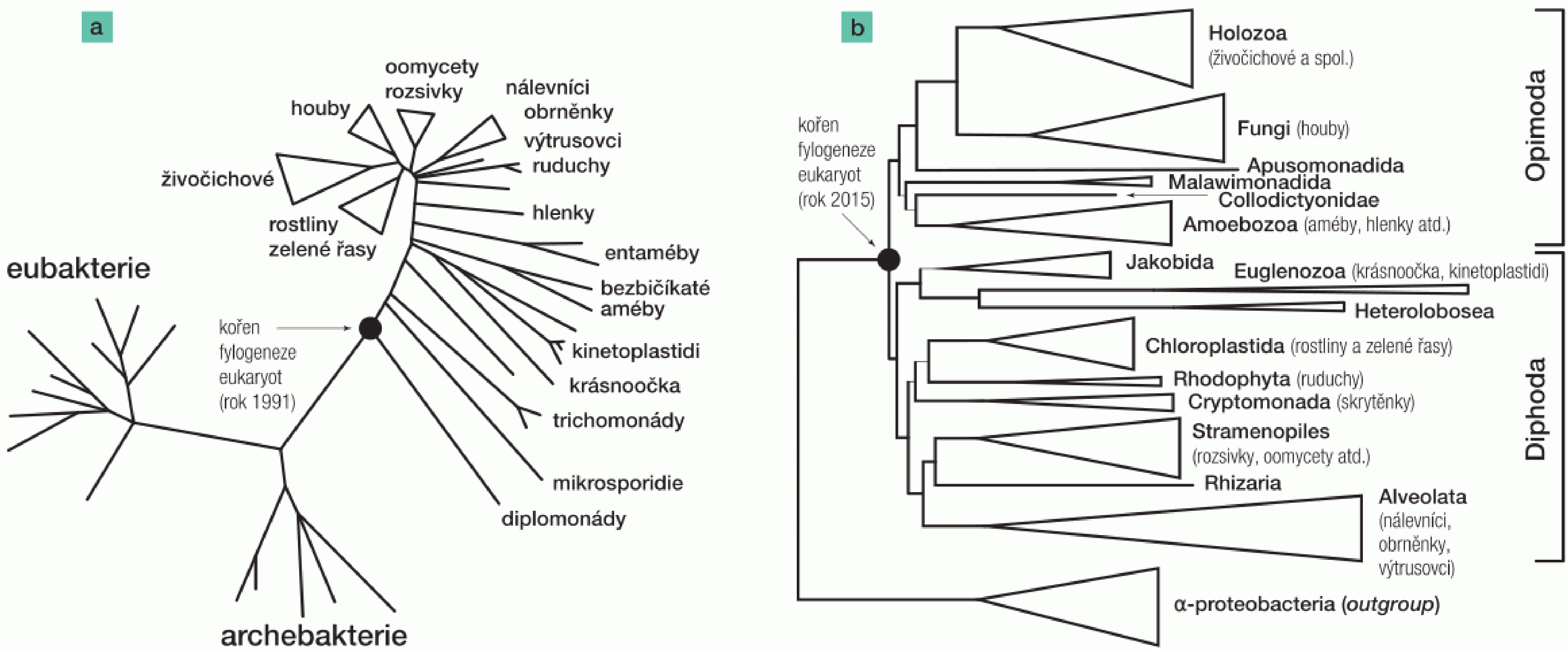










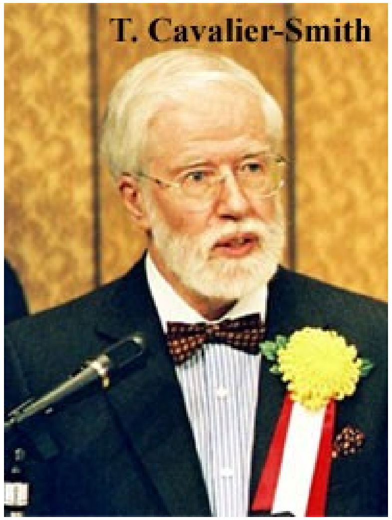


a
oomycety
rozsivky
nálevníci
houby
obrněnky
výtrusovci
ruduchy
živočichové
hlenky
rostliny
zelené řasy
entaméby
eubakterie
bezbičíkaté
améby
kořen
fylogeneze
eukaryot
(rok 1991)
kinetoplastidi
krásnoočka
trichomonády
mikrosporidie
diplomonády
archebakterie
b
Holozoa
(živočichové a spol.)
Fungi (houby)
Apusomonadida
Malawimonadida
Collodictyonidae
Amoebozoa (améby, hlenky atd.)
Opimoda
kořen
fylogeneze
eukaryot
(rok 2015)
Jakobida
Euglenozoa (krásnoočka, kinetoplastidi)
Heterolobosea
Chloroplastida (rostliny a zelené řasy)
Rhodophyta (ruduchy)
Cryptomonada (skrytěnky)
Stramenopiles
(rozsivky, oomycety atd.)
Rhizaria
Alveolata
(nálevníci,
obrněnky,
výtrusovci)
Diphoda
α-proteobacteria (*outgroup*)

Thomas Cavalier-Smith:

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

invagination of membrane → ER



Prokaryotic cytoskeleton:

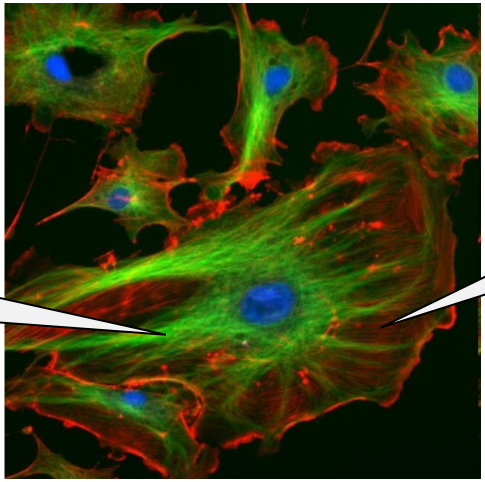
FtsZ: tubuline analogue, function in cell division

MreB: actin analogue, rod-shaped cell shape

Crescentin: analogue of intermediary microfilaments, helix creation

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

microtubules



microfilaments

exaptation

Origin of cell organelles:

Konstantin Sergeyevich 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)

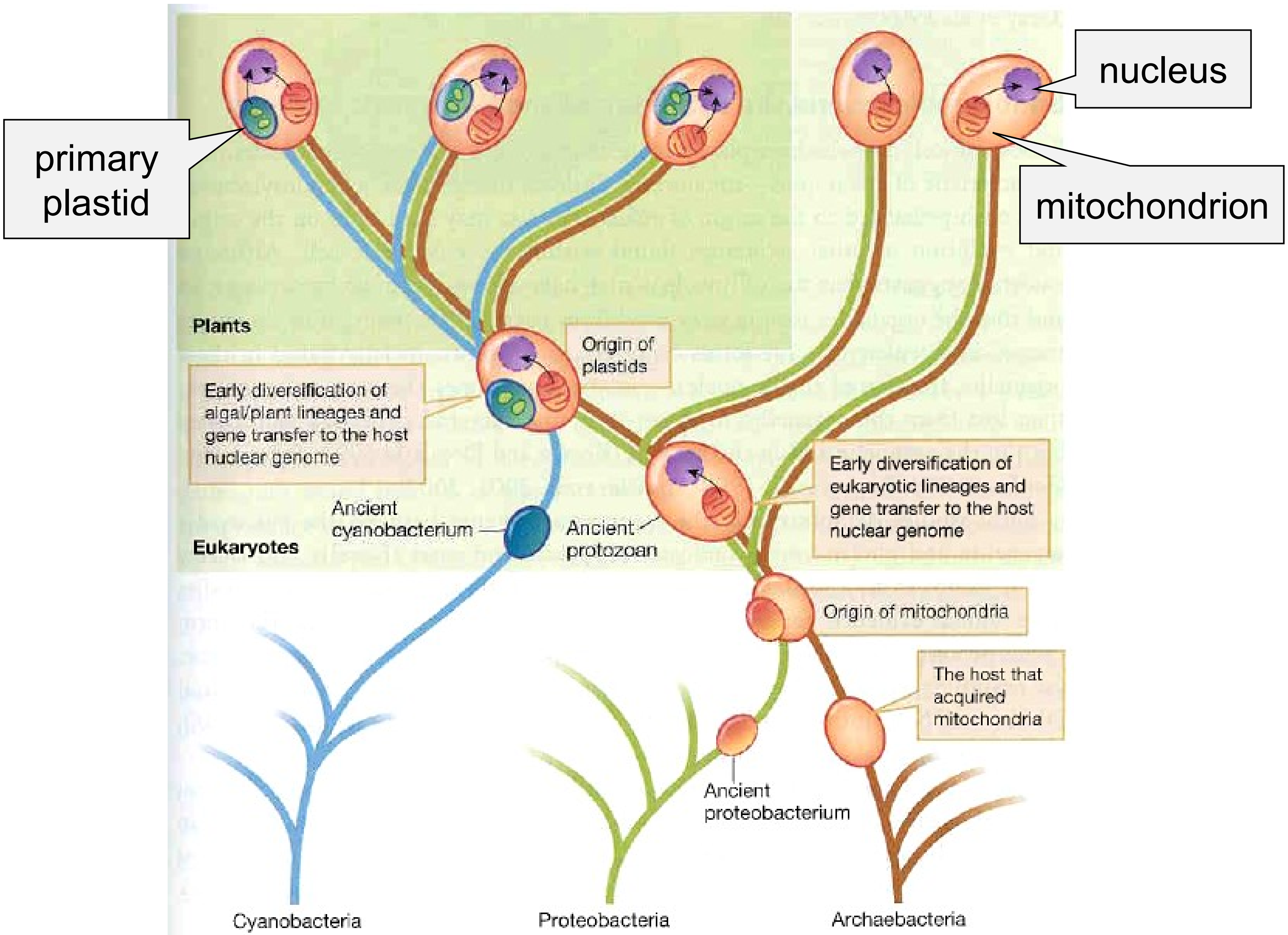
K.S. Merežkovskij

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

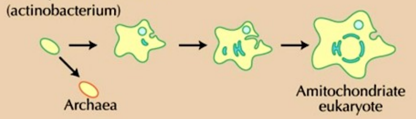
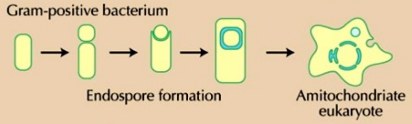
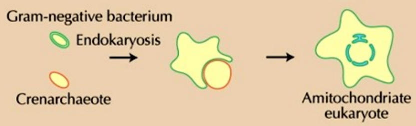
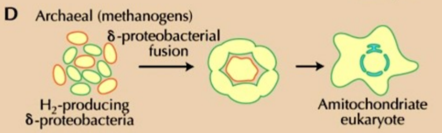
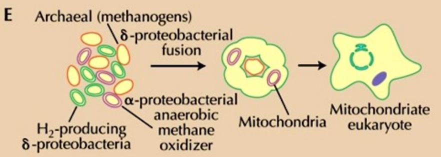
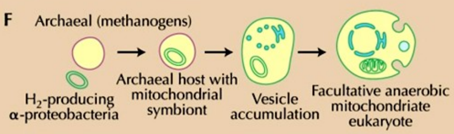
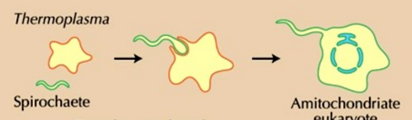
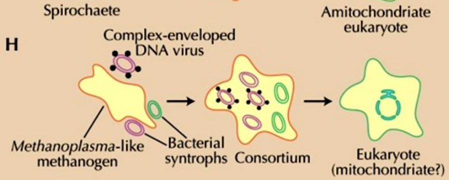


primary plastid
nucleus
mitochondrion
Plants
Origin of plastids
Early diversification of algal/plant lineages and gene transfer to the host nuclear genome
Ancient cyanobacterium
Eukaryotes
Ancient protozoan
Early diversification of eukaryotic lineages and gene transfer to the host nuclear genome
Origin of mitochondria
The host that acquired mitochondria
Ancient proteobacterium
Cyanobacteria
Proteobacteria
Archaebacteria

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

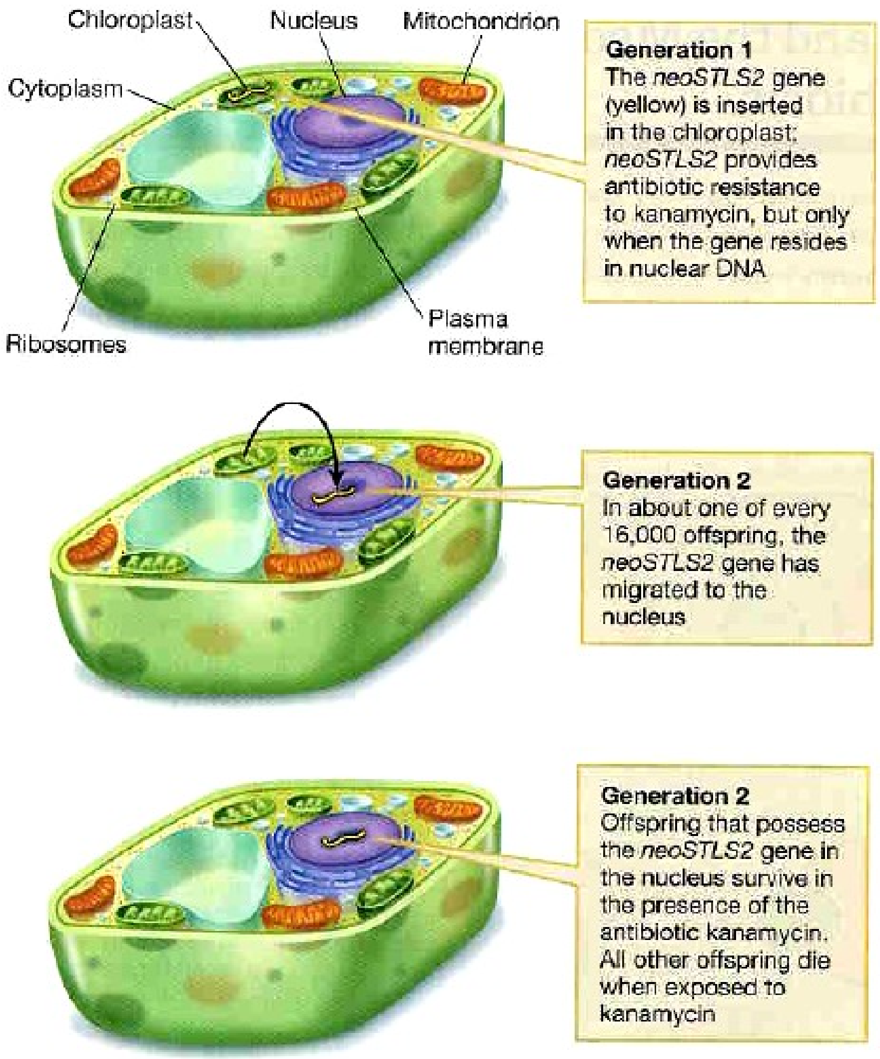
TABLE 8.2. Schematic summary of various models for the origin of the nucleus

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
A 	Plasma membrane of a bacterium	Bacterial cytoplasm
B 	Plasma membrane of a bacterium	Bacterial endospore
C 	Plasma membranes of a bacterium and an archaea	Archaeal cytoplasm
D 	Plasma membranes of several bacteria	Archaeal cytoplasm
E 	Plasma membranes of several bacteria	Archaeal cytoplasm
F 	Vesicles of bacterial lipids synthesized in an archaea cytoplasm	Archaeal cytoplasm around the chromosome
G 	Plasma membranes of a bacterium and an archaea	Spirochaete cytoplasm
H 	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:

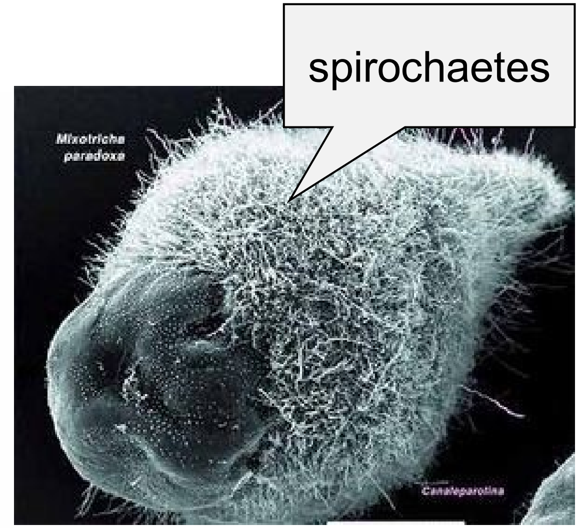
eg. *neoSTLS2* gene, tobacco chloroplast → in 16 of 250 000 (≈ 1/16 000) daughter cells transfer of the gene to nucleus ⇒ kanamycin resistence



peroxisomes: G+ bacteria

microtubules: spirochaetes

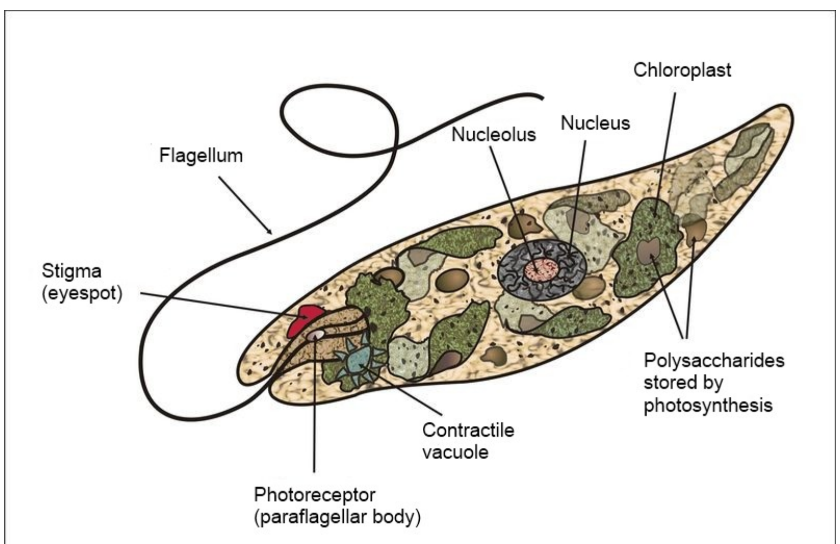
× současné poznatky nepotvrzují



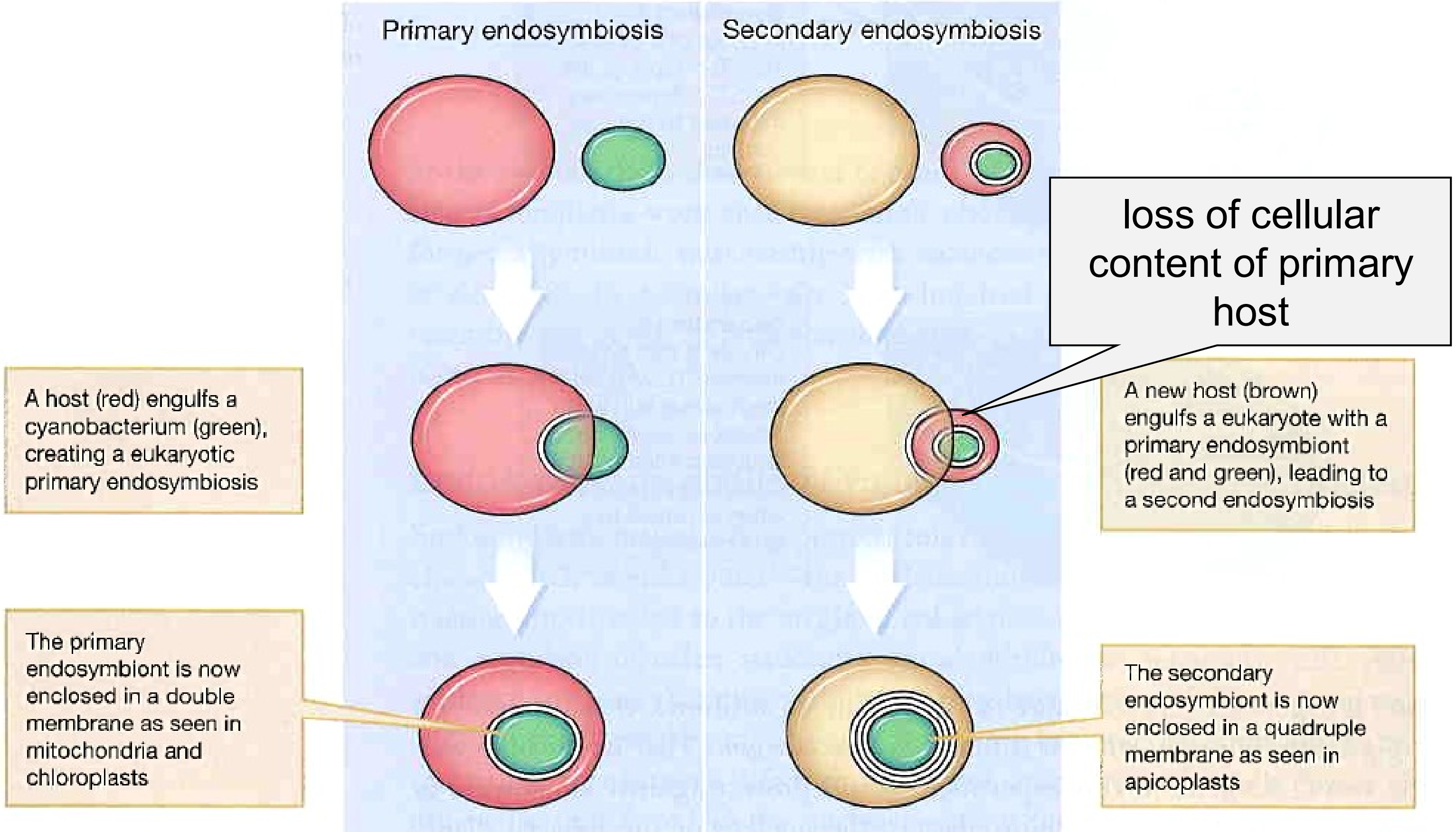
Mixotricha paradoxa

secondary and tertiary endosymbiosis

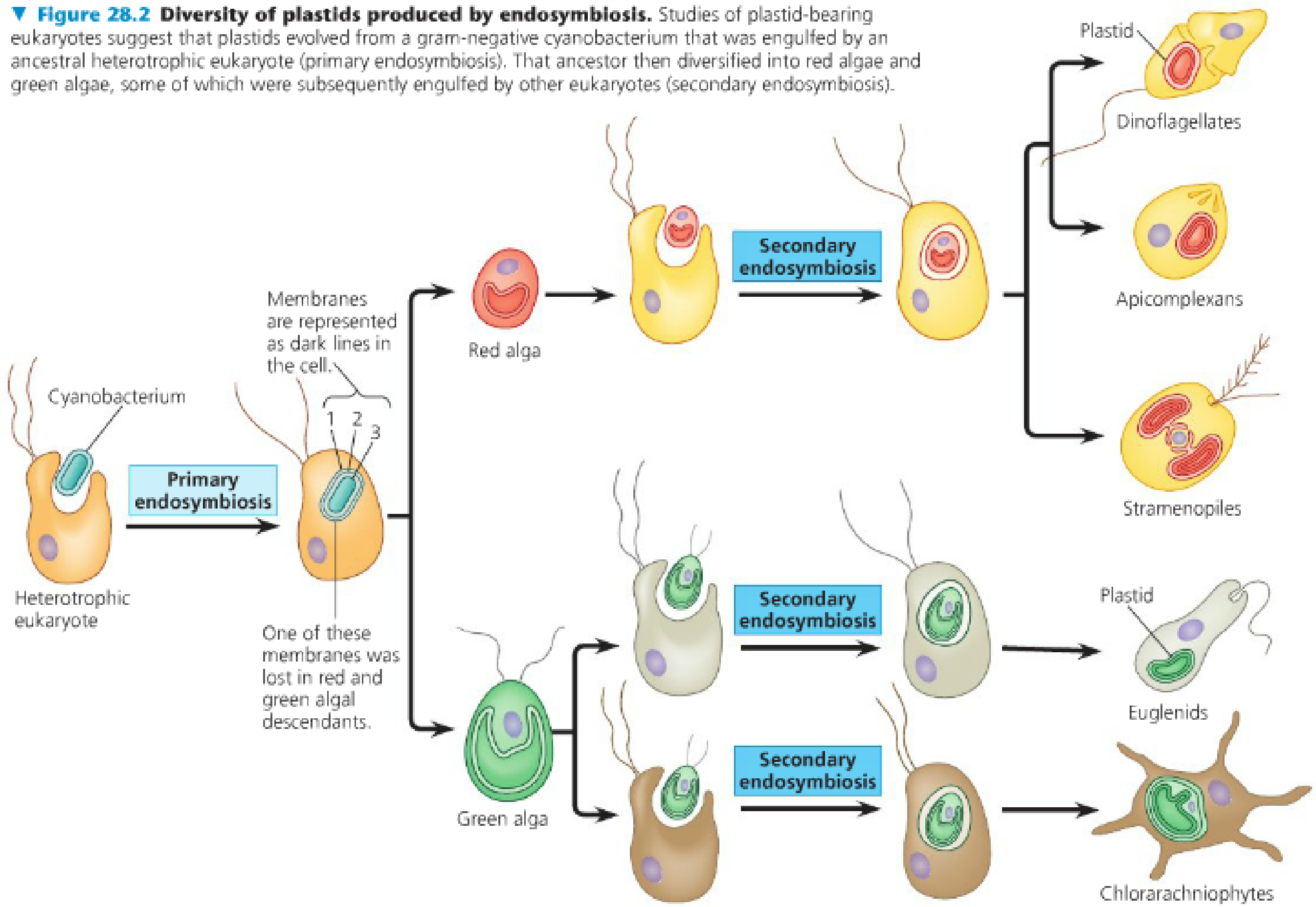
→ complex plastids: eg. euglena + green alga



Secondary endosymbiosis:

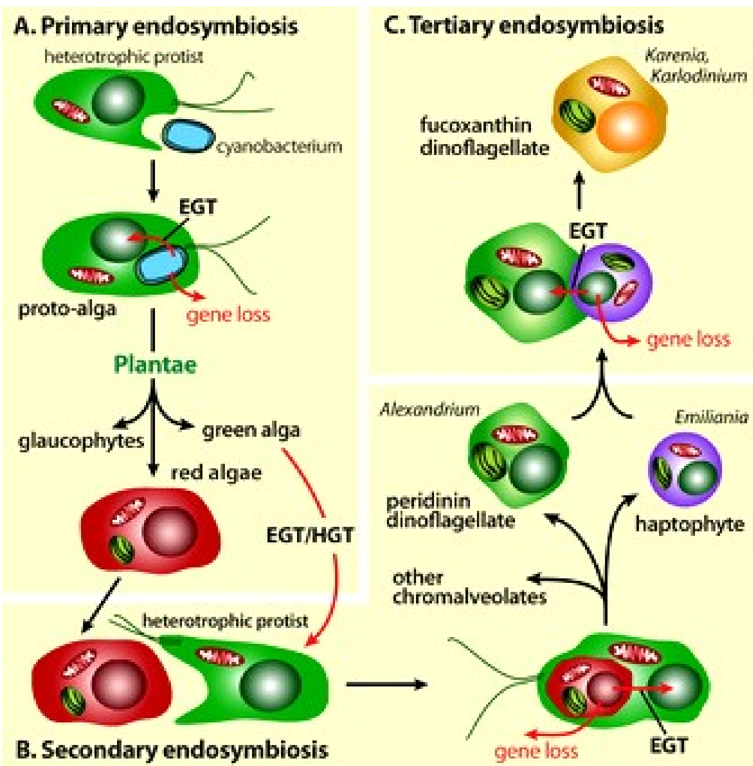


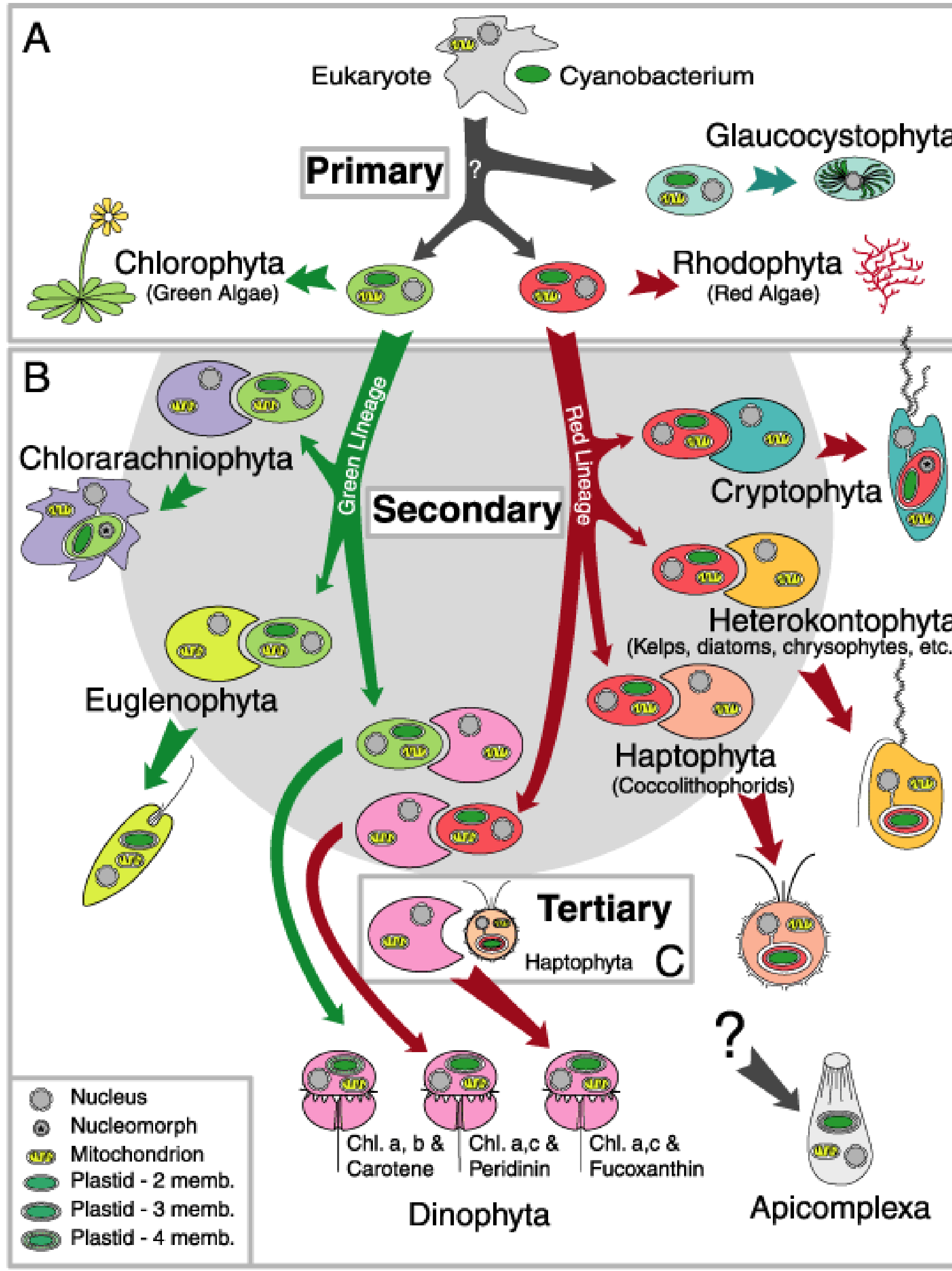
Secondary endosymbiosis:



▼ **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:

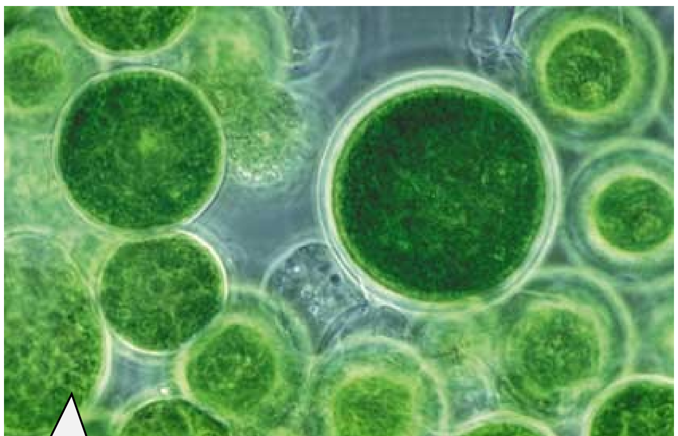




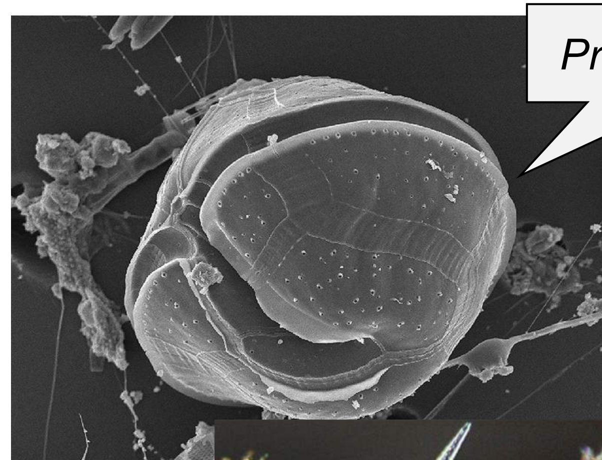
Modified from Delwiche, C.F. 1999. Tracing the thread of plastid diversity through the tapestry of life. Am. Nat. 154:S164-S177.

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



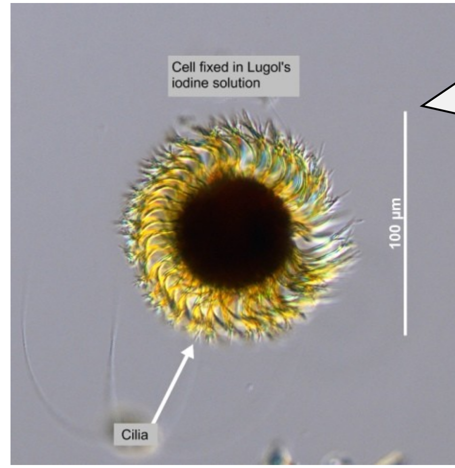
Protoperidinium

haptophyte *Gephyrocapsa*

Ceratium

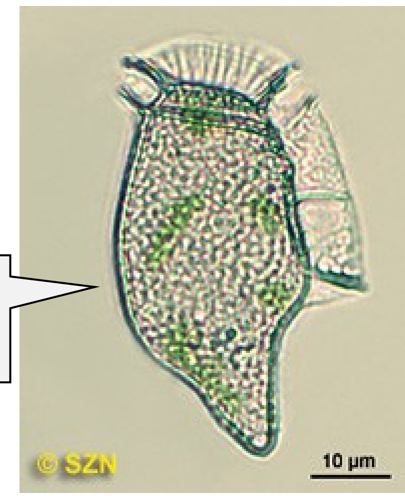
„kleptoplastids“ (eg. ciliate *Myrionecta rubra*, dinoflagellate of the genus *Dinophysis*, marine gasteropod *Elysia viridis*)

Elysia viridis

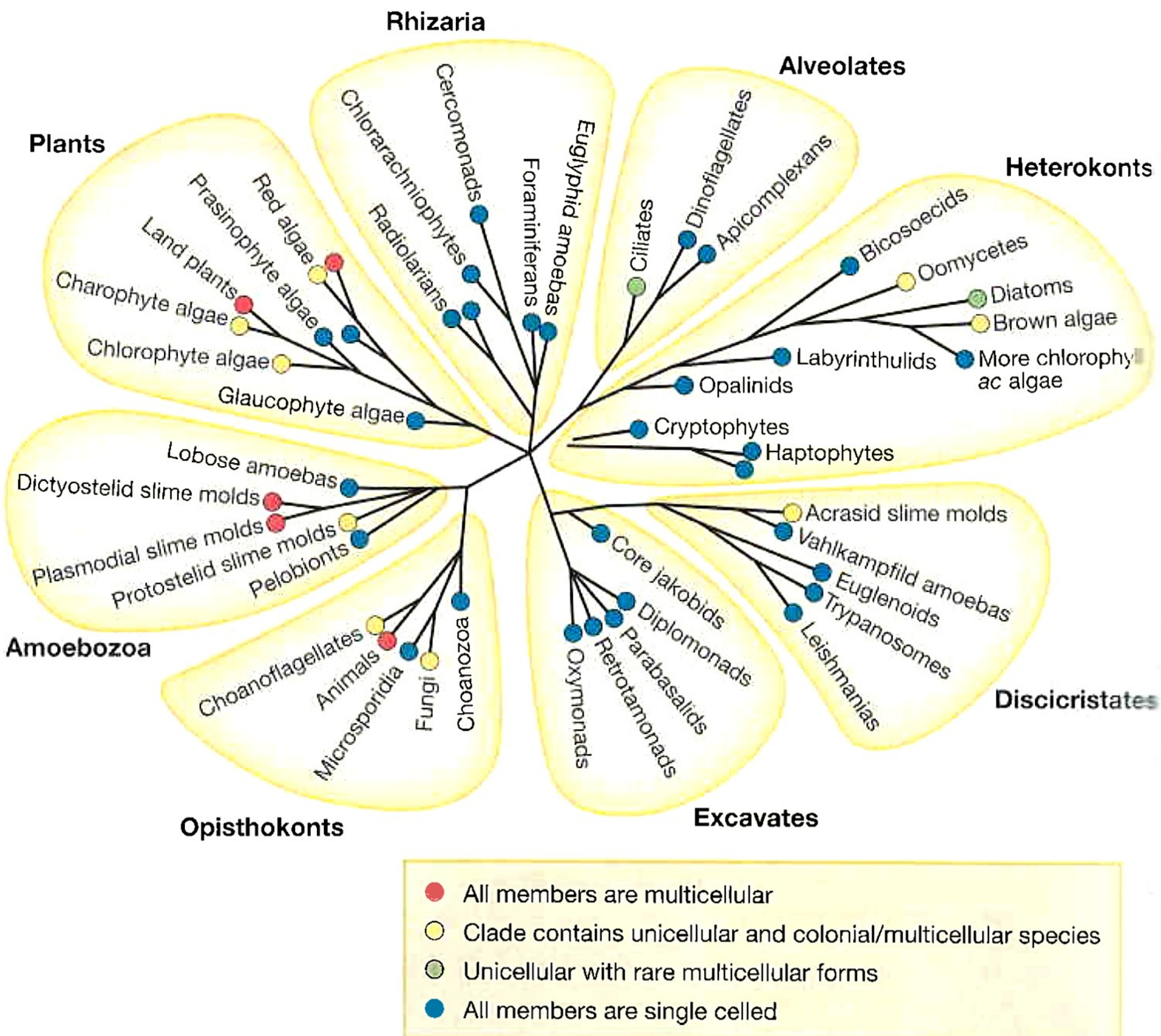


Myrionecta rubra

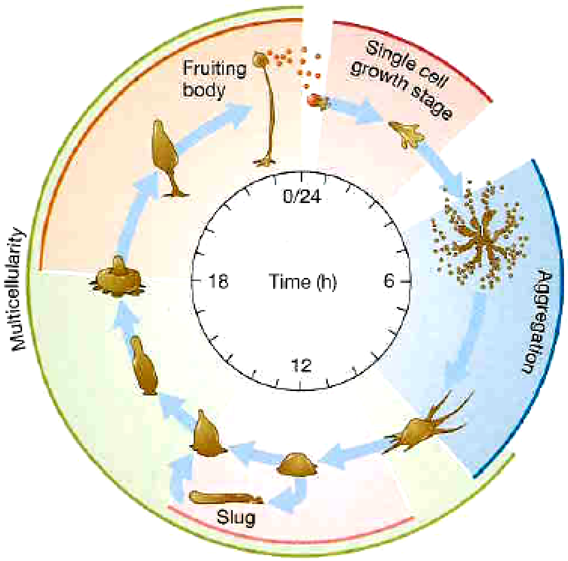
Dinophysis caudata

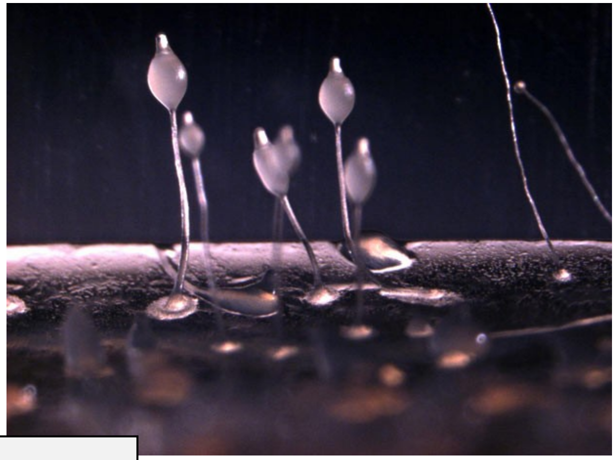


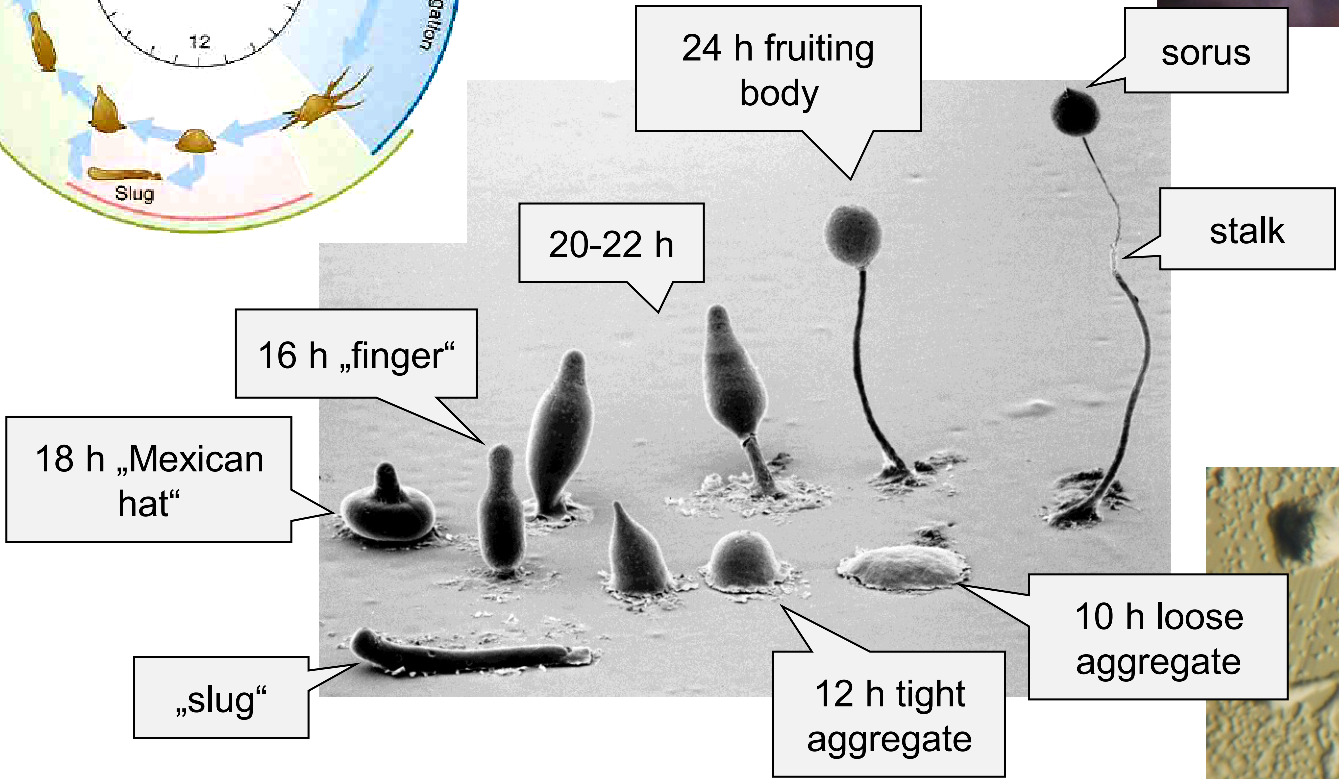
Origin of multicellular organisms

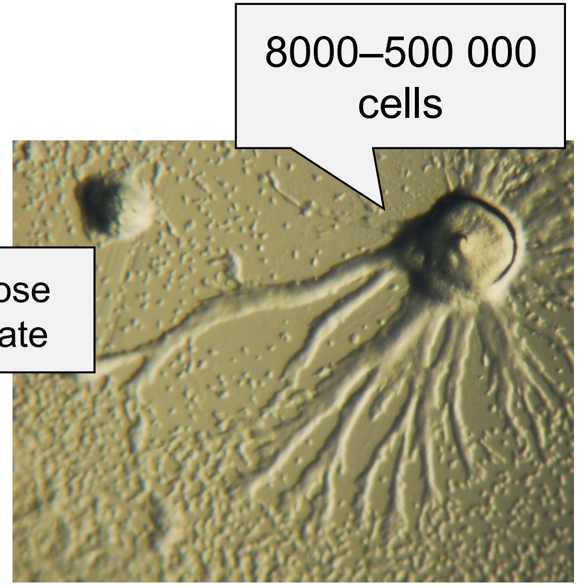


slime molds, eg. *Dictyostelium discoideum*







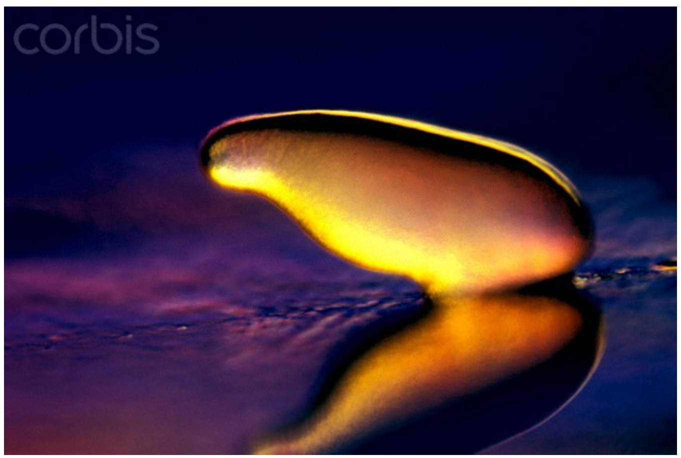


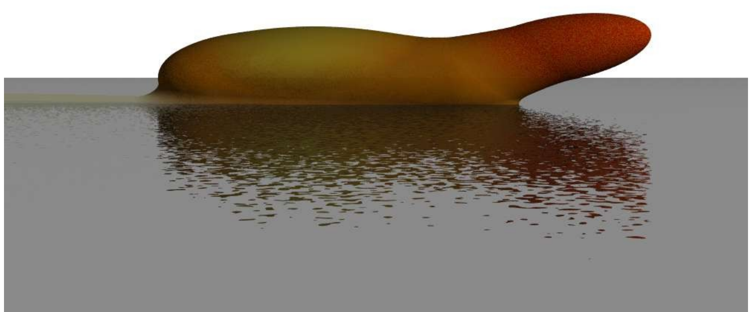
How can „slug“, composed of independent amoebas, orient itself in its environment?

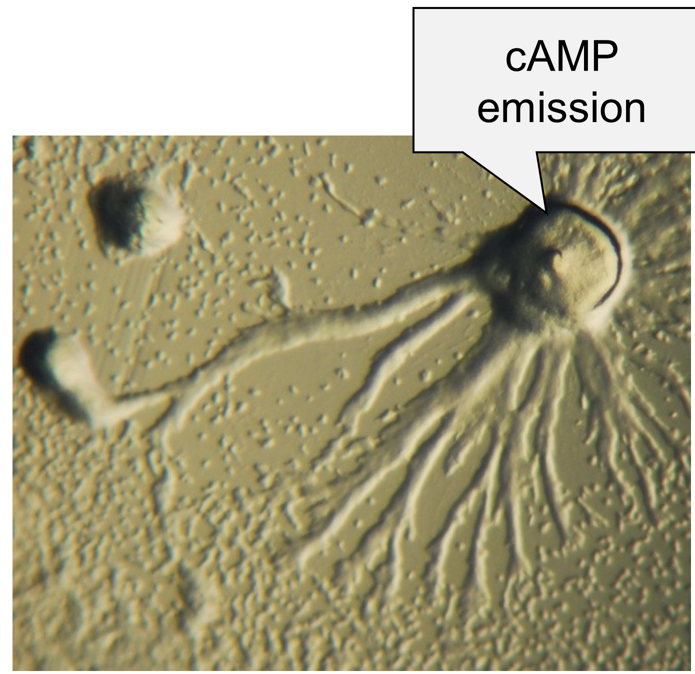
cAMP (cyclic adenosine monophosphate): emission in area of the densest aggregation → signal for „downstream“ cells → gradual aggregation

production of protein enabling mutual attachment of amoebas

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



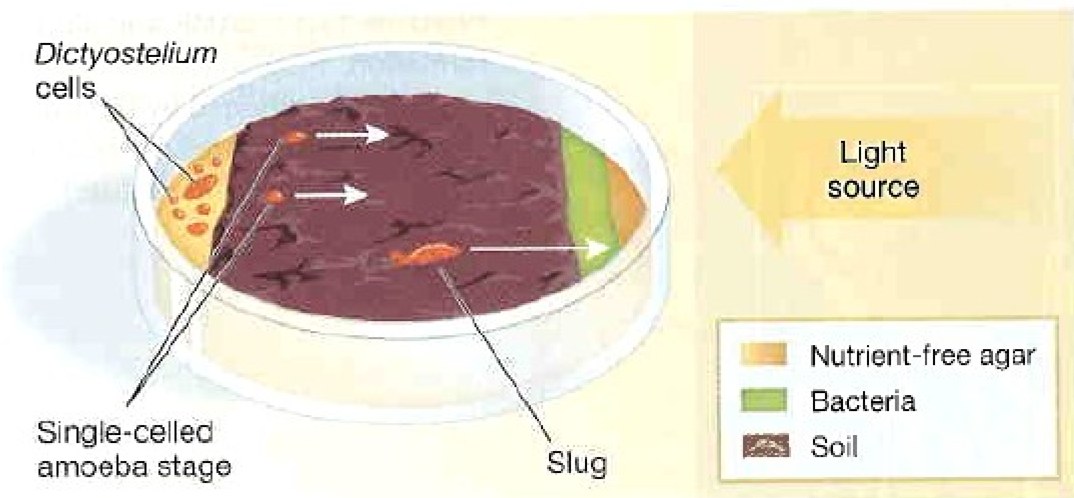


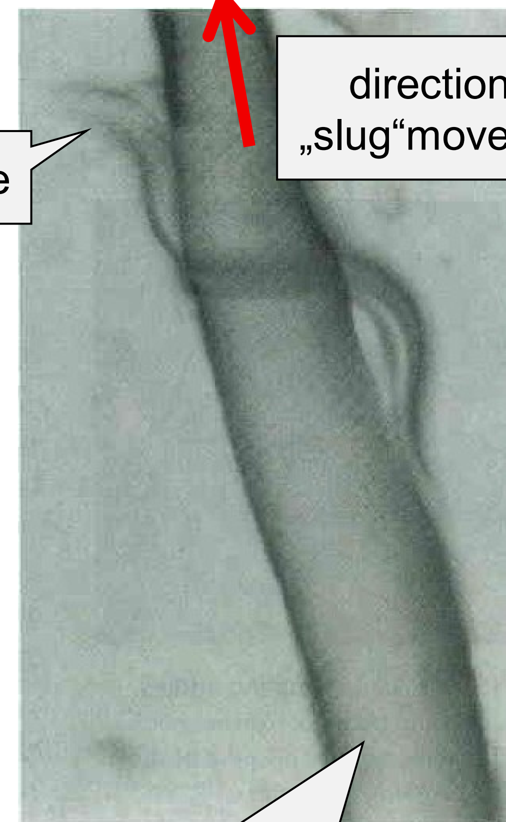


Advantages of *D. discoideum* aggregation?

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

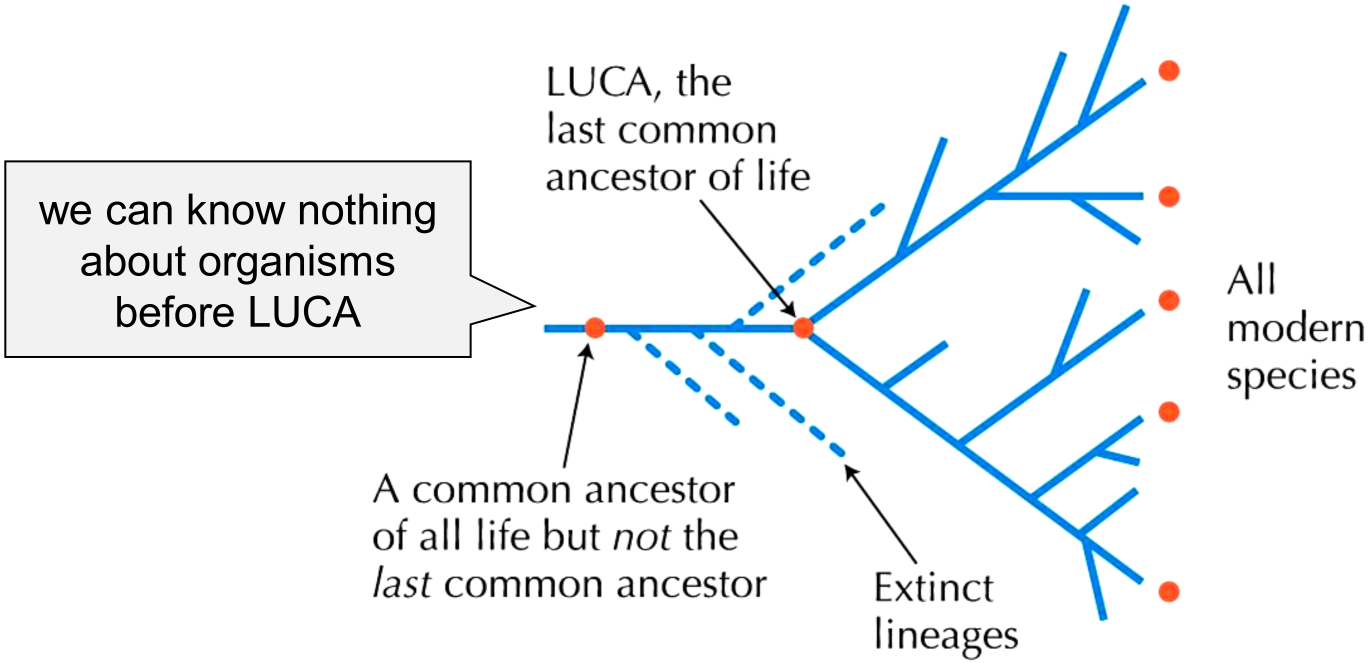
faster movement



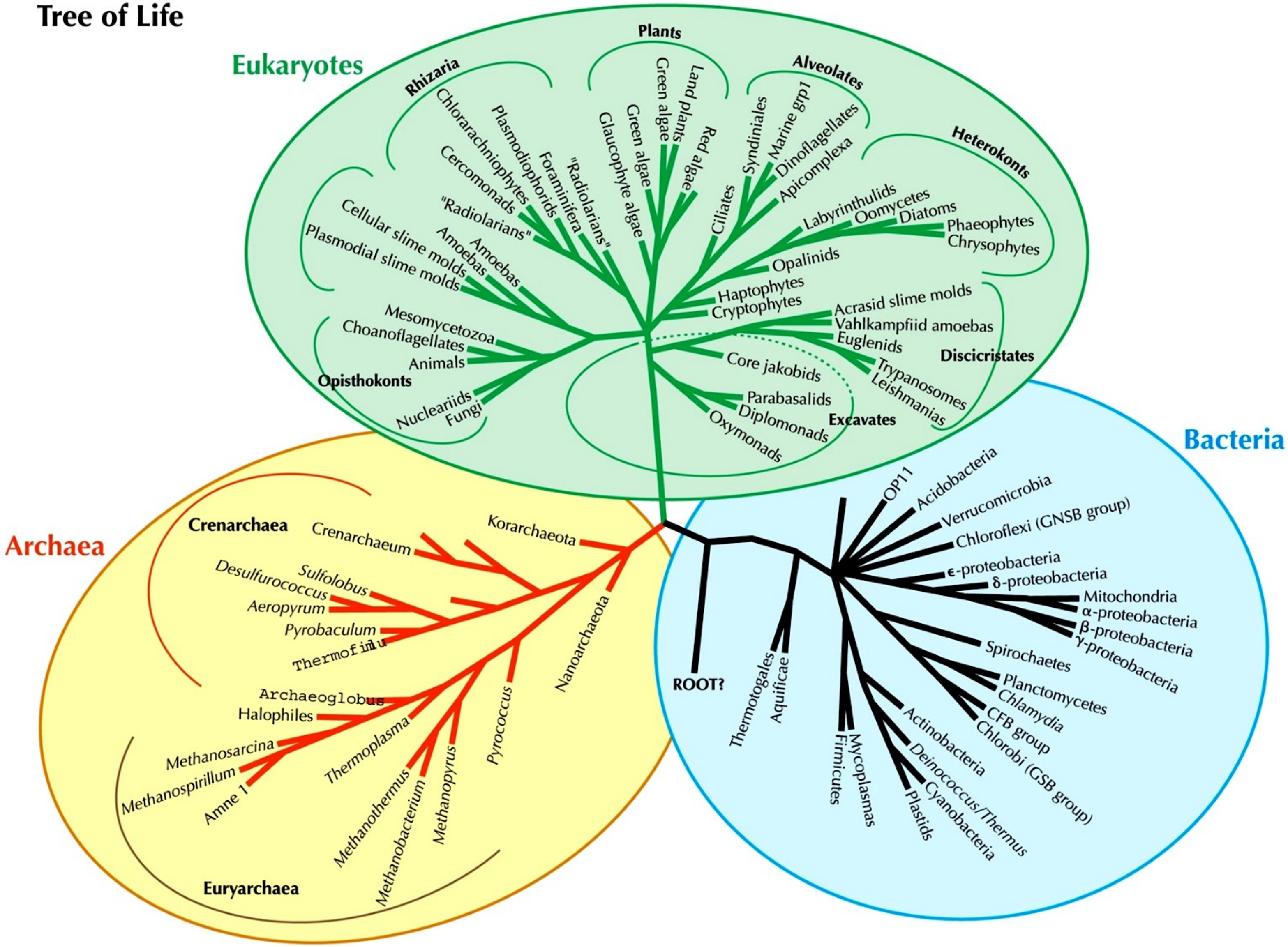


Tree of life:

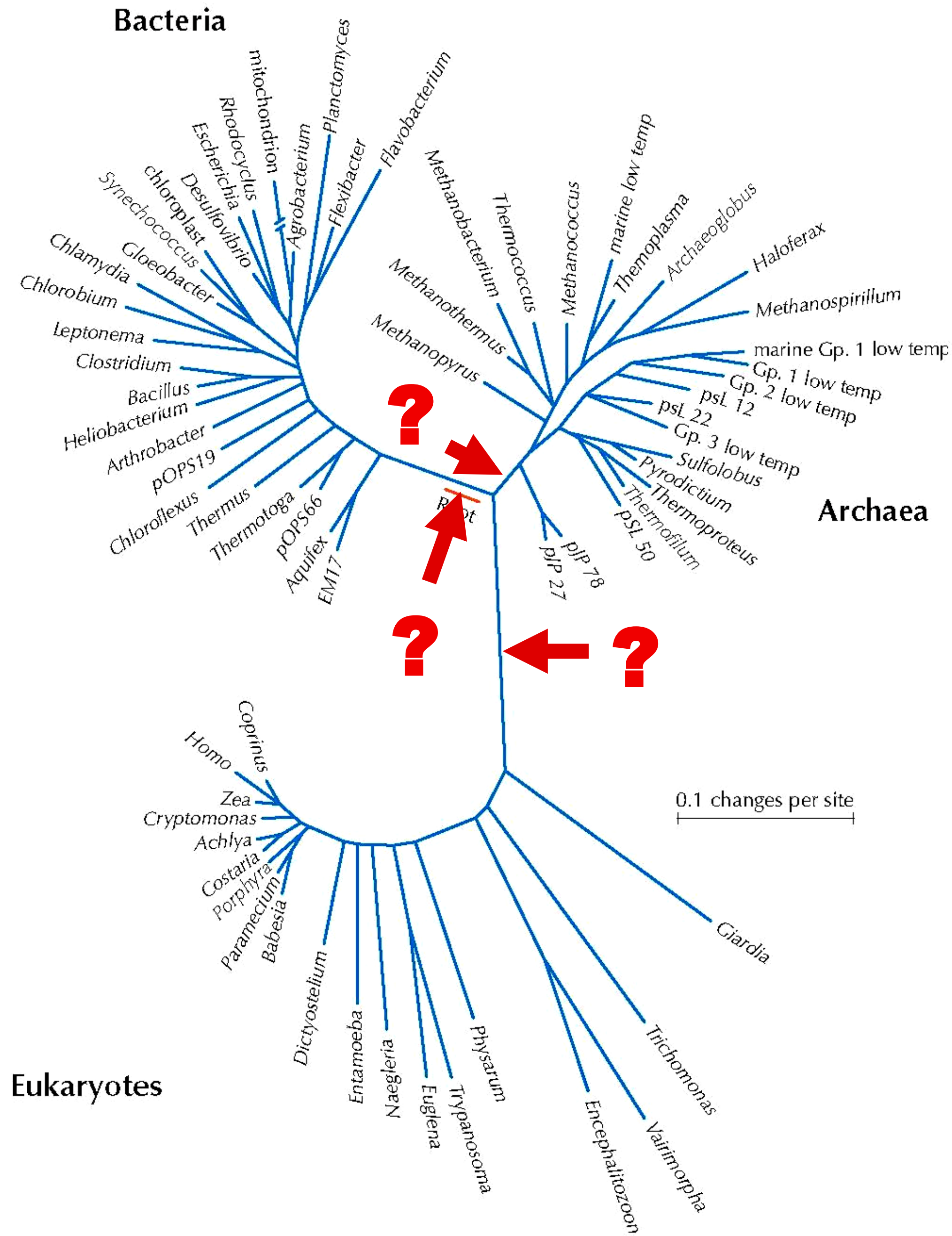
Last Universal Common Ancestor (LUCA)



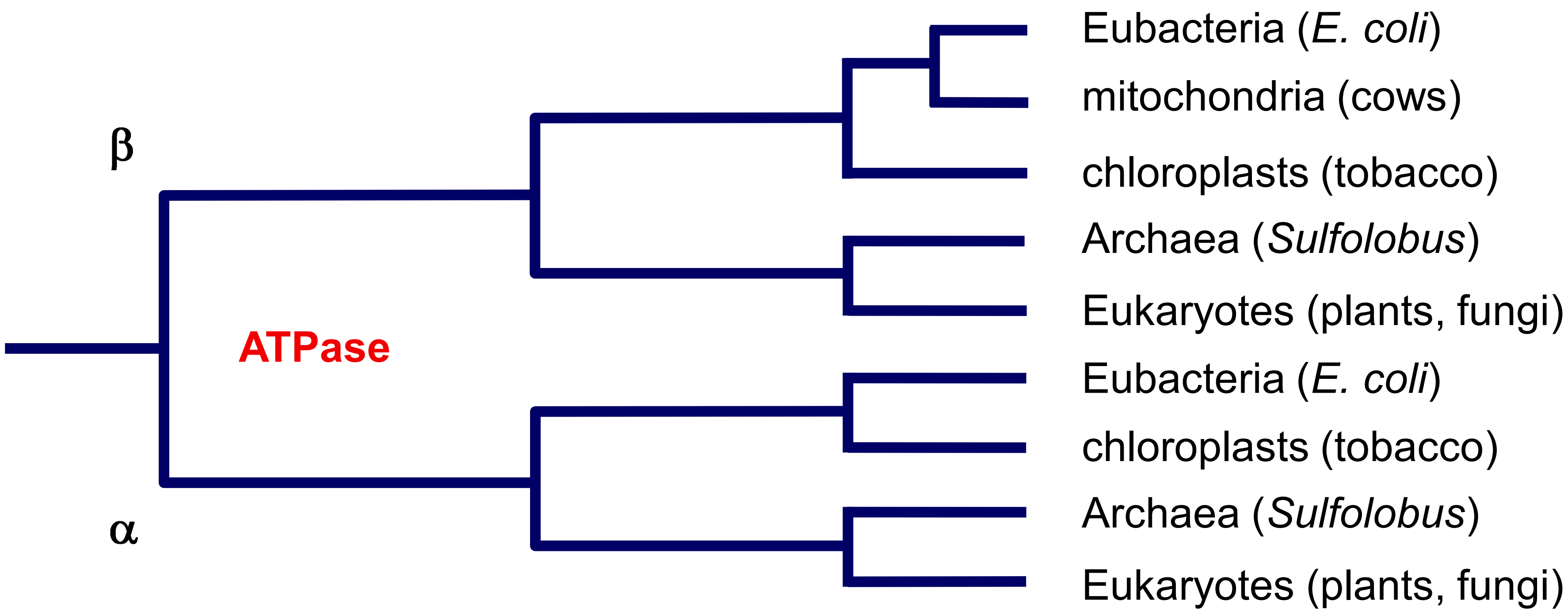
Tree of Life



Eukaryotes
Plants
Green algae
Land plants
Red algae
Green algae
Glaucophyte algae
Rhizaria
Chlorarachniophytes
Plasmodiophorids
Foraminifera
"Radiolarians"
Cercomonads
"Radiolarians"
Alveolates
Syndiniales
Marine grp1
Dinoflagellates
Apicomplexa
Ciliates
Heterokonts
Labyrinthulids
Oomycetes
Diatoms
Phaeophytes
Chrysophytes
Opalinids
Haptophytes
Cryptophytes
Cellular slime molds
Amoebas
Amoebas
Plasmodial slime molds
Mesomycetozoa
Choanoflagellates
Animals
Opisthokonts
Nucleariids
Fungi
Acrasid slime molds
Vahlkampfiid amoebas
Euglenids
Discicristates
Trypanosomes
Leishmanias
Core jakobids
Parabasalids
Diplomonads
Oxymonads
Excavates
Bacteria
OP11
Acidobacteria
Verrucomicrobia
Chloroflexi (GNSB group)
ϵ-proteobacteria
δ-proteobacteria
Mitochondria
α-proteobacteria
β-proteobacteria
γ-proteobacteria
Spirochaetes
Planctomycetes
Chlamydia
CFB group
Chlorobi (GSB group)
Actinobacteria
Deinococcus/Thermus
Cyanobacteria
Plastids
Mycoplasmas
Firmicutes
Thermotogales
Aquificae
ROOT?
Archaea
Crenarchaea
Crenarchaeum
Korarchaeota
Desulfurococcus
Sulfolobus
Aeropyrum
Pyrobaculum
Thermofilum
Nanoarchaeota
Archaeoglobus
Halophiles
Methanosarcina
Methanospirillum
Amne 1
Thermoplasma
Methanothermus
Methanobacterium
Methanopyrus
Pyrococcus
Euryarchaea

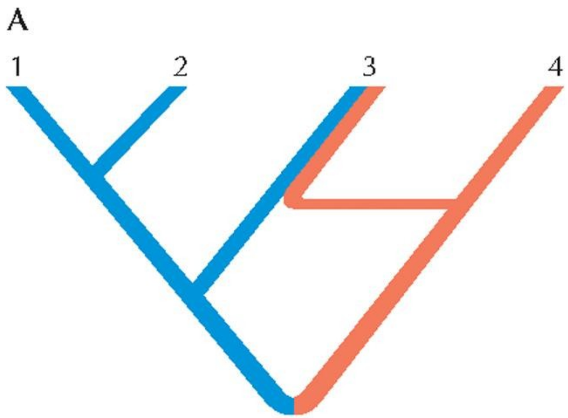


Bacteria
Archaea
Eukaryotes
0.1 changes per site
Root
?
?
?
mitochondrion
Planctomyces
Flavobacterium
Agrobacterium
Flexibacter
Rhodocyclus
Escherichia
Desulfovibrio
chloroplast
Synechococcus
Gloeobacter
Chlamydia
Chlorobium
Leptonema
Clostridium
Bacillus
Heliobacterium
Arthrobacter
pOPS19
Chloroflexus
Thermus
Thermotoga
pOPS66
Aquifex
EM17
Methanobacterium
Thermococcus
Methanococcus
marine low temp
Themoplasma
Archaeoglobus
Haloferax
Methanospirillum
Methanothermus
Methanopyrus
marine Gp. 1 low temp
Gp. 1 low temp
Gp. 2 low temp
psL 12
psL 22
Gp. 3 low temp
Sulfolobus
Pyrodictium
Thermoproteus
Thermofilum
pSL 50
pJP 78
pJP 27
Coprinus
Homo
Zea
Cryptomonas
Achlya
Costaria
Porphyra
Paramecium
Babesia
Dictyostelium
Entamoeba
Naegleria
Euglena
Trypanosoma
Physarum
Encephalitozoon
Vairimorpha
Trichomonas
Giardia

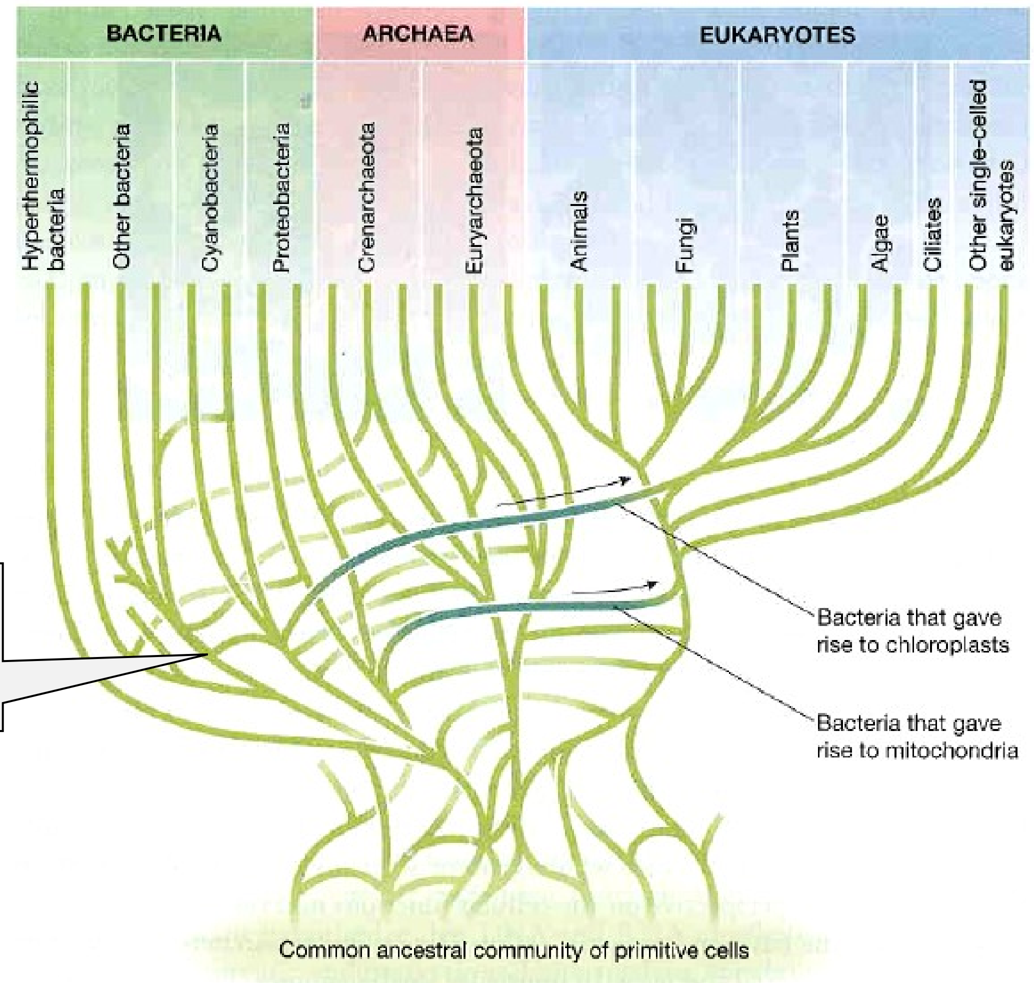


β
ATPase
α
Eubacteria (*E. coli*)
mitochondria (cows)
chloroplasts (tobacco)
Archaea (*Sulfolobus*)
Eukaryotes (plants, fungi)
Eubacteria (*E. coli*)
chloroplasts (tobacco)
Archaea (*Sulfolobus*)
Eukaryotes (plants, fungi)

Horizontal transfer of genes



reticulate evolution



$\Rightarrow$ no LUCA of recent organisms $\times$ trees for individual genes <u>can</u> have LUCA

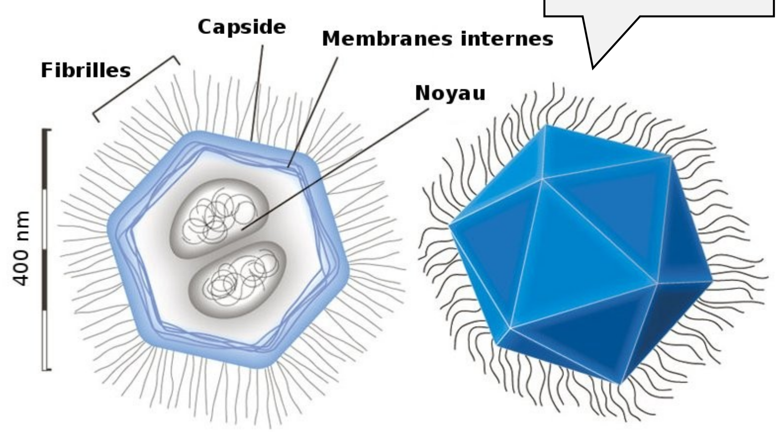
Where to place viruses on the Tree of Life?

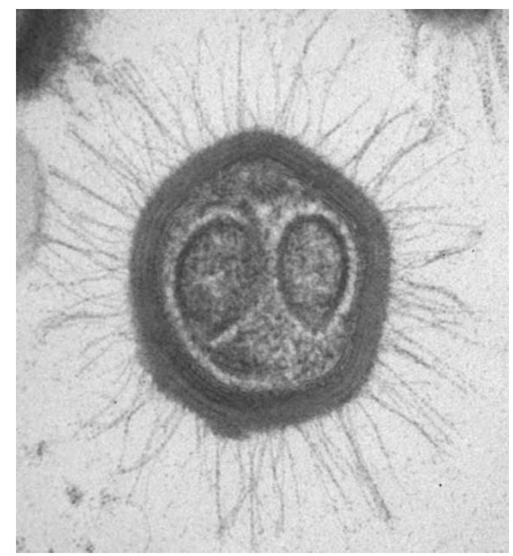
1. relics of pre-cellular world: some processes and genes ancient
   many genes only very distantly related to their cellular counterparts
   × how could they independently exist in pre-cellular world?

2. similarity with transposons → „escaped“ parts of cellular organisms
   – (eg. RNA or DNA elements, plasmids)

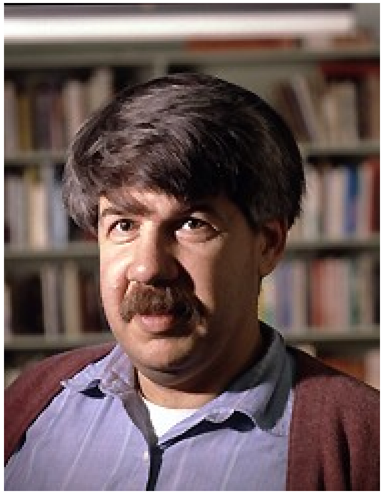
3. originally free-living organisms
   eg. mimivirus: genome size = 1,2 Mb, > 900 proteins, ie. more than
   some bacteria and archaebacteria!

mimivirus





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)

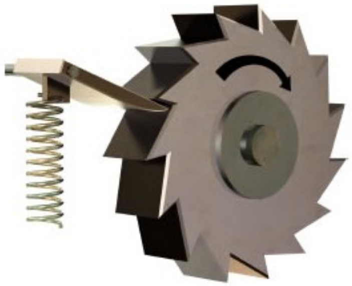
×

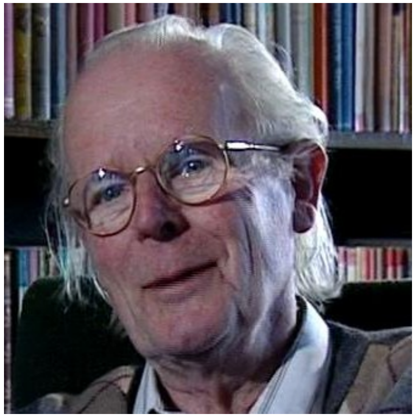
John Maynard Smith a Eörs Szathmáry:

the contingent irreversibility theory): steady tendency to increase of complexity

major transitions

complexity emrges withou selection





Major transitions in evolution:

origin of replicators

compartmentation, origin of cell

origin of chromosomes

origin of genetic code, DNA

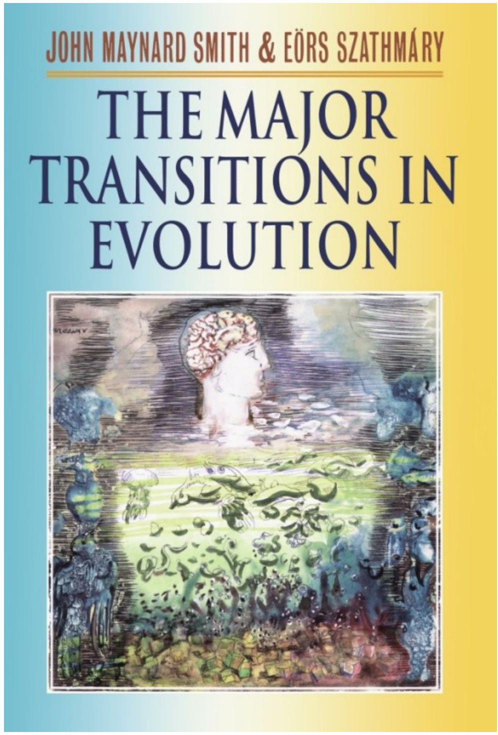
origin of Eukaryotes

origin of sex

multicellularity

societies

origin of language



Individuals cease to reproduce independently

Bigger size → bigger pray, 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 $\times$ B chromosomes, transposition

fair meiosis $\times$ meiotic drive

differentiation of somatic cells $\times$ oncogenic growth

non-reproducing castes $\times$ egg-laying workers