

Vývojová biologie rostlin

rostliny nejsou zelení
živočichové

Studijní materiál ke zkoušce:

Úvod do fyziologie vyšších rostlin

Jiří Luštinec a Viktor Žárský

Karolinum 2003, **kap. 10 ONTOGENEZE** (příp. 11 a 12)

a také Fyziologie rostlin , Doc. Libuše Pavlová, Karolinum.
Na stránkách KFR on-line; Kap. 8-11

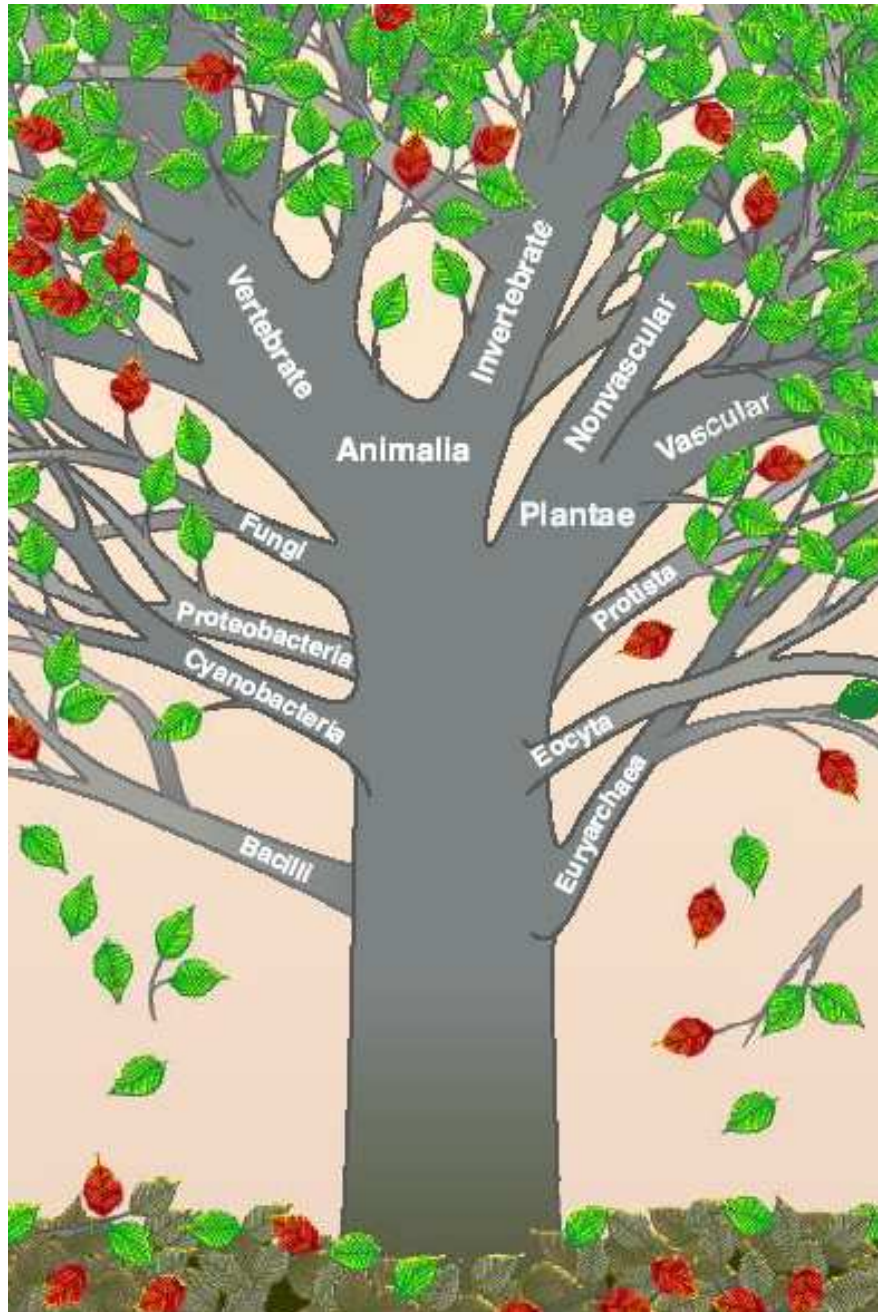
<http://kfrserver.natur.cuni.cz/kfrserver/studium/prednasky/vyvojrost/index.htm>

Pro hlubší zájemce:

http://www.plantsci.cam.ac.uk/Haseloff/teaching/Index_teaching.htm

Evoluční dějiny rostlinné buňky

aneb co jsou (a co už nejsou) rostliny



Building the Tree of Life. A current view of the Tree of Life (7). Information is biased toward vertebrate animals and vascular plants (the thick branches); lesser-known groups such as bacteria, fungi, and protists are largely underrepresented. Also shown are species known to science (green leaves), extinct species (leaf litter, brown), endangered species (falling leaves), and species for which "barcode" information is available (red leaves).

Crandall and Buhay, Science 306:1144, 2004

Co jsou rostliny?

- Fotosyntetizující (zelená) (eukaryota) ...
„**Viridiplantae**“
- (To, co studuje botanika)
- ALE: ruduchy, sinice ... lišejníky
- V řadě situací se rozumí **Embryophyta**

Pohled na fylogenezi eukaryot

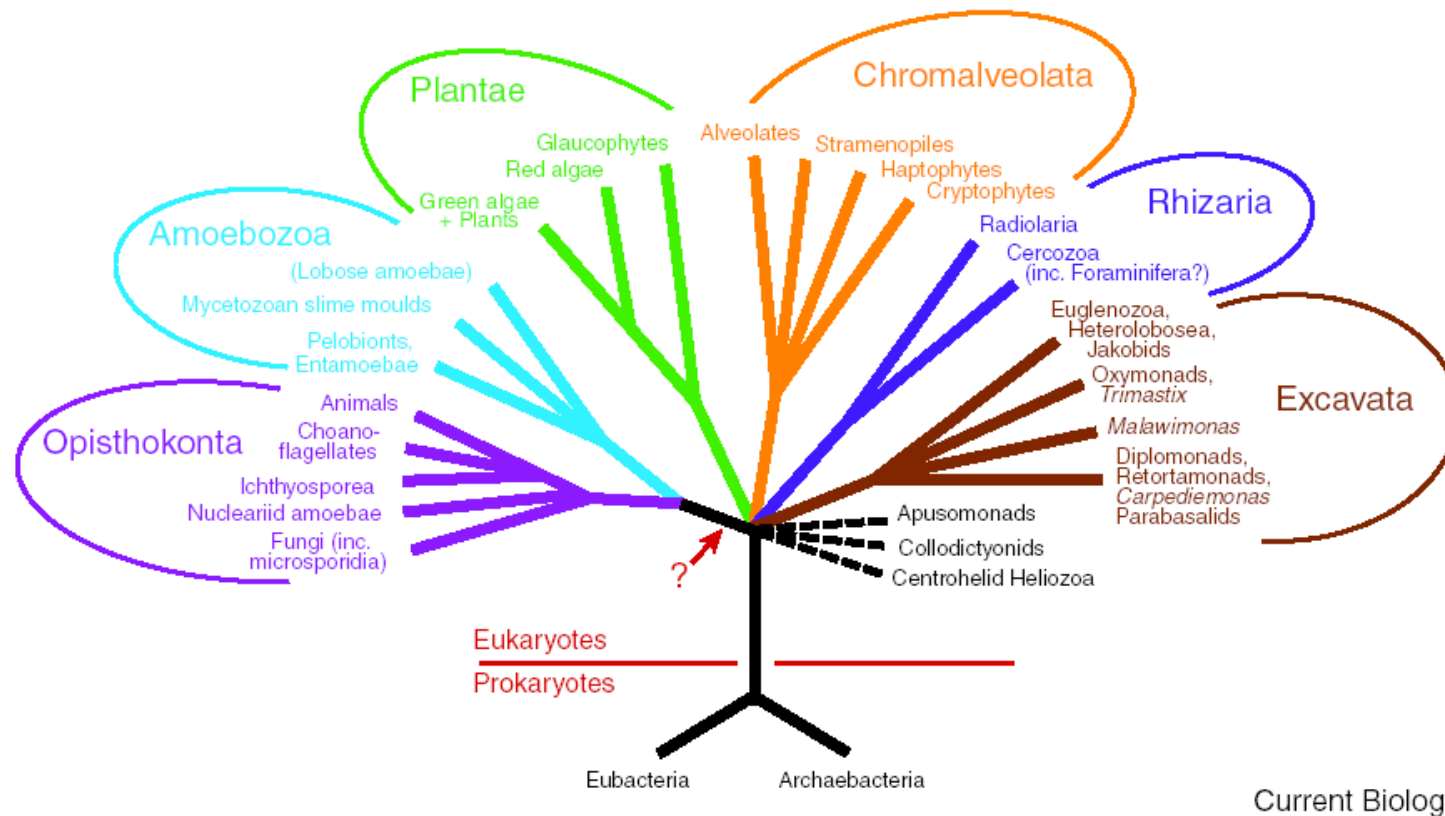
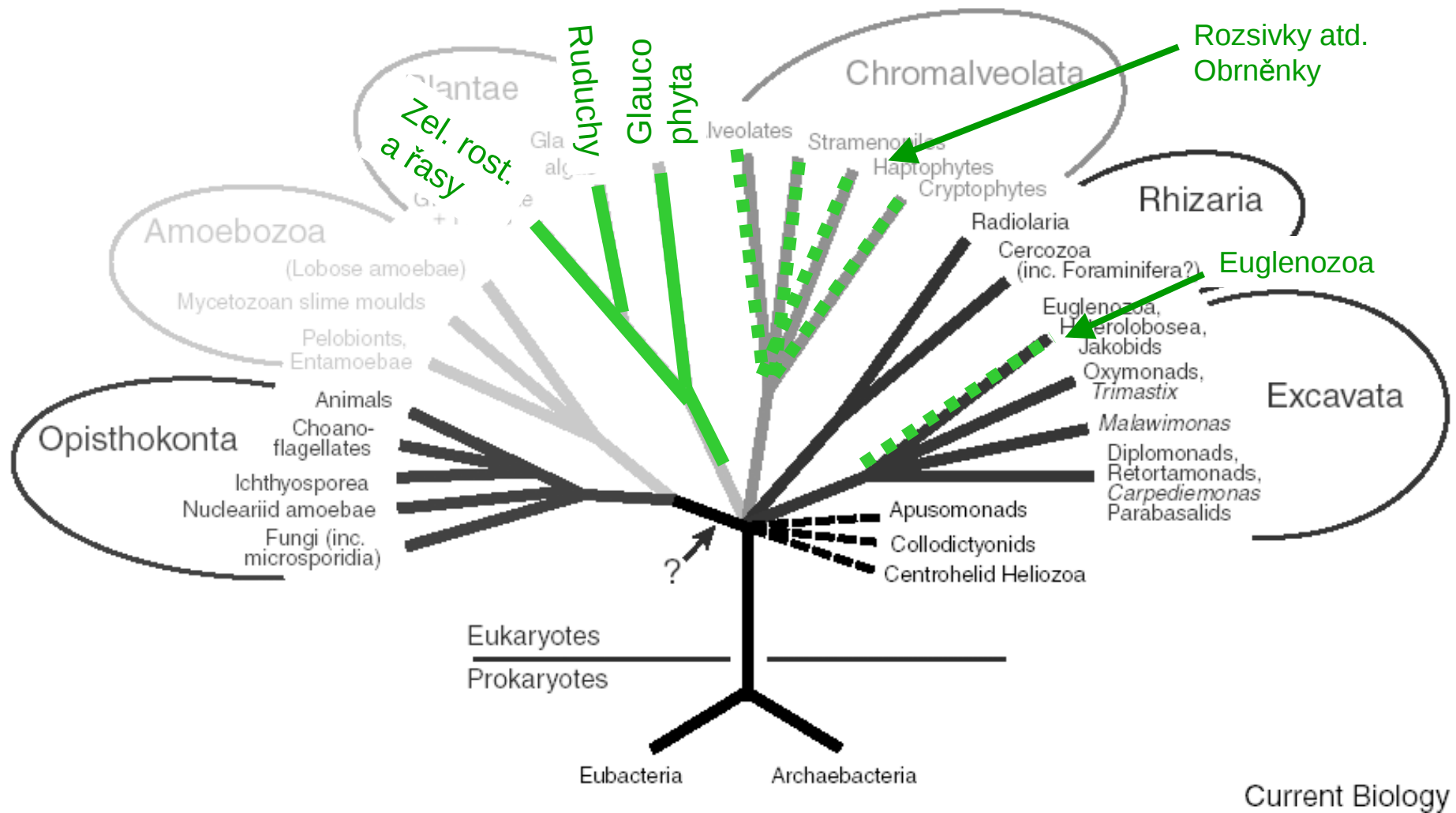


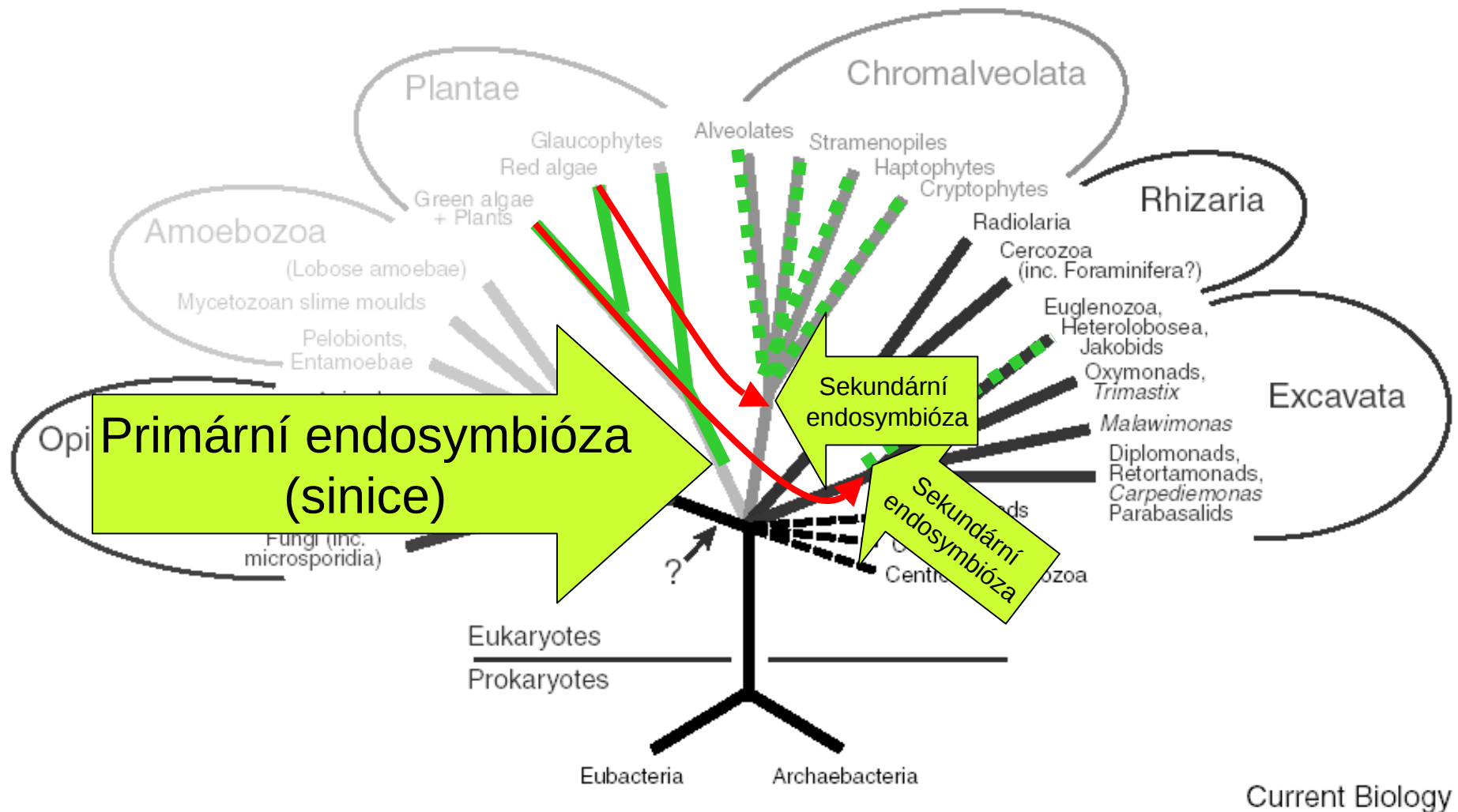
Figure 1. A diagrammatic tree depicting the organisation of most eukaryotes into six major groups. The relationships amongst most of the major groups and the position of the 'root' of the tree are shown as unresolved (note however, the grouping of Opisthokonta and Amoebozoa). The arrow shows a possible precise placement of the root, based on gene fusion data (see text).

(Simpson and Roger, Curr. Biol. 14:R693, 2005)

Fotosyntetické organismy v rámci 6 říší

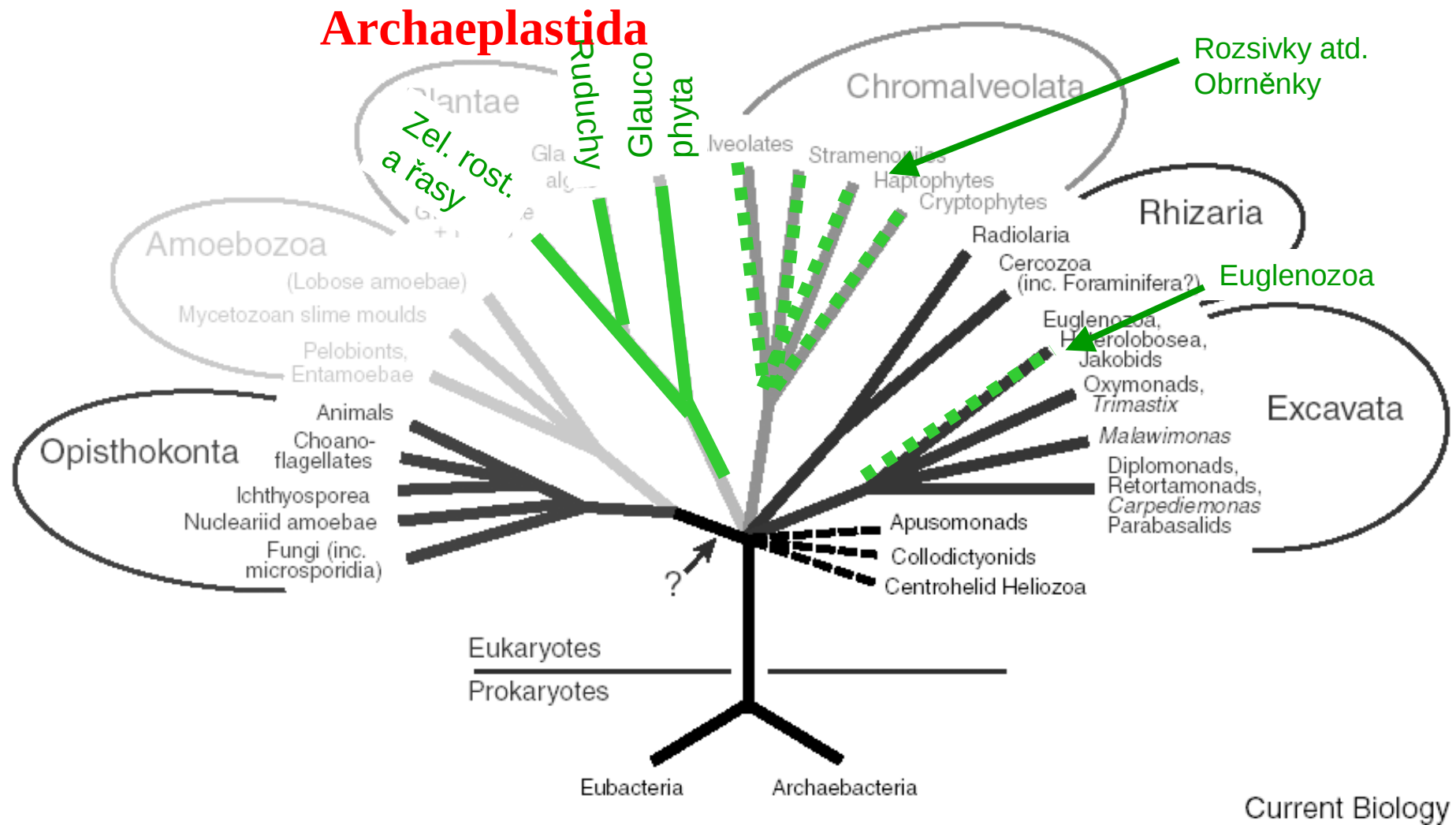


Původ plastidů: jednou a přece víckrát!

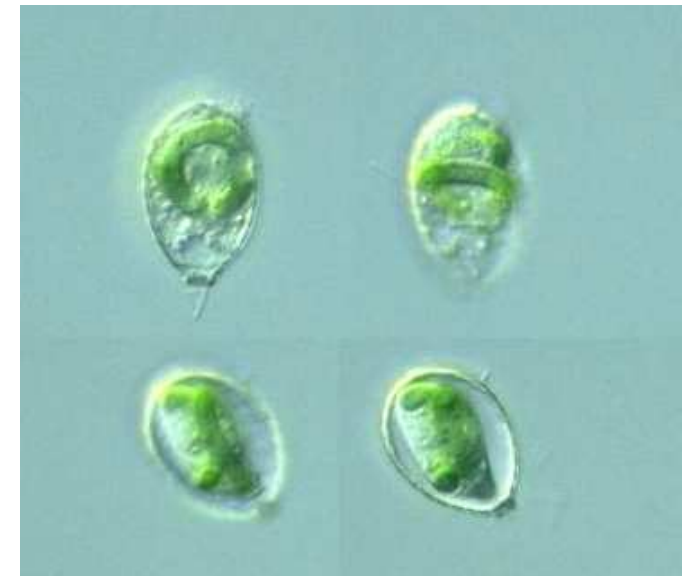
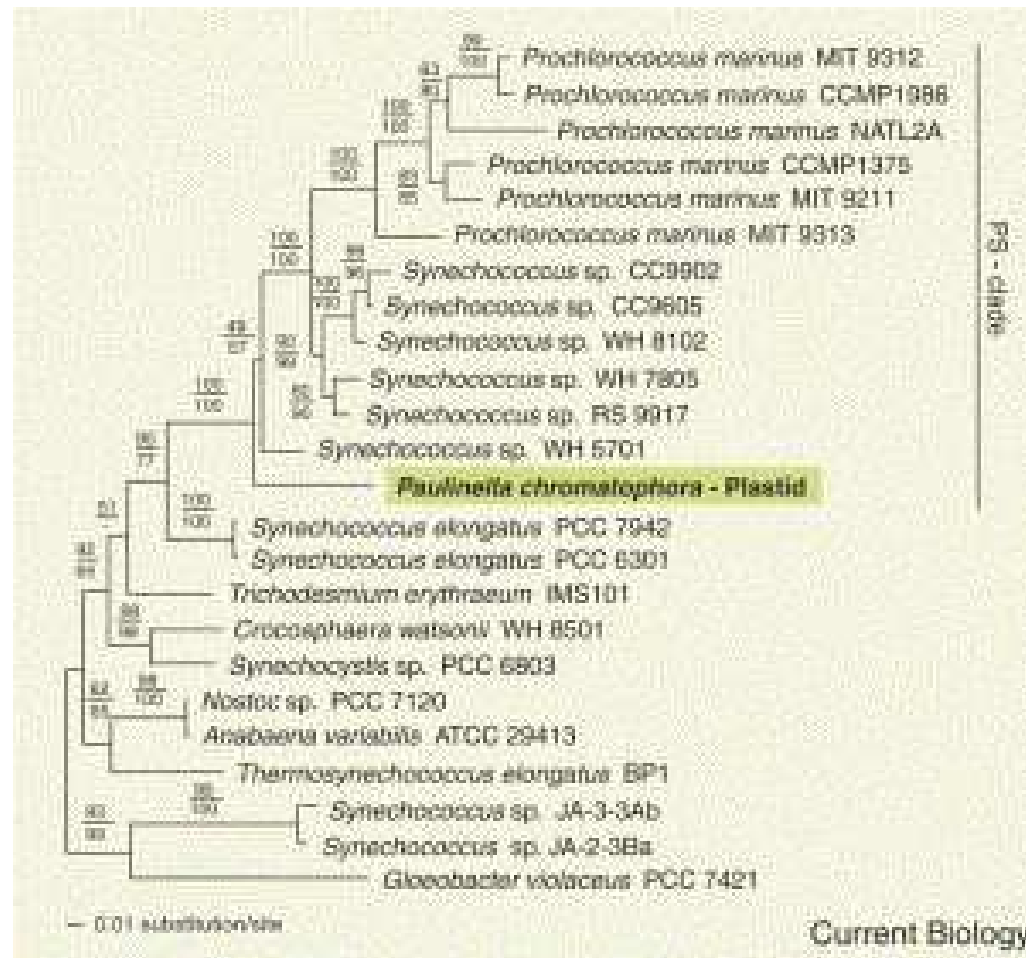


U sekundárních endosymbiontů je plastid vlastně řasa, z jádra někdy „nukleomorf“.

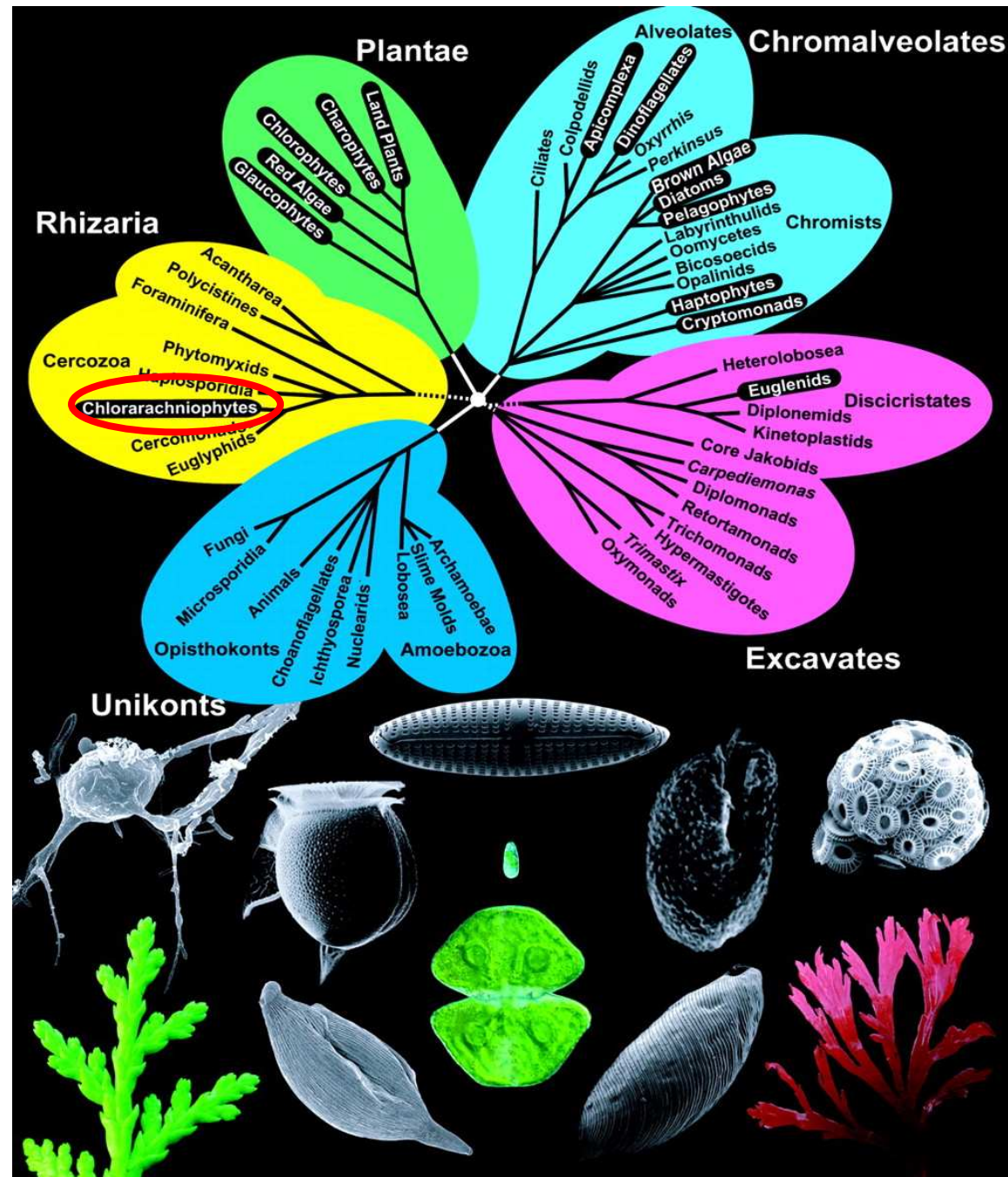
Fotosyntetické organismy v rámci 6 říší



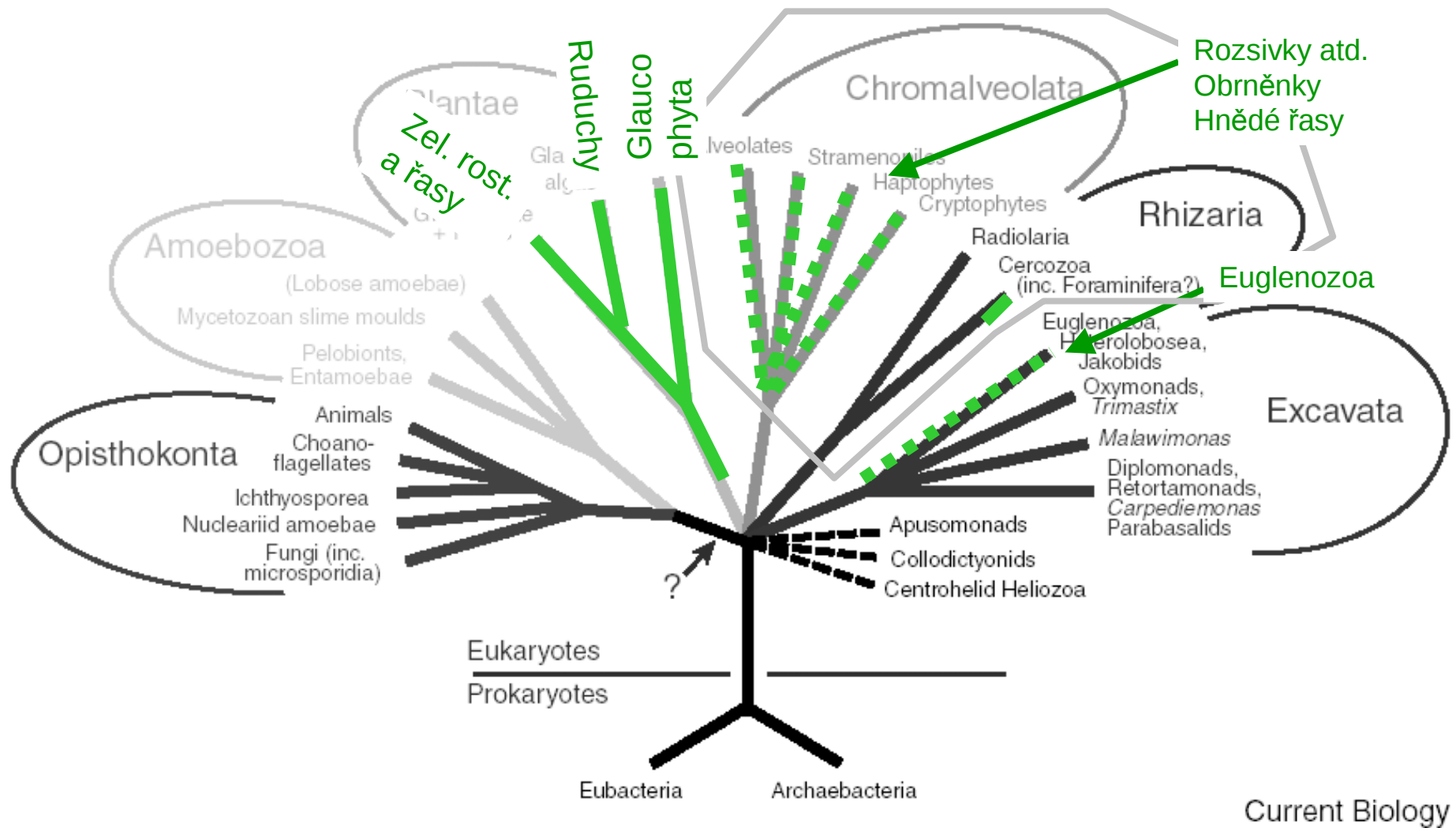
Paulinella chromatophora



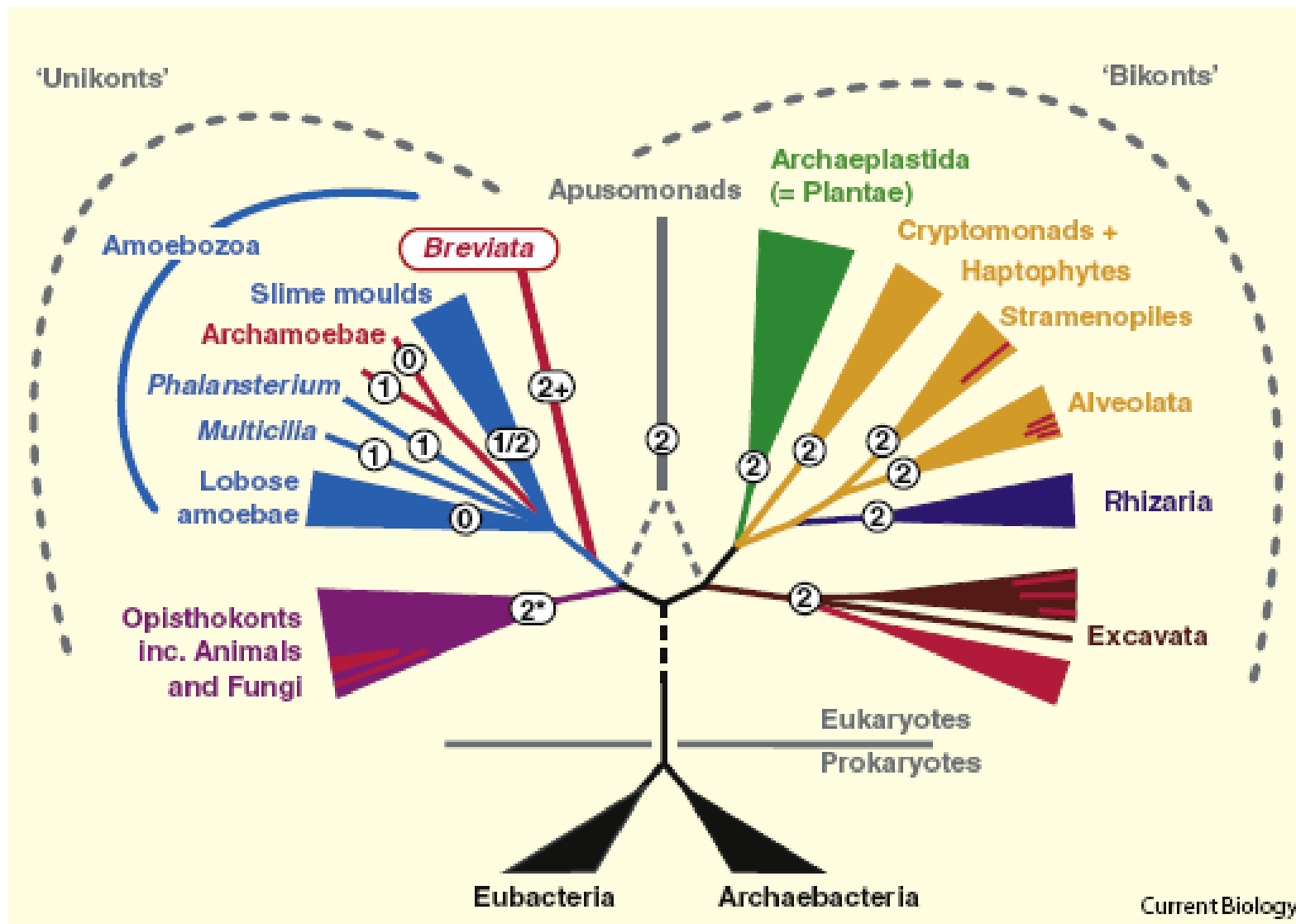
860 genů
25% pův.



Fotosyntetické organismy v rámci 5 říší

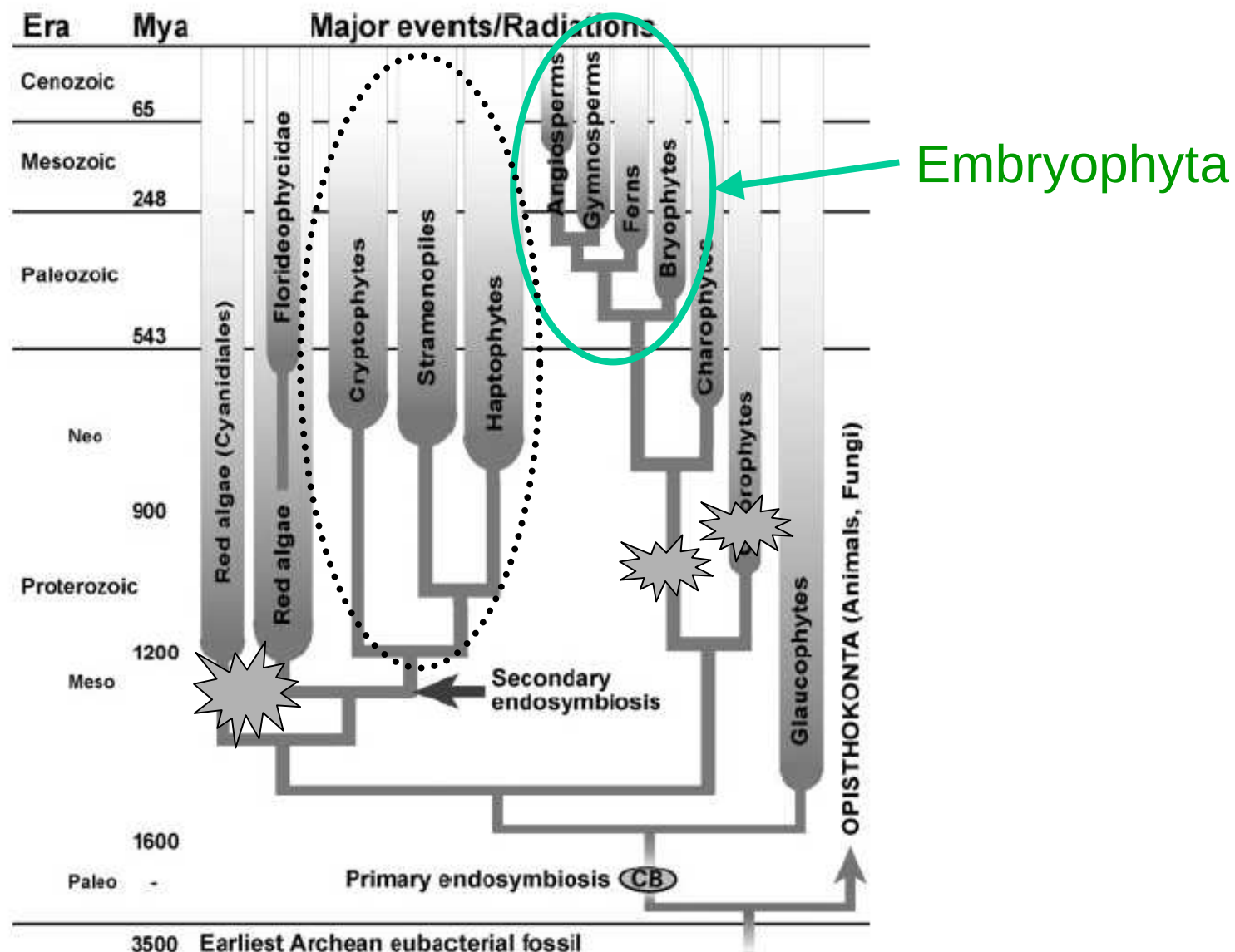


Kolik bičíků?



(Roger a Simpson 2008)

Mnohobuněčnost vznikla u rostlin několikrát



(Yoon, Mol. Biol. Evol. 21:809, 2004)

Mnohobuněčnost rostlin je evolučně nepříbuzná mnohobuněčnosti živočichů

PLANT EVOLUTION AND DEVELOPMENT IN A POST-GENOMIC CONTEXT

Quentin C. B. Cronk

Large-scale gene-sequencing projects that have been undertaken in animals have involved organisms from contrasting taxonomic groups, such as worm, fly and mammal. By contrast, similar botanical projects have focused exclusively on flowering plants. This has made it difficult to carry out fundamental research on how plants have evolved from simple to complex forms — a task that has been very successful in animals. However, in the flowering plants, the many completely or partially sequenced genomes now becoming available will provide a powerful tool to investigate the details of evolution in one group of related organisms.

Plant evolution has exerted a controlling influence on the geochemical and climatic evolution of our planet. Through photosynthesis, plants have altered the atmosphere by producing oxygen and providing a sink for carbon dioxide. The colonization of the land by plants created the terrestrial biosphere. The evolution of the root by early land plants promoted soil formation from weathered rock. Finally, the enormous ecological and morphological diversity achieved by the angiosperms supports an even more staggering diversity of insect forms, and the evolution of the leaf, which has a higher concentration of protein than stems do, permits the survival of significant numbers of large complex animals. All these innovations have been driven by genetic changes. The study of plant evolution, at its grandest, is the study of how mutations in genes have affected the way in which the planet functions. In this article, I review the principal morphological landmarks that have characterized the evolution of plants and address how knowledge that has been accrued over the centuries by plant morphologists, systematists and developmental biologists can be integrated with genomic information to address the most intriguing evolutionary question of all — the nucleotide basis of development and adaptation.

New phase of the study of evolution

Before the completion of the *Arabidopsis* genome-sequencing project, which was announced in February 2000 (REF. 1), the complexity of the genome was a strong barrier to understanding the specific relationships between genotype and evolution. This is no longer the case. With the advent of rapid sequencing methods, the study of plant evolution has shifted from the gene level to the nucleotide level. It is now possible to investigate how nucleotide changes affect phenotype through altering developmental processes and how selection acts on these phenotypes to drive evolutionary change, both past and present. The use of genomic information is, therefore, set to enhance markedly the study of the evolution of development (known as 'evo-devo'). The great endeavour for the twenty-first century will be to discover the nucleotide basis of morphological differences between organisms, so marking a third phase in the study of natural selection (BOX 1). The completion of this endeavour will require the integration of four disciplines: development, morphology, systematics and evolutionary biology. Systematics, by revealing the pattern of character change in the evolution of particular taxonomic groups, is an essential underpinning of plant evo-devo. The development of molecular systematics has been particularly important in providing accurate organism^{2,3} (BOX 1) and gene^{4,6} phylogenies. This

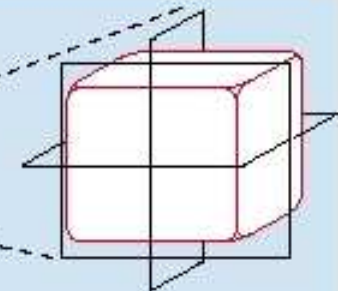
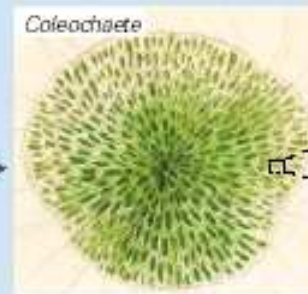
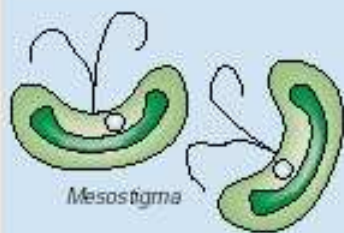
Institute of Cell and Molecular Biology,
University of Edinburgh,
Kings Buildings,
Mayfield Road,
Edinburgh EH9 3JH, UK,
and Royal Botanic Garden,
20A Inverleith Row,
Edinburgh EH3 5JF, UK.
e-mail: q.cronk@rbg.org.uk

Rostliny kolonizovaly souši jen
jednou
a jen zelené rostliny

Z 1. rozměru do prostoru – význam orientace dělení a dloužení.

Box 3 | Outline summary of some important innovations of plant evolution

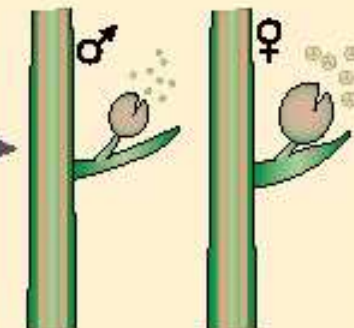
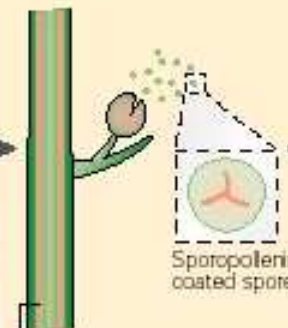
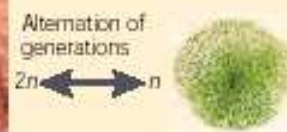
Aquatic Algal level



Unicellular to filamentous transition. Products of mitosis do not separate, thus forming long filaments. Plane of division is always parallel to the direction of growth. Filaments can produce mats, which, by trapping evolved oxygen, can rise to the water surface (the photic zone). Evolved: several times. *Klebsormidium* image © Yuuji Tsukii, Japan.

Filamentous to parenchymatous cell division. A complex multicellular organism can form only if cell division occurs in more than one plane. This requires sophisticated control of a developmental mechanism that regulates cell division in response to external signals. Evolved: several times. Example: *Coleochaete* image © Mike Clayton, USA.

Terrestrial Colonization of the land



Secretion of a hydrophobic chemical layer onto the surface of the plant (cuticle). Evolved: once. With the evolution of the cuticle, an alternative system for gas exchange is needed, rather than diffusion across the plant surface. Cuticularized parts of bryophytes have stomata (breathing pores), as do the pteridophytes and seed plants. Evolved: probably once.

All land plants have sporopollenin-coated spores, which is thought to protect the spore from the hostile aerial environment. The microspore cannot avoid travelling through this hostile aerial environment, as it is a principal instrument of gene flow in the population of otherwise stationary organisms. Evolved: once. *Cooksonia* and *Rhynia* images © Hans Stenr, The Netherlands.

Conducting tissue. All land plants have some sort of water-conducting tissue. In mosses, this is called a hydrome. In vascular plants, this is better developed and is called xylem. Evolved: probably once.

Homospory to HETEROSPORY transition. The evolution of a large female megaspore with more resources than the small microspore represents an important evolutionary division of function, requiring a new developmental control of sex expression. Evolved: several times (at least six, probably nine), but once in the seed-plant lineage.

Klíčový význam lignifikace

Rodozměna

- Tendence k rozvoji/převládnutí sporofytu
- Jak vůbec vznikl mnohobuněčný sporofyt?

Dvě hypotézy o vzniku dvou generací u rostlin

- **Interpolační teorie** - předek měl diploidní jen zygotu (tak je tomu u parožnatek). Oddálení meiózy po mitotickém dělení zygoty vede ke vzniku sporofytu.
- **Transformační teorie** - předek suchozemských rostlin vyvinul simultánně mnohobuněčný gametofyt i sporofyt (analog. Ulva).

Stará dobrá „Coleochaete“ hypotéza mluví pro IT.

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Hlavní evoluční novinky suchozemských rostlin

- Kutikula a průduchy.
- Evoluce listu.
- Evoluce květu a semenných obalů

Listy

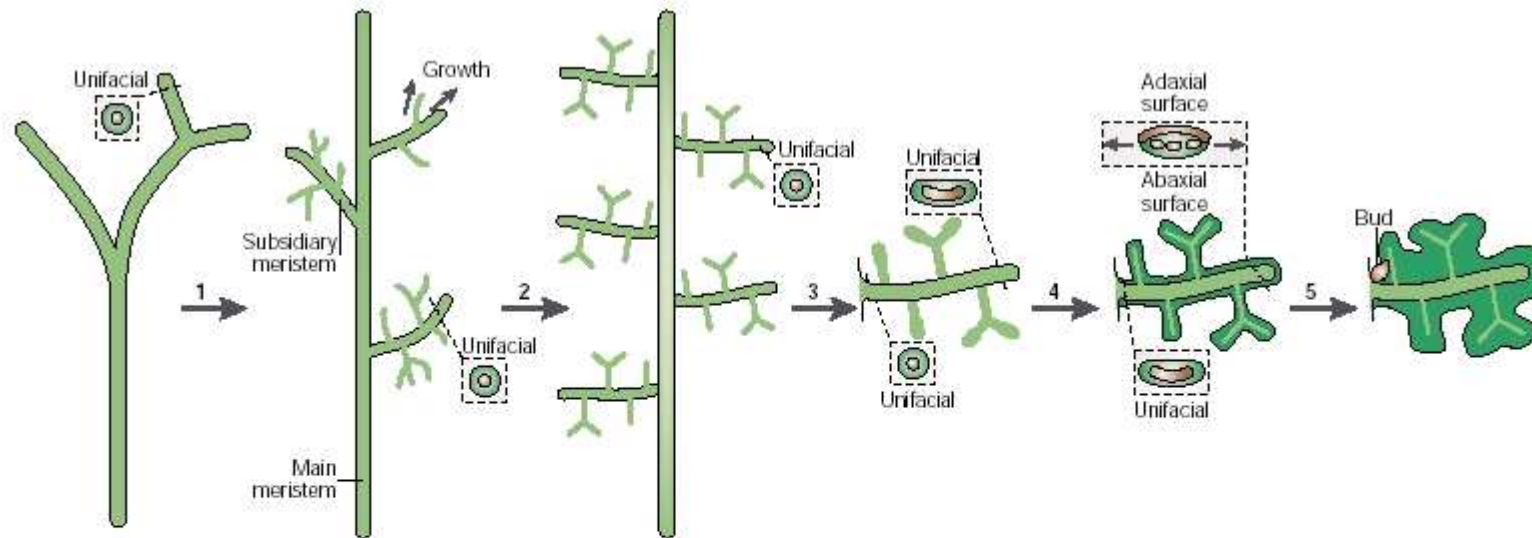


Figure 2 | **Five-step hypothesis of seed-plant leaf evolution.** Leaf evolution requires the recruitment of at least five broadly defined gene systems, each consisting of several different, but interacting, developmental genes. Recruitment of such systems in the following order would be consistent with both the observed morphology of leaves and with the fossil record: 1, a monopodality system — the division of meristem into main and subsidiary meristems, probably through an increase in complexity of meristem control networks; 2, a determination system — cessation of growth at tips in lateral branch systems. Originally, this probably involved the late downregulation of *KNOX* genes by *PHANTASTICA* (*PH*)/*ROUGH SHEATH2* homologues, which in evolution have become expressed earlier and earlier; 3, a dorsoventrality system — lateral branch systems of some fossils are unifacial but show internal dorsoventrality. This requires asymmetric, abaxial or adaxial (ventral or dorsal) gene expression, promoting stable adaxial or abaxial expression of key regulators, such as *PHB*, and of the *YABBY* gene family; 4, a lamination system (production of a large flat sheet of tissue) — the evolution of an adaxial surface (extreme dorsoventrality) is correlated with the activity of a marginal meristem. This might have arisen through the interaction between adaxial–abaxial identity genes (such as *PHB*) and *KNOX* genes. As the marginal meristem (located along the margin of the leaf primordium and that forms the blade) is always active at the junction of adaxial and abaxial domains, crosstalk between the domains might constitute the stimulus for lamination; 5, an axillary bud system — the constant association of a new meristem with the adaxial side of the leaf, which could have arisen by signalling between likely adaxial identity genes (such as the homeodomain-zip gene *REVOLUTA*) and meristem identity genes. Although for several of these functions we are in a position to suggest candidate genes, much further work needs to be carried out on the comparative evolution of the gene networks involved.

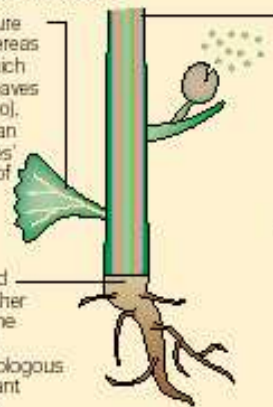
Vyvinuly se několikrát (min.3x) nezávisle, podobně kořeny.

Květy

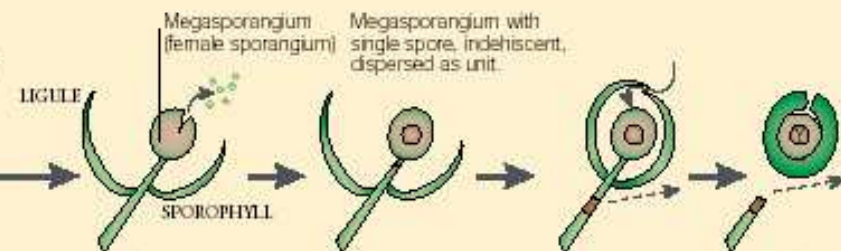
Filling the terrestrial ecospace

Leaves are a unique feature of the land flora, and whereas the first land plants of which we have fossils had no leaves (Silurian 440–410 Myr ago), by the end of the Devonian (410–360 Myr ago) 'leaves' had evolved a minimum of six times.

Roots might have evolved twice (in lycopods and other pteridophytes). If this is the case, lycopod roots and other roots are non-homologous and should show important differences in the genetic systems underpinning their development. This hypothesis can only be tested if more is known about the molecular genetics of root development generally, and about the molecular genetics of root development in lycopods specifically.



A means of secondarily thickening the stem after primary growth is needed to support large-stature plants. This has been solved in pteridophytes and in seed plants by the differentiation of a vascular cambium, which is an encircling meristem (unifacial in lycopods), producing new cells around the stem. Evolved: several times.

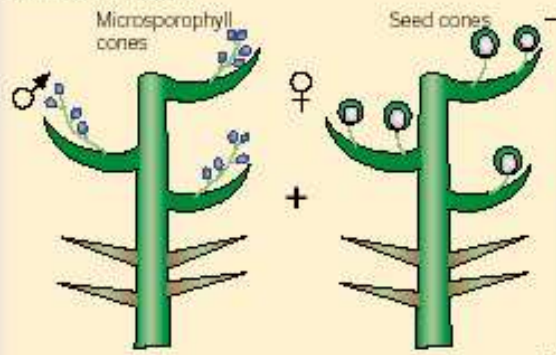


Evolution of the seed. The seed reduces the requirement for external water in which the gametes swim, by enclosing the female gametophyte in sporophyte tissue. In gymnosperms, this forms a chamber into which liquid (pollen drop) is secreted. The enclosing sporophyte tissue also provides protection when the seed is dispersed. Evolved: several times.

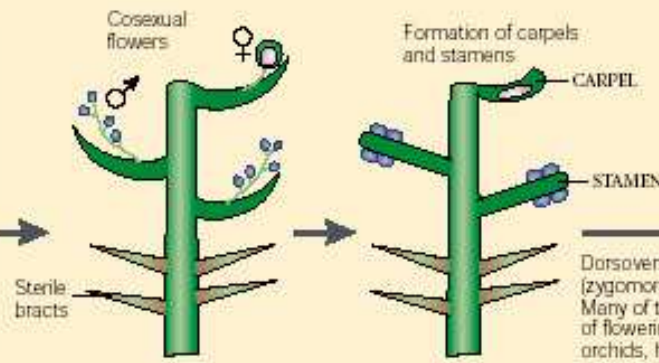
Megasporangium protected by investing bracts past which microspores have to pass.

Investing bracts form a seed coat.

Flower evolution

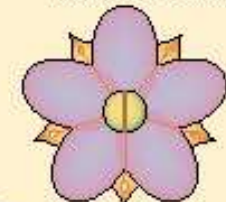


Production of male and female sporangia in a cosexual structure (the hermaphrodite flower). The extant gymnosperms have separate male and female cones (and this is probably true of the ancestor of gymnosperms and angiosperms), whereas the angiosperm flower is essentially a bisexual cone. Evolved: once in the ancestor of extant hermaphrodite seed plants (angiosperms), but independently in some extinct groups of gymnosperms (Example: *Bennettitales*).

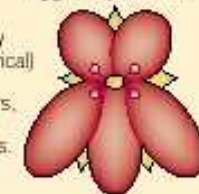


Dorsoventral asymmetry (zygomorphy) of the flower. Many of the largest families of flowering plants, such as the orchids, have such dorsoventrally asymmetrical (bilaterally symmetrical) flowers, and it is possible that adaptation to specialist pollinators, aided by zygomorphy, promotes speciation. Evolved: several times.

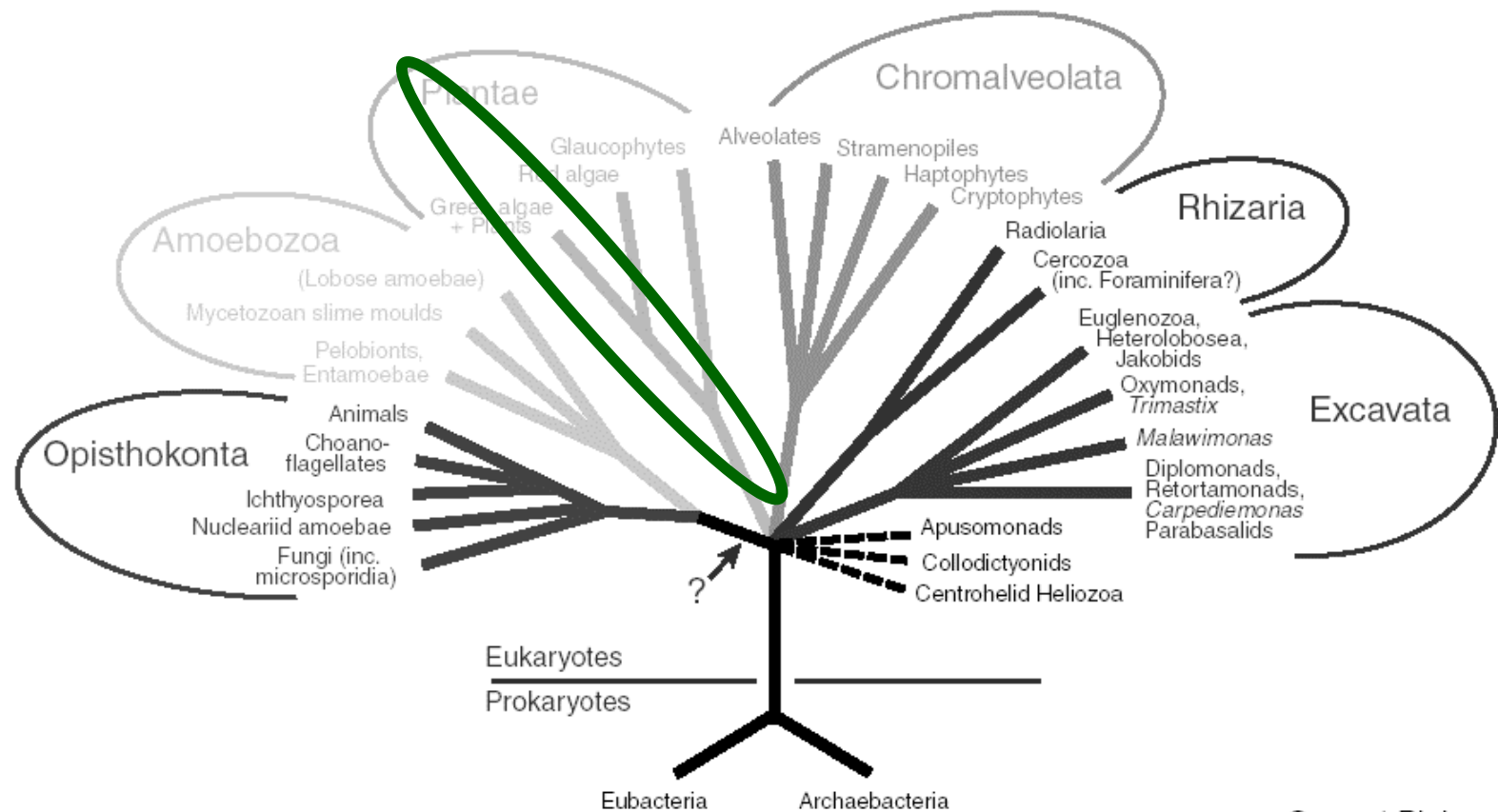
Establishment of four whorls in radial flower



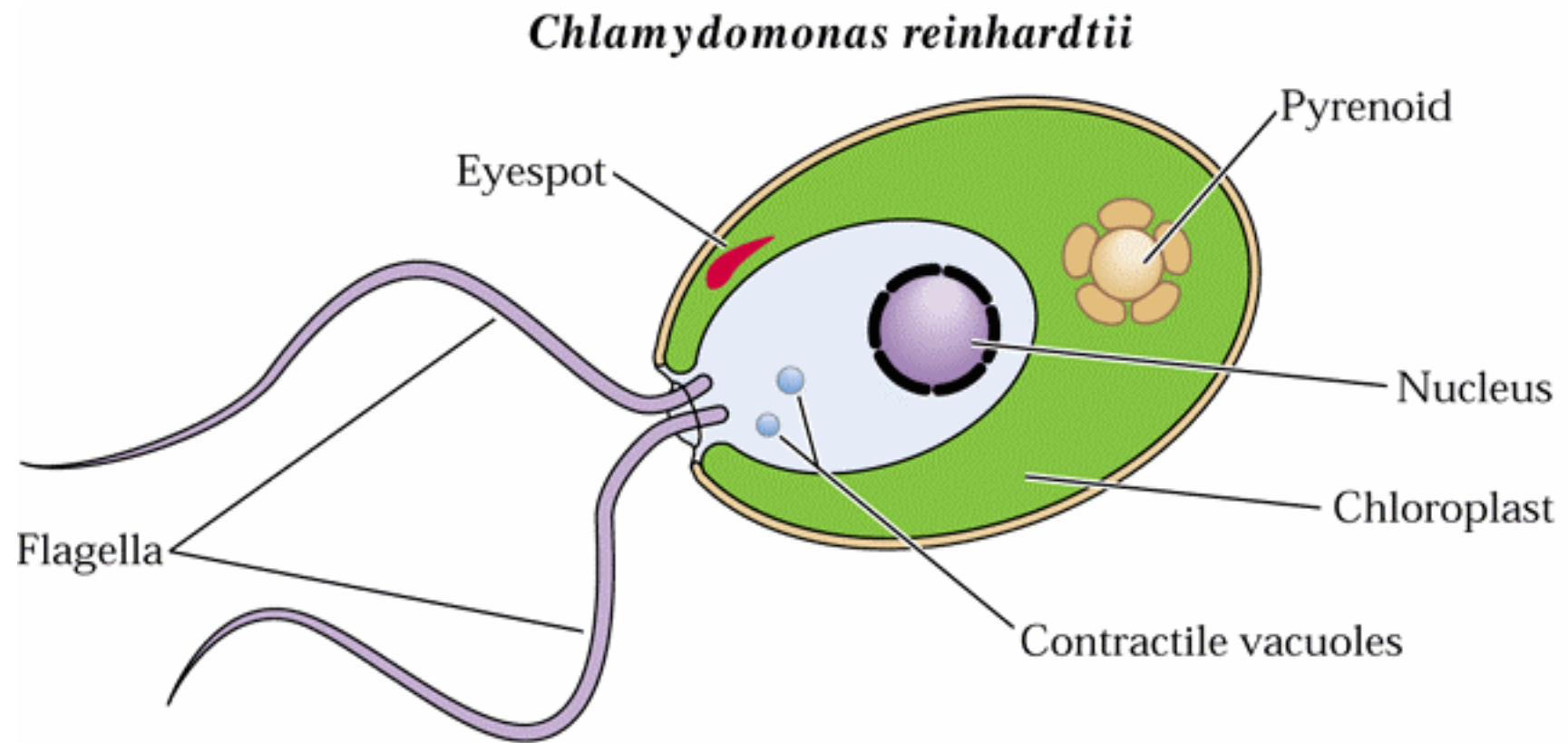
Zygomorphic flower



Modelové organismy rostlinné vývojové biologie

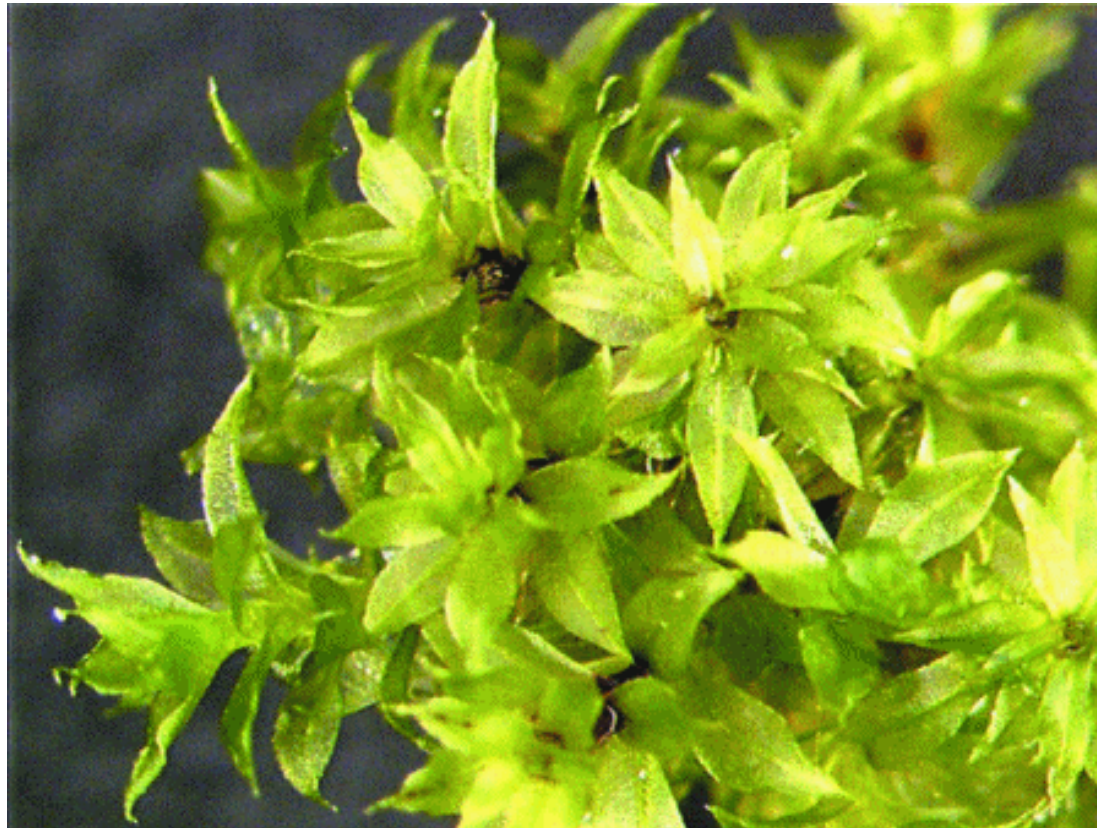


Current Biology



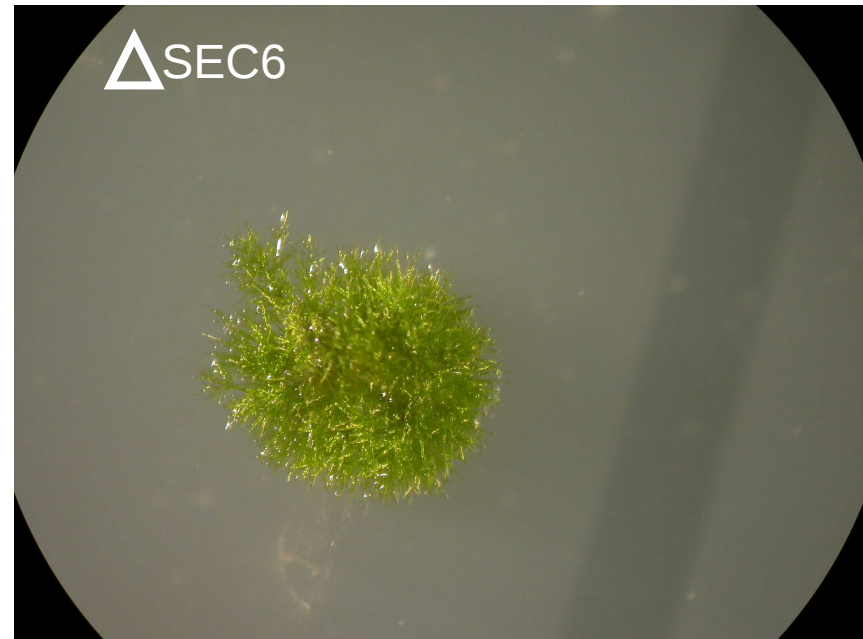
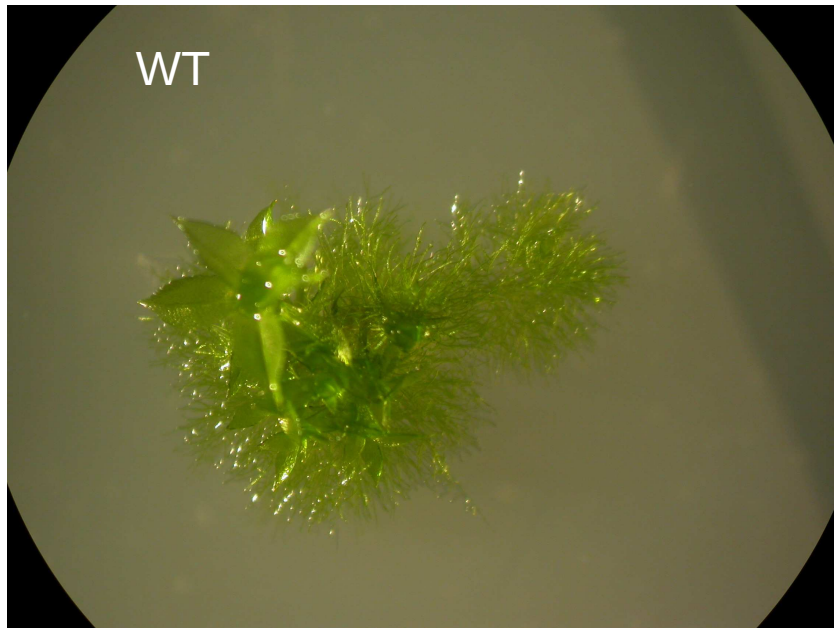
Skvělý model pro studium plastidů a fotosyntézy.

Mech ***Physcomitrella patens*** je dosud jediný rostlinný model, který umožňuje homologní rekombinace - tzv. gene knock-out



Základní tropické a fytohormonální systémy jako u vyšších rostlin.

Partial SEC6 deletion in *Physcomitrella patens*



In collaboration with Fabien NOGUE, INRA, Versailles, France

***Zea mays* nejstarší vývojově-genetický model kytosemenných
mutace *knotted***



***Arabidopsis* - 10^7 pb (A) a *Fritillaria* - 10^{11} pb (B)**

Rostliny se zcela srovnatelnou komplexitou pletiv a orgánů se liší 10 000x obsahem DNA.

(A)

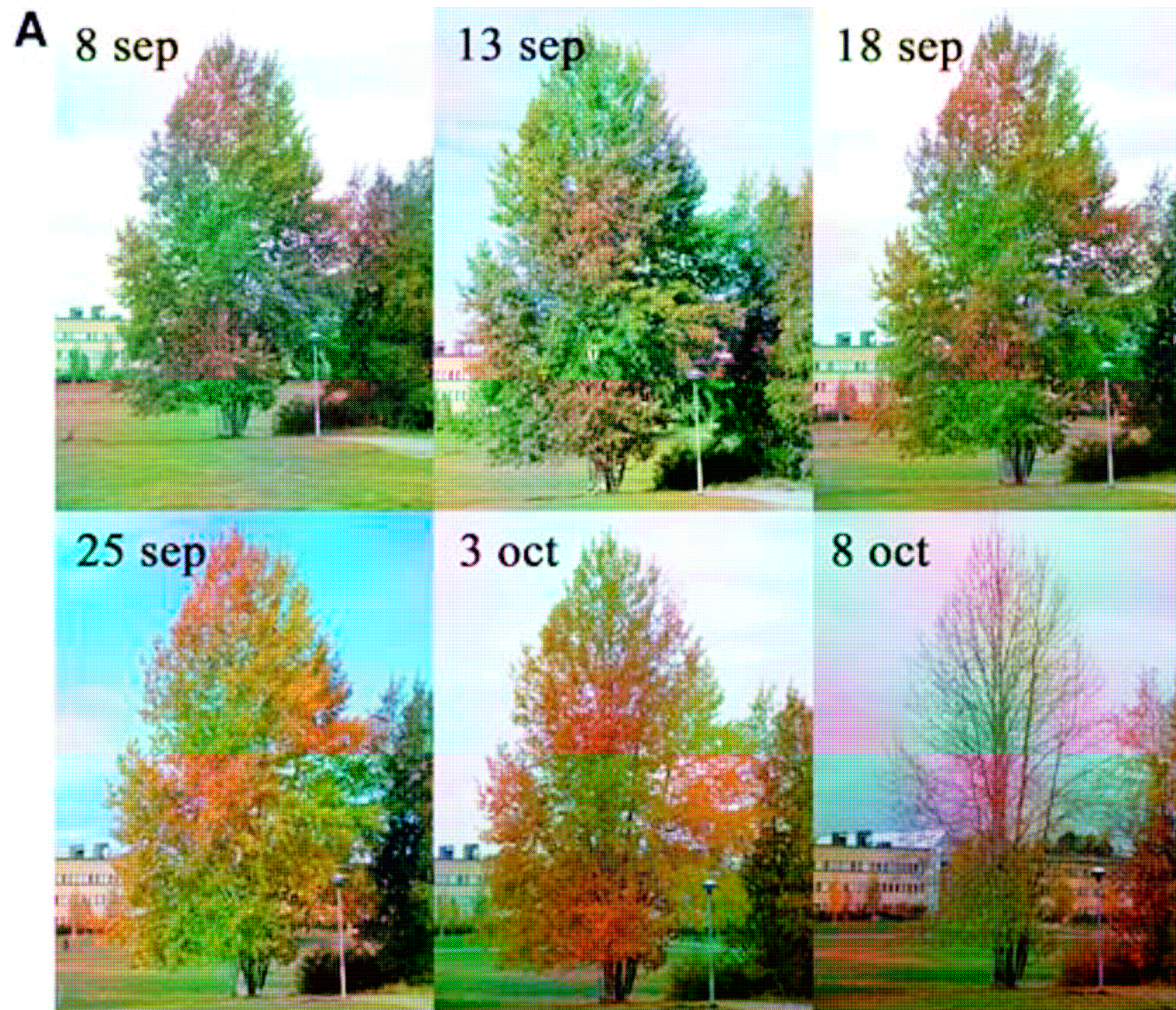


(B)



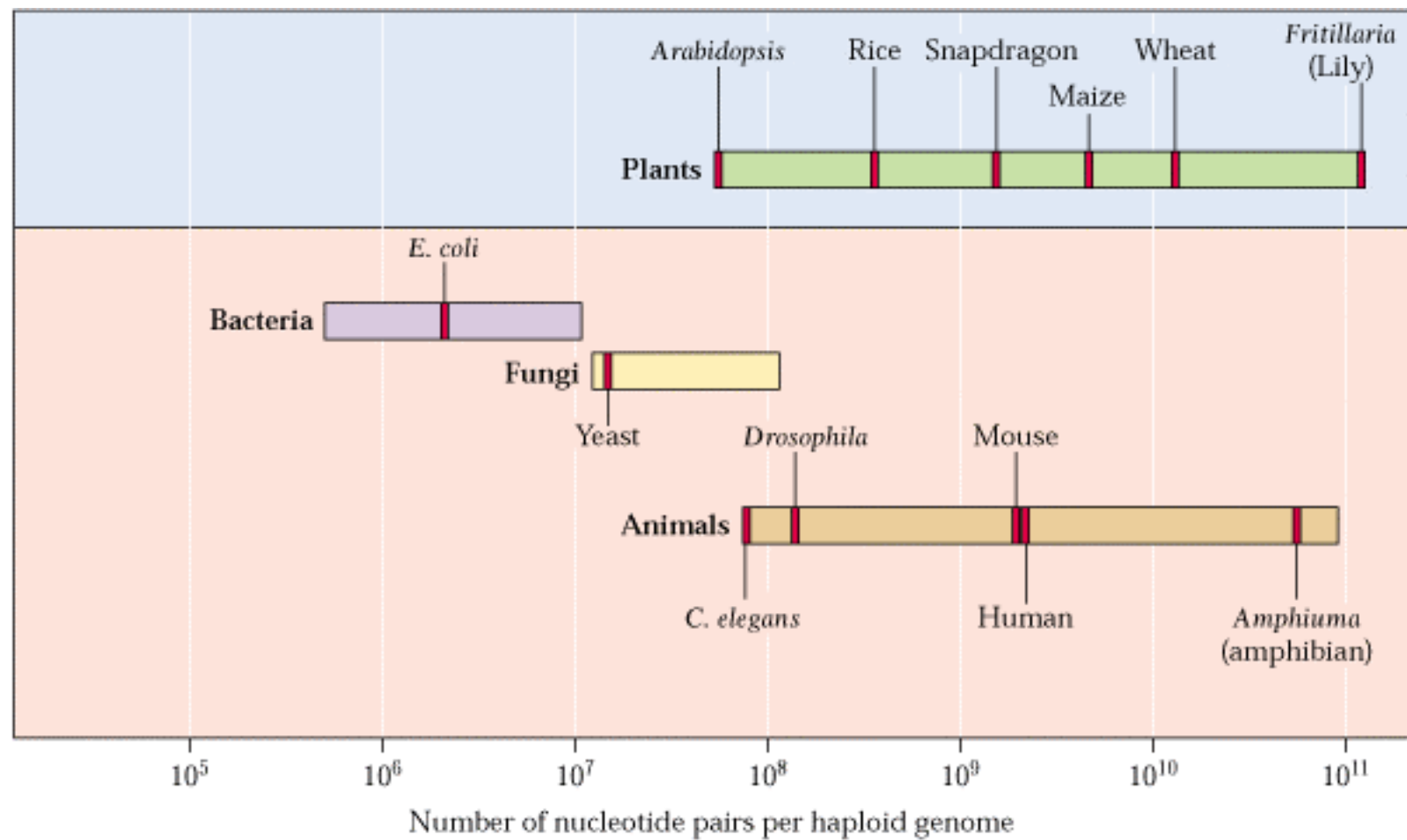
Osekvenované genomy rostlin

- ALE UŽ TAKÉ MODELOVÁ OBILNINA **RÝŽE** A
- MODELOVÝ STROM **TOPOL**
- (*Populus trichocarpa*)

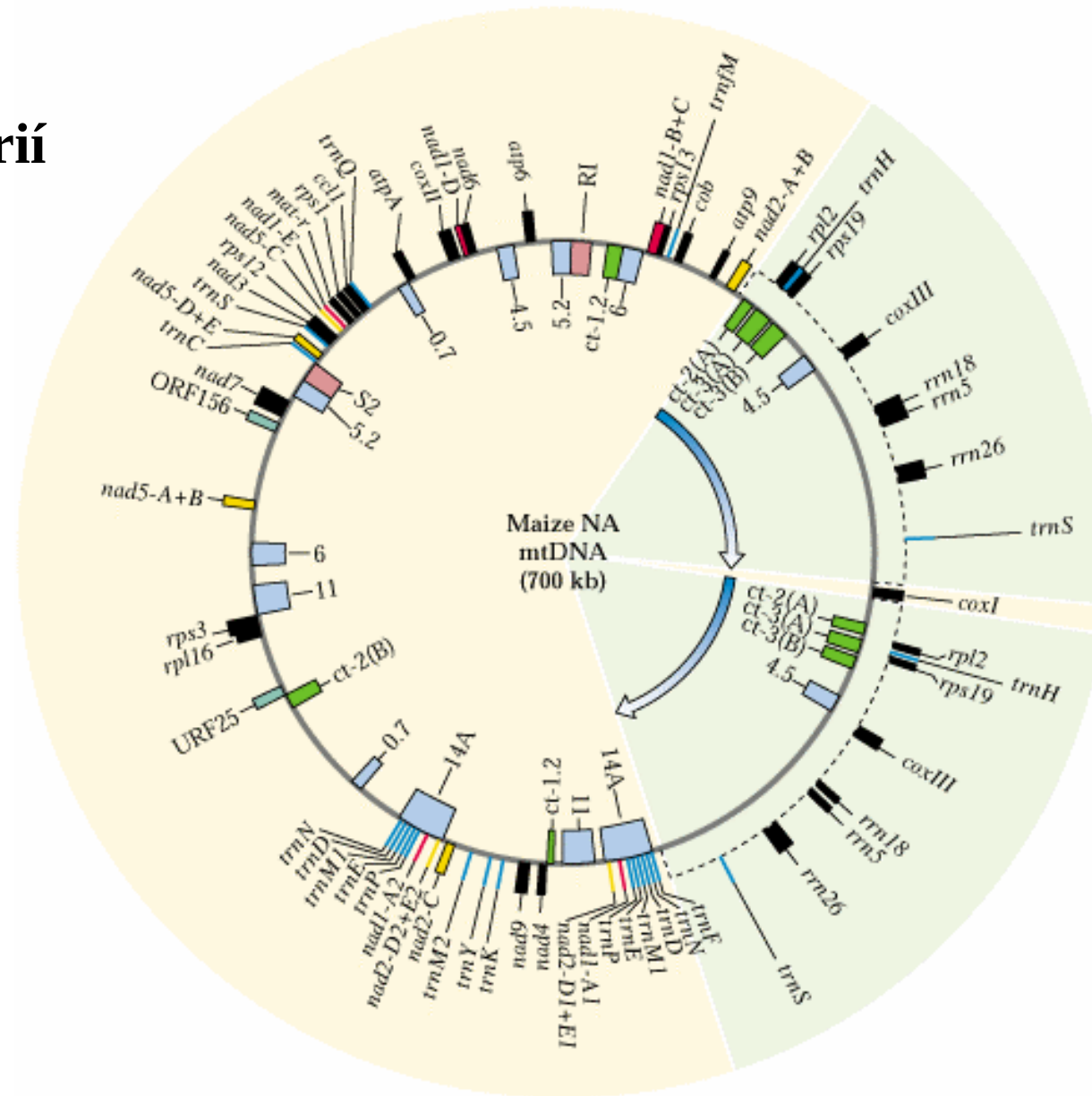


Campus Umea – **modelový jedinec**

- GENOMY ROSTLINNÉ BUŇKY
- PROBLÉM KOORDINACE TŘÍ GENOMŮ V JEDNOM ORGANISMU
- „Stěhování“ genů z organel do jádra.

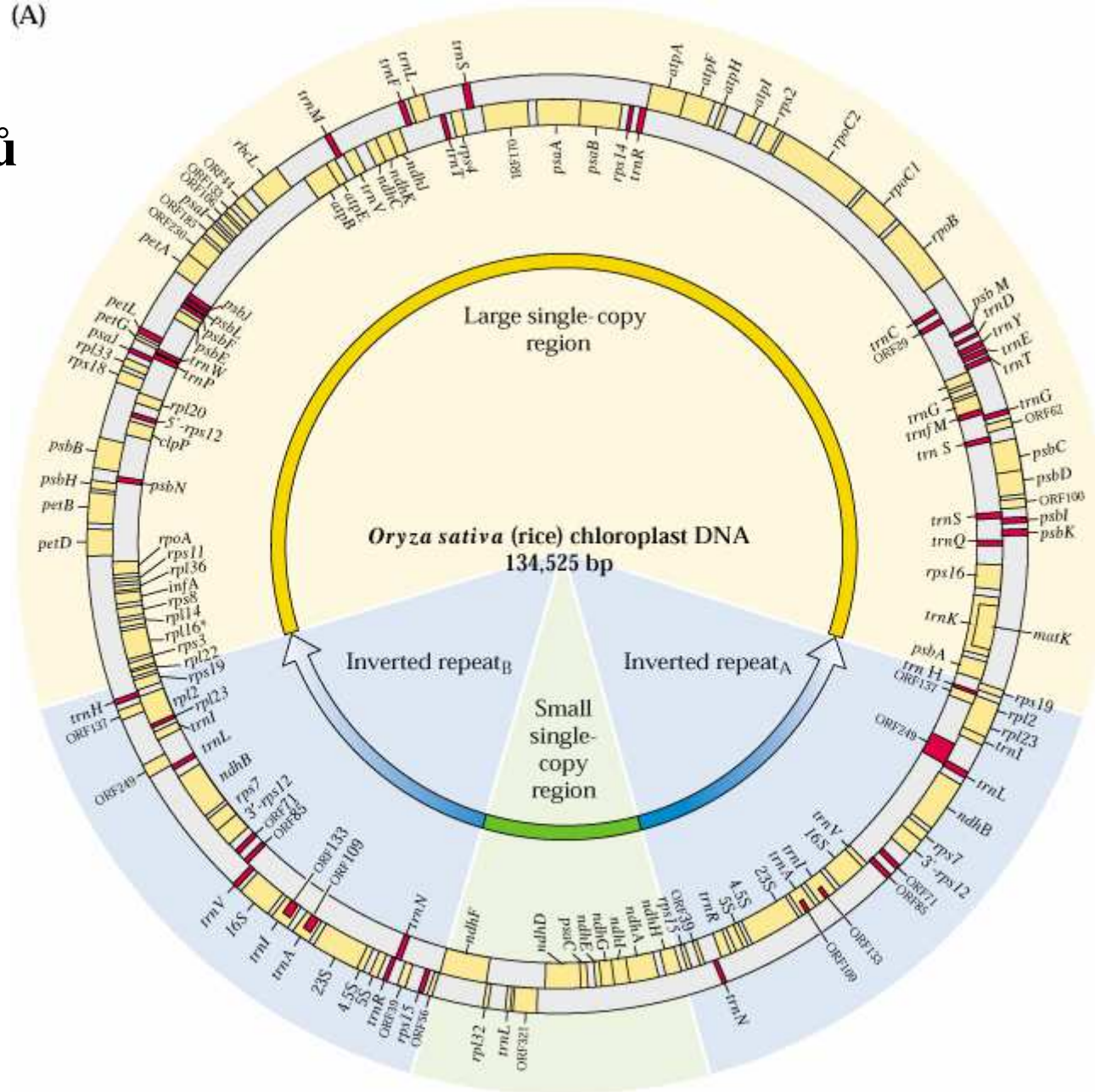


Genom Mitochondrií



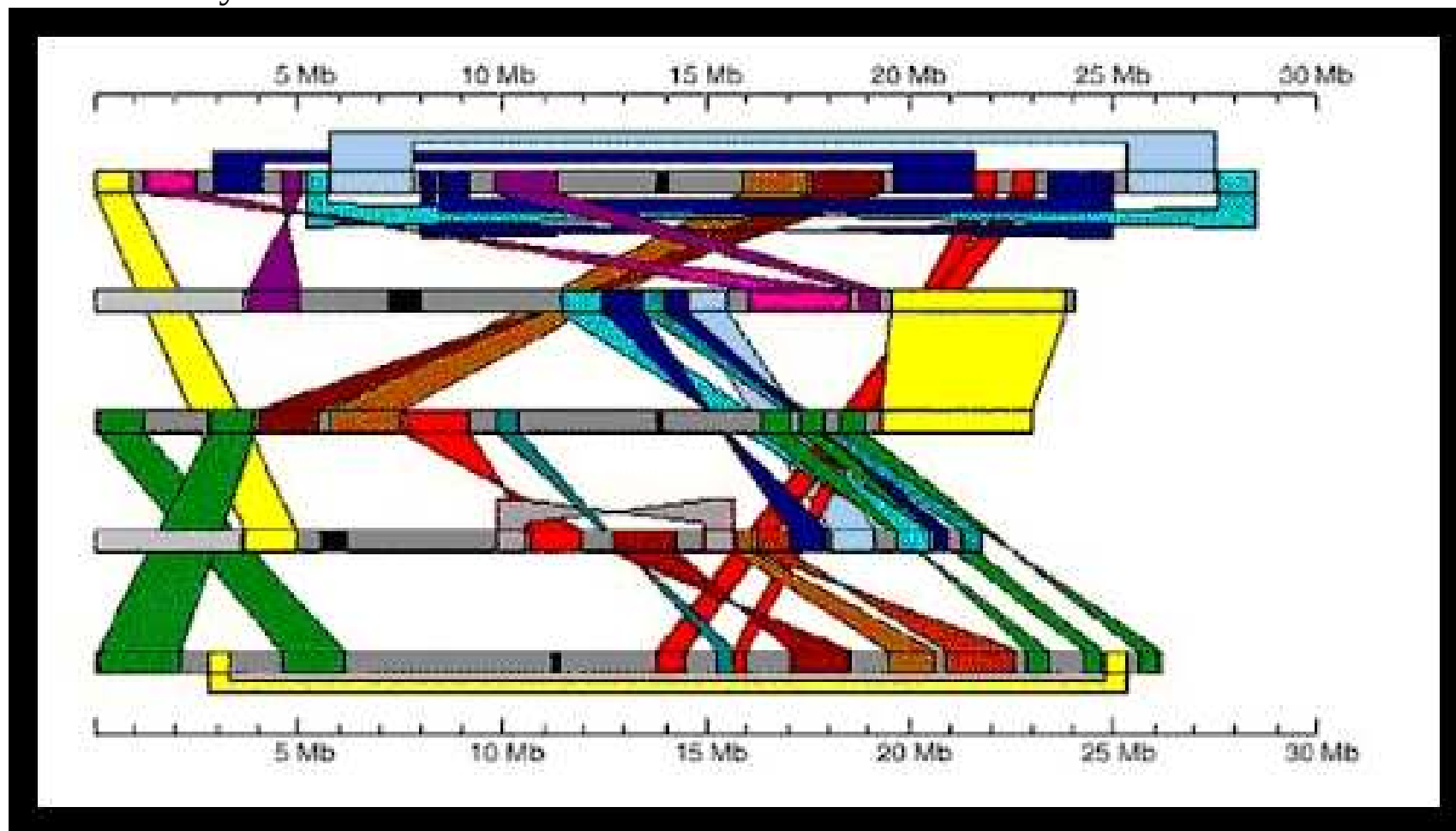
Vetšina mt transkriptů je editována.

Genom Plastidů



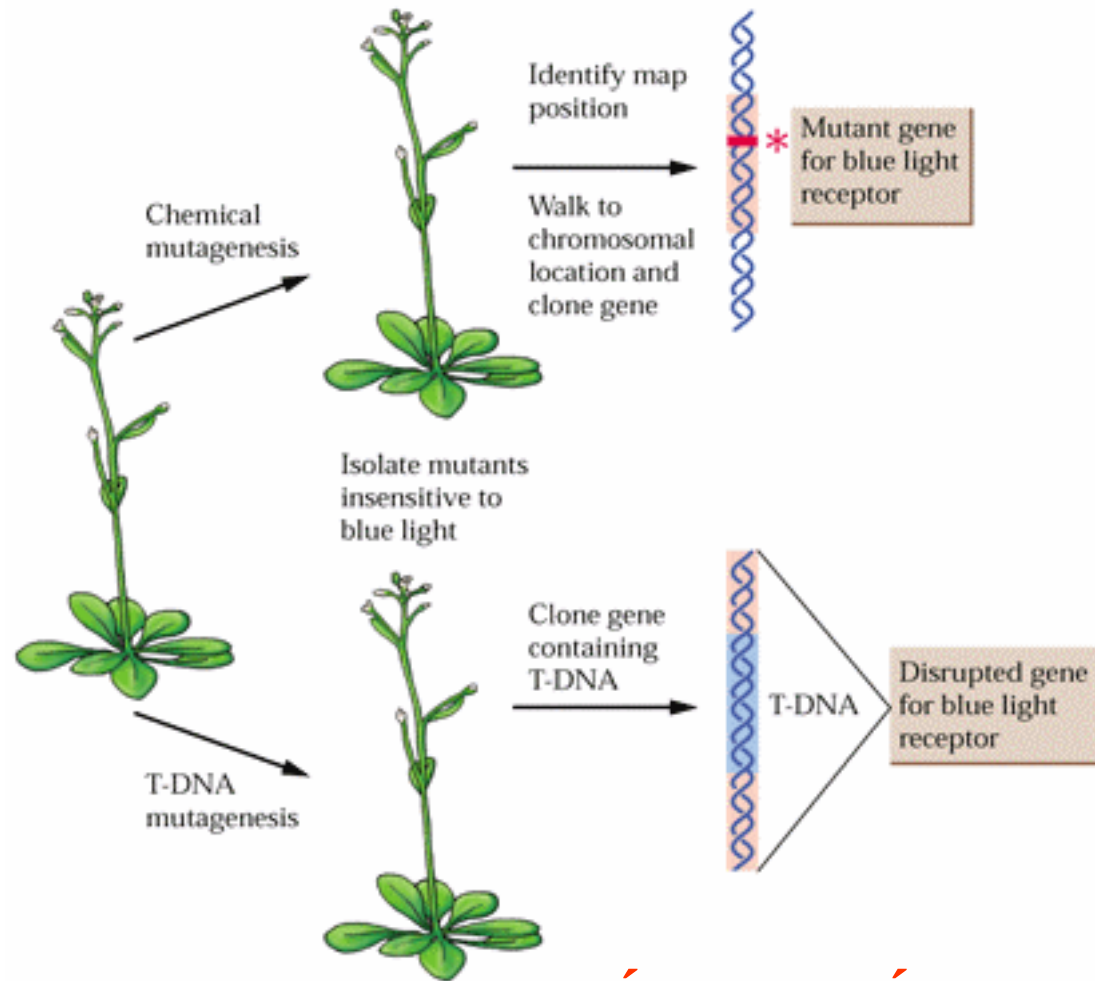
Hybridizace a polyploidizace/genomové duplikace jsou běžnou součástí speciace rostlin.

Jako pozůstatek dávné polyploidizační události se i v genomu *Arabidopsis* vyskytují některé úseky chromozomů dvakrát

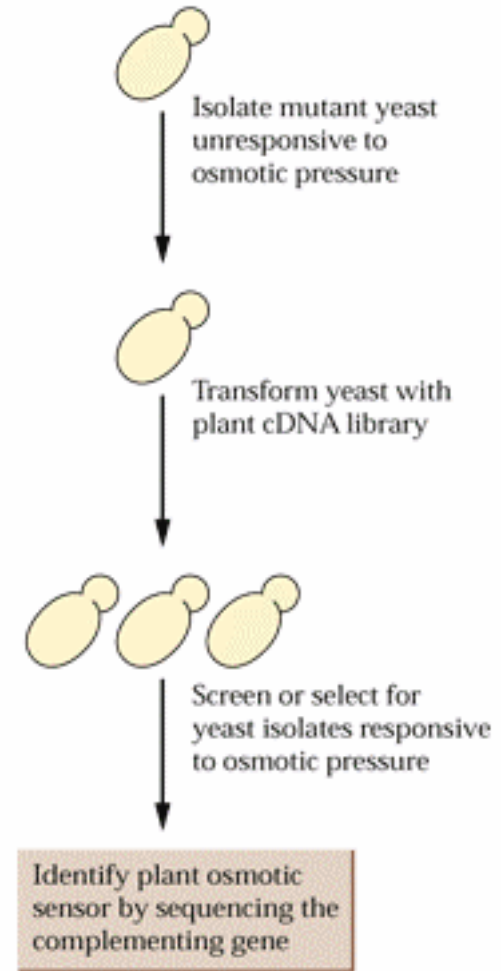


Metody studia rostlinných genů řídících ontogenezi.

(A) Chemical mutagenesis vs. T-DNA mutagenesis



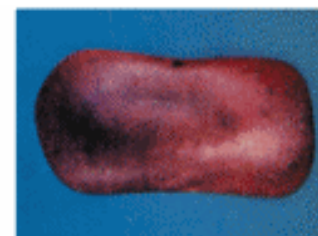
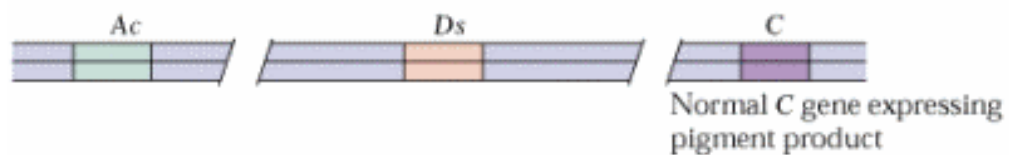
(B) Complementation of mutant yeast



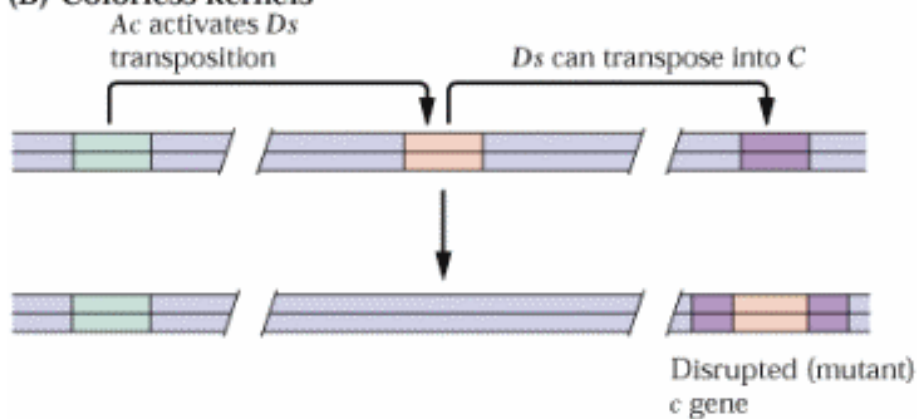
VÝVOJOVÁ GENETIKA

Mutageneze transpozonom může být reversibilní

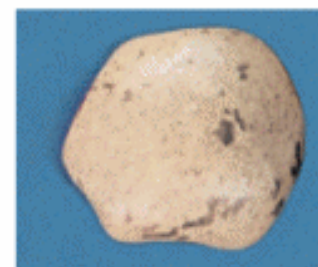
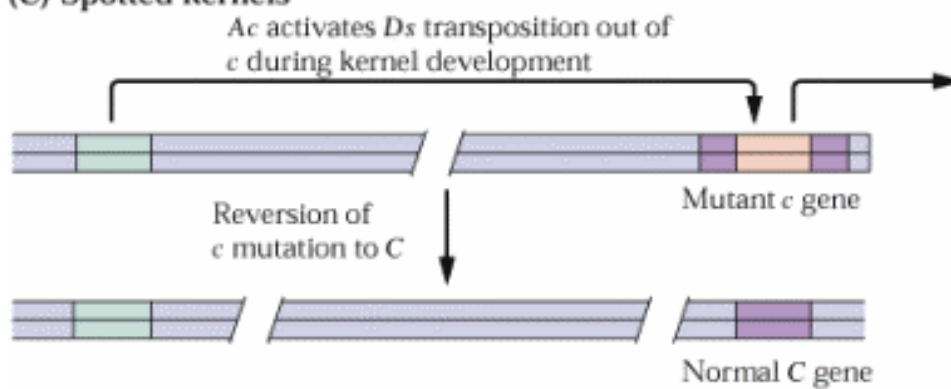
(A) Purple kernels



(B) Colorless kernels



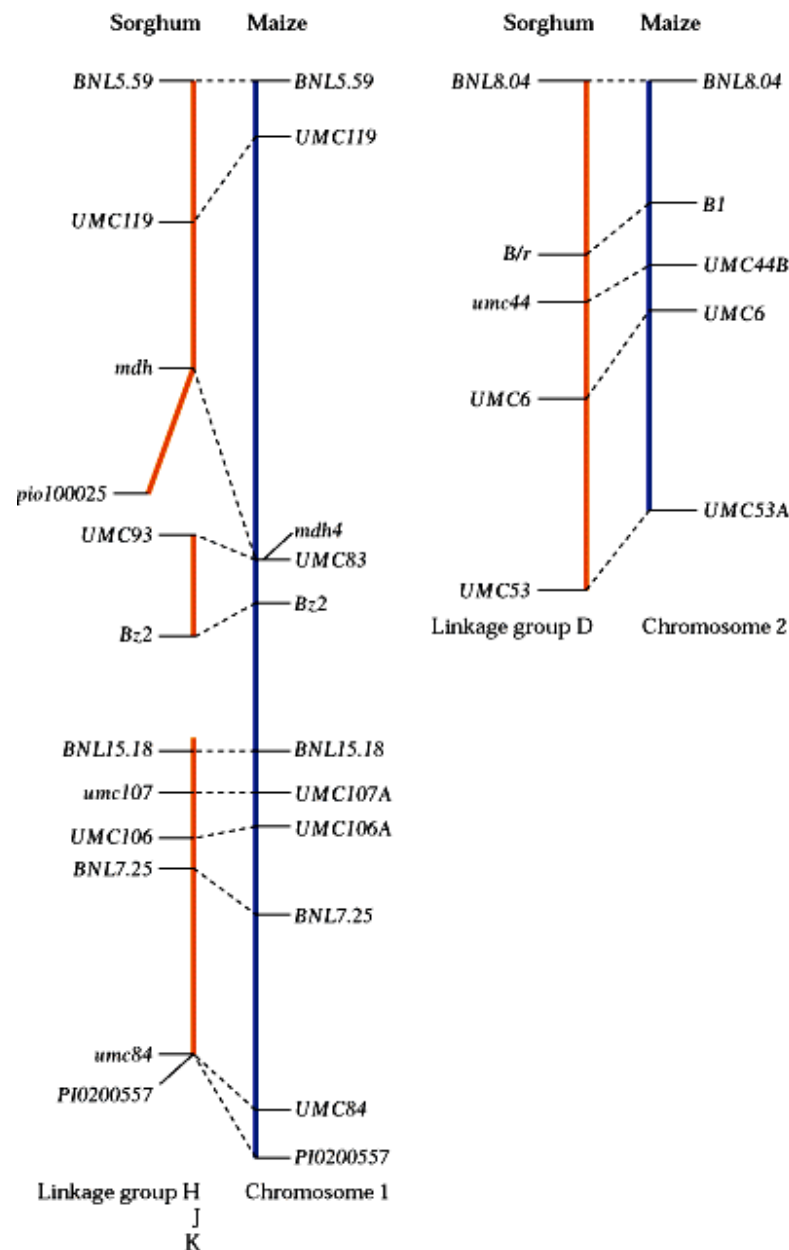
(C) Spotted kernels



SYNTENIE či KOLINEARITA GENOMŮ

Příbuzné druhy rostlin mají obdobnou lokální architekturu genomu - pořadí genů na homologních úsecích chromosomů.

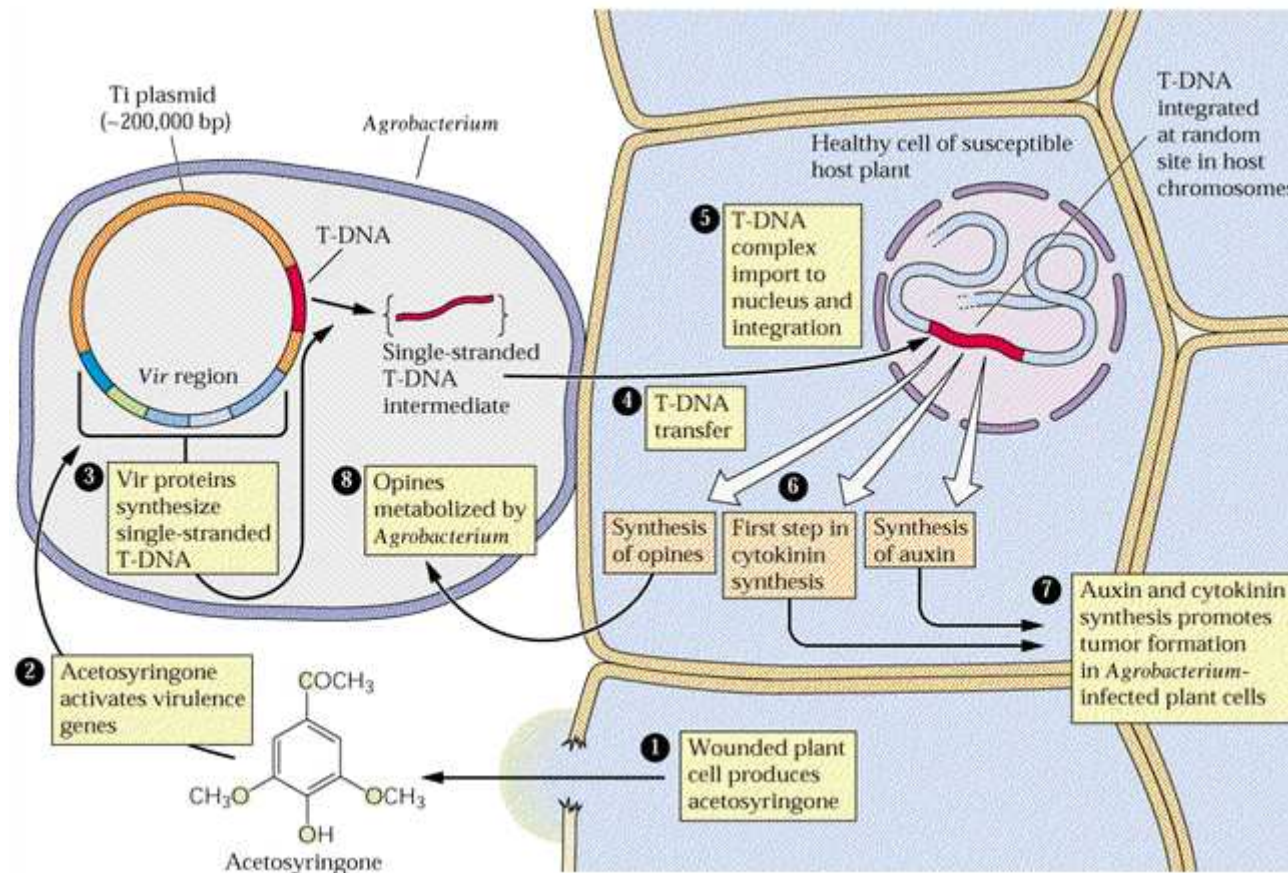
Sorghum=čirok (už také osekvenovaný genom)



T-DNA JAKO NÁSTROJ ROSTLINNÉ EXPERIMENTÁLNÍ BIOLOGIE

Mechanismus přenosu T-DNA

„Agrotransformace“ jako důležitý nástroj studia i modifikací rostlin

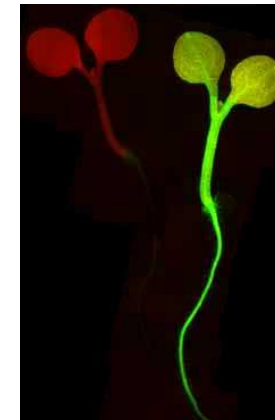


Reporter Gene Systems – GFP a GUS

Use of a reporter gene – gene whose expression is easy to observe. Used to “report” gene expression - regulation and localization

- Green fluorescent protein (GFP)

Protein identified from luminescent jellyfish *Aequorea victoria*. GFP has now been produced in a number of heterologous cell types and there appears to be little requirement for specific additional factors for post-translational modification of the protein, which may be autocatalytic or require ubiquitous factors. Many structural variants now available commercially (e.g. red fluorescent protein)



A. thaliana C24 wild type (left)
35S-mgfp4-ER transformed (right)

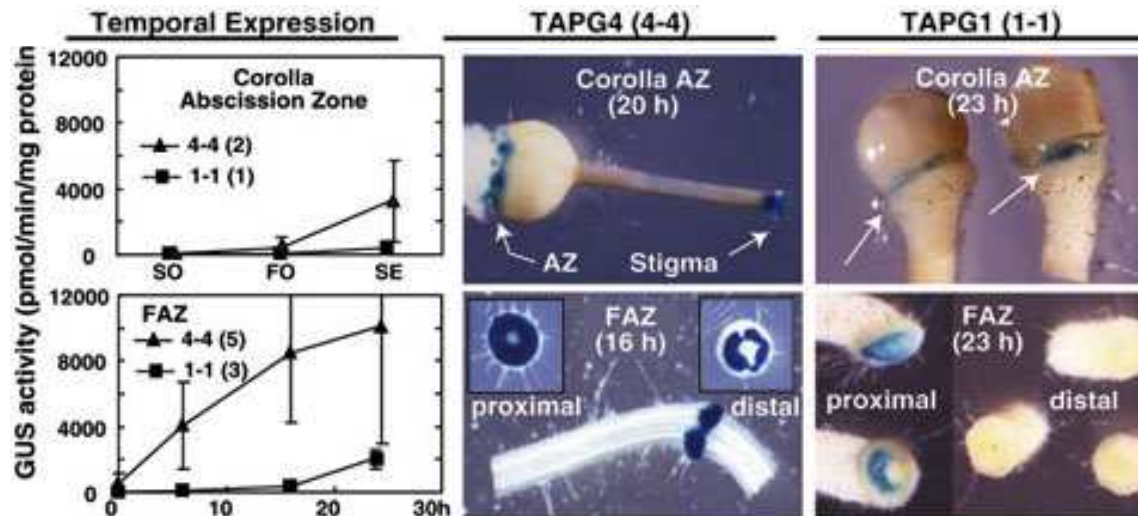
Aequorea victoria

<http://www.plantsci.cam.ac.uk/Haseloff/GFP/GFPbackgrnd.html>
http://pantheon.cis.yale.edu/~wfm5/gfp_gateway.html

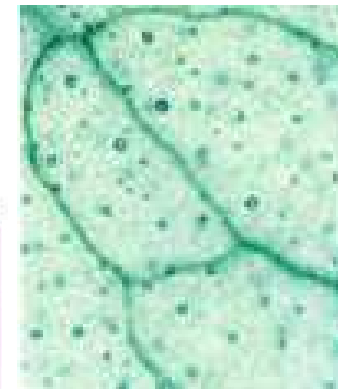
- GUS (*uidA*) gene

X-Glc $\xrightarrow{\beta\text{-glucuronidase}}$ Blue precipitate

5-bromo-4-chloro-3-inolyl
- β -D-glucuronic acid



ABA-inducible expression



Guard cells

Roots

<http://home.ust.hk/~rocklab/dc3gus/>

http://bldg6.arsusda.gov/mtucker/Public/images/F2_TAPG_GUS.html

Koncept rostlinného organismu

1. **Neukončená organogeneze/embryogeneze**
2. **Modulární stavba - FYTOMERA**
3. **Neoddělená zárodečná linie**
4. **Totipotence rostlinných buněk**
5. **Střídání n a $2n$ generací – rodozměna**
6. **Velká vývojová plasticita – stresová odolnost.**

1. Neukončená organogeneze/embryogeneze

2. Modulární stavba - FYTOMERA

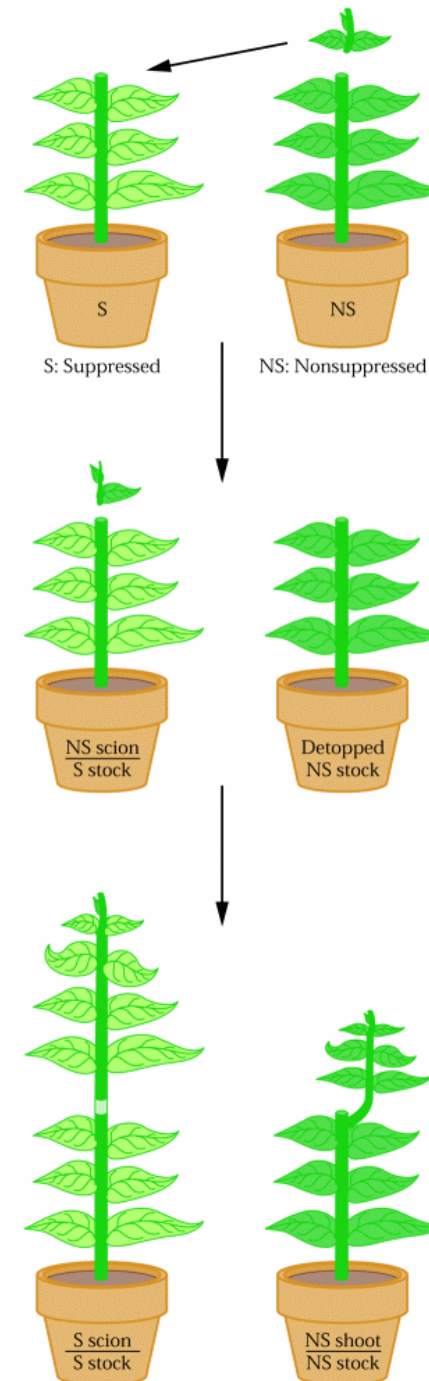
Modulární stavba rostlinného organismu

Pravidelné opakování základní konstrukční jednotky - **fytomery** - mj. umožňuje roubovat fytoomeru jedné rostliny na druhou.

Fytomera se skládá z **nodu s listem** (příp. úžlabními pupeny) a **internodia**.

Apikální dominance

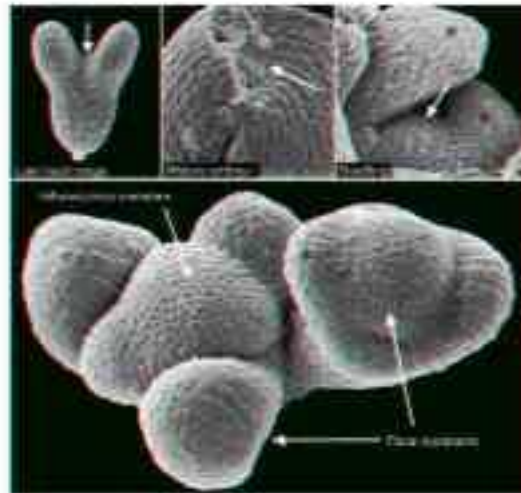
Souvisí s produkcí **IAA = auxinu** ve vzrostném vrcholu a jeho bazipetálním transportem



Zdrojem fytomer je meristém -

Jak porozumět vzniku jejich pravidelného uspořádání
=

FYLOTAXE ?



V řízení fylotaxe hraje důležitou **roli IAA...**

Modely diferenciačních procesů

ALLAN
TURING

Pracoval na luštění šifer
nacistických armád – ENIGMA.



Alan Mathison Turing on election to Fellowship of the Royal Society, 1951

Reakčně-difusní model vzniku pravidelného uspořádání

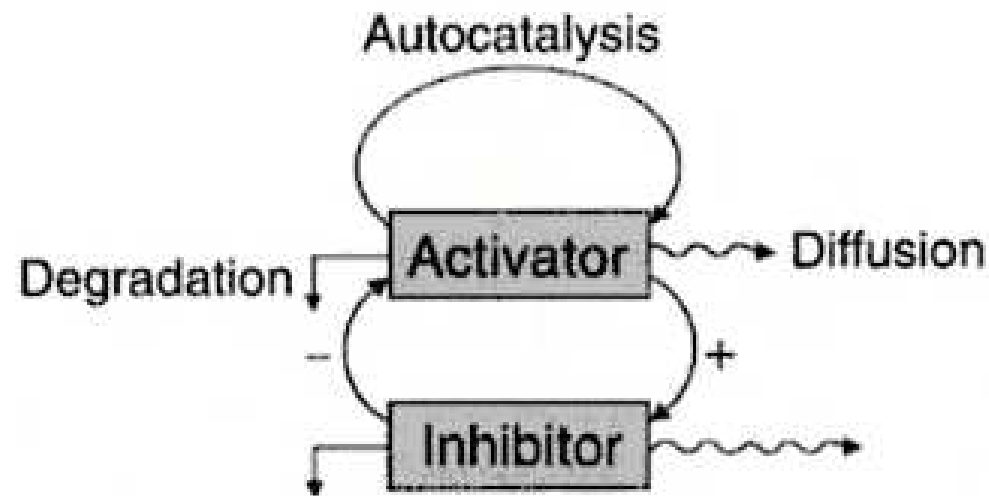


Fig. 4.2 How an activator–inhibitor scheme works. The activator generates more of itself by autocatalysis, and also activates the inhibitor. The inhibitor disrupts the autocatalytic formation of the activator. Meanwhile, the two substances diffuse through the system at different rates, with the inhibitor migrating faster.

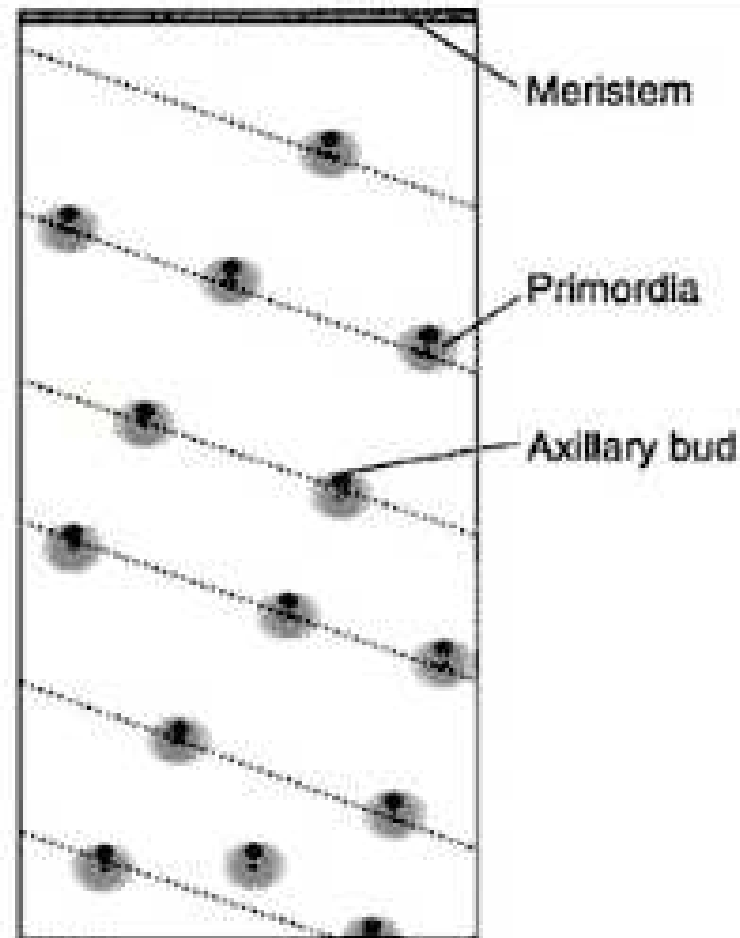
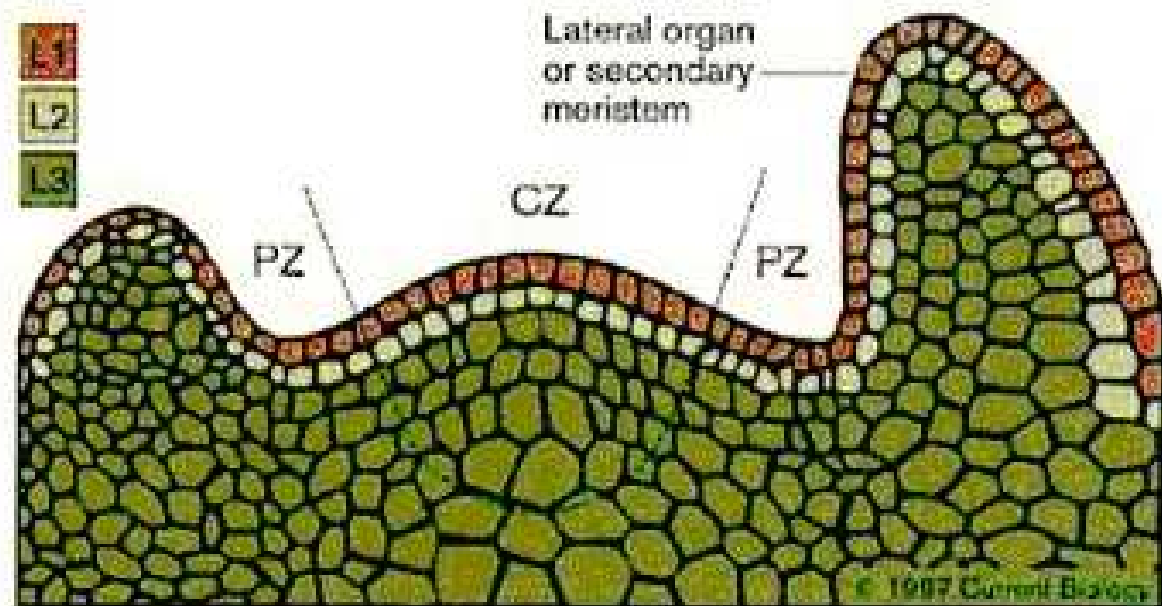


Fig. 4.43 Spiral phyllotaxis can be generated in a reaction–diffusion model of patterning on a cylindrical plant stem, here shown rolled out into a flat sheet. The spiral sequence of primordia is indicated by dashed lines. New primordia develop below the meristem at the top of the cylinder. (After: Koch and Meinhardt 1994.)

Tunika a korpus

**Neoddělená
zárodečná linie**

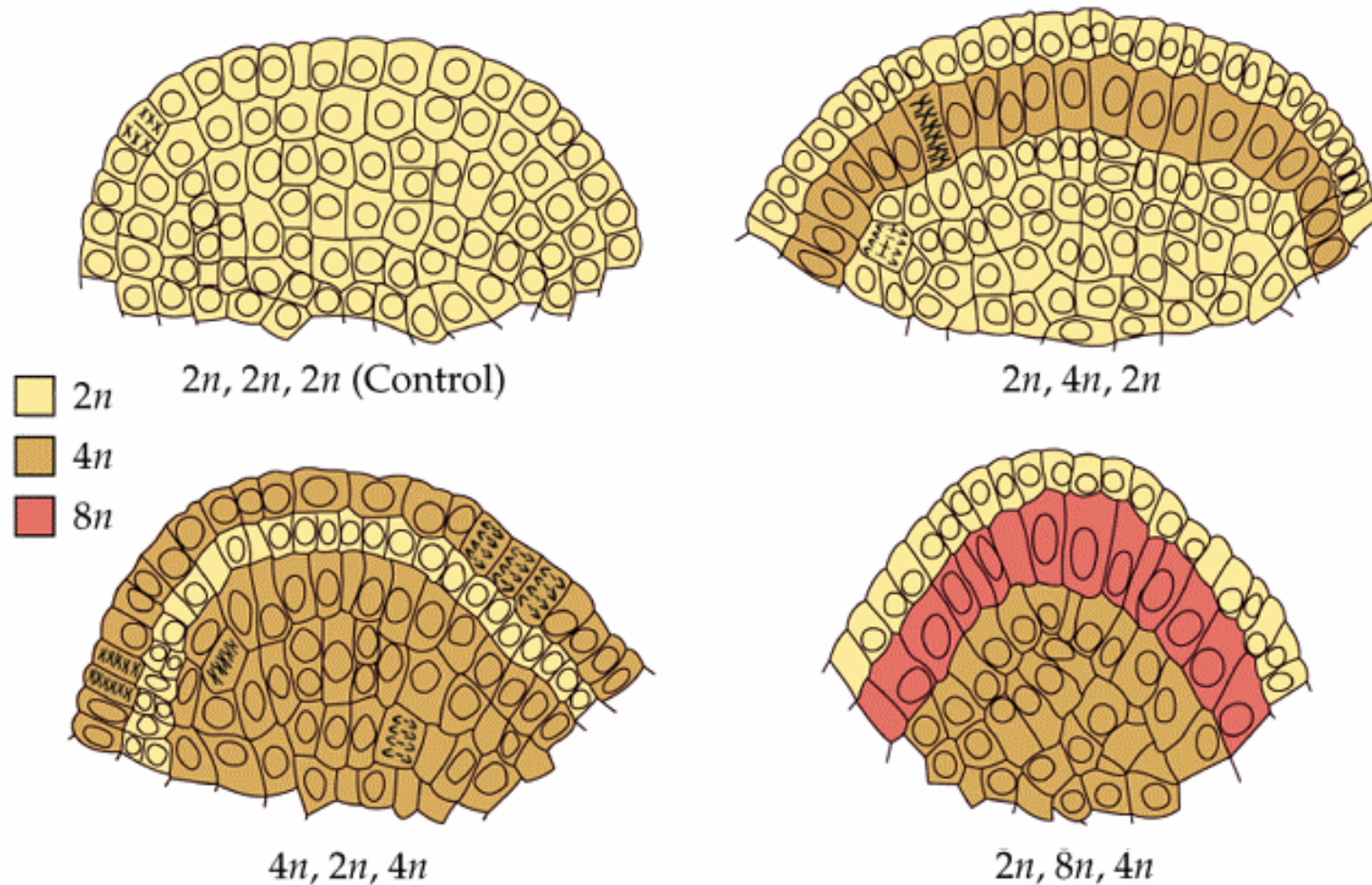
V tunice převládají **antiklinální** = kolmá k povrchu
buněčná dělení (Trávy mají jen jednovrstevnou
tuniku) ;v korpusu také **periklinální**.



Structure of a shoot apical meristem. Cell division in the L1 and L2 layers is anticlinal – perpendicular to the surface – so that these layers seldom contribute progeny to other layers and thus remain clonally distinct lineages. The region proposed to correspond to a central zone of stem cells is indicated (CZ), as is the peripheral zone (PZ) where lateral organs or meristems initiate.

Vliv ploidie na velikost buněk u **periklinálních** meristémových **chimér**

Buněčné vrstvy mají schopnost kompenzovat změny ve velikosti buněk v sousedních vrstvách = důkaz komunikace a celistvosti



Velká vývojová plasticita

I když se buňky dělí „neorganizovaně“...

ROSTLINA VLÁDNE BUŇKÁM

nejen buňky rostlině

**Klíčovou koordinačně-regulační funkci v morfogenezi
hraje epidermis.**