Cell Biology and Developmental Genetics

Lectures by

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Mitochondria, ageing, and sex – energy versus fidelity

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Lecture 1

Endosymbiosis and the origin of bioenergetic organelles.
Some history

What are bioenergetic organelles?

What are bioenergetic organelles?

- Chloroplasts

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  - Membrane-bound compartments in eukaryotic cells

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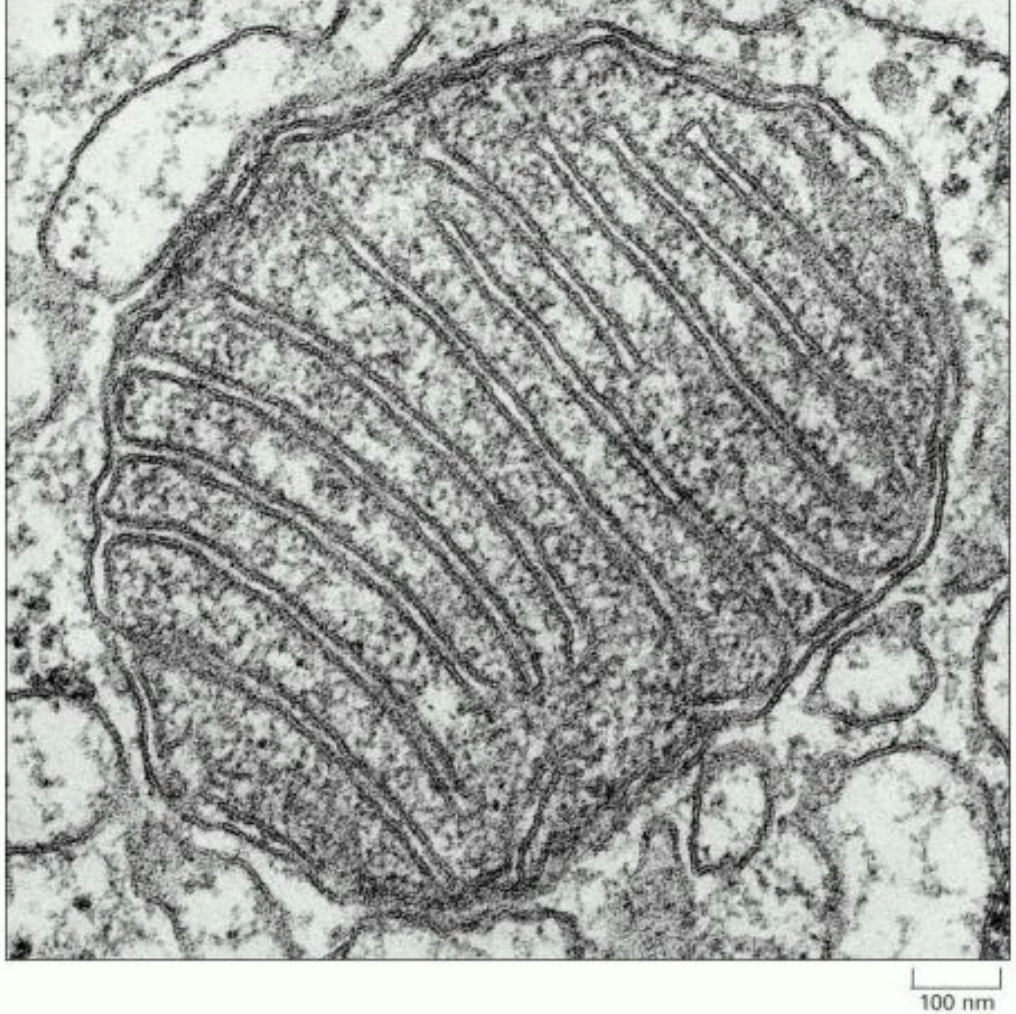
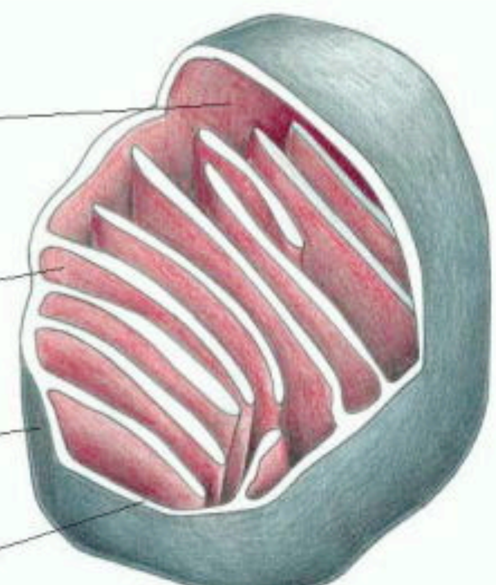


Matrix. This large internal space contains a highly concentrated mixture of hundreds of enzymes, including those required for the oxidation of pyruvate and fatty acids and for the citric acid cycle. The matrix also contains several identical copies of the mitochondrial DNA genome, special mitochondrial ribosomes, tRNAs, and various enzymes required for expression of the mitochondrial genes.

Inner membrane. The inner membrane *(red)* is folded into numerous cristae, greatly increasing its total surface area. It contains proteins with three types of functions: (1) those that carry out the oxidation reactions of the electron-transport chain, (2) the ATP synthase that makes ATP in the matrix, and (3) transport proteins that allow the passage of metabolites into and out of the matrix. An electrochemical gradient of H^+, which drives the ATP synthase, is established across this membrane, so the membrane must be impermeable to ions and most small charged molecules.

Outer membrane. Because it contains a large channel-forming protein (called porin), the outer membrane is permeable to all molecules of 5000 daltons or less. Other proteins in this membrane include enzymes involved in mitochondrial lipid synthesis and enzymes that convert lipid substrates into forms that are subsequently metabolized in the matrix.

Intermembrane space. This space *(white)* contains several enzymes that use the ATP passing out of the matrix to phosphorylate other nucleotides.



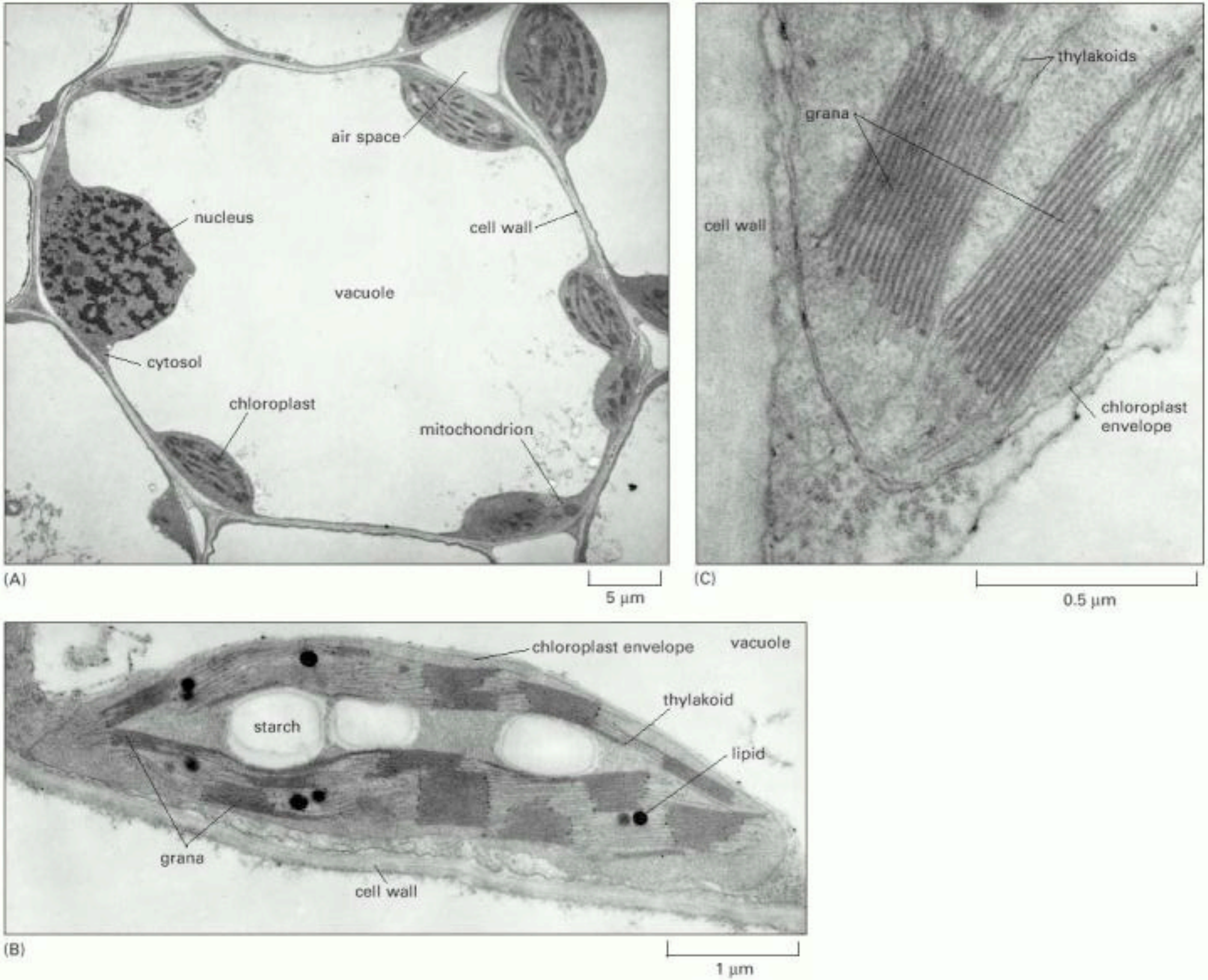


Figure 14-34. Electron micrographs of chloroplasts. (A) In a wheat leaf cell, a thin rim of cytoplasm—containing chloroplasts, the nucleus, and mitochondria—surrounds a large vacuole. (B) A thin section of a single chloroplast, showing the chloroplast envelope, starch granules, and lipid (fat) droplets that have accumulated in the stroma as a result of the biosyntheses occurring there. (C) A high-magnification view of two grana. A granum is a stack of thylakoids. (Courtesy of K. Plaskitt.)

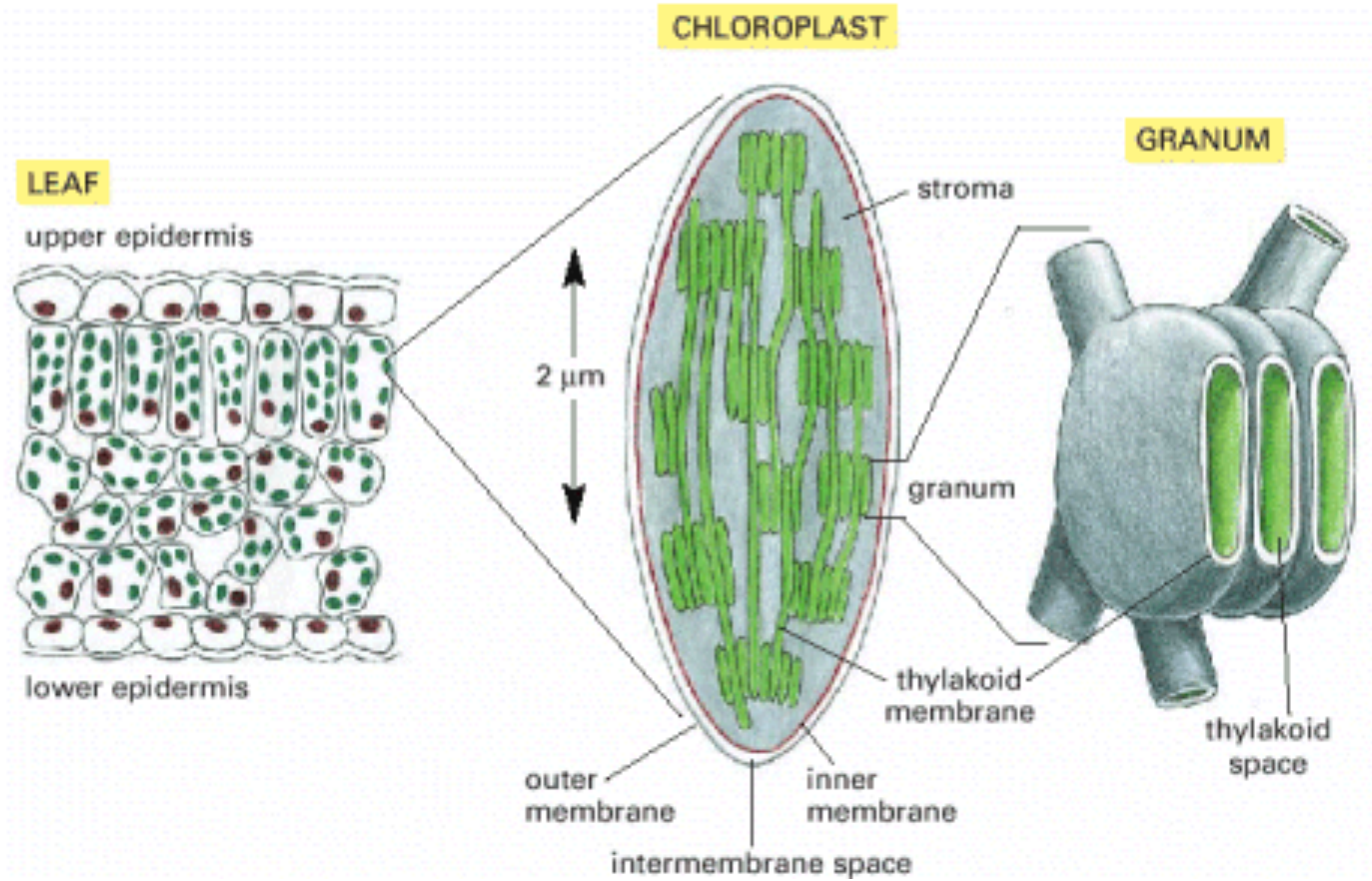


Figure 14-35. The chloroplast. This photosynthetic organelle contains three distinct membranes (the outer membrane, the inner membrane, and the thylakoid membrane) that define three separate internal compartments (the intermembrane space, the stroma, and the thylakoid space). The thylakoid membrane contains all the energy-generating systems of the chloroplast, including its chlorophyll. In electron micrographs, this membrane seems to be broken up into separate units that enclose individual flattened vesicles (see Figure 14-34), but these are probably joined into a single, highly folded membrane in each chloroplast. As indicated, the individual thylakoids are interconnected, and they tend to stack to form grana.

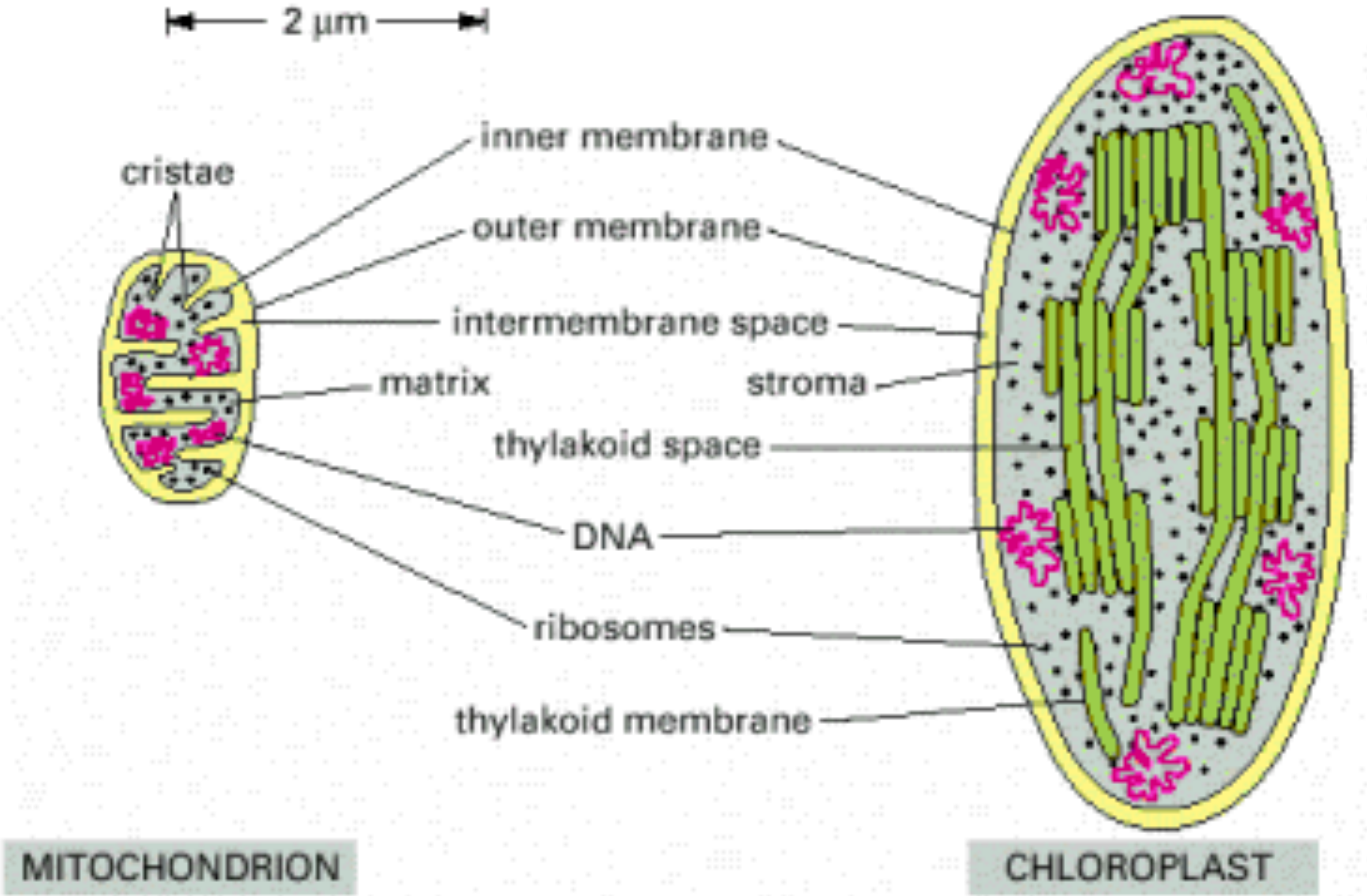
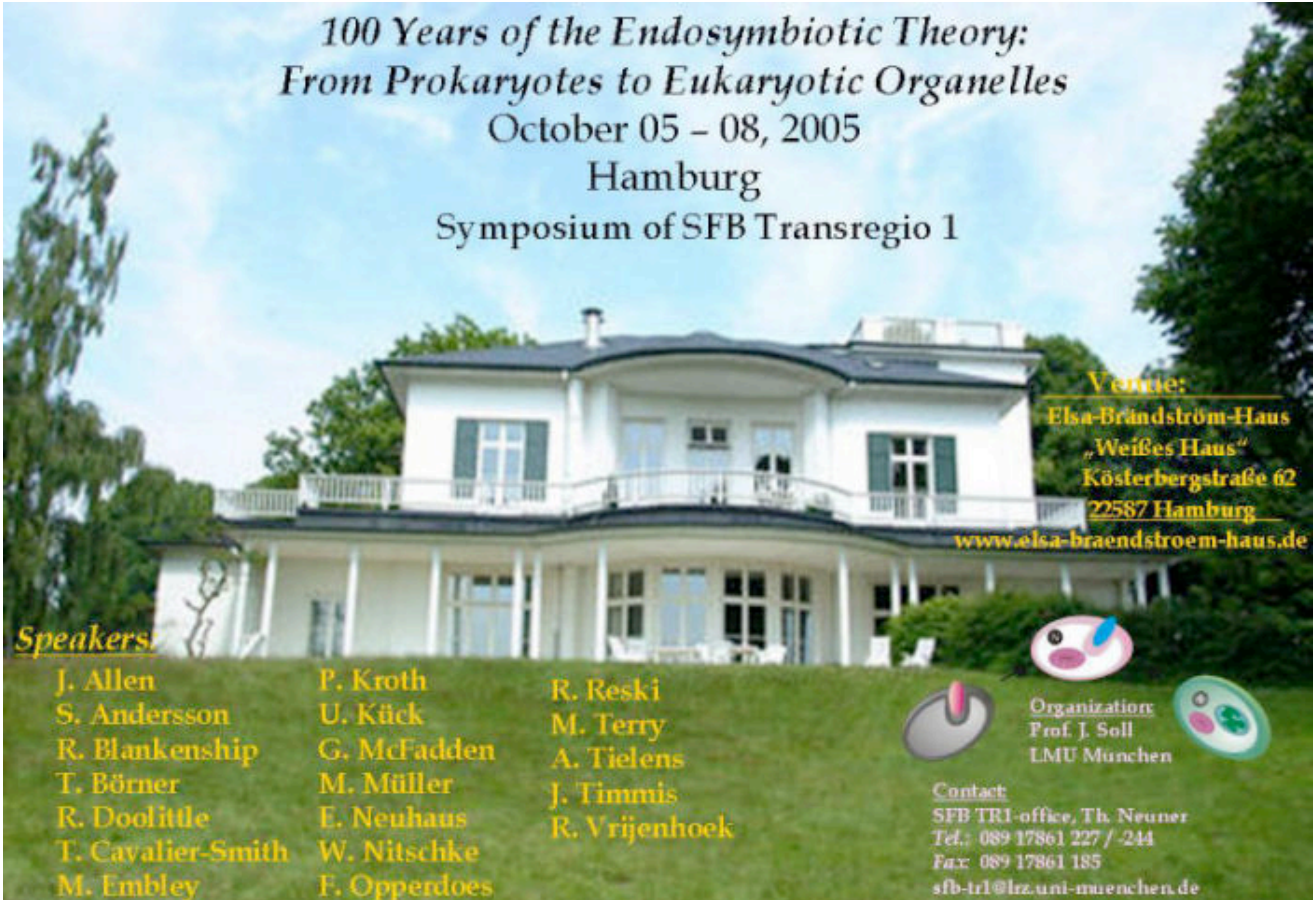


Figure 14-36. A mitochondrion and chloroplast compared. A chloroplast is generally much larger than a mitochondrion and contains, in addition to an outer and inner membrane, a thylakoid membrane enclosing a thylakoid space. Unlike the chloroplast inner membrane, the inner mitochondrial membrane is folded into cristae to increase its surface area.

What is symbiosis?

- Simon Schwendener (1867) discovered that lichens are a consortium of two organisms - a fungus and an alga
- Heinrich Anton de Bary (1878) used “symbiosis” (“same living”) to describe this association

The origin of the Endosymbiont hypothesis



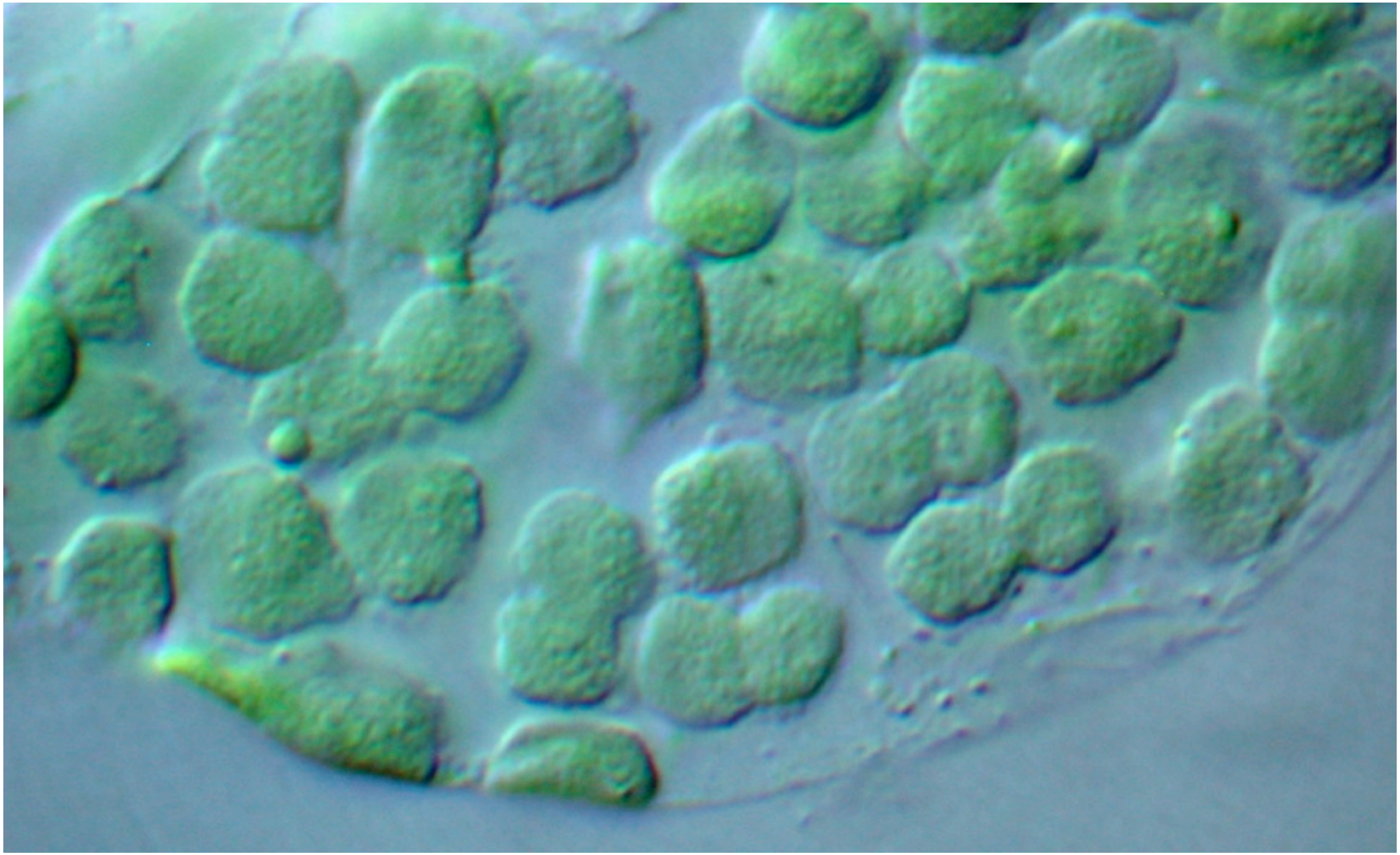
Konstantin Sergejewicz Mereschkowsky (1855-1921)

http://en.wikipedia.org/wiki/Konstantin_Mereschkowski

Constantin Mereschkowsky,'Über Natur und Ursprung der Chromatophoren im Pflanzenreiche'. *Biol. Centralbl.*, 25 (1905): 593–604.

English translation by Martin, W. And Kowallik, K. (1999) *Eur. J. Phycol.* 34: 287-295.

Background to the endosymbiont hypothesis, I:



plastids in *Arabidopsis thaliana*

- plastids multiply by division
- as observed repeatedly in plants and algae in 19th century

Background to the endosymbiont hypothesis, 2:

cyanobacteria	plastids
Small, blue-green, round or oval bodies of very simple structure	Small, green (probably blue-green originally, as with *Cyanomonas*), round or oval bodies of very simple structure
The green pigment saturates the plasm uniformly or is distributed therein in the form of small droplets	The green pigment saturates the stroma uniformly or is distributed therein in the form of small droplets

Background to the endosymbiont hypothesis, 3:

cyanobacteria	plastids
Do not possess a true nucleus, rather just certain structures (nucleic granules) that can be viewed as a predecessor of the nucleus	Do not possess a true nucleus, rather certain structures (pyrenoids) that can be viewed as a transformed, primitive nucleus
Nutrition: assimilation of CO_2 in the light	Nutrition: assimilation of CO_2 in the light
Reproduction: through division	Reproduction: through division

Plastids are organs

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- accepted view was that plastids were organs

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- autonomously derived from cytoplasm

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- accepted view was that plastids were organs
- autonomously derived from cytoplasm
- Mereschkowsky: '…this notion is, by no means, a finding supported by direct observation…'

Plastids are organs

soybean

Plastids are organs

soybean

- why was it thought plastids arose *de novo*?

Plastids are organs

soybean

- why was it thought plastids arose *de novo*?
- plant parts that are kept in the dark turn green when exposed to light

Plastids are organs

soybean

- why was it thought plastids arose *de novo*?
- plant parts that are kept in the dark turn green when exposed to light
- Schimper (1885) showed that chlorophyll arises *de novo* but not its carriers

Plastids are *not* organs

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- plastids do not arise *de novo* but from pre-existing (sometimes colourless) plastids

Plastids are *not* organs

- plastids do not arise *de novo* but from pre-existing (sometimes colourless) plastids

- Mereschkowsky: *'this hypothesis is...founded upon an error in logic. And those who wish to maintain their view...reveal that they lack a proper grasp of the nature of heredity'*

Continuity of plastids

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- plastids arise from pre-existing plastids, never *de novo*

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- so, at one stage, a plastid established itself in a plant lineage

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- therefore, plastids must be ‘foreign bodies’ or symbionts

Plastids are independent

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- nucleus is central to cell

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- if nucleus is removed, cells do not proliferate

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- grow and multiply by division
- assimilate CO_2

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- plastids function biochemically even *in vitro*

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- plastid produce lipids that are distinct from those from the rest of the cell

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- plastids have a colourless mass (pyrenoid) similar to bacteria (this is their DNA but unknown at the time) and produce protein

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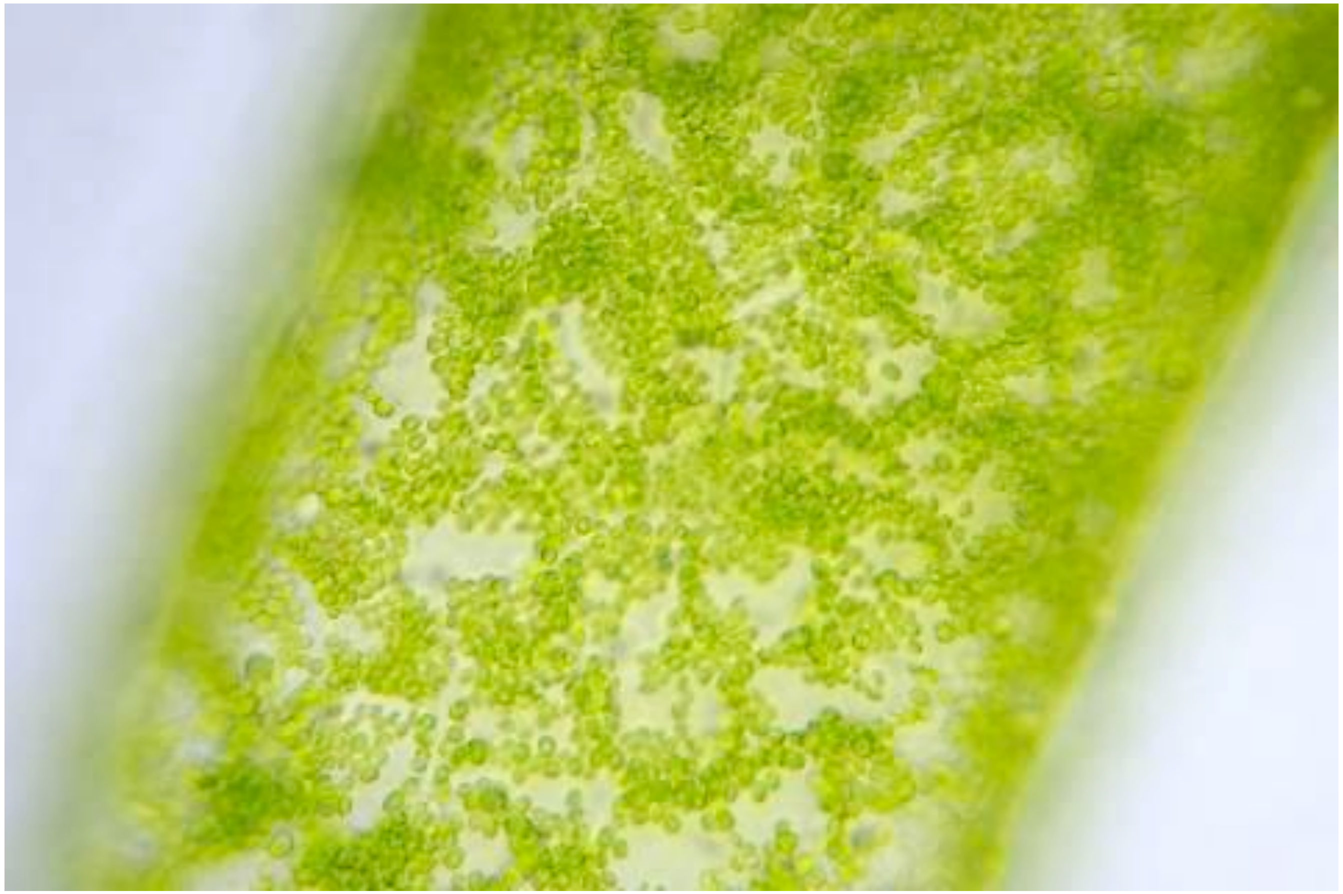
- plastids function biochemically even *in vitro*

- plastid produce lipids that are distinct from those from the rest of the cell

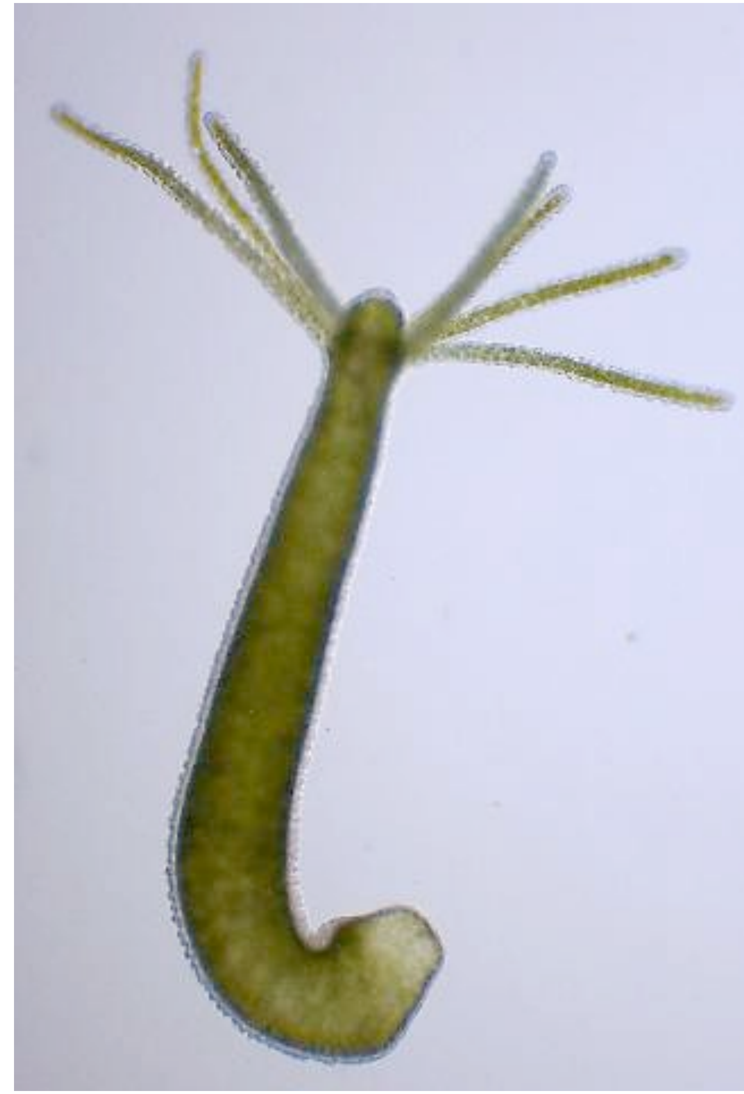
- plastids have a colourless mass (pyrenoid) similar to bacteria (this is their DNA but unknown at the time) and produce protein

- so, plastids behave like independent organisms

Analogy with hydra



polyp *Hydra viridis* contains endosymbiotic zoochlorellae (algae)



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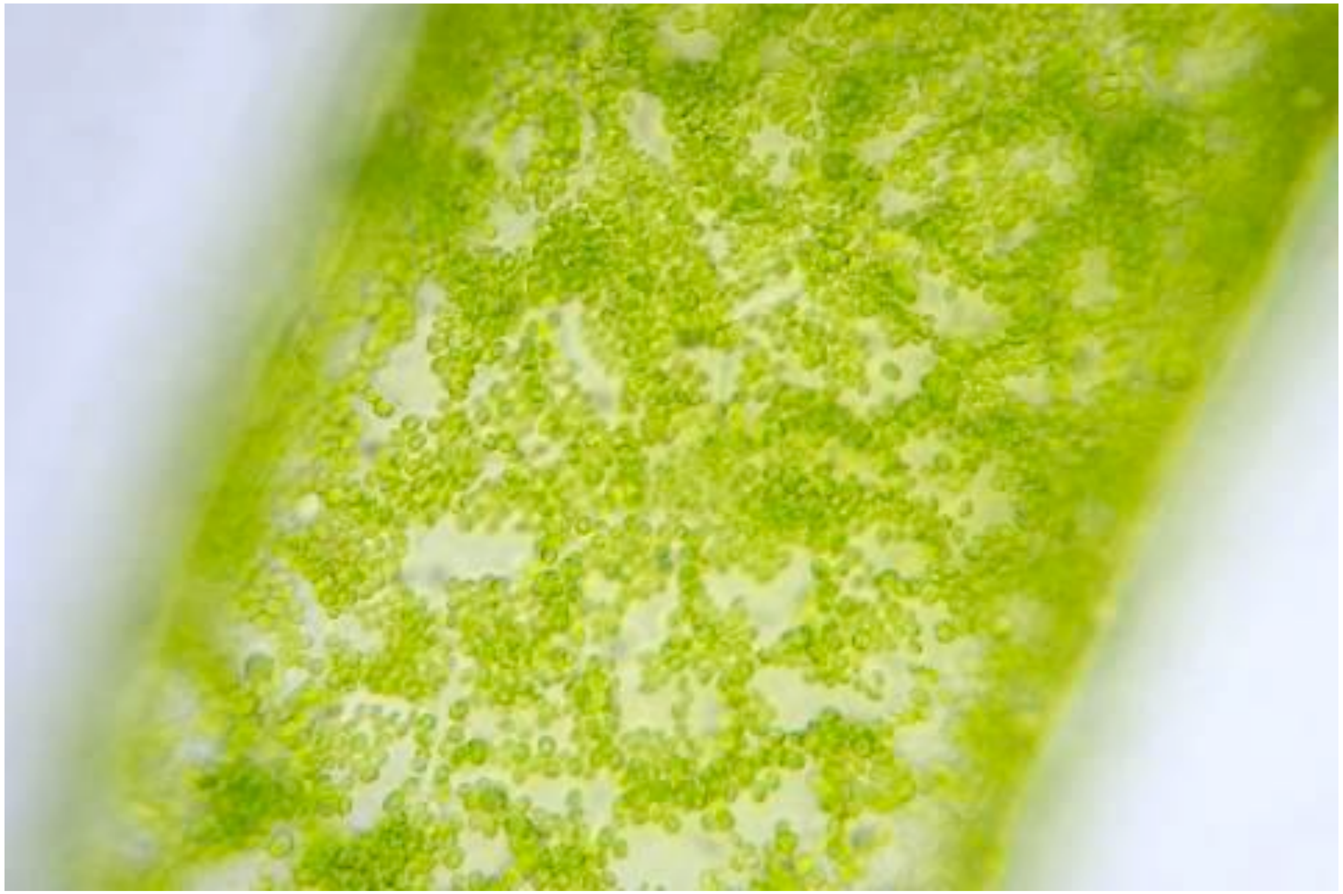

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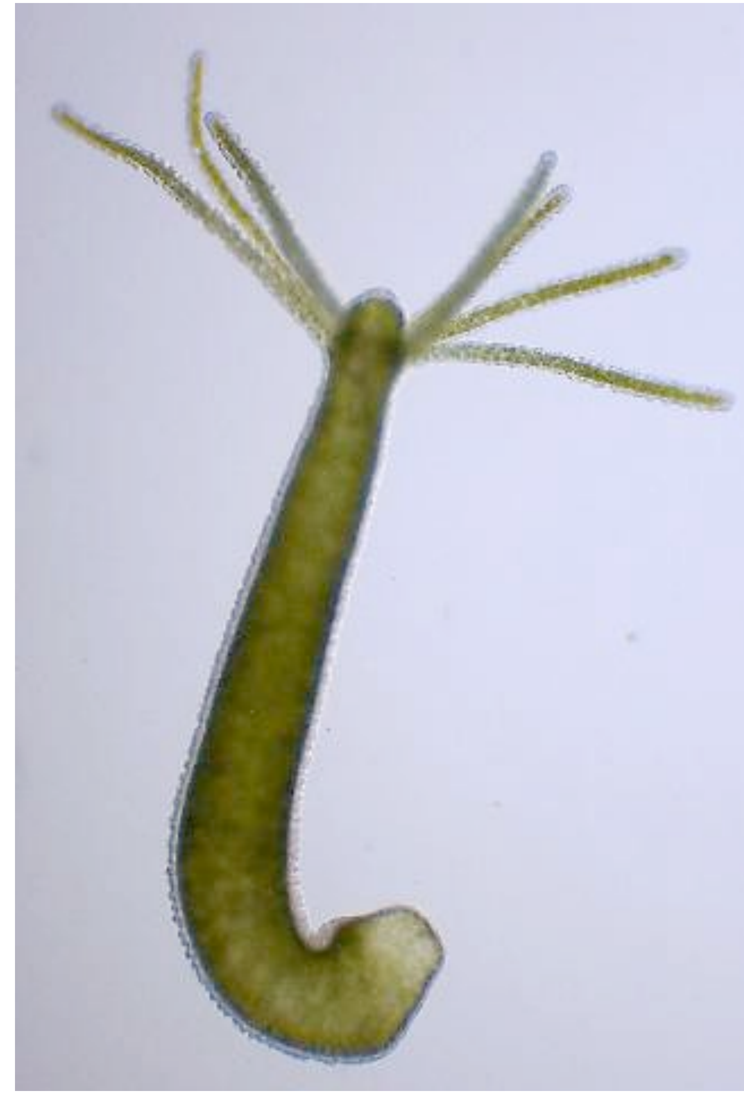
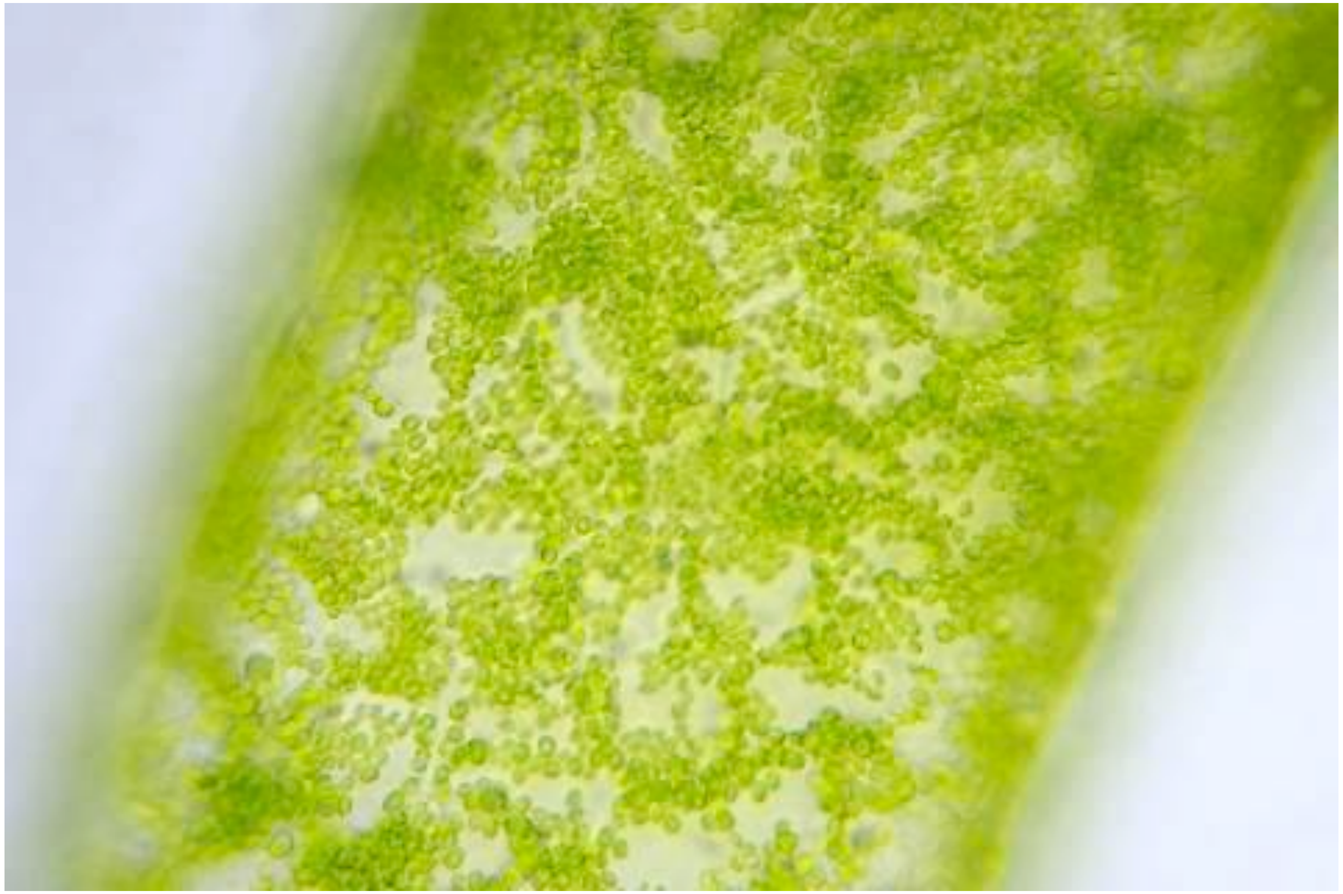
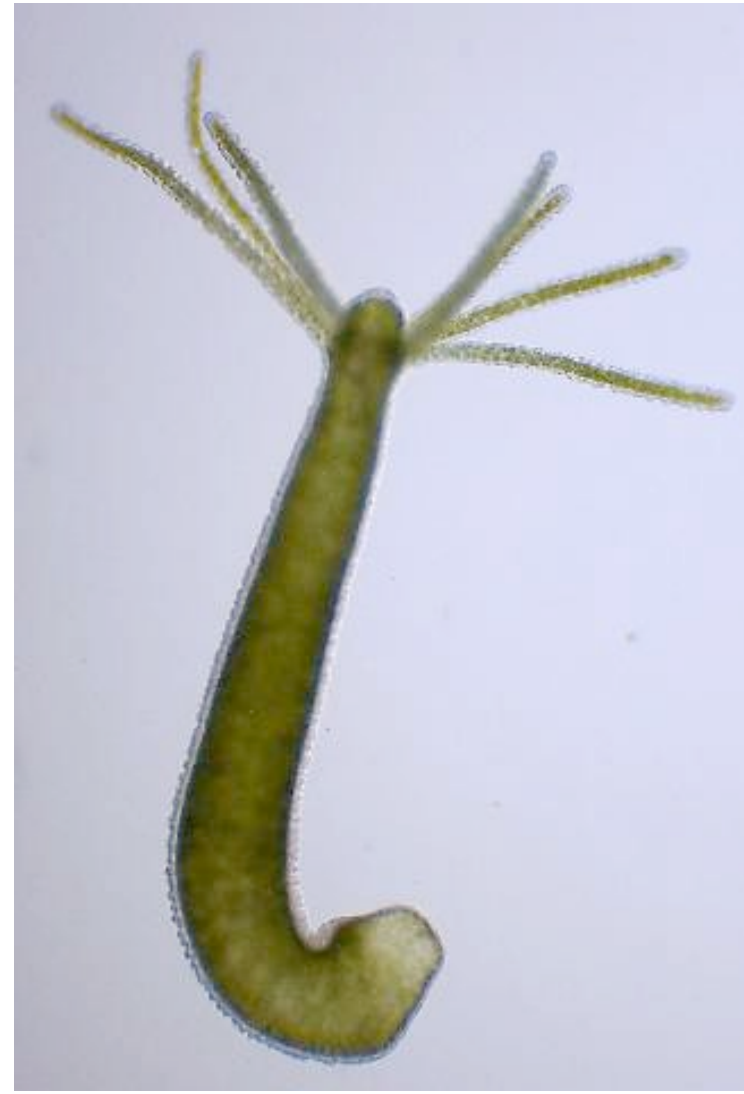


- some hydra contain symbionts that behave as plastids in plants

Analogy with hydra

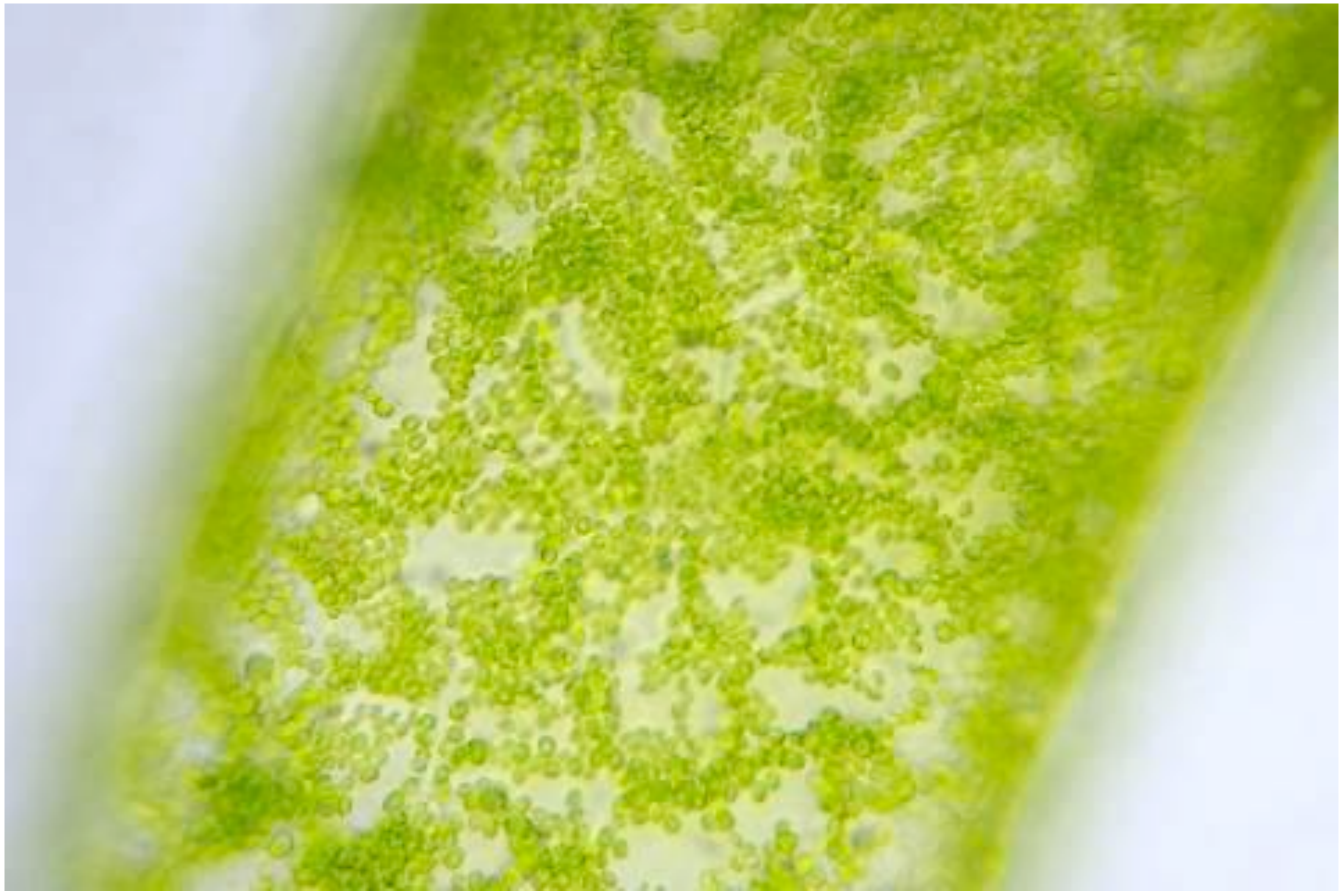




polyp *Hydra viridis* contains endosymbiotic zoochlorellae (algae)

- some hydra contain symbionts that behave as plastids in plants
- these also originate by division

Analogy with hydra



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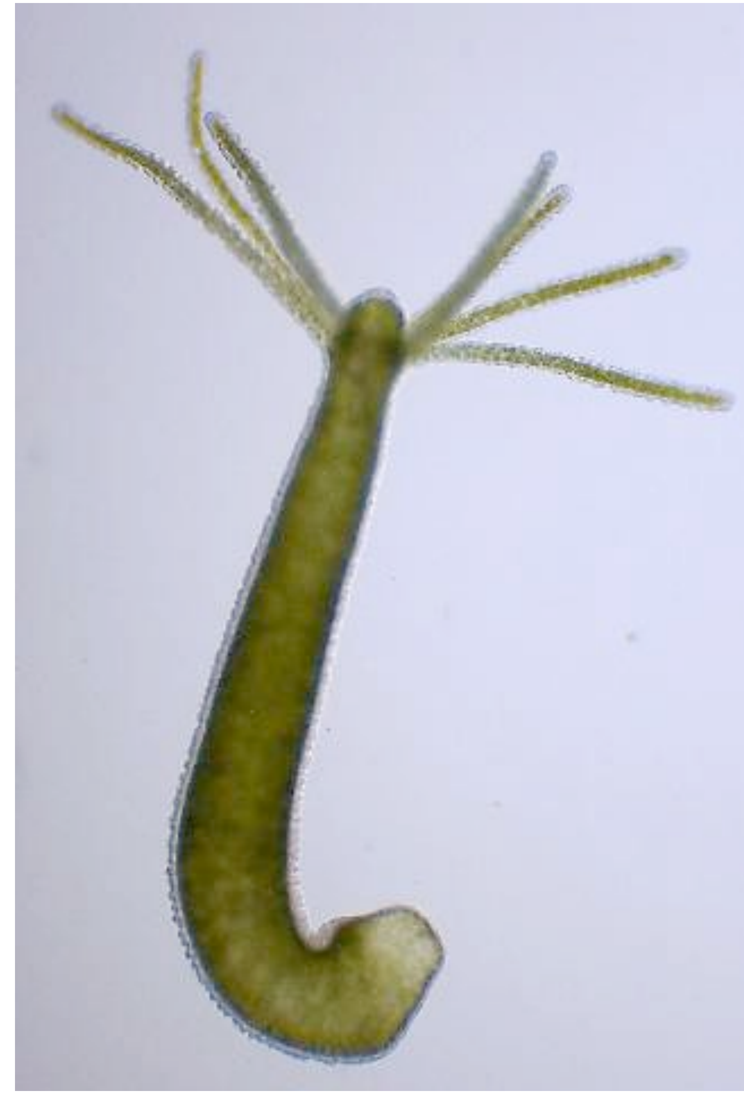
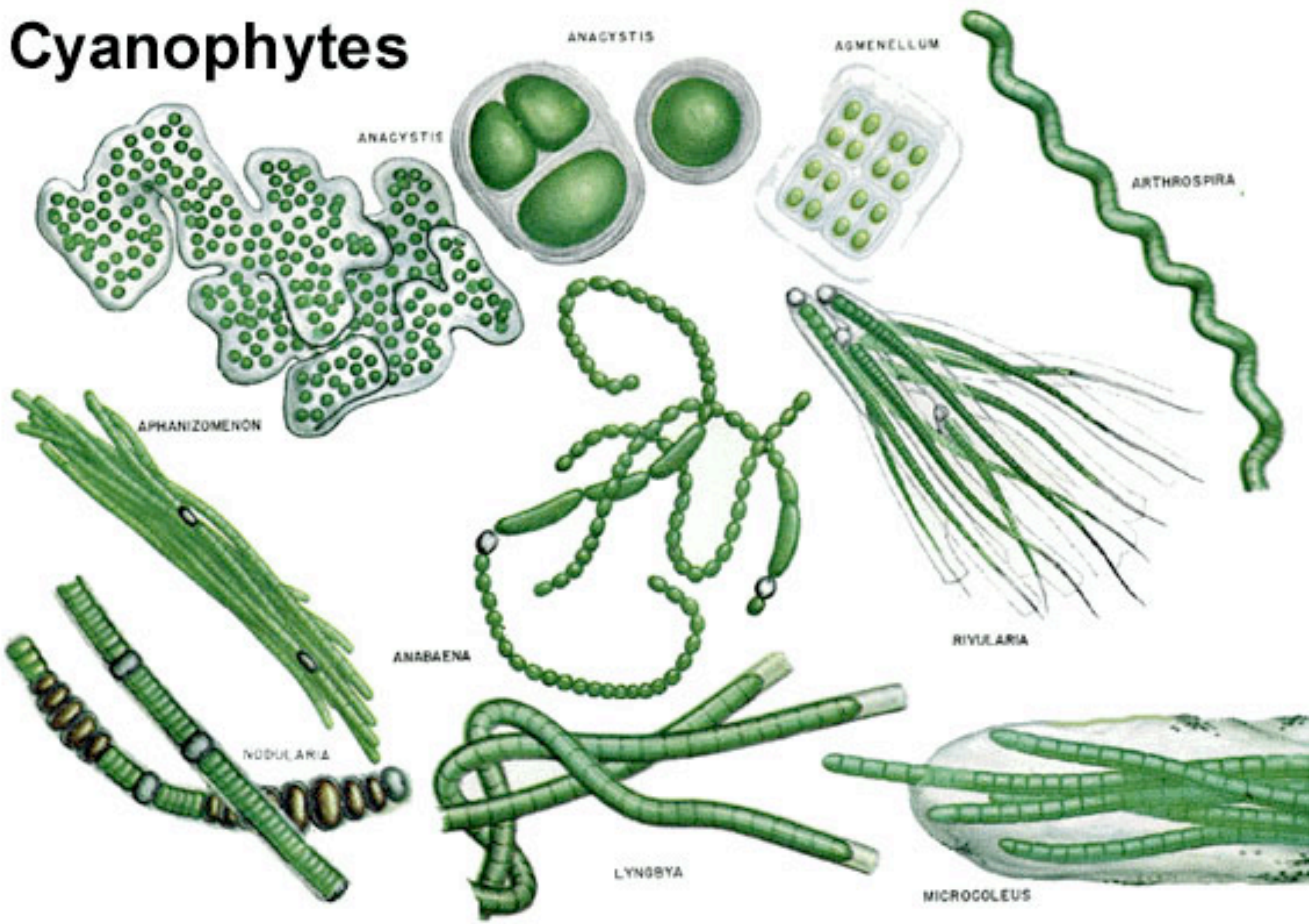


- some hydra contain symbionts that behave as plastids in plants
- these also originate by division
- these symbionts can live outside the host

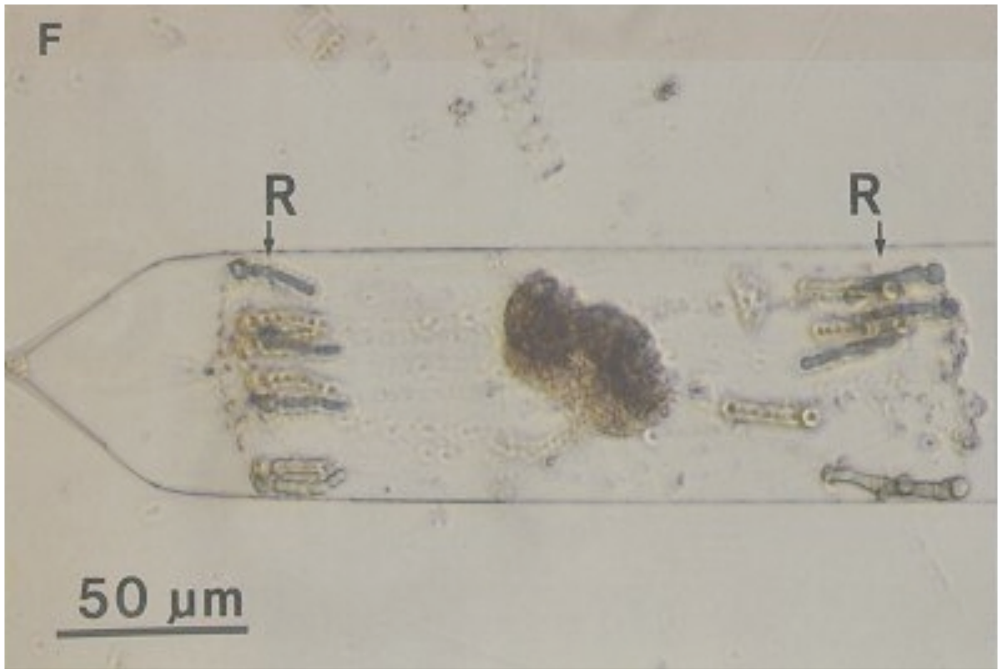
Free-living plastids..?



- Mereschkowsky: 'A theory such as the one suggested here would gain considerably...if...free-living organisms with similarity to the symbionts could be demonstrated'
- cyanobacteria (cyanophytes; blue-green algae)

Anabaena cylindrica
Watercolour, 1946, by G. E. Fogg

Endosymbiosis with cyanobacteria



cyanobacterium, *Richelia intercellularis* in a diatom, Rhizosolenia styliformis

rhizopod *Paulinella chromatophora* parasitized by cyanobacteria

- Living examples are known

Plastids are endosymbionts

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Plastids are endosymbionts

- plastids arise by division from previous plastids
- plastids continue to function normally in enucleated cells
- plastids make protein
- cyanobacteria seem very similar to plastids
- cyanobacteria are known that live in symbioses with other organisms

Further consequences

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- ‘According to this theory, the plant cell is nothing other than an animal cell with cyanobacteria that have invaded it’

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- ‘the green, the brown and the red algae could have thus originated independently’

Further consequences

- ‘According to this theory, the plant cell is nothing other than an animal cell with cyanobacteria that have invaded it’

- ‘the green, the brown and the red algae could have thus originated independently’

- ‘All of the peculiarities that are characteristic for plants and that distinguish them from animals, are…the natural result of a symbiosis between an animal cell and a CO_2-assimilating cyanobacterium’

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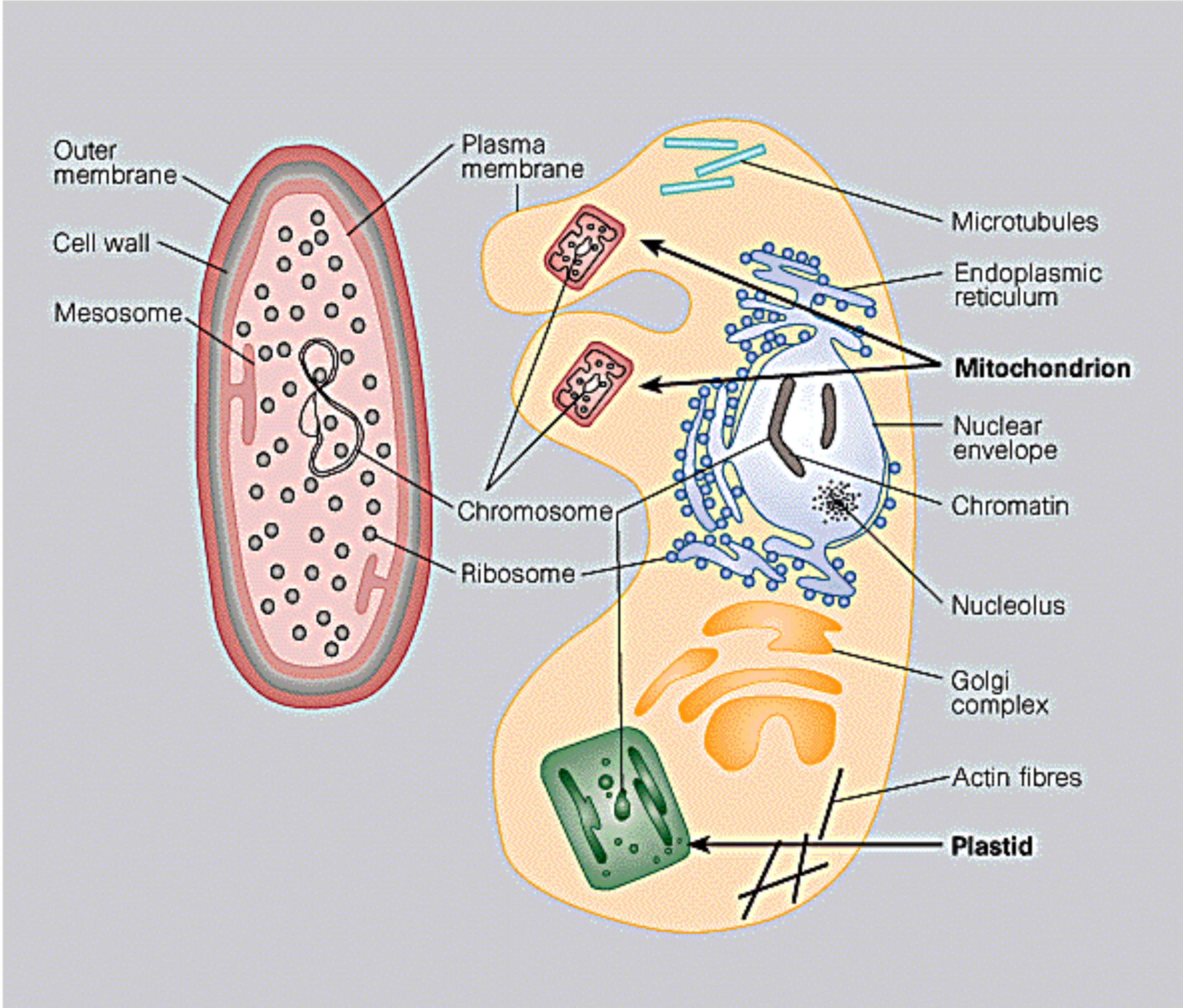
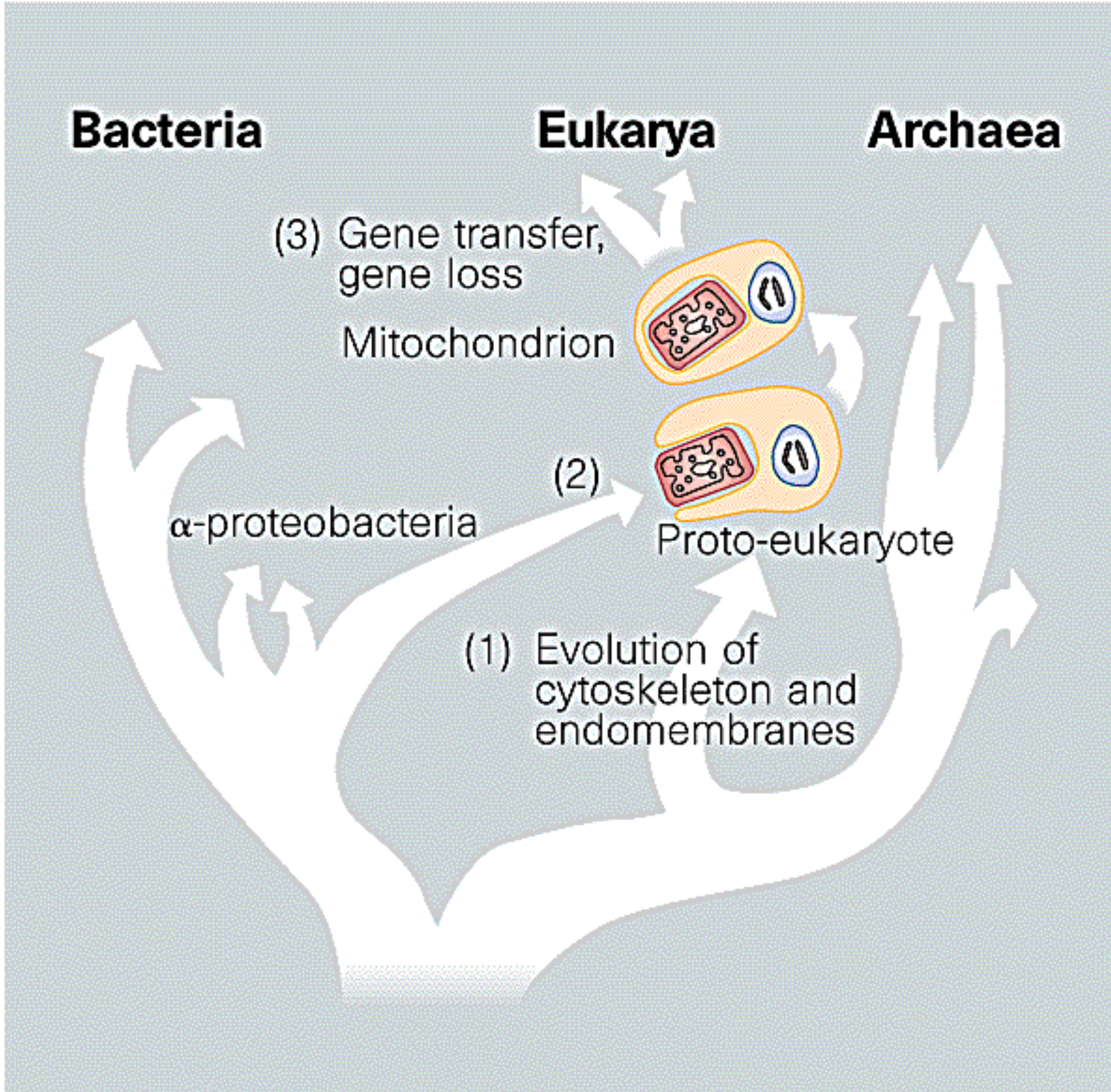
- These hypotheses were made before molecular biology, before it was known that DNA was the hereditary material



Typical prokaryotic (left) and eukaryotic (right) cells.

W. Ford Doolittle *Nature* **392,** 15-16, 1998



The endosymbiont hypothesis for the origin of mitochondria.

W. Ford Doolittle *Nature* **392**, 15-16, 1998

Summary

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- Mereschkowsky proposed 100 years ago that the bodies - ‘chromatophores’ found in green plants and algae are ‘enslaved ’ cyanobacteria

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- The **endosymbiont hypothesis** for the origin of chloroplasts and mitochondria is now orthodox, but there is controversy over the nature of the symbionts and their place in eukaryote evolution

The origin of the Endosymbiont hypothesis

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http://en.wikipedia.org/wiki/Konstantin_Mereschkowski

The renaissance of the Endosymbiont hypothesis

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Margulis, Lynn, 1992, *Symbiosis in Cell Evolution: Microbial Communities in the Archean and Proterozoic Eons*, W.H. Freeman

Lynn Margulis (b. 1938)
http://en.wikipedia.org/wiki/Lynn_Margulis

Lecture 2. October 28th, 2010. 11.00 a.m.

Endosymbiosis and the origin of bioenergetic organelles.
A modern view