# Лекция 3

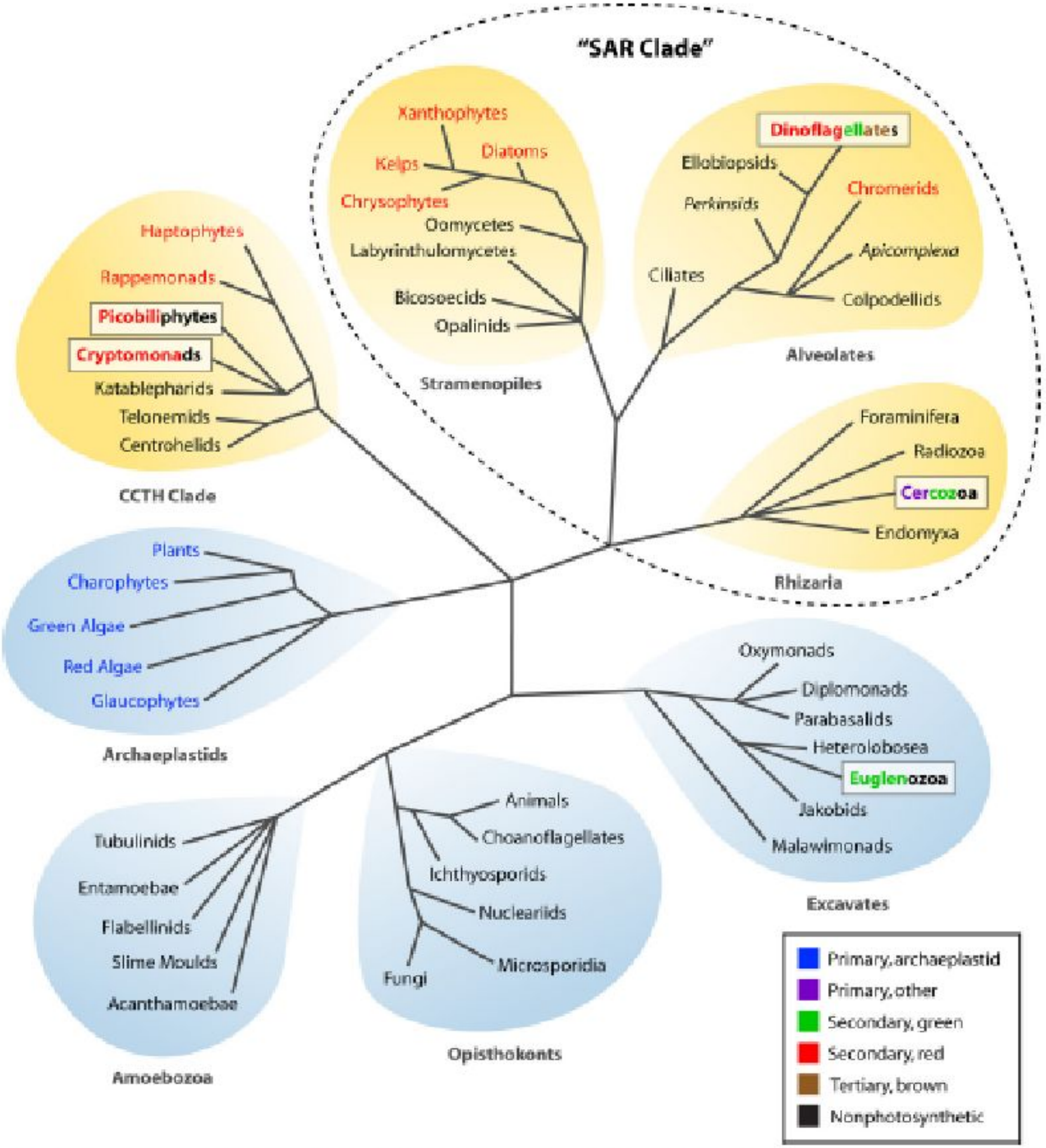


FIG. 2. Algae across the eukaryotes. Presented is a tree of eukaryotes, based on data from reference 123, showing the six "supergroups." For ease of visualization, the SAR clade has been split into its three constituent lineages (stramenopiles, alveolates, and rhizaria). Chromalveolate groups are shaded in orange. Photosynthetic phyla are shown in colored text to indicate the chloroplast lineage, as shown in the key. The majority have just one lineage, but for some (dinoflagellates and cercozoa) there are two or more. Nonphotosynthetic phyla that contain organelles believed to be derived from ancestral chloroplasts are in italics.

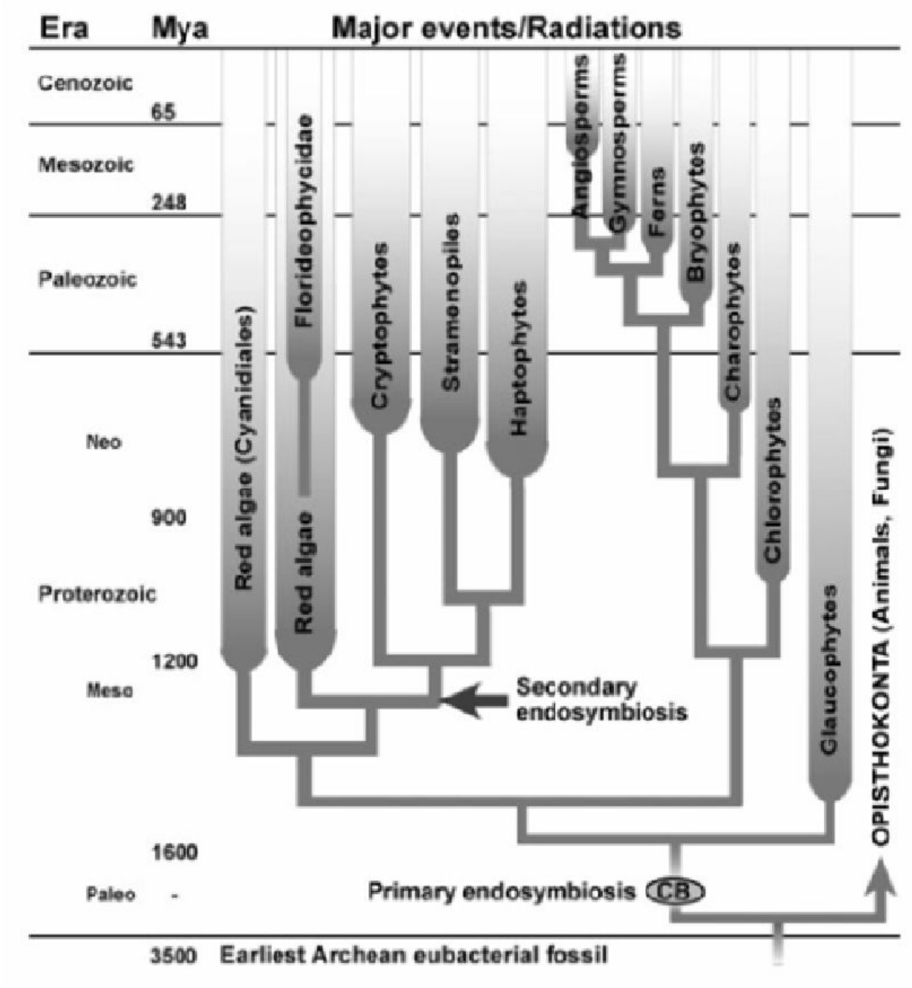
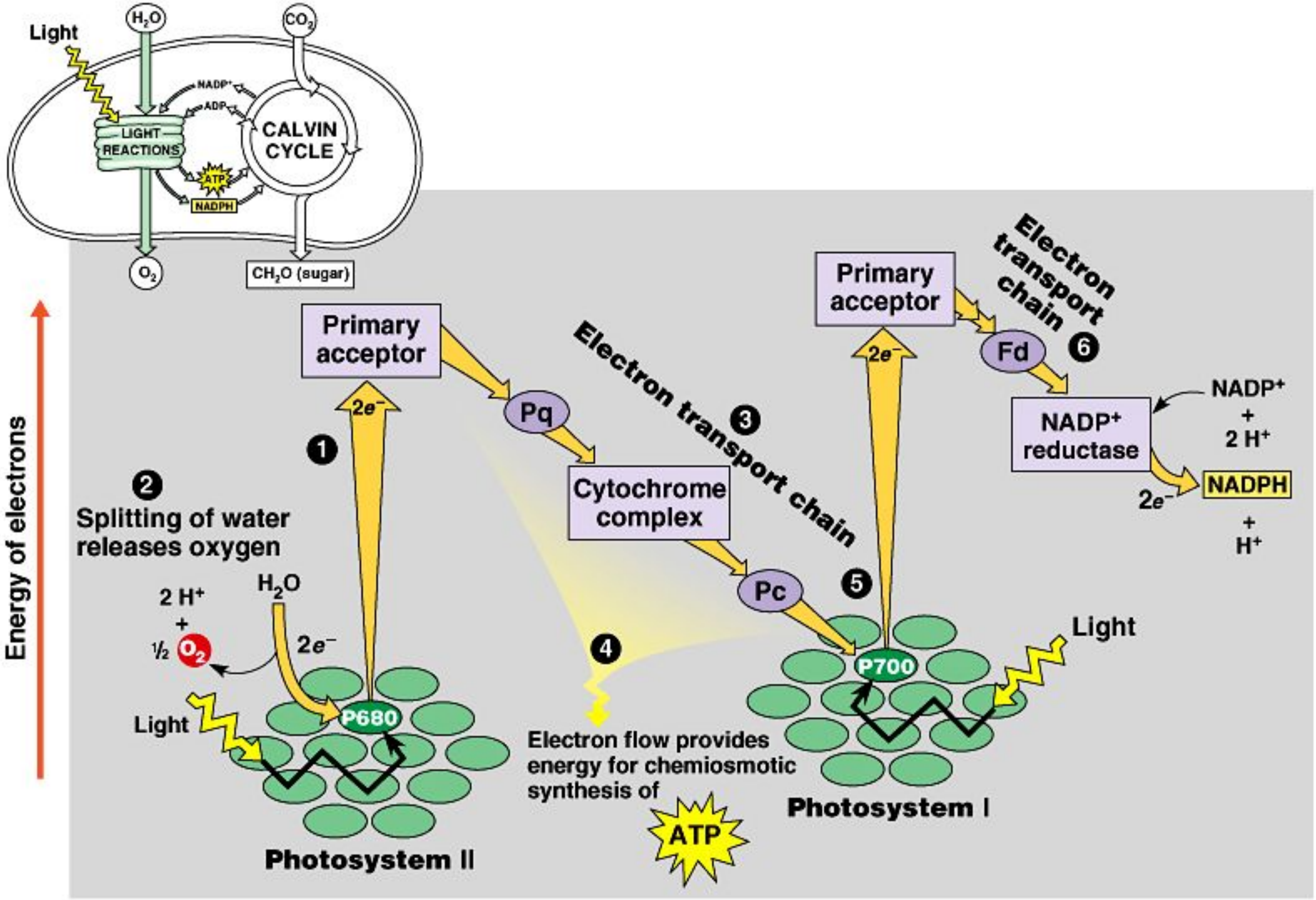


**Figure 7.** Schematic representation of the evolutionary relationships and divergence times for the red, green, glaucophyte and chromist algae, according to Yoon *et al.*[64]. The branches on which the cyanobacterial (CB) primary and red algal chromist secondary endosymbioses occurred are shown. Divergence times in the evolution of eukaryotic phototrophs; Mya, million years; CB, Paleo, Paleozoic.


Light
$H_2O$
$CO_2$
$NADP^+$
ADP
LIGHT REACTIONS
CALVIN CYCLE
ATP
NADPH
$O_2$
$CH_2O$ (sugar)
Energy of electrons
Primary acceptor
$2e^-$
①
②
Splitting of water releases oxygen
2 $H^+$
+
½ $O_2$
$H_2O$
$2e^-$
P680
Light
Photosystem II
Pq
Cytochrome complex
③
Electron transport chain
Pc
④
Electron flow provides energy for chemiosmotic synthesis of
ATP
⑤
Primary acceptor
$2e^-$
P700
Light
Photosystem I
Electron transport chain
⑥
Fd
$NADP^+$ reductase
$NADP^+$
+
2 $H^+$
$2e^-$
NADPH
+
$H^+$

В отличие от эукариот, некоторые цианобактерии (в том числе и прохлорофиты) способны использовать сероводород в качестве донора электронов, образуя серу *(Oscillatoria Lyngbya*, *Phormidium*, *Synechocystis*, *Prochlorothrix, Microcoleus).*

- $2H_2S + CO_2 \rightarrow CH_2O + 2S + H_2O$

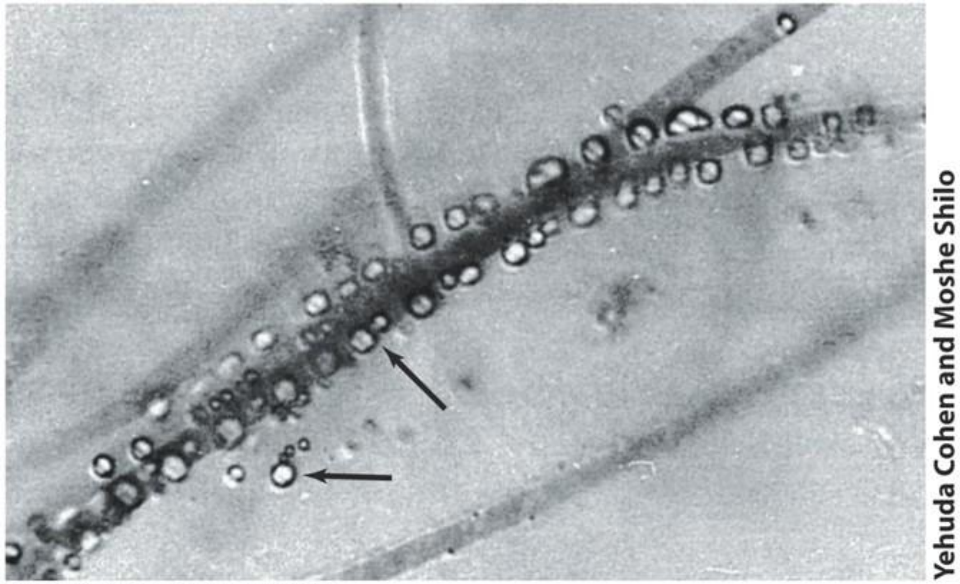
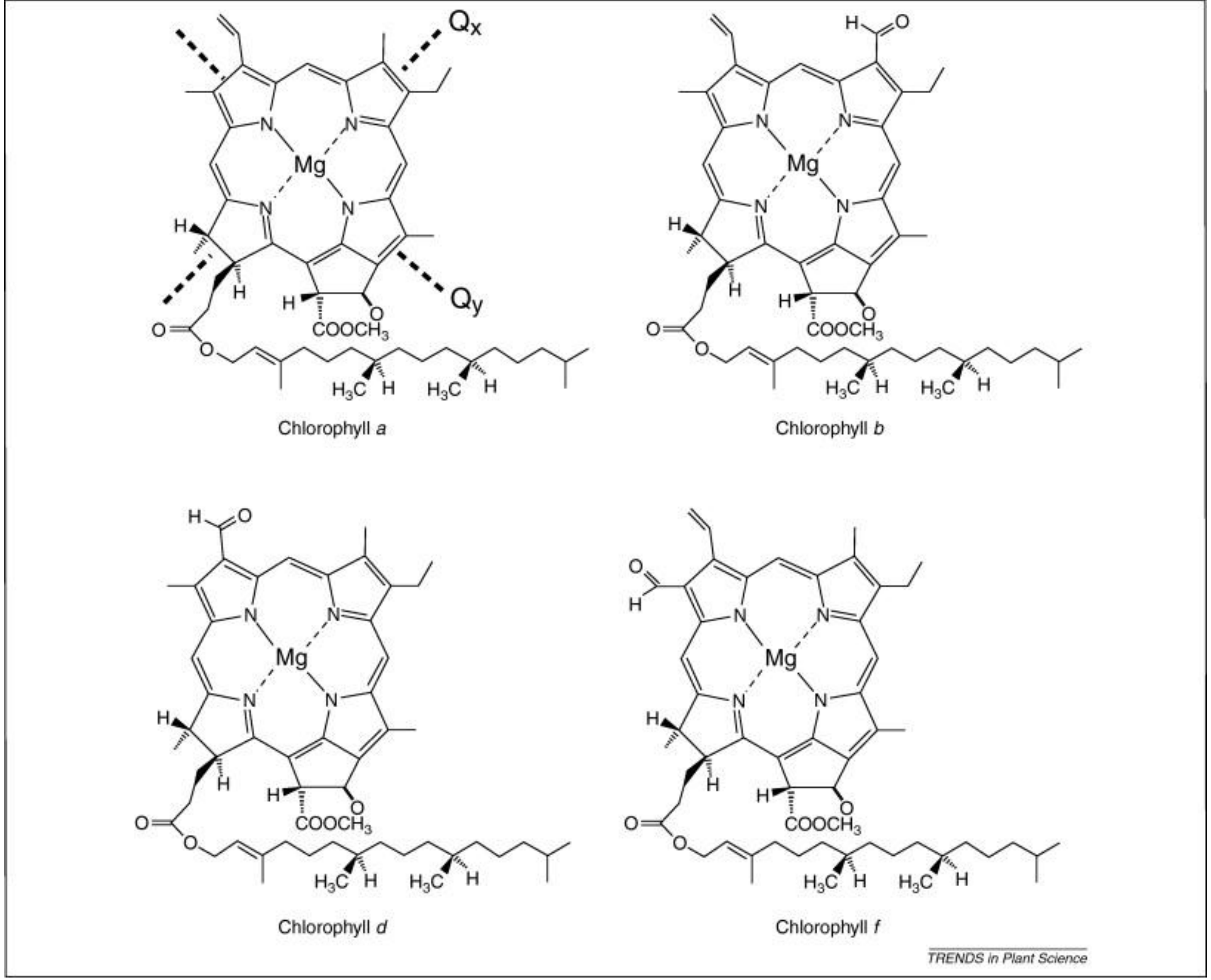


Figure 17-20 Brock Biology of Microorganisms 11/e

Такие цианобактерии – факультативно аноксигенные фототрофы, они могут обитать при достаточном освещении в анаэробных условиях богатых серой. Например, *Oscillatoria limnetica*, обитающая в гиперсалинном озере Солар-Лейк в районе залива Эйлат (Красное море).



*TRENDS in Plant Science*

Figure 2 Chemical structures of Chl a, b d and f. The x and y molecular axes are shown for Chl a but are the same for the other pigments.

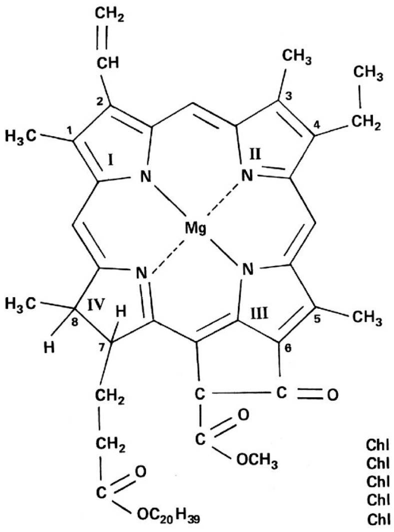
Min Chen , Robert E. Blankenship

**Expanding the solar spectrum used by photosynthesis**

Trends in Plant Science, Volume 16, Issue 8, 2011, 427 - 431

http://dx.doi.org/10.1016/j.tplants.2011.03.011

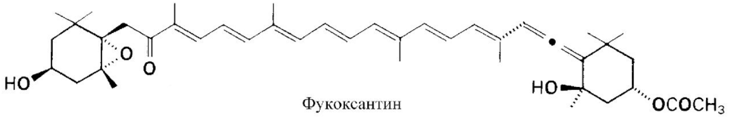
|  | Хлорофилл *a* | Хлорофилл *b* | Хлорофилл *c* – подобный | Хлорофилл *d* |
|---|---|---|---|---|
| *Prochlorothrix* | + | + |  |  |
| *Prochloron* | + | + | + |  |
| *Prochlorococcus* | +<br>форма $a_2$ | +<br>форма $b_2$ | + |  |
| *Acaryochloris marina* | < 5% |  |  | >95% |
| Все остальные цианобактерии | + |  |  |  |



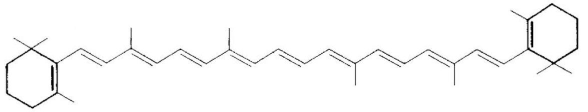
Chl *a*: как показано на рисунке
Chl *b*: II–3 = CHO
Chl *d*: I –2 = CHO
Chl $c_1$: IV–7 = CH=CHCOOH; двойная связь при IV–7, 8
Chl $c_2$: IV–7 = CH=CHCOOH; двойная связь при IV–7, 8
II–4 = $CH{=}CH_2$

Рис. 27. Структура хлорофиллов

Каротиноиды цианобактерий:
β-каротин у них содержится в больших пропорциях, чем у эукариот, встречаются α-каротин, зеаксантин эхиненон, миксоксантофилл, осциллаксантин , кантаксантин



Фукоксантин



β- Каротин

Рис.28. Структура фукоксантина и β- каротина.

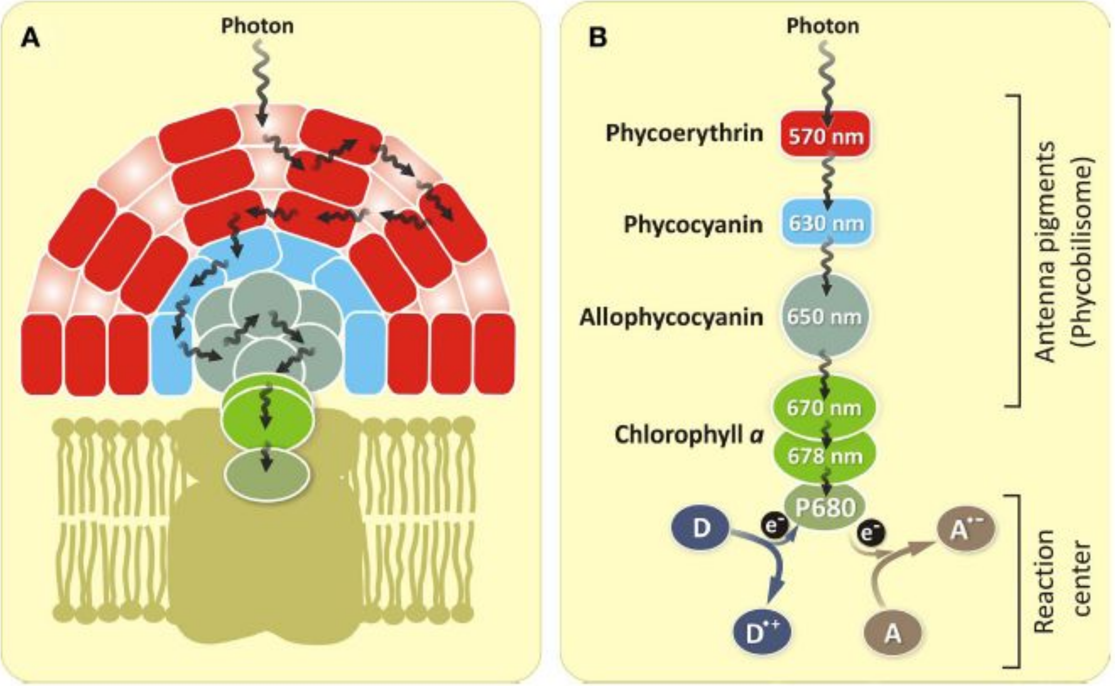
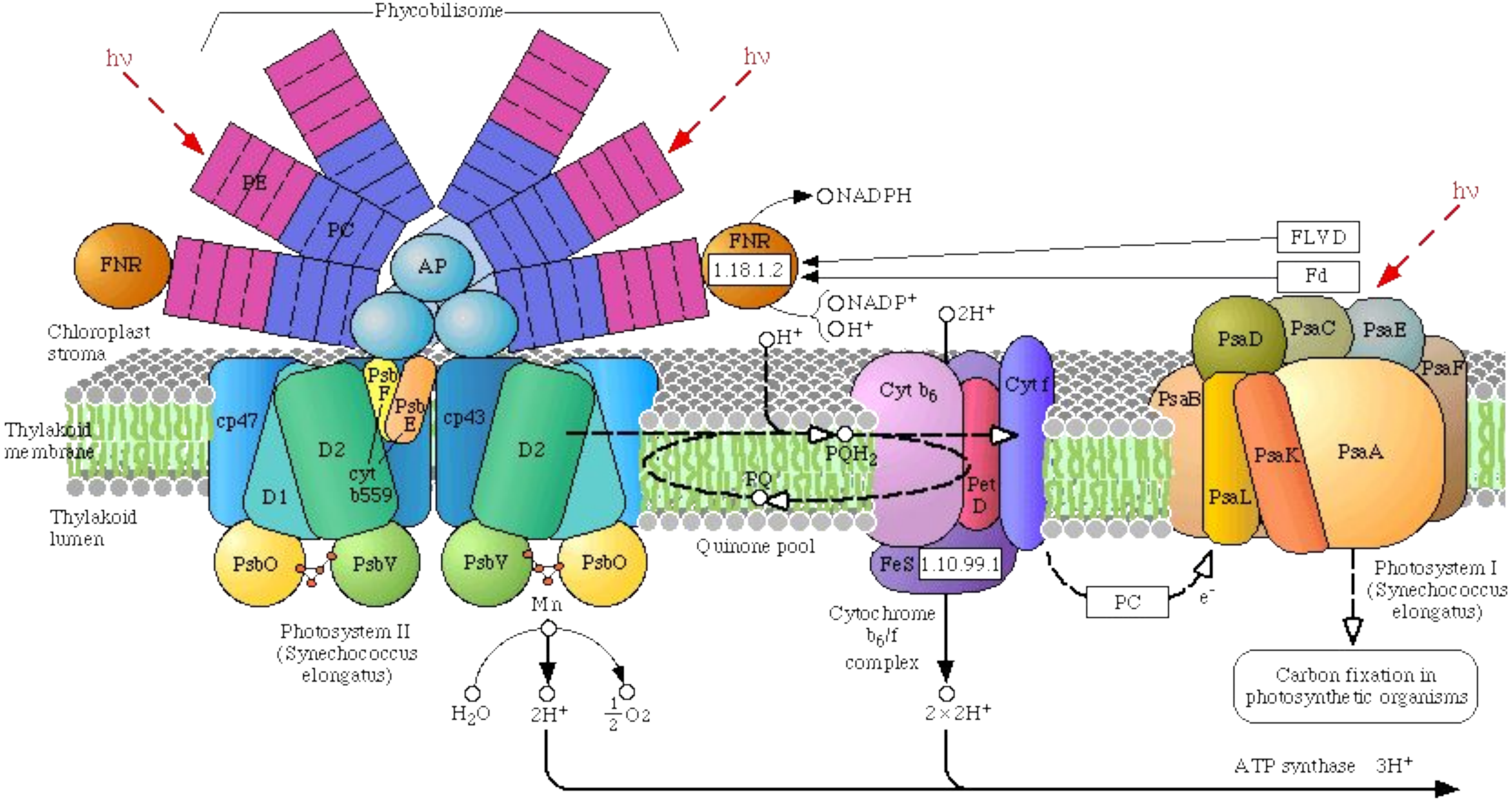
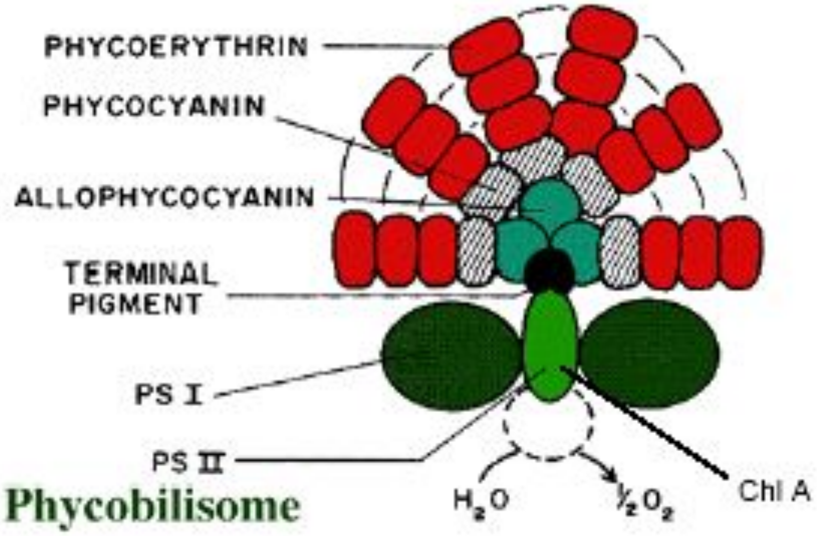


**FIGURE 2 | Structural organization of the antenna system of PSII for red algae and cyanobacteria (A) and energy transfer steps including charge separation (photochemical reaction) at the PSII RC (B) for cyanobacteria.** The energy of absorbed photons is passed through a number of antenna molecules [phycoerythrin (absent in most cyanobacteria) → phycocyanin → allophycocyanin] until it reaches the RC Chl *a* (P680). The excited P680 donates its electron, which is in the excited state of the molecule, to an electron acceptor (A). The electron vacancy of the Chl *a* is filled by the electron from an electron donor (D). The wavelength numbers (nm) inside the circles represent pigments corresponding to the long wavelength absorption maxima of these pigments.

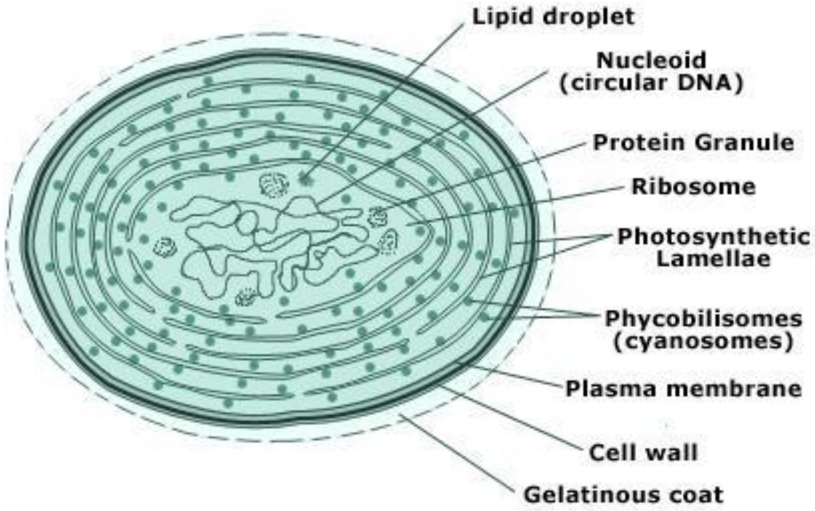

Phycobilisome
hν
hν
hν
PE
PC
AP
FNR
FNR
1.18.1.2
NADPH
FLVD
Fd
NADP⁺
H⁺
2H⁺
H⁺
Chloroplast stroma
Thylakoid membrane
Thylakoid lumen
cp47
D2
D1
cyt b559
Psb F
Psb E
cp43
D2
PsbO
PsbV
PsbV
PsbO
Mn
Photosystem II (Synechococcus elongatus)
H₂O
2H⁺
½O2
PQH₂
PQ
Quinone pool
Cyt b₆
Cyt f
Pet D
FeS
1.10.99.1
Cytochrome b₆/f complex
2×2H⁺
PC
e⁻
PsaD
PsaC
PsaE
PsaF
PsaB
PsaL
PsaK
PsaA
Photosystem I (Synechococcus elongatus)
Carbon fixation in photosynthetic organisms
ATP synthase 3H⁺

# Light Capturing "Antennae"

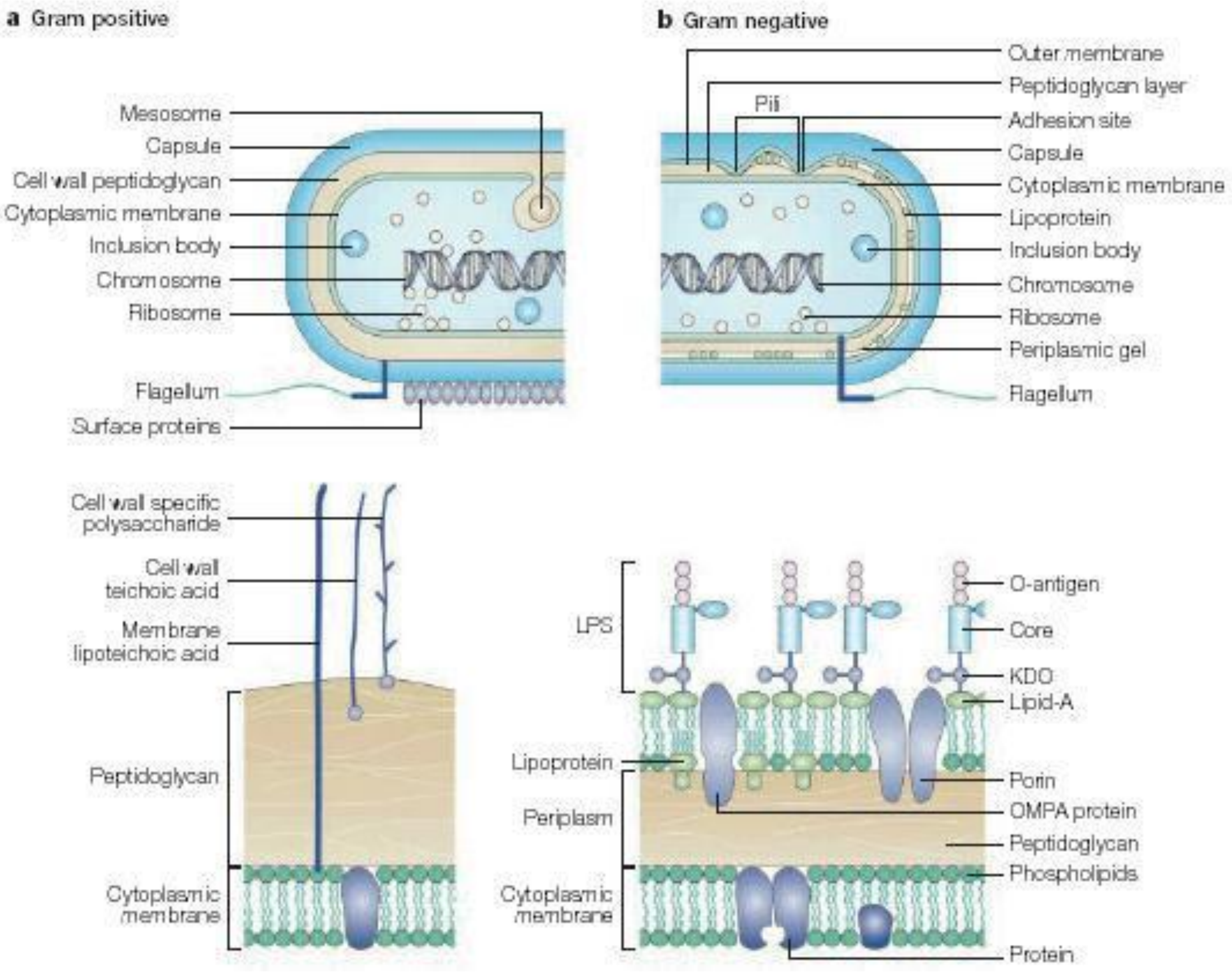
- phycobiliproteins act as both light antennae and reserves of cellular nitrogen

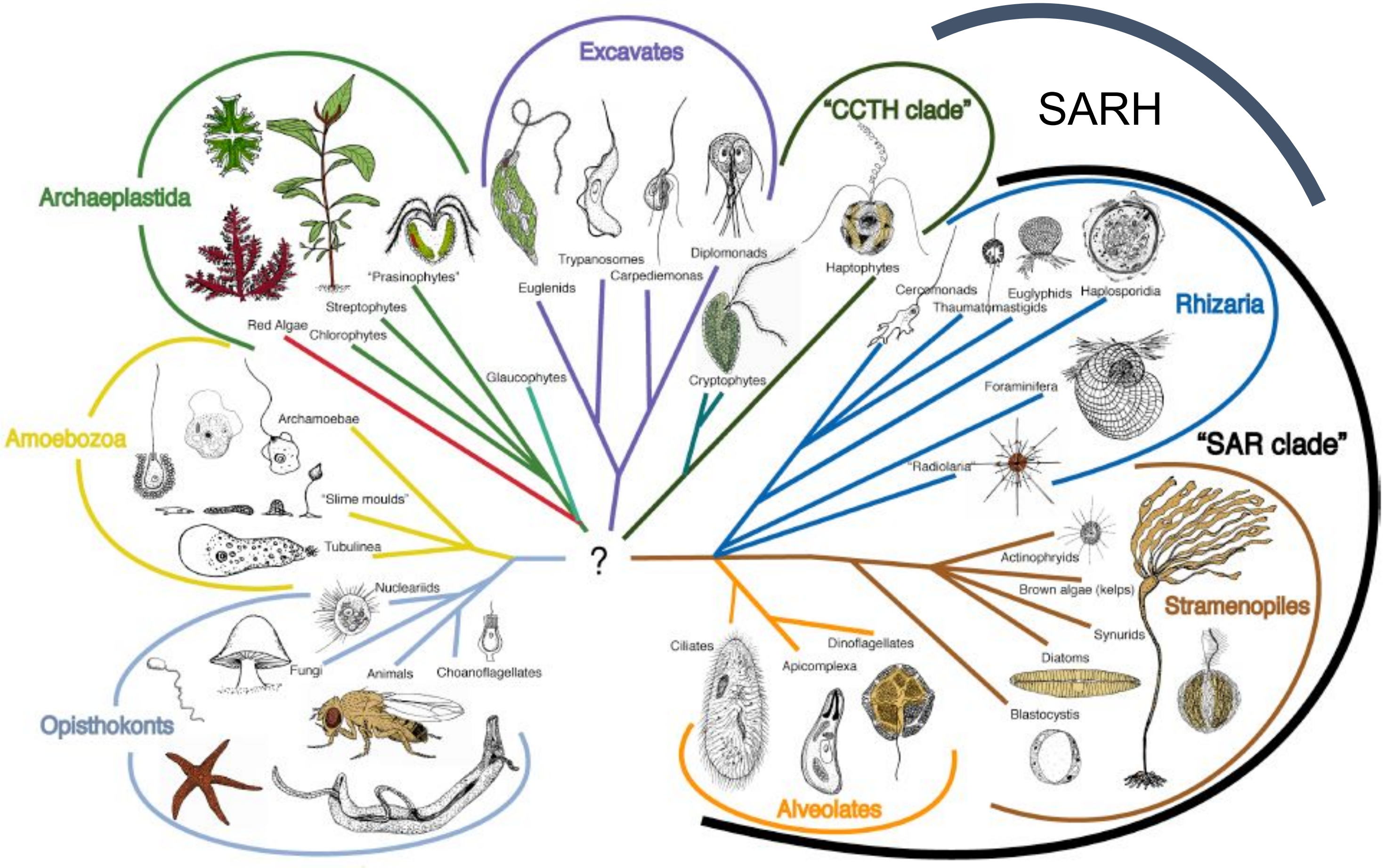


**Phycobilisome**



Chromatic adaptation: green light ↑ phycoerythrin, red light ↑ phycocyanin

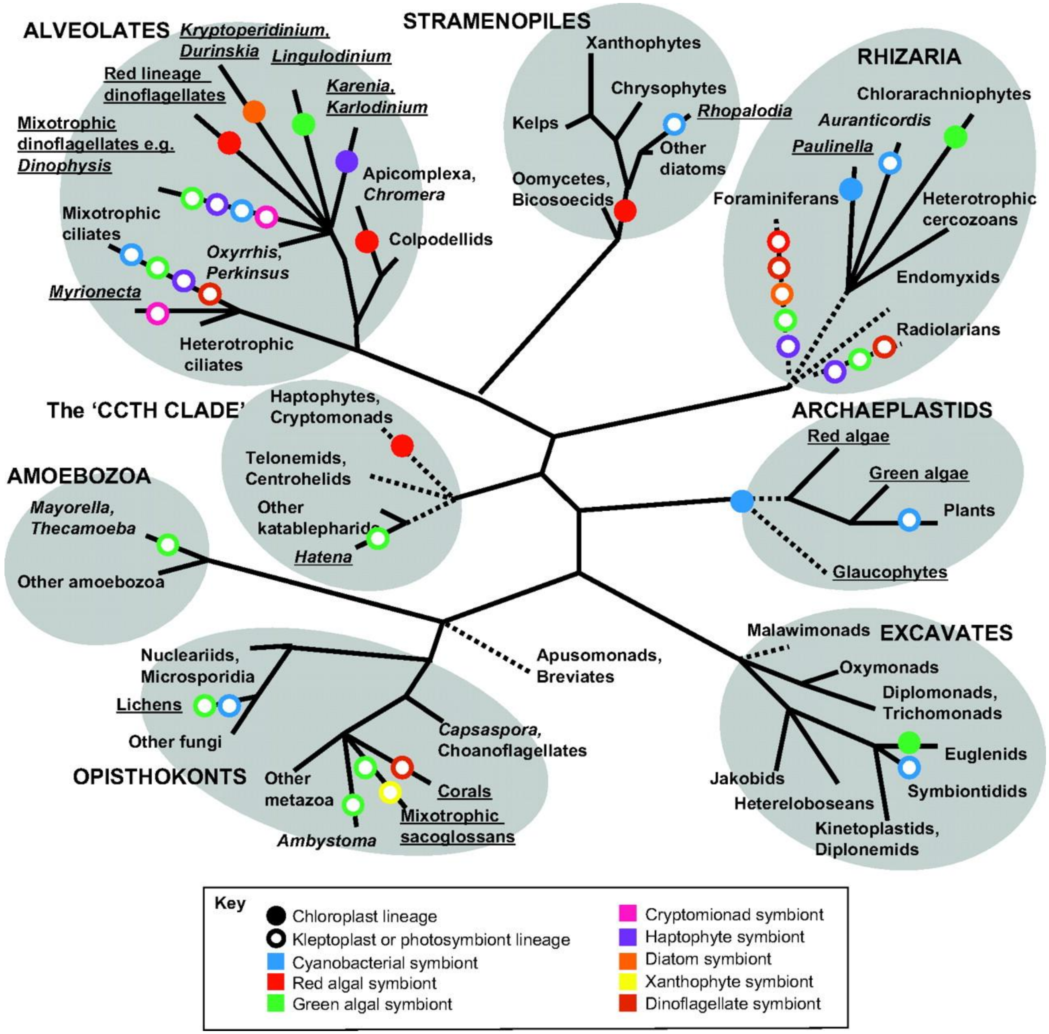

a Gram positive
Mesosome
Capsule
Cell wall peptidoglycan
Cytoplasmic membrane
Inclusion body
Chromosome
Ribosome
Flagellum
Surface proteins
b Gram negative
Outer membrane
Peptidoglycan layer
Pili
Adhesion site
Capsule
Cytoplasmic membrane
Lipoprotein
Inclusion body
Chromosome
Ribosome
Periplasmic gel
Flagellum
Cell wall specific polysaccharide
Cell wall teichoic acid
Membrane lipoteichoic acid
Peptidoglycan
Cytoplasmic membrane
LPS
O-antigen
Core
KDO
Lipid-A
Lipoprotein
Porin
OMPA protein
Periplasm
Peptidoglycan
Phospholipids
Cytoplasmic membrane
Protein



*Supplementary online material to:*

Walker G., Dorrell R.G., Schlacht A., Dacks J.B. (2011): Eukaryotic systematics: a 2011 user's guide for cell biologists and parasitologists. *Parasitology* **138,** 1-26.

# The distribution of photosynthesis across the eukaryotes.



Dorrell R G , Howe C J J Cell Sci 2012;125:1865-1875

Journal of Cell Science
jcs.biologists.org

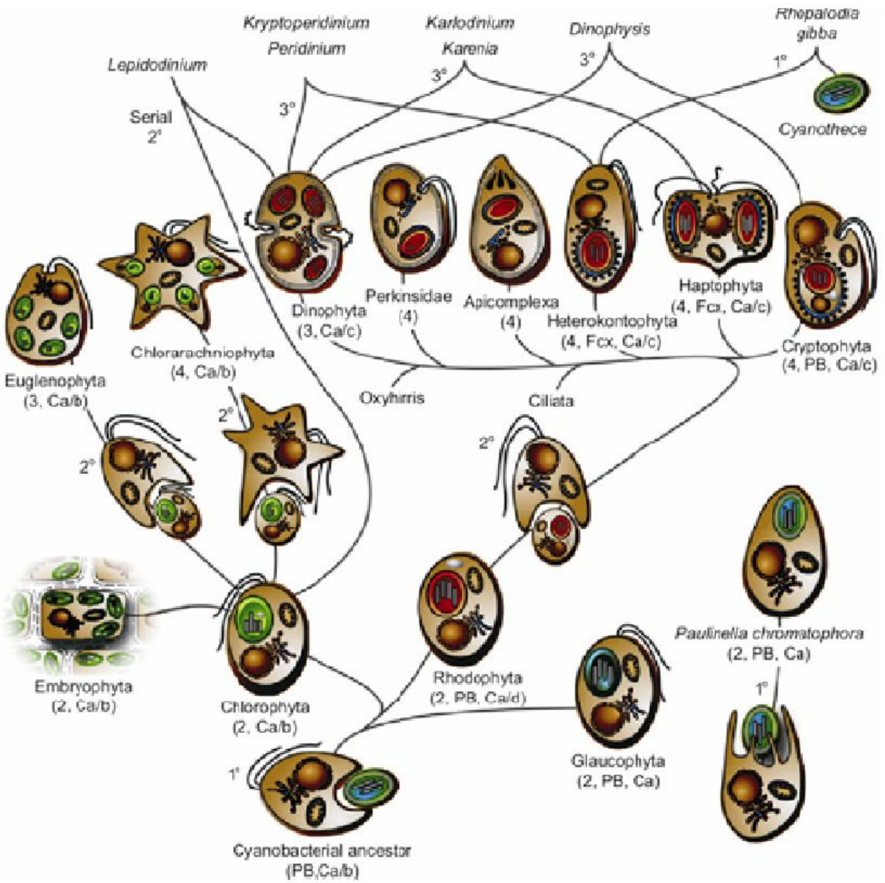


**Figure 6.** Evolutionary relations of plastids. The main branches diverging from the primary endosymbiotic event are those going to Chlorophyta (the 'green line') and Rhodophyta (the 'red line'), but even before their divergence the Glaucophyta plastids branch-off. For an explanation of other relationships, see text. From Gould *et al.*[59]. Reprinted, with permission, from the *Annual Review of Plant Biology*, vol. 59. © 2008 by Annual Reviews http://www.annualreviews.org/.

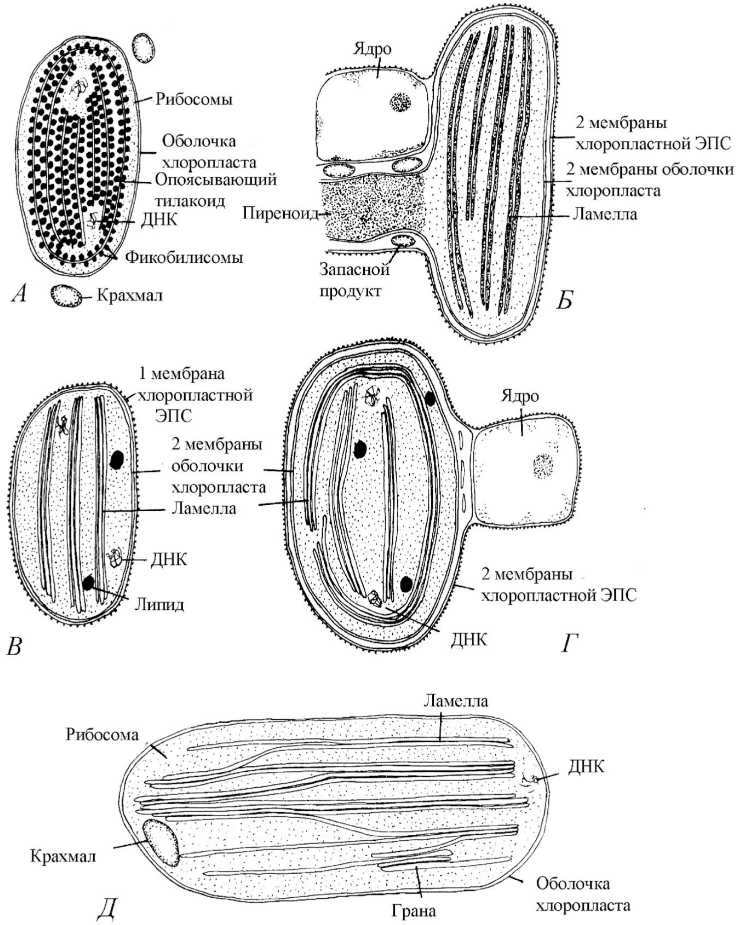
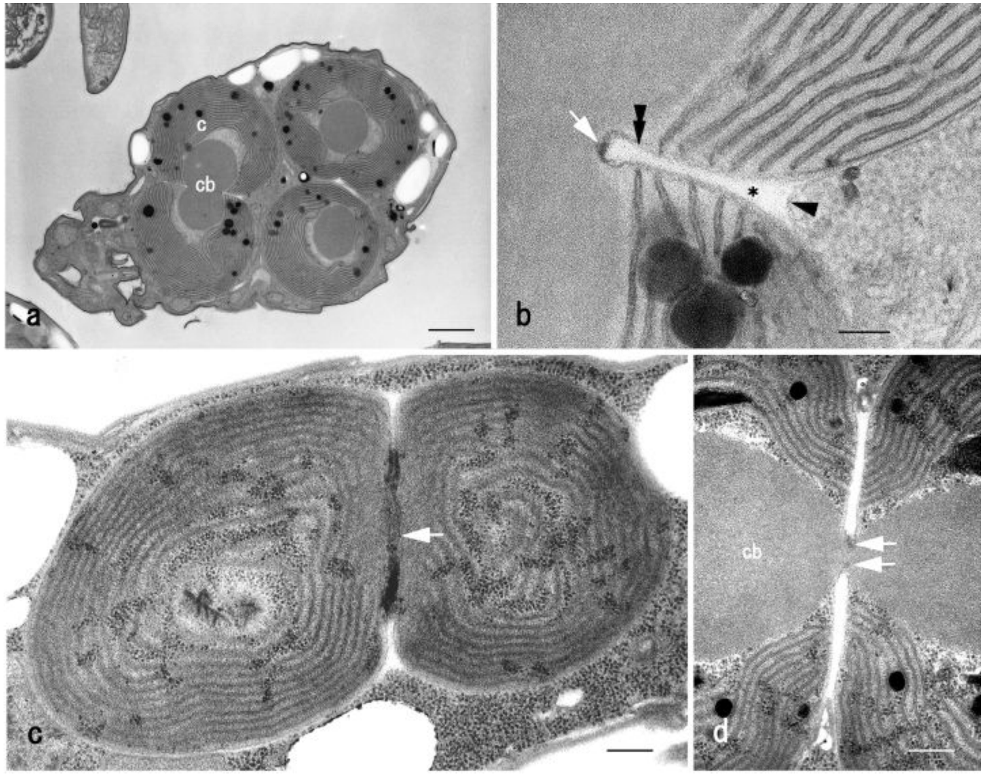
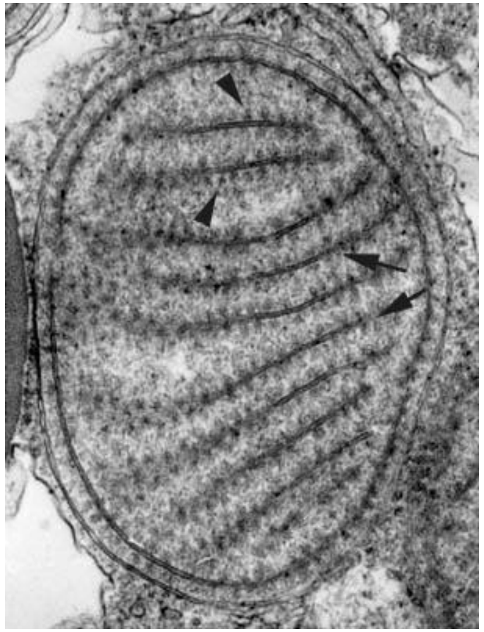


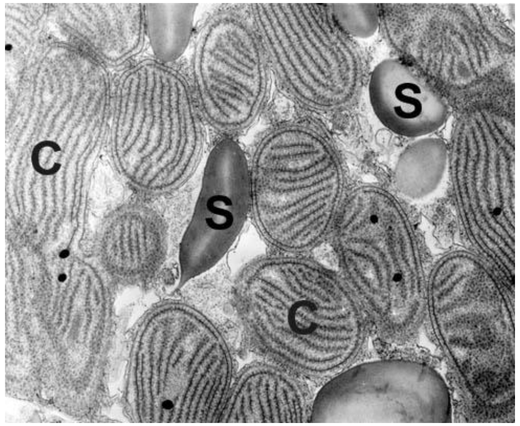
Рис. 24. Схема строения хлоропластов у эукариотных водорослей (по: Lee, 1999). *А* - тилакоиды расположены по одному, отсутствует хлоропластная ЭПС (Rhodophyta); *Б* - ламеллы двухтилакоидные, две мембраны хлоропластной ЭПС (Cryptophyta); *В* - трехтилакоидные ламеллы, одна мембрана хлоропластной ЭПС (Dinophyta, Euglenophyta); *Г* - ламеллы трехтилакоидные, две мембраны хлоропластной ЭПС (Ochrophyta, Prymnesiophyta); *Д* - двух- шеститилакоидные ламеллы, отсутствует хлоропластная ЭПС (Chlorophyta, Charophyta).

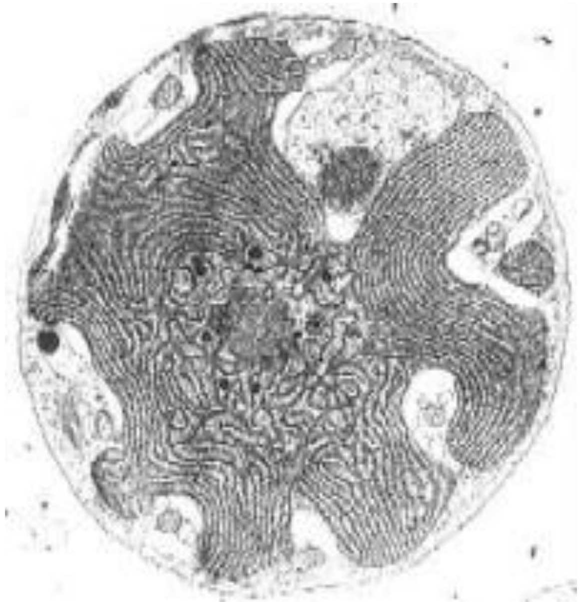
# Отдел Glaucocystophyta



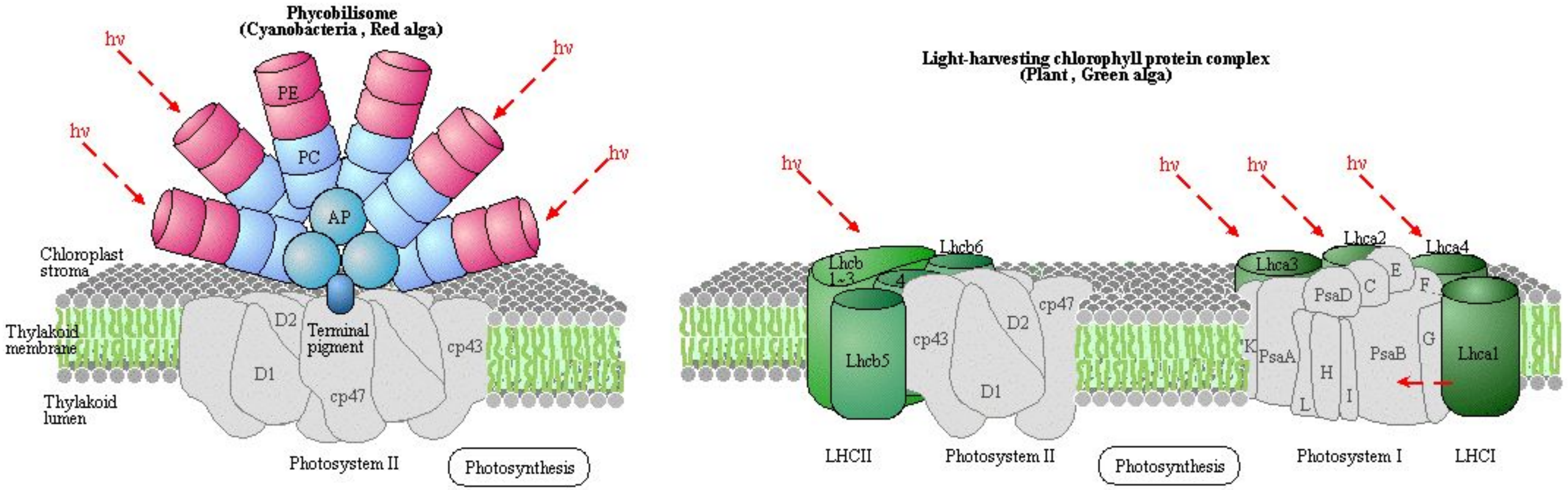
# Отд Rhodophyta







# PHOTOSYNTHESIS - ANTENNA PROTEINS



Allophycocyanin(AP)

| | | | | | |
|---|---|---|---|---|---|
| ApcA | ApcB | ApcC | ApcD | ApcE | ApcF |

Phycocyanin(PC) / Phycoerythrocyanin(PEC)

| | | | | | | |
|---|---|---|---|---|---|---|
| CpcA | CpcB | CpcC | CpcD | CpcE | CpcF | CpcG |

Phycoerythrin(PE)

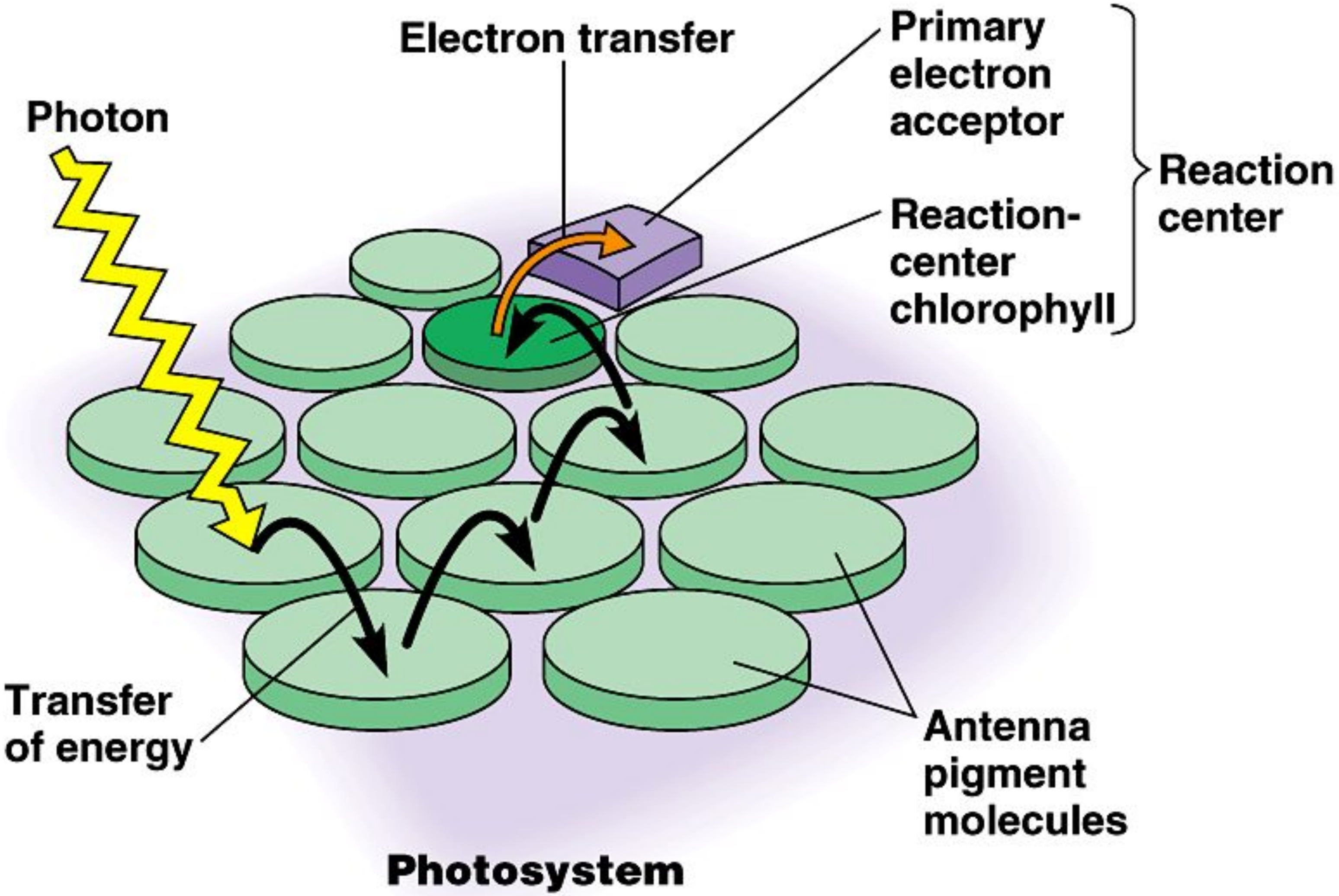
| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| CpeA | CpeB | CpeC | CpeD | CpeE | CpeR | CpeS | CpeT | CpeU | CpeY | CpeZ |

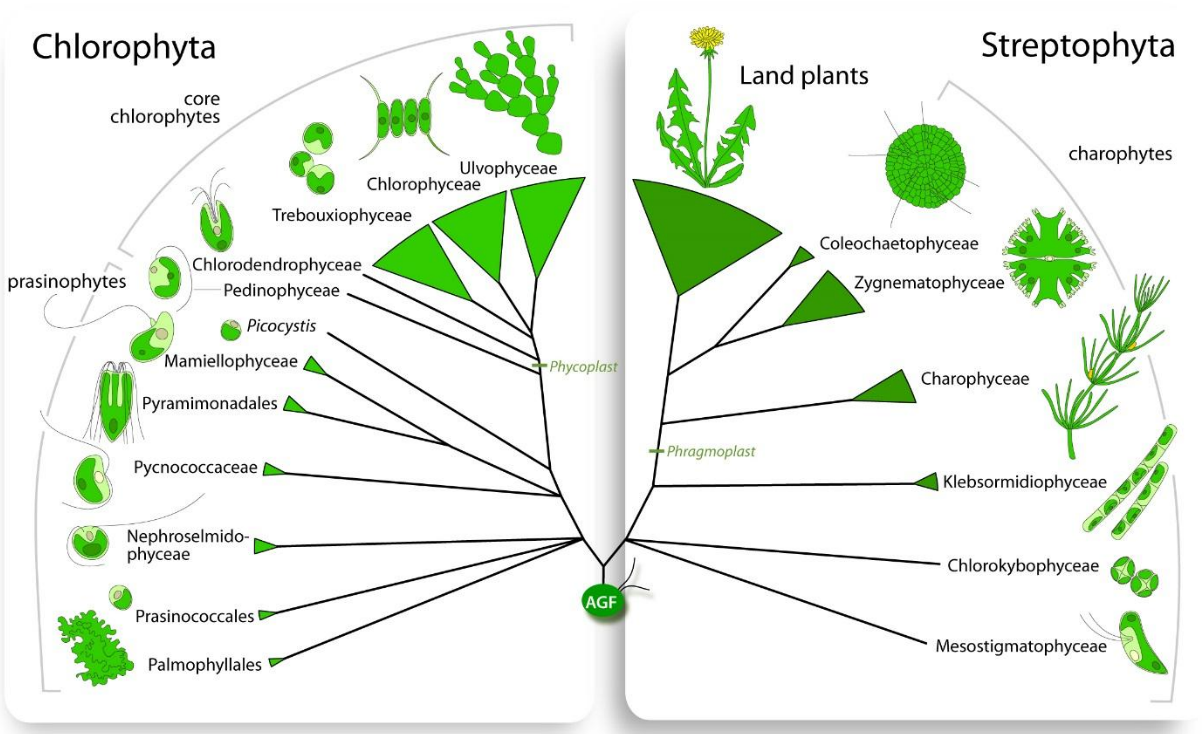
Light-harvesting chlorophyll protein complex(LHC)

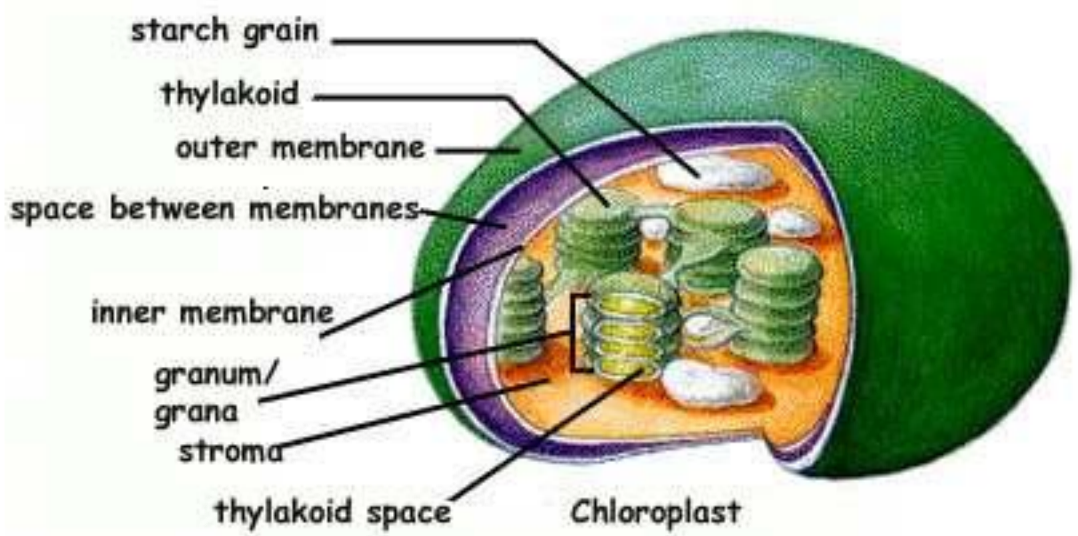
| | | | | |
|---|---|---|---|---|
| Lhca1 | Lhca2 | Lhca3 | Lhca4 | Lhca5 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Lhcb1 | Lhcb2 | Lhcb3 | Lhcb4 | Lhcb5 | Lhcb6 | Lhcb7 |

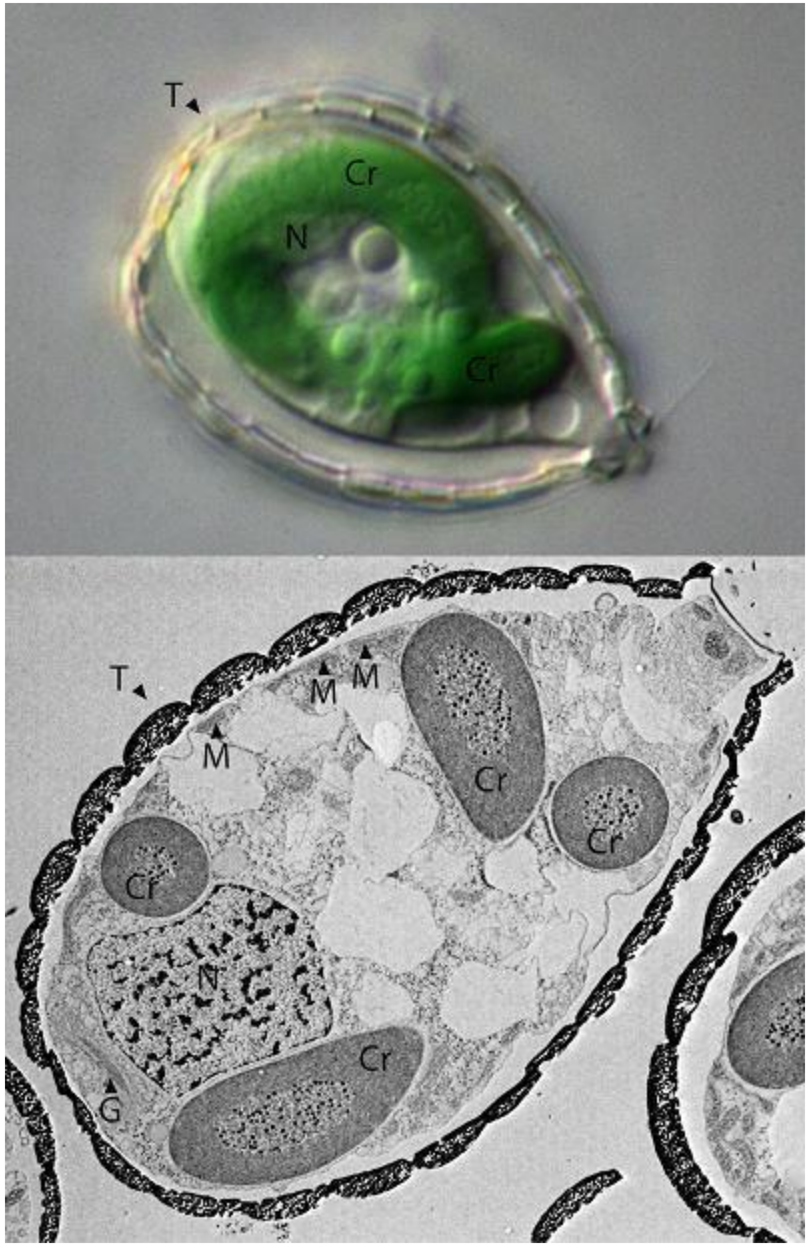
00196 11/16/10


Electron transfer
Primary electron acceptor
Photon
Reaction center
Reaction-center chlorophyll
Transfer of energy
Antenna pigment molecules
Photosystem


Chlorophyta
core chlorophytes
Ulvophyceae
Chlorophyceae
Trebouxiophyceae
Chlorodendrophyceae
Pedinophyceae
prasinophytes
Picocystis
Mamiellophyceae
Pyramimonadales
Pycnococcaceae
Nephroselmido-phyceae
Prasinococcales
Palmophyllales
Phycoplast
AGF
Streptophyta
Land plants
charophytes
Coleochaetophyceae
Zygnematophyceae
Charophyceae
Phragmoplast
Klebsormidiophyceae
Chlorokybophyceae
Mesostigmatophyceae


starch grain
thylakoid
outer membrane
space between membranes
inner membrane
granum/ grana
stroma
thylakoid space
Chloroplast

The rhizarian amoeba *Paulinella chromatophora* harbors two photosynthetically active and deeply integrated cyanobacterial endosymbionts acquired ~60 million years ago. Recent genomic analyses of *P. chromatophora* have revealed the loss of many essential genes from the endosymbiont's genome, and have identified more than 30 genes that have been transferred to the host cell's nucleus through endosymbiotic gene transfer (EGT).



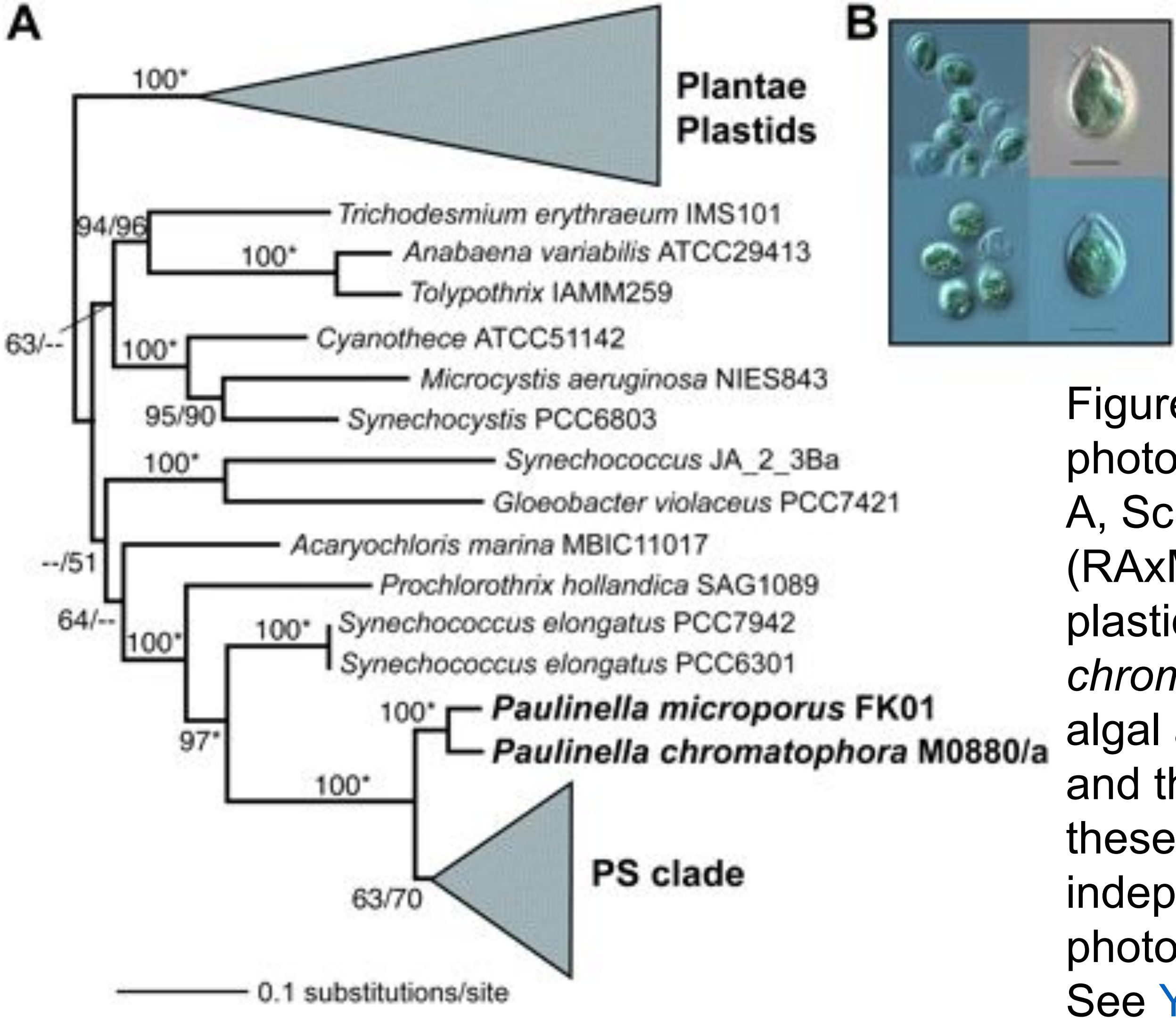
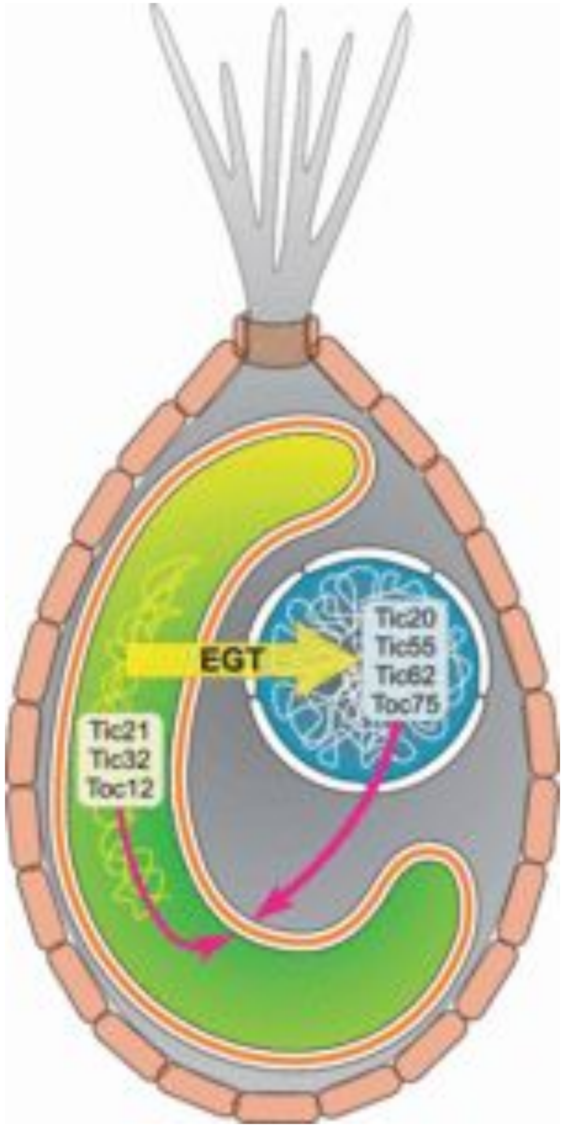
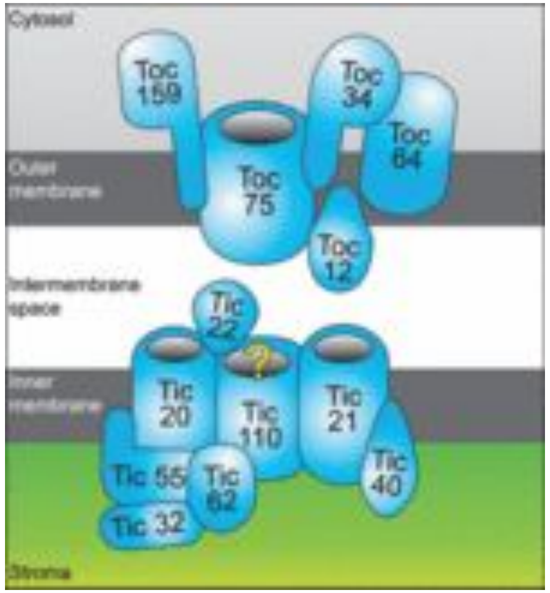


Figure 2. Evolution of photosynthetic *Paulinella* species. A, Schematic maximum likelihood (RAxML) phylogenetic tree of plastid-derived 16S rDNA from *P. chromatophora*, *P. microporus*, algal and plant (Plantae) plastids, and the cyanobacterial donors of these organelles. Note the clear independent origins of Plantae and photosynthetic *Paulinella* plastids. See Yoon et al. (2009) for details. B, Light micrograph images of *P. chromatophora* (top two images) and *P. microporus* (bottom two images). The scale bar indicates 5 µm.

The endosymbiont genome has already been reduced compared to free-living cyanobacteria, but not as much as the primary plastids of the Archaeplastida


EGT
Tic20
Tic55
Tic62
Toc75
Tic21
Tic32
Toc12


Cytosol
Toc 159
Toc 34
Toc 64
Outer membrane
Toc 75
Toc 12
Intermembrane space
Tic 22
?
Inner membrane
Tic 20
Tic 110
Tic 21
Tic 55
Tic 62
Tic 40
Tic 32
Stroma

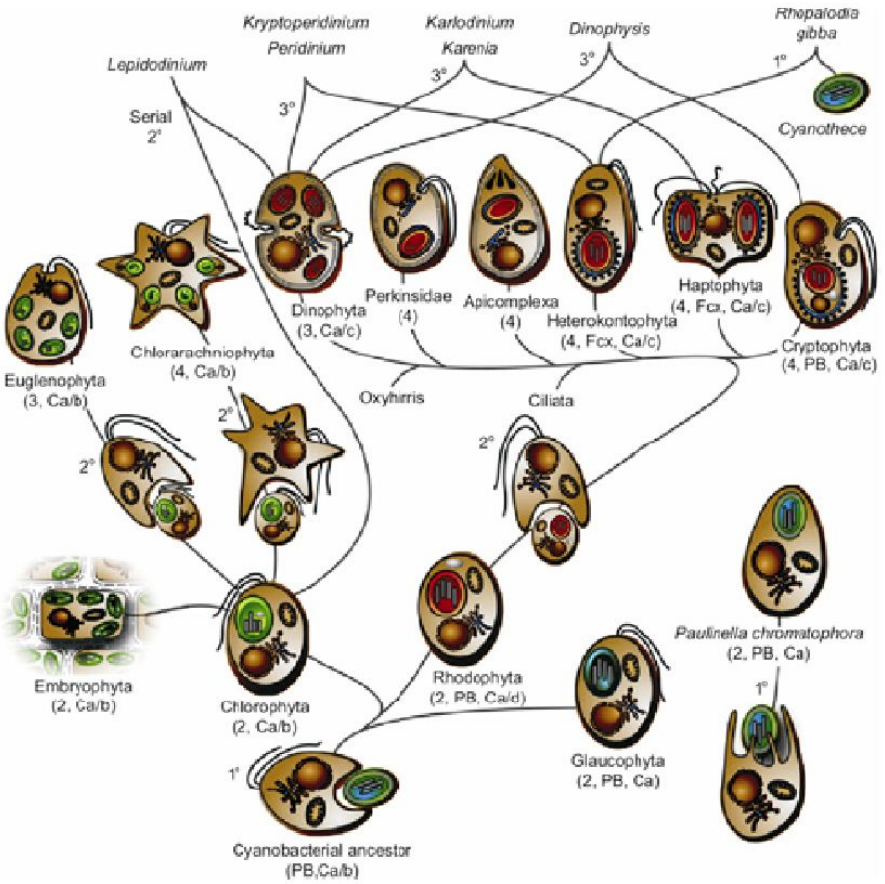
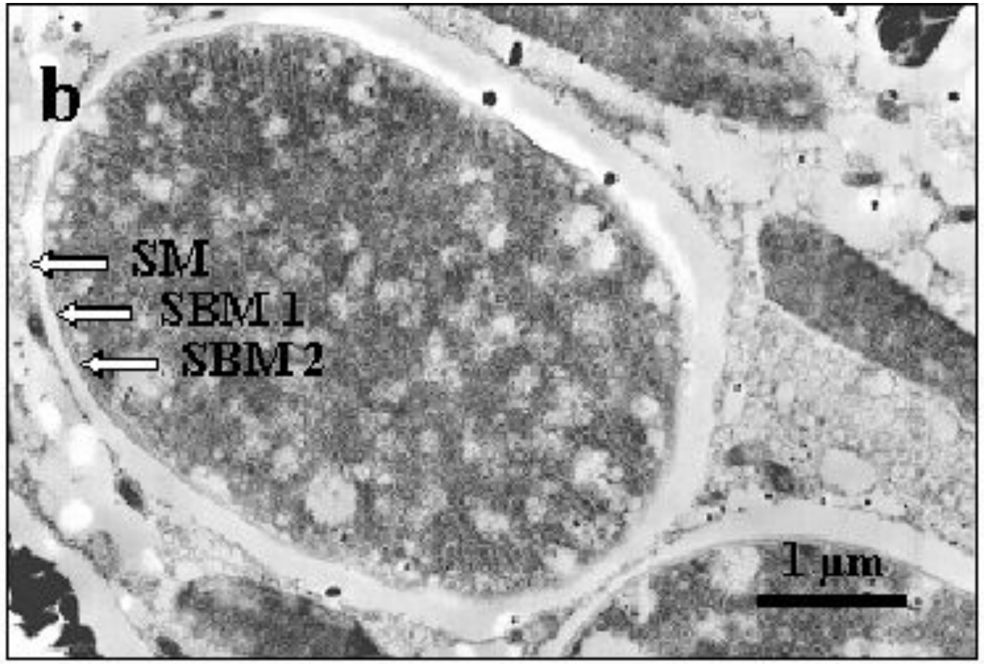
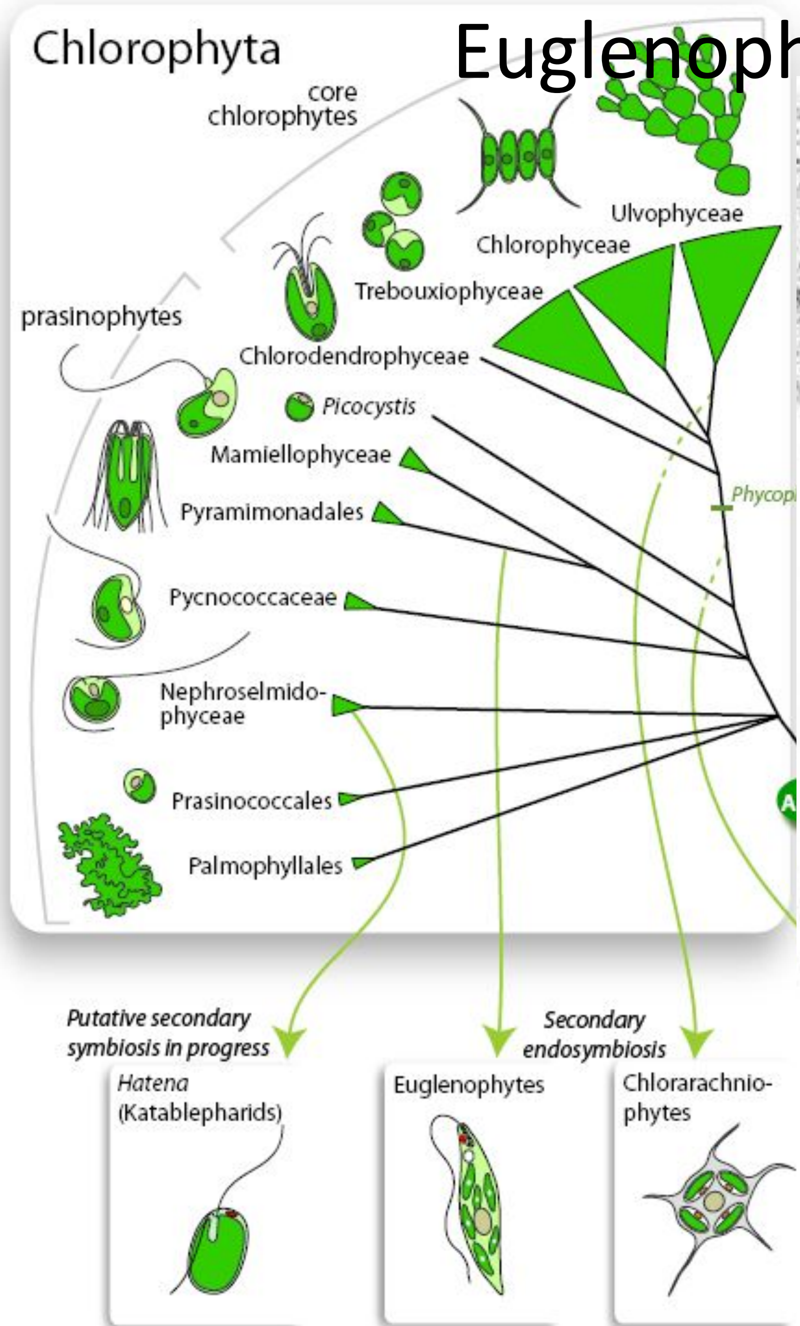


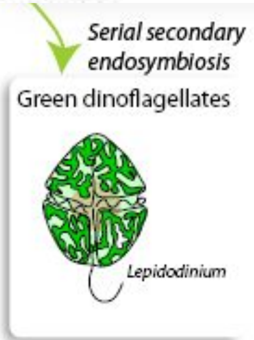
**Figure 6.** Evolutionary relations of plastids. The main branches diverging from the primary endosymbiotic event are those going to Chlorophyta (the 'green line') and Rhodophyta (the 'red line'), but even before their divergence the Glaucophyta plastids branch-off. For an explanation of other relationships, see text. From Gould *et al.*[59]. Reprinted, with permission, from the *Annual Review of Plant Biology*, vol. 59. © 2008 by Annual Reviews http://www.annualreviews.org/.

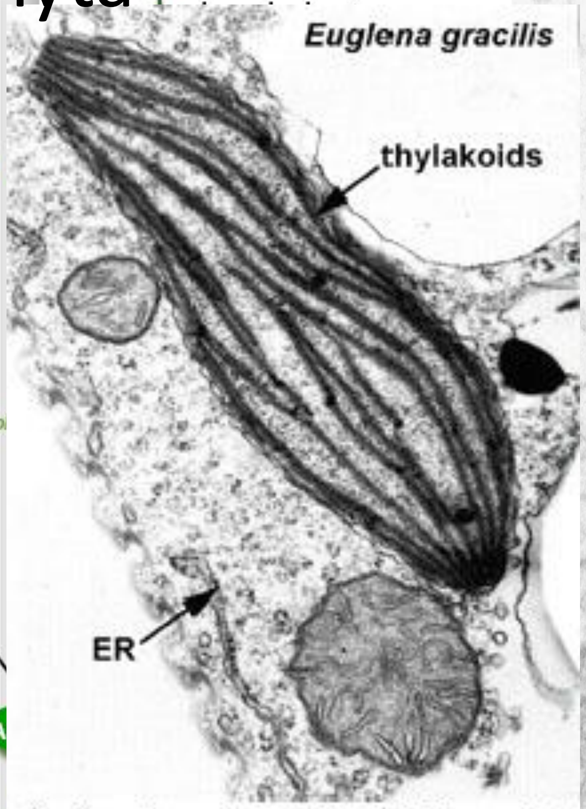


b) A Spheroid body of the diatom *Rhopalodia gibba*. SM: Symbiontophoric membrane SBM: Spheroid body membrane.

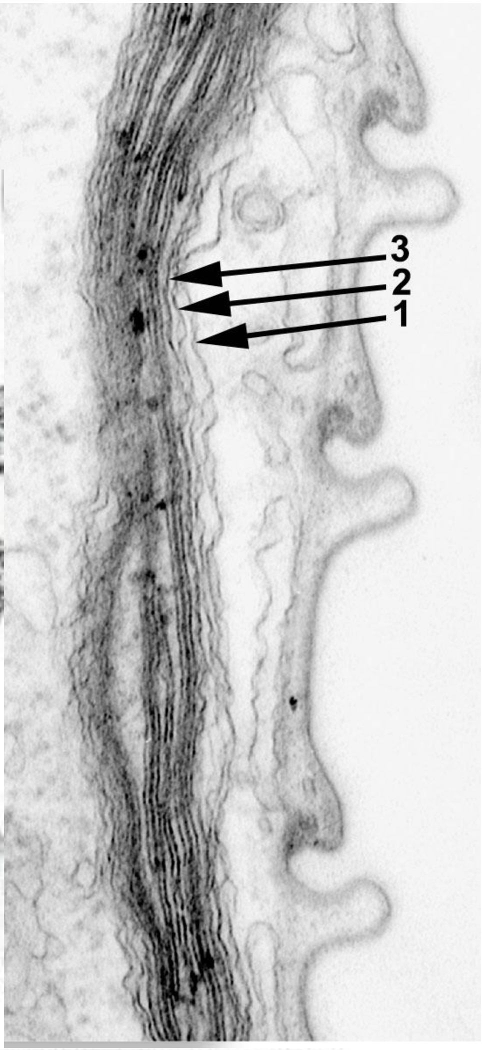
# Отдел Euglenophyta

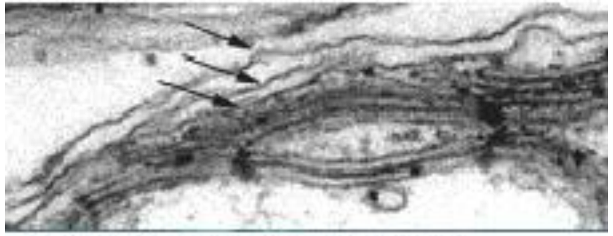






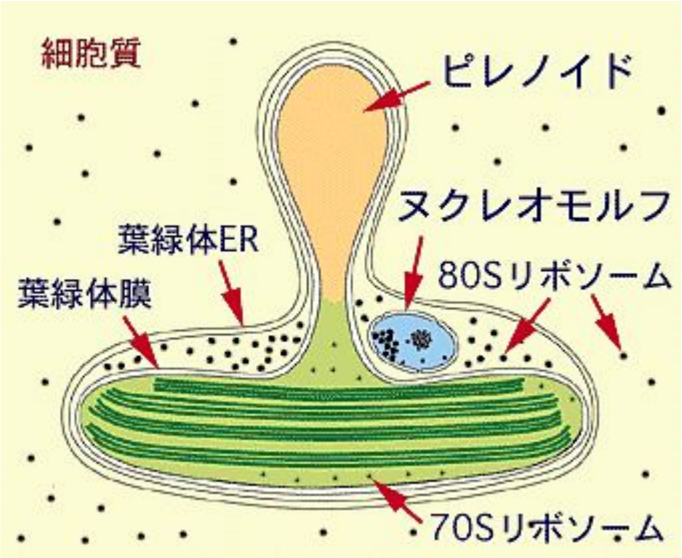
**Section through a euglenoid chloroplast. The thylakoids are stacked in groups of three.**

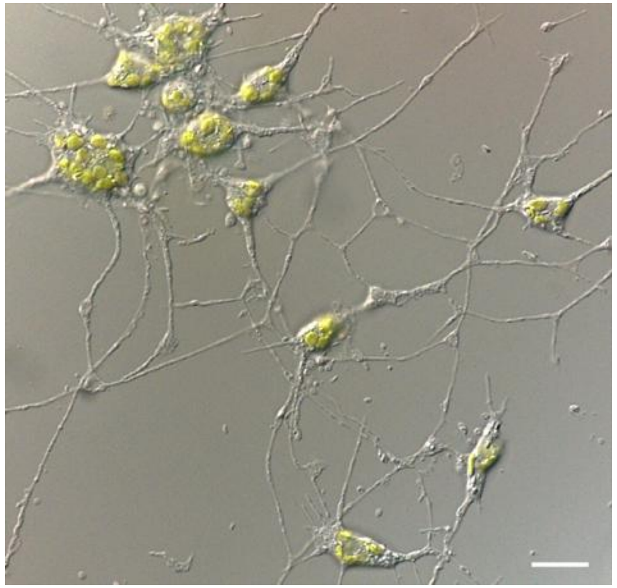




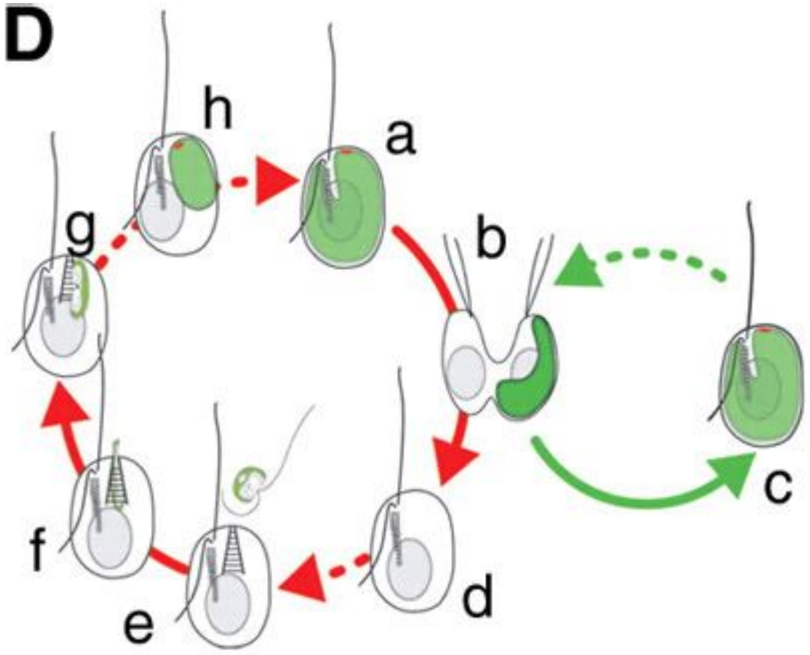
**High magnification view of the chloroplast envelope showing the three surrounding membranes.**

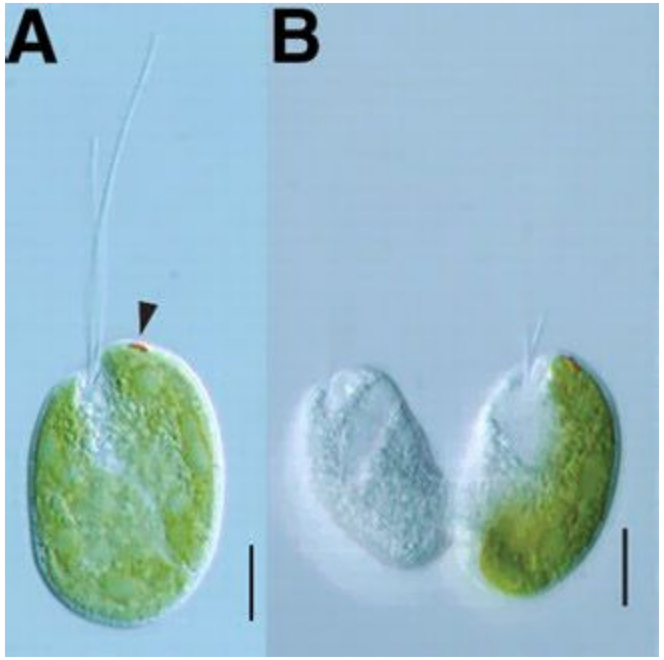
# Отдел Chlorarachniophyta

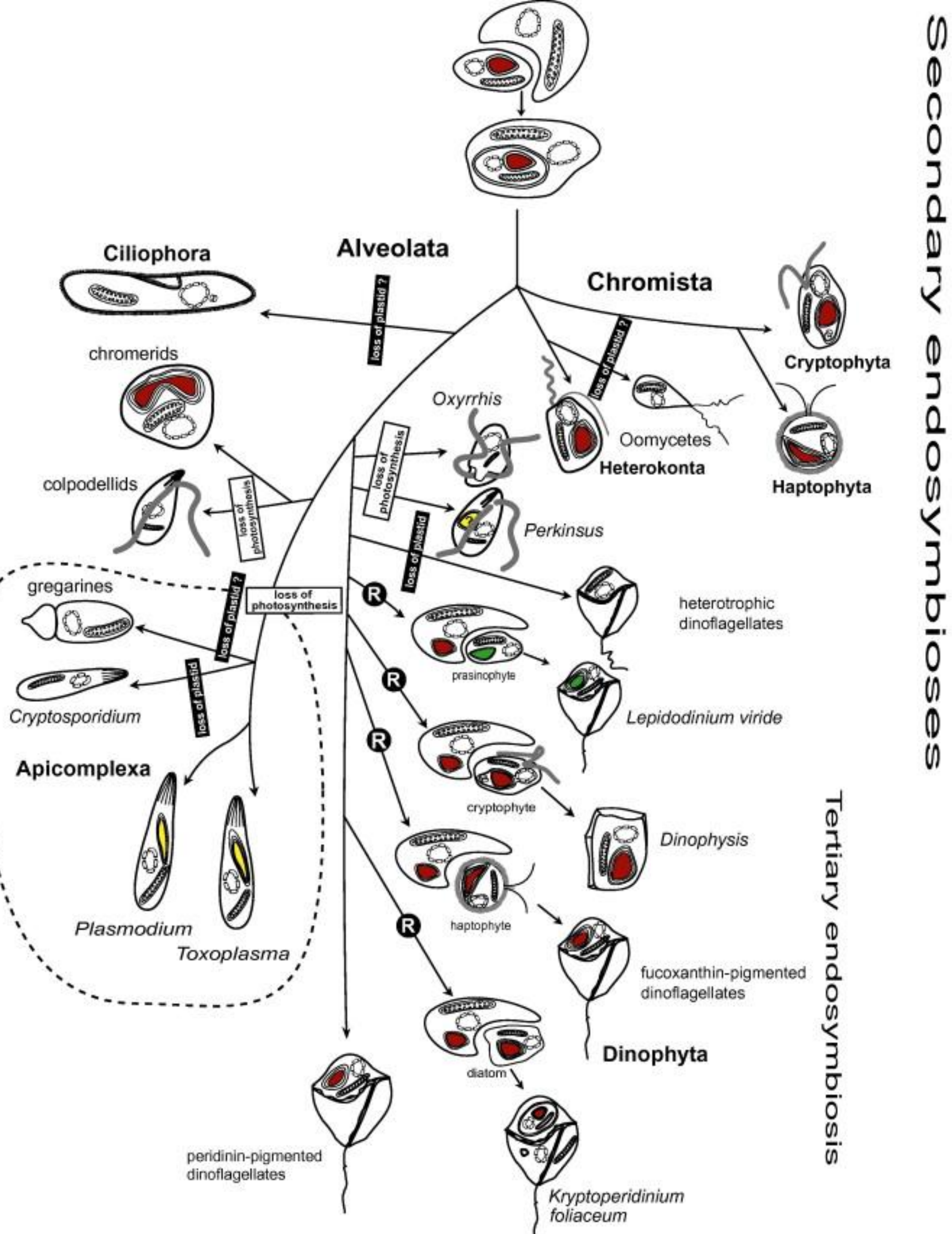


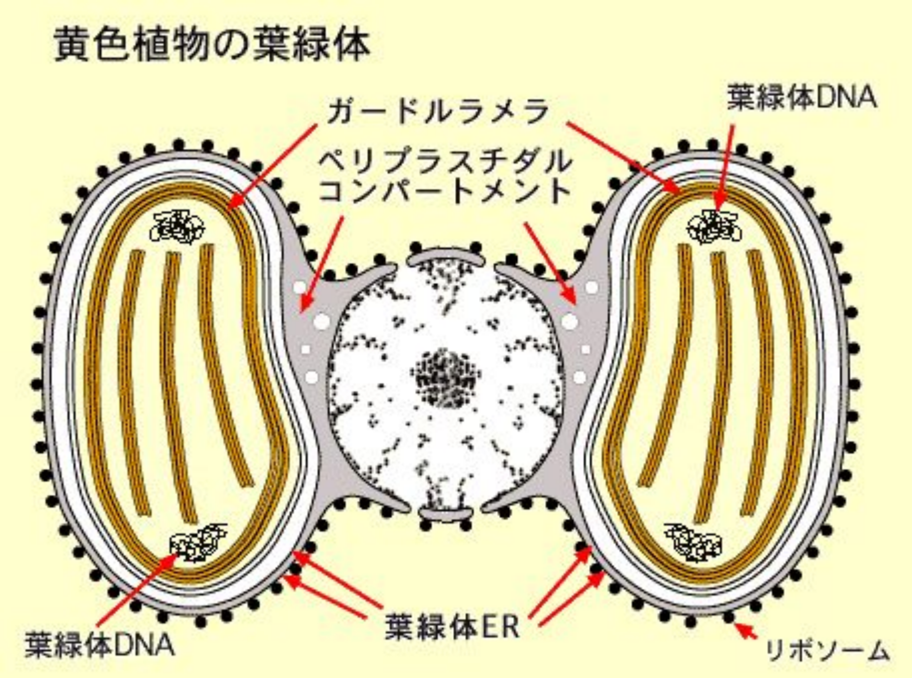


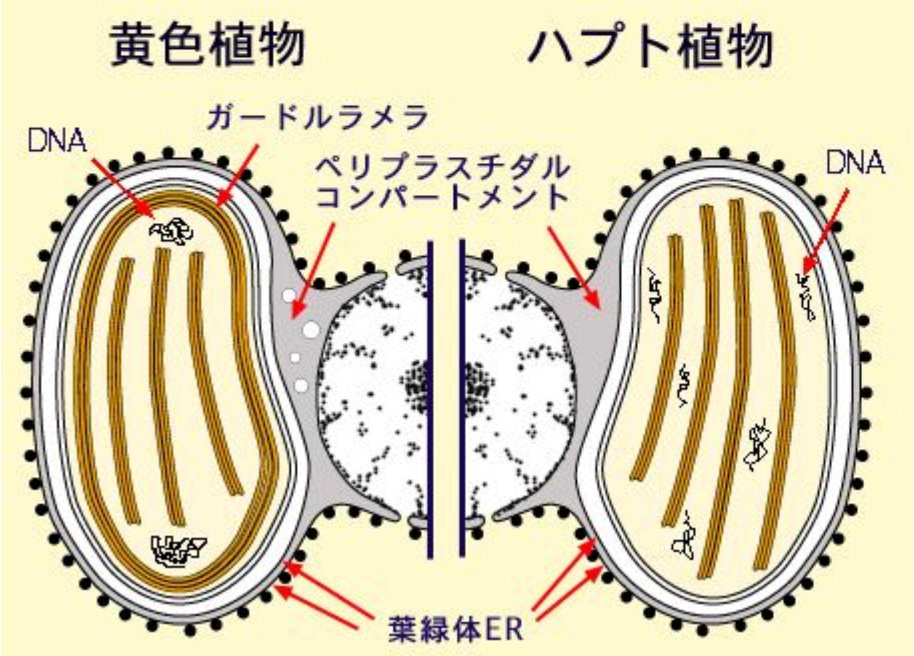
# *Hatena*






Secondary endosymbioses
Alveolata
Chromista
Ciliophora
loss of plastid ?
chromerids
colpodellids
loss of photosynthesis
Oxyrrhis
loss of photosynthesis
Perkinsus
loss of plastid
Heterokonta
Oomycetes
loss of plastid ?
Cryptophyta
Haptophyta
gregarines
loss of plastid ?
loss of photosynthesis
Cryptosporidium
loss of plastid
Apicomplexa
Plasmodium
Toxoplasma
heterotrophic dinoflagellates
R
prasinophyte
Lepidodinium viride
R
cryptophyte
Dinophysis
R
haptophyte
fucoxanthin-pigmented dinoflagellates
R
diatom
Dinophyta
Kryptoperidinium foliaceum
peridinin-pigmented dinoflagellates
Tertiary endosymbiosis


黄色植物の葉緑体
ガードルラメラ
葉緑体DNA
ペリプラスチダル
コンパートメント
葉緑体DNA
葉緑体ER
リボソーム


黄色植物
ハプト植物
DNA
ガードルラメラ
ペリプラスチダル
コンパートメント
DNA
葉緑体ER

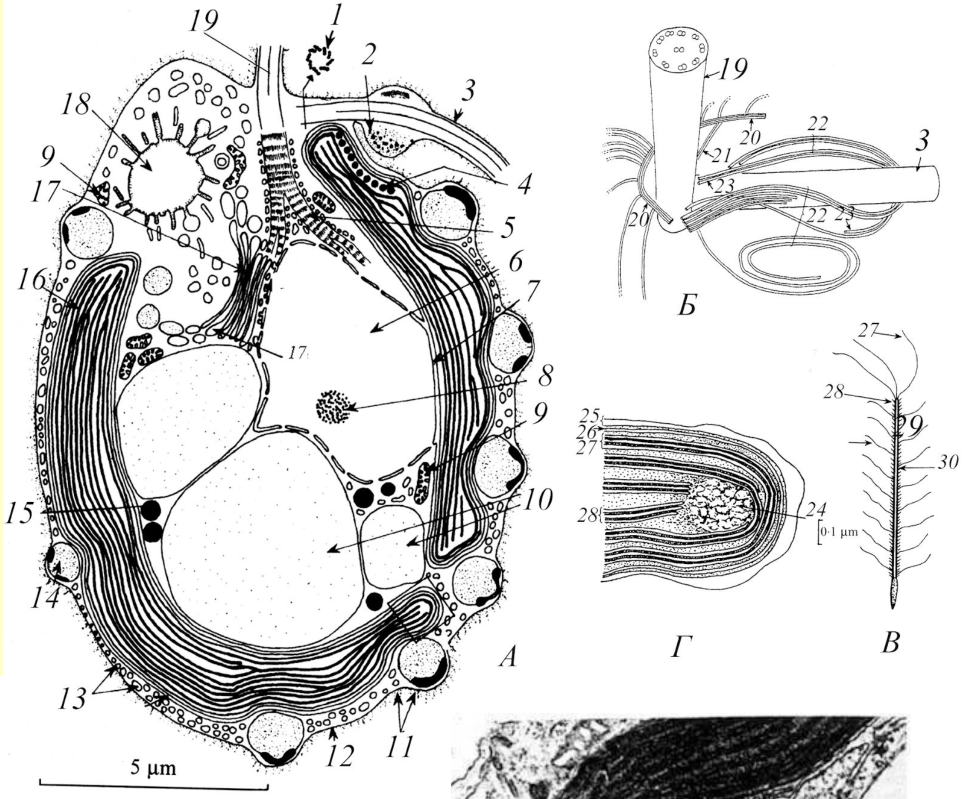
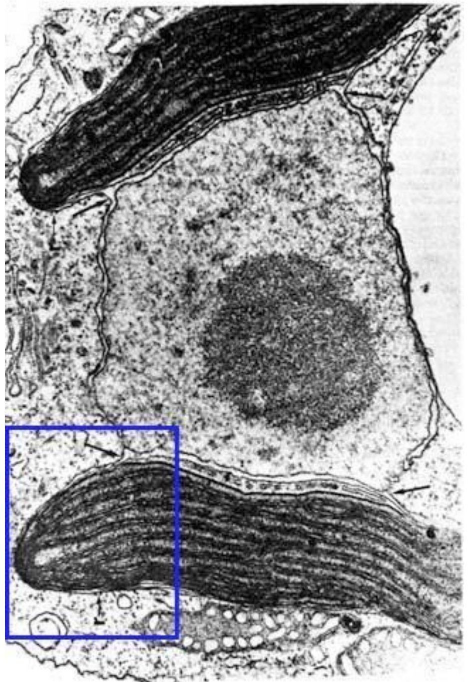

19
1
2
3
18
4
9
17
5
6
16
7
17
8
9
15
10
14
13
12
11
A
5 µm
19
20
21
22
3
23
20
22
23
Б
25
26
27
27
28
24
0·1 µm
Г
27
28
29
30
В

Рис. 247



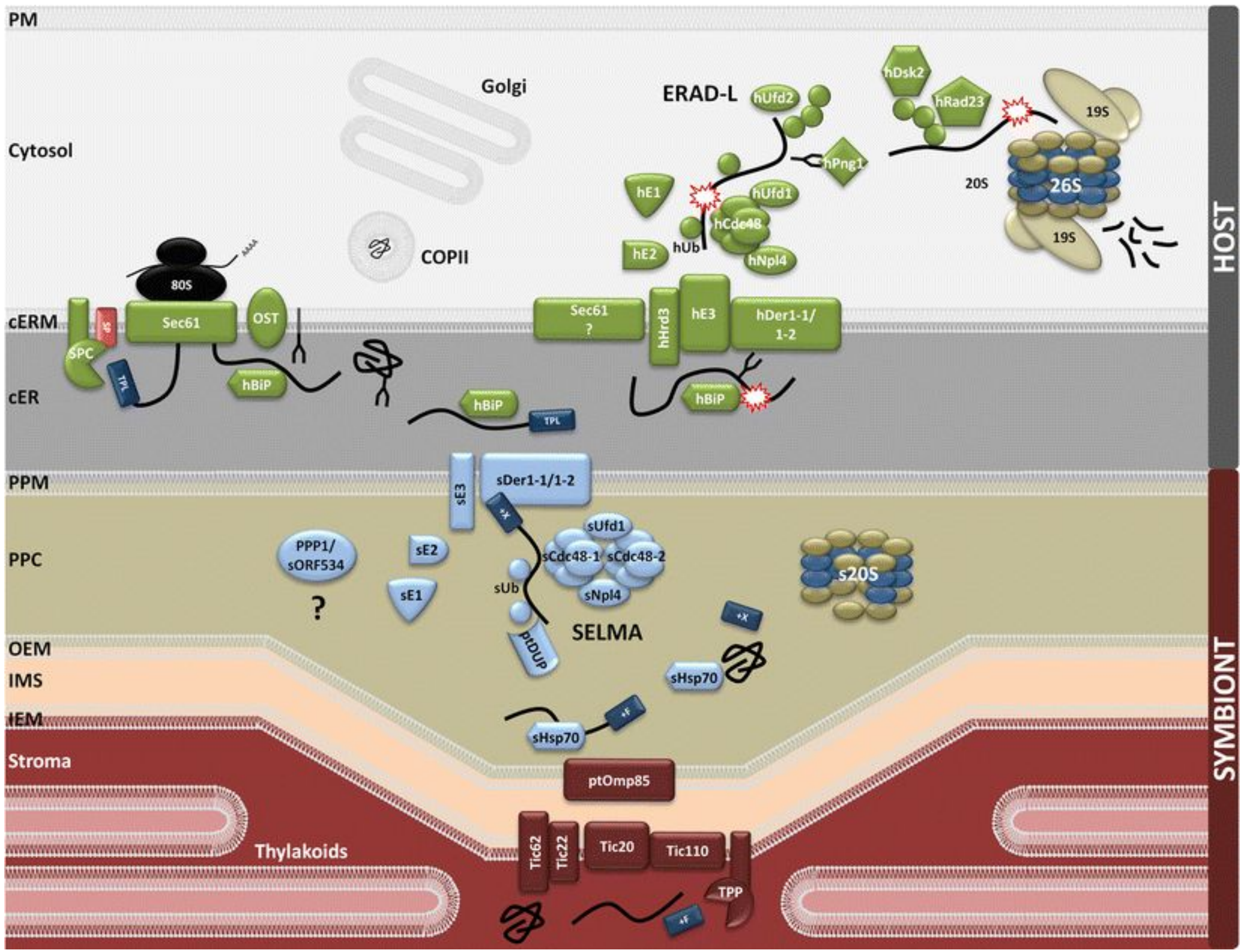


**Fig. 1**ERAD, SELMA, and protein import into complex plastids of diatoms. Entry into the (chloroplast) ER is host-derived (*h*): nucleus-encoded preproteins are equipped with an N-terminal signal peptide (*SP*) and enter the (*c*)*ER* cotranslationally through the Sec61 complex. During translocation, the SP of ER-resident or secretory proteins and, most likely, plastidal preproteins is cleaved off by the signal peptidase complex (*SPC*). The majority of ER or secretory proteins are N-glycosylated in the (c)ER lumen by an oligosaccharyl transferase (*OST*), folded into their native conformation via chaperones (*hBiP*) and are further transported through vesicles (e.g., *COPII*) towards the endomembrane system. The host machinery of the ERAD-L pathway recognizes misfolded or defective proteins (*asterisks*) in the (c)ER lumen, translocates them into the cytosol and polyubiquitinates the substrates for proteasomal degradation. For detailed information on the hostERAD-L system, see text. Passage of the second outermost membrane (*PPM*) and subsequent transport steps are symbiont derived (*s*): In addition to a SP, plastidal preproteins possess a transit peptide-like sequence (*TPL*) at their N-terminus, which is recognized in the cER lumen by an as yet unknown factor. Preproteins cross the PPM through the symbiont-specific ERAD-like machinery (*SELMA*), representing a recycled symbiontic ERAD system installed for translocation of plastidal preproteins. The ubiquitin-dependent translocation is supposed to be mediated by the AAA-ATPase Cdc48 with its cofactors (see text). PPC-resident proteins (+*X*) are processed by an as yet unidentified transit peptide peptidase and folded in the PPC. In addition to the SELMA system, an incomplete proteasomal s20S complex is present in the PPC of diatoms, which is believed to be uncoupled from translocation. Passage of the two inner membranes: stromal preproteins (+*F*) are further transported across the two inner membranes of the complex plastid via TOC- (*ptOmp85*) and TIC-related systems prior processing and folding in the stroma. Note that vesicular traffic (not shown) may be an alternative model for transport of stromal preproteins between PPM and OEM. *Question mark* unknown function; *cER* chloroplast endoplasmic reticulum;*OEM*/*IEM* outer/inner chloroplast envelope membrane; *IMS* intermembrane space; *TOC*/*TIC* translocon at the outer/inner chloroplast membrane

# Отдел Cryptophyta

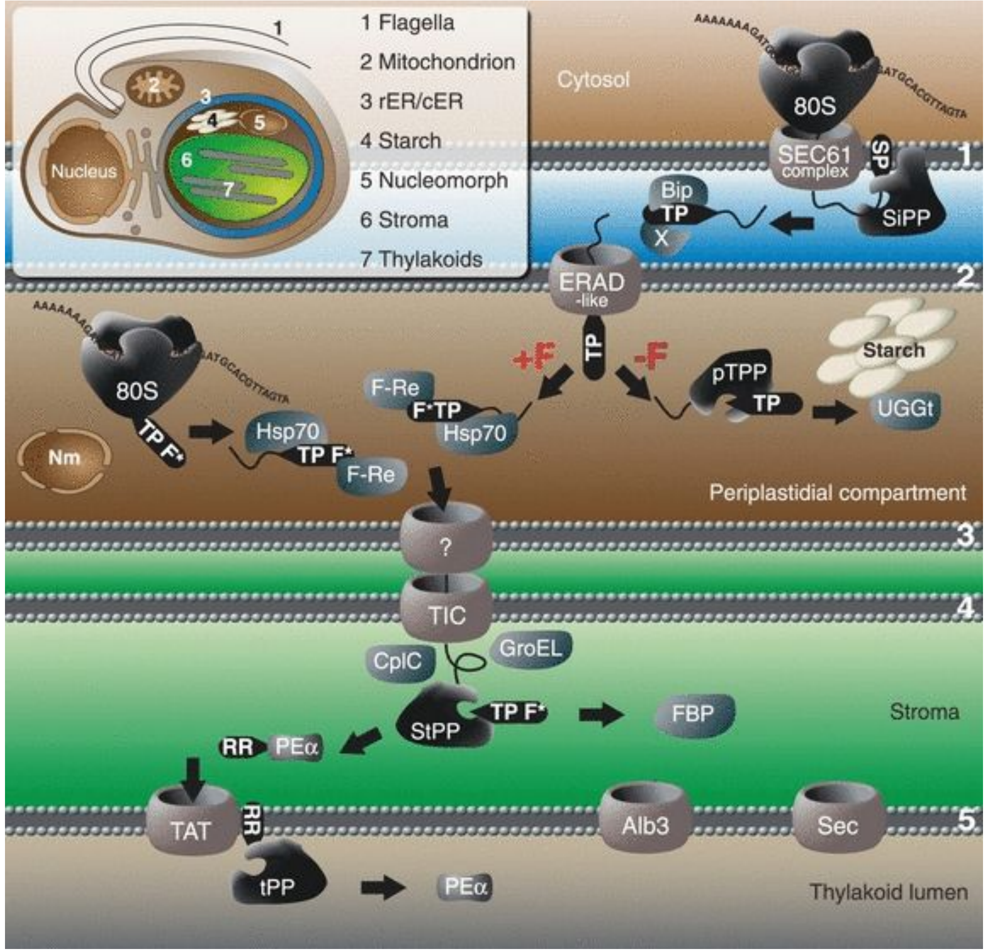
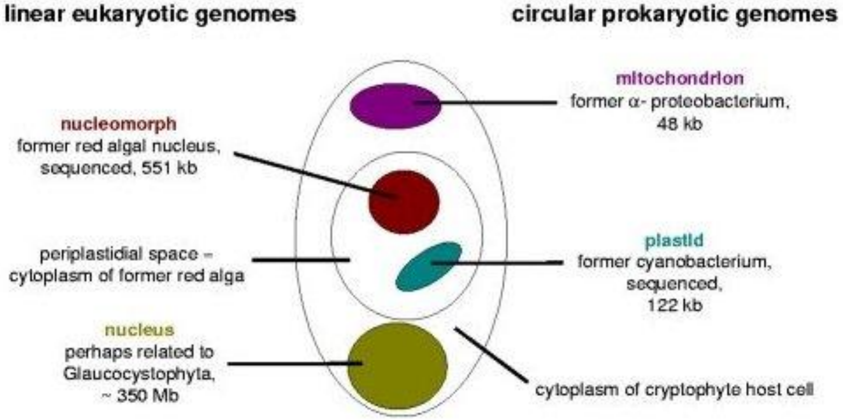
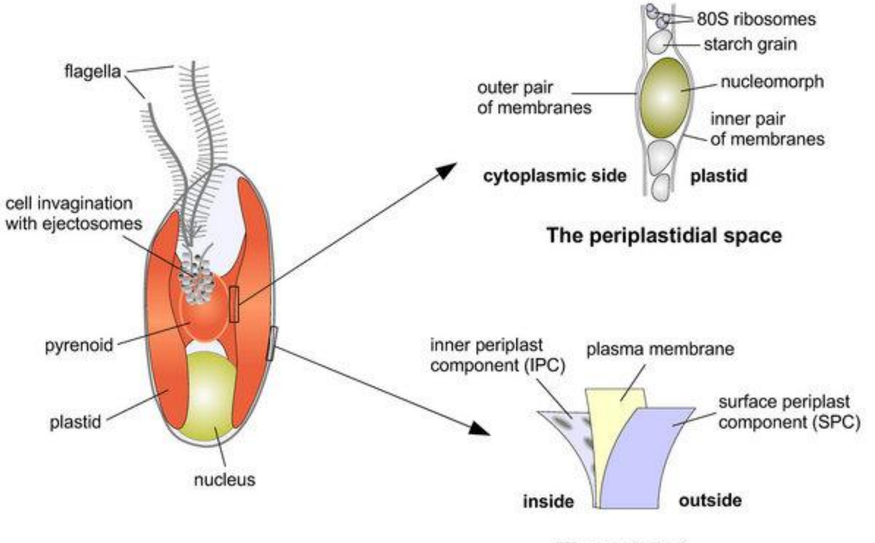


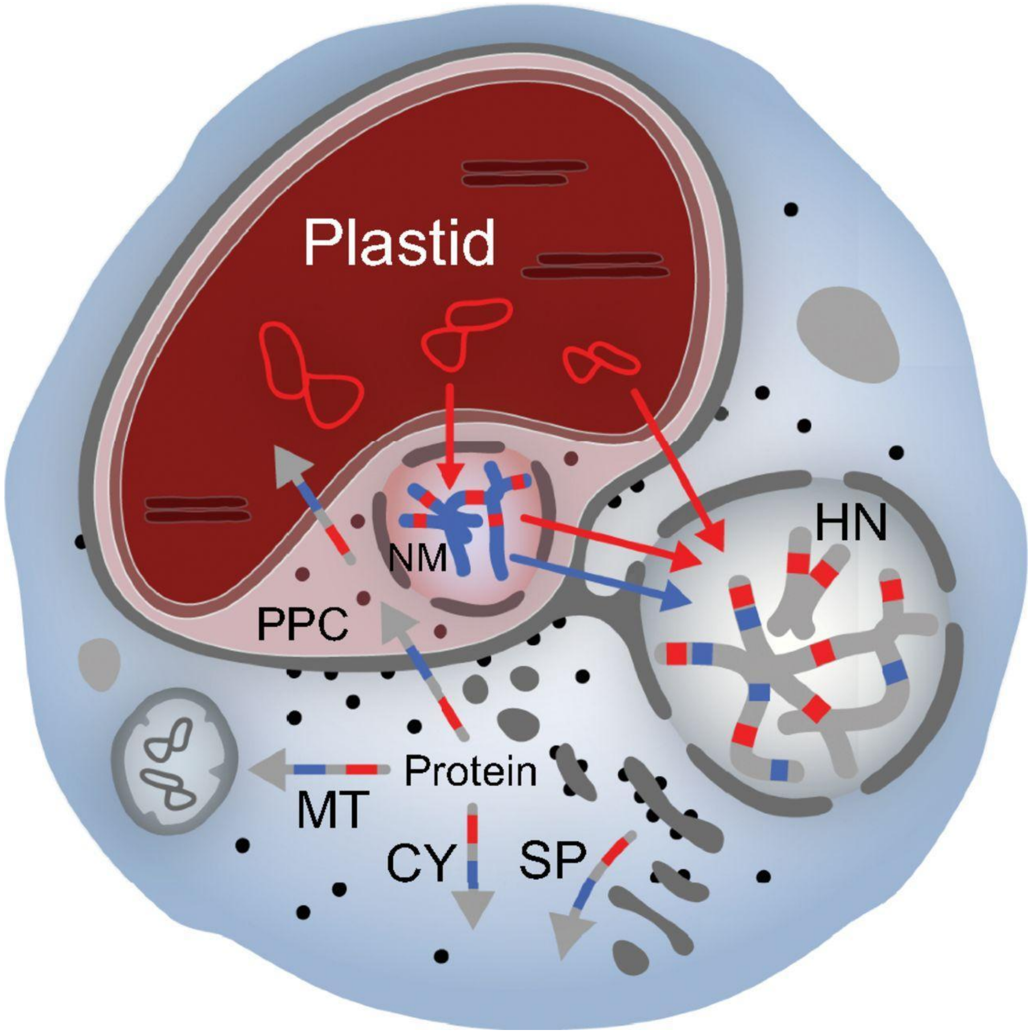
Fig. 5.
Genome sizes of the four genomes of the cryptophyte *Guillardia theta* according to Douglas et al. (2001). Nature 410: 1091-1096





Morphology of a cryptophyte cell

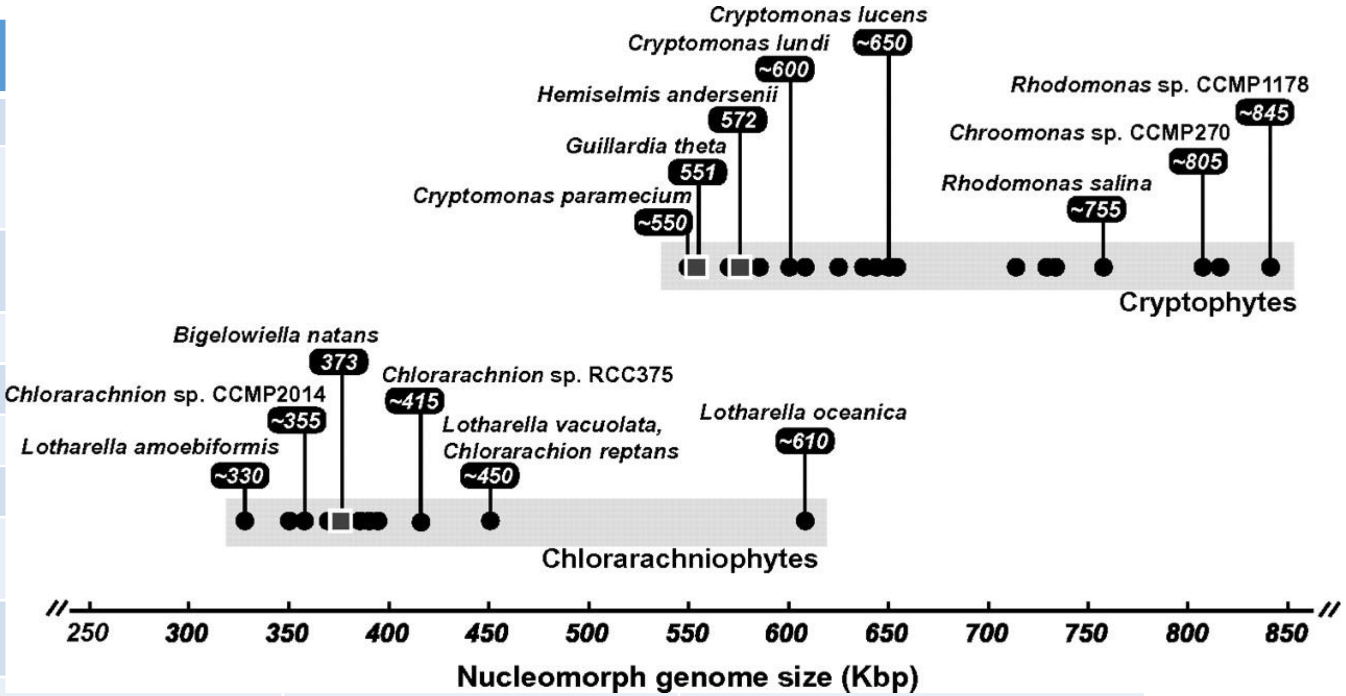
# Genome and proteome mosaicism in complex algae.



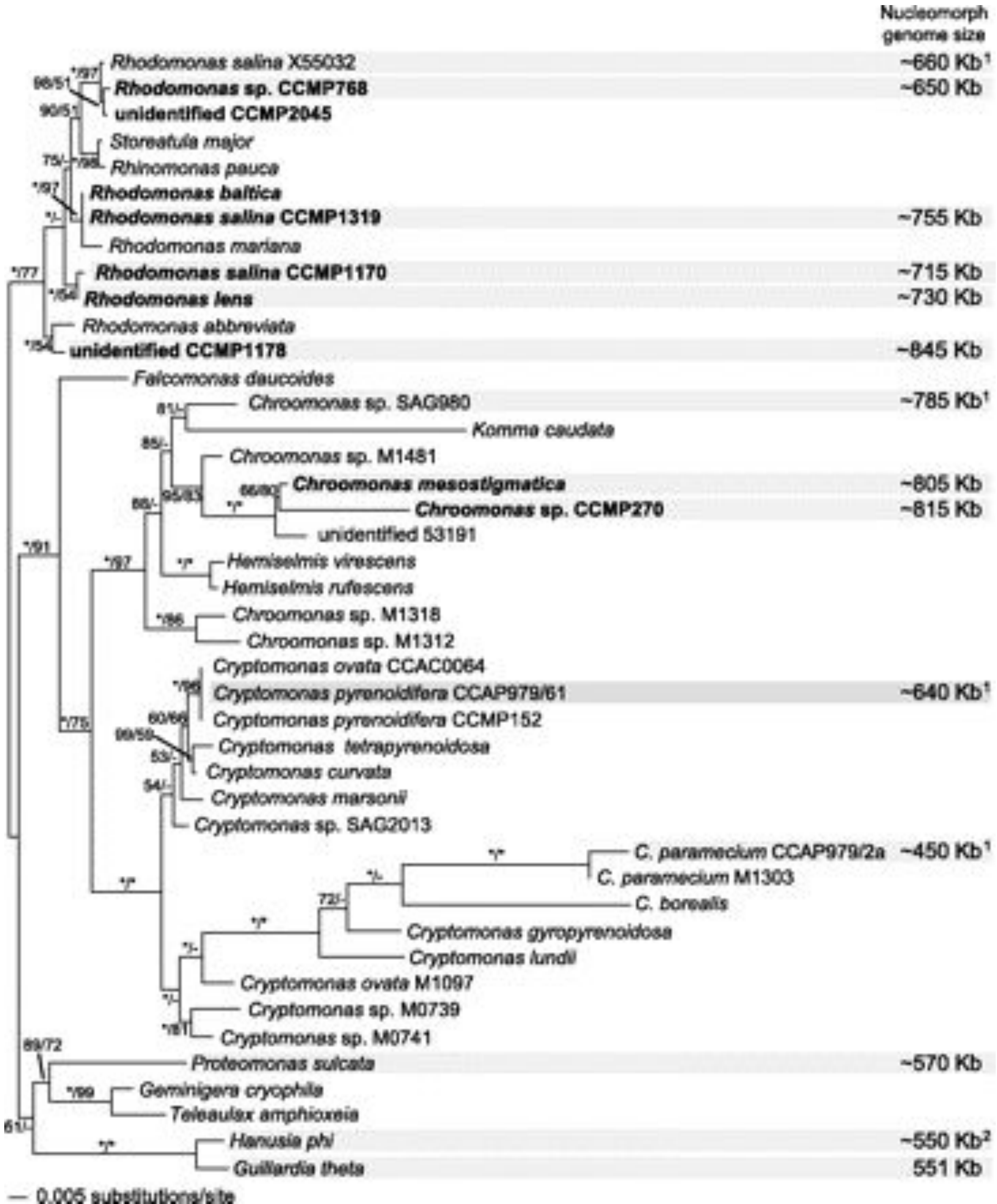
John M. Archibald PNAS 2015;112:10147-10153

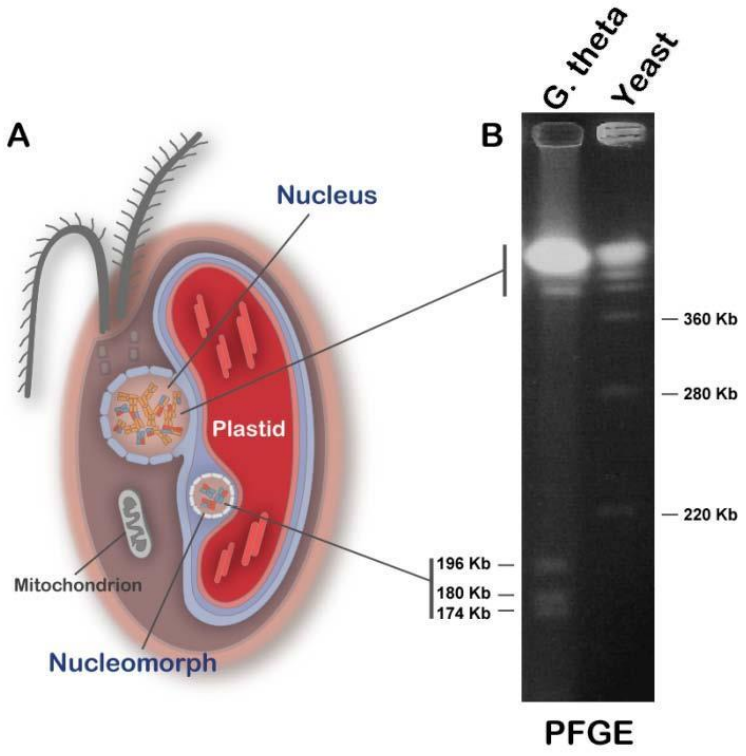
# Summary of known or estimated nucleomorph genome sizes in cryptophyte and chlorarachniophyte algae

| | | | |
|---|---|---|---|
| Guilardia theta CCMP327 | 551 | | |
| Hanusia phi CCMP325<br>Proteomonas sulcata | ~550<br>~570 | | |
| Chroomonas sp. CCMP270<br>Chroomonas sp. SAG980 | ~815<br>~785 | | |
| Ch. mesostigmatica CCMP1168 | ~805 | | |
| Hemiselmis tepida CCMP443 | ~640 | | |
| H.rufescens RCC659 | ~640 | | |
| H.andersenii CCMP644 | 572 | | |
| Cryptomonas erosa CCAP979/67<br>C.pyrenoidifera CCAP979/61 | ~655<br>~640 | | |
| C.tetrapyrenoidosa CCAP979/63 | ~635 | | |
| C.lundii CCAP979/69 | ~600 | | |
| C.lucens CCAP979/52 | ~650 | | |
| Cryptomonas sp. CCAP979/52 | ~640 | | |
| C.ovata CCAC0064 | ~640 | | |
| **C.paramecium 9772a** | **~450** | | |
| Rhodomonas salina X55032<br>R. salina CCMP 1170 | ~660<br>~715 | | |
| R.salina CCMP1319<br>Rhodomonas sp. CCMP768 | ~755<br>~650 | | |
| R.lens<br>**Unindentified CCMP1178** | ~730<br>**~845** | | |

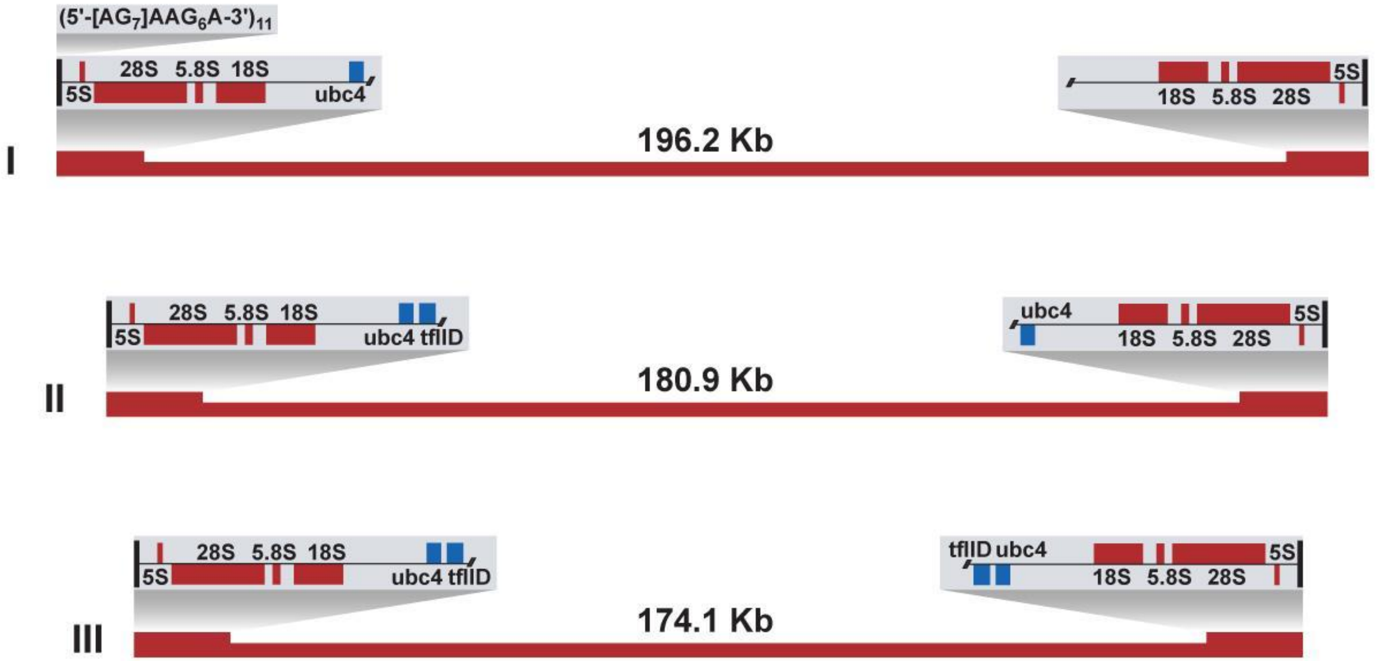


Archibald, J. M. et al. J Hered 2009 100:582-590


Nucleomorph genome size
Rhodomonas salina X55032 ~660 Kb¹
Rhodomonas sp. CCMP768 ~650 Kb
unidentified CCMP2045
Storeatula major
Rhinomonas pauca
Rhodomonas baltica
Rhodomonas salina CCMP1319 ~755 Kb
Rhodomonas mariana
Rhodomonas salina CCMP1170 ~715 Kb
Rhodomonas lens ~730 Kb
Rhodomonas abbreviata
unidentified CCMP1178 ~845 Kb
Falcomonas daucoides
Chroomonas sp. SAG980 ~785 Kb¹
Komma caudata
Chroomonas sp. M1481
Chroomonas mesostigmatica ~805 Kb
Chroomonas sp. CCMP270 ~815 Kb
unidentified 53191
Hemiselmis virescens
Hemiselmis rufescens
Chroomonas sp. M1318
Chroomonas sp. M1312
Cryptomonas ovata CCAC0064
Cryptomonas pyrenoidifera CCAP979/61 ~640 Kb¹
Cryptomonas pyrenoidifera CCMP152
Cryptomonas tetrapyrenoidosa
Cryptomonas curvata
Cryptomonas marsonii
Cryptomonas sp. SAG2013
C. paramecium CCAP979/2a ~450 Kb¹
C. paramecium M1303
C. borealis
Cryptomonas gyropyrenoidosa
Cryptomonas lundii
Cryptomonas ovata M1097
Cryptomonas sp. M0739
Cryptomonas sp. M0741
Proteomonas sulcata ~570 Kb
Geminigera cryophila
Teleaulax amphioxeia
Hanusia phi ~550 Kb²
Guillardia theta 551 Kb
*/97
98/51
90/51
75/-
*/98
*/97
*/-
*/77
*/54
*/54
81/-
85/-
88/-
95/83
66/80
*/*
*/*
*/97
*/86
*/91
*/99
60/66
99/59
53/-
54/-
*/75
*/*
*/*
*/-
72/-
*/*
*/-
*/-
*/81
89/72
*/99
61/-
*/*
0.005 substitutions/site

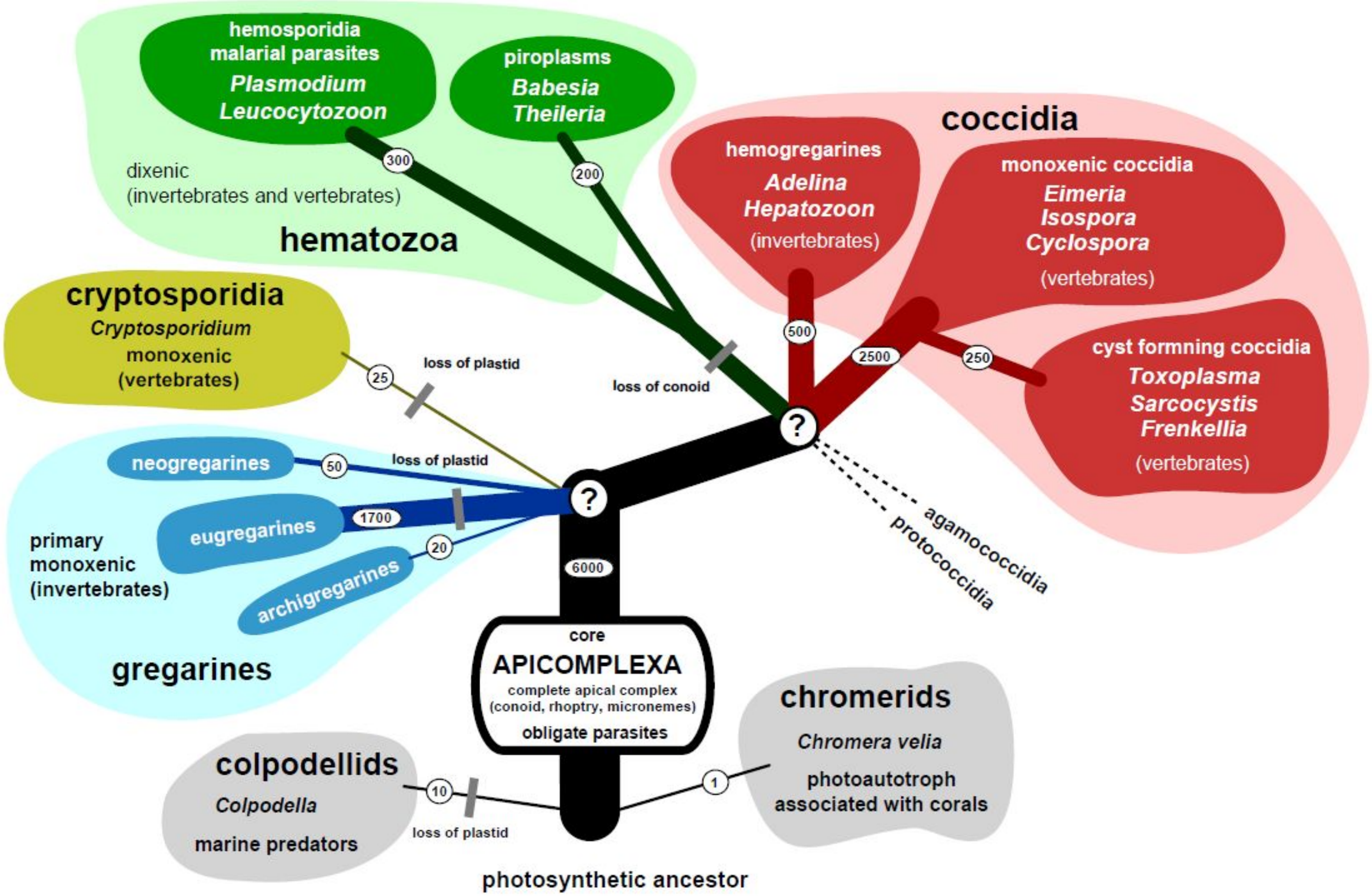


## *Guillardia theta* nucleomorph genome (551 Kb)



# Характеристики геномов нуклеоморф

| Genome characteristics | *Guillardia theta* | *Hemiselmis andersenii* | *Bigelowiella natans* |
|---|---|---|---|
| Evolutionary origin | Red algae | Red algae | Green algae |
| Genome size (bp) | 551 264 | 571 872 | 372 870 |
| Chromosome number/size | 3 (196.2, 180.9, 174.1 kbp) | 3 (207.5, 184.7, 179.6 kbp) | 3 (140.6, 134.1, 98.1 kbp) |
| Chromosome structure | Subtelomeric inverted repeats including rDNA genes | Subtelomeric inverted repeats, only 3 with complete rDNAs | Subtelomeric inverted repeats including rDNA genes |
| Telomeric sequence/length | $([AG]_7AAG_6A)_{11}$ | $(G[A]_{17})_{4–7}$ | $(TCTAGGG)_{25–45}$ |
| Genomic A + T content | ~55 | ~60 | ~50 |
| Inverted repeats (including rDNA) (%) | | | |
| Single-copy DNA (%) | 65–77 | ~ 75 | >65 |
| Number of genes | | | |
| Protein genes | 465 | 472 | 293 |
| Non-mRNA (rRNA, tRNA, snRNA, and snoRNA) | 67 | 53 | 42 |
| Pseudogenes | 1 | 1 | 5 |
| Total | 513 | 525 | 340 |
| Gene density | 1.07 kb/gene | 1.09 kb/gene | 1.10 kb/gene |
| Introns and size range | 17 (42–52 bp) | None | 852 (18–21 bp) |
| Plastid genes | 30 | 30 | 17 |

hemosporidia
malarial parasites
***Plasmodium***
***Leucocytozoon***
piroplasms
***Babesia***
***Theileria***
dixenic
(invertebrates and vertebrates)
hematozoa
300
200
coccidia
hemogregarines
***Adelina***
***Hepatozoon***
(invertebrates)
monoxenic coccidia
***Eimeria***
***Isospora***
***Cyclospora***
(vertebrates)
cyst formning coccidia
***Toxoplasma***
***Sarcocystis***
***Frenkellia***
(vertebrates)
500
2500
250
loss of conoid
?
agamococcidia
protococcidia
cryptosporidia
*Cryptosporidium*
monoxenic
(vertebrates)
25
loss of plastid
neogregarines
50
loss of plastid
eugregarines
1700
archigregarines
20
primary
monoxenic
(invertebrates)
gregarines
?
6000
core
APICOMPLEXA
complete apical complex
(conoid, rhoptry, micronemes)
obligate parasites
chromerids
*Chromera velia*
photoautotroph
associated with corals
1
colpodellids
*Colpodella*
marine predators
10
loss of plastid
photosynthetic ancestor

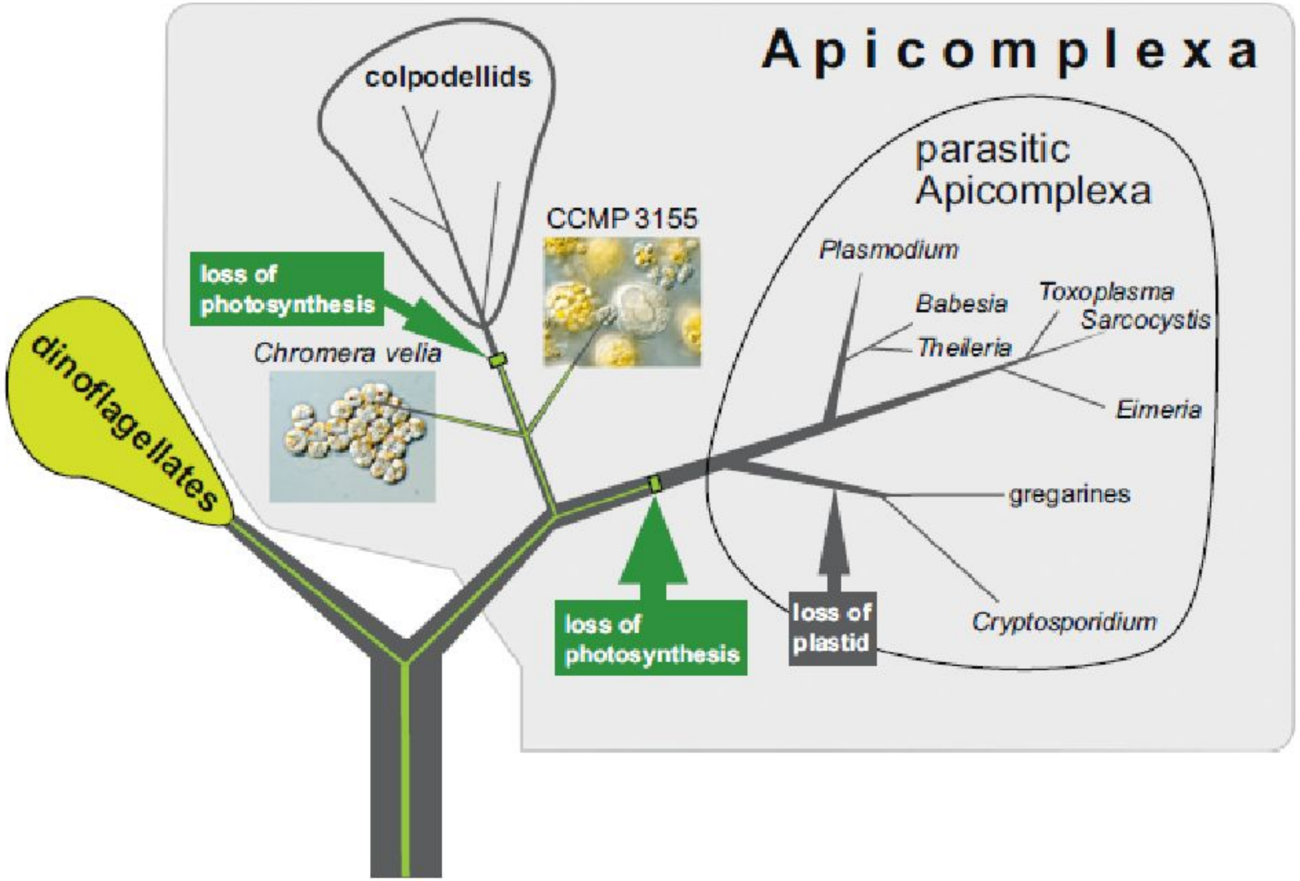
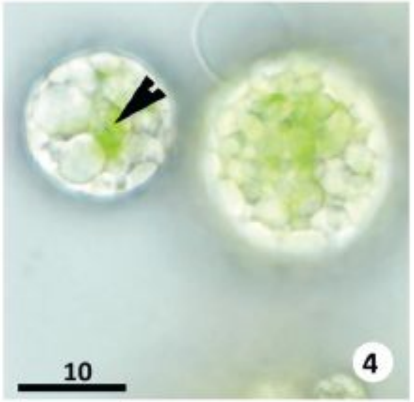
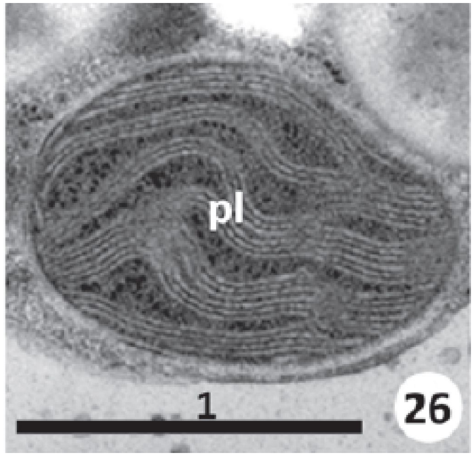


**Figure 55.** Current view of the evolution of chromerids. A schematic tree shows evolutionary relationships among chromerids and apicomplexans. The green line in the tree indicates photosynthetic organisms. Losses of photosynthesis or plastids are indicated. We propose that photosynthesis was lost once in chromerids with respect to colpodellids and once in the lineage evolving to apicomplexan parasites. We suppose chromerids to form a sister groups, mainly based on their unique pigmentation and molecular phylogeny.

# *Vitrella brassicaformis*





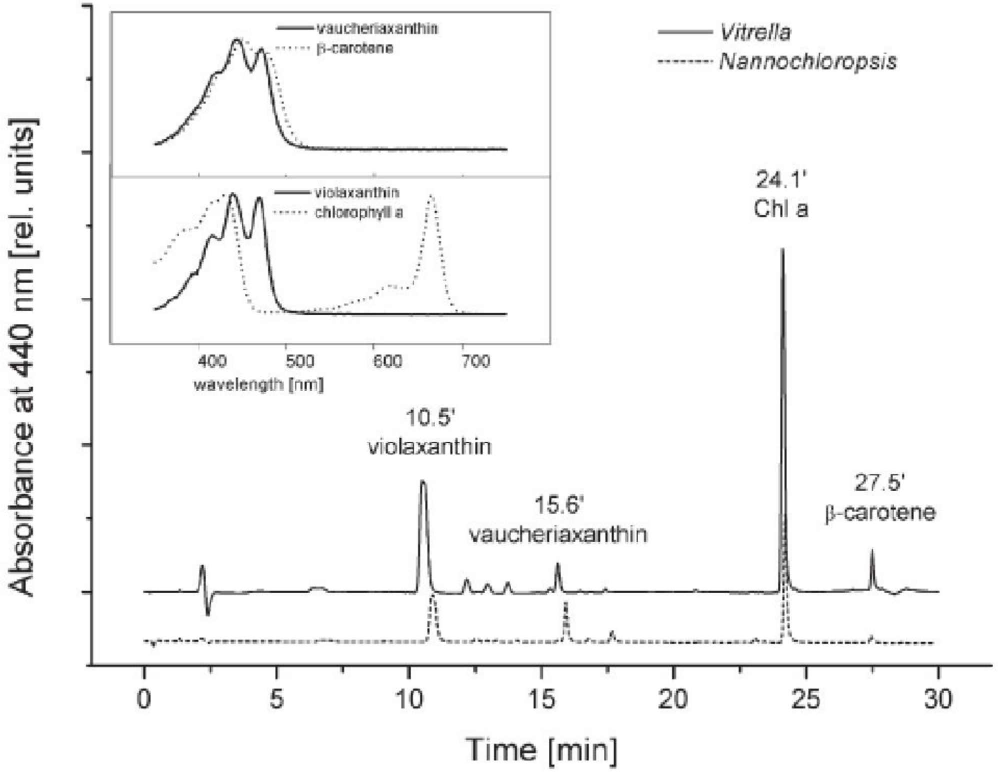
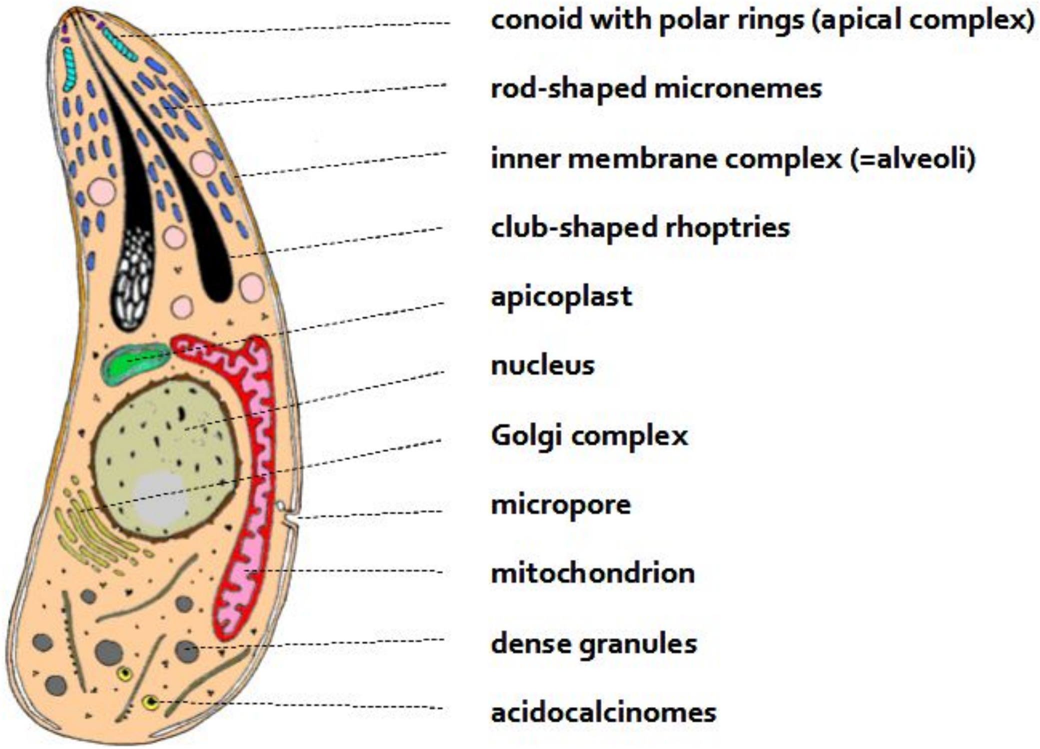
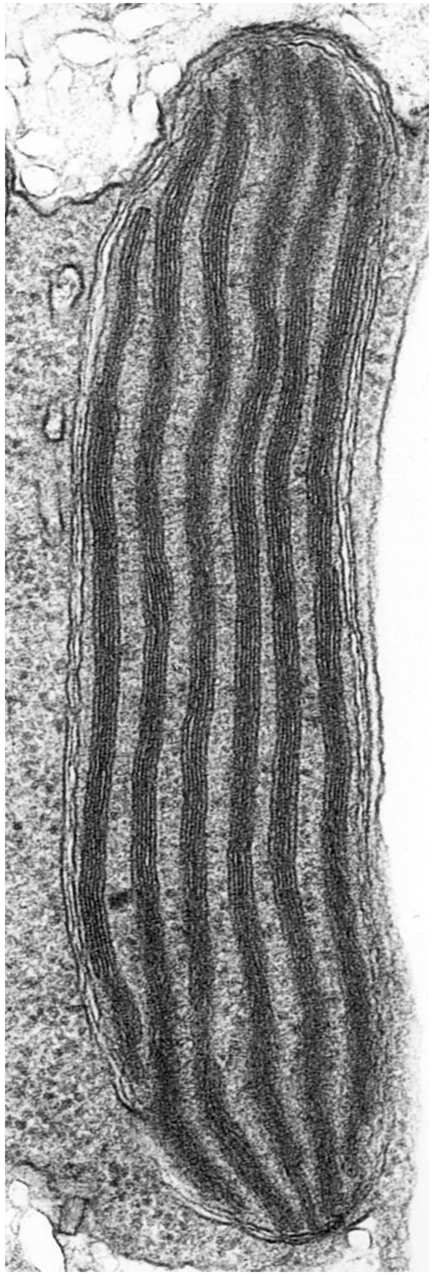


**Figure 54.** Composition of the photosynthetic pigments in *Vitrella brassicaformis* and *Nannochloropsis limetica*.


conoid with polar rings (apical complex)
rod-shaped micronemes
inner membrane complex (=alveoli)
club-shaped rhoptries
apicoplast
nucleus
Golgi complex
micropore
mitochondrion
dense granules
acidocalcinomes



Наиболее часто встречающийся тип пластид у динофитов – перидинин содержащие, окруженные тремя мембранами. В этих пластидах обнаружена **форма II РуБисКо**, известная также для некоторых бактерий, состоящая только из 2-х больших субъединиц и кодирующаяся ядерным геномом. У ряда динофитовых с такими пластидами **хлоропластный геном сильно редуцирован** (осталось менее 20 действующих генов) и пластидная ДНК фрагментирована на отдельные кольцевые фрагменты 2-3 кб, содержащие по одному гену. Такая форма хлоропластной ДНК и максимальная передача хлоропластных генов в ядро - уникальна для водорослей. В хлоропластах встречаются пиреноиды различной формы.

4. Пресноводные формы запасают преимущественно **крахмал**, откладываемый в цитоплазме, а морские – **липиды и стеролы.**

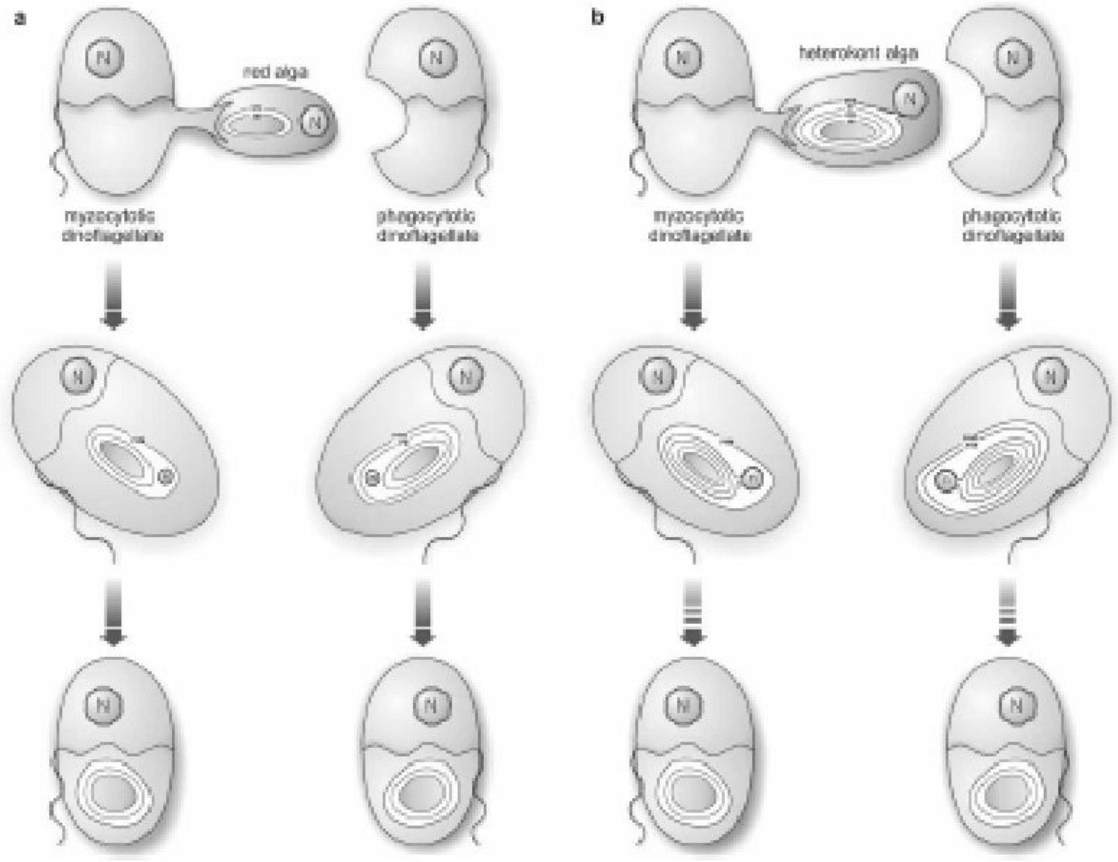


**Fig. 1.** Models explaining evolutionary origin of the peridinin plastid. (a) According to the secondary model, the peridinin plastid evolved from a red alga that harboured a cyanobacterium-derived plastid surrounded by two membranes: the inner membrane (IM) and the outer membrane (OM). There are two versions of this model: a myzocytotic scenario (left) and phagocytotic scenario (right). In myzocytotic engulfment of the red alga, the peridinin plastid would be surrounded by three membranes: IM, OM, and the phagosomal membrane of the host (PHM). In phagocytotic engulfment, the envelope initially would be composed of four membranes (IM, OM, the endosymbiont plasmalemma (EP), and PHM) and one of them would have to be lost. It is assumed that this membrane was the EP. (b) The tertiary model postulates that the peridinin plastid is derived from a heterokont alga which possessed a red alga-derived plastid surrounded by four membranes: IM, OM, EP, and the plastid endoplasmic reticulum (PER). There is a myzocytotic (left) and phagocytotic (right) version of this model. In myzocytotic engulfment of the heterokont, the peridinin plastid would be initially surrounded by five membranes: IM, OM, EP, PER, and PHM. In phagocytotic engulfment, its envelope would additionally contain the plasmalemma of the heterokont endosymbiont (PHE). This means that the ancestral peridinin plastid must have lost two (myzocytotic scenario) or three (phagocytotic scenario) membranes. Regardless of the scenario followed, it currently is unclear which membranes were eliminated. N: typical eukaryotic nucleus; n: highly reduced eukaryotic nucleus known as the nucleomorph.

- Prasinophyte-производные «пластиды»:
- Постоянные зеленые хлоропласты в *Lepidodinium* (Watanabe et al. 1991, Elbrächter and Schnepf 1996, Hansen et al. 2007). Ряд генов из эндосимбионта перемещен в ядро хозяина (Ming

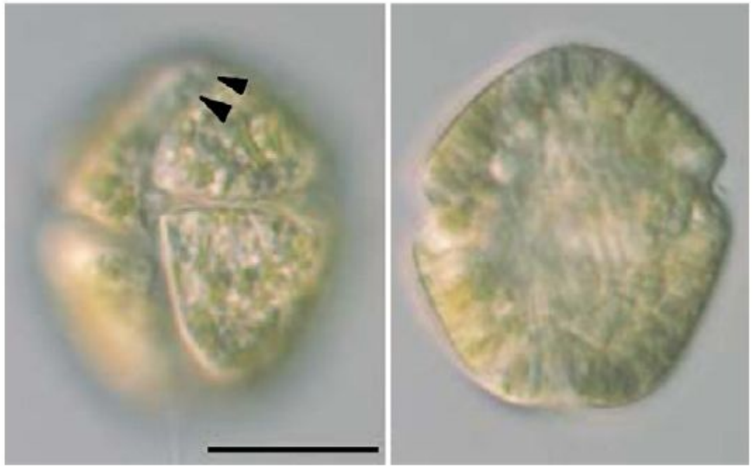
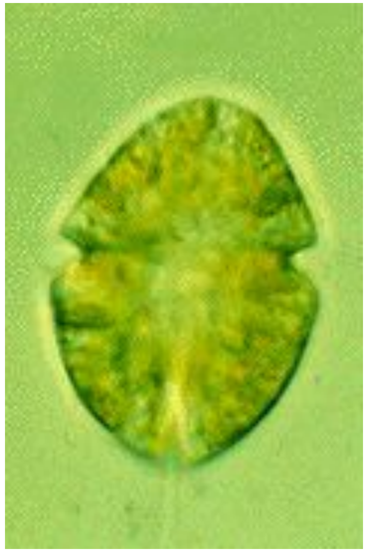
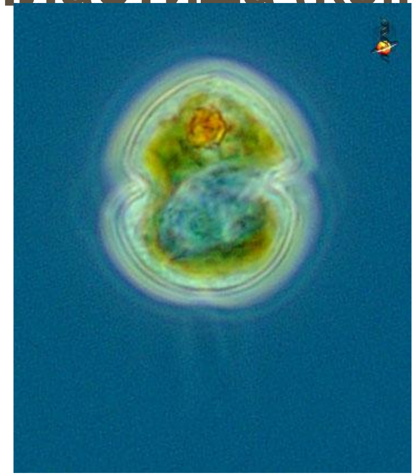


Fig. 1. Light micrographs of a live cell of *Lepidodinium chlorophorum* showing general morphology. Left: Appearance near the surface of cell. Note the apical groove (arrowheads), shape of chloroplasts and both cingulum and sulcus. Right: different focus image near the center of cell, showing the nucleus located in the center of the cell. Scale bar=20 µm.



- **Haptophyte-произошедшие пластиды:**
- **В этой ветви (*Karenia, Karlodinium, Takayama*) фотосинтезирующие органеллы представляют настоящие пластиды – гены для многих белков, участвующие в фотосинтезе, находятся в ядре** (Ishida and Green 2002,
Patron et al. 2006, Nosenko et al. 2006). **При таком типе возникновения пластид, эукариота съела другую эукариоту, у которой пластида произошла в результате вторичного эндосимбиоза. Такой тип эндосимбиоза называется третичным. У *Dinophysis mitra* гаптофит существует как клептопластида** (Koike et al. 2005).

*Karenia brevis*

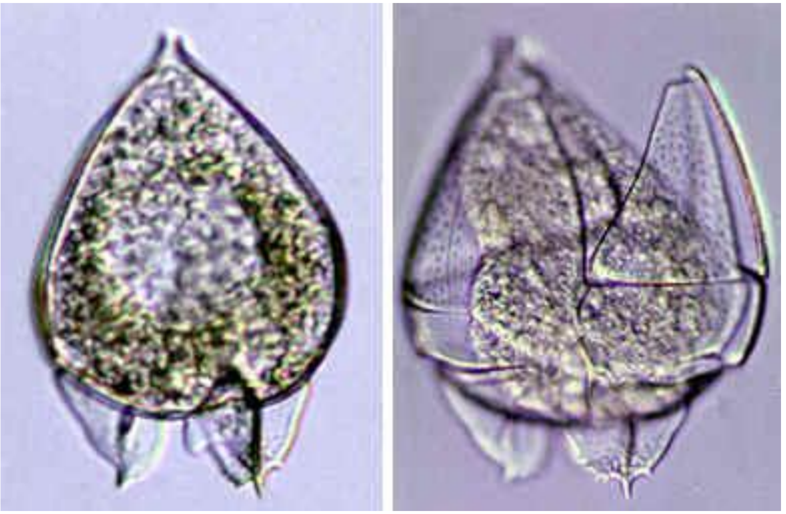


*Karlodinium micrum*

- Dictyophyte-производные пластиды:

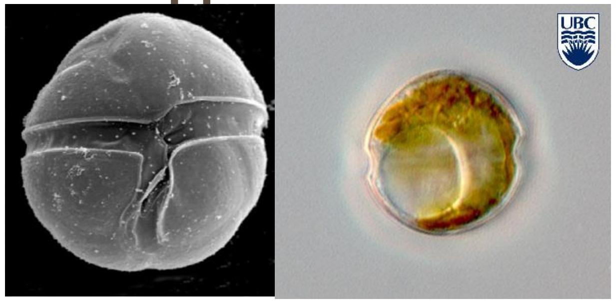
**Один вид динофлагеллят (*Podolampas bipes*) содержит постоянный диктиохофициевый эндосимбионт с хлоропластами и ядром**

(Schnepf and Elbrächter 1999, Schweikert and Elbrächter 2004).

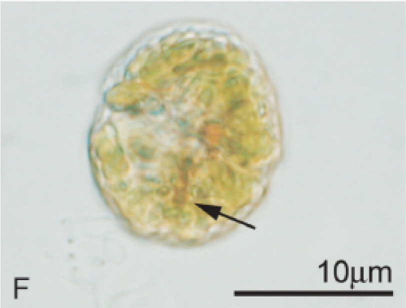


•

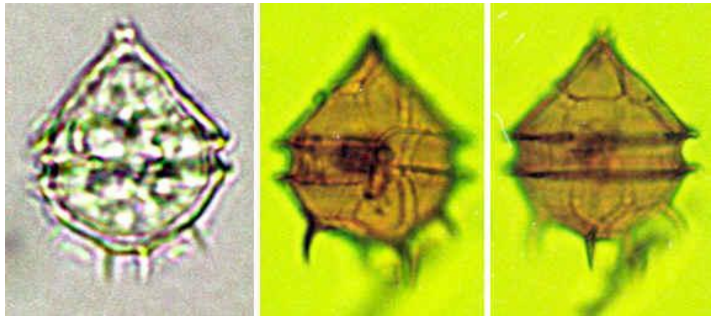
- **Diatom-производные фотосинтезирующие эндосимбионты**: некоторые динофдагелляты (e.g., *Durinskia baltica, Kryptoperidinium foliaceum, Peridinium quinquecorne*) постоянно содержат диатомовые эндосимбионты с хлоропластами и ядром (e.g., Dodge 1971, Horiguchi and Pienaar 1991, 1994, Schnepf and Elbrächter 1999). Такие водоросли содержат 2 ядра. Диатомоморфные динофлагелляты культивируются, более года поддерживаются в культуре. Одноядерные нефотосинтезирующие представители некоторых из этих видов встречаются в природе, указывая, что эндосимбиоз произошел недавно.



*Durinskia baltica*



*Galeidinium rugatum*



*Peridinium quinquecorne*

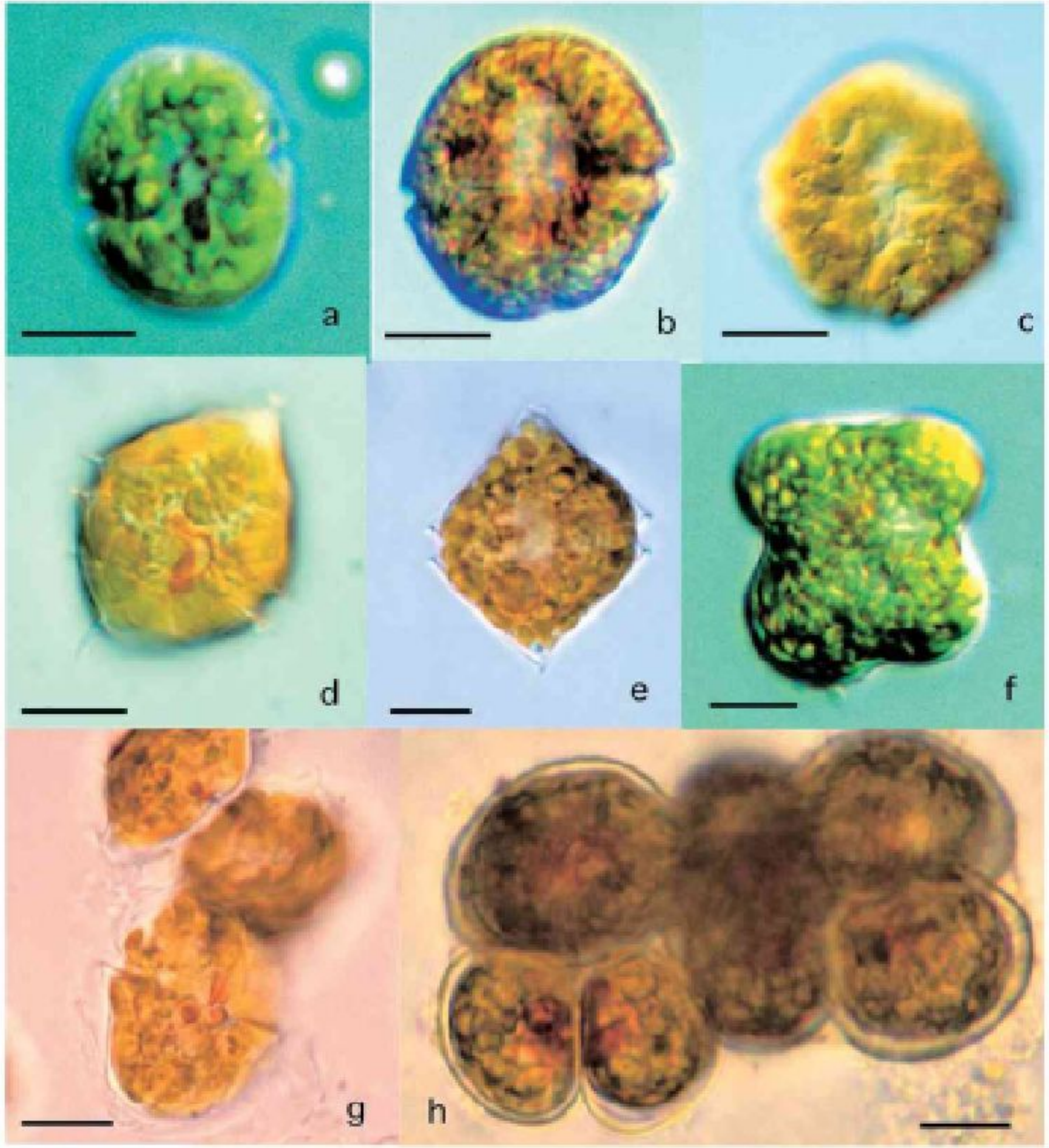
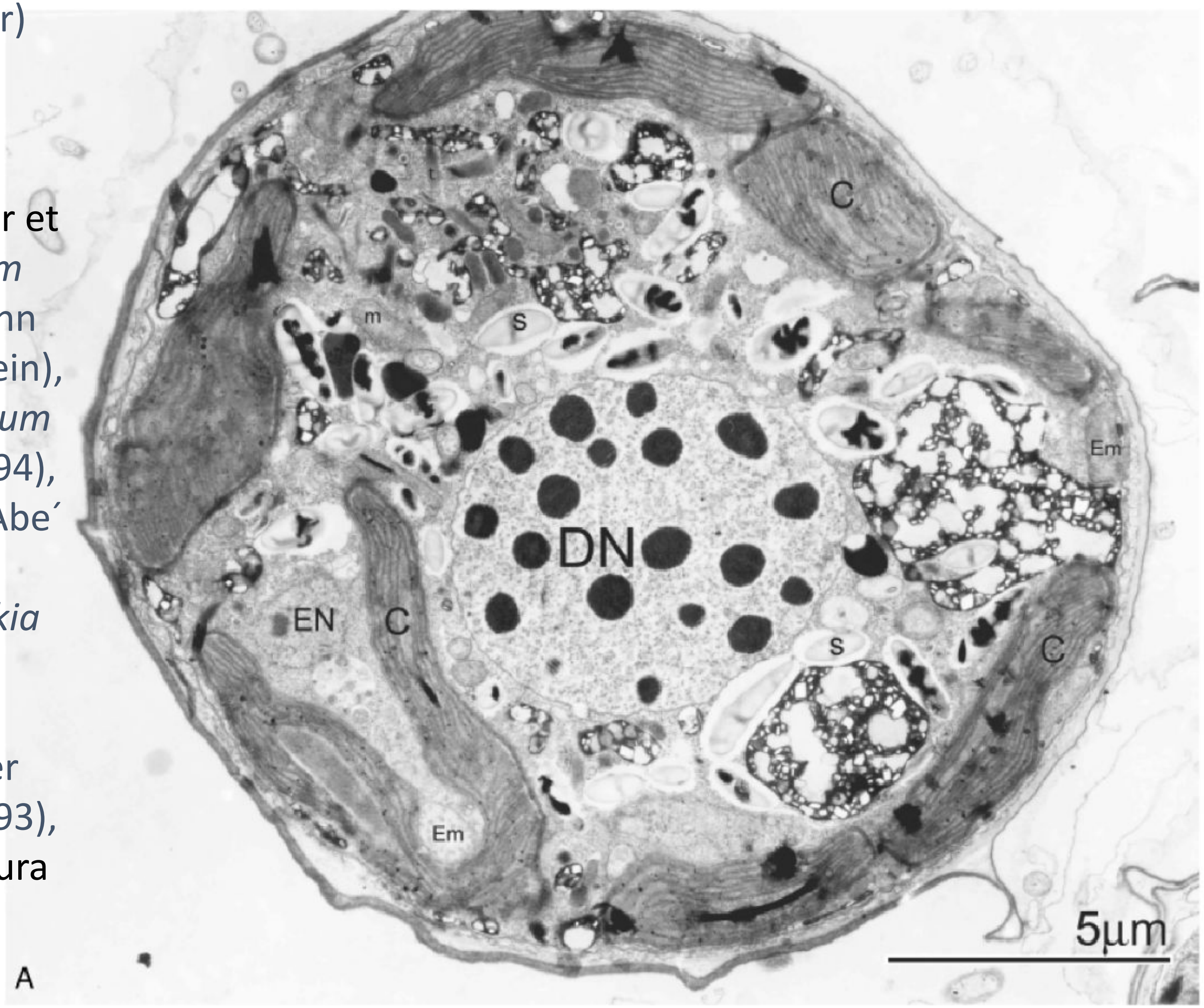


**Fig. 1** Dinoflagellates with a diatom endosymbiont. a. *Durinskia baltica*, b. *Durinskia* sp. c. *Kryptoperidinium foliaceum*, d. *Peridinium quinquecorne*, e. *Peridiniopsis rhomboids*, f. *Gymnodinium quadrilobatum*, g. P-18 strain from Palau, h. *Dinothrix paradoxa*. Scale bars = 10 μm

These include *Durinskia baltica* (Levander) Carty et Cox (=Peridinium balticum (Levander) Lemmermann), *Durinskia capensis* (Pienaar et al., 2007), *Kryptoperidinium foliaceum* (Stein) Lindemann (=Peridinium foliaceum Stein), *Gymnodinium quadrilobatum* (Horiguchi and Pienaar 1994), *Peridinium quinquecorne* Abe´ (Horiguchi and Pienaar 1991), *Durinskia* sp. (Horiguchi and Pienaar 1988), *Dinothrix paradoxa* Pascher (Horiguchi and Chihara 1993), *Galeidinium rugatum* Tamura et Horiguchi.



J. Phycol. 41, 658–671 (2005)

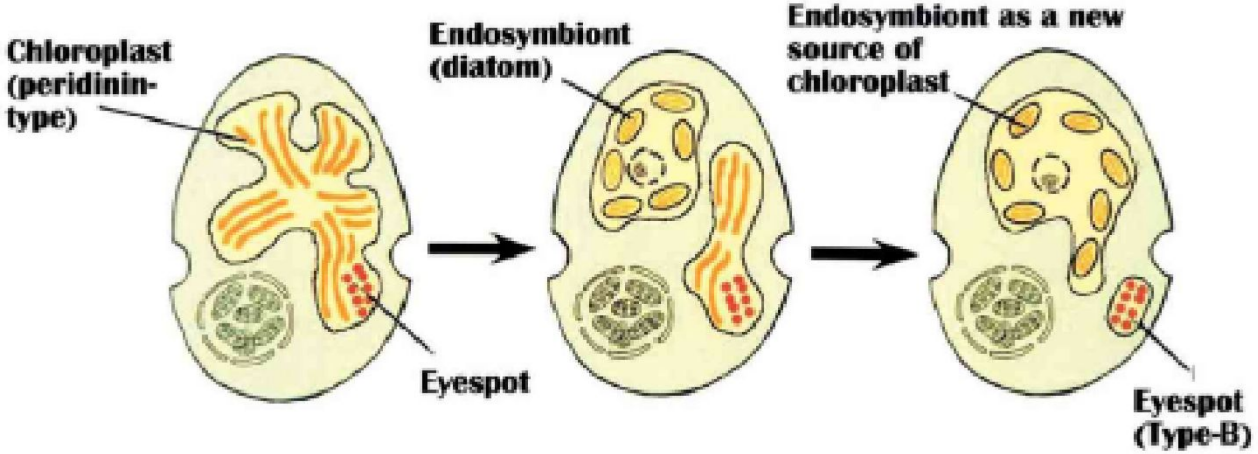
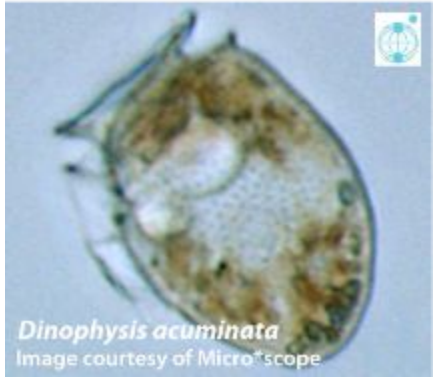


**Fig. 2** Hypothesis regarding the origin of a diatom-harboring dinoflagellate as well as type B eyespot.

- Cryptophyte-клептохлоропласты:
  - Большинство видов рода *Dinophysis* содержат или целые криптомонады или только их хлоропласты (Schnepf and Elbrächter 1988, 1999, Janson 2004). D.acuminata содержит пластиды, покрытые только 2 мембранами, отсутствуют нуклеоморфа и ядро криптомонады. Показано, что 5 ядерных генов кодируют хлоропластные белки (Wisecaver and Hackett BMC Genomics 2010, 11:366)

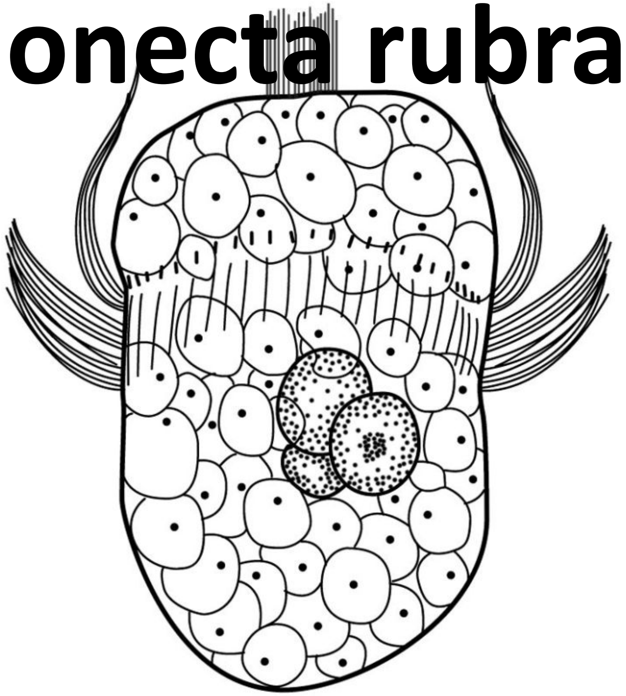
*Dinophysis tripos*

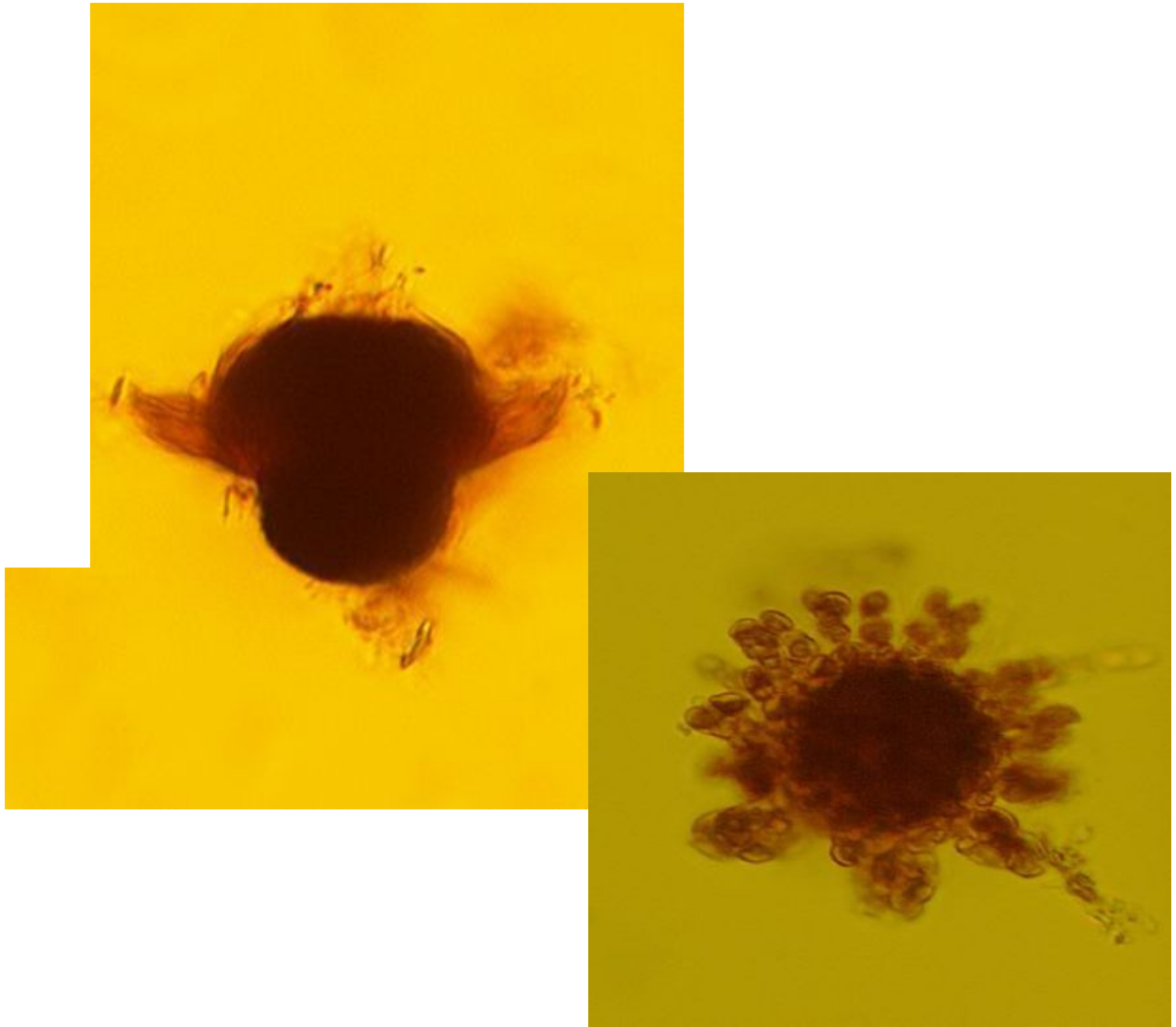


*Dinophysis acuminata*

Image courtesy of Micro*scope

# Myrionecta rubra





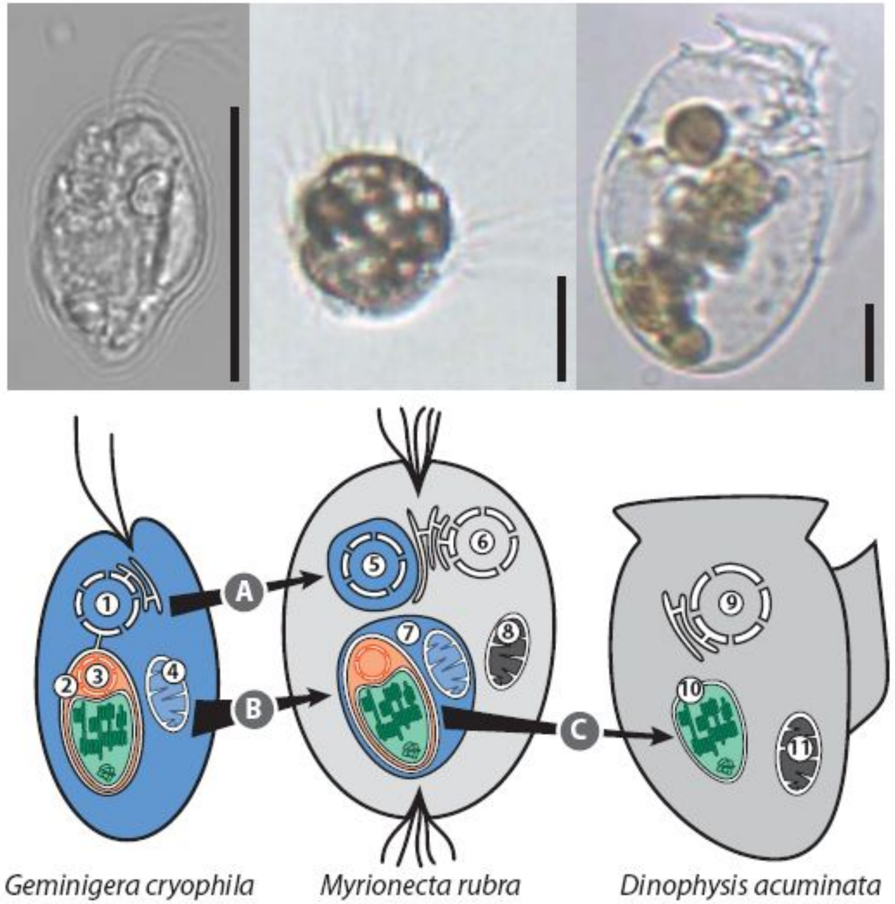
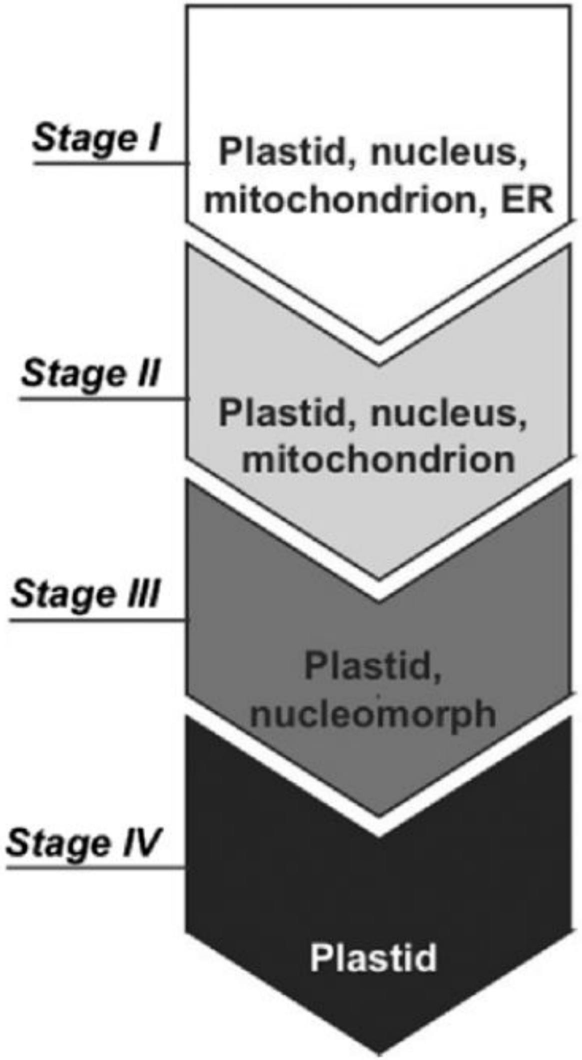


**Figure 1 Kleptoplast acquisition in *M. rubra* and *D. acuminata*.** The cryptophyte nucleus (A) and complete cryptophyte plastid and mitochondria (B) are retained in *M. rubra*. When the plastid is acquired by *D. acuminata* the outer two membranes and nucleomorph are lost (C). 1, cryptophyte nucleus; 2, plastid; 3, nucleomorph; 4, cryptophyte mitochondrion; 5, cryptophyte nucleus and cytoplasm surrounded by host membrane; 6, ciliate nucleus; 7, plastid-mitochondrial complex surrounded by host membrane; 8, ciliate mitochondrion; 9, dinoflagellate nucleus; 10, kleptoplast; 11, dinoflagellate mitochondrion. Light photomicrographs of the cells are shown above the cartoon for each organism (scale bar = 10 μm).

**Contents of symtiont**



***Stage I***

**Plastid, nucleus, mitochondrion, ER**

Host feeds on prey cells.

Digestion of a prey cell delayes.
Host and symbiont develope specificity.

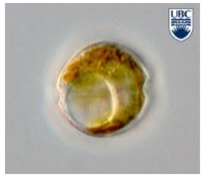
e.g. *Amphidinium latum, A. poecilochroum, Gymnodinium acidotum*

***Stage II***

**Plastid, nucleus, mitochondrion**

Cell cycles are coupled.

e.g. *Durinskia baltica, Kryptoperidinium foliaceum*



***Stage III***

**Plastid, nucleomorph**

Host cell compensate symbiont's house keeping function.

e.g. the cryptophytes, the chlorarachniophytes

***Stage IV***

**Plastid**

Symbiont is integrated as a plastid

e.g. *Lepidodinium viride, Gymnodinium chlorophorum, Karenia* brevis, *K. mikimotoi, Karlodonoium micrum*

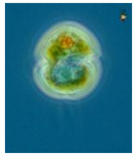
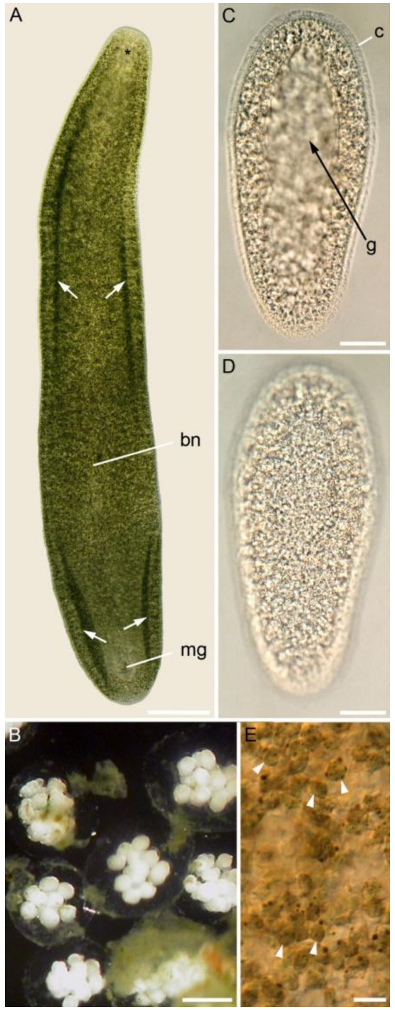
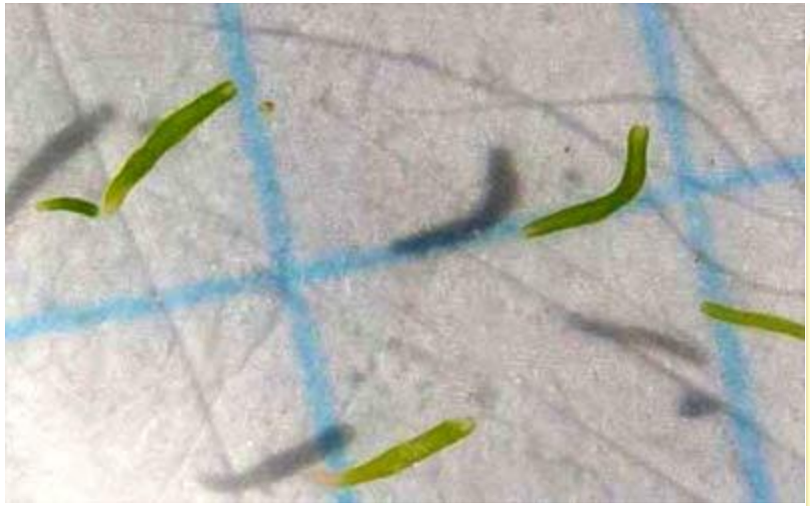
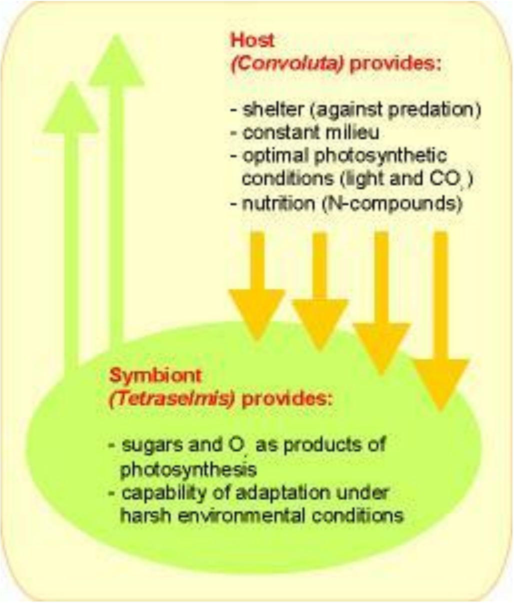


**Figure 3.** Hypothetical intermediate steps of plastid integration.

# The relationship between *Convoluta roscoffensis* and *Tetraselmis convolutae*







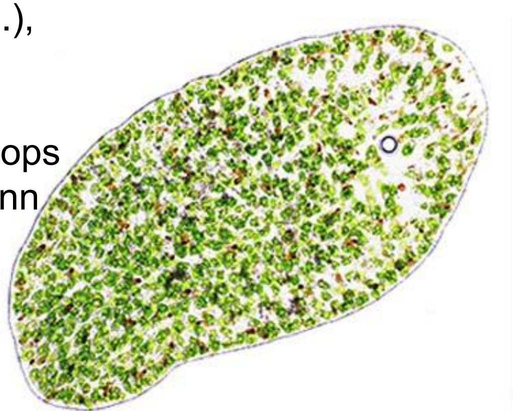
**Host (*Convoluta*) provides:**

- shelter (against predation)
- constant milieu
- optimal photosynthetic conditions (light and $CO_2$)
- nutrition (N-compounds)

**Symbiont (*Tetraselmis*) provides:**

- sugars and $O_2$ as products of photosynthesis
- capability of adaptation under harsh environmental conditions

Tetraselmis spp. in Symsagittifera (=Convoluta) spp.), diatoms (Licmophora spp. in Convoluta convoluta (Abildgaard 1806)) and dinoflagellates (Amphidinium spp. in Amphiscolops spp.;e.g. Douglas, 1992; McCoy & Balzer, 2002; Venn et al., 2008).



***Symsagittifera roscoffensis***

2–7.$10^4$ endosymbionts per animal

- Функционирующие клептопласты широко распространены среди моллюсков рода Elysia (менее 10 дней у *E. hedgpethi* (Greene, 1970), до 6 недель для *E. (=Tridachia) crispata, E. (=Tridachiella) diomedea* и *Placobranchus ianthobapsus*) (R.Trench, 1969; Greene,1970), до нескольких месяцев (три у *E. viridis*) (Hinde and Smith, 1972), 9 и более у *E.chlorotica*) (Pierce *et al.*, 1996; Rumpho *et al.*, 2001;Mondy and Pierce, 2003).
- *E.viridis - Codium fragile;*
- *Elysia timida - Acetabularia acetabulum;*
- *E. furvacauda - Codium* и *Microdictyon* , красные водоросли и бурая Sargassum
- *E. crispata* (R. Trench *et al.*, 1969) и *E.diomedea* (R. Trench,1975) - *Caulerpa*.

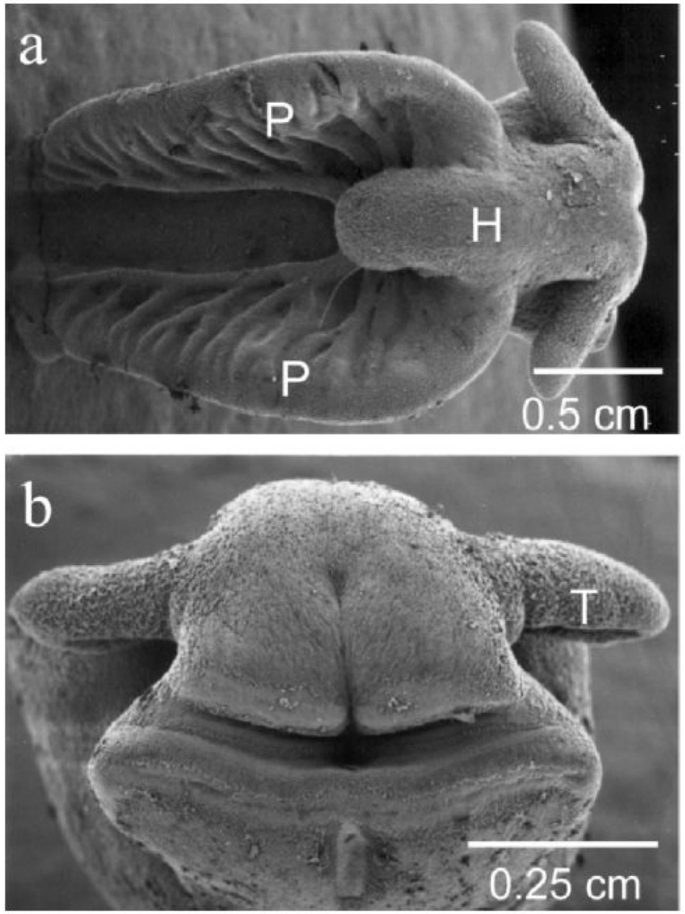
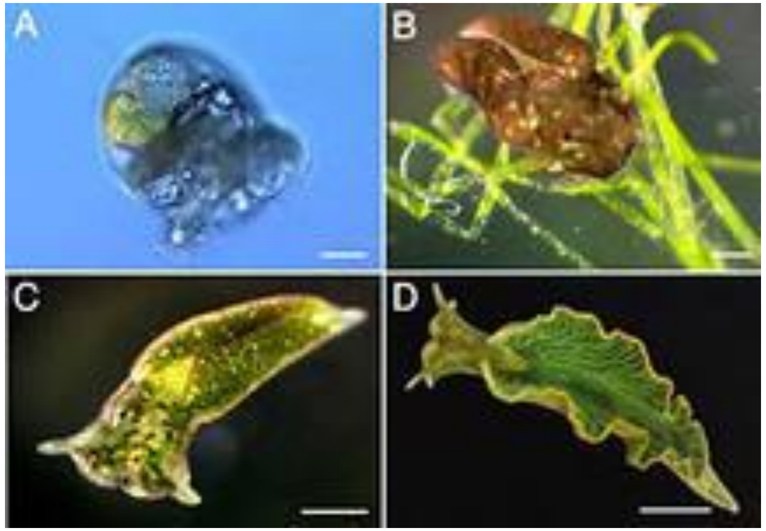
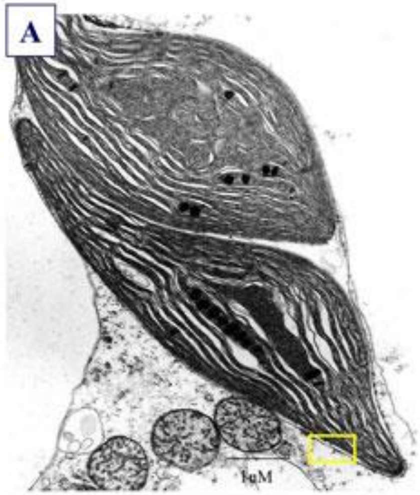
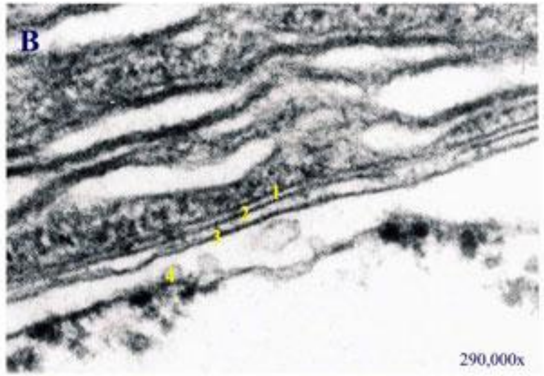


*Fig. 5.* Scanning electron micrographs of the mollusc *E. chlorotica*. Young, small (about 3 to 4 mm in length) animals were fixed in 2% glutaraldehyde, processed and their external structure examined with an AMRay 1000 scanning electron microscope. (a) Dorsal image illustrating the extensive vascular system which branches from the heart as two major ducts and spreads throughout the animal. The raised pericardium which houses the heart is very obvious in this image. (b) Head image illustrating the sensory tentacles and recessed, sucking mouth. Within the mouth structure are the uniserate radular teeth used to puncture the algal filaments prior to sucking out the chloroplasts. H, heart; P, parapodia; T, tentacle.



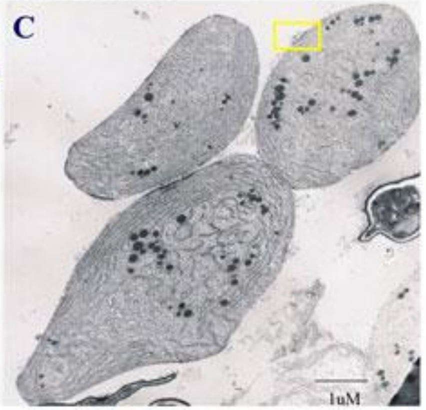
**Chloroplasts in algal filament**

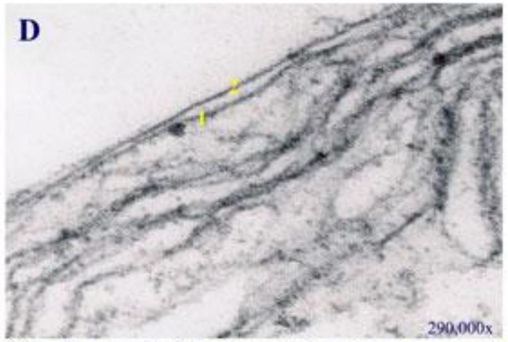




Four membranes surround the plastids in the alga.

**Isolated algal chloroplasts (0 hr)**





Only the standard double envelope is seen around the isolated plastids (C&D) and also in the sea slug (not shown).

# Species of Costasiella investigated.

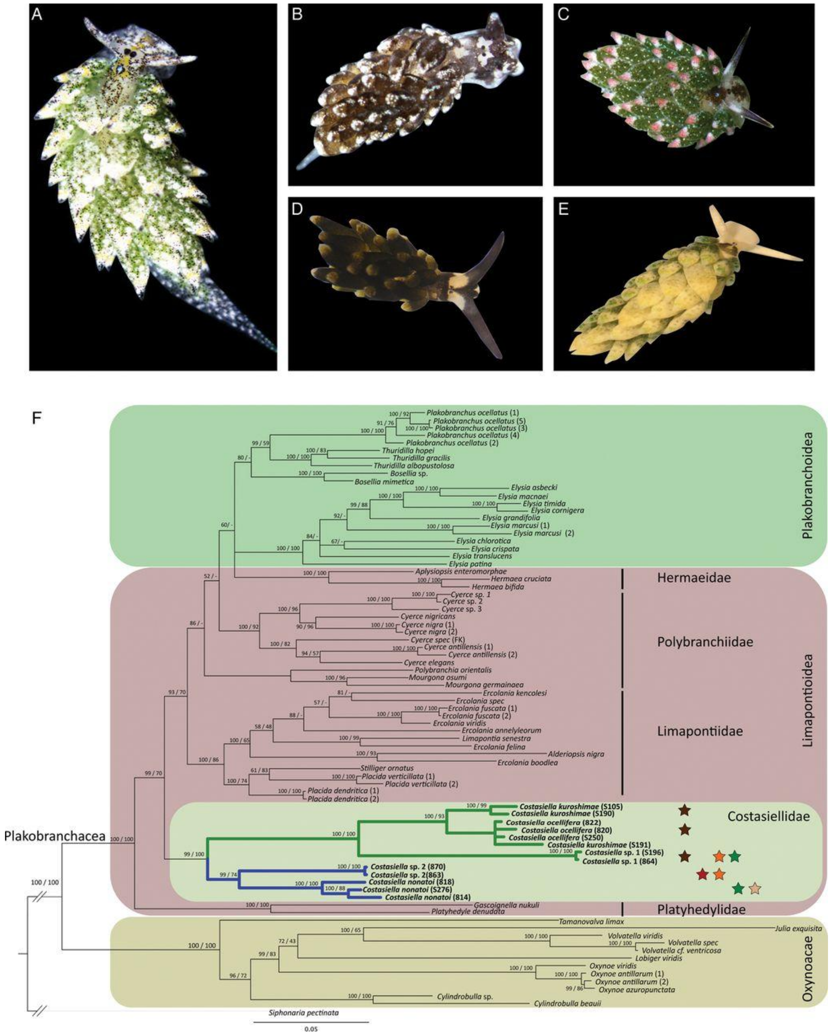
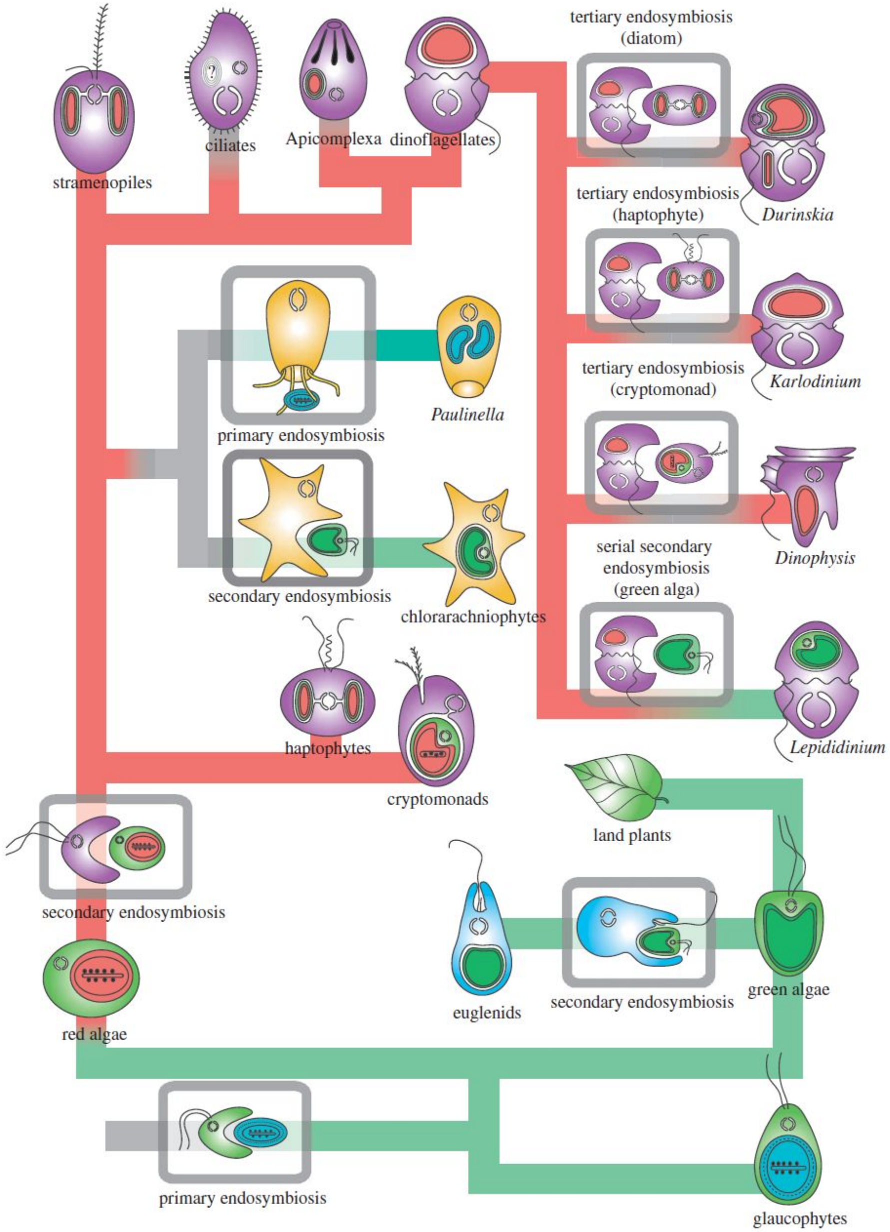


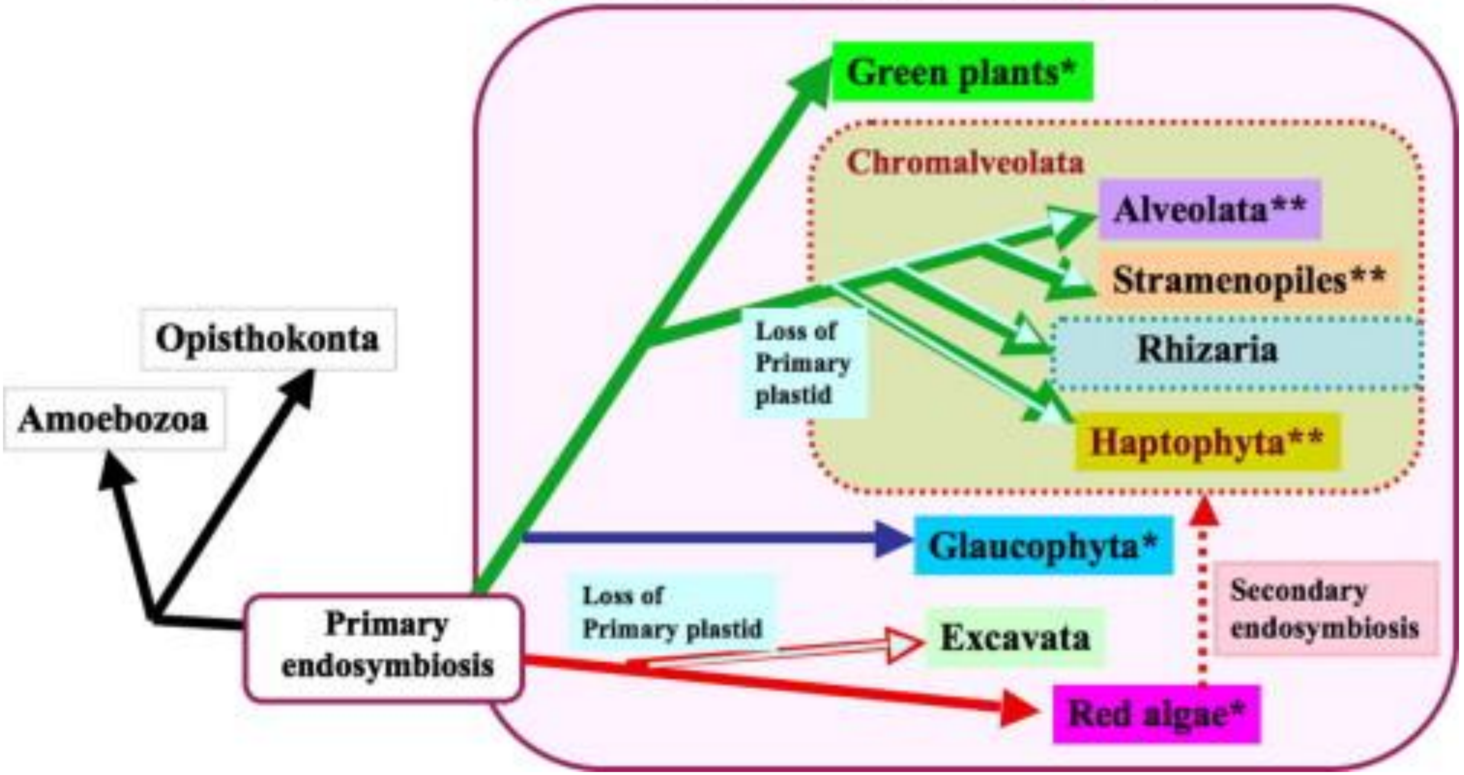
Figure 1. Species of Costasiella investigated. A. C. ocellifera (Florida Keys). B. C. nonatoi (Florida Keys). C. C. kuroshimae (Guam). D. C. sp. 2 (Guam).
E. C. sp. 1 (Guam). F. Phylogenetic relationship of Costasiella based on partial sequences of 16S, 1st and 2nd positions of COI, H3 and 28S. Shown is a 50% majority-rule tree based on a Bayesian analysis. Numbers at nodes represent posterior probabilities (Bayesian analysis) and bootstrap values (maximum-likelihood analysis). Siphonaria pectinata was chosen as outgroup. Stars indicate food sources of Costasiella species identified by barcoding using rbcL: brown, Avrainvillea; red, Tydemania; orange, Rhipilia; green, Pseudochlorodesmis; beige, Bryopsis. Blue clade shows Costasiella with no functional retention of kleptoplasts, green clade indicates species with functional retention.

**Christa G et al. J. Mollus. Stud. 2014;mollus.eyu026**

Journal of
Molluscan Studies


stramenopiles
ciliates
Apicomplexa
dinoflagellates
tertiary endosymbiosis (diatom)
Durinskia
tertiary endosymbiosis (haptophyte)
Karlodinium
tertiary endosymbiosis (cryptomonad)
Dinophysis
serial secondary endosymbiosis (green alga)
Lepididinium
primary endosymbiosis
Paulinella
secondary endosymbiosis
chlorarachniophytes
haptophytes
cryptomonads
secondary endosymbiosis
red algae
land plants
euglenids
secondary endosymbiosis
green algae
primary endosymbiosis
glaucophytes

# “Super” Plant Kingdom (Bikonts)



Opisthokonta

Amoebozoa

Primary endosymbiosis

Green plants*

Chromalveolata

Alveolata**

Stramenopiles**

Loss of Primary plastid

Rhizaria

Haptophyta**

Glaucophyta*

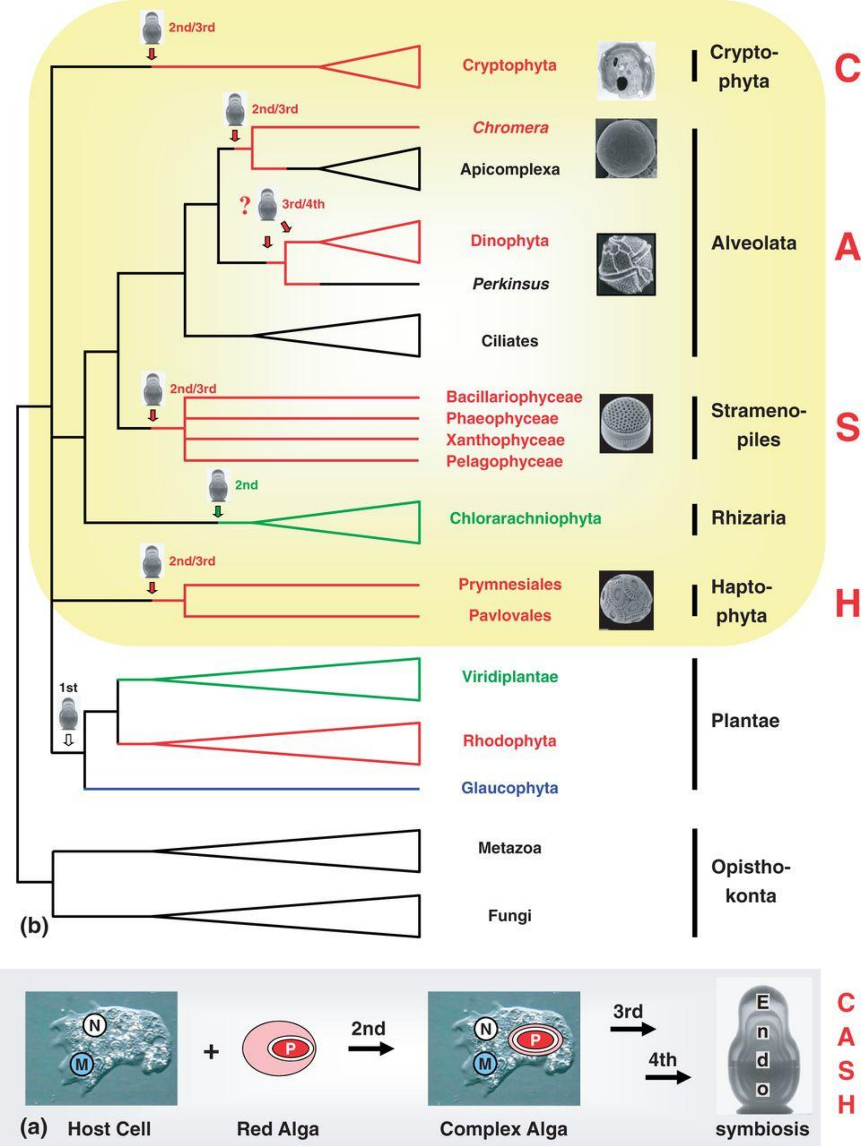
Loss of Primary plastid

Excavata

Secondary endosymbiosis

Red algae*

# (a) Origin of complex algae with red plastids via a single secondary endosymbiosis with a red alga and successive tertiary and quaternary endosymbioses.



N: nucleus; M: mitochondrion; P: plastid. (*b*) Scenario of plastid evolution among CASH lineages according to the rhodoplex hypothesis. X-ray images of the Russian Matryoshka dolls indicate independent events of plastid endosymbioses. All CASH plastids originate from an initial engulfment of a rhodophyte (see [*a*]), but the genuine secondary endosymbiont and the order of subsequent endosymbioses remains to be determined (indicated by 2nd/3rd and 3rd/4th). The typical plastid of PCD may represent a reduced apicomplexan alga (see current study). The gain of rhodophycean plastids as well as the loss of photosynthesis/plastids is indicated by the red horizontal lines. With respect to stramenopiles, only a subset of separate lineages is shown. Micrograph courtesy of Peter Vontobel, Sven Gould, Woody Hastings, and Manfred Rohde.

**Petersen J et al. Genome Biol Evol 2014;6:666-684**

Genome Biology and Evolution