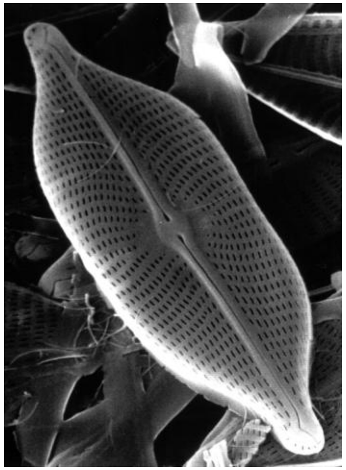
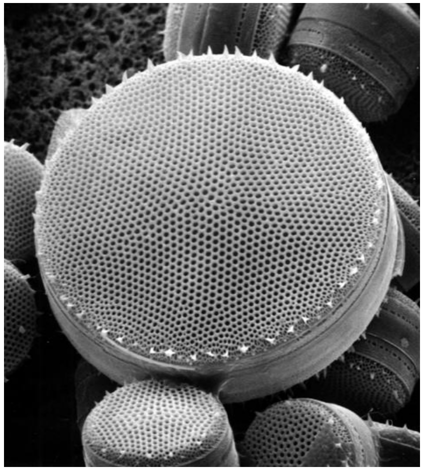
EBS 566/555 3/3/2010

Lecture 15

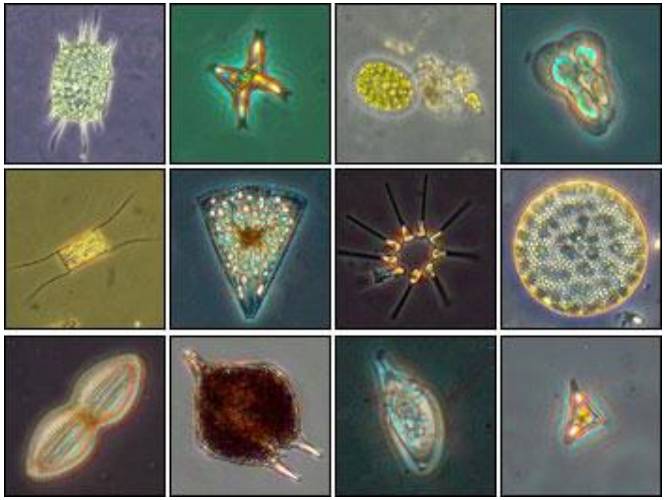
Blooms, primary production and types of phytoplankton (Ch 2, 3)





Topics

- Finish blooms
- Major taxa of phytoplankton
- How to measure phytoplankton
- Primary production

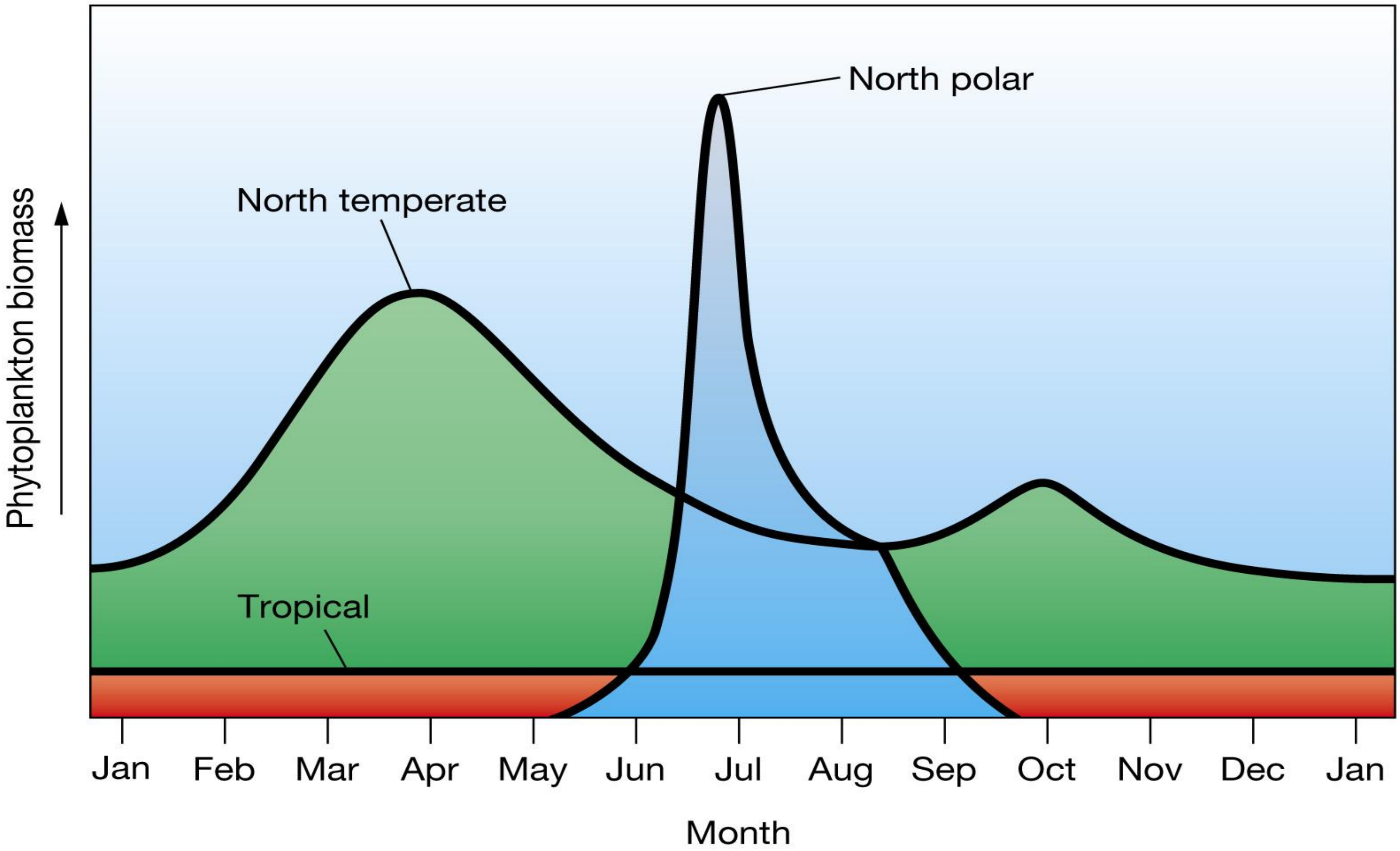


http://cmore.soest.hawaii.edu

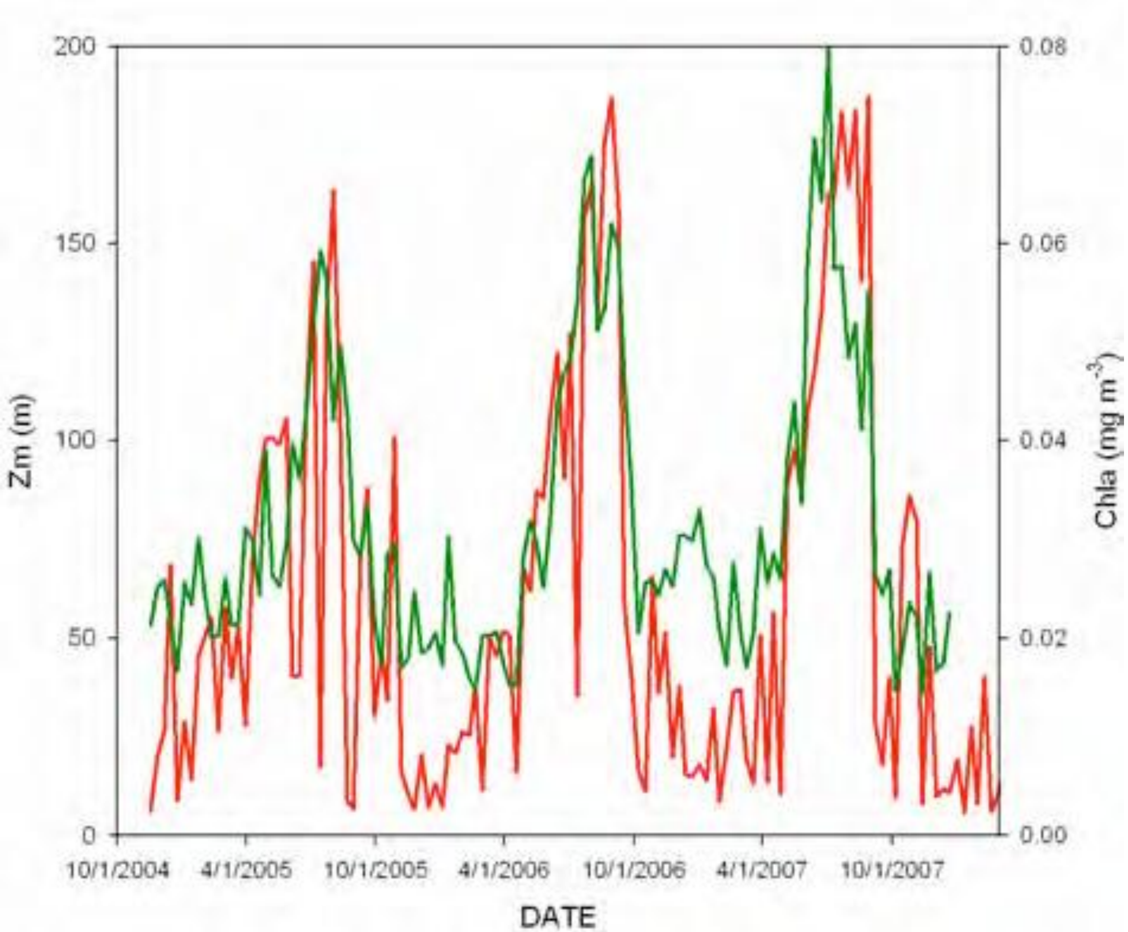
Alternatives to the Spring Bloom

- Polar and tropical seas
- Shallow water case: stratification not important for bloom initiation, only light is important
- Estuaries (Cloern and Jassby 2008, 2009)
- Extremely oligotrophic regions
- Iron limitation (e.g. subarctic North Pacific)
  - But also applies to spring bloom!
- Grazing regime
- Upwelling systems (coastal, equatorial)

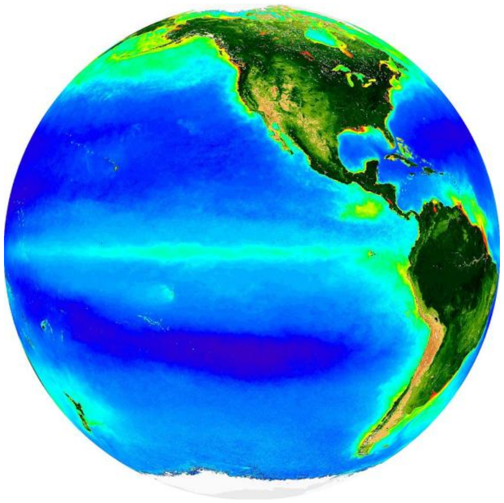
Global comparison of phytoplankton biomass



In South Pacific Gyre, chl *a* is highest in winter compared to summer

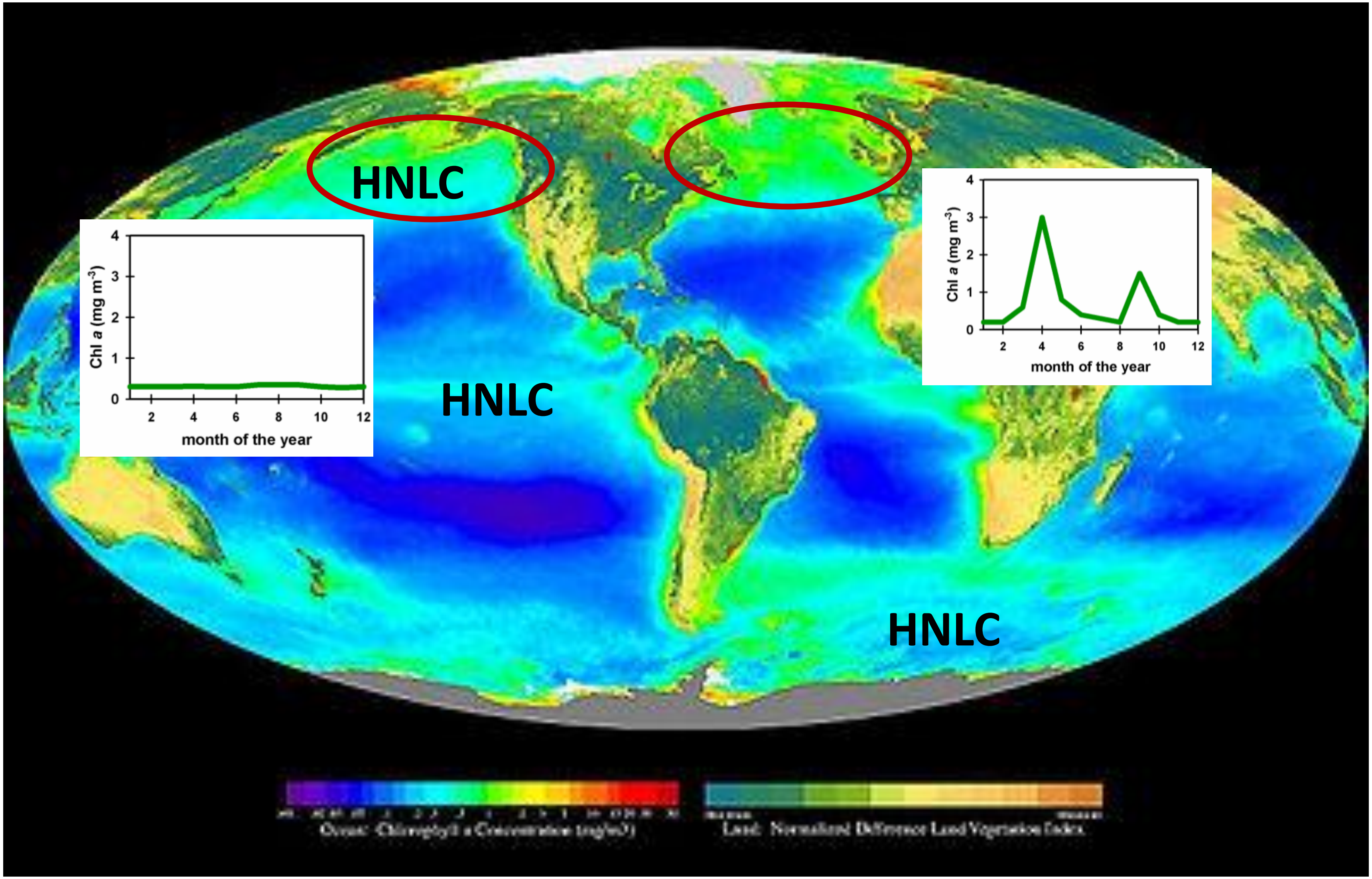


Green = chl a
Red = mixed layer depth (determined from Argo float)



Claustre, unpubl.

Annually averaged chl *a*



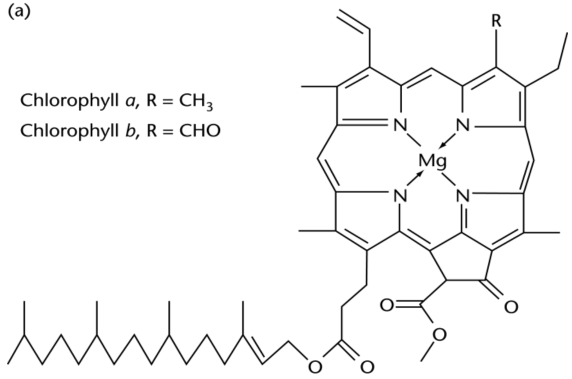
Fate of bloom phytoplankton

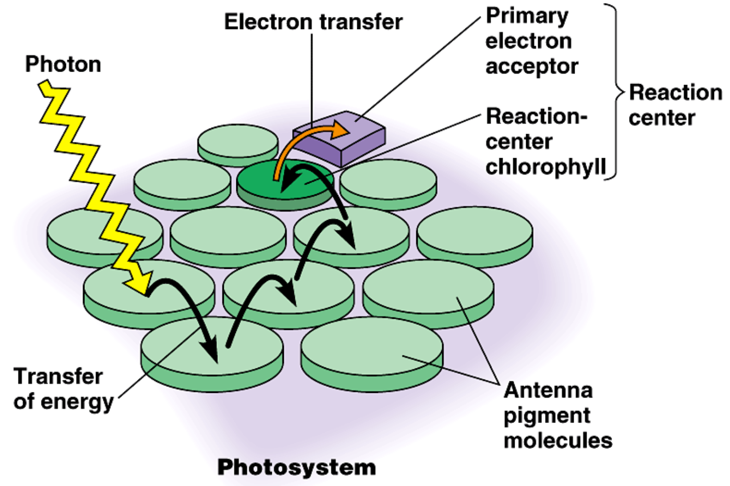
- Shallow decomposition (→ microbial loop, regeneration)
- Export
  - To deep ocean
  - Burial in sediments (→ sedimentary record)
- Grazing
  - Mesozooplankton
  - Microzooplankton
  - Excretion → regenerated nutrients

We can estimate algal biomass using the photosynthetic pigment, chlorophyll *a*

(a)

Chlorophyll *a*, R = CH_3
Chlorophyll *b*, R = CHO





Plant Cell Chloroplast Structure

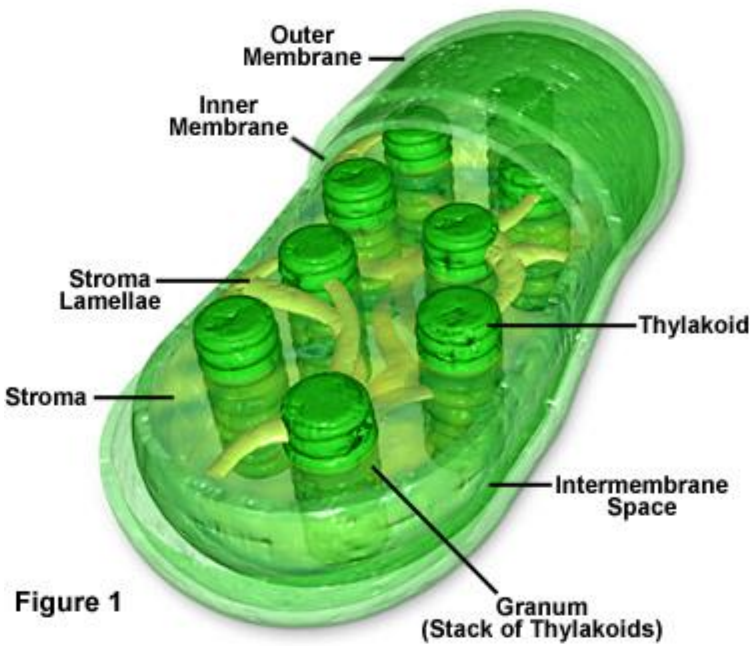
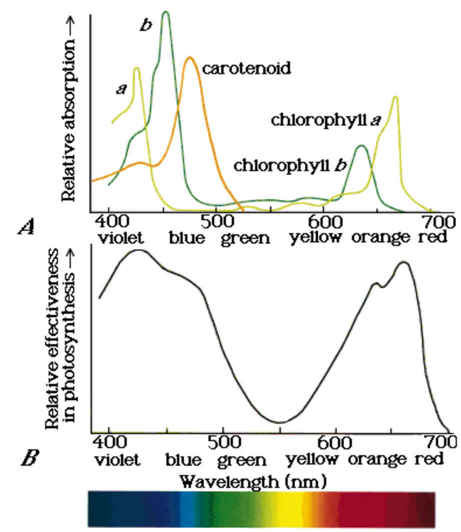


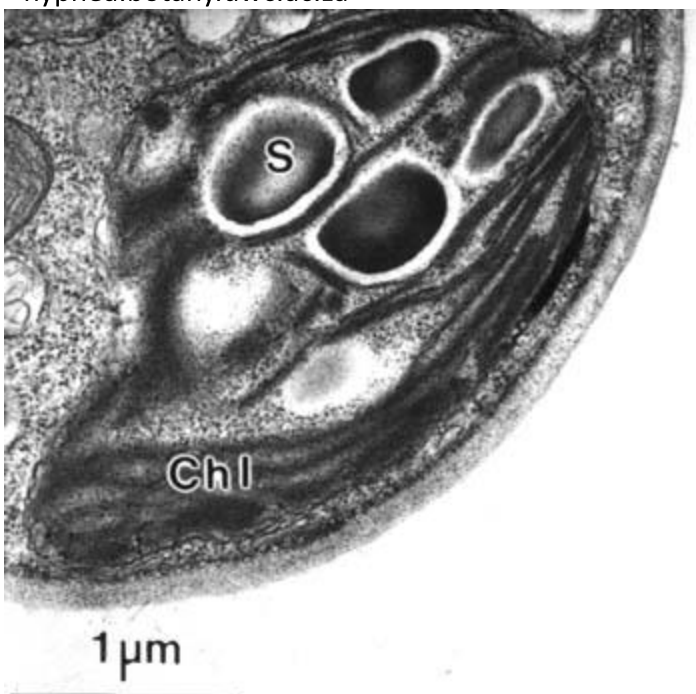
Figure 1



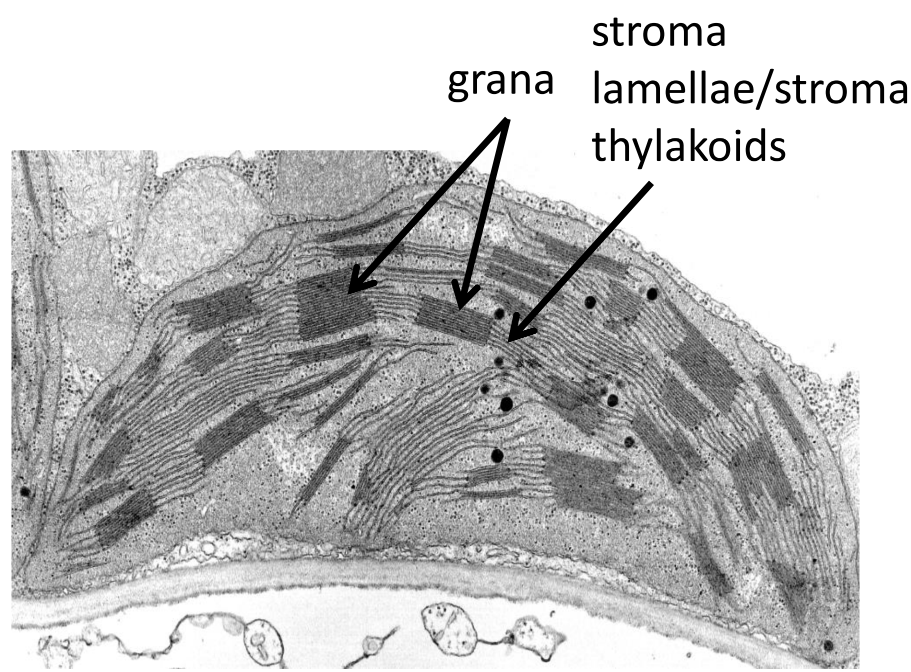
micro.magnet.fsu.edu

http://www.agen.ufl.edu

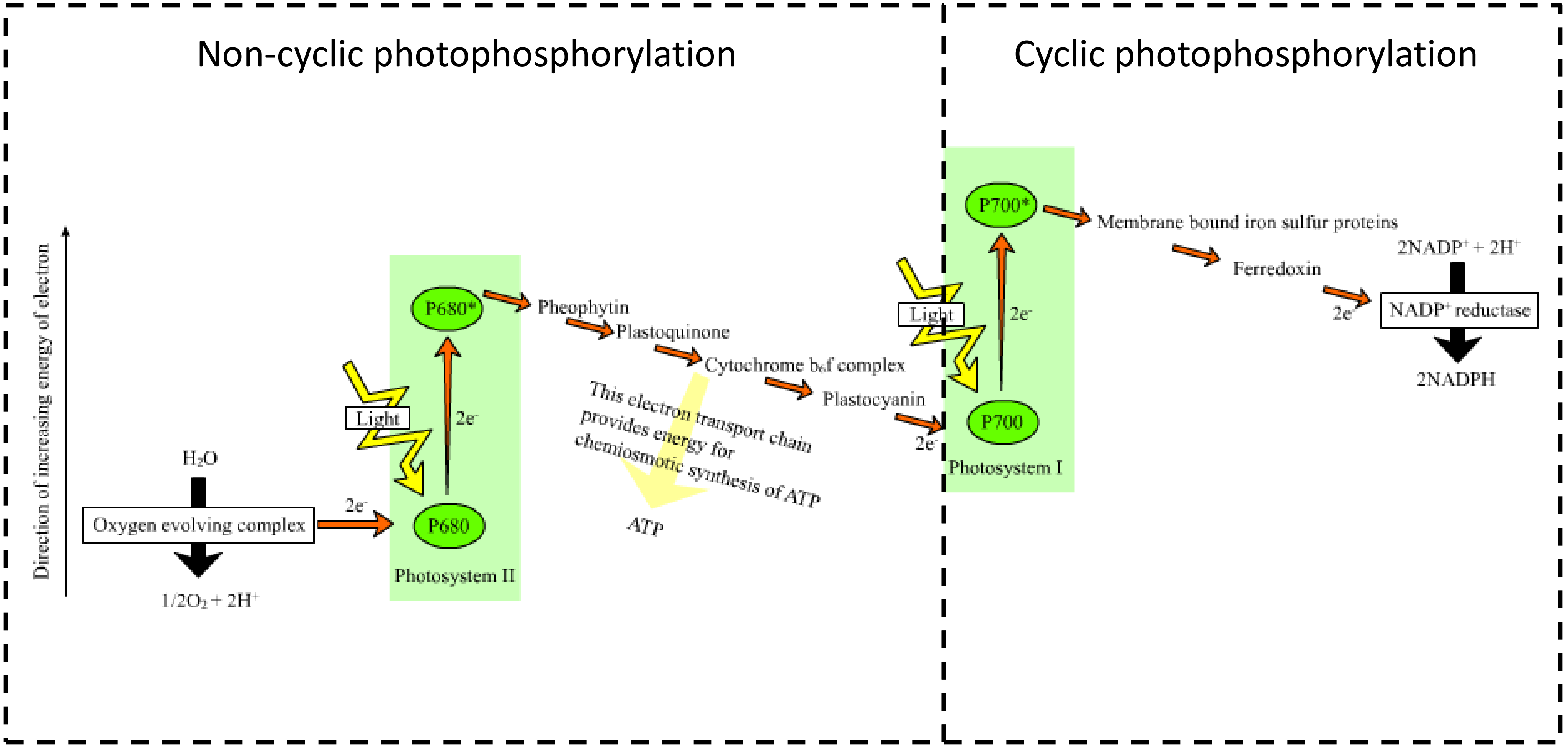
hypnea.botany.uwc.ac.za



left: Chloroplast of *Chlamydomonas*, a unicellular green alga. Note the chloroplast (Chl) with stacked thylakoids, and starch (s). TEM image by Richard Pienaar

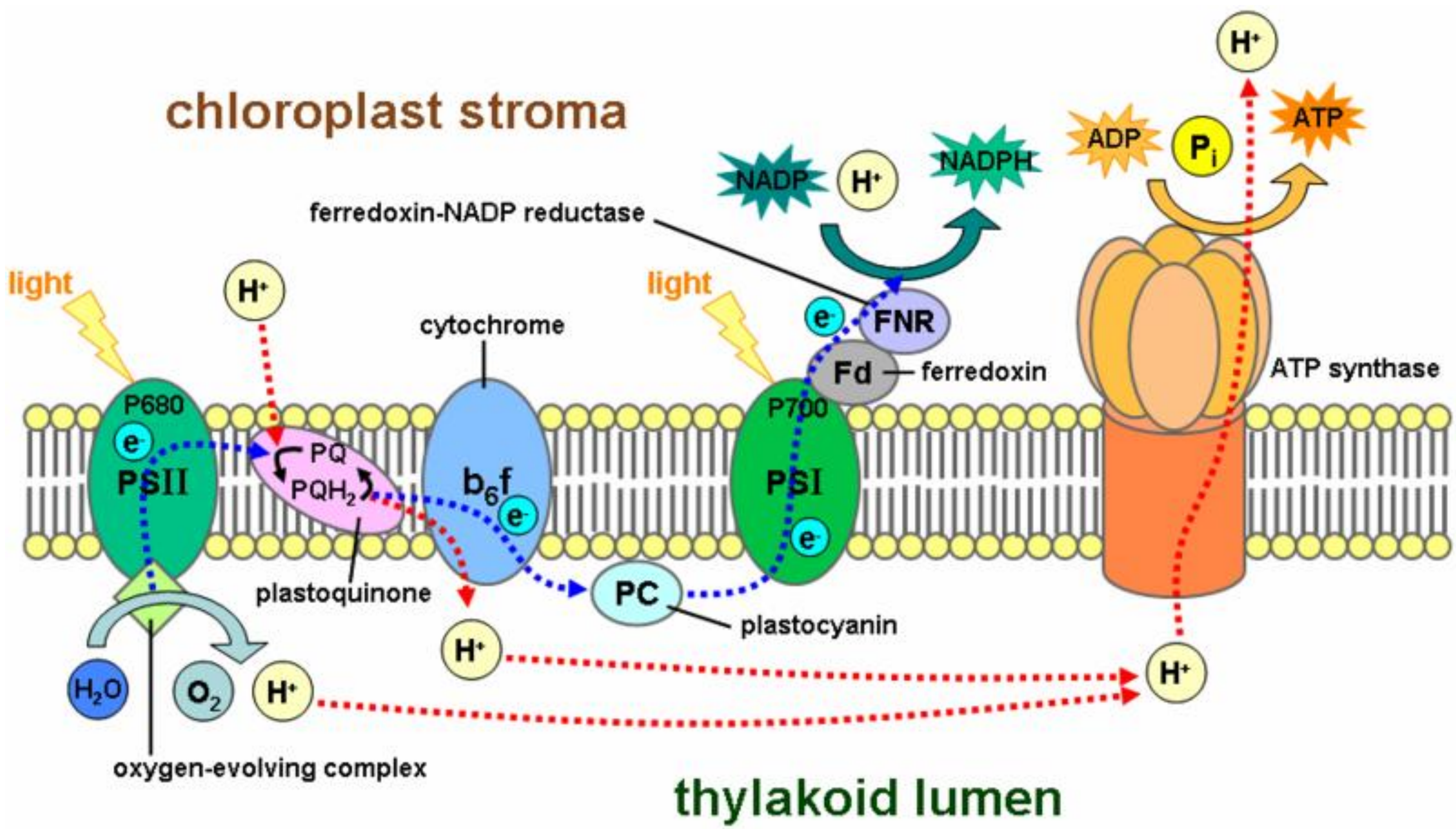


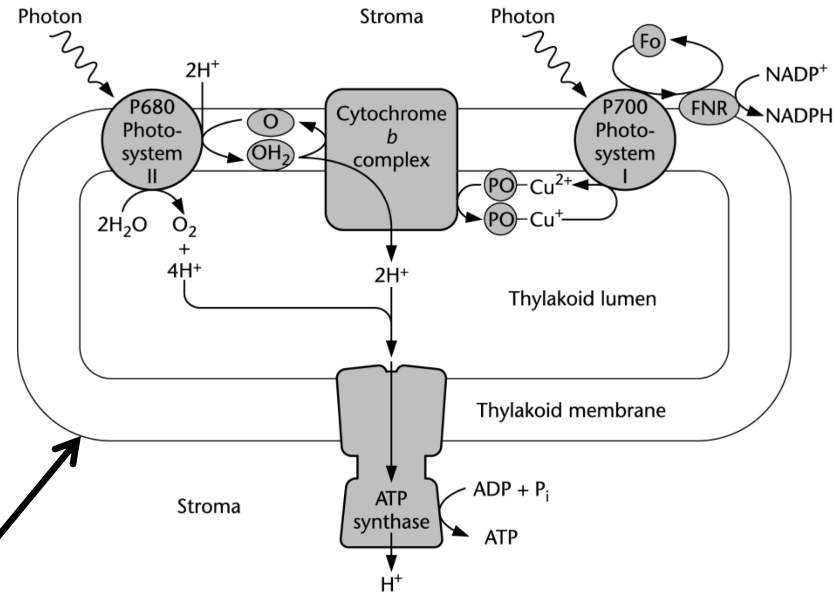
The 'Z' scheme



Light reactions: O_2 evolution

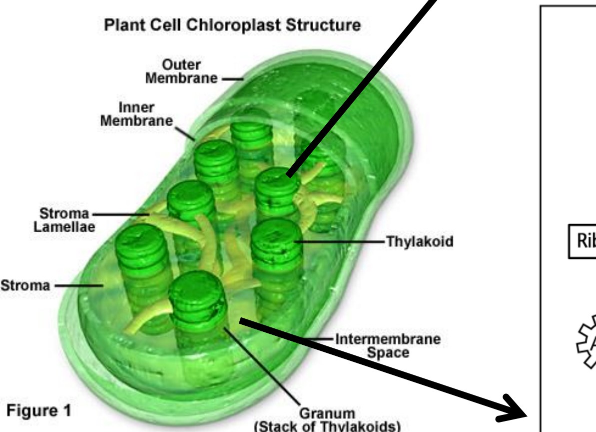
Occurs in thylakoid membranes

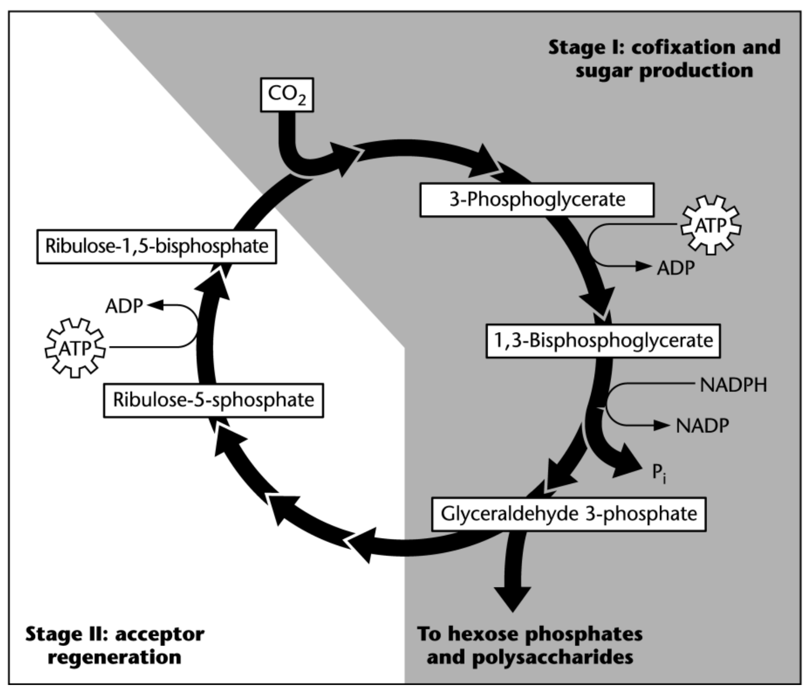

chloroplast stroma
light
H+
cytochrome
light
NADP
H+
NADPH
ADP
Pi
ATP
H+
ferredoxin-NADP reductase
e-
FNR
Fd
ferredoxin
ATP synthase
P680
e-
PSII
PQ
PQH2
b6f
e-
P700
PSI
e-
plastoquinone
PC
plastocyanin
H+
H2O
O2
H+
H+
oxygen-evolving complex
thylakoid lumen



Light reactions

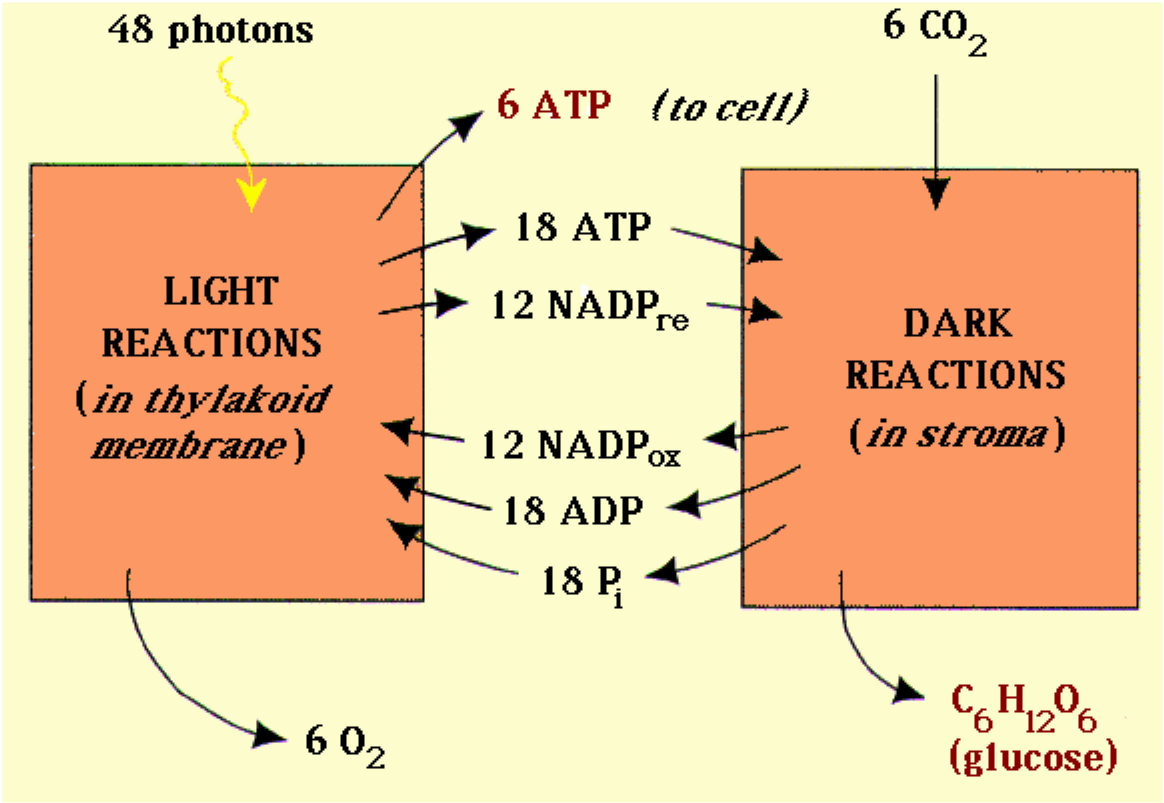
Occurs in thylakoid membrane; O_2 evolution



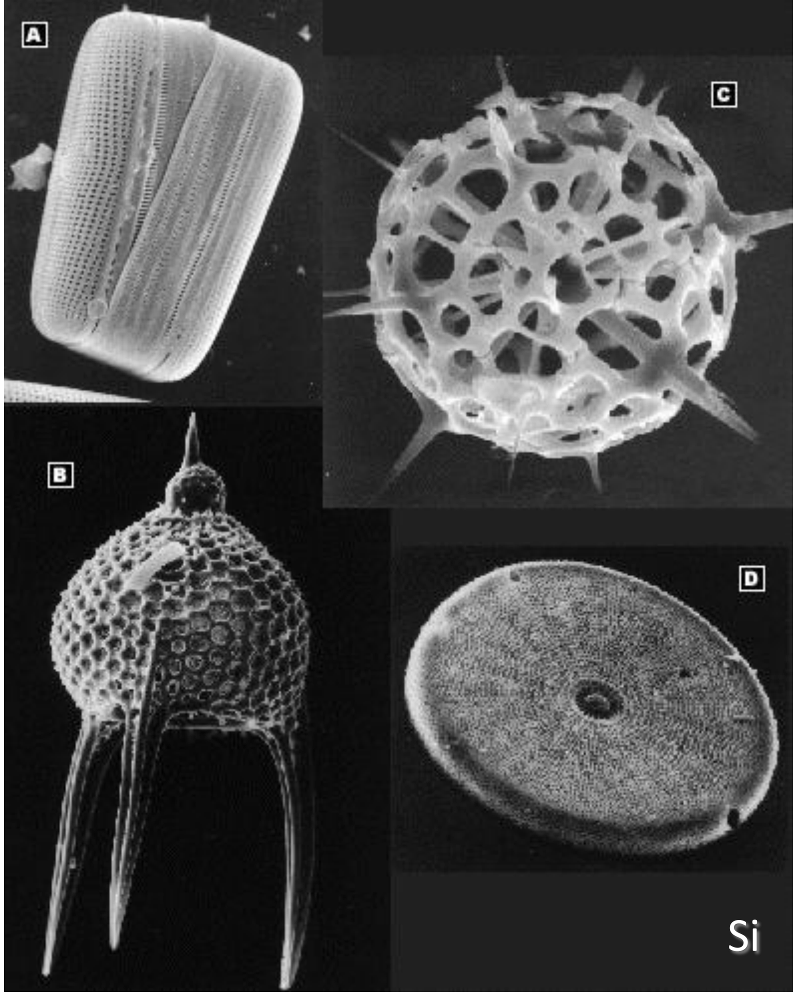


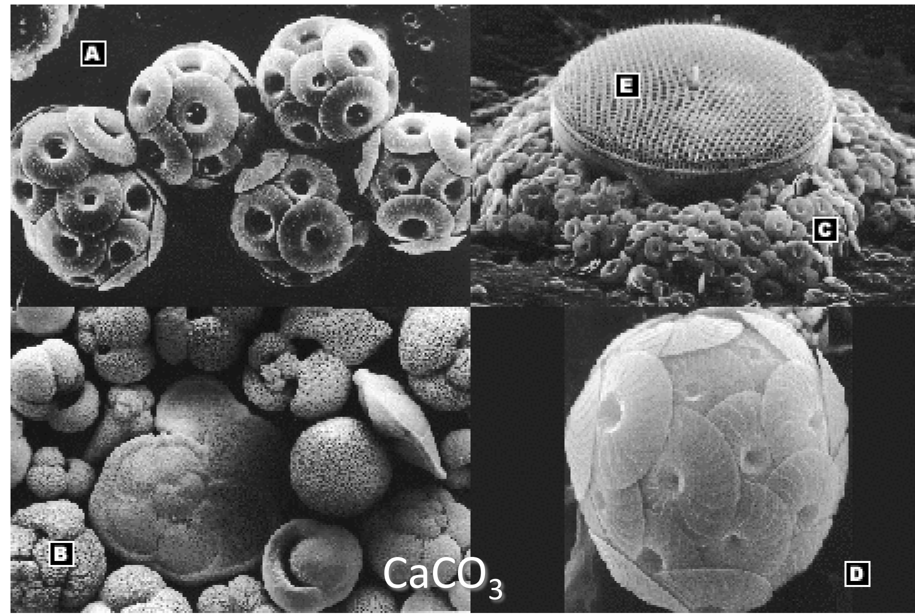
Dark reactions

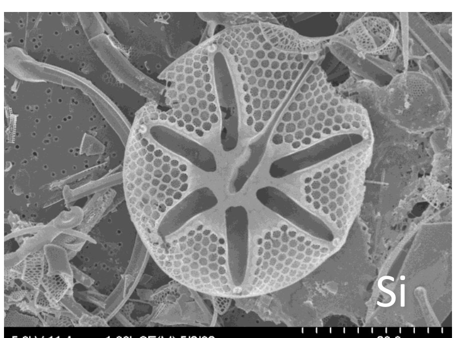
Occurs in stroma; production of glucose

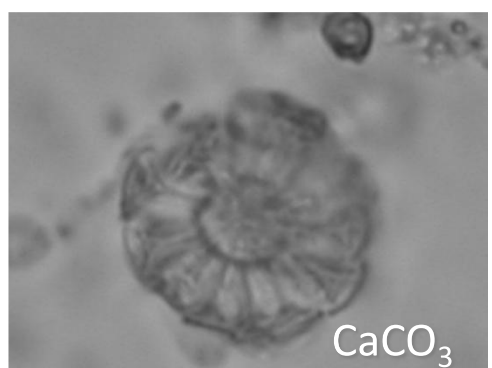

48 photons
6 ATP (to cell)
6 CO_2
LIGHT REACTIONS
(in thylakoid membrane)
18 ATP
12 $NADP_{re}$
12 $NADP_{ox}$
18 ADP
18 P_i
DARK REACTIONS
(in stroma)
6 O_2
$C_6H_{12}O_6$
(glucose)

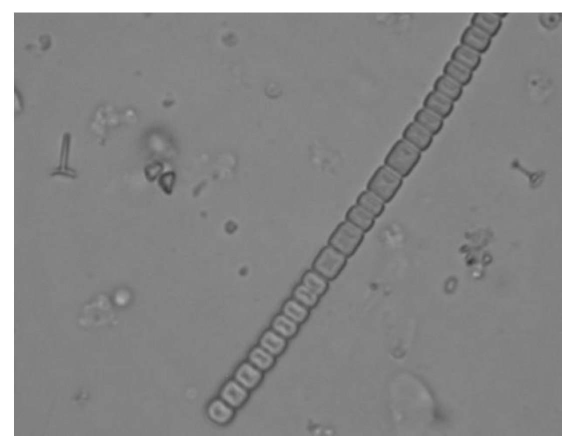
Planktonic forms











Classifying phytoplankton

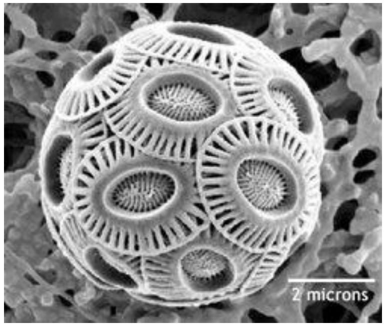
- Size (last time)
- Pigments (photosynthetic pigments, includes chl a, antenna pigments and protective pigments)
- Evolutionary relationships
  - How are they related?
- Functional groups
  - What do they do?

How they are classified depends on how they are measured, and on the question at hand

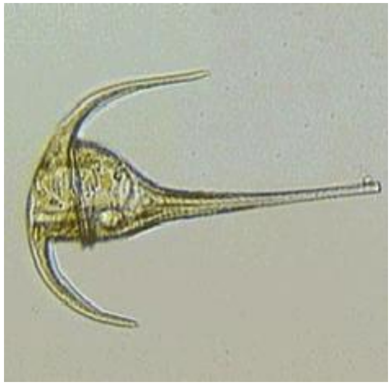
Cyanobacteria oxygenated Earth (>2 billion years ago); harmful algal blooms (more later)

Diatoms great at drawing down CO_2: reduce global temperatures

Coccolithophores alter and are altered by ocean's pH; produce DMS (trace gas connected to climate)



Dinoflagellates – harmful algal blooms, extraordinary diversity of form & function



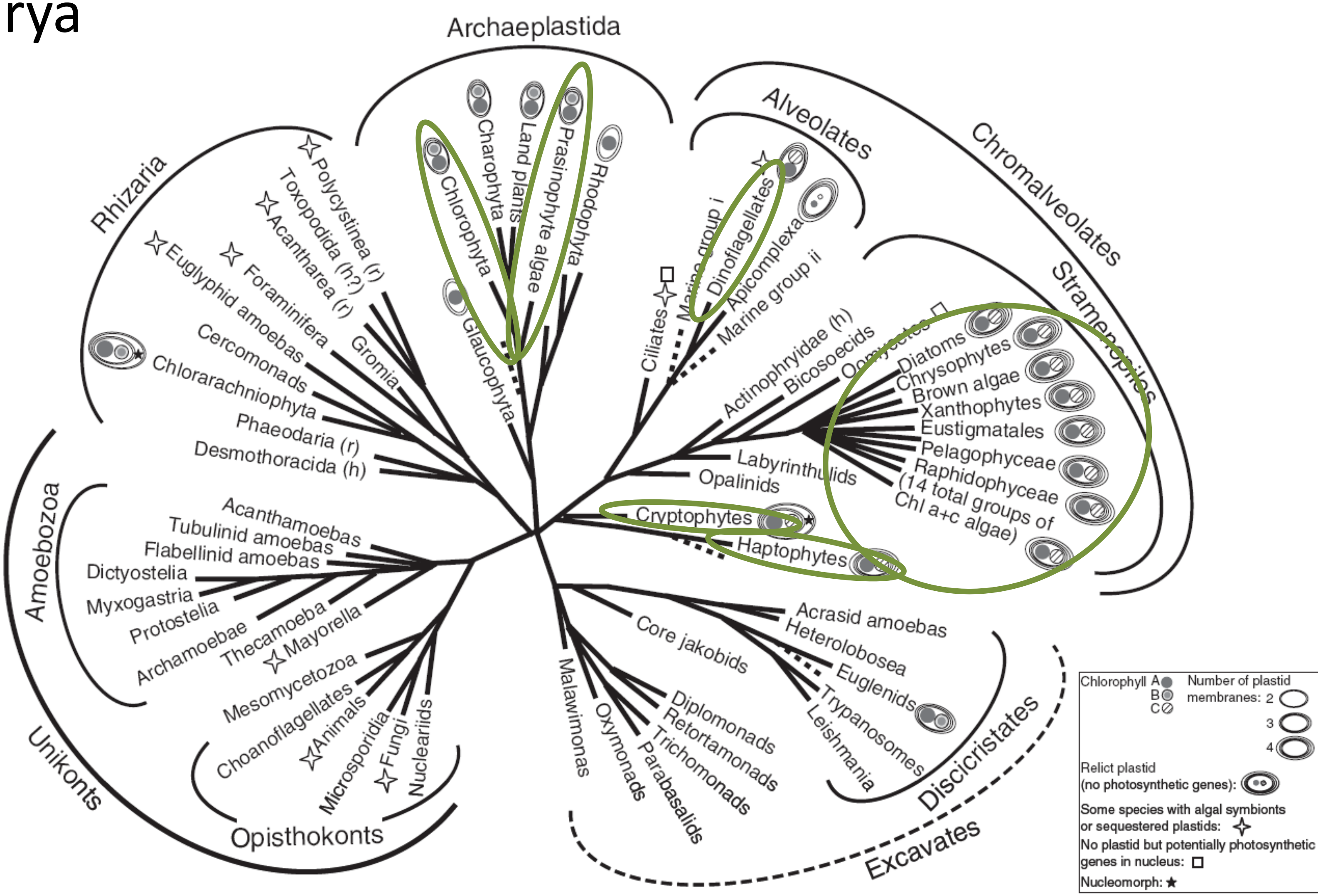
Phytoplankton in the eukaryotic tree of life

- Phylogeny/taxonomy is complicated and continuously being revised; see Adl et al. 2005 (on website) for recent classification scheme

Domain Eukarya

Supergroup	First rank	Second rank (examples)
Archaeplastida	Chloroplastida	Chlorophyta, Prasinophyta
Chromalveolata	Cryptophyceae	Cryptomonadales
	Haptophyta	Pavlovophyceae, Prymnesiophyceae
	Stramenopiles (= Heterokontophyta)	Bacillariophyta, Chrysophyceae, Dictyochophyceae, Pelagophyceae, Raphidophyceae, Synurales, Xanthophyceae, Dinozoa
Excavata	Euglenozoa	Euglenida

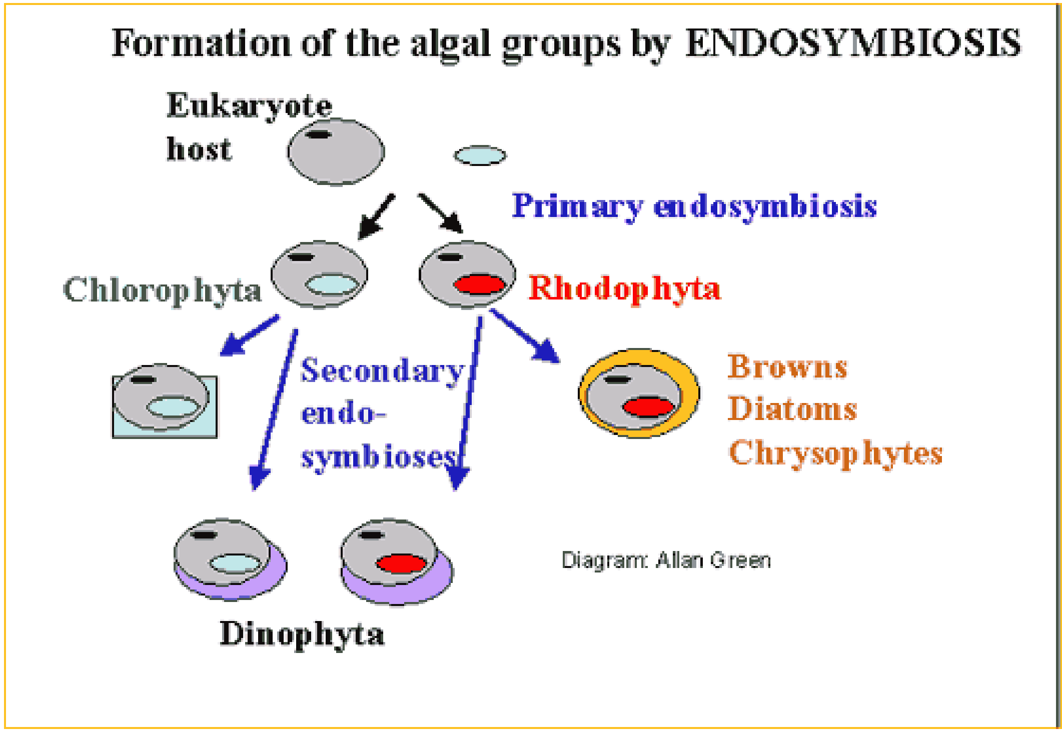
Eukarya

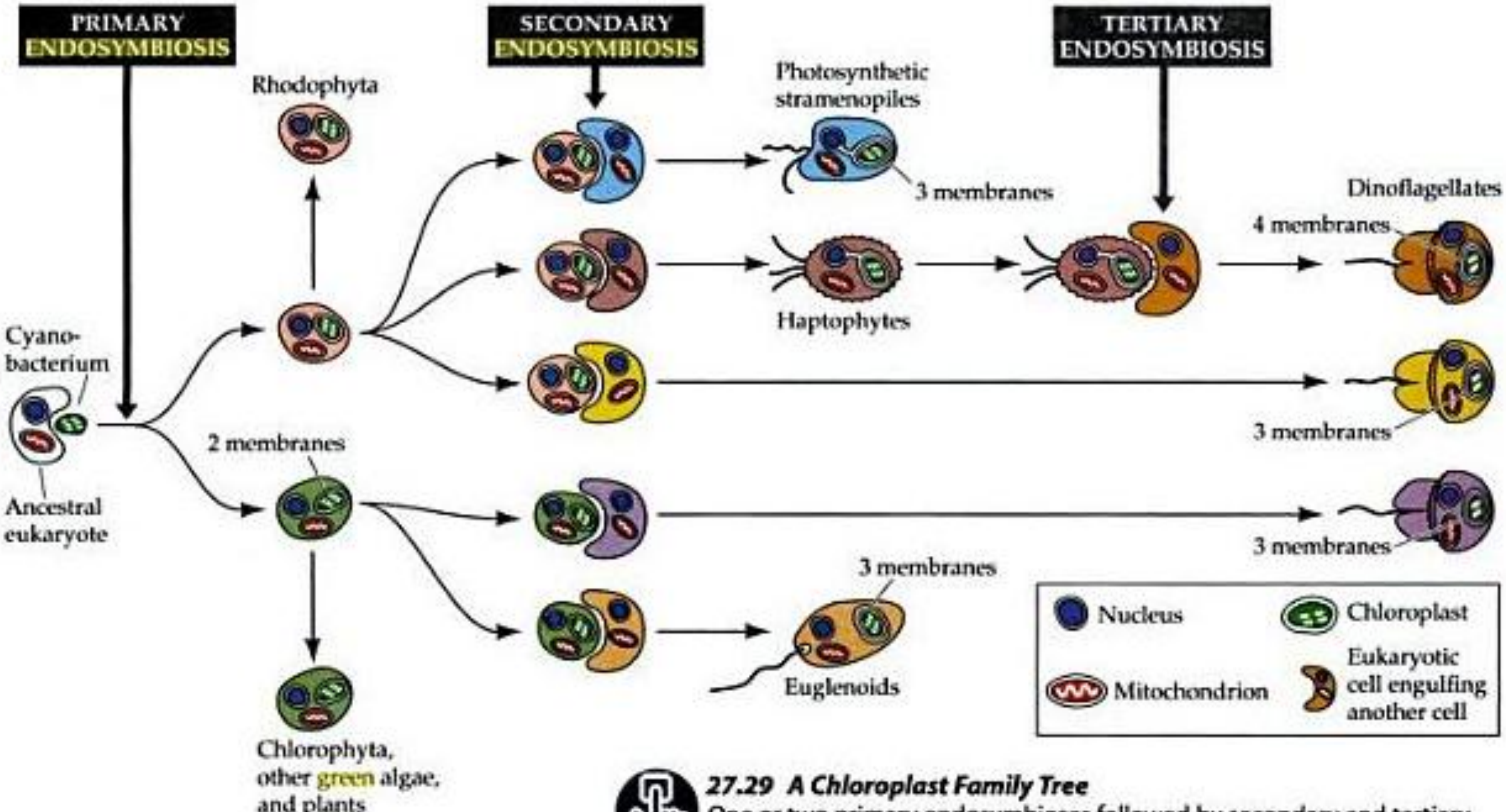


Fehling et al., 2007

Evolutionary relationships

- Endosymbiotic theory (serial endosymbiosis)
- Eukaryote engulfed a prokaryote
  - Photosynthetic: chloroplast; nonphotosynthetic: mitochondrion
  - Green and red lineages





27.29 A Chloroplast Family Tree
One or two primary endosymbioses followed by secondary and tertiary endosymbioses gave rise to all of today's chloroplasts.

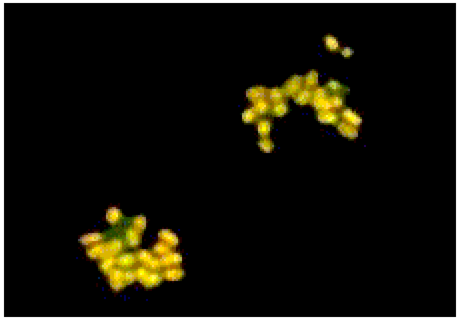
Life, the science of biology
By William K. Purves

Major classes of phytoplankton

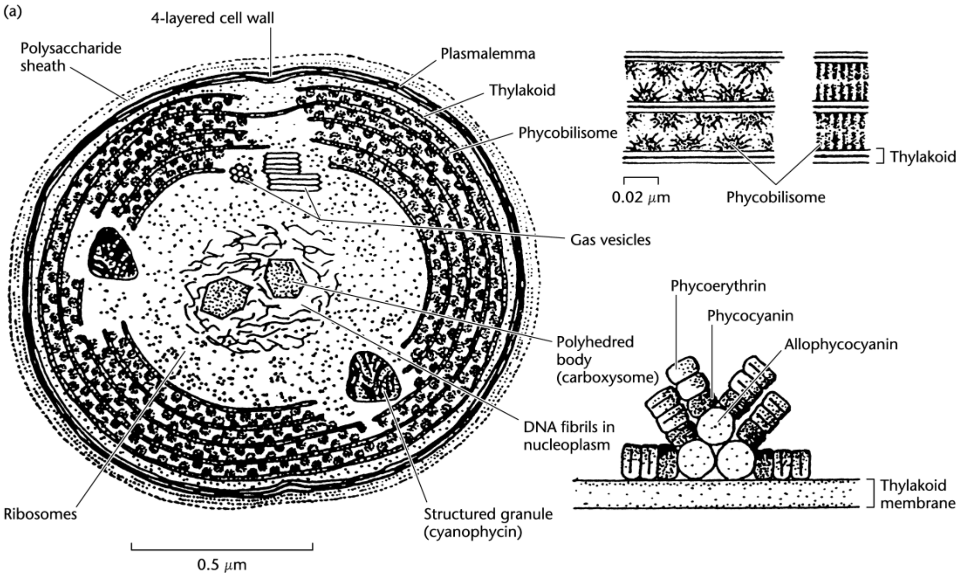
- Bacteria
  - Cyanophyceae and Prochlorophyceae (Bacteria)
- Eukarya
  - **Archaeplastida**: Chloroplastida (Chlorophyceae, Prasinophyceae)
  - **Chromalveolata**: Cryptophyceae (Cryptomonodales), Haptophytes (Pavlophyceae, Prymnesiophyceae), Heterokonts (Bacillariophyta, Chrysophyceae, Dictyochophyceae, Pelagophyceae, Raphidophyceae, Synurales, Xanthophyceae, Dinozoa)
  - **Excavata**: Euglenozoa (Euglenida/Euglenophyceae)

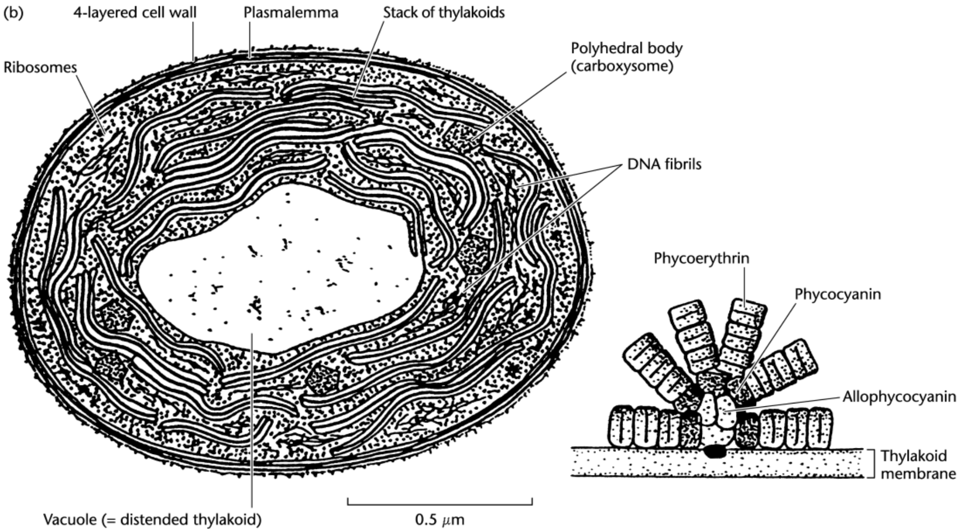
Cyanobacteria

- Bacteria
- Chlorophyll, but no chloroplasts
- Syn: Phycocyanin, Phycoerythrin, allophycocyanin
- Pro: divinyl chlorophyll b
- Cell wall of murein



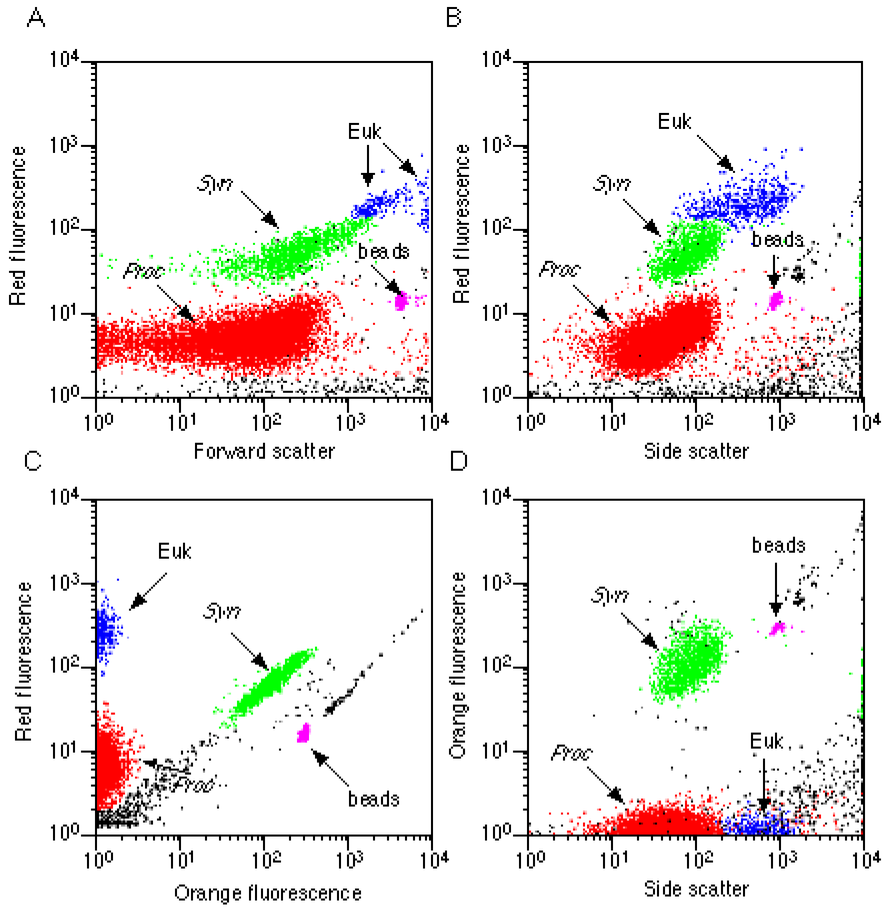
Synechococcus sp.



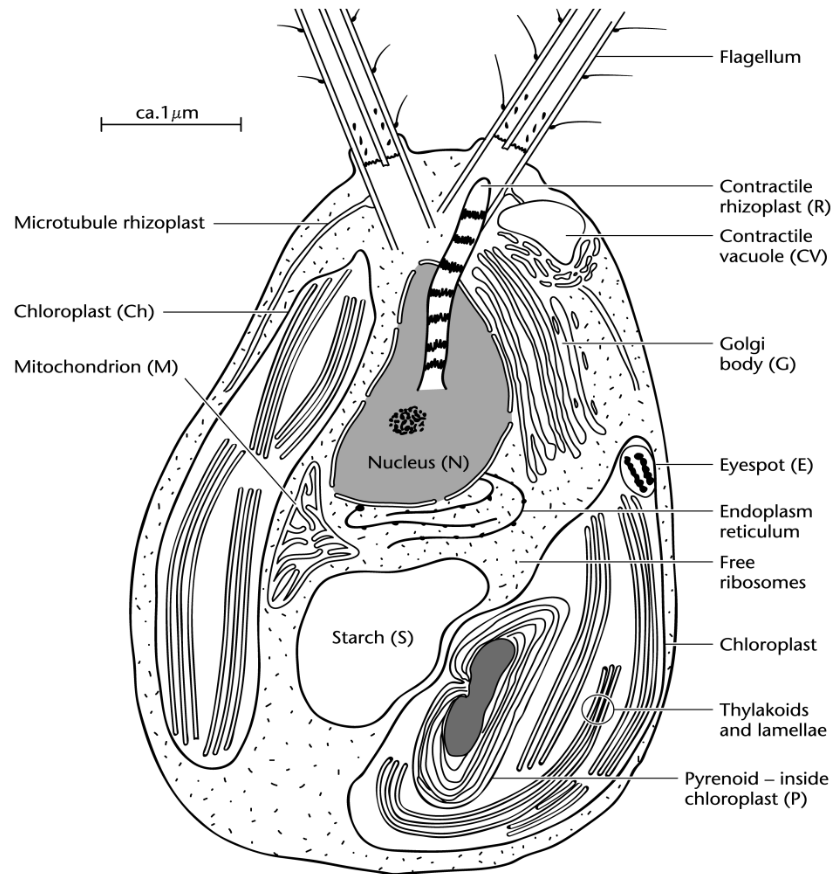


Prochlorococcus marinus

Synechococcus and *Prochlorococcus* as viewed by a flow cytometer

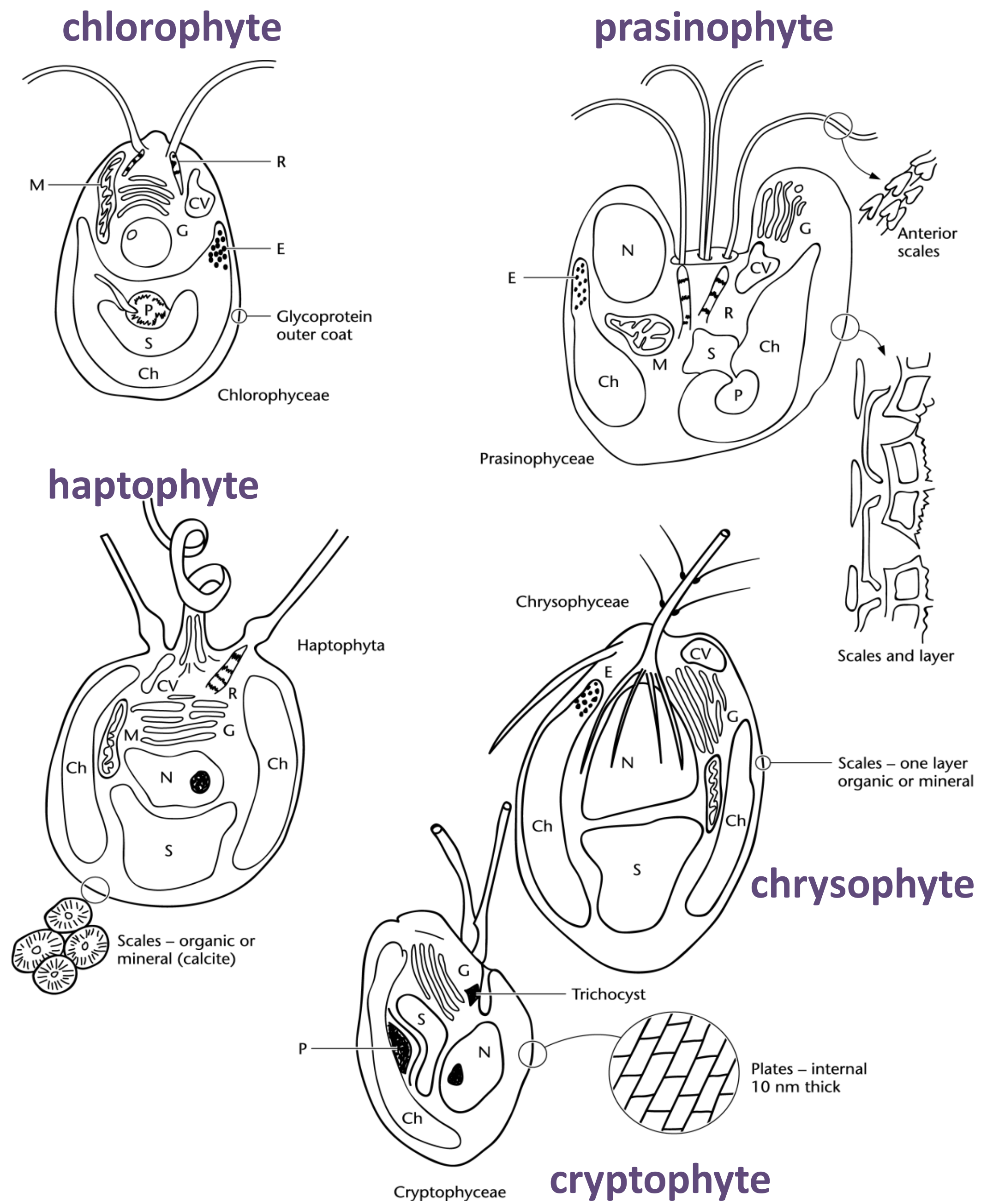


Generalized "microflagellate"



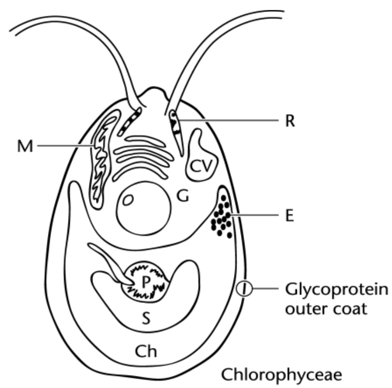
Types of microflagellates

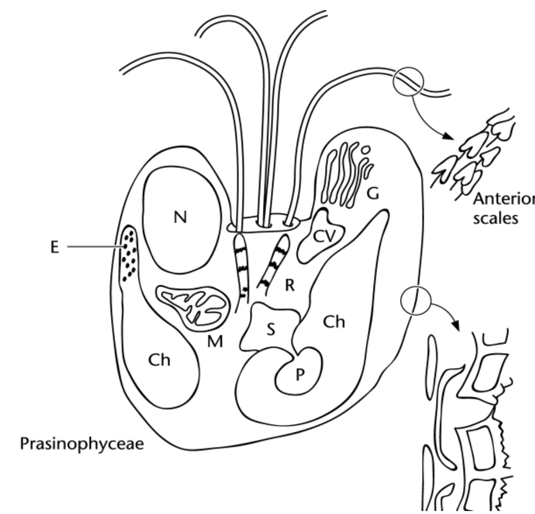
- Differ according to pigments, cell wall material, number of flagella
- Very diverse group
- Artificial grouping (not related – polyphyletic, many origins)
- If classified based on size, they have similar characteristics; if measured by pigments, can be quite different



Archaeplastida: Chloroplastida (Chlorophyceae, Prasinophyceae)

- possess chl *a* and chl *b*
- possess flagella that are similar in structure, can have two or more
- chloroplast is surrounded by two membranes
- accessory pigments include lutein, zeaxanthin, violaxanthin, anteraxanthin, neoxanthin
- some possess pyrenoids (proteinaceous product involved in starch formation)
- storage product is starch, present as grains



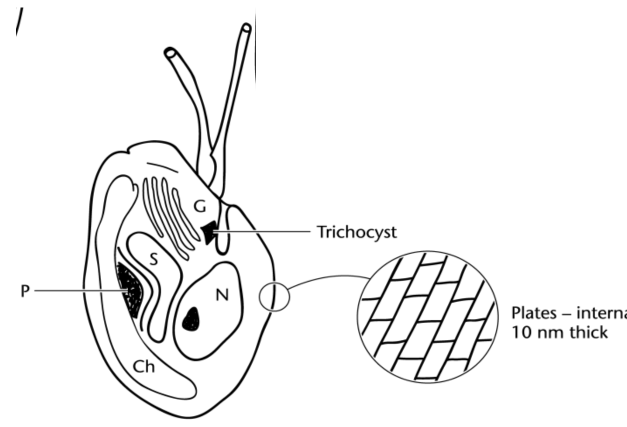


Chromalveolata

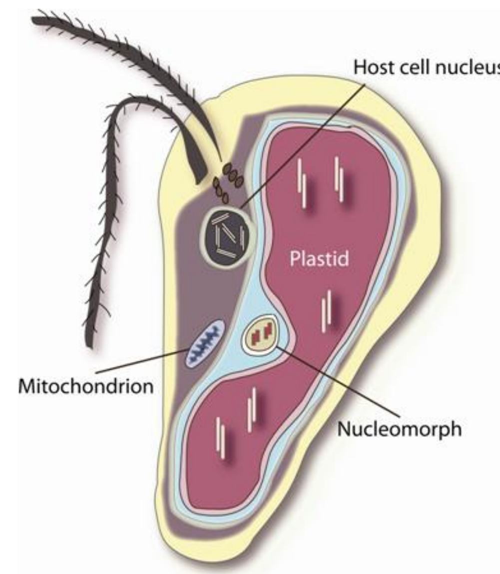
- **Cryptophyceae** (Cryptomonodales)
- Haptophytes (Pavlophyceae, **Prymnesiophyceae**)
- Heterokonts (**Bacillariophyta**, Chrysophyceae, Dictyochophyceae, Pelagophyceae, Raphidophyceae, Synurales, Xanthophyceae, **Dinozoa**)

Cryptophyceae

- Two flagella which differ in length
  - longer flagellum bears two rows of mastigonemes (stiff lateral hairs), shorter flagellum bears a single row of shorter mastigonemes
  - flagella covered with tiny organic scales
- Dorsal side is convex, while ventral side is flat, with a shallow longitudinal groove
- Gullet on the ventral side at the anterior end of the flagellar groove – gullet is lined with trichocysts (releases small protein thread into medium for rapid movement)
- Chloroplasts surrounded by a fold of endoplasmic reticulum
- Chloroplasts contain chl *a* and c_2; accessory pigments include phycocyanin, phycoerythrin, a-carotene, alloxanthin, zeaxanthin, monadoxanthin, crocoxanthin
- No phycobilisomes

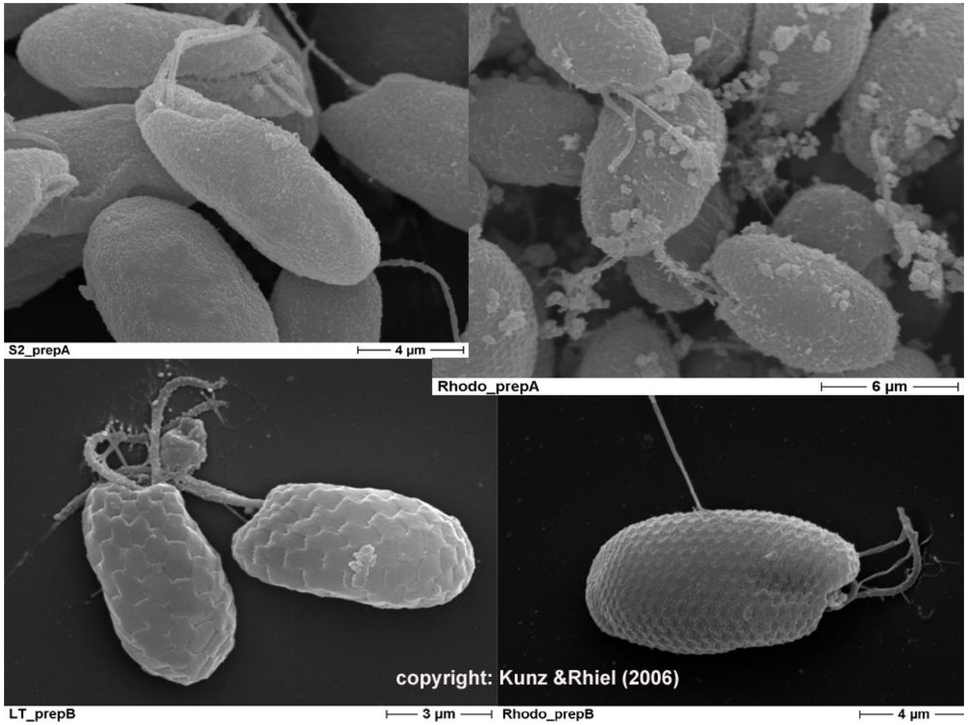


Cryptophyceae



- Storage material is starch
- Cell is enclosed by stiff, proteinaceous periplast, usually made up of rectangular or polygonal plates
- A nucleomorph is present in the space between the chloroplast and the chloroplast ER (contains DNA and a nucleolus-like structure; interpreted as the vestigial nucleus of a photosynthetic eukaryotic endosymbiont)
- Found in both fresh and marine waters

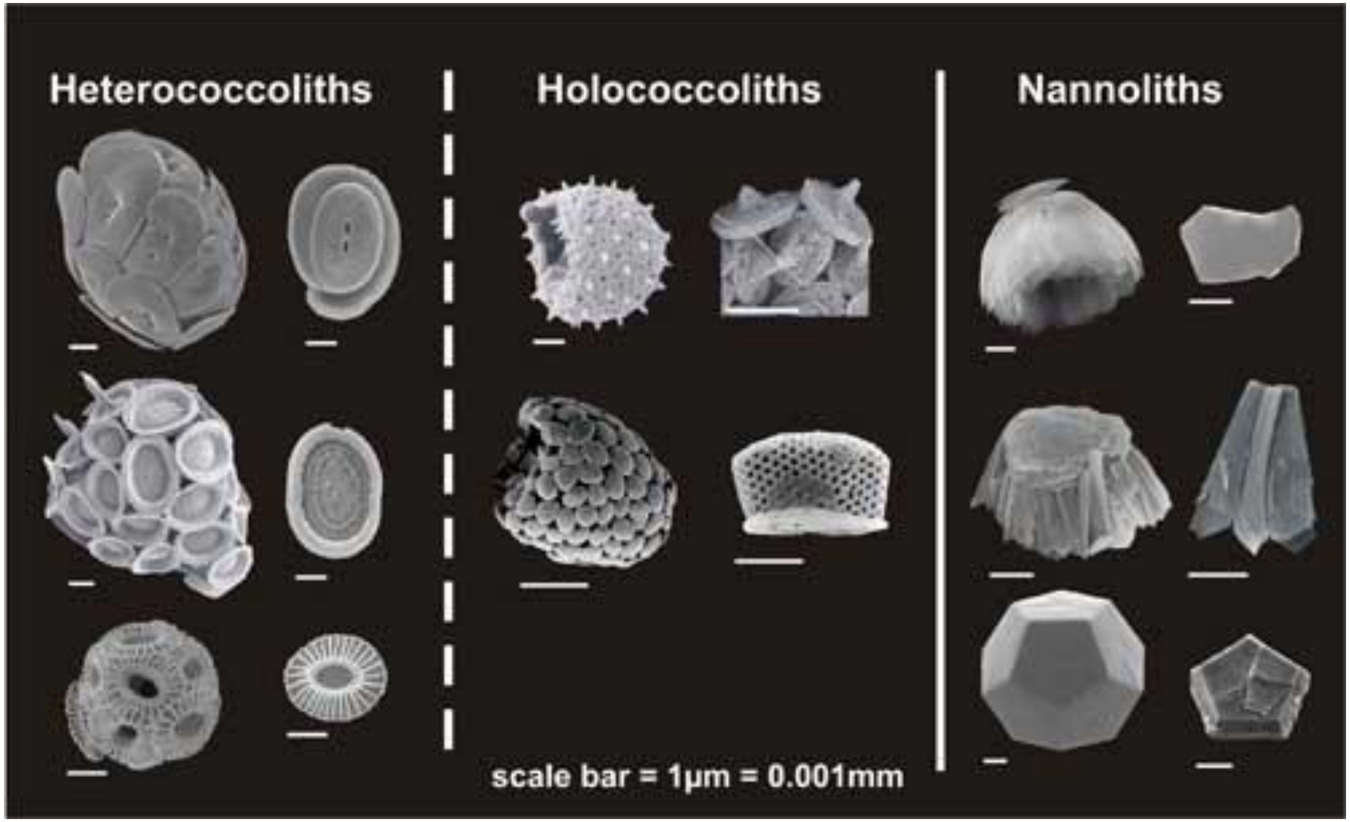
Cryptophyceae



Haptophytes (= Prymnesiophytes)

- Majority are unicellular
- Possess two flagella without mastigonemes plus a haptonema (thin, filamentous appendage which may be short or very long – not a flagellum, different structure)
- Often possess pyrenoids
- Contain chl a, c1 and/or c3, c2; accessory pigments include 19'hexanoyloxyfucoxanthin, 19'butanoyloxyfucoxanthin, and fucoxanthin, plus b-carotene, diadinoxanthin, and diaoxanthin
- Storage product is chrysolaminarin (polysaccharide)
- Cell surface covered in scales, granules of organic matter (cellulose), or else calcified scales (coccoliths)

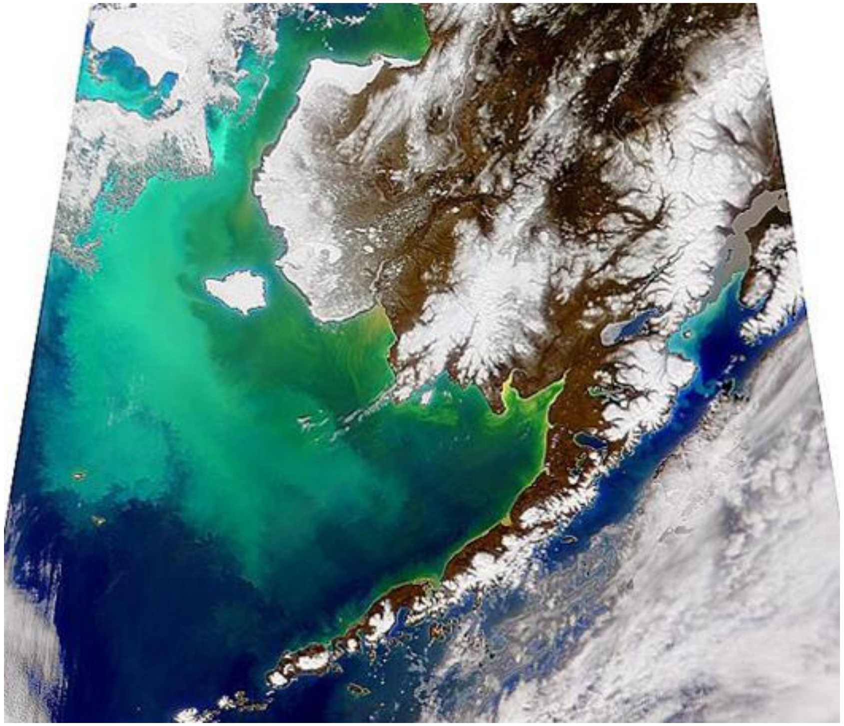
Haptophytes

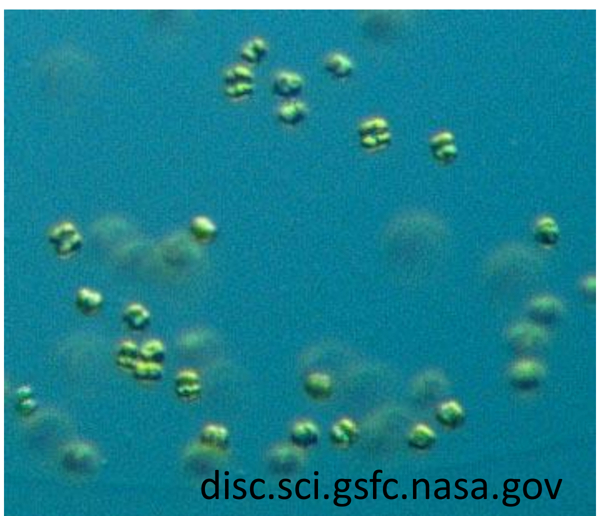


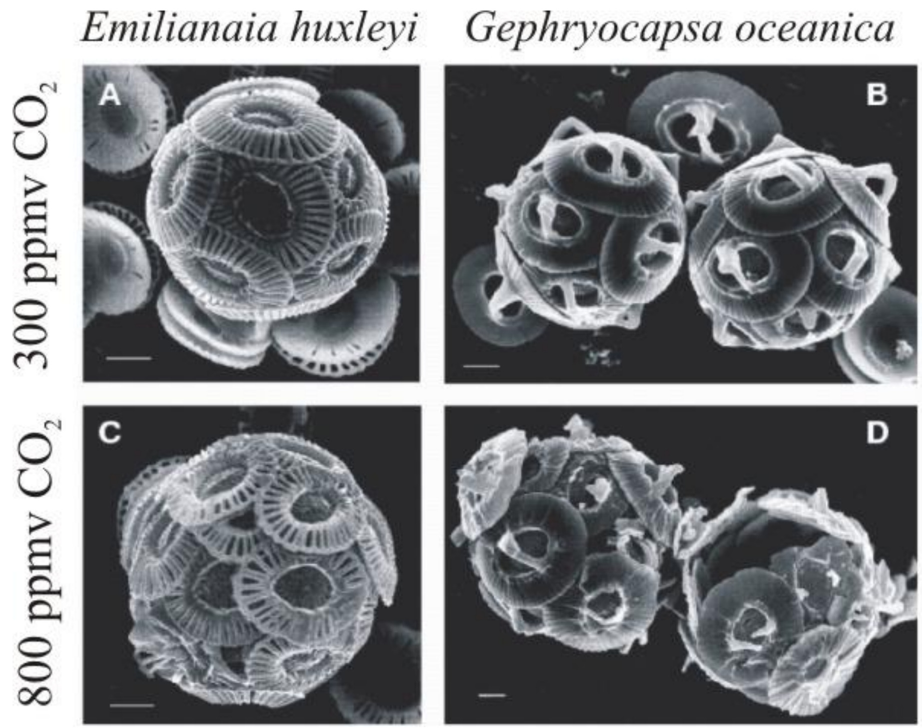
Chrysochromulina sp.

www.glerl.noaa.gov

Haptophytes







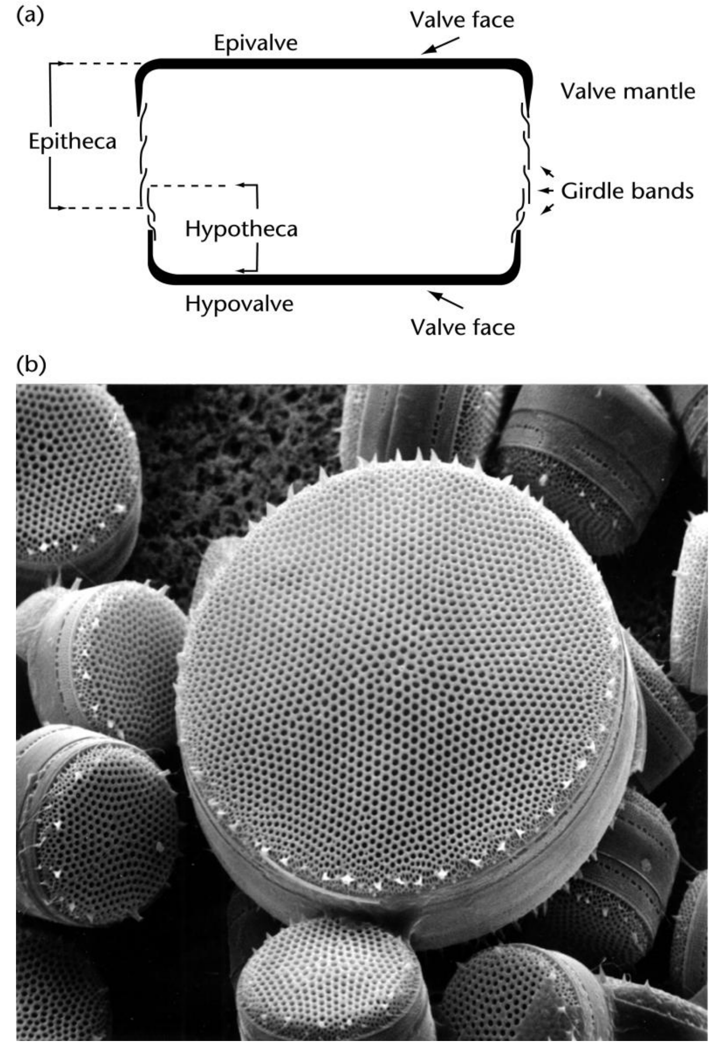
Riebesell et al.

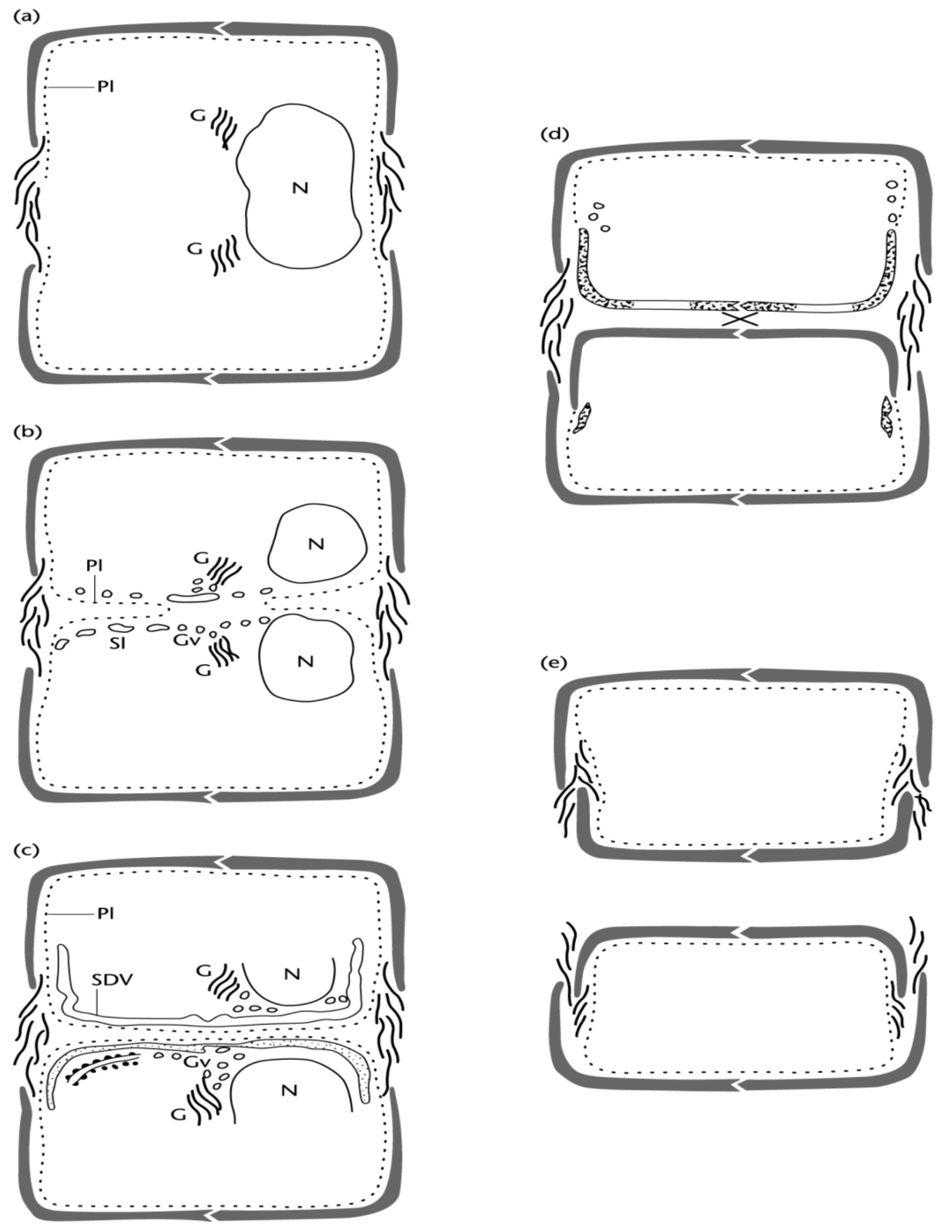
Heterokontophyta/Stramenopiles

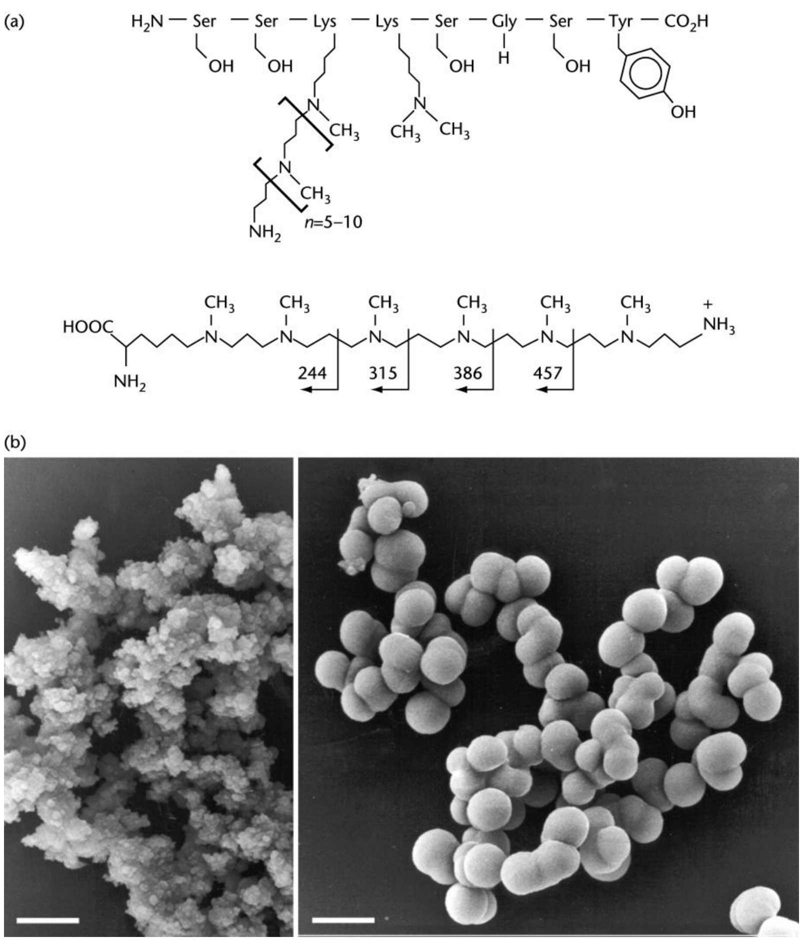
- Heterokonts have two flagella, one long pleuronematic (= flimmer or tinsel) flagellum with stiff hairs (mastigonemes) directed forward during swimming and a shorter smooth flagellum that points backwards along the cell
- Chloroplast enclosed by double membrane and by a fold of endoplasmic reticulum (called chloroplast ER)
- Chloroplasts contain chl *a*, c_1 and c_2, with fucoxanthin as principal accessory pigment in some groups (Chrysophyceae, Bacillariophyceae, some Raphidophyceae) or vaucheriaxanthin in other groups
- Main reserve polysaccharide is chrysolaminarin (β-1,3 linked glucan) found outside the chloroplasts inside special vaculoles

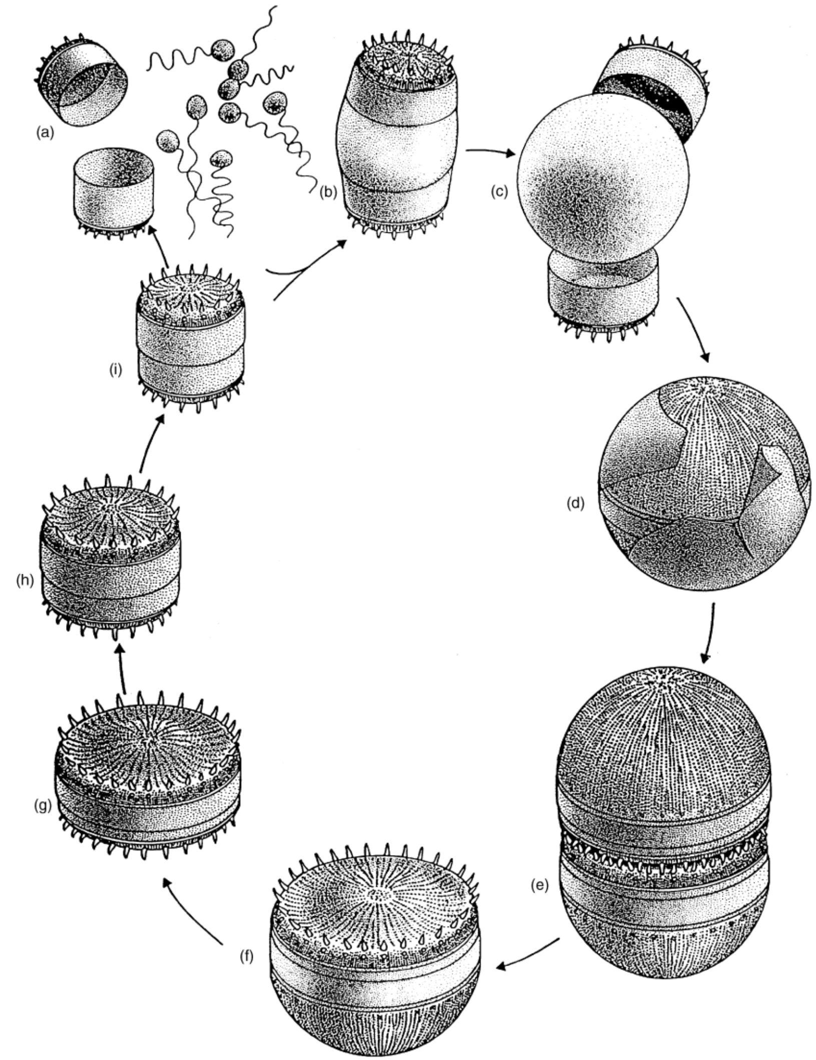
Diatoms

- Bacillariophyceae
- Pigments: chl *a*, chl c_2, fucoxanthin, diadinoxanthin, β-carotene, diatoxanthin, chl c_1
- Cell wall: amorphous silica (opal)
- Centric (radially symmetric) and pennate (bilaterally symmetric)

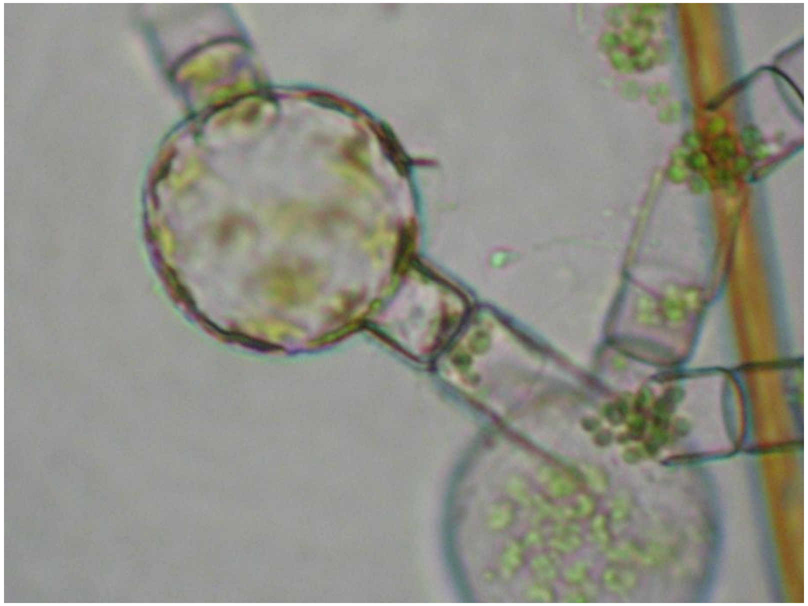


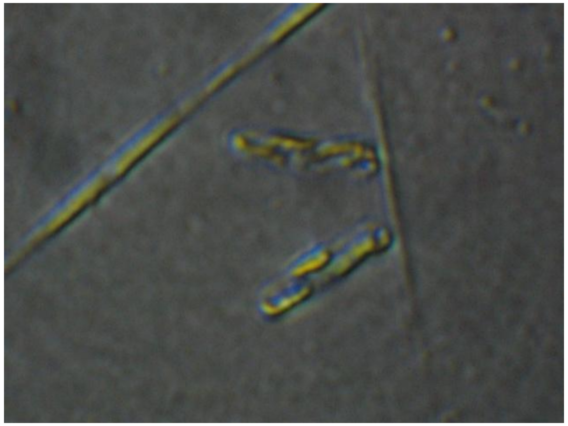

(a)
Pl
G
N
G
(b)
N
Pl
G
Sl
Gv
G
N
(c)
Pl
G
N
SDV
Gv
G
N
(d)
(e)


(a)
H2N — Ser — Ser — Lys — Lys — Ser — Gly — Ser — Tyr — CO2H
OH
H
CH3
n=5–10
NH2
HOOC
NH3
244
315
386
457
(b)


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)

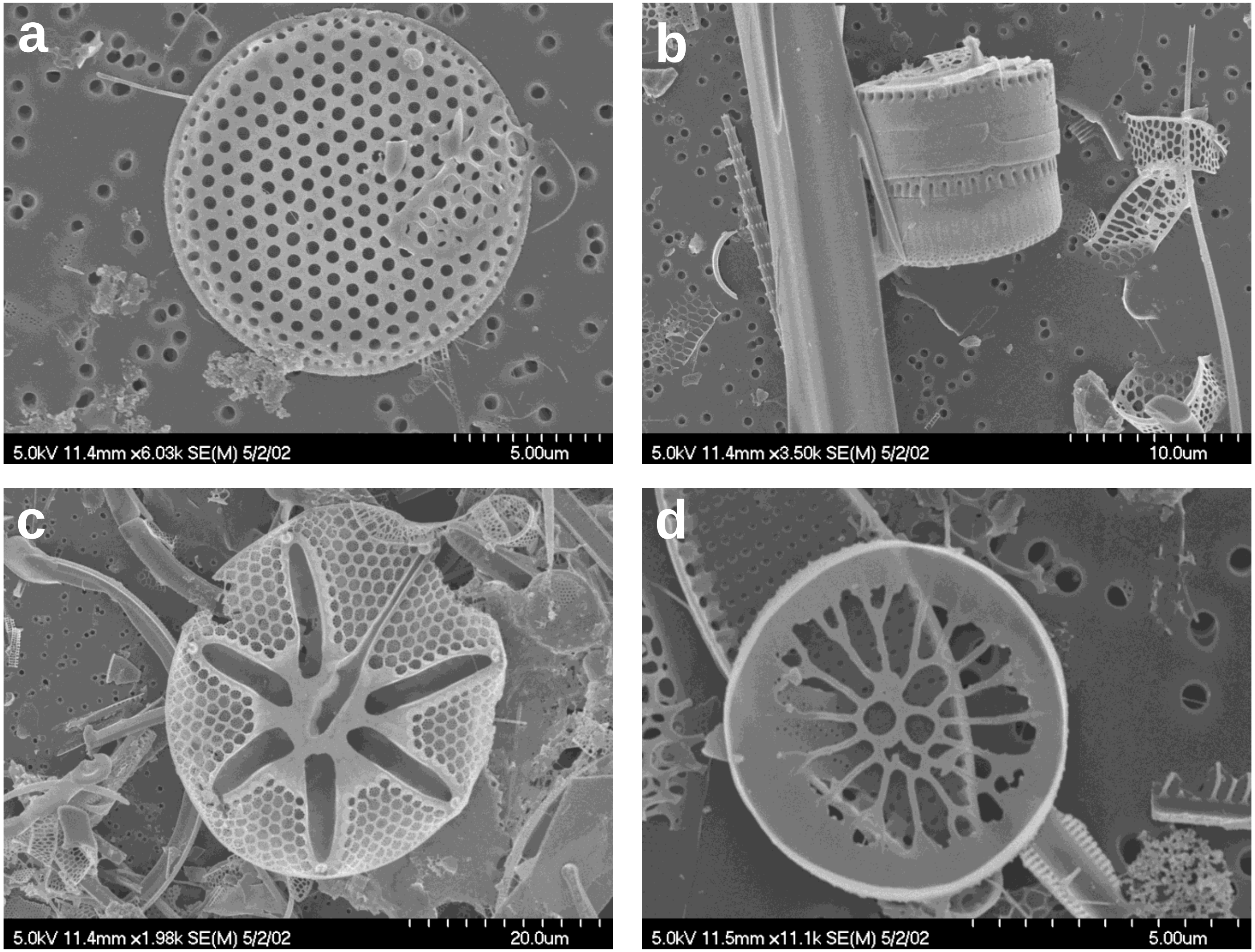
Auxospores of *Aulacoseira* sp.

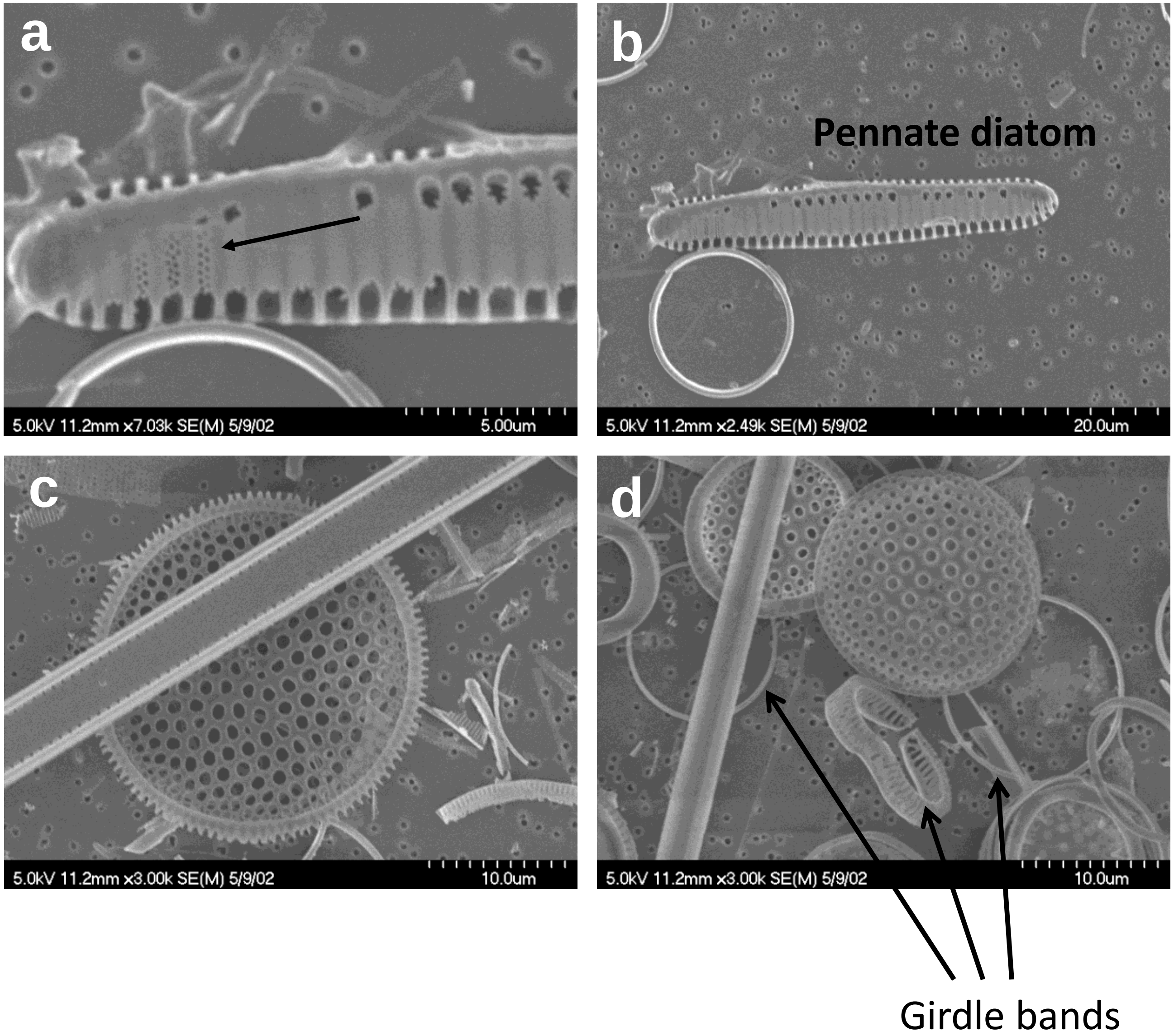


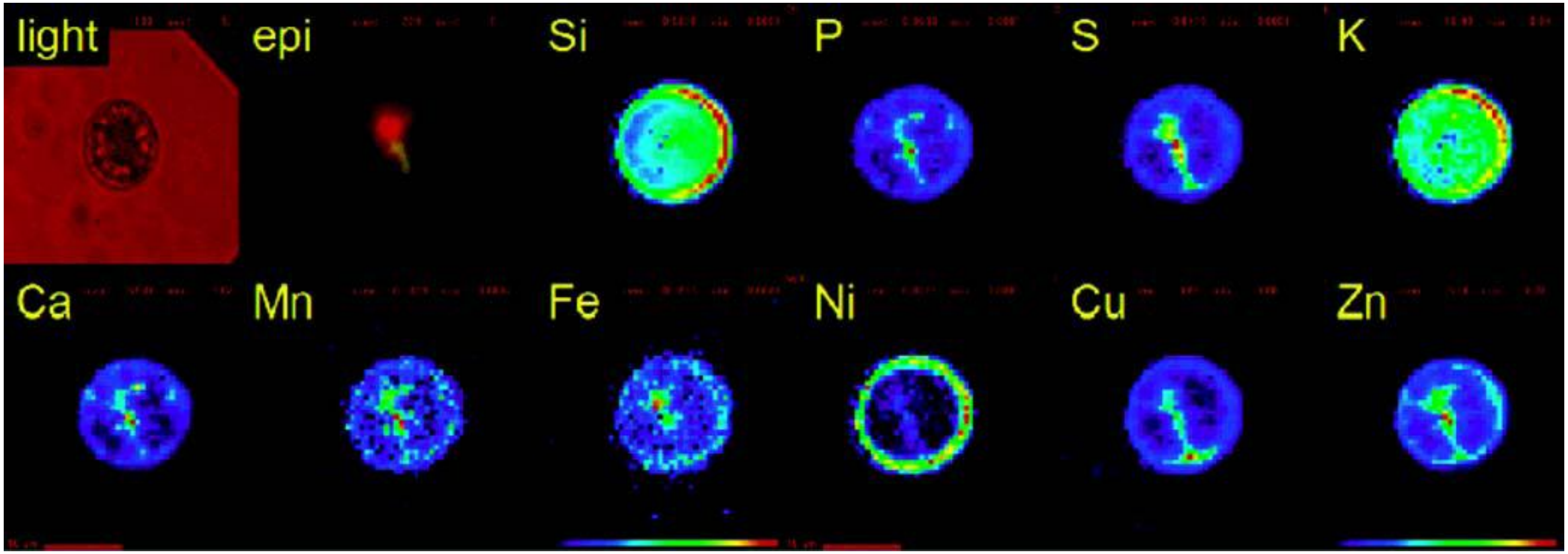


Pennate diatoms – initial cells produced by non-motile gametes

Diatoms from the Gulf of Alaska




a
5.0kV 11.2mm x7.03k SE(M) 5/9/02
5.00um
b
Pennate diatom
5.0kV 11.2mm x2.49k SE(M) 5/9/02
20.0um
c
5.0kV 11.2mm x3.00k SE(M) 5/9/02
10.0um
d
5.0kV 11.2mm x3.00k SE(M) 5/9/02
10.0um
Girdle bands



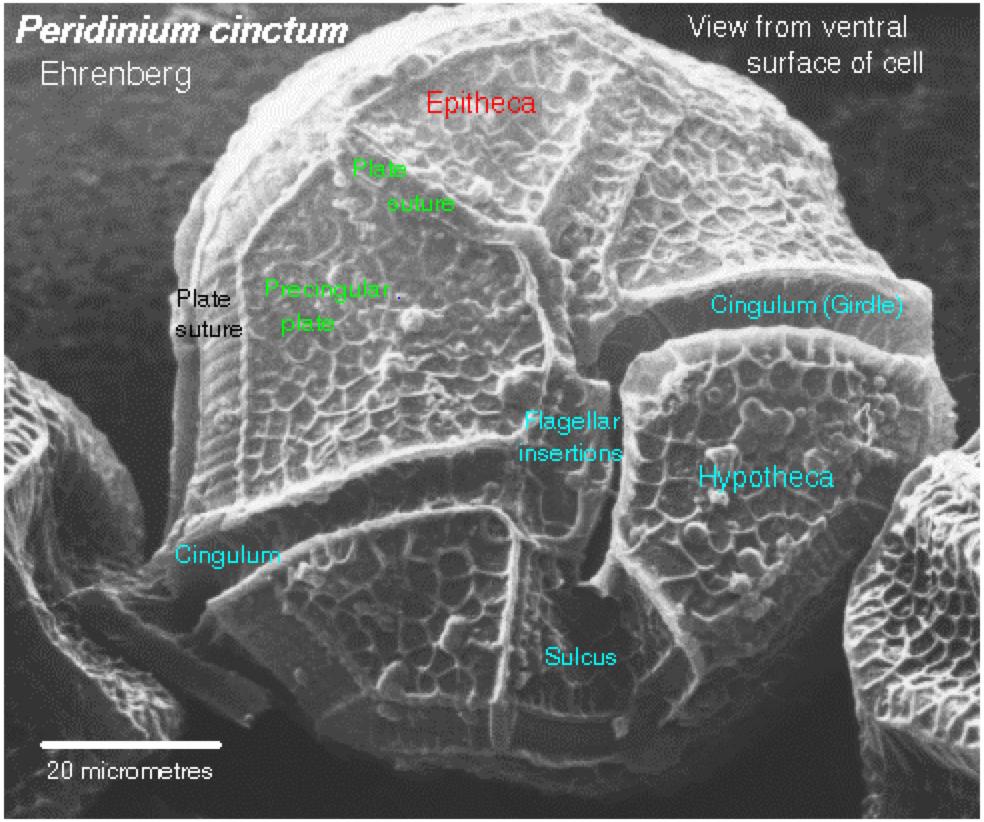
Using synchrotron x-ray fluorescence to map out elements in a diatom cell (Zhao & Le, 2007)

Dinophyceae

- Most unicellular, some colonial
- Complex group, including autotrophs, heterotrophs, and mixotrophs
- Two dissimilar flagella; one is transverse (‘side-to-side’) and one is longitudinal (‘up-down’) each bearing fine lateral hairs; both arise on the ventral side of the cell
- Transverse furrow and longitudinal groove present in most taxa
- Chloroplasts surrounded by 3 membranes
- Chl *a*, chl c_2; accessory pigments are peridinin, β-carotene, and other xanthophylls
- Pyrenoids present
- Reserve polysaccharide is starch
- Cell wall made of cellulose arranged in plates (thecal plates) – pellicle made up of cell membrane externally and underlain by flattened vesicles (plates)
- Many have eyespots
- Possess trichocysts (discharge explosively when simulated, throwing out transversely striated, four-sided threads)

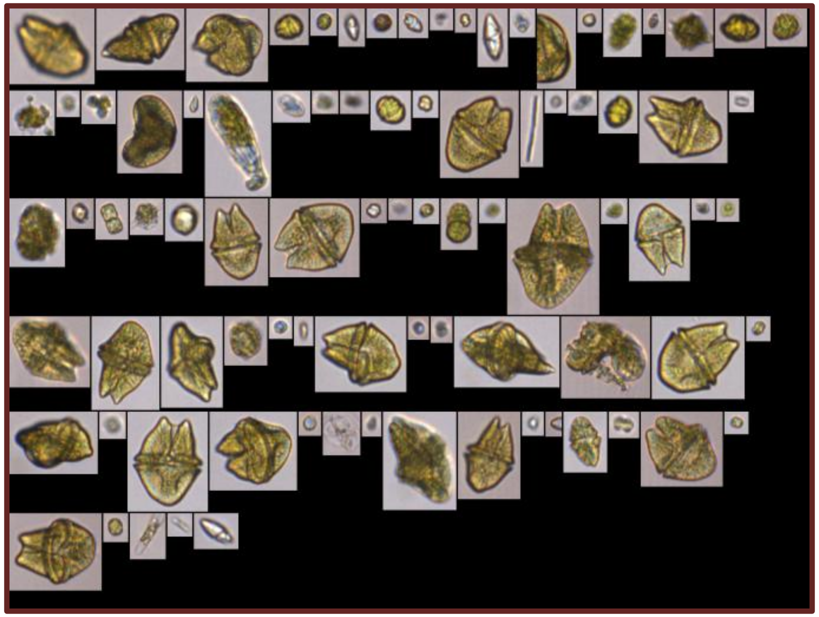
Dinoflagellates

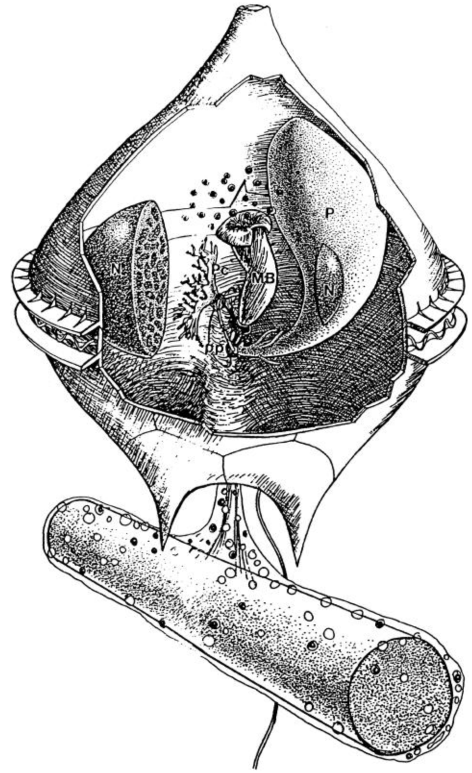
-theca (robust 'envelope')
-epitheca (=epicone)
-hypotheca (= hypocone)
-transverse groove (cingulum or girdle)
-longitudinal groove (sulcus)
-dino = 'spinning' – swim in a turning motion
-many produce toxins and are considered to be harmful algal bloom species



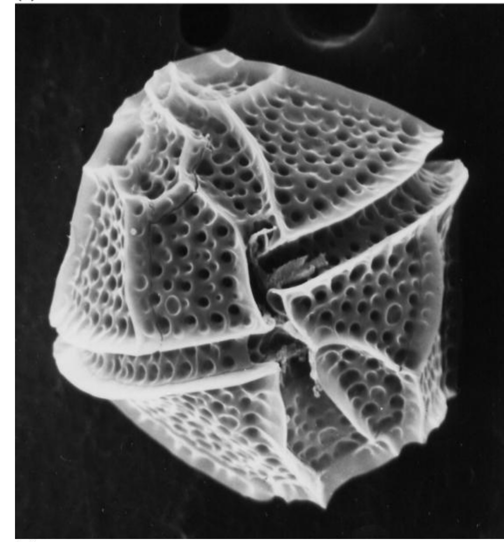
www.jochemnet.de

Dinophyceae

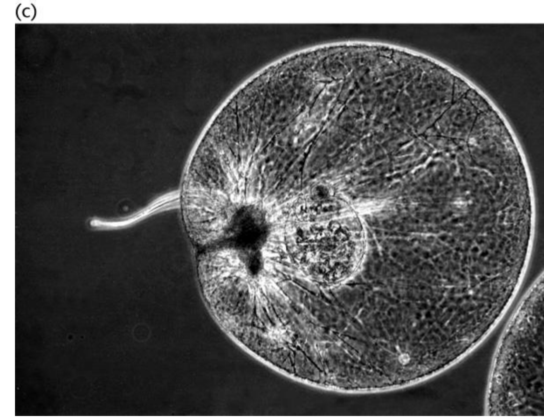


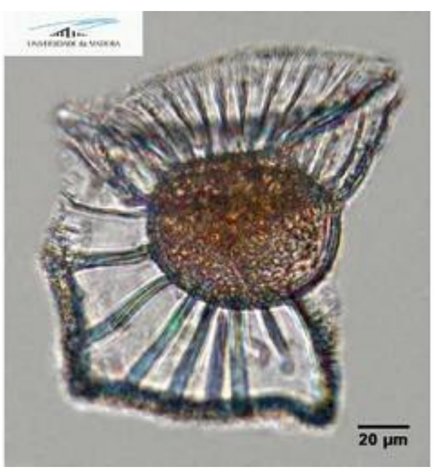


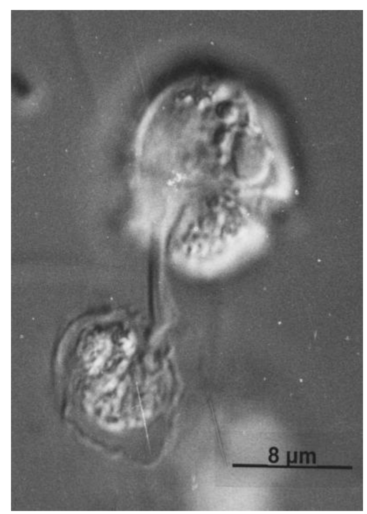
(a)



(c)



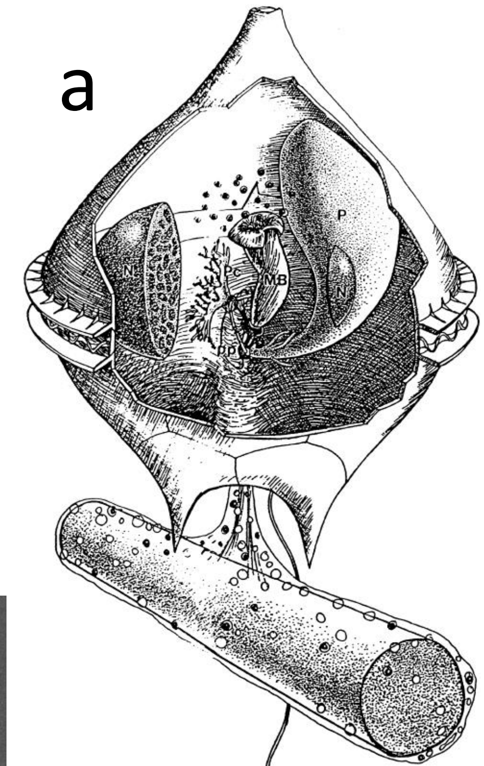




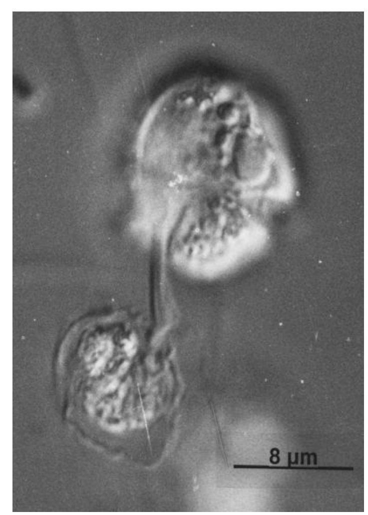
Dinophyceae as predators

- Some dinoflagellates prey on other organisms using an extracellular net of fibers or mucus-like material (a pallium); extruded through pallial pore located in the sulcus; digestion occurs in the pallial sac (a)
- Another strategy is to insert a peduncle into the tissue of the prey (b)

a



b



Chrysophyceae

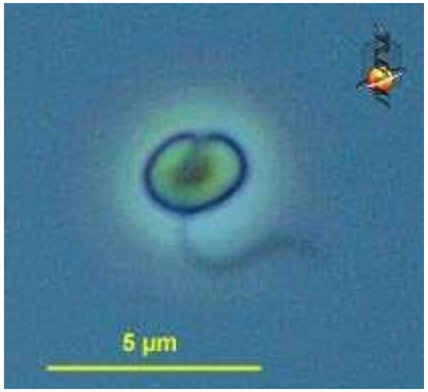
- Unicellular or colonial
- May or may not be flagellate
- Flagella inserted near the apex of the cell (not laterally)
- Golden-brown chloroplasts (chl is masked by the accessory pigment, fucoxanthin); may also possess zeaxanthin, antheraxanthin, violaxanthin, diatoxanthin, diadinoxanthin
- Some species bear siliceous scales
- Freshwater and marine
- Chrysolaminarin as storage product
- Common in oligotrophic lakes; greater diversity in freshwater

www.conncoll.edu

http://www.members.shaw.ca

Pelagophyceae

- Small, flagellated cells
- Some form ‘brown tides’ (e.g. *Aureococcus anophagefferens*)
- Coastal and open ocean environments

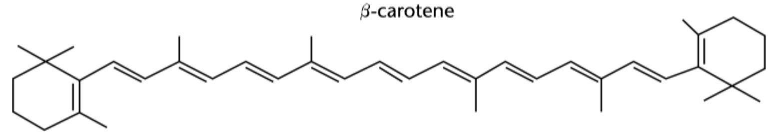



www.bayshorewatershed.org

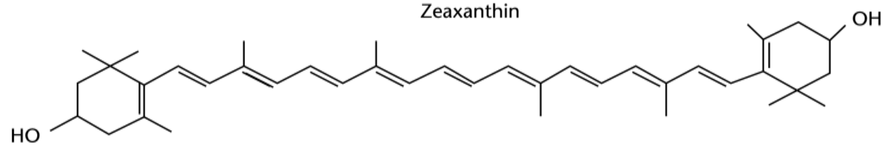
Encyclopedia of Life

(b)

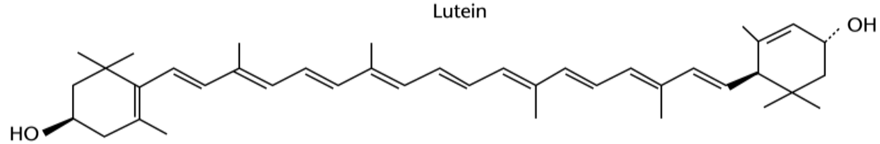
β-carotene



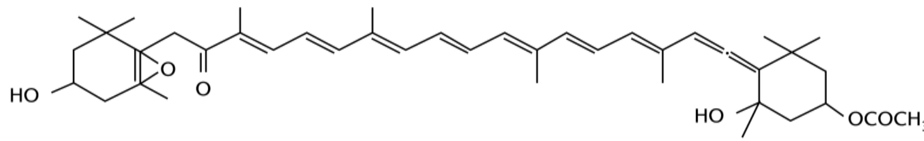
Zeaxanthin



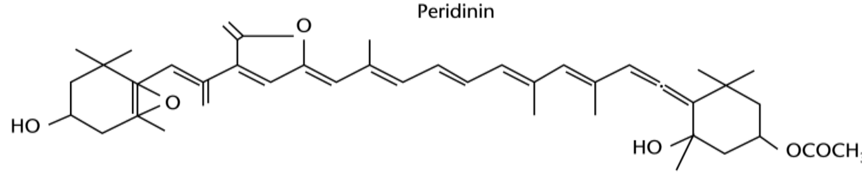
Lutein



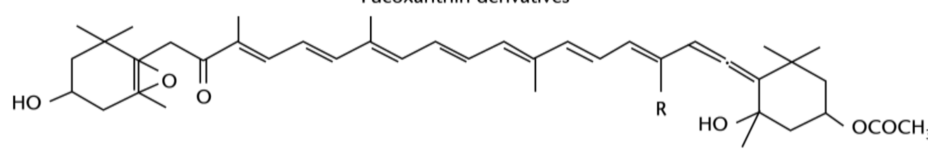
Fucoxanthin



Peridinin



Fucoxanthin derivatives

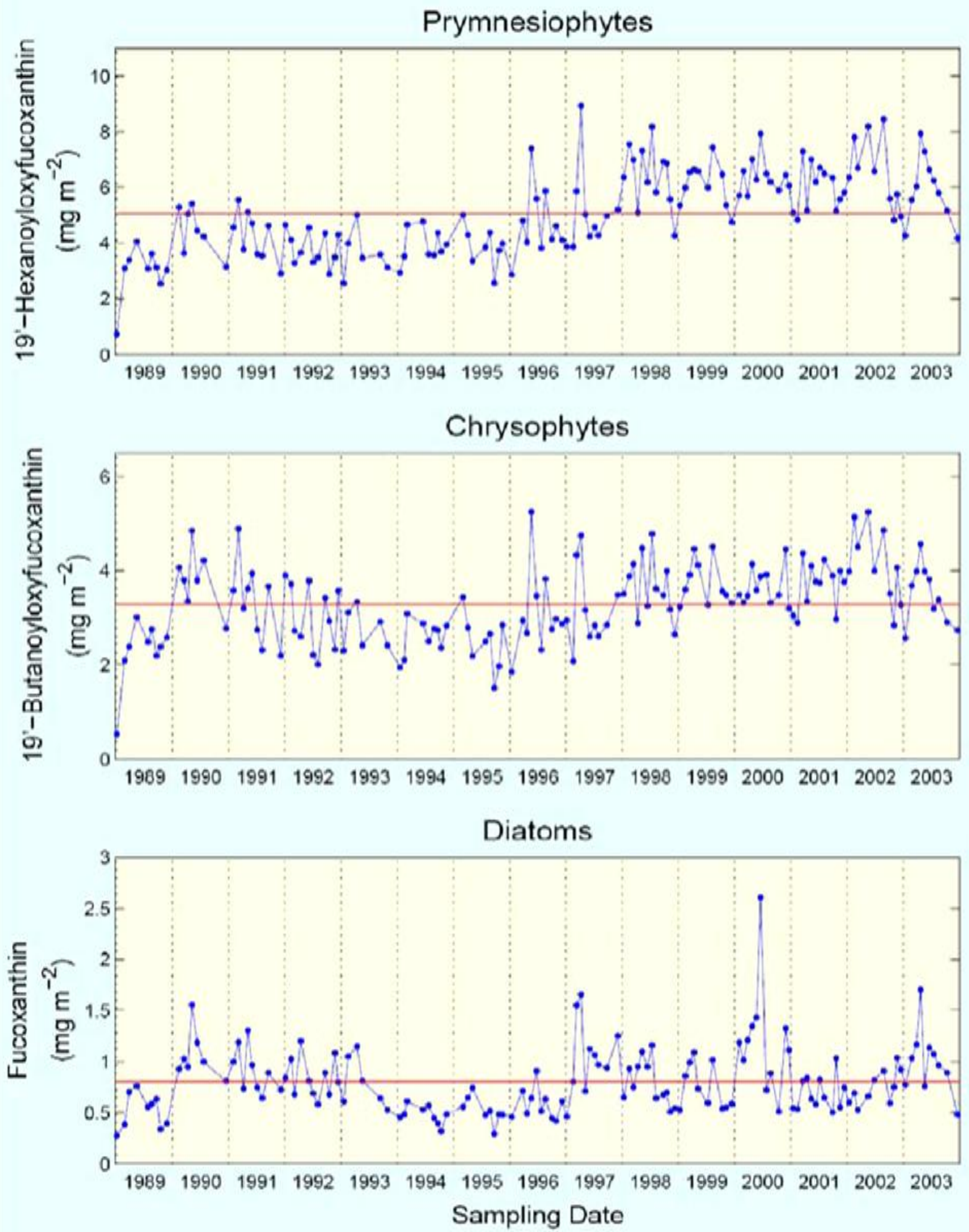


19'-hexanoyloxy-fucoxanthin, R = CH_2 — O — C — C_3H_7

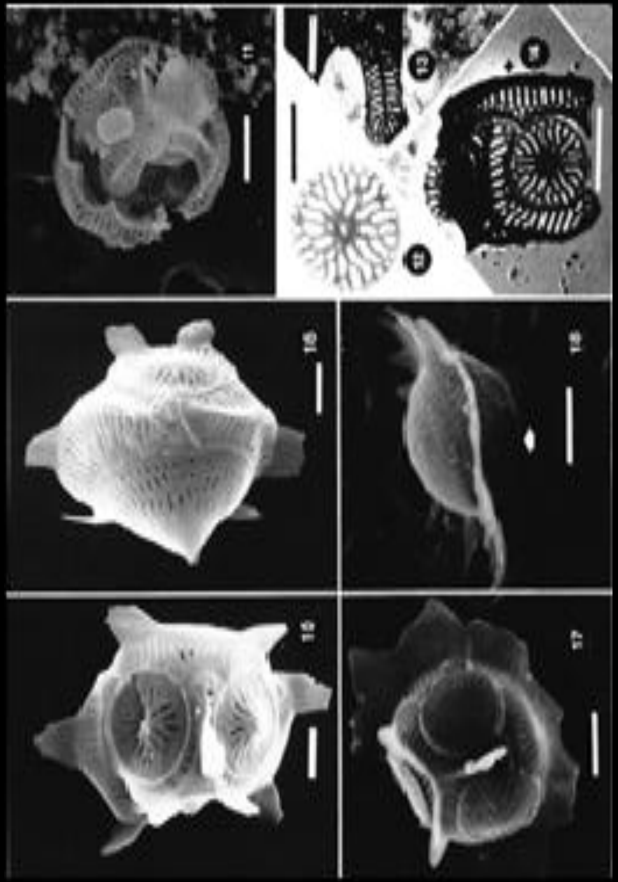
19'-butanoyloxy-fucoxanthin, R = CH_2 — O — C — C_5H_{11}

Class	Pigments	Diagnostic pigment
Bacillariophyceae	Chl *a*, chl c_2, fucoxanthin, diadinoxanthin, β-carotene, diatoxanthin, chl c_1	Fucoxanthin
Chlorophyceae	Chl *a*, chl *b*, β-carotene, lutein, violaxanthin, zeaxanthin, neoxanthin	Chl *b*
Chrysophyceae	Chl *a*, chl c_1, c_2, fucoxanthin, 19'butanoyloxyfucoxanthin, diadinoxanthin	Chl c_1, c_2
Cryptophyceae	Chl *a*, chl c_2, β-carotene, alloxanthin, phycoerythrin & phycoerythrin (cryptophyte types)	Alloxanthin
Cyanophyceae	Chl *a*, β-carotene, zeaxanthin, phycocyanin, allophycocyanin, phycoerythrin	Zeaxanthin
Prochlorophyceae	Chl *a*, divinyl chl b, β-carotene, zeaxanthin	Divinyl chl b

Class	Pigments	Diagnostic pigment
Dinophyceae	Chl *a*, c_2, β-carotene, peridinin, dinoxanthin, diadinoxanthin	Peridinin
Haptophyceae	Chl *a*, chl c_1 or c_3, chl c2, β-carotene, fucoxanthin, 19'hexanoyloxyfucoxanthin, 19'but, diadinoxanthin, diatoxanthin	19' hexanoyloxyfucoxanthin
Prasinophyceae	Chl *a*, chl *b*, prasinoxanthin	Prasinoxanthin
Pelagophyceae	Chl *a*, chl c_2, chl c_3, diatoxanthin, fucoxanthin, β-carotene, diadinoxanthin, 19'butanoyloxyfucoxanthin	19'butanoyloxyfucoxanthin
Euglenophyceae	Chl *a*, chl *b*, β-carotene, diadinoxanthin, zeaxanthin, neoxanthin	Violaxanthin, chl *b*
Raphidophytes	Chl *a*, c_1, c_2, fucoxanthin, β-carotene, violaxanthin	



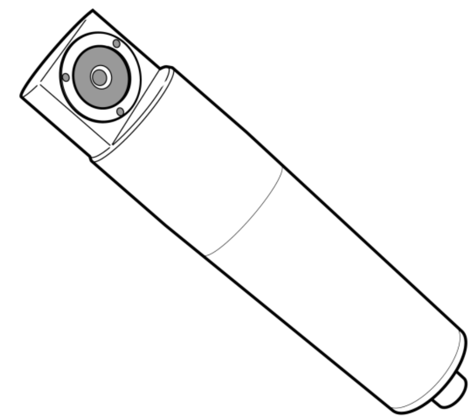
The various groups (or 'taxa') respond to changes in the environment in different ways



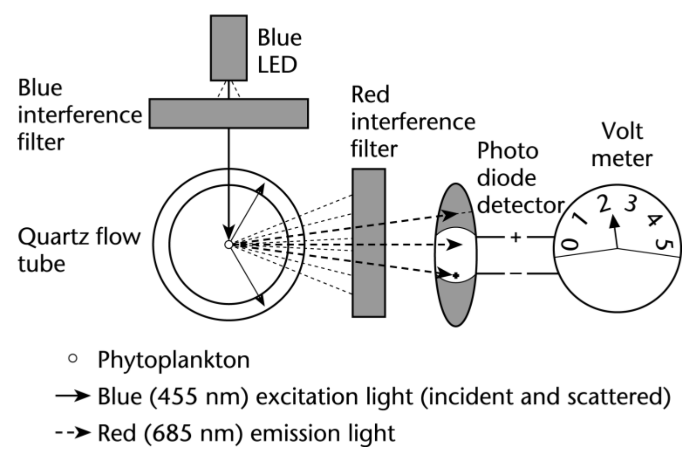
Letelier, 2006

Measuring phytoplankton

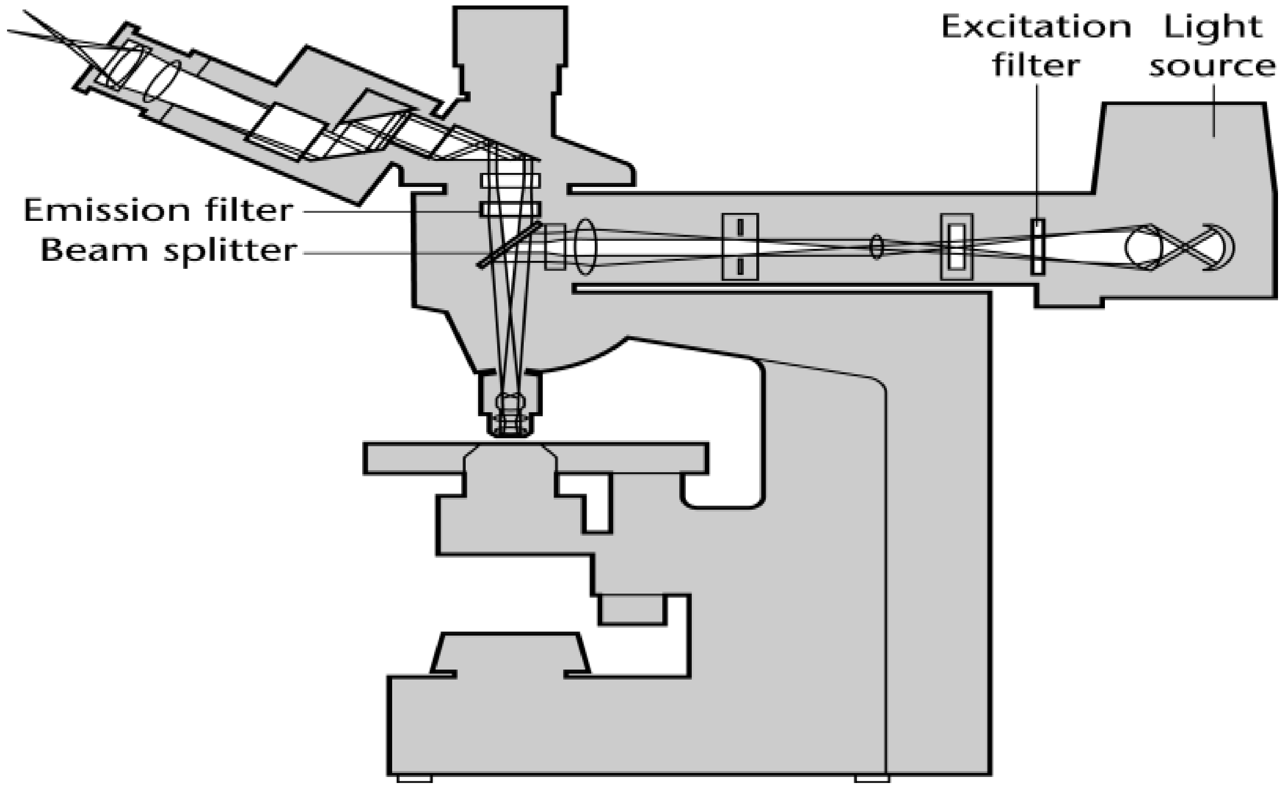
- Use chlorophyll *a* as a proxy
  - Spectrophotometer (absorption)
  - Fluorometer (fluorescence)
- Note: artifactual day-night and depth variation
  - fluorescence varies strongly with external illumination
  - chlorophyll decouples in the dark from the energy transfer system in the chloroplasts of the plant and fluoresces more strongly



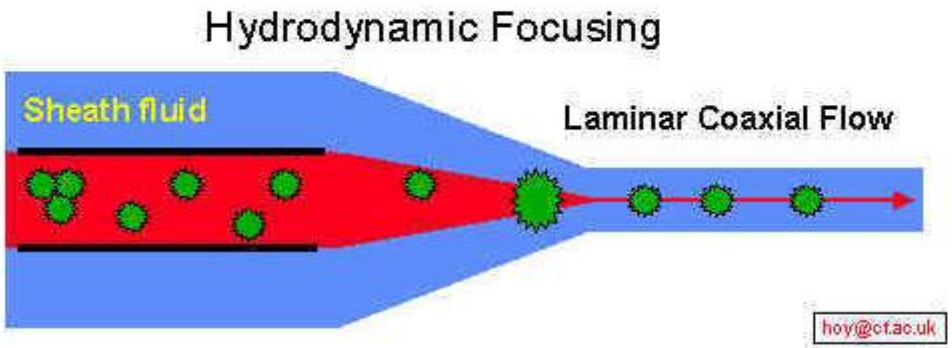
Theory of operation

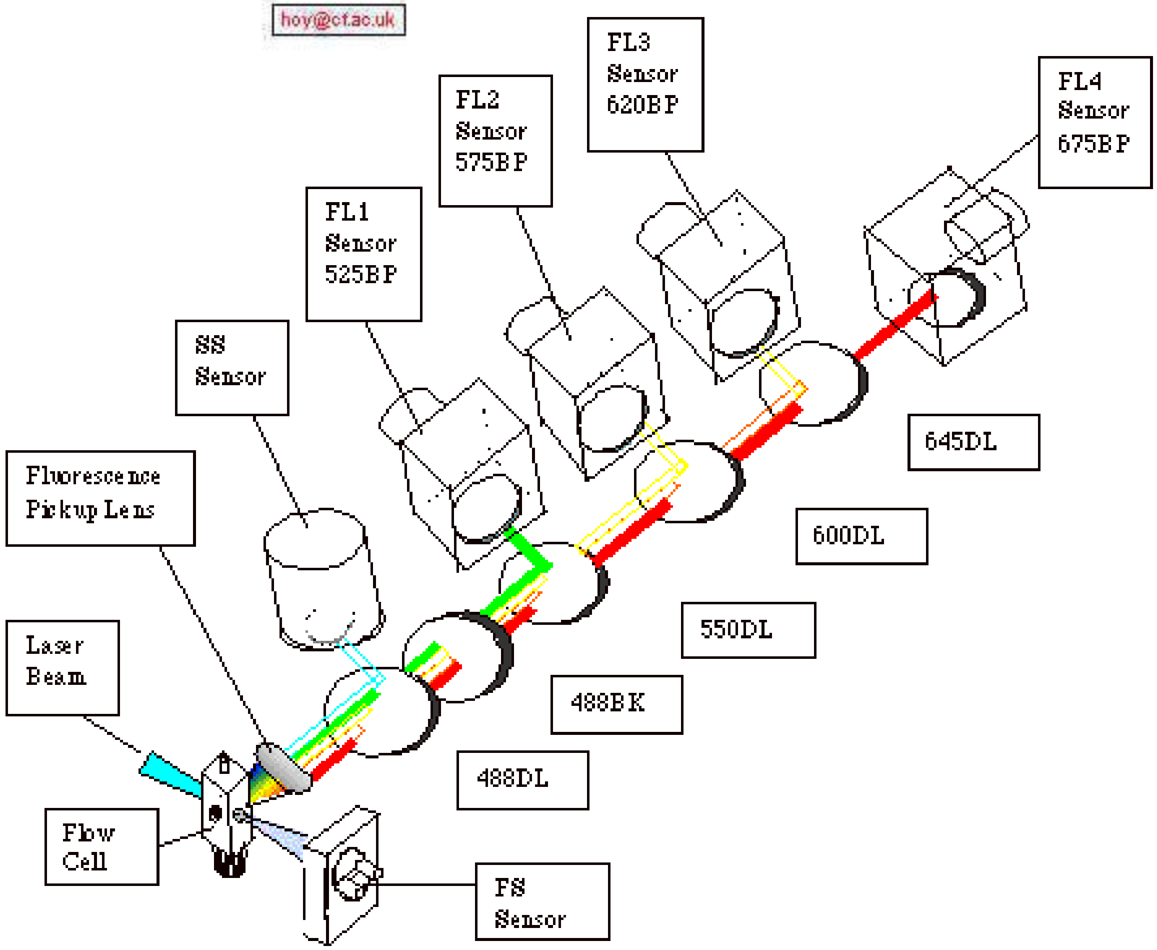


Epifluorescence microscope



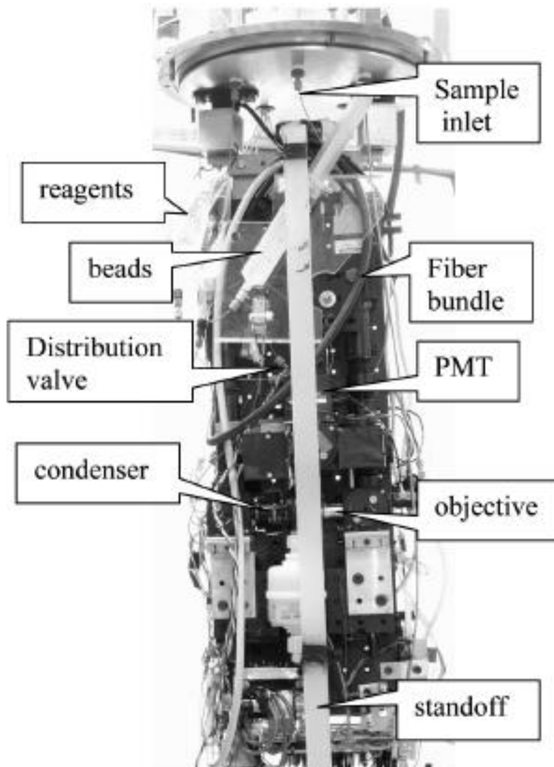
Flow cytometer

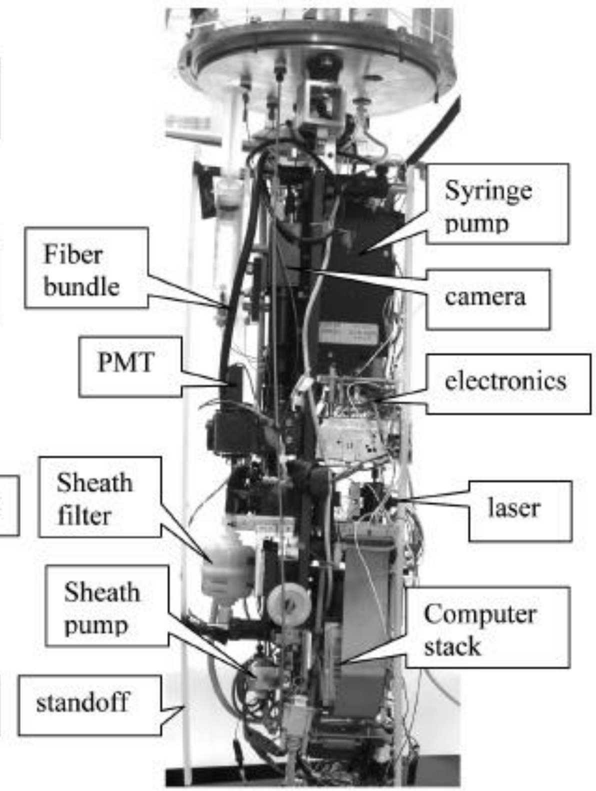


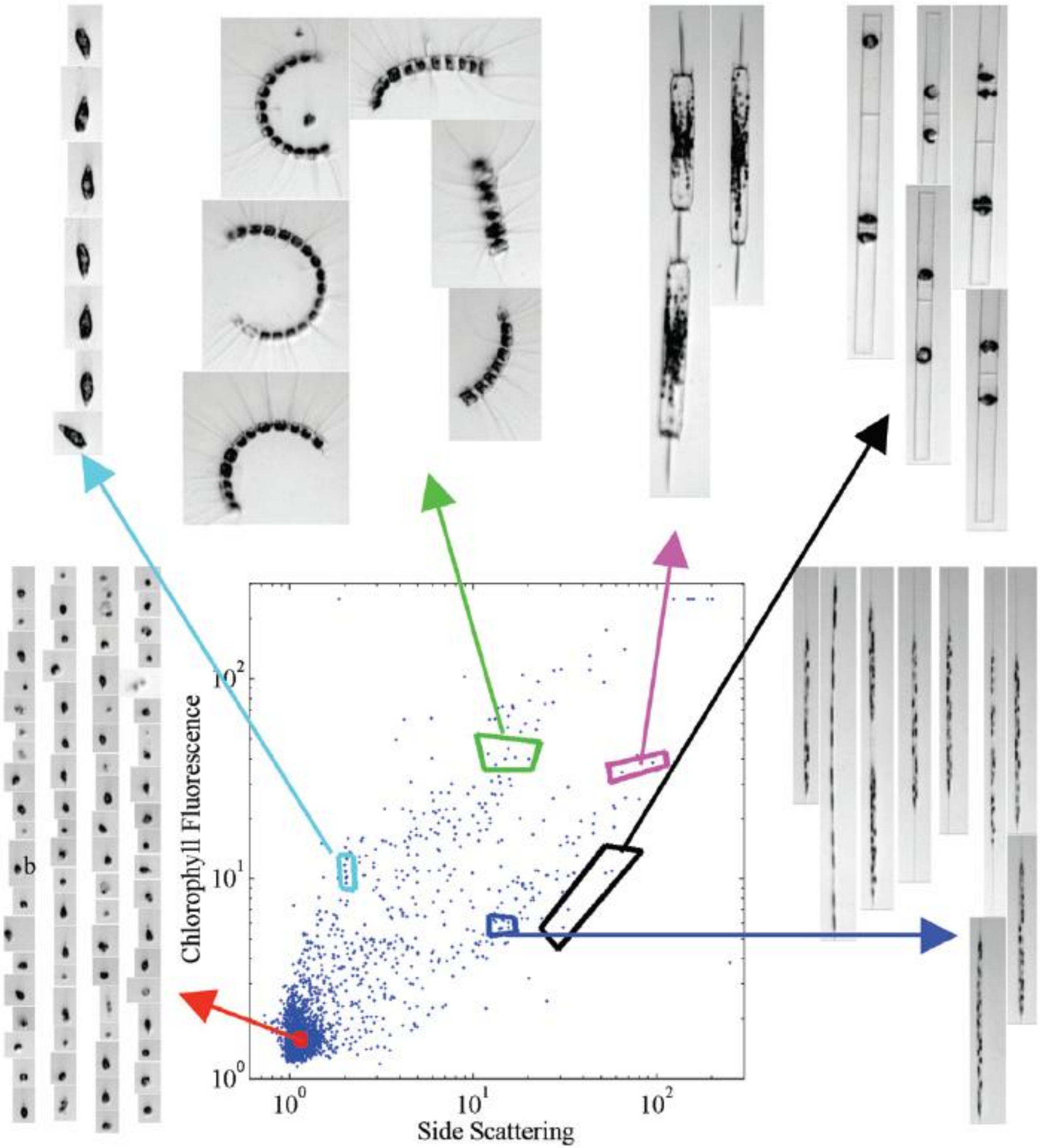


Olson and Sosik, Woods Hole Oceanographic Institute

FlowCytobot and Imaging FlowCytobot



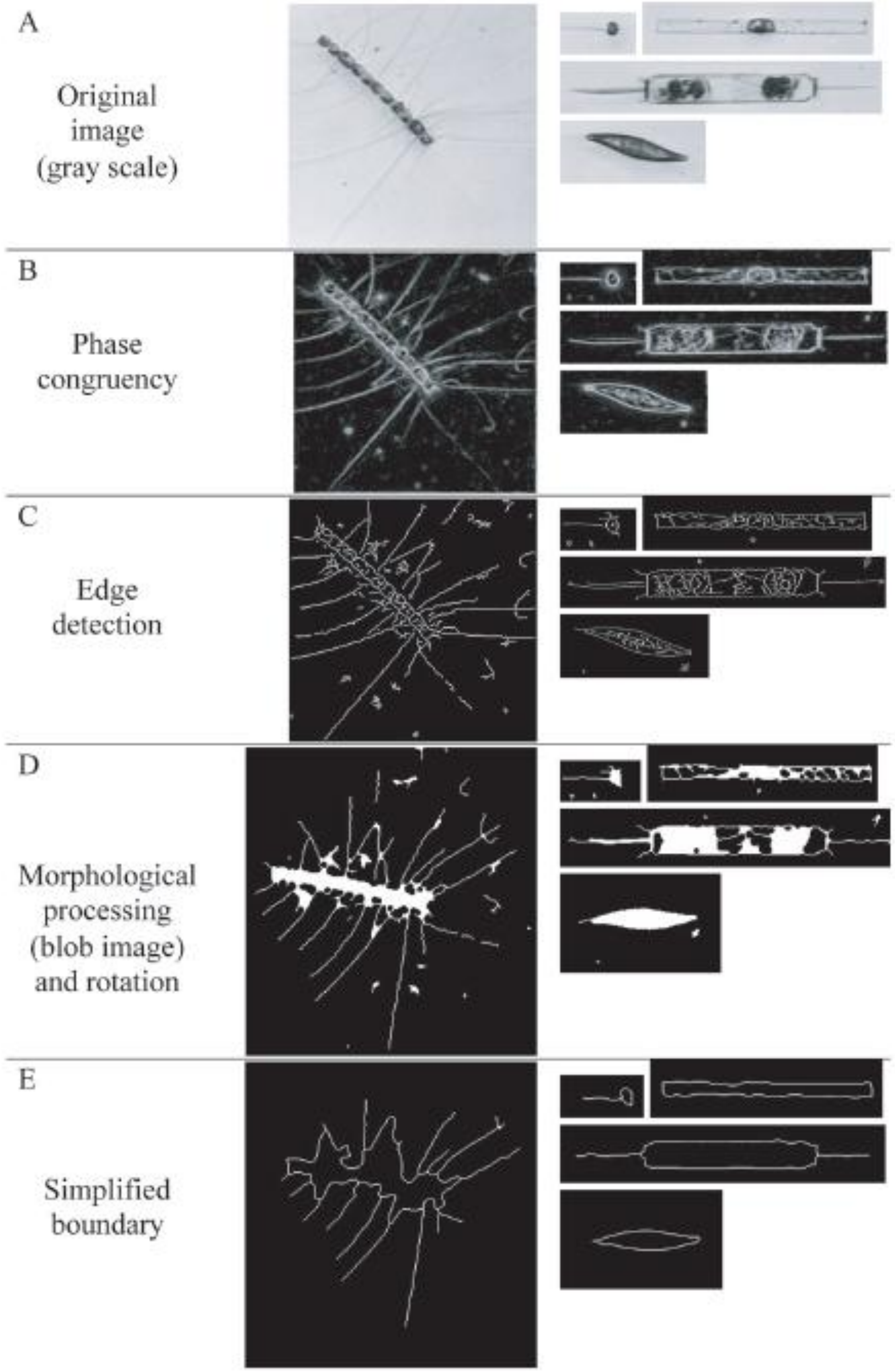




Chlorophyll Fluorescence
Side Scattering
10^0
10^1
10^2
b

Image processing steps for Flow CytoBot

Sosik & Olsen, 2007



FlowCAM: Flow Cytometer And Microscope

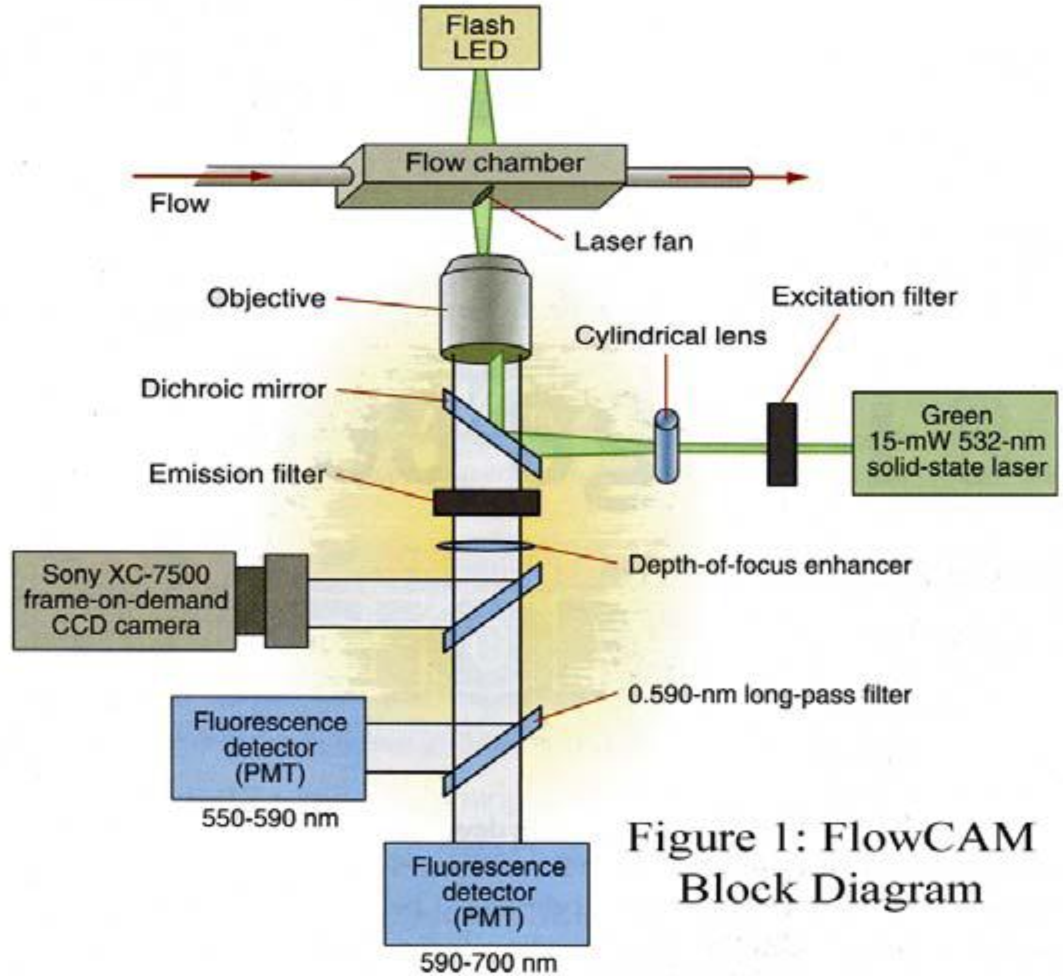
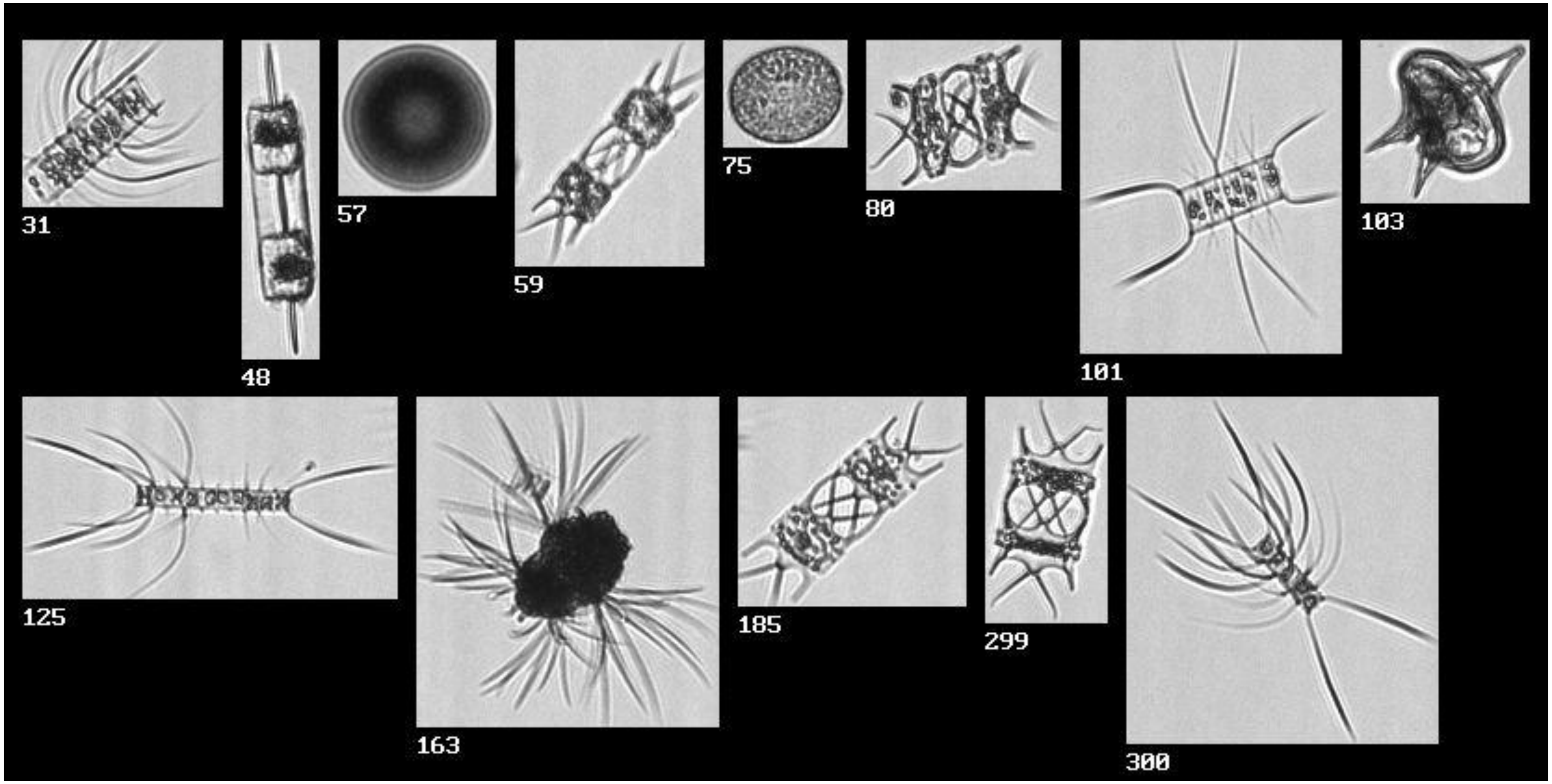
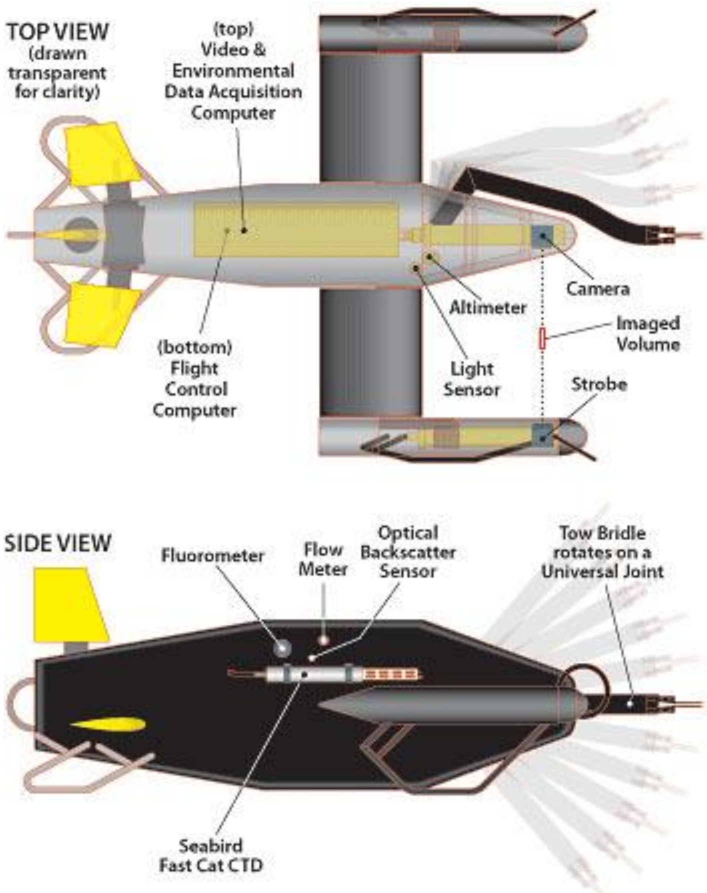
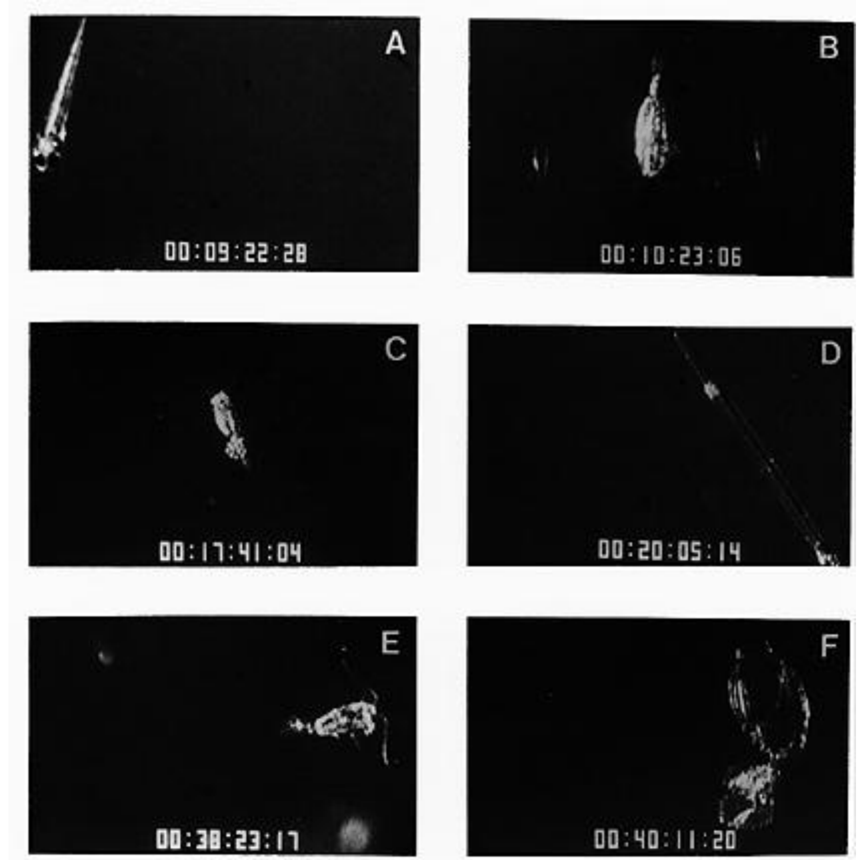


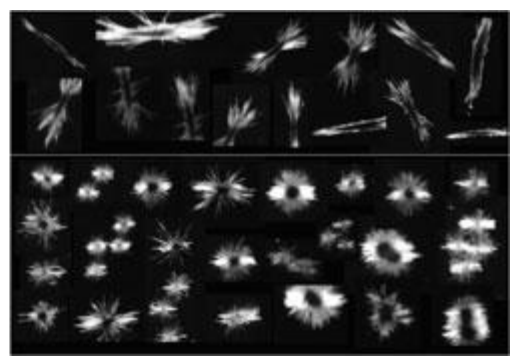
Figure 1: FlowCAM Block Diagram

Marine sample from the coast of Oregon

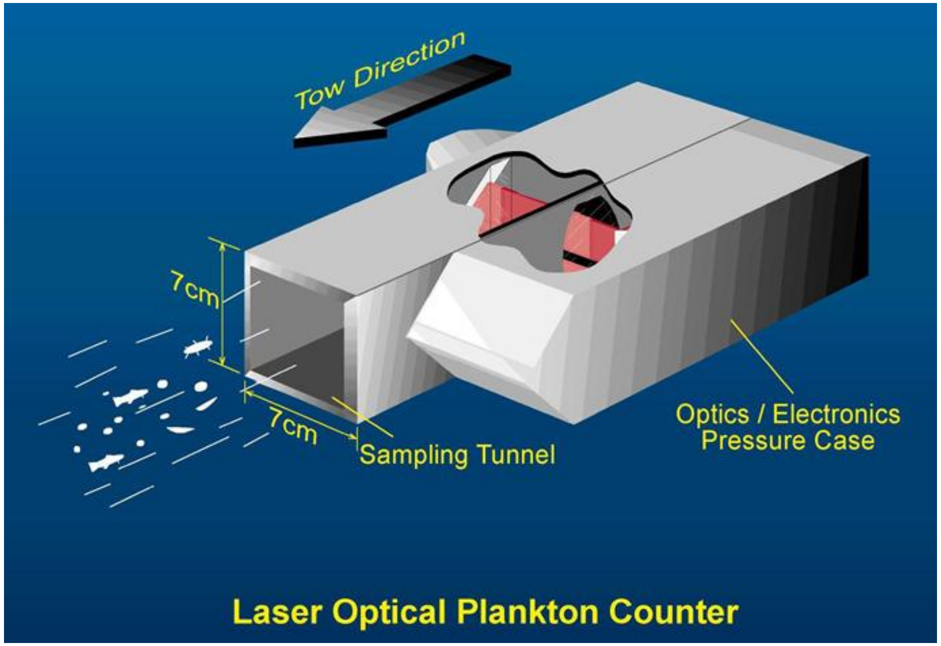


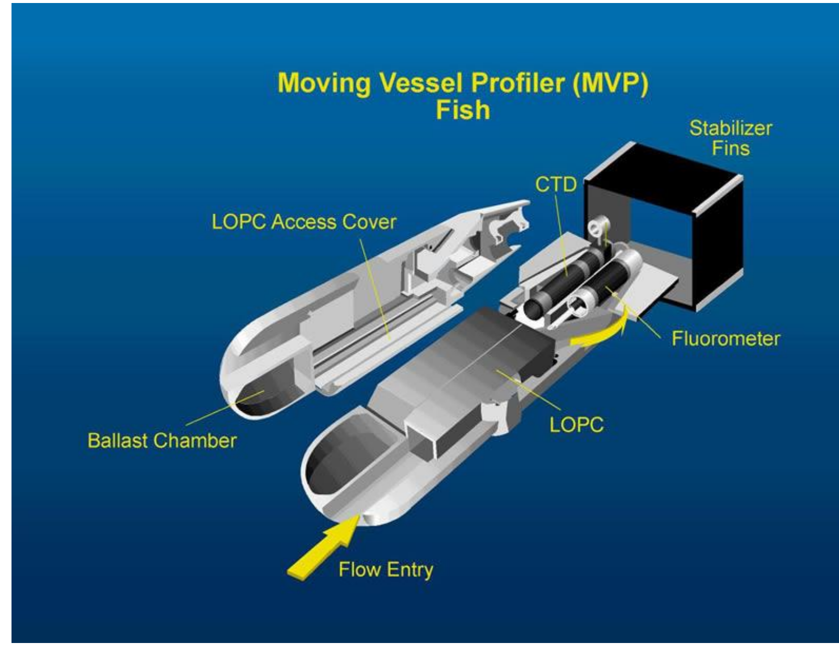






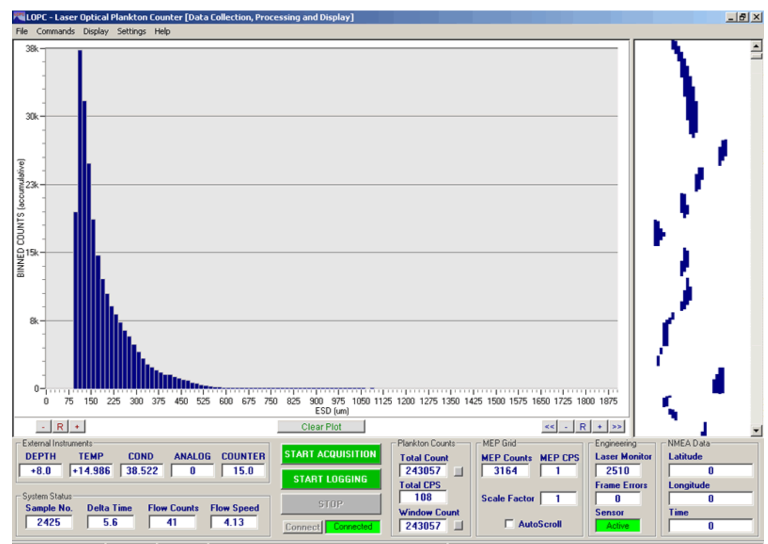
Video Plankton Recorder





(A) Wide Tunnel LOPC - Batfish Tow

Shape profiles obtained from an LOPC mounted on a Batfish vehicle towed at 8 knots. Silhouettes show profiles of euphausiids and copepods of a variety of sizes. Credit: ©Alex Herman, Bedford Institute of Oceanography.

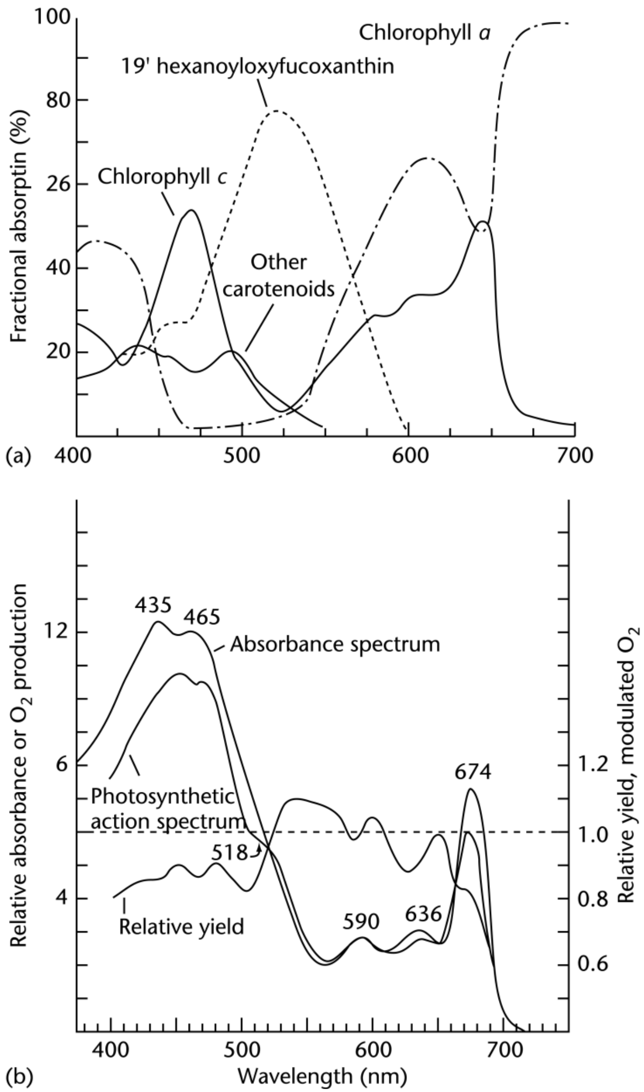


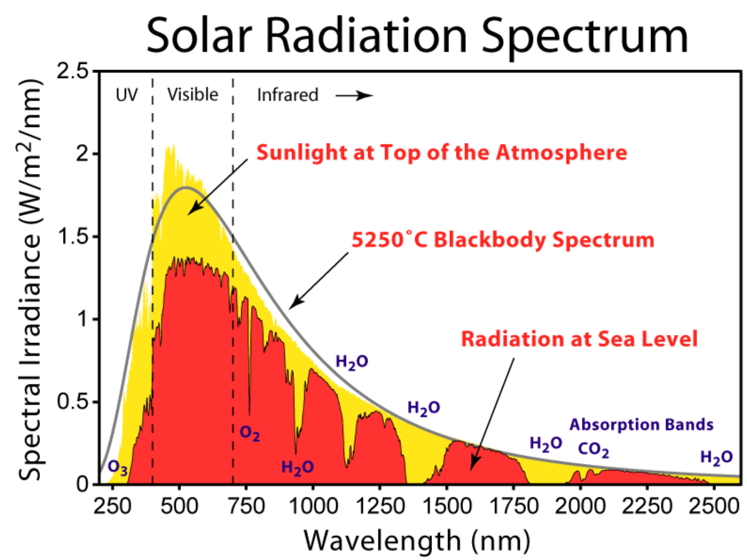
Primary production

- Fixation of inorganic carbon using energy from the sun to make organic carbon (through the process of photosynthesis)
- **Primary production** = organic matter produced (speak of a *rate* of primary production)
- Primary productivity = rate of organic matter production – ***never*** say 'rate' of primary productivity
- Generally measured using a tracer of carbon uptake ($H^{14}CO_3^-$ or $H^{13}CO_3^-$) or by appearance of oxygen (since oxygen evolution is the product of photosynthesis)
- Geochemical ways: apparent oxygen utilization, etc.
- **New production**: Dugdale, 1967
  - Ratio of uptake of nitrogen species used tells us about what is getting exported in a steady-state system ('f ratio')
  - 'new' nitrogen is nitrate (and N_2 gas), while regenerated nitrogen is ammonium and organic nitrogen (e.g. urea)
  - This concept is losing favor as we discover many intricacies in the nitrogen cycle

$$f\,ratio = \frac{\rho NO_3^-}{\rho NO_3^- + \rho NH_4^+}$$

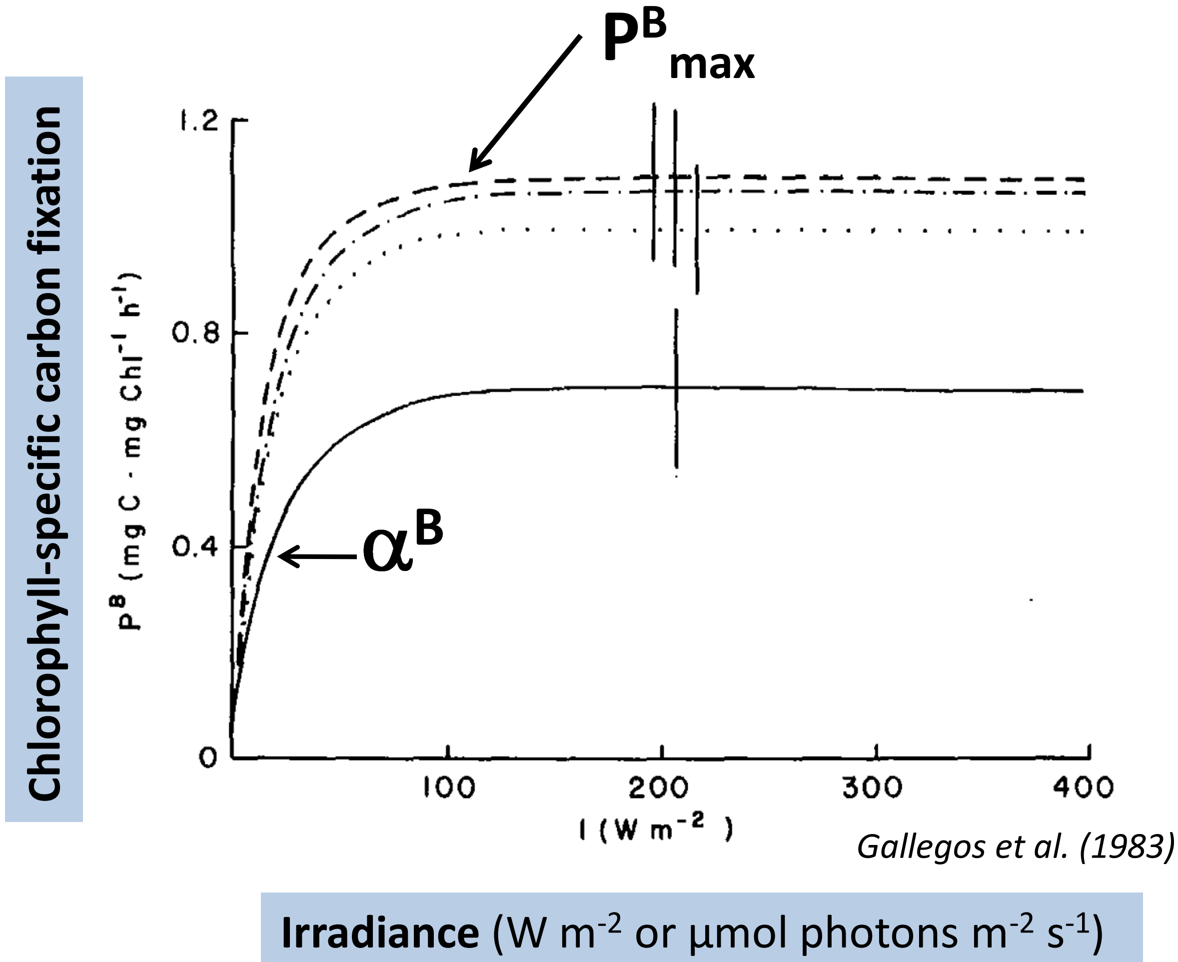
There is a correspondence between spectra of pigment absorption and solar radiation





Photosynthesis vs. irradiance (P vs. E) curves

- Alpha (α): initial slope of the PE curve
- P^B_{max}: maximum chlorophyll-specific rate of C-fixation



Gallegos et al. (1983)

Beta (β)

Photoinhibition

- β: slope of the PE curve that reflects photoinhibition
- Photoinhibition: light-induced reduction in photosynthetic capacity caused by damage to photosystems (mainly PS-II)