Physiology and Cultivation of Algae and Cyanobacteria

2.

Summaries of the ten algal divisions

- Historically
  - classified on basis of: pigmentation, chem. structure of storage products, thylakoid membrane organization, chemistry, structure of cell wall, number, arrangement, and ultrastructure of flagella, occurrence of special features, sex.cycles
- Recently
  - comparison of sequence of 5S; 18S; 28S rRNA, internal genetic coherence

TABLE 1.4
The Main Pigments, Storage Products, and Cell Coverings of the Algal Divisions

Division	Pigments				Storage Products
	Chlorophylls	Phycobilins	Carotenoids	Xanthophylls	
Cyanophyta	*a*	*c*-Phycoerythrin *c*-Phycocyanin Allophycocyanin Phycoerythrocyanin	β-Carotene	Myxoxanthin Zeaxanthin	Cyanophycin (argine and asparagine polymer) Cyanophycean starch (α-1,4-glucan)
Prochlorophyta	*a, b*	Absent	β-Carotene	Zeaxanthin	Cyanophycean starch (α-1, 4-glucan)
Glaucophyta	*a*	*c*-Phycocyanin Allophycocyanin	β-Carotene	Zeaxanthin	Starch (α-1,4-glucan)
Rhodophyta	*a*	*r,b*-Phycoerythrin *r*-Phycocyanin Allophycocyanin	α- and β-Carotene	Lutein	Floridean starch (α-1,4-glucan)
Cryptophyta	*a, c*	Phycoerythrin-545 *r*-Phycocyanin	α-, β-, and ε-Carotene	Alloxanthin	Starch (α-1,4-glucan)
Heterokontophyta	*a, c*	Absent	α-, β-, and ε-Carotene	Fucoxanthin, Violaxanthin	Chrysolaminaran (β-1,3-glucan)
Haptophyta	*a, c*	Absent	α- and β-Carotene	Fucoxanthin	Chrysolaminaran (β-1,3-glucan)
Dinophyta	*a, b, c*	Absent	β-Carotene	Peridinin, Fucoxanthin, Diadinoxanthin Dinoxanthin Gyroxanthin	Starch (α-1,4-glucan)
Euglenophyta	*a, b*	Absent	β- and γ-Carotene	Diadinoxanthin	Paramylon (β-1,3-glucan)
Chlorarachniophyta	*a, b*	Absent	Absent	Lutein, Neoxanthin, Violaxanthin	Paramylon (β-1,3-glucan)
Chlorophyta	*a, b*	Absent	α-, β-, and γ-Carotene	Lutein Prasinoxanthin	Starch (α-1,4-glucan)

	Cyanophyta	Prochlorophyta	Glaucophyta	Rhodophyta	Heterokontophyta Chrysophyceae	Heterokontophyta Xanthophyceae	Heterokontophyta Eustigmatophyceae	Heterokontophyta Bacillariophyceae	Heterokontophyta Raphidophyceae	Heterokontophyta Dictyochophyceae	Heterokontophyta Phaeophyceae	Haptophyta	Cryptophyta	Dinophyta I	Dinophyta II	Euglenophyta	Chlorarachniophyta	Chlorophyta
chlorofyly																		
chlorofyl a	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
chlorofyl b		*														*	*	*
chlorofyl c_1					*	+		*	*	} +[4]	*	*			*			} ±[8]
chlorofyl c_2					*	+		*	*		*	*	*	*	*			
chlorofyl c_3					±			*			*							
fykobiliny																		
fykocyanín	*		*	*									*					
alofykocyanín	*		*	*														
fykoerytrín	*			*									*					
fykobilizómy	*		*	*														
karotény																		
α-karotén				*	+							+	*		+			±
β-karotén	*	*	*	*	*	*	*	*	*	*	*	*	±	*	*	*		*
γ-karotén																±		±
ε-karotén					+			+			+		±					
xantofyly																		
zeaxantín	*	*	*	*	+		±		+[3]		±		+			±		+
echinenón	*	+						+				+		+		±		±
kantaxantín	*						+	+				+		+				
myxoxantofyl	*																	
oscillaxantín	*																	
α-kryptoxantín				±	+		±					+						
β-kryptoxantín	+	+	+	±		±	±									±		±
izokryptoxantín	+	+																
mutatochróm	+	+																
luteín				+						+							+	*
anteraxantín				±	+		+				+							+
violaxantín				±	+		*		+[3]		*						+	*
fukoxantín					*			*	*[3]	*	*	*			*			
neofukoxantín					+			+							+			
fukoxantín- der.[1]												*[5]			*[5]			
fukoxantín- der.[2]												*[5]						
diatoxantín					+	*		*		+	+	*			*	±		
diadinoxantín					+	*		*	*	+	+	*		*	*	+		
vaucheriaxantín						*	*		+									
heteroxantín						*			+									
aloxantín													*					
dinoxantín									+			+		+				
peridinín														*				
neoxantín					+	+	+	+	+		+					*	+	*
sifoneín																		+[6]
sifonoxantín																		+[6,7]
krokoxantín													+					
monadoxantín													+					
pyrroxantín														+				

[1,2] deriváty fukoxantínu, [3] v morských druhoch, [4] bližšie nešpecifikovaný chlorofyl c, [5] v niektorých druhoch, [6] v Bryopsidophyceae, [7] roztrúsene v niekoľkých triedach, [8] pigment podobný chlorofylu c, v asi piatich zelených riasach triedy Prasinophyceae

Tab. 2.: Najdôležitejšie zásobné látky rias (upravené podľa van den Hoeka)

	Cyanophyta	Prochlorophyta	Glaucophyta	Rhodophyta	Heterokontophyta Chrysophyceae	Heterokontophyta Xanthophyceae	Heterokontophyta Eustigmatophyceae	Heterokontophyta Bacillariophyceae	Heterokontophyta Raphidophyceae	Heterokontophyta Dictyochophyceae	Heterokontophyta Phaeophyceae	Haptophyta	Cryptophyta	Dinophyta	Euglenophyta	Chlorarachniophyta	Chlorophyta
cyanofycínové zrná *(bohaté na arginín a asparagín)*	*																
α-1,4 glukány																	
sinicový škrob	*	*															
florideový škrob				*													
škrob			*										*	*			*
β-1,3 glukány																	
chryzolaminarín					*	*	*	*	?	?	*	*					
paramylón												*[1]			*	?	

[1] v rode Pavlova.

Cyanophyta

- together with prochlorophyta – non-motile G- eubacteria

- 1-cell. to filament (un-/branched), & colonial aggr.
- widely distrib.; planctonic, blooms, picoplancton, benthic, soil, mud, hot springs; symbiotic
- Pigm.: chl *a*, blue & red phycobilins, carotenes
- phycobilisomes in rows on outher surface of thylakoids
- Thylacoids – free in cytoplasm, non-stacked, singled&equidistant
- Res.polysach.: cyanophycean starch (granules betw. thylakoids), cyanophycin
- some marine contain gas vesicles
- some filamentous form heterocysts & akinetes
- some produce hepato-, neurotoxins

Prochlorophyta

- 1-cell. / filamentous (un-/branched)
- free-living component of pelagic nanoplancton, obligate symbionts within didemnid ascidians & holoturians
- mainly limited to tropical&subtropical env.
- Pigm.: chl *a*, chl *b*, β-carotene, xanthophyls lack phycobilins,
- Thylakoids – free in cytoplasm, stacked
- Res.polysach.: cyanophycean starch (starch-like)

Cyan.&Prochlor.

- able to fix nitrogen
- contain polyhedral bodies (carboxysomes) with RuBisCO
- in cell wall peptidoglycane layer
- obligate photoautotrophs
- asexual reproduction (cell division / fragmentation of colonies)

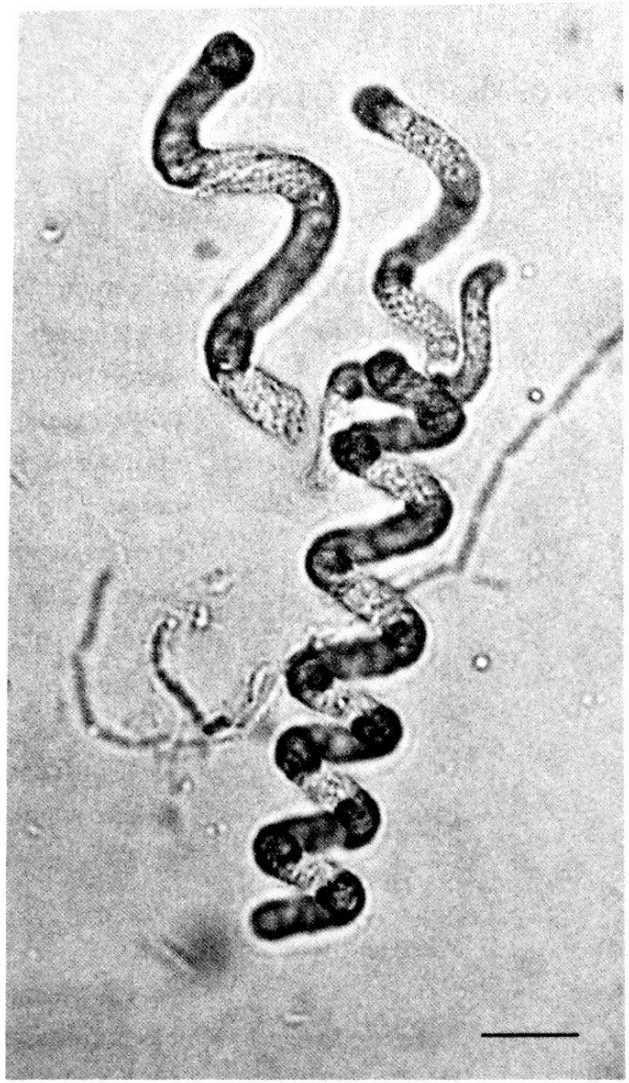


FIGURE 1.25 Trichome of *Arthrospira* sp. (Bar: 20 μm.)

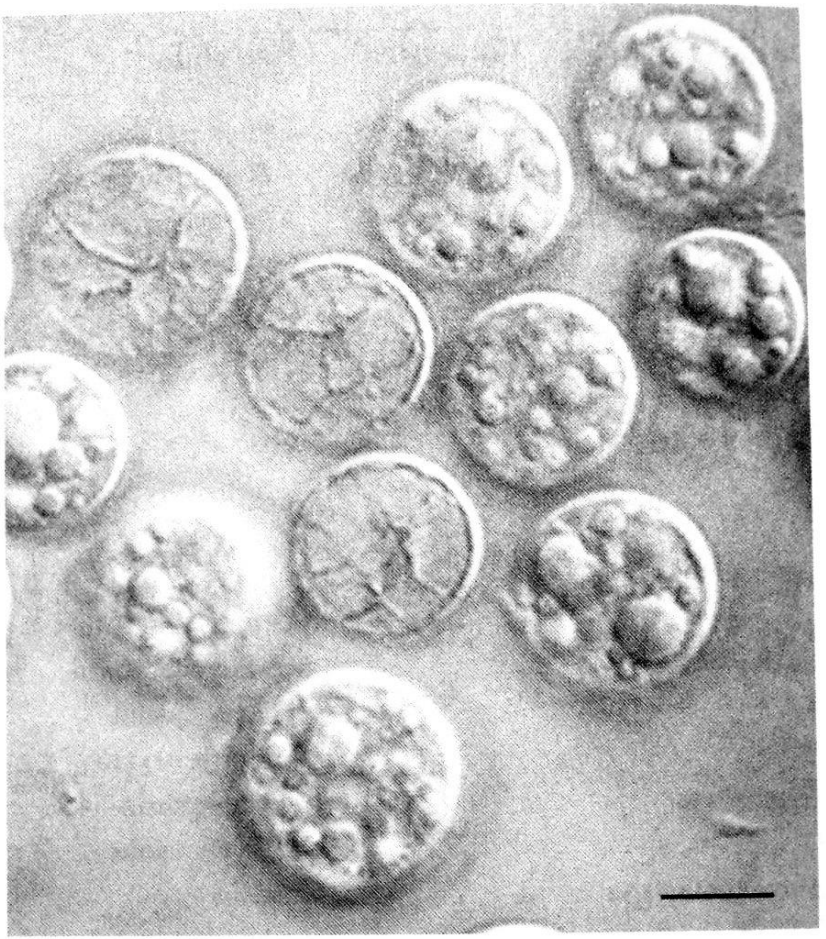


FIGURE 1.26 Cells of *Prochloron* sp. (Bar: 10 μm.)

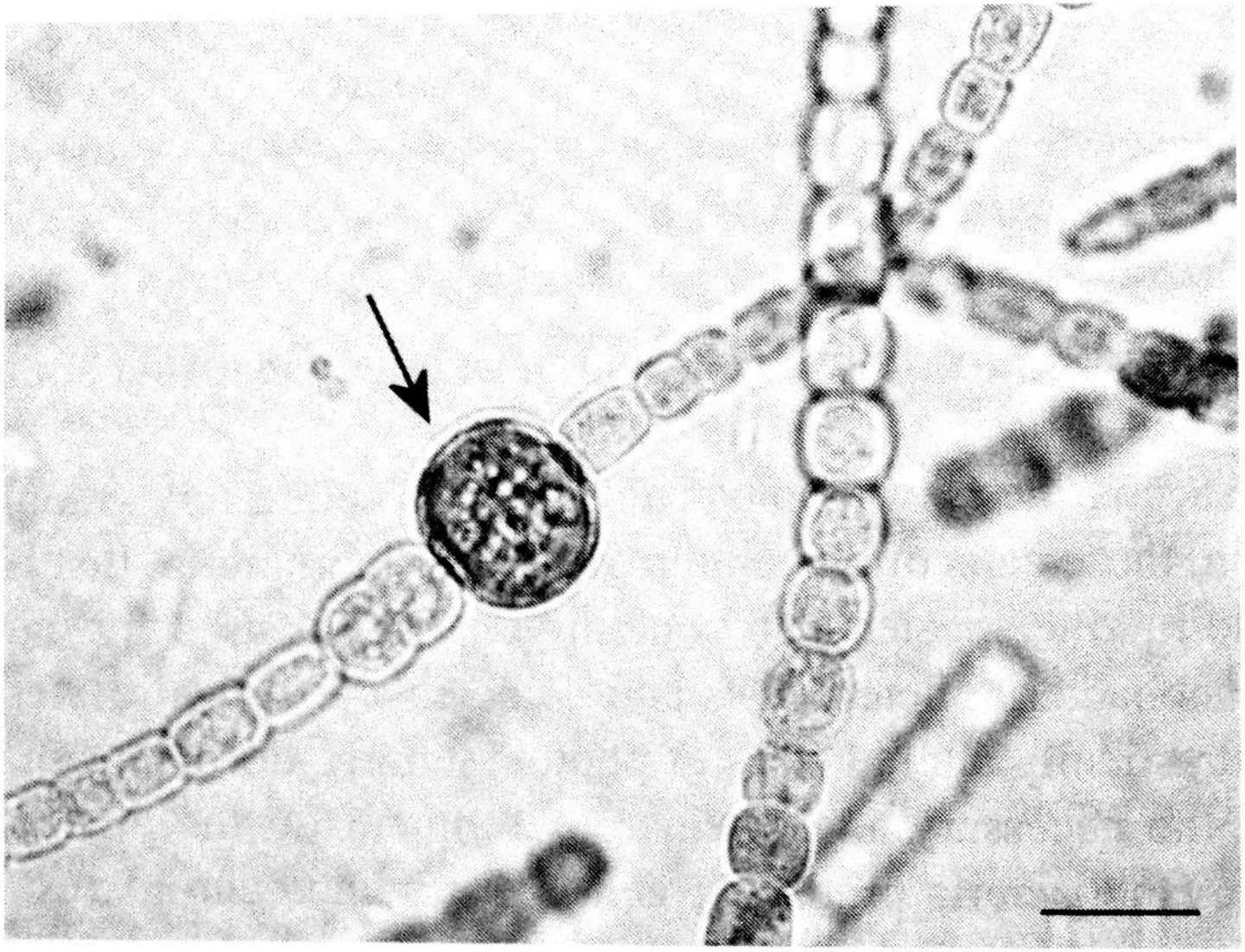


FIGURE 1.27 Heterocyst (arrow) of *Anabaena azollae*. (Bar: 10 μm.)

Glaucophyta

- 1-cell., flagellate, dorsiventral construction, 2 unequal flagella inserted in shallow depression below apex
- marine, rare freshw., solme soil
- Pigm.: chl *a*, acces.pigm.: phycoerythrocyanin, phycocyanin, allophycocyanin in phycobilisomes, carotenoids
- Chlpl. lie ni spec. vacuole, present thin peptidoglycan wall betw. 2 outher plastid membranes
- Thylacoids non-stacked
- ctDNA in center of chlpl. near carboxysomes (RuBisCO)
- Res.polysach.: starch (granules in cytoplasm outside of chlpl.)
- photoautotrophs with blue-green plastids – **cyanelles**
  - presumed to be phylogenetically derived from endosymbiotic cyanobacterium
- unknown sex. reproduction

Glaucocystis sp. / from Kanazawa, Ishikawa Pref., Japan / Microscope:Leica DMRD (DIC)

Rhodophyta

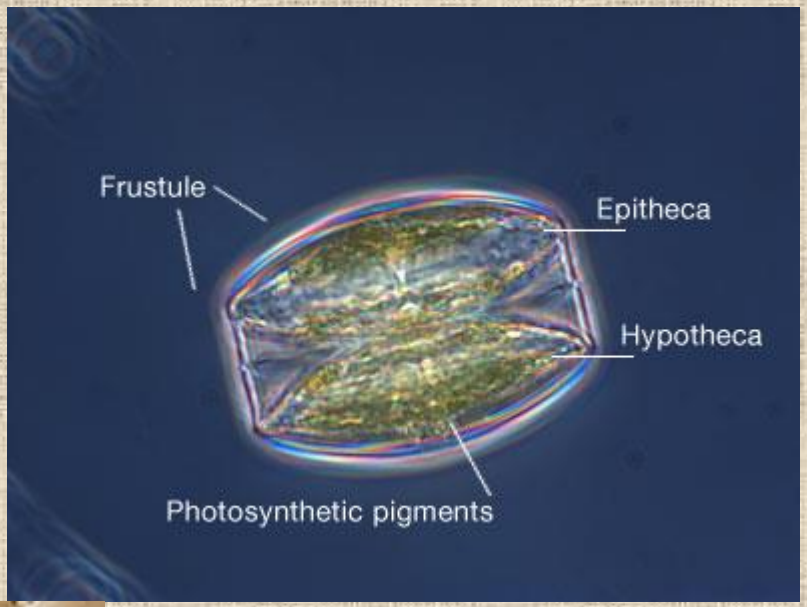
- red algae, mostly seaweeds, can free-living 1-cell.
- mostly marine
- lack flagellate stages
- Pigm.: chl *a*, phycobiliproteins in phycobilisomes
- Chlpl. 2-membrane enclosure
- thylakoids – non-stacked, single&equidistant within chlpl.
- ctDNA scattered throughout chlpl.
- Res.polysach.: floridean starch & α-1.4-glucan polysach. – grains in cytoplasm
- mostly photoautotrophs
- Repr.
  - in majority – cytokinesis incomplete >> pit connection >> proteinacous plug >> plug
  - sexual.: isomorphic / heteromorphic diplohaplontic life cycle

Rhodophyllis ***Divaricata - http://www.algaebase.org/search/species/detail/?species_id=121***

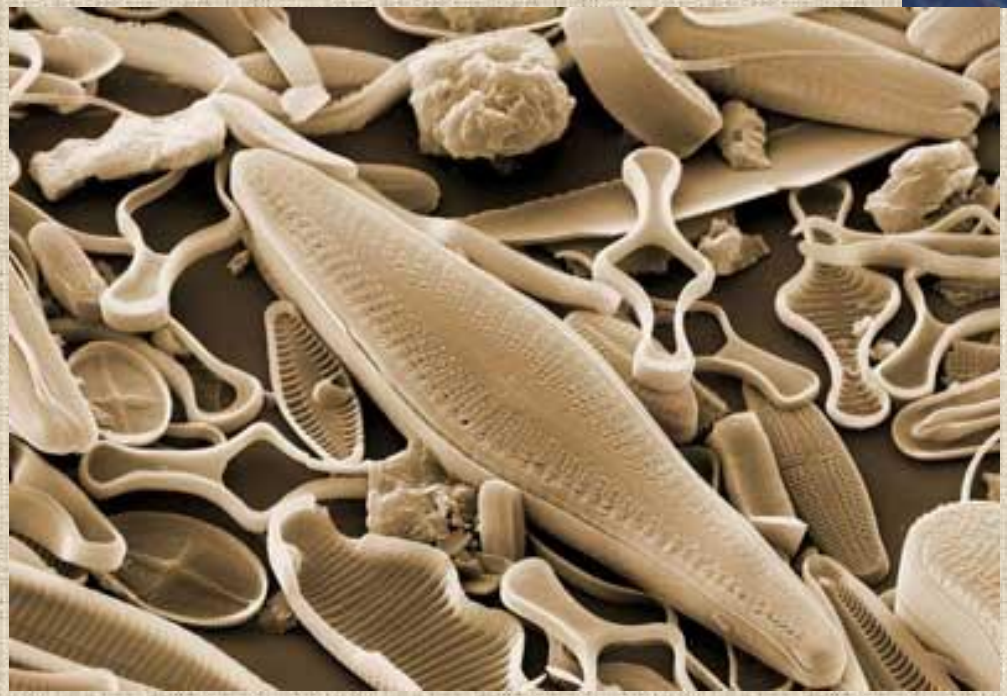
Heterokontophyta

- when 2 flagella they are different
- flagelate cells – **heterokont** – long mastigonemate flagellum directed forward during swimming & short smooth fl., points backwards along the cell
- 1-cell-to-colonial, filamentous, siphonous, multicellular complex kelp; various type of flagellum
- mostly marine (can freshw,&terestrial)
- Pigm.: prepoderance of carotenoids over chlorophylls
  - chl *a*, c_1, c_2, c_3, access.: b-carotene, fucoxanthin, vaucheriaxanthin
- thylakoids stacked in three – **lamellae**
    - one lamellae usually runs along whole chlpl. = **girdle lamellae**
- chlpl. 2-membrane & fold of ER
- ctDNA – ring-shaped
- Res.polysach.: chrysolaminarin in cytoplasm in spec. vacuole
- eyespot – layer of globules, enclosed within chlpl. together with photoreceptor loc. in smooth flagellum, forms photoreceptive apparatus
- photoautotrophy can be combine with heterotrophy
- sex. reproduc.: life cycle – haplontic (Chrysophyceae), diplontic (Bacillariophyceae), diplohaplontic (Phaeophyceae)

http://www.urbanrivers.org/drawingdiatoms/diatoms.html



http://oceandatacenter.ucsc.edu/PhytoGallery/dinos%20vs%20diatoms.html



http://www.calacademy.org/science_now/archive/academy_research/sarah_spaulding.php

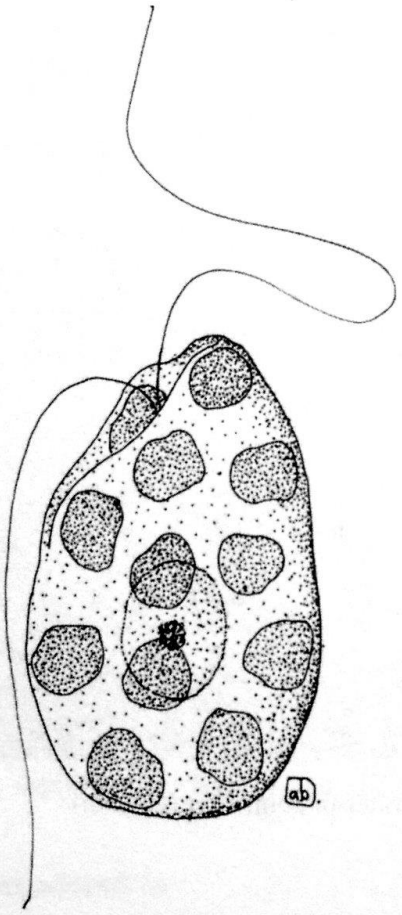


FIGURE 1.32 Unicell of *Heterosigma akashiwo.*

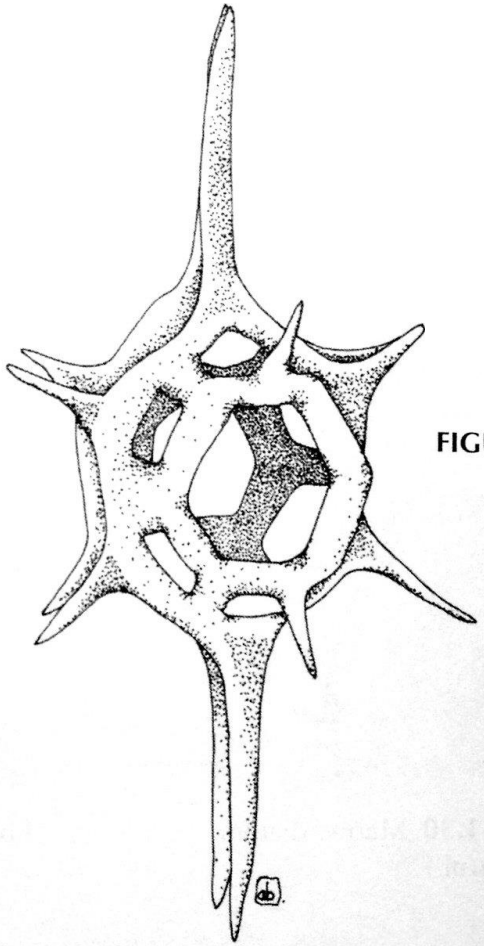


FIGURE 1.33 The silicoflagellate *Distephanus speculum.*

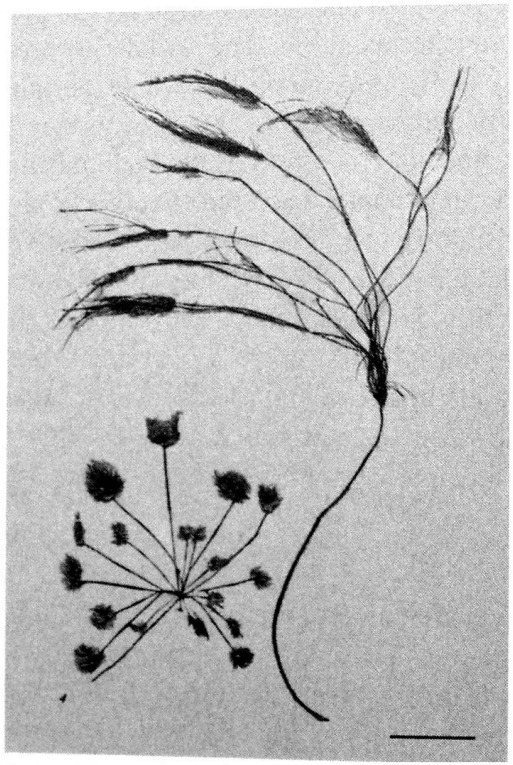


FIGURE 1.34 Frond of *Bellotia eriophorum.* (Bar: 5 cm.)

Haptophyta

- mostly 1-cell., motile, palmelloid / coccoid (rare colonial/filament.)
- generaly marine
- flagellate cells – 2 naked flagella inserted laterally or apically (may have diff. lenght)
- **haptonema** – typically long organelle flagellar structure (diff ultrastruct.)
- Pigm.: chl *a*, c_1, c_2, access.: fucoxanthin, β-carotene, xanthins
- Chlpl. enclosed within fold of ER
- Thylakoids – stacked in three, no girdle lamellae
- ctDNA – nucleoid scattered in chlpl.
- can be eyespot – row of globules inside chlpl., no associated flagellar struct.
- Res.polysach.: chrysolaminarin
- Cell surface – tiny celulosic scales or calcified scales bearing spoke-like fibrils
- Phototrophs / heterotrophs, phagotrophy in forms that lack cell covering
- Sex. reprod.: heteromorphic diplohaplontic life cycle

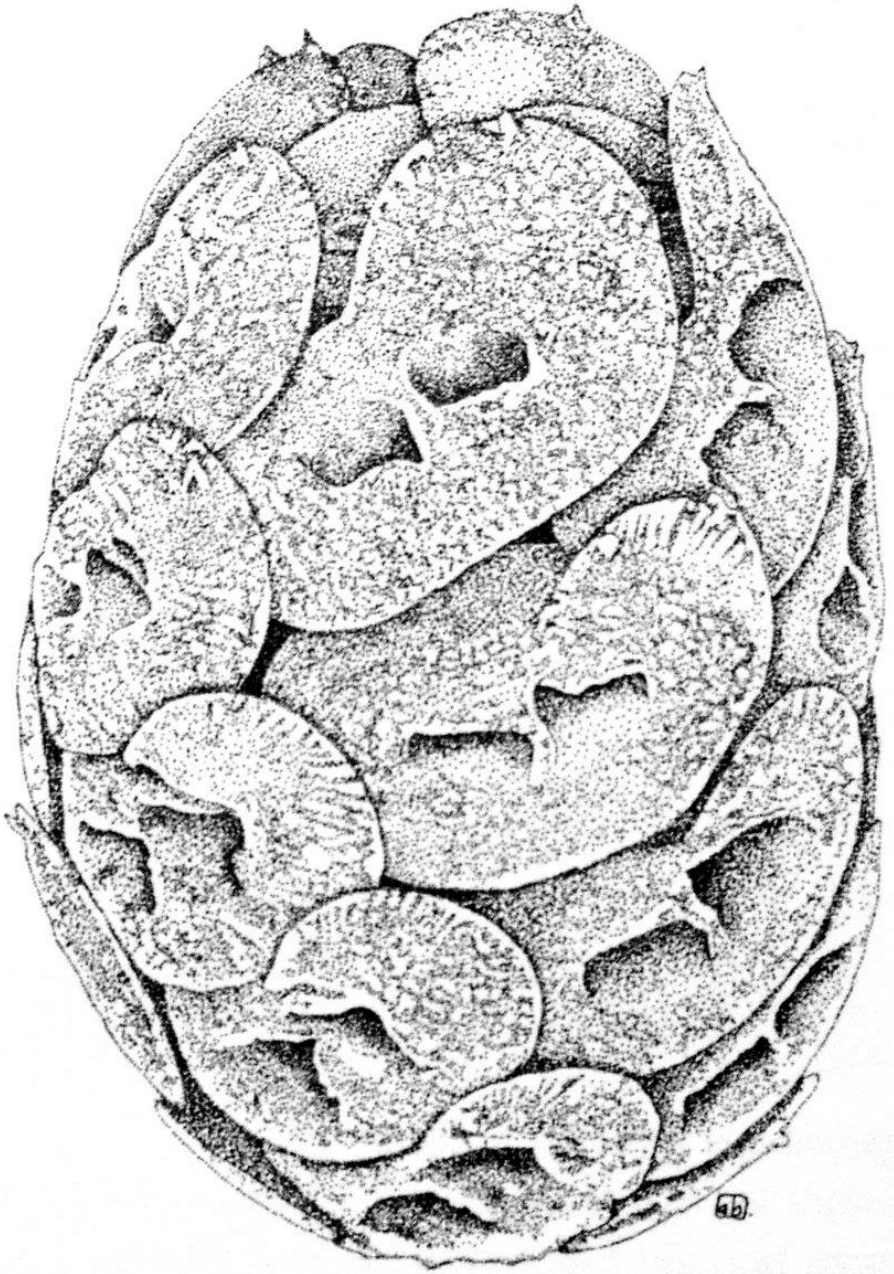


FIGURE 1.35 Unicell of *Helicosphaera carteri.*

Cryptophyta

- 1-cell. flagellate
- assymetric cells, dorsiventrally constructed
- 2 unequal hary flagella, subapically inserted, emerging from above gullet loc. on ventral side of cell – lined by ejectosomes
- free-swimming in freshw. & marine
- Pigm.: chl *a, c2,* phycobilins in thylakoid lumen > in phycobilisomes
- Chlpl. – 1 - 2 per cell, surrounded by fold of ER - in these intermembrane space – peculiar organemme – **nucleomorph -** ? nucleus of red algal symbiont
- Thylakoids in pairs, no girdle lamellae
- Pyrenoid projects out from the inner side of chlpl.
- ctDNA condensed in small nucleoid inside chlpl.
- Res.polysach.: starch ganules in periplastidial space
- eyespot sometimes inside plastid, no association with flagella
- Cell enclosed in stiff, proteinaceous periplast – polygonal plates
- mostly photosynthetic nutrition, can be heterotrophs
- Repr.: primary longitudinal cell division, can be sexual

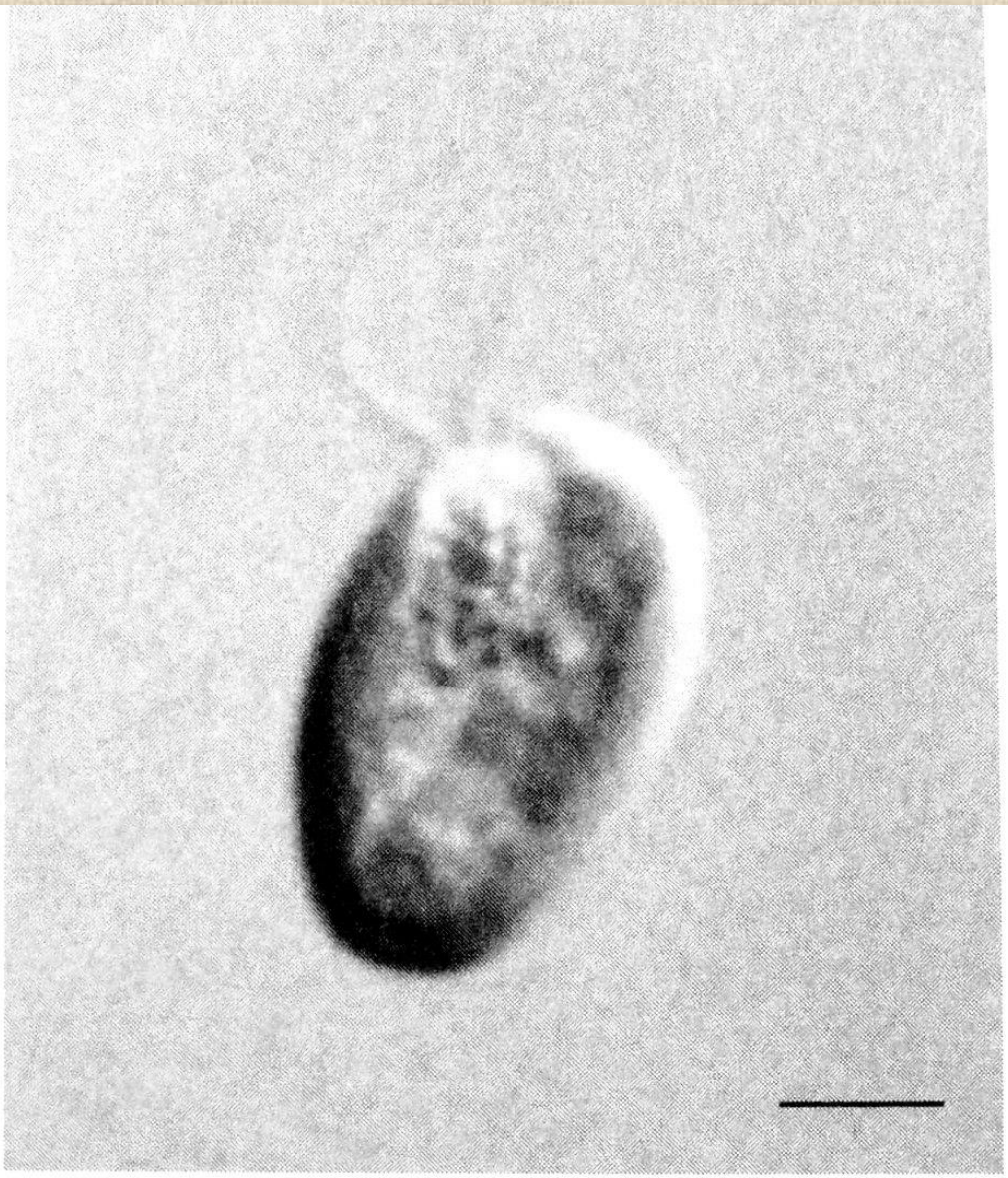


FIGURE 1.36 Unicell of *Cryptomonas* sp. (Bar: 6 μm.)

Dinophyta

- 1-cell., flagelates (can be ameboid, coccoid, palmelloid or filament.)
- 2 flagella with independent beating pattern (1st - training, 2nd - girdling) >> rotatory whirling motion
- characteristic cell covering components beneath cell membrane (layer of flat, polygon. vesicles – empty or celulose filled)
- dinokont type – **theca** – bi-partite armor (upper, anterior [epiconus]; lower, posterior [hypoconus]) separated by groove (cingulum) loc. transversal flagellum; smaller groove (sulcus) – extended posteriorly – host longitudinal flagellum
- important freshw. & marine microplancton
    - consumed by filterfeeders; parasites; endosymbionts of tropical corals
- Pigm.: chl *a, b, c1, c2,* fucoxanthin, carotenoids, xanthophylls
- Chlpl. (if present) surrounded by 3 membranes
- Thylakoids stacked in 3; ctDNA in small nodules scattered in whole chlpl.
- complex photoreceptive system "compound eye" (Warnowiaceae) – lens & retinoid
- Dinocaryon – eukaryotic nucleus, chromosomes condensed during mitosis, karyotheca unbroken – endomitosis
- Res.polysach.: starch - grains in cytoplasm; oil droplets in some genera
- At cell suraface – trichocysts – discharge explosively when stimulated
- Photoautotrophy & hi. diversity of nutrit. types
- can form blooms, possib. bioluminiscence
- Sex. reproduct. – haplontic life cycle; can form hypnospores

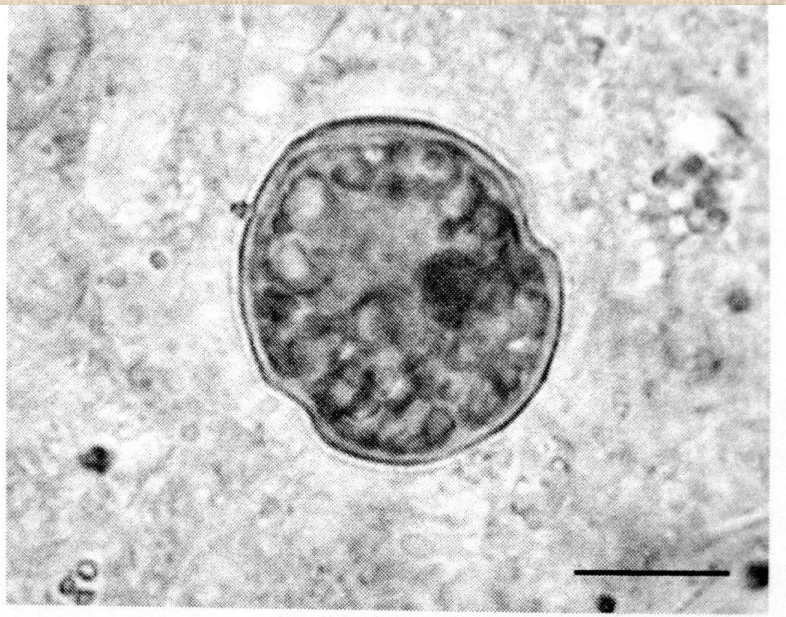


FIGURE 1.37 A marine dinoflagellate. (Bar: 30 μm.)

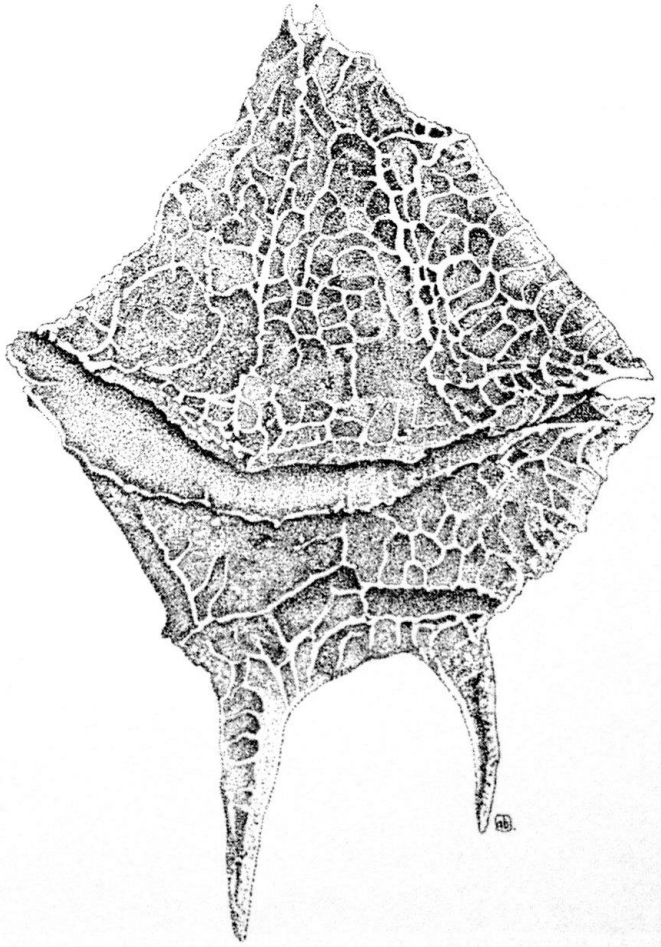


FIGURE 1.38 Dorsal view of *Gonyaulax* sp., a brackish water dinoflagellate.

Euglenophyta

- mostly unicell.flagellates, can be colonial
- widely distributed, freshwater, brakish & marine, abundant in hi. heterotrophic env.
- flagella arise from bottom of cavity – reservoir (loc. in anterior end of cell); can live in mud; presence of pellicle – proteinaceous wall inside cytoplasm – spiral construction
- Pigm.: chl *a* & *b*, β & γ-carotenes, xanthins, some spec. can absent plastids
- Chlpl.- 3 membrane envelope
- Thylakoids – group of three without girdle lamella
- photoreceptive system – orange eyespot loc. free in cytoplasm; true photoreceptor loc. at base of flagellum
- Res.polysach.: paramylon (β-1,3-glucan); granules inside cytoplasm(not in chlpl.)
- obligate mixotrophs, require vitamins of B group; colorless can be phagotrophs, osmotrophs
- Reproduction – only asexual

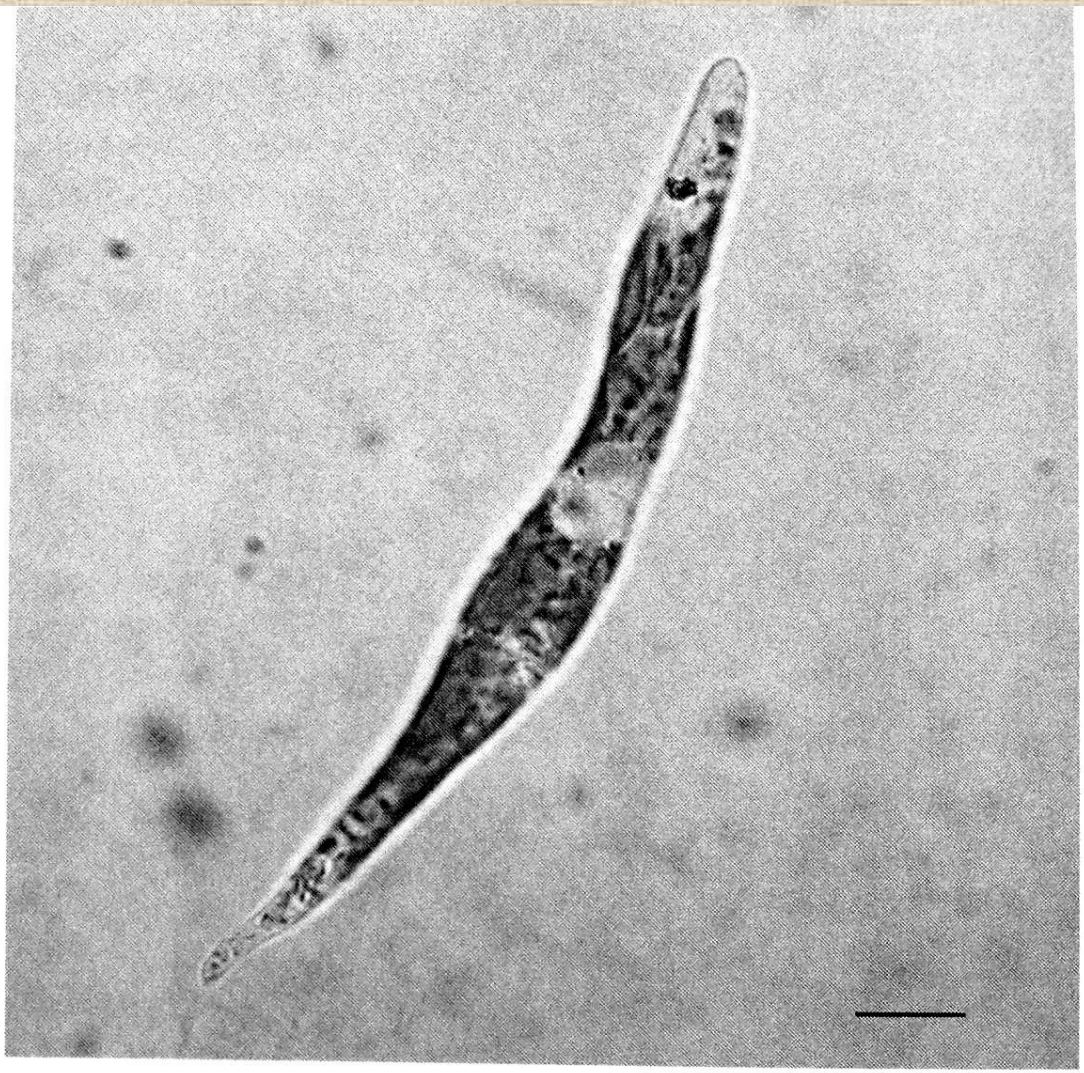


FIGURE 1.39 Unicell of *Euglena mutabilis.* (Bar: 10 μm.)

Chlorarachniophyta

- naked, unicell., form net-like plasmodium via filopodia
- life cycle forms – amoeboid, coccoid, flagellate stages
- ovoid zoospores bear single flagellum
- marine
- Pgm.: chl *a* & *b*
- Chlpl. – 4-membrane envelope, each has prominent projecting pyrenoid
- Thylakoids – stacked in one to three
- nucleomorph present btw. 2nd and 3th membrane originated from green algal endosymbiont
- Res.polysach.: paramylon (β-1,3-glucan)
- phototrophs & phagotrophs engulfs bacteria, flagelates & eukaryotic algae
- Repr. – mostly asexual – mitosis or zoospore formation
  - heterogamy rarely

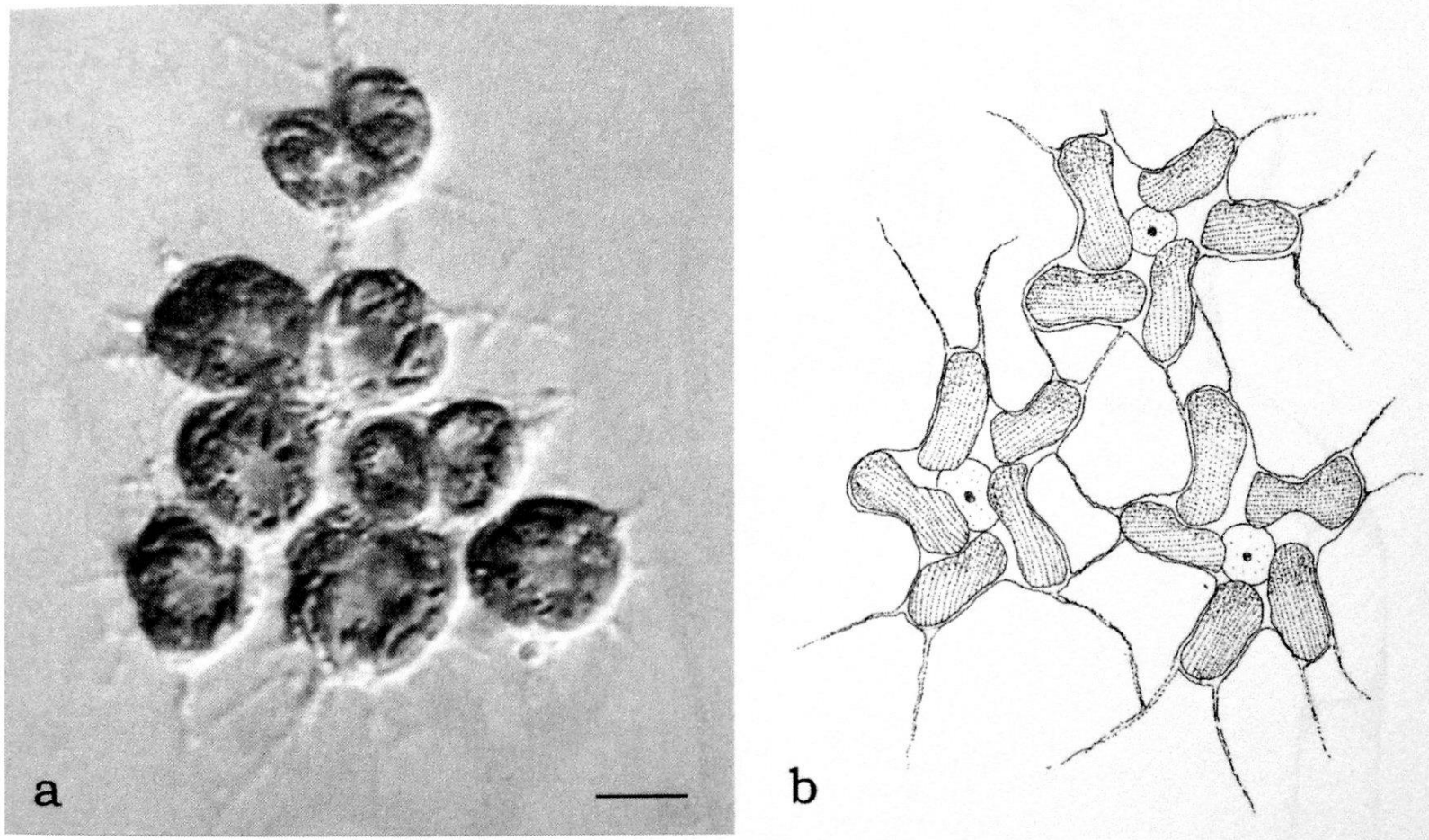


FIGURE 1.40 Plasmodial reticulum of *Chlorarachnion*, bright field microscope image (a) and schematic drawing (b). (Bar: 4 μm.)

Chlorophyta

- great range of somatic differentiation (flagellates to differentiated multicell. thalli)
- thallus organization <--> basis of classification
- flagella -wide diversity in number & arrangement (1-8 in apical / subapical region)
- zoids are isokont (similar struct. but can differ in lenght)
- freshwater, marine & terestrial
- Pigm.: chl. *a* & *b*, β & γ-carotenes, xanthophylls
- Chlpl. – 2-membrane envelope
- Thylakoids – stacked, form grana
- pyrenoid (if present) in chlpl.
- ctDNA – circular
- Res.polysach.: starch – most important – grain inside chlpl.
- glucan & β-1,4-mannan can present in cell wall
- eyespot (if present) loc. inside chlpl.
- photoautotrophs, can be heterotrophs
- Repr. – sex. – variety of life cycle – group specific
  - similarity to higher plants - *Trentepohliaceae* – cell division using phrogmoplast disc where the cells will divide
- probably land plants derived directly from these freshwater algae

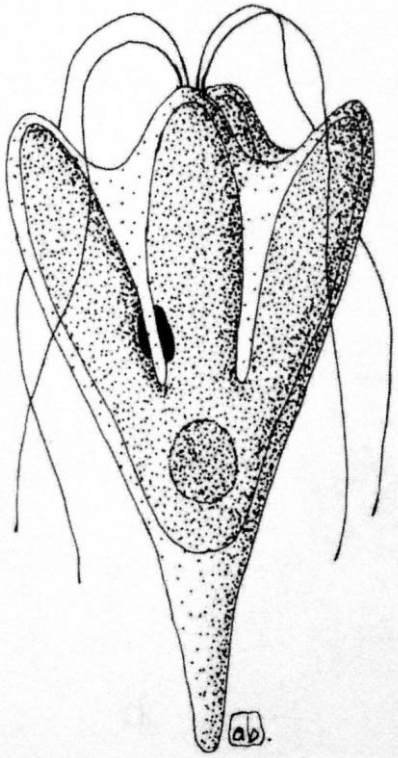


FIGURE 1.41 Unicell of *Pyramimonas longicauda.*

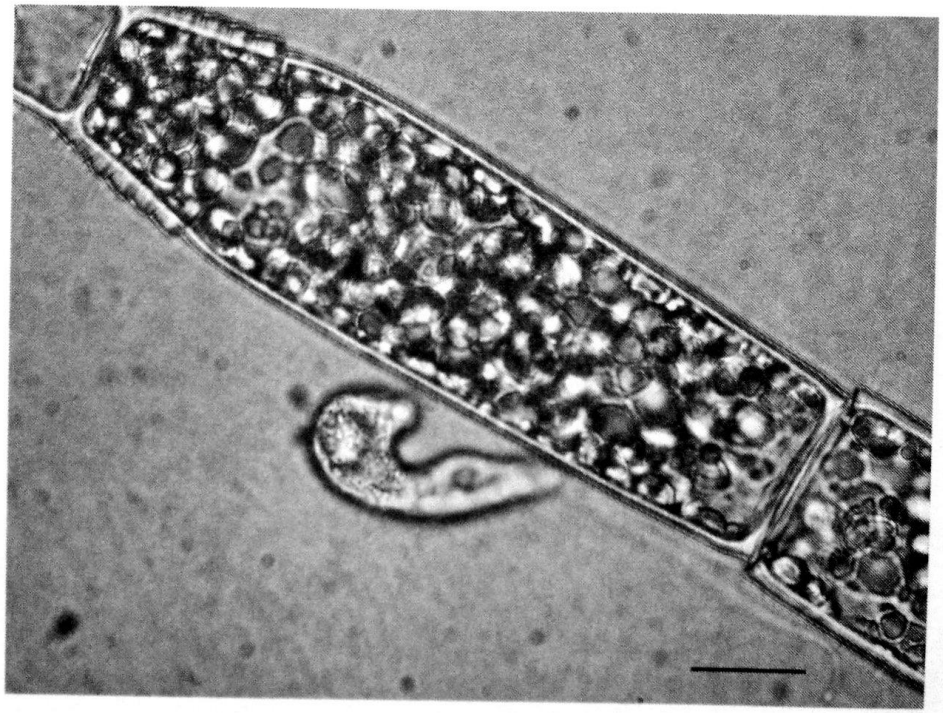


FIGURE 1.42 Filament of *Oedogonium* sp., with a *Peranema* sp. cell. (Bar: 20 μm.)

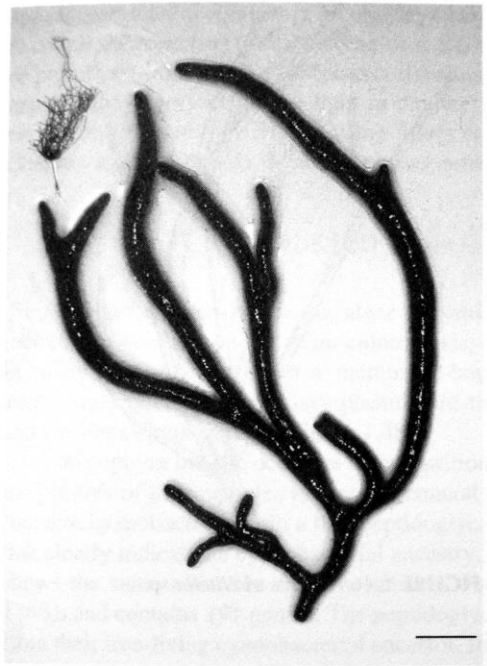


FIGURE 1.43 Thallus of *Codium* sp. (Bar: 2 cm.)

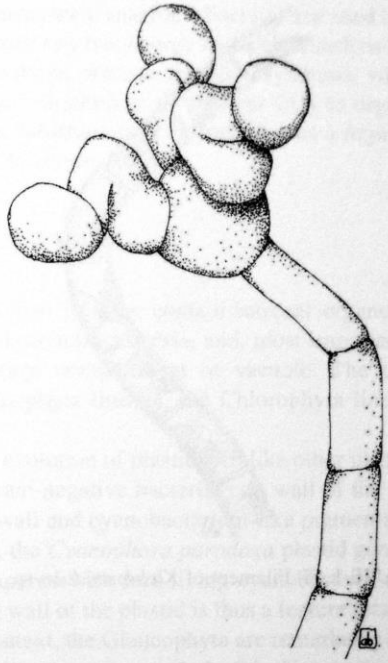


FIGURE 1.44 Thallus of *Trentepohlia arborum.*

FIGURE 1.47 Portion of the thallus of *Acetabularia* sp.

FIGURE 1.45 Filament of *Klebsormidium* sp.

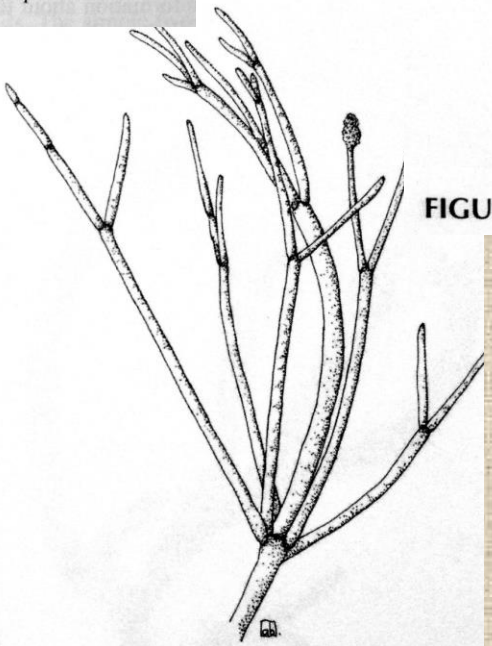


FIGURE 1.46 Thallus of *Nitella* sp.

Endosymbiosis & origin of eukaryotic algae

- procaryotic ancestor → endosymbiotic events → primary plastid
- secondary / tertiary endosymbiosis → plastid (sec. eukaryotic cell)
- arrangement of cellular compartments inside the the other – info about evolut. history
- Cyanobacteria
  - evolved >2.8 bill. years ago
  - fundamental roles in ocean carbon, oxygen, nitrogen fluxes
  - turning point in biogeochemistry of Earth
  - photosynthesis – energy of VIS, oxidation of H2O, reduction of CO2
  - $CO_2 + H_2O + \text{light} \xrightarrow{\text{chl } a} (CH_2O)n + O_2$

Three major algal lineages of primary plastids

- Glaucophyta lineage
  - plastids – thin peptidoglycan cell wall & cyanobacter.-like pigments
    - » cyanobacterial ancestry
  - neither green nor red plastid present
  - any secondary plastid derived from Glacophyta is known

Endosymbiosis & origin of eukaryotic algae

- Chlorophyta lineage "green algae"
  - green algal plastid
  - 2-membrane system surround.
    - chl *b* – sec. pigment, phycobiliproteins lost
  - other – prochlorophyte based hypothesis
  - major role in oceanic food webs & carbon cycle from -2.2 bill. years until Permian extinction (-250mil y.)
  - origin of land plants

  - >Secondary endosymbiosis → Euglenophyta (3-membrane plastid) & Chlorarachniophyta (4-membrane plastid
- Rodophyta leneage " red algae"
  - red algal plastid
  - 2-membrane system
    - chl *a* & phycobiliproteins organized into phycobilisomes attached on thylakoid membrane
    - Thylakoids with phycobilisomes don't form stacks – similar to cyanobacteria

  - >Secondary endosysmbiosis → Cryptomonades (Cryptophyta)
    - (4-membrane plastid) + chl *c* (also Haptophyta, Heterocontophyta & Dinophyta)

  - stacked thylakoids found in lineages lacking phycobilisomes

  - >a few groups of Dinoflagelates Tertiary endosymbiosis – uptake of secondary plastid containing endosymbiont

  - All these groups are relatively modern org.
  - dinoflagelates & coccolithophorids rise paralel with dinosaurs
  - diatoms rise with mammals

members of red lineages in shallow seas in Jurassic period provide petroleum

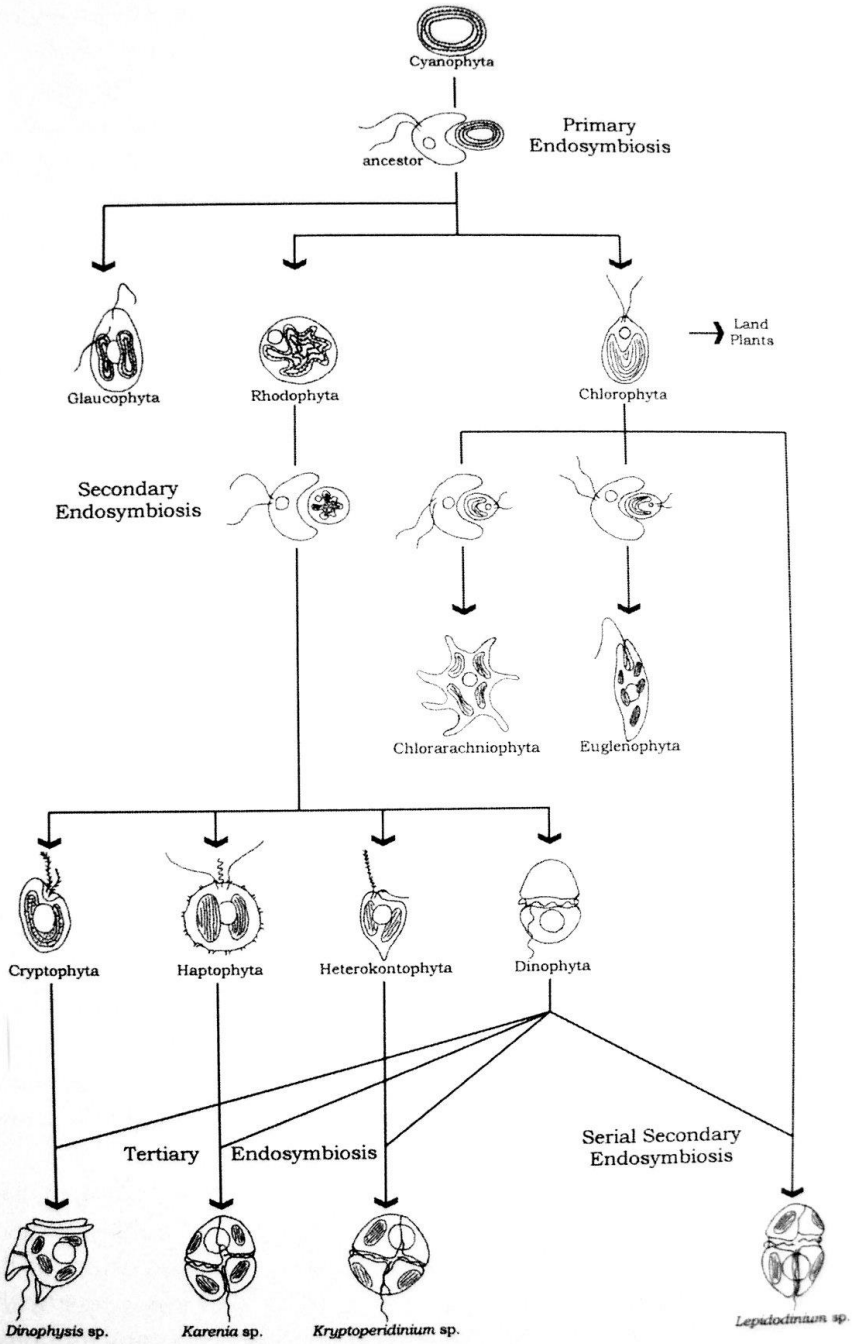


FIGURE 1.48 Algal evolution and endosymbiotic events.