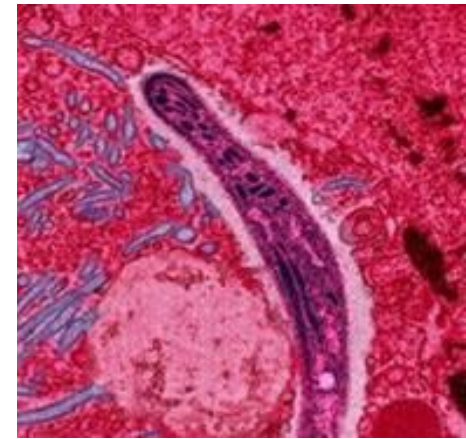
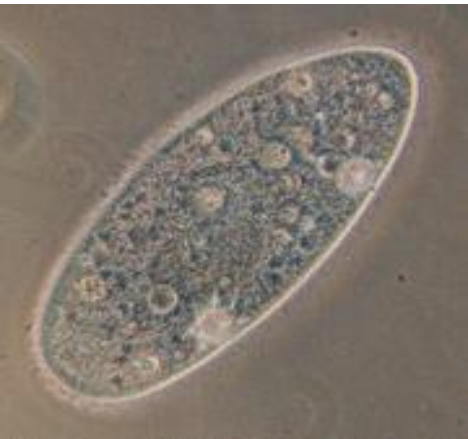


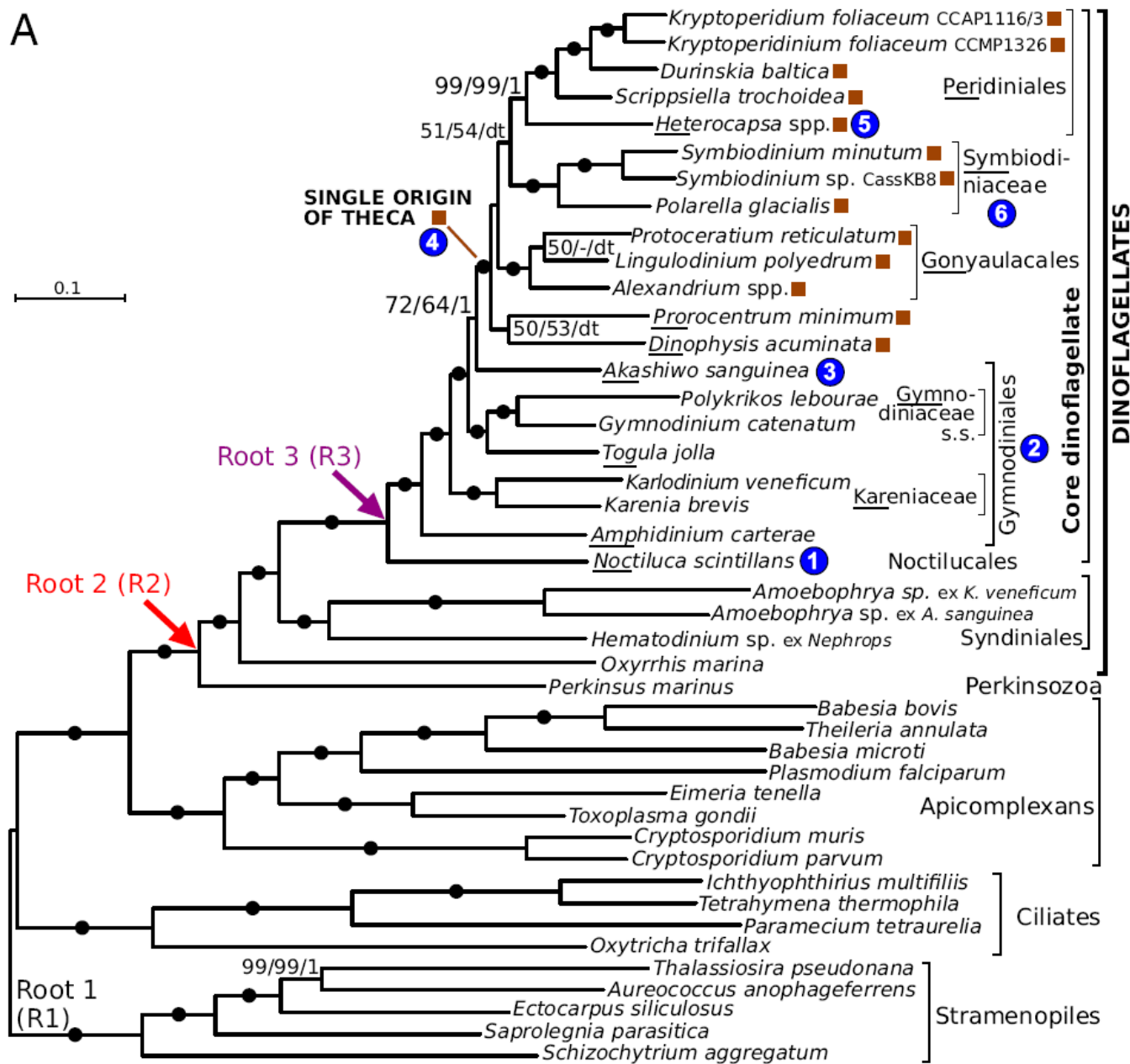
Dinophyta II. – Diversity, Evolution

- Alveolata (Ciliates, Dinophyta, Apicomplexa)
- traditional systematics (Dodge 1982) - 12 orders



Dinoflagellate evolution history

A



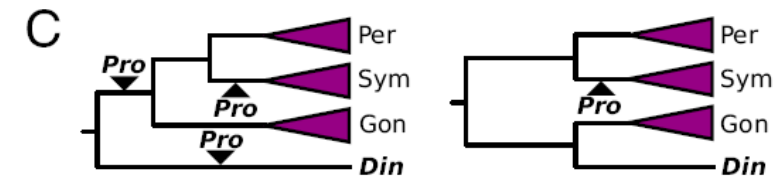
Principal findings:

- 1** Noctiluca (and Amphidinium) early-branching
 - 2** Gymnodiales paraphyletic to thecate, and Togula sister group of Gymnodiniaceae s.s.
 - 3** Akashiwo sister group to thecate
 - 4** Thecate monophyletic (unambiguous support)
 - 5** Heterocapsa with other Peridinales (not early-branching)
 - 6** Symbiodiniaceae nested within thecate (not intermediate)
- Cellulosic thecal plates

B

Clade	Matrix	All	Species presence All - Din	All - Pro	All - Din & Pro
Noc + other core dino.	R1 R2	● 100/100/dt	● 100/100/dt	● 100/100/dt	● 100/100/dt
1 Noc+Amp	R1 R2	dt/dt/dt dt/dt/.99	dt/dt/dt dt/dt/.99	dt/dt/dt dt/dt/.99	dt/dt/dt dt/dt/.99
Kar + Gym, Tog Aka+thecates	R1 R2 R3	● 100/100/.95 100/100/.98	● 100/100/.94 100/100/.98	● 100/100/.82 100/100/.92	● 100/100/.94 100/100/.92
2 Gym, Tog+Aka + thecate	R1 R2 R3	● ● ●	● ● ●	● ● ●	● ● ●
3 Aka + thecates	R1 R2 R3	72/64/1 88/85/1 90/87/1	68/62/1 86/86/1 90/87/1	62/54/1 86/84/1 85/88/1	56/48/1 84/87/1 84/84/1
4 Thecate	R1 R2 R3	● ● ●	● ● ●	97/95/1 99/100/1	● ● ●
5 Het + other Per	R1 R2 R3	99/99/1 100/99/1 ●	98/98/1 97/99/1 99/97/1	● ● ●	● ● ●
Sym + Per	R1 R2 R3	51/54/dt dt/dt/dt dt/dt/1	dt/dt/dt dt/dt/dt dt/dt/1	100/100/1 99/99/1 98/99/1	99/98/1 96/96/1 93/93/1
6 Sym + Pro	R1 R2 R3	dt/dt/1 57/48/1 57/65/dt	84/87/1 80/67/1 84/79/dt	not applicable	not applicable

C



Dinophysiales I

CRYPTO



D. norvegica

Dinophysiales II

HAPTO



D. mitra

Kryptoperidinium

BACILLARIO



Durinskia, *P. quinquecorne*

Karenia

HAPTO



Karenia sp.

Lepidodinium

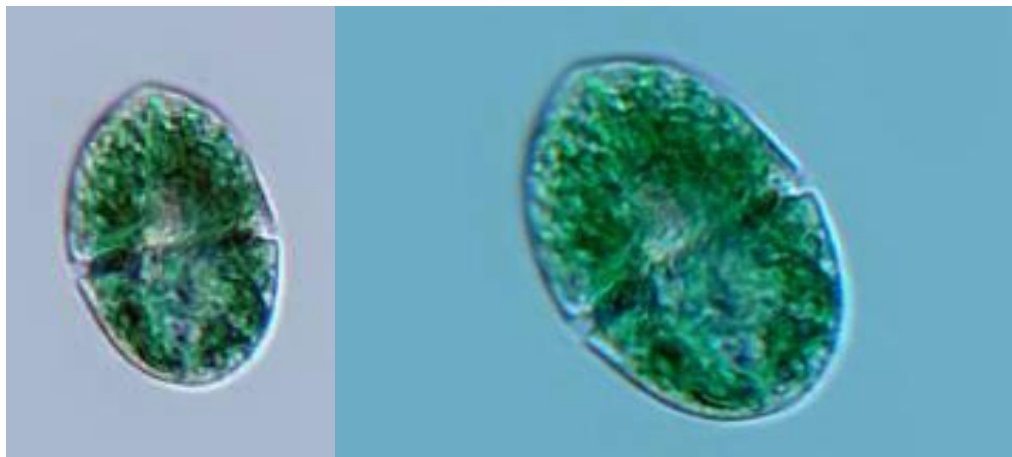
CHLORO



L. viride

Nusuttodinium aeruginosum

CRYPTO



Podolampas

DICTYOCHO



P. bipes

traditional features to recognize particular genera

- naked vs. thecate
- cingulum position (displacement)
- differences in plate ornamentation

features correlated with molecular data

- type of apical groove
- ultrastructural features (stigma types)

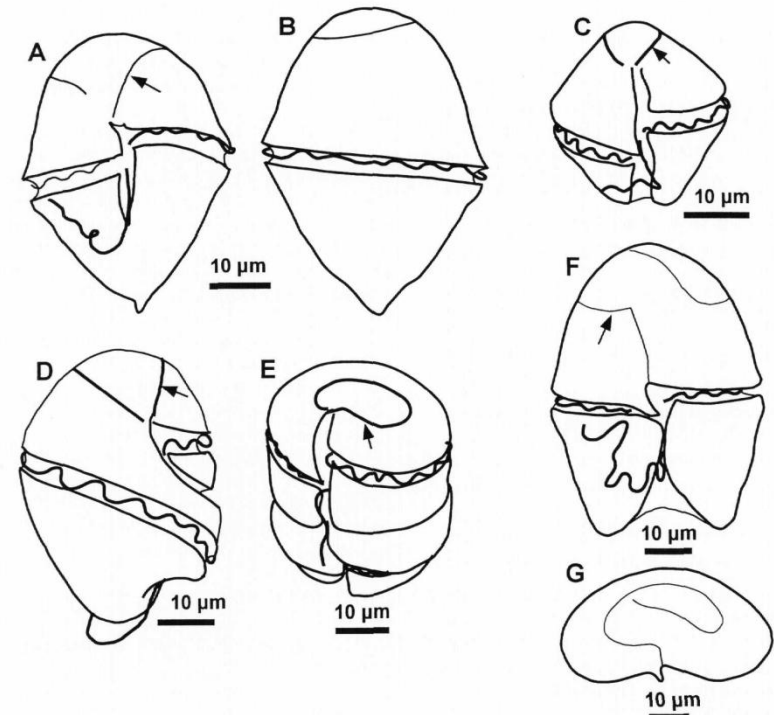
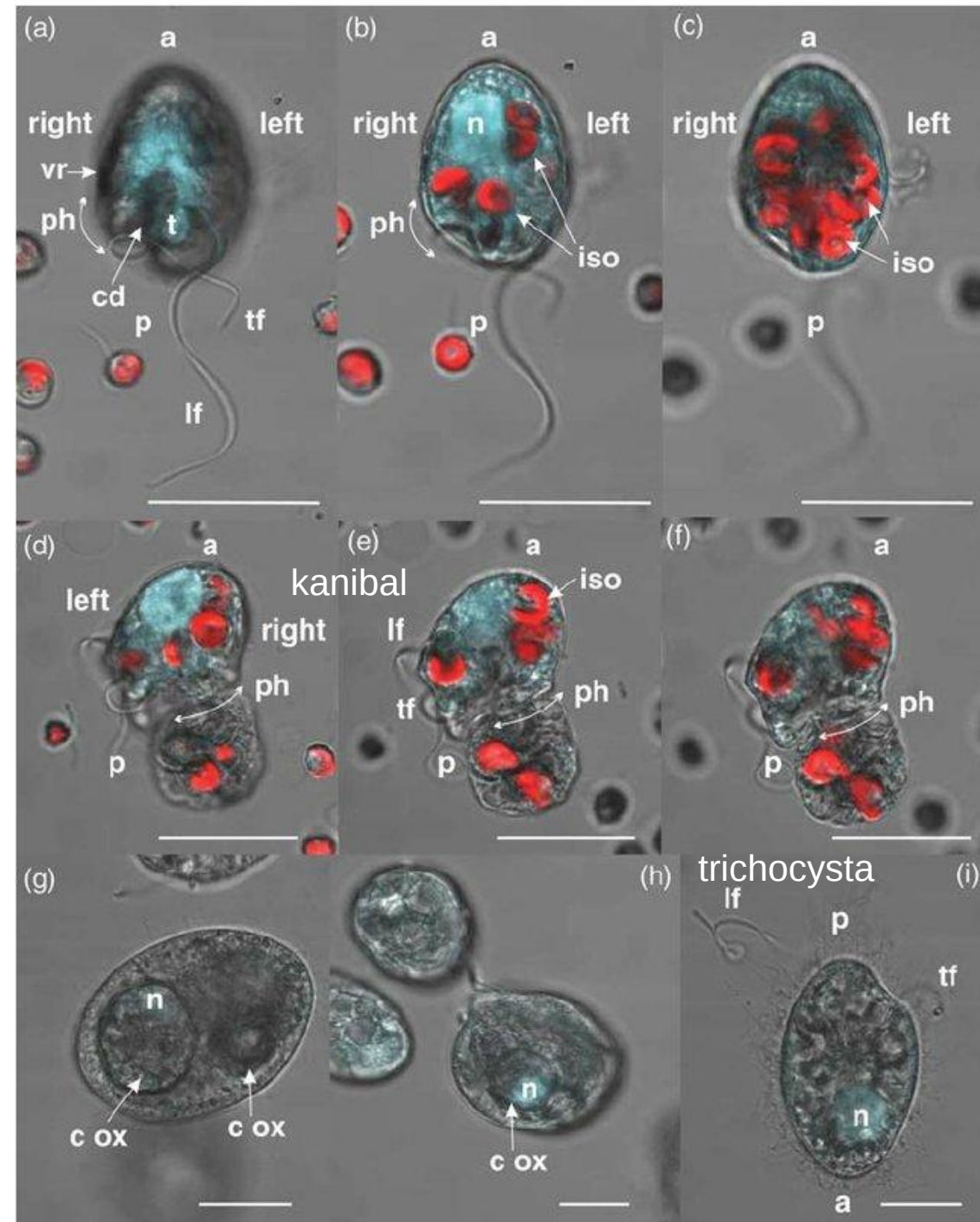
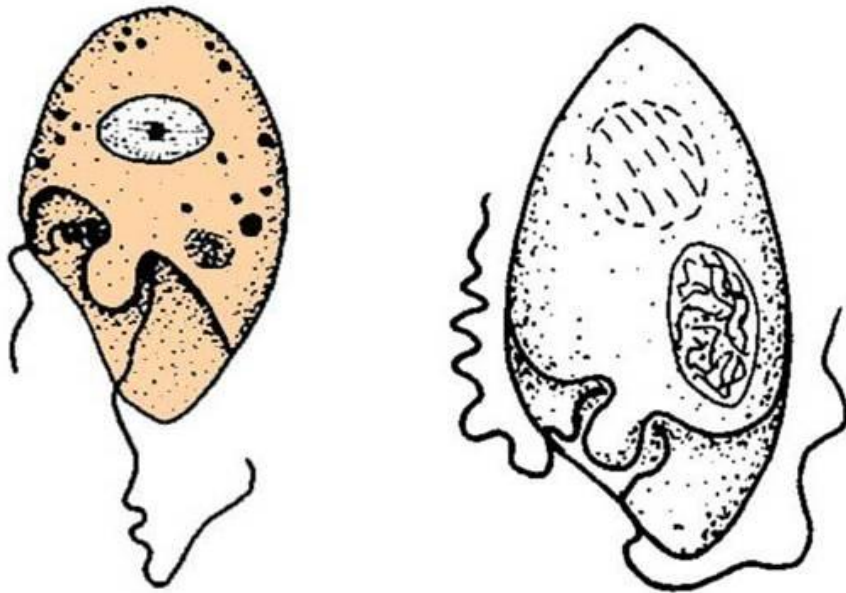


Fig. 2. Apical grooves (arrows) of unarmoured dinoflagellates (drawings based on Hansen *et al.* 2000b; Takayama 1985, 1998; Roberts *et al.* 1992; Hansen, unpublished observations). (A, B) *Gymnodinium fuscum*, ventral and dorsal view, respectively. (C) *Gymnodinium aureolum*. (D) *Nematodinium armatum*. (E) *Polykrikos kofoidii*. (F, G) *Akashiwo sanguinea*, ventral and apical views, respectively.

Oxyrrhinales (M)

Oxyrrhis marina

- the oldest lineage of dinoflagellates
- brackish species, toxic red tides
- primitive features: open mitosis, histons



Syndiniales ^(M)

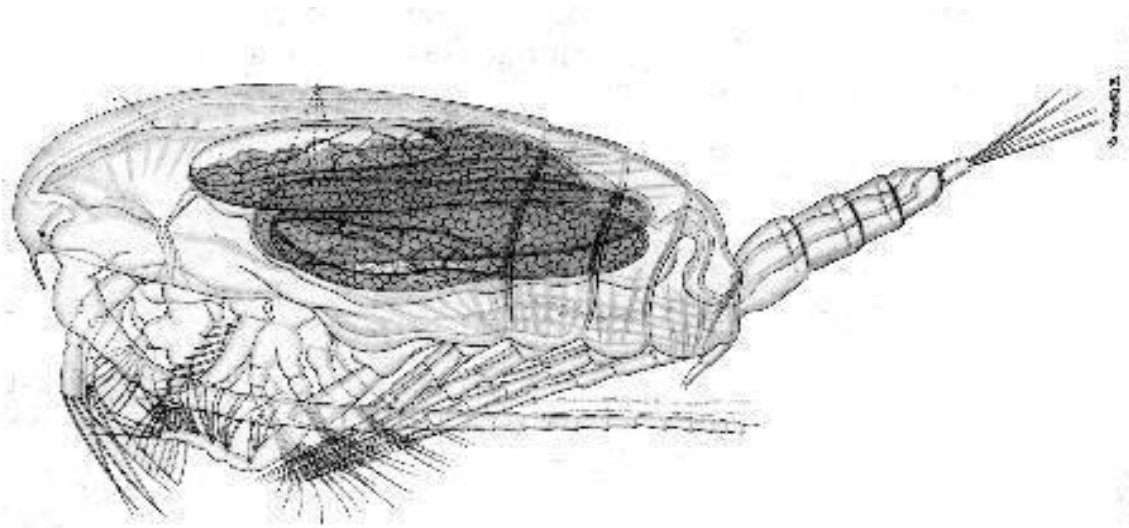
- ecto- and endoparasites of marine invertebrates and fish



***Syndinium* – release of zoospores**

Syndiniales ^(M)

endoparasite in Copepods

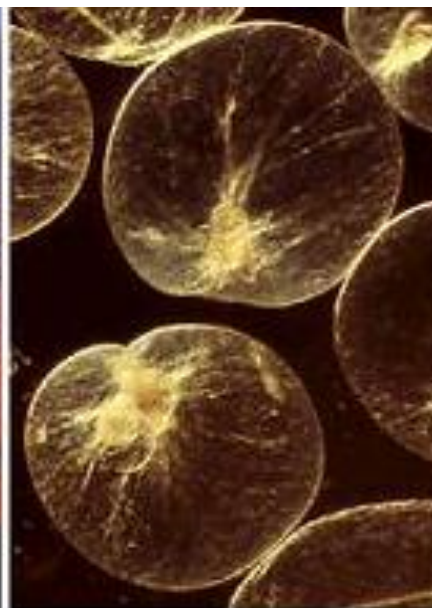


Blastodinium



Noctilucales (M)

- marine *Noctiluca scintillans*
- free-living flagellates without plates, large vacuolised cells (up to 1.2 mm in diameter) – Na^+ , K^+ replaced by H^+
- heterotrophic
- epitheca and hypotheca are not differentiated in adult cells, cingulum transformed in groove with tentacle



Red Tide caused by *Noctiluca scintillans*
occurred in Seto Inland Sea, Japan (May 6, 1976)

Noctilucales (M)

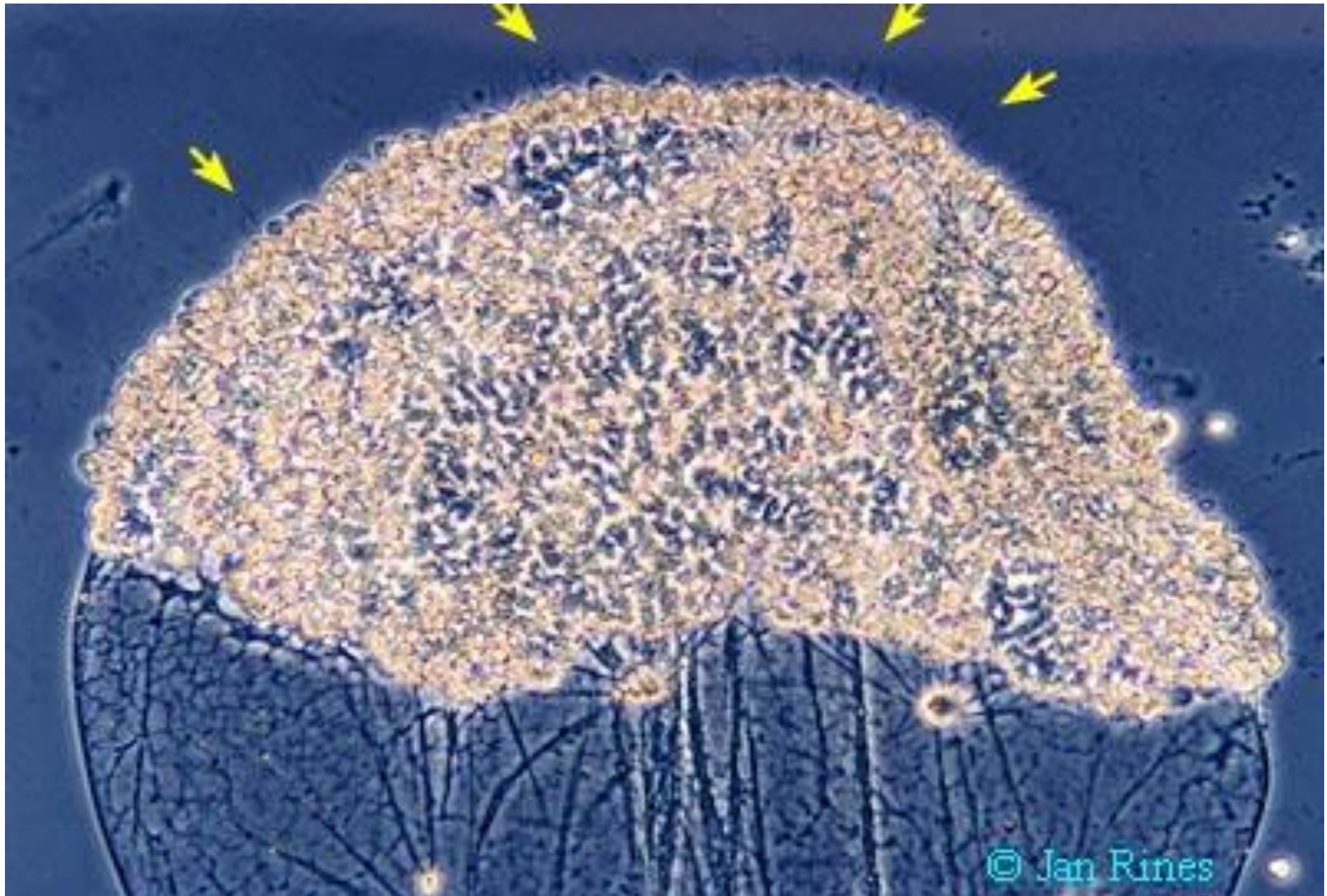
bioluminescence



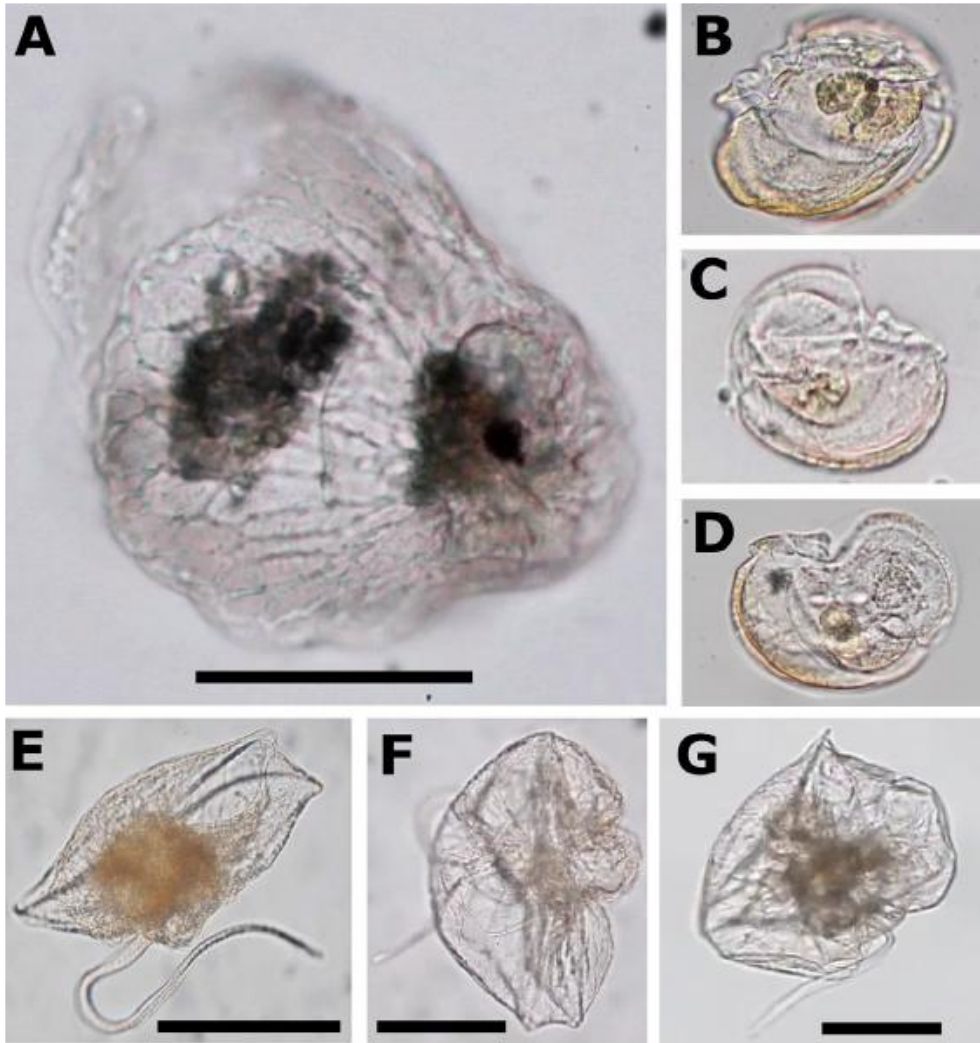
© Jan Rines

Noctilucales (M)

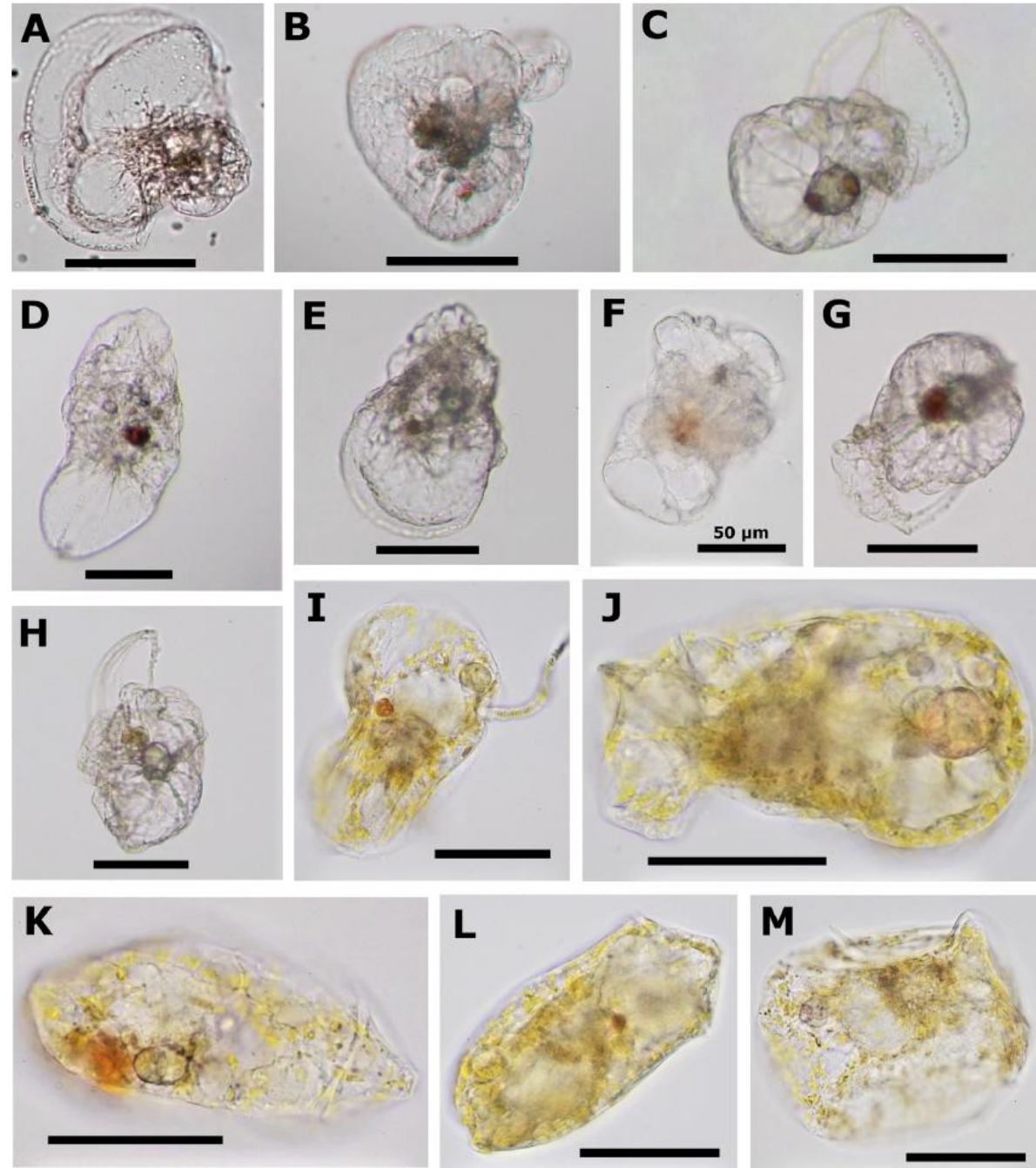
zoosporogenesis



Noctilucales (M)



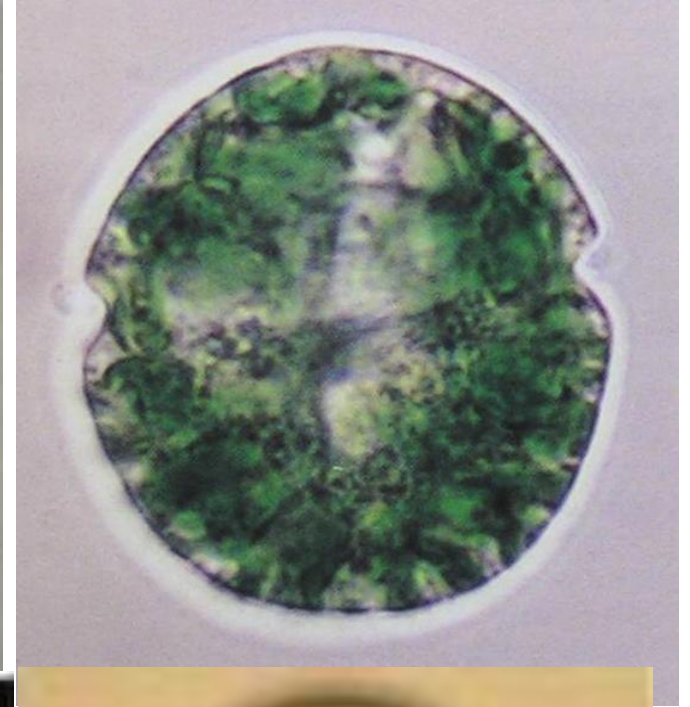
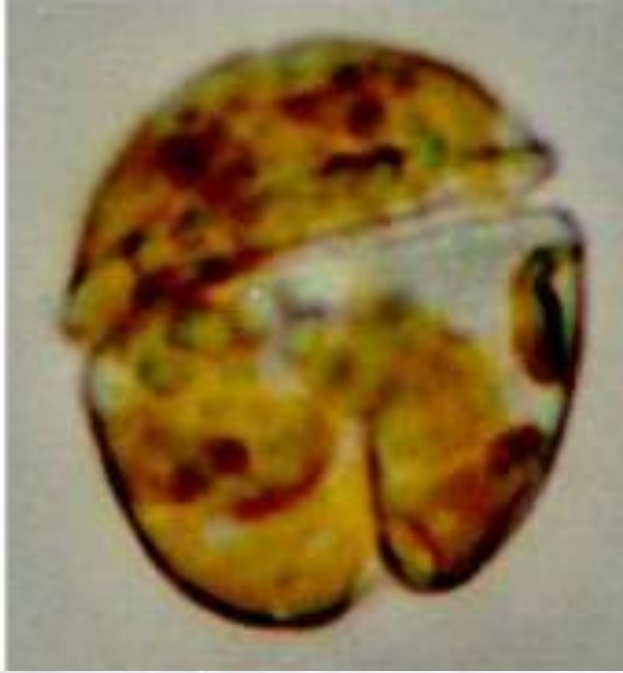
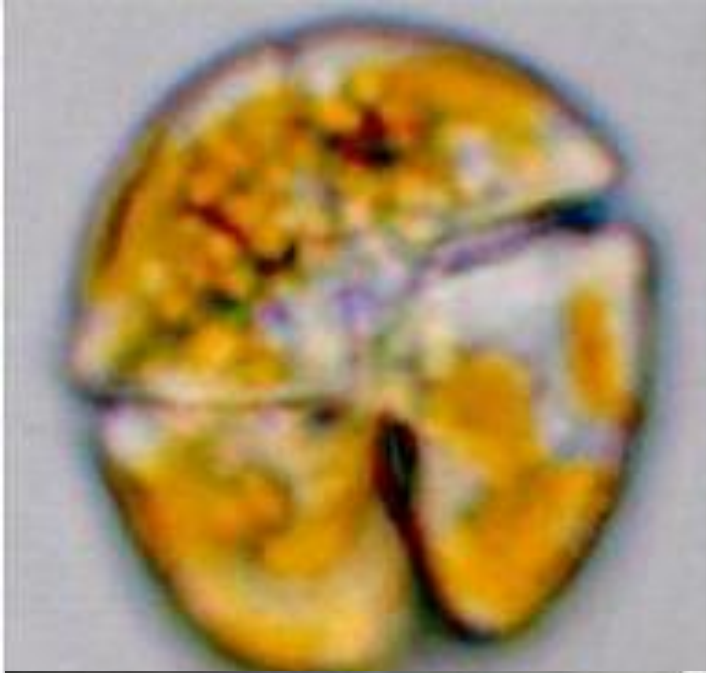
Fabadinium



Kofoidinium, Spatulodinium

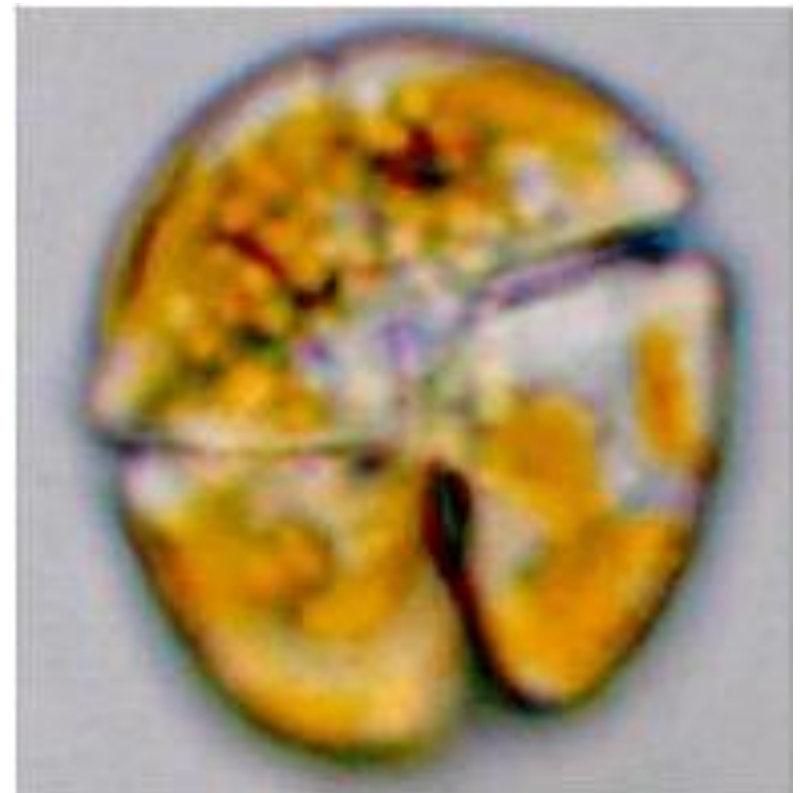
Gymnodiniales

- unarmored dinoflagellates



Gymnodinium

- free-living flagellates, sulcus + cingulum
- dorsiventrally flattened cells without visible plates
- autotrophic and heterotrophic species
- freshwater and marine



Gymnodinium (M)



Gymnodinium
catenatum
Graham

saxitoxin - PSP !

Microphoto by
Yasuwo Fukuyo and
Haruyoshi Takayama

WESTPAC-HAB
T0006

Gymnodinium (F)



SINICE
& RASY.cz

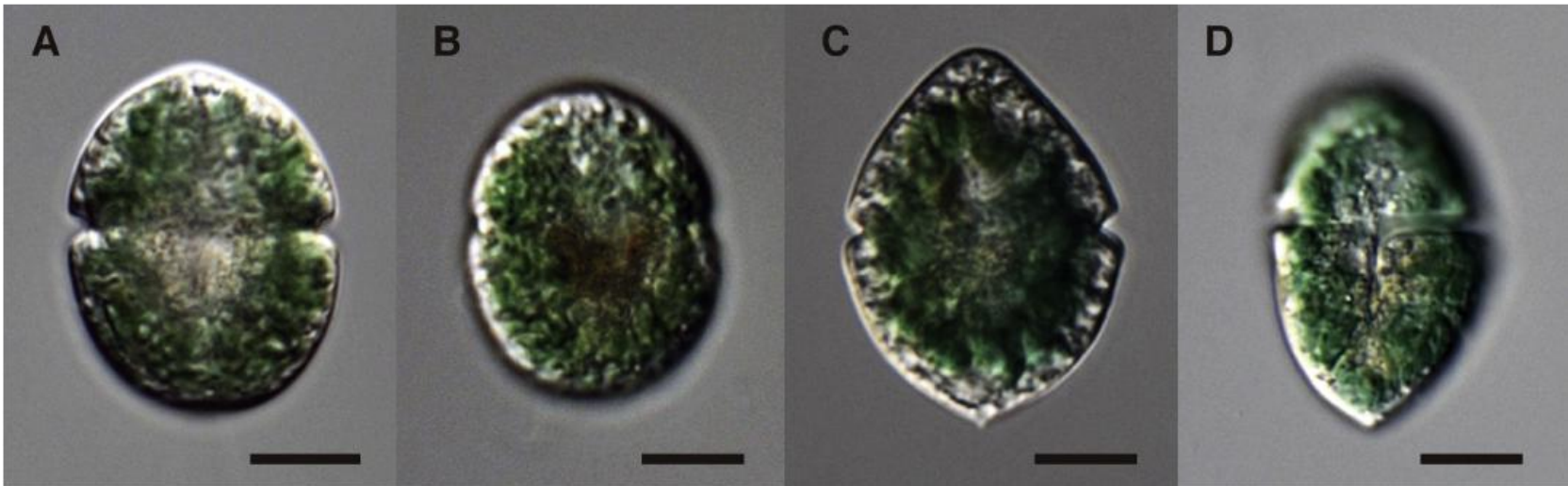
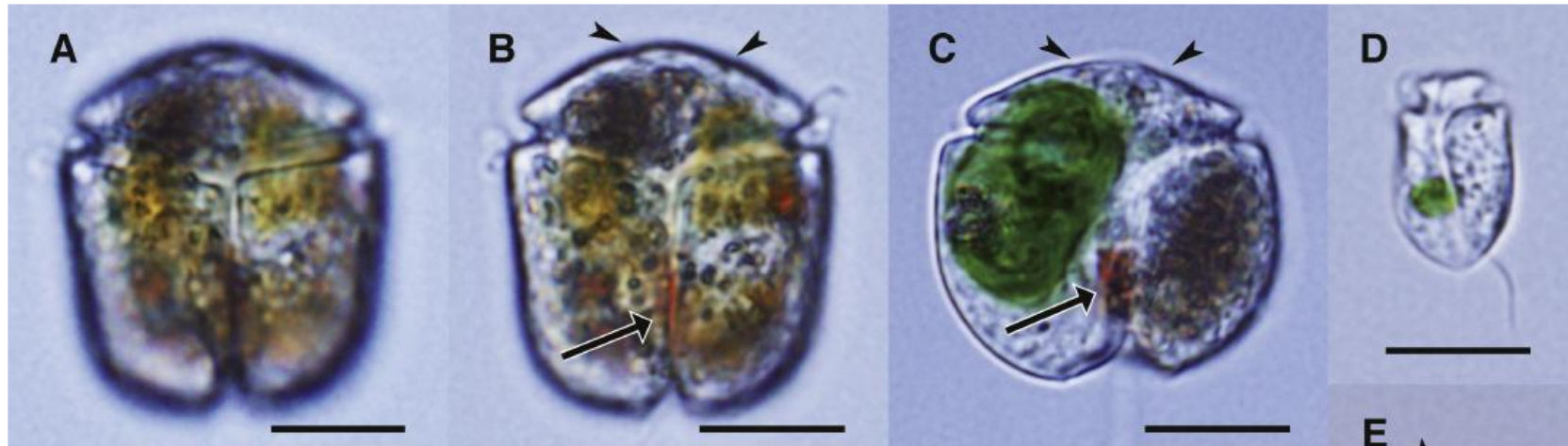


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G. fuscum

Nusuttodinium (F, M)

- kleptoplastidic = chloroplasts derived from endosymbiotic, periodically acquired and temporarily retained cryptomonads

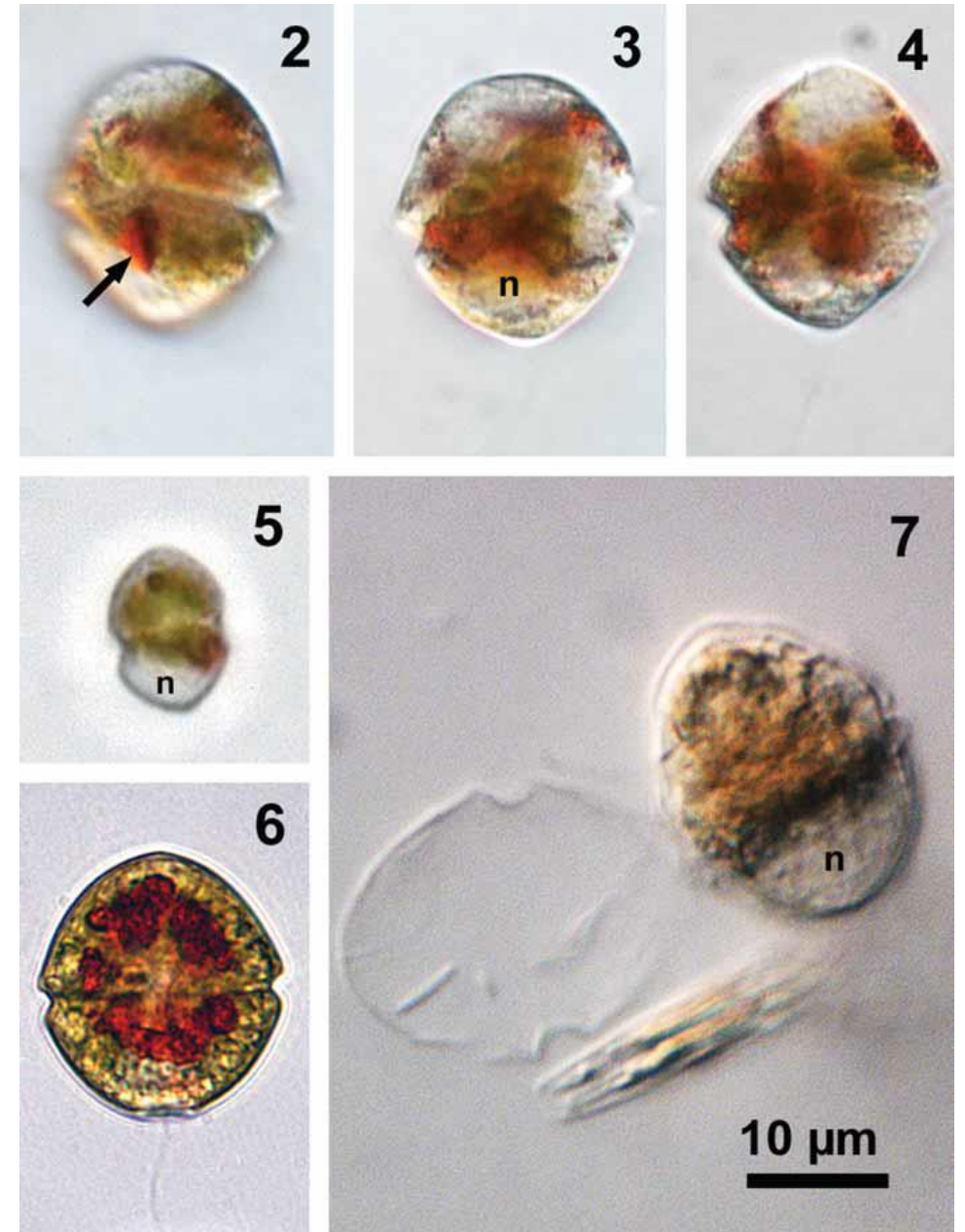
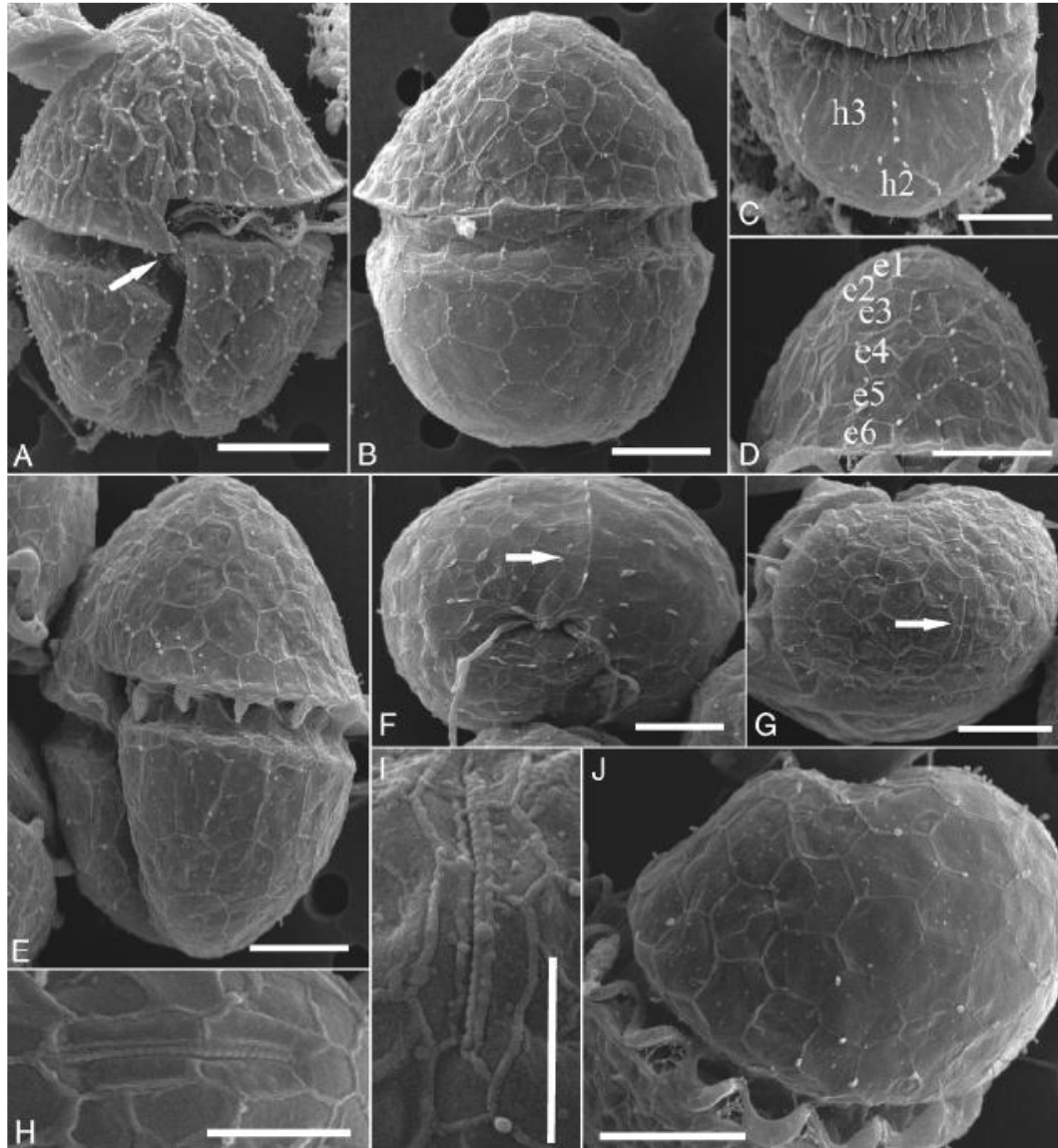


Nusuttodinium aeruginosum

Woloszynskia, *Tovelia* (F)

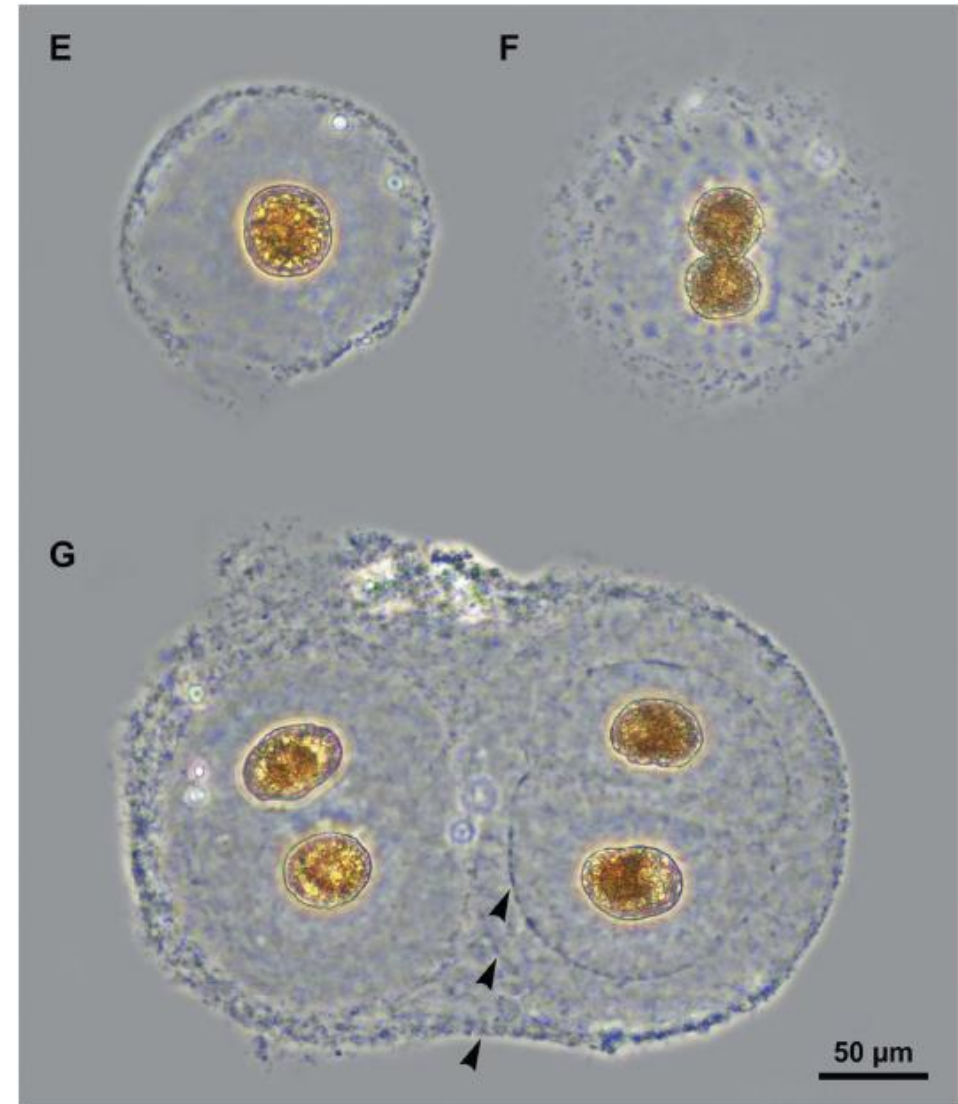
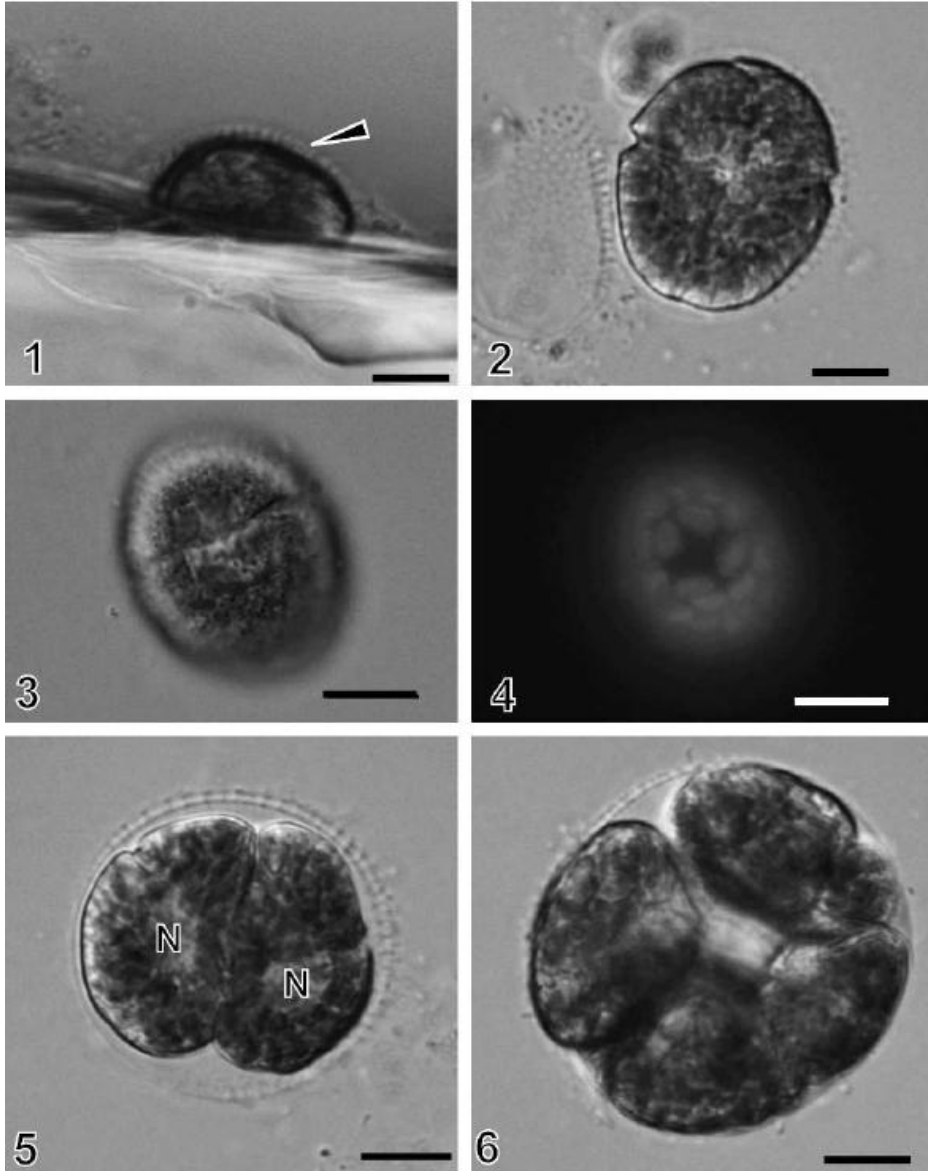
- a number of thin, hexagonal plates visible only on empty cells

Tovelia sanguinea



Spiniferodinium (F, M)

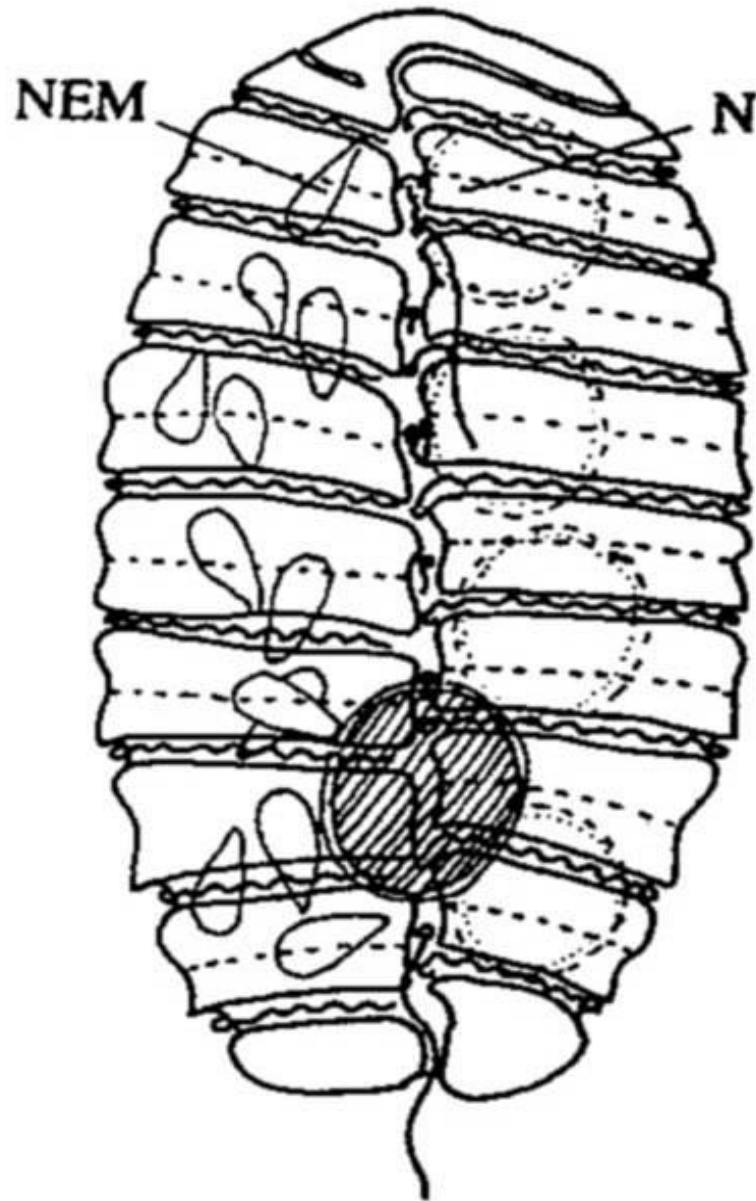
- a unique transparent, spiny, helmet-shaped cell covering, termed the 'helmet shell'



Spiniferodinium limneticum

Polykrikos, Phaeopolykrikos (M)

coenocytic organisation



*Polykrikos
schwartzii*

Amphidinium (F, M)

conspicuously small epitheca



Amphidinium carterae



Amphidinium operculatum

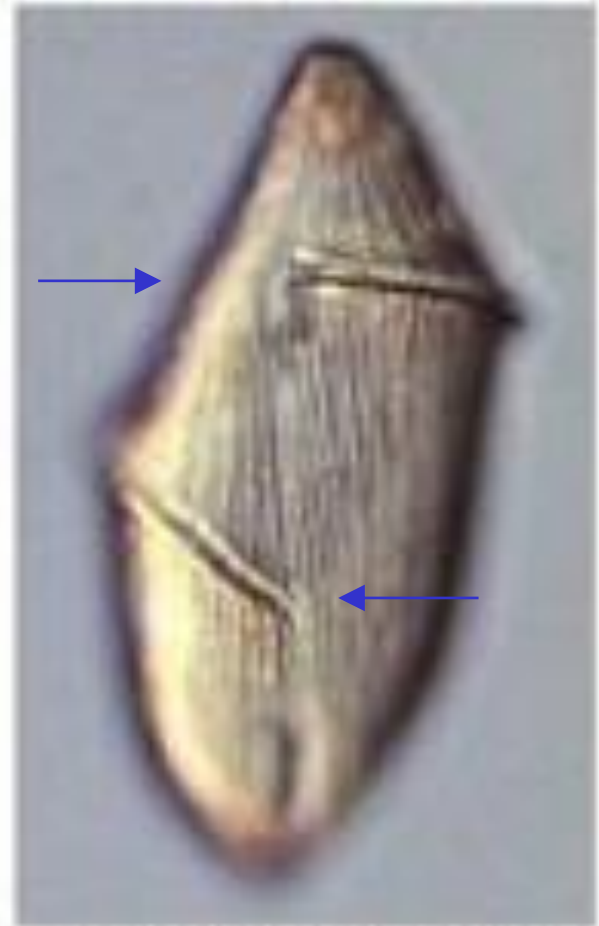
ciguatoxin - CFP !

Gyrodinium (F, M)

strongly displaced cingulum



Gyrodinium instriatum

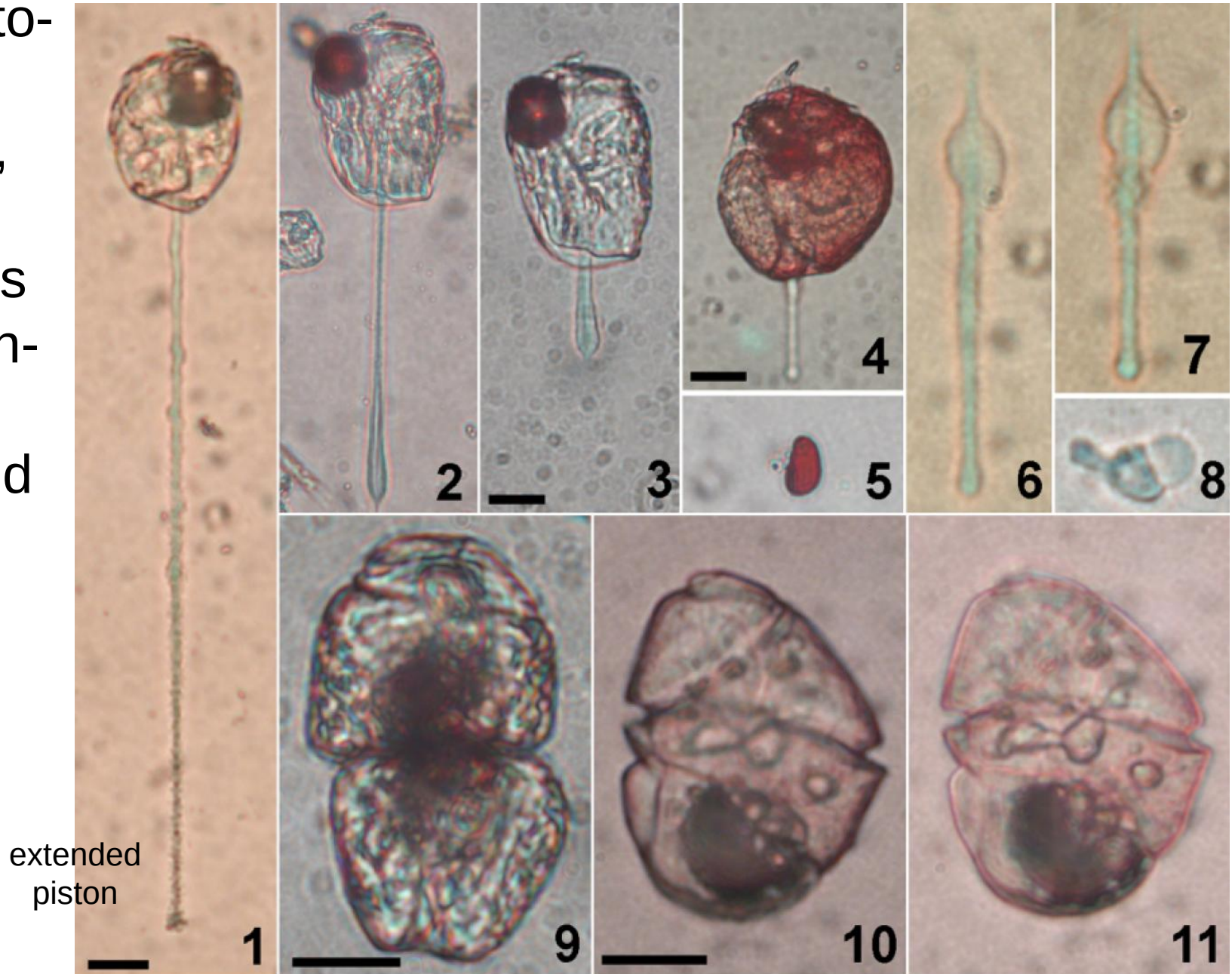


Gyrodinium spirale

Erythropsidinium, *Warnowia* (M)

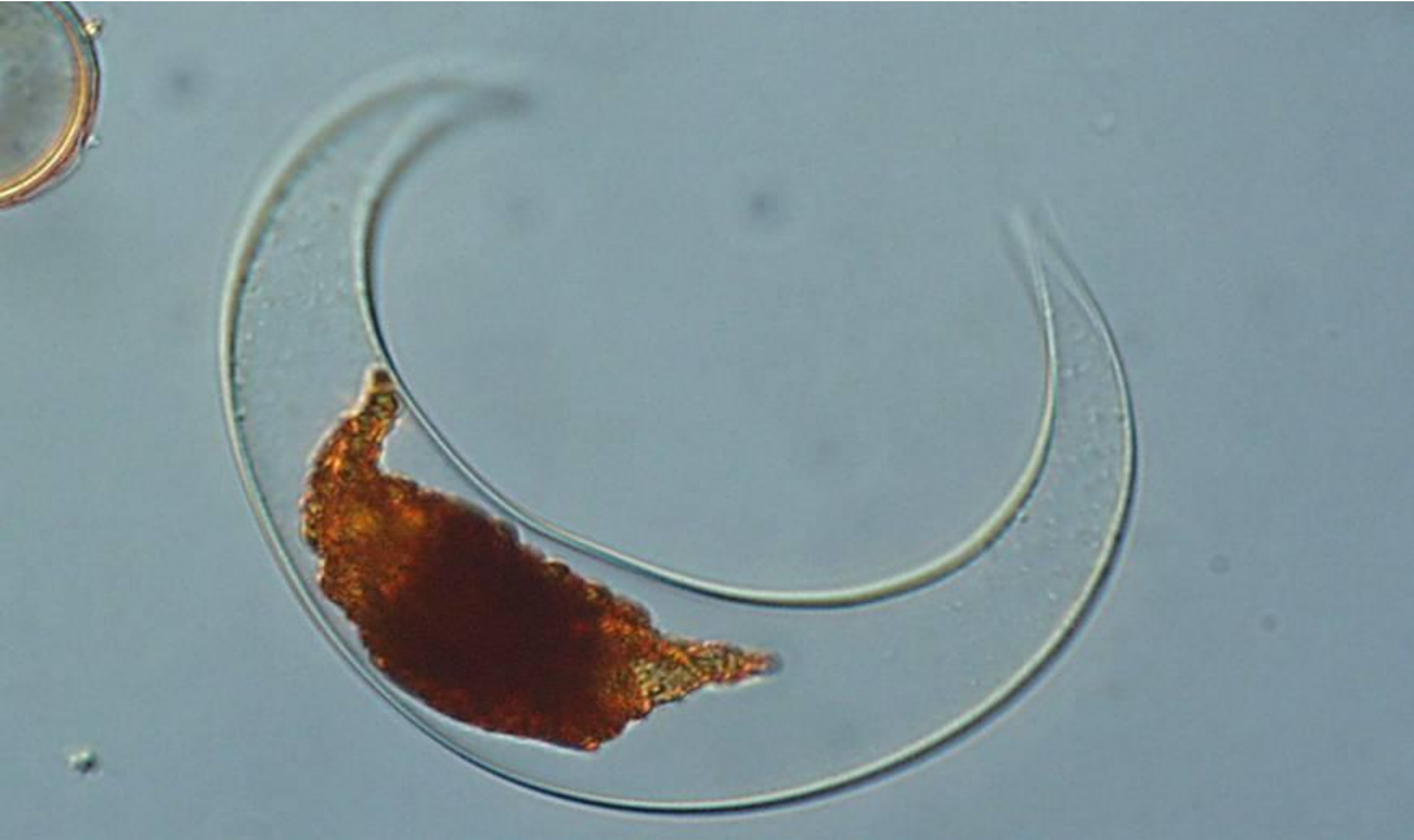
complex organells:

- **ocelloid**: a photo-receptor system with cornea, lens, and pigment cup-like structures
- **piston**: an extensible appendage for locomotion and prey location



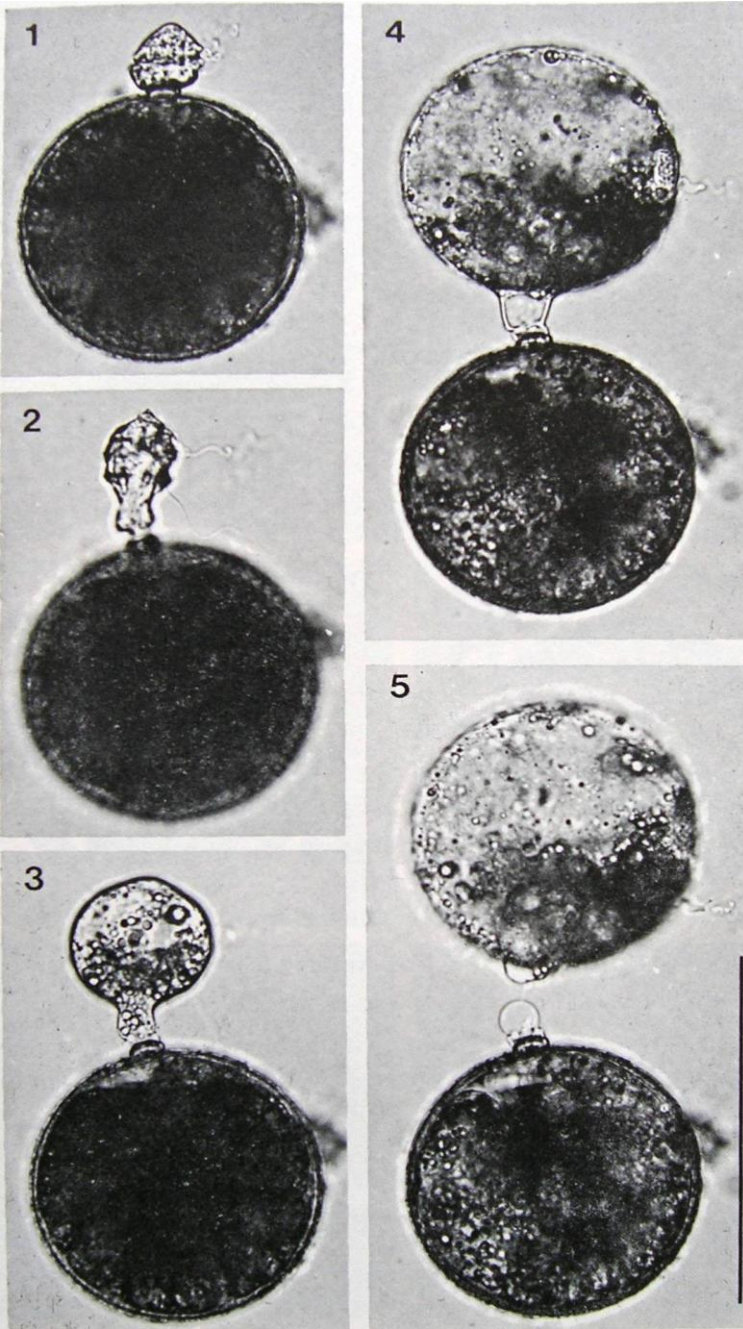
Dissodinium pseudolunula (M)

parasite on crustacean eggs



Dissodinium pseudolunula (M)

parasite on crustacean eggs



1 – dinospore is attaching the cell

5 – trophont separation (after 90 min)

Dissodinium pseudolunula (M)

parasite on crustacean eggs



1 – dinospore is attaching the cell

5 – trophont separation (after 90 min)

6 – several trophonts on one cell

10 – primary cyst

12 – secondary cyst

13 – secondary cysts with mature dinospores

Dissodinium pseudolunula (M)

parasite on crustacean eggs

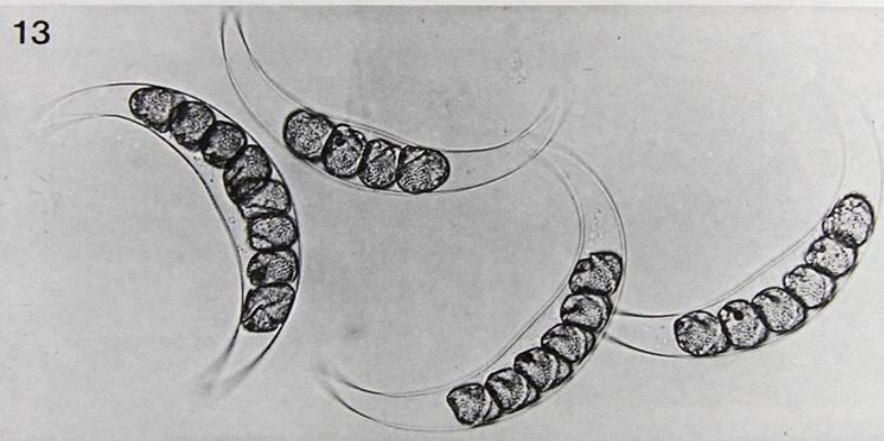


1 – dinospore is attaching the cell

5 – trophont separation (after 90 min)

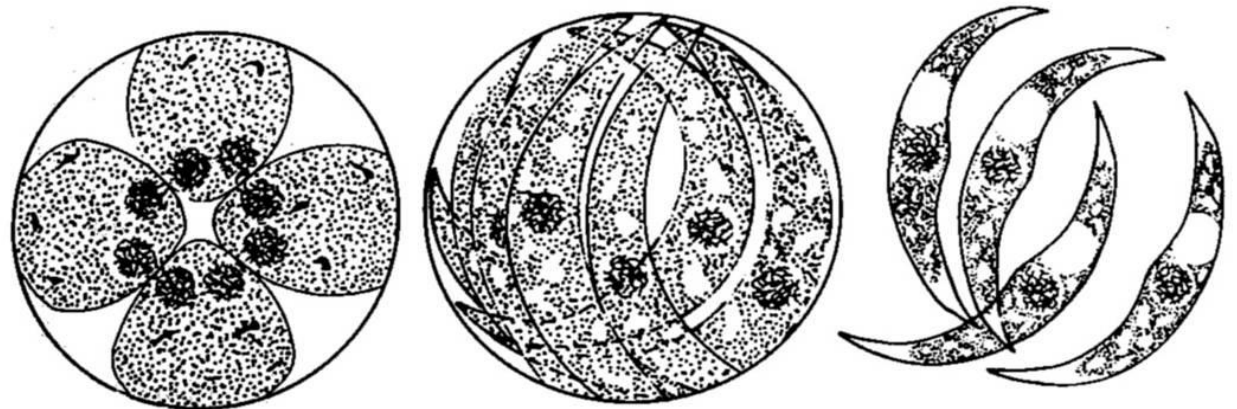
6 – several trophonts on one cell

10 – primary cyst



12 – secondary cyst

13 – secondary cysts with mature dinospores



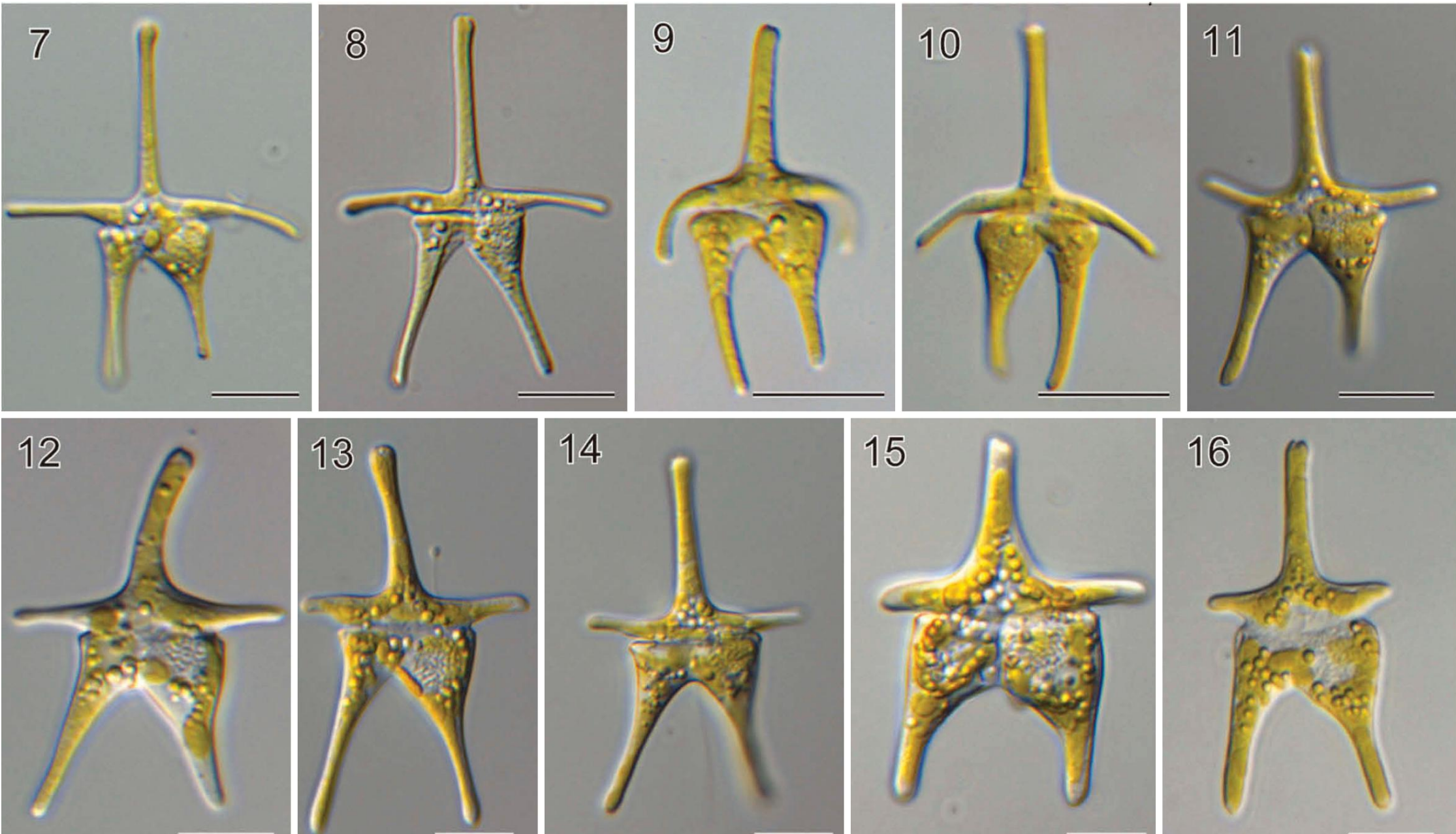
Karlodinium (M)

- massive blooms in coastal waters, toxin production
- paralysis and mortality of finfish, copepods, nematods, and even polychaete-larvae



Asterodinium (M)

- star-shaped, unarmored dinoflagellate from Japan



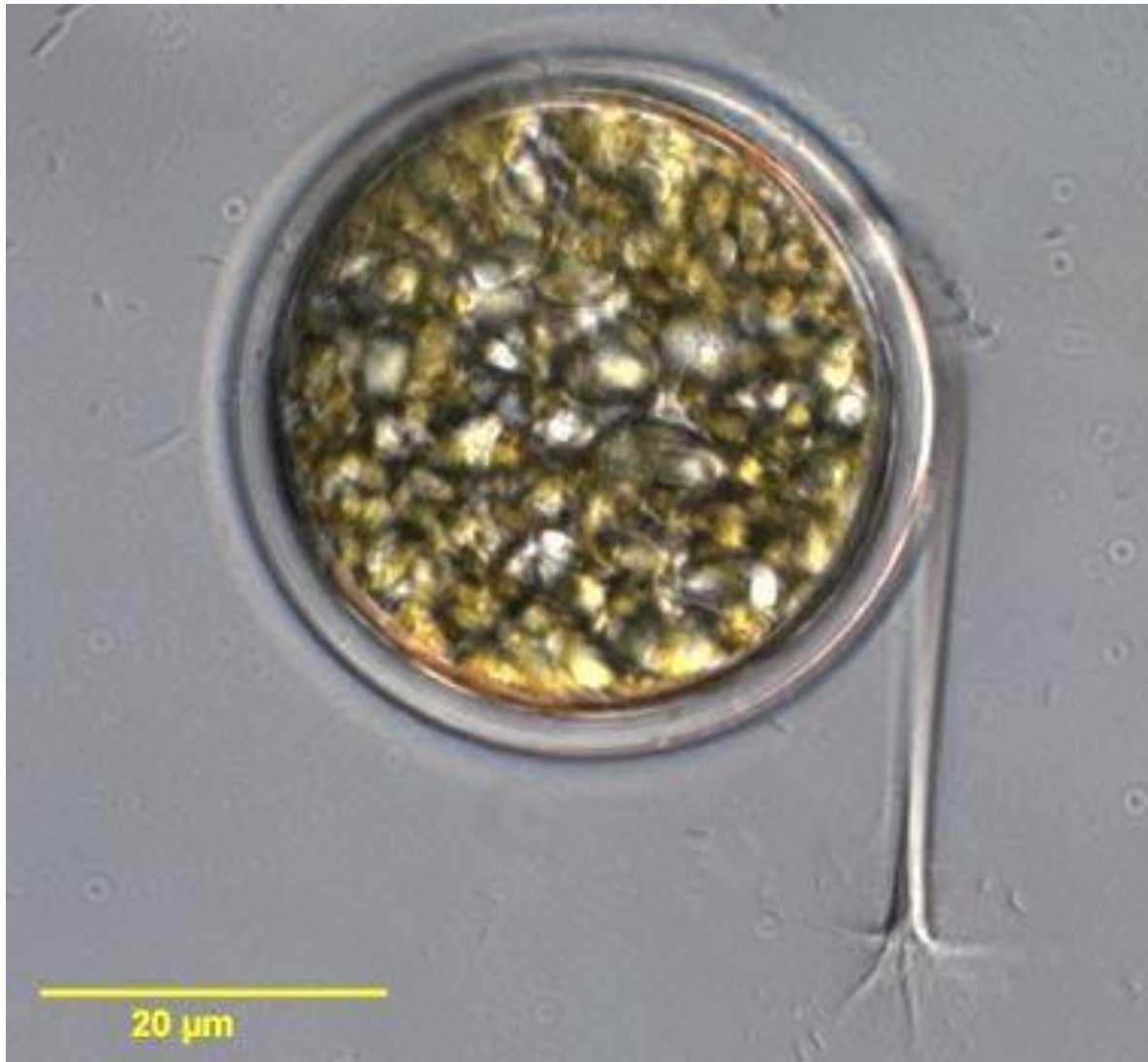
Akashiwo sanguinea (M)

- a distinct lineage unrelated to any order
- forming blooms that result in red tides not harmful to humans

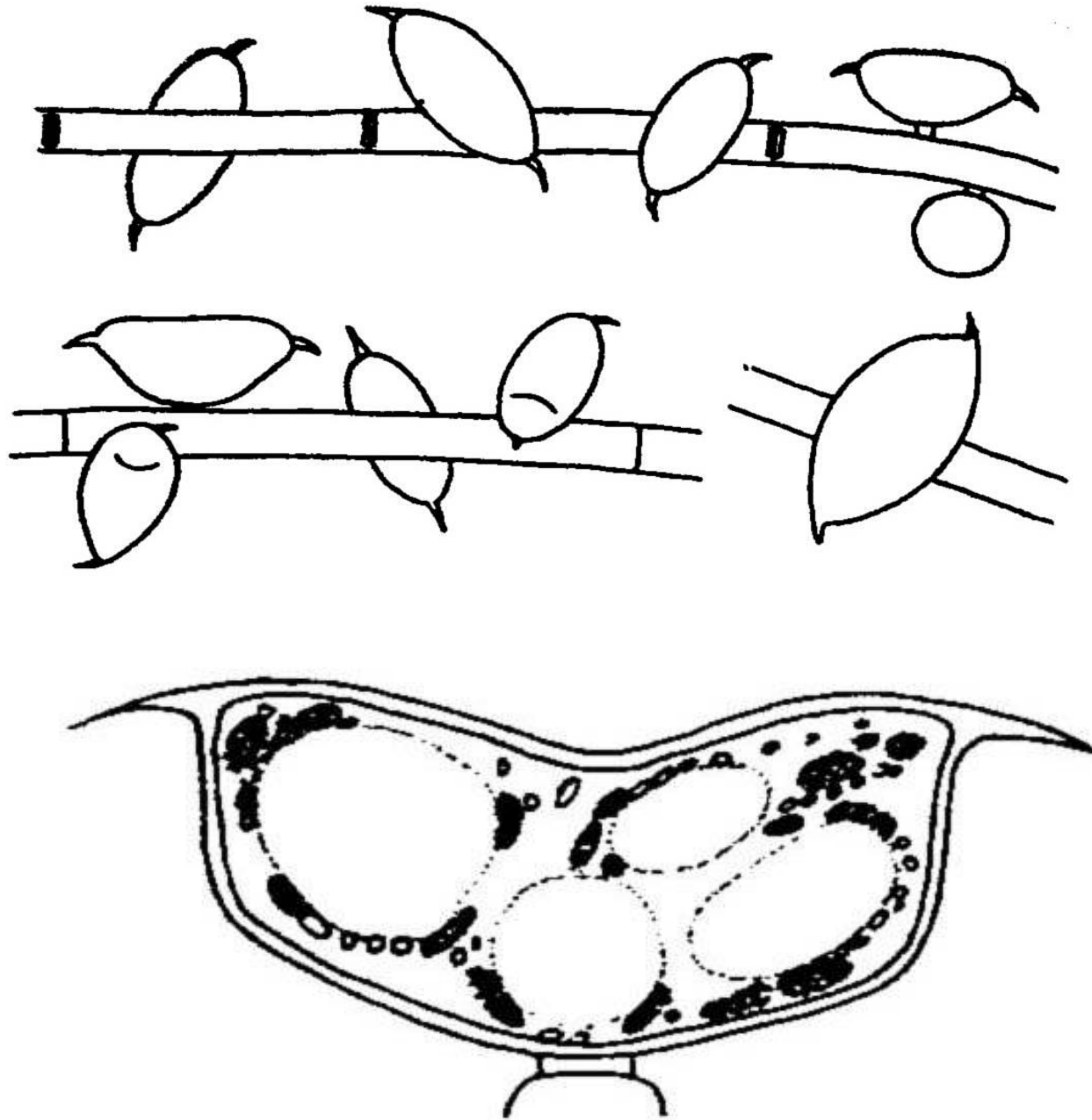


Phytodiniales

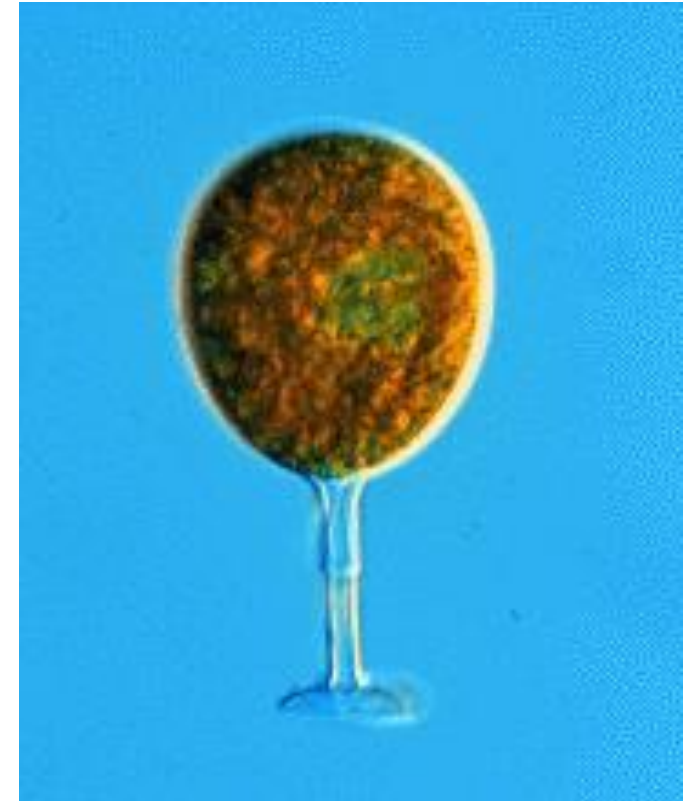
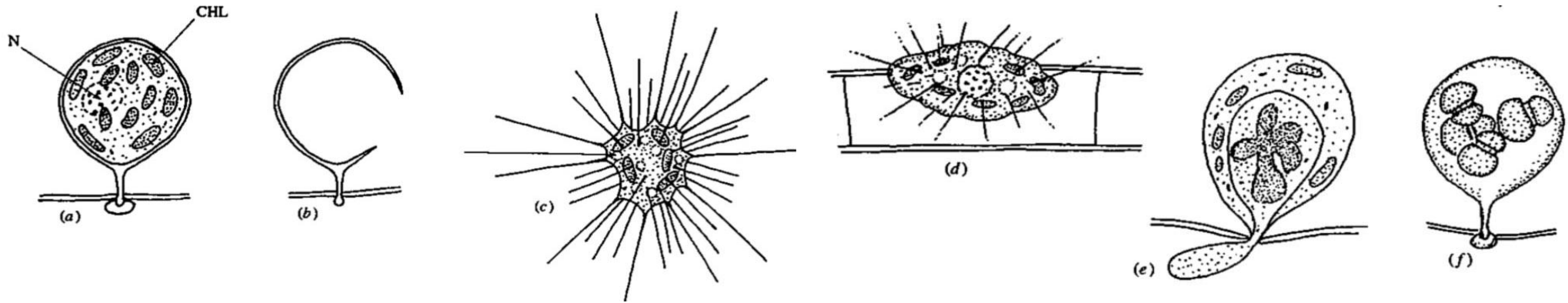
- coccoid dinoflagellates
- epiphytes on filamentous algae



Dinococcus (F)

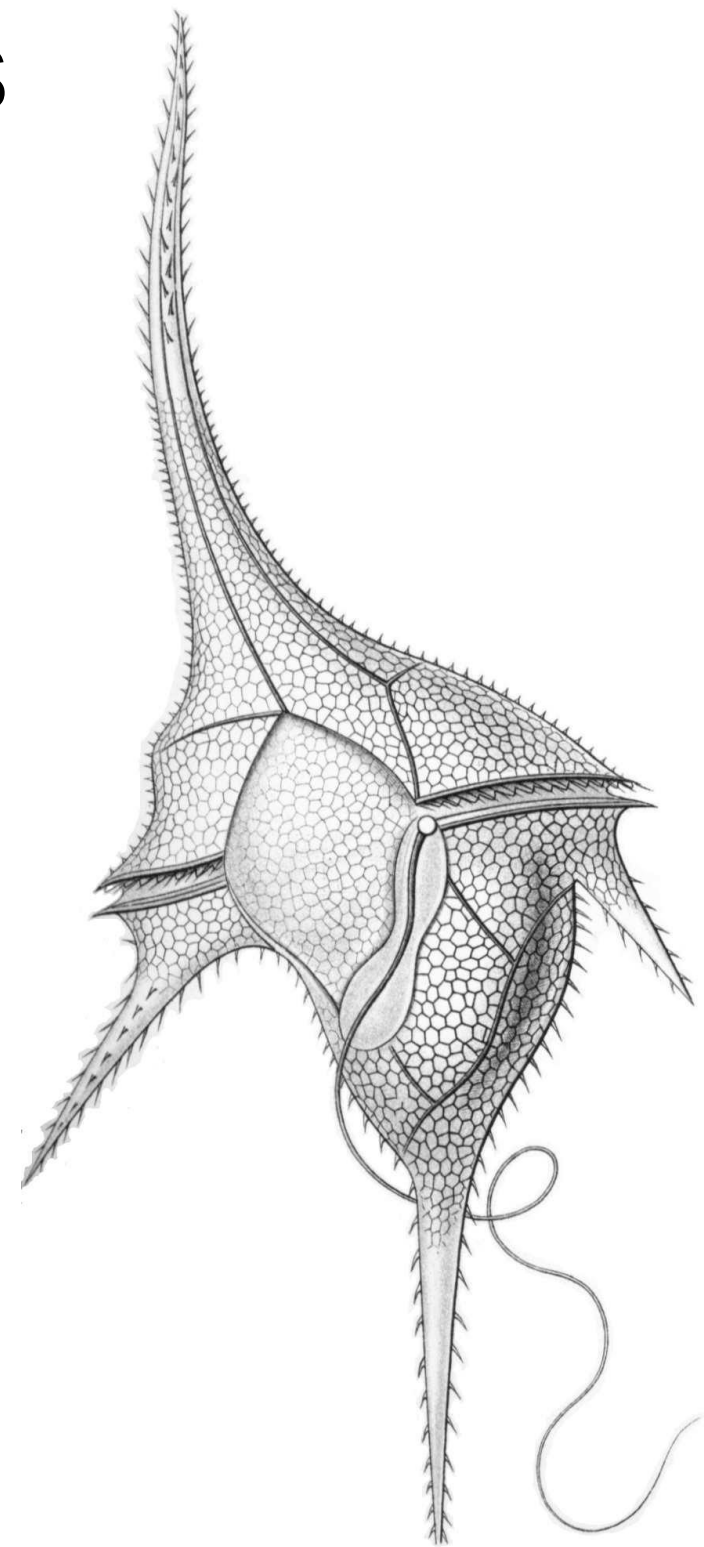
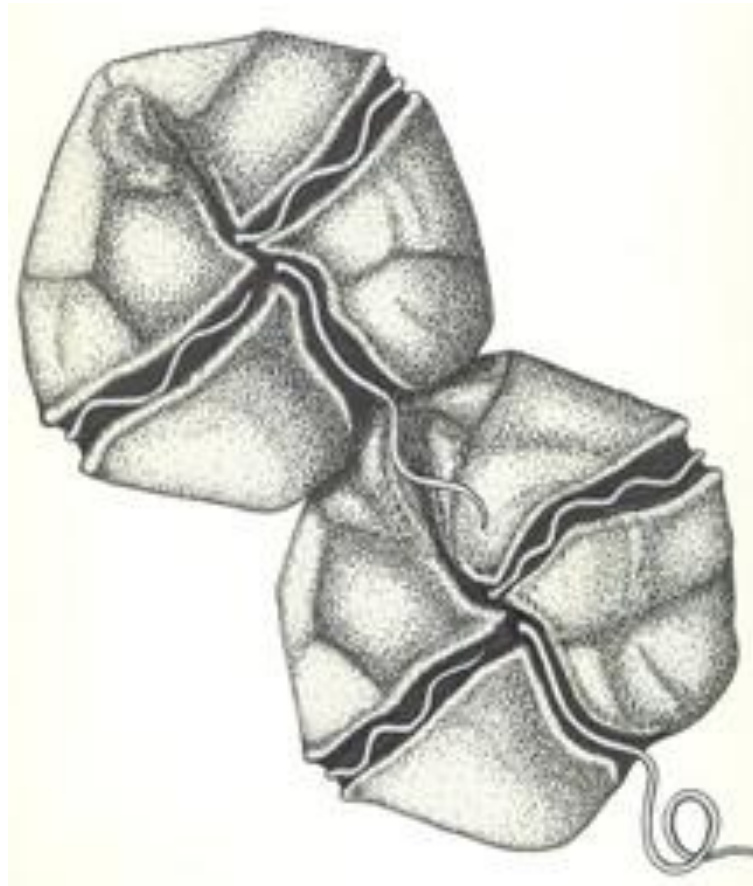
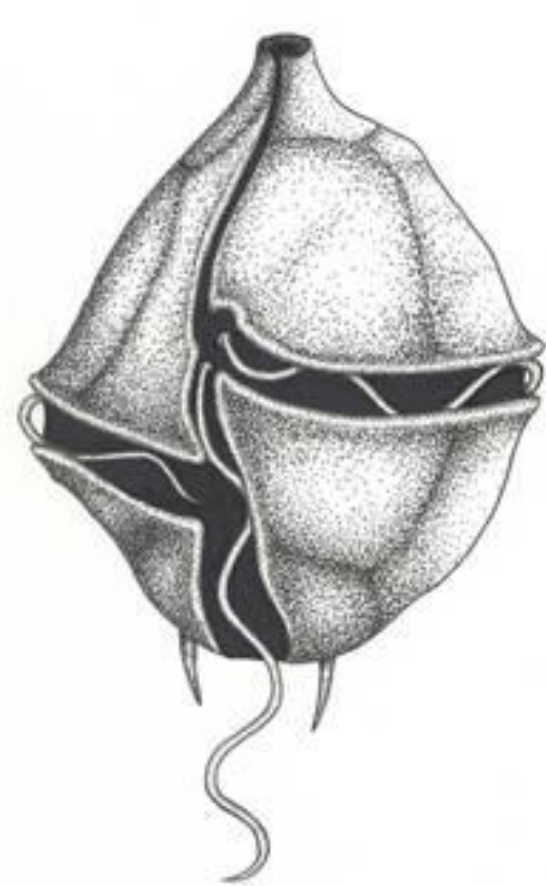


Stylodinium (F)



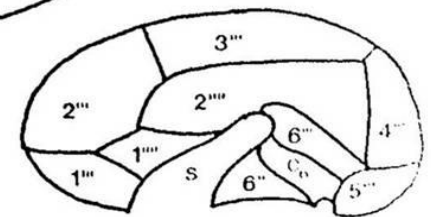
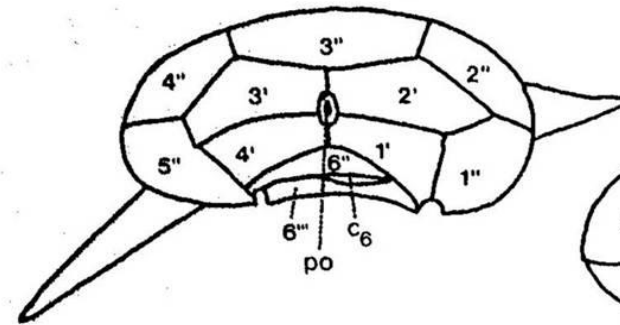
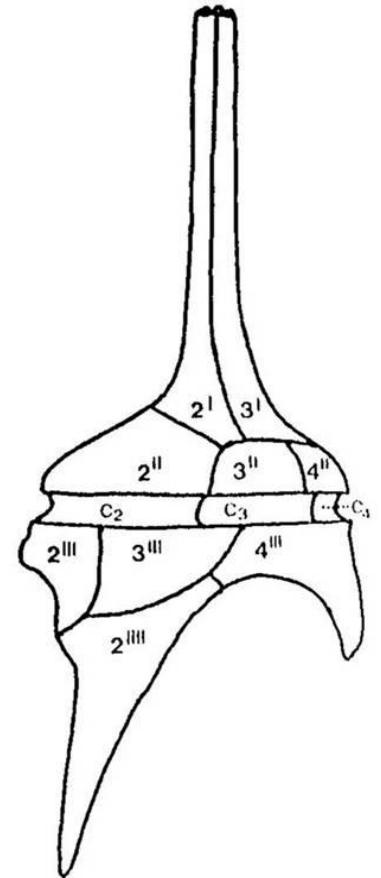
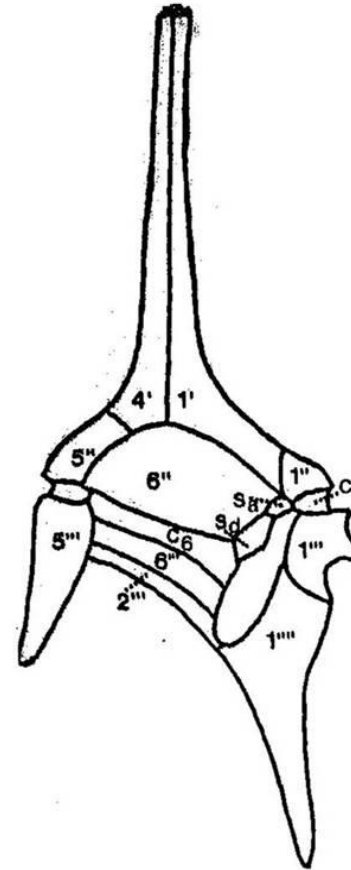
Gonyaulacales

- armored flagellates
- distinguished from the Peridinales mostly by the arrangement and number of the thecal plates
- the first apical plate assymetrical



Ceratum (F)

formula 4', 5'', 5''', 2''''



Ceratium (F)



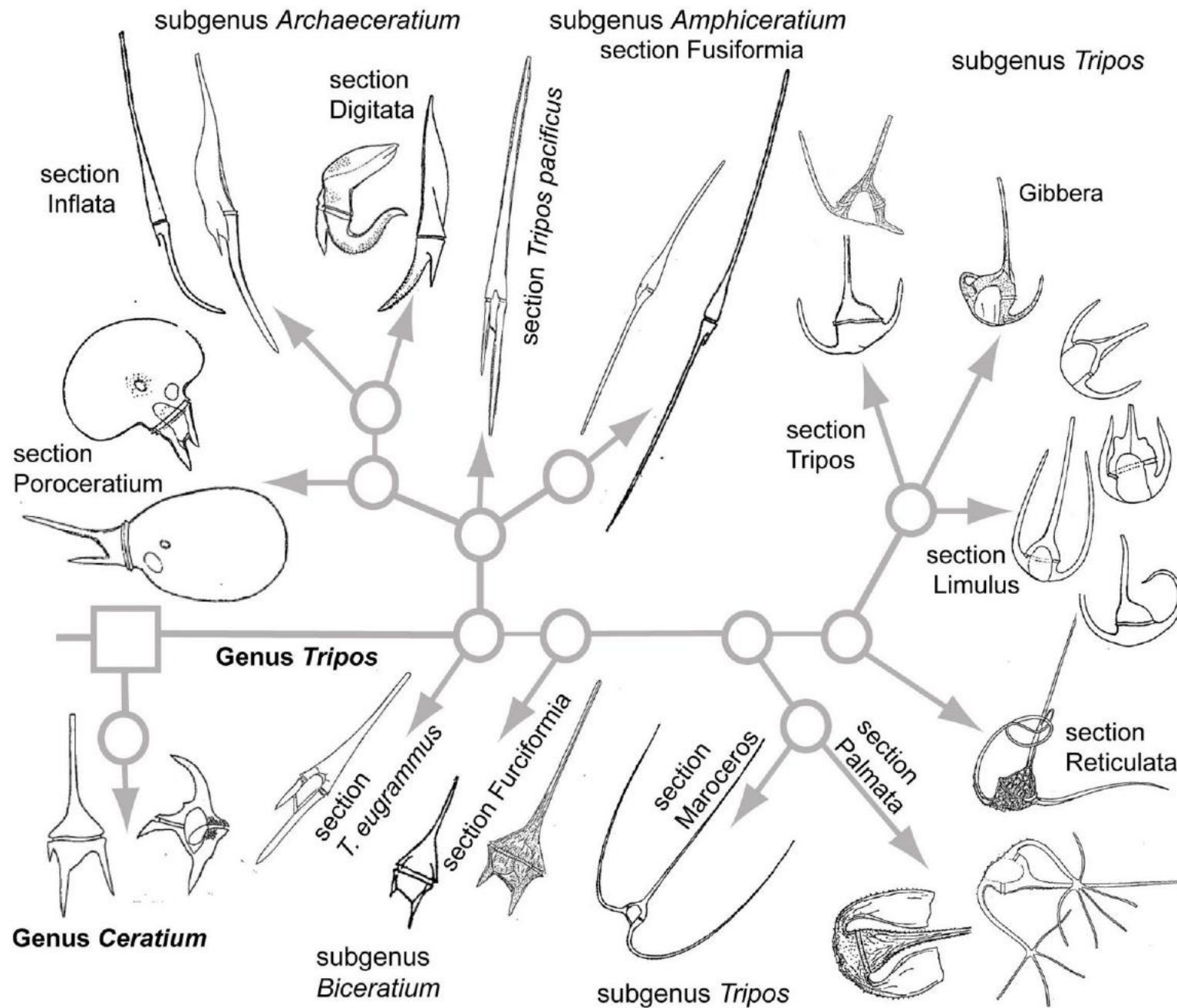
Ceratium hirundinella



Ceratium cornutum

Triplos (M)

formula 4', 5'', 5''', 2''''



Triplos ^(M)



T. furca



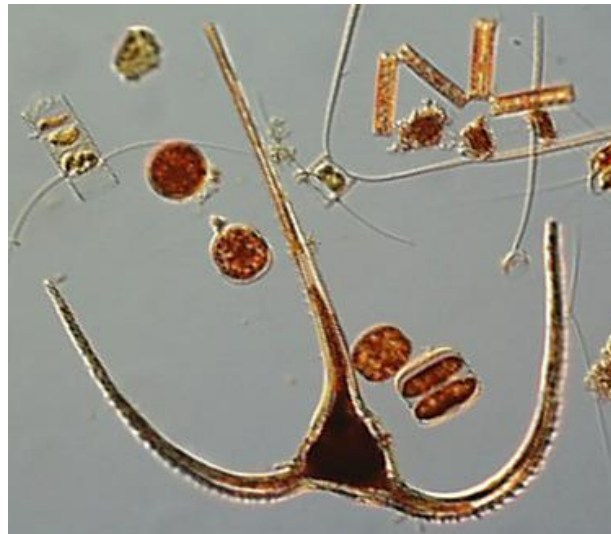
T. lineatus



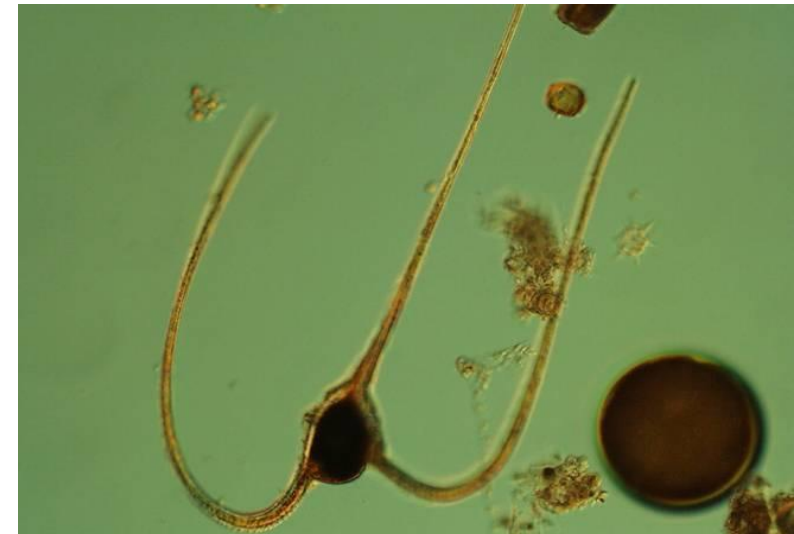
T. fusus



T. muelleri



T. longipes



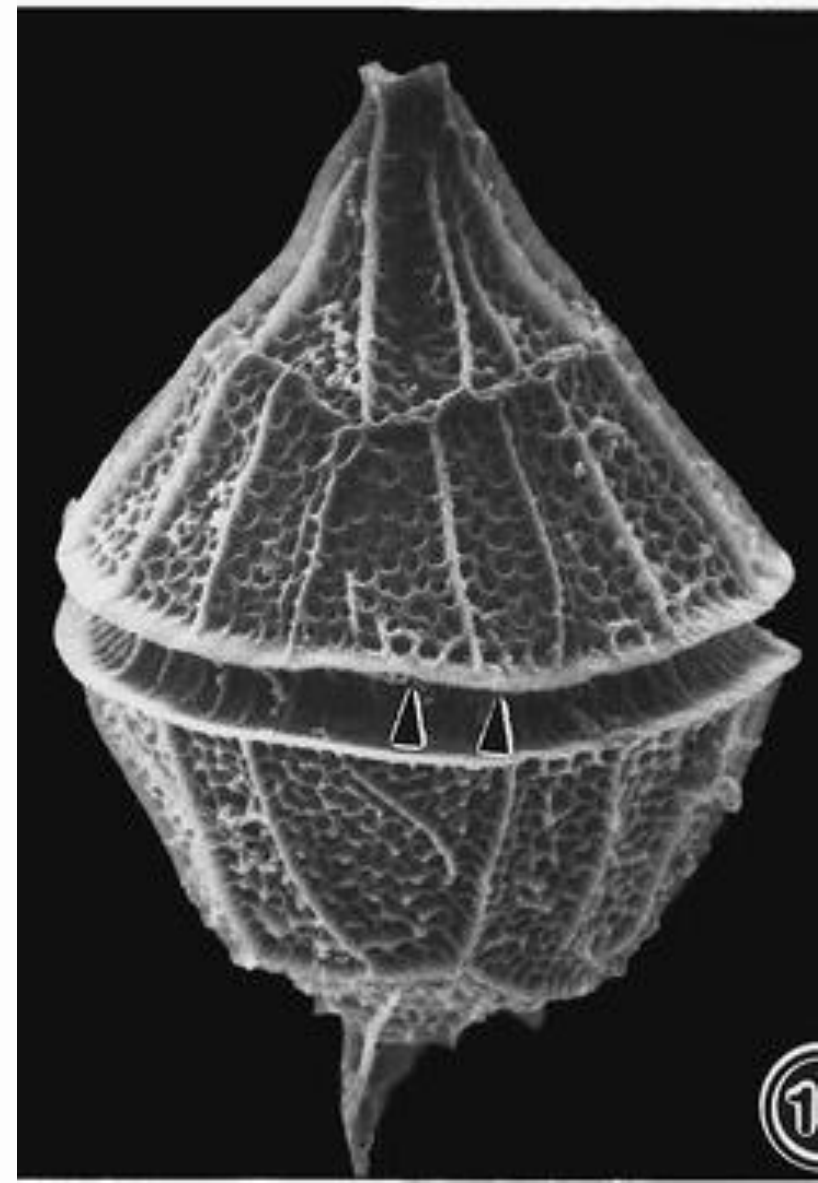
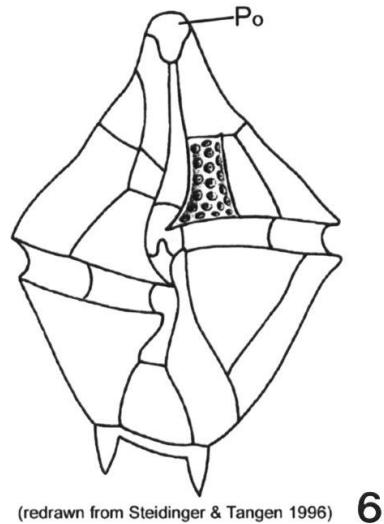
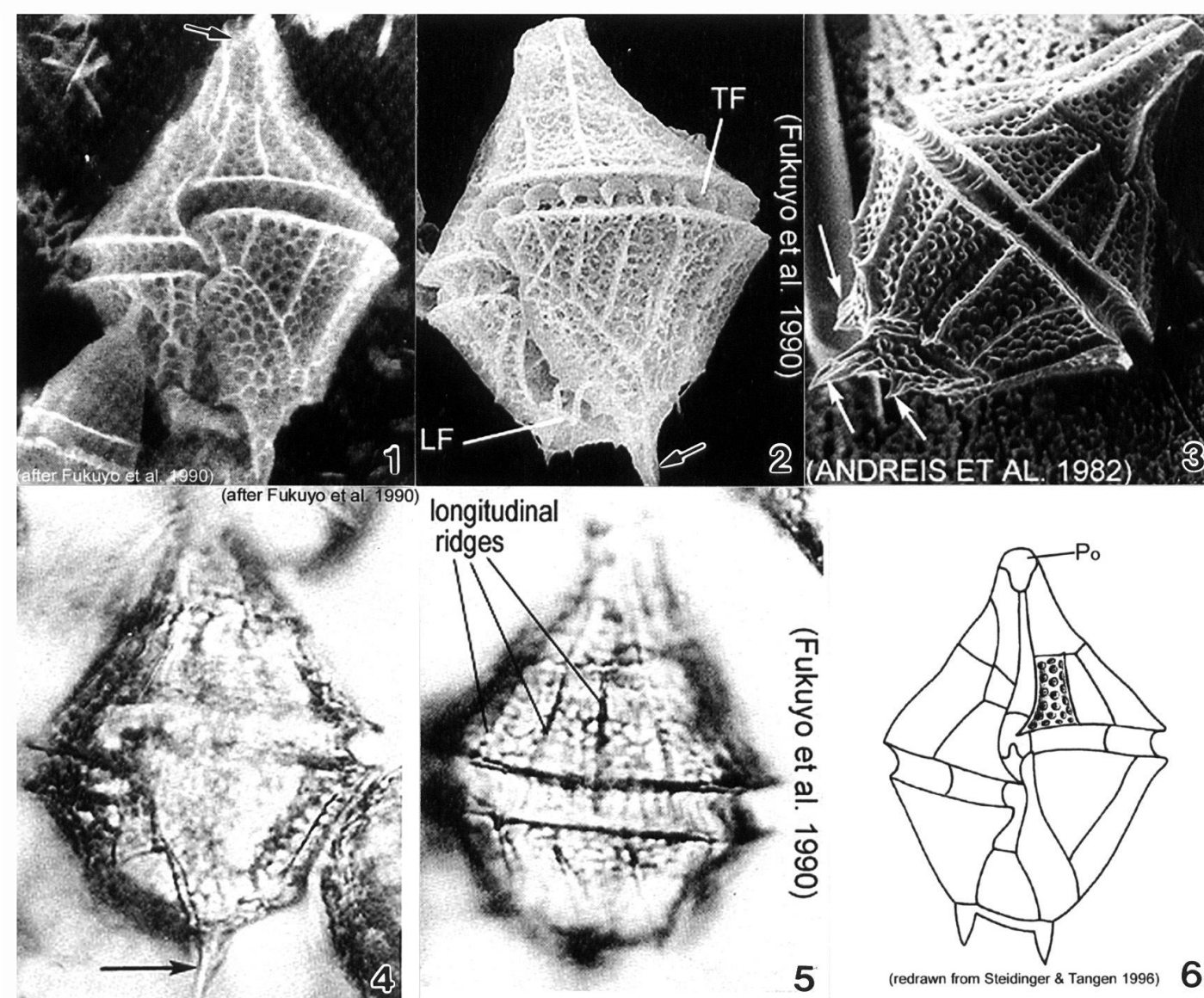
T. macroceros

Triplos (M)



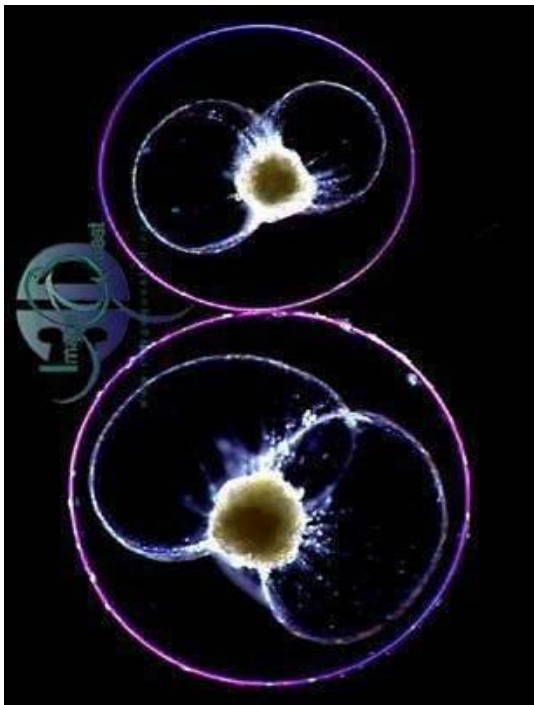
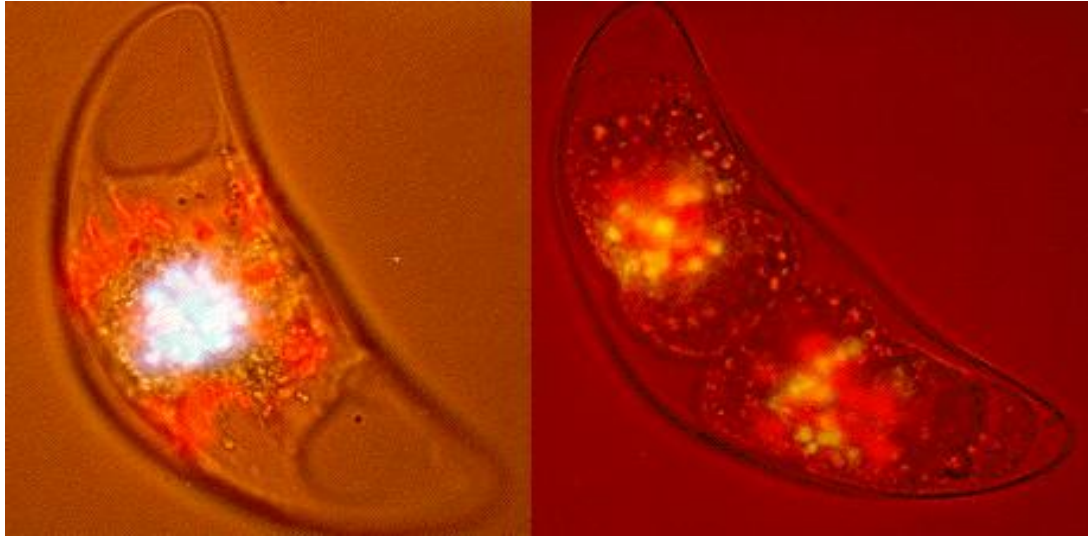
Gonyaulax (F, M)

thick, ornamented plates, species determined according to the hypotheca morphology, hard to determine particular species



Pyrocystis ^(M)

bioluminescence



Pyrocystis noctiluca



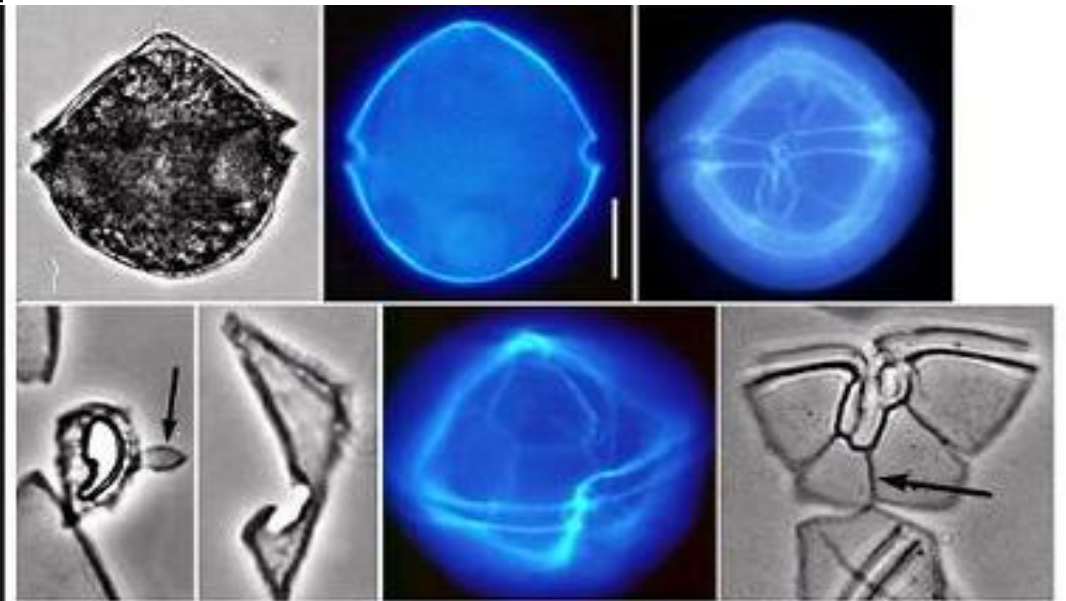
Pyrocystis fusiformis

Alexandrium ^(M)

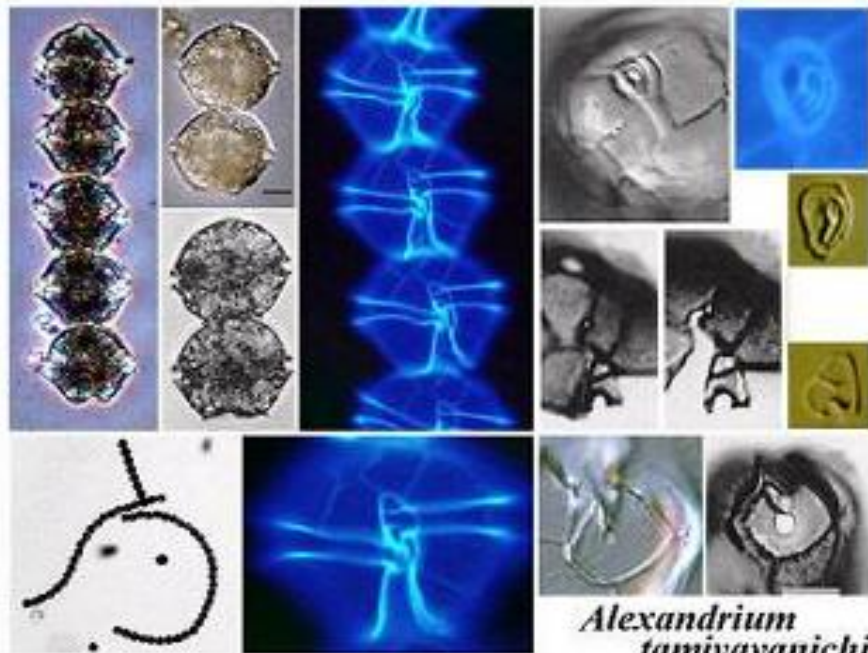
thin plates, pore at 1' plate, often filamentous



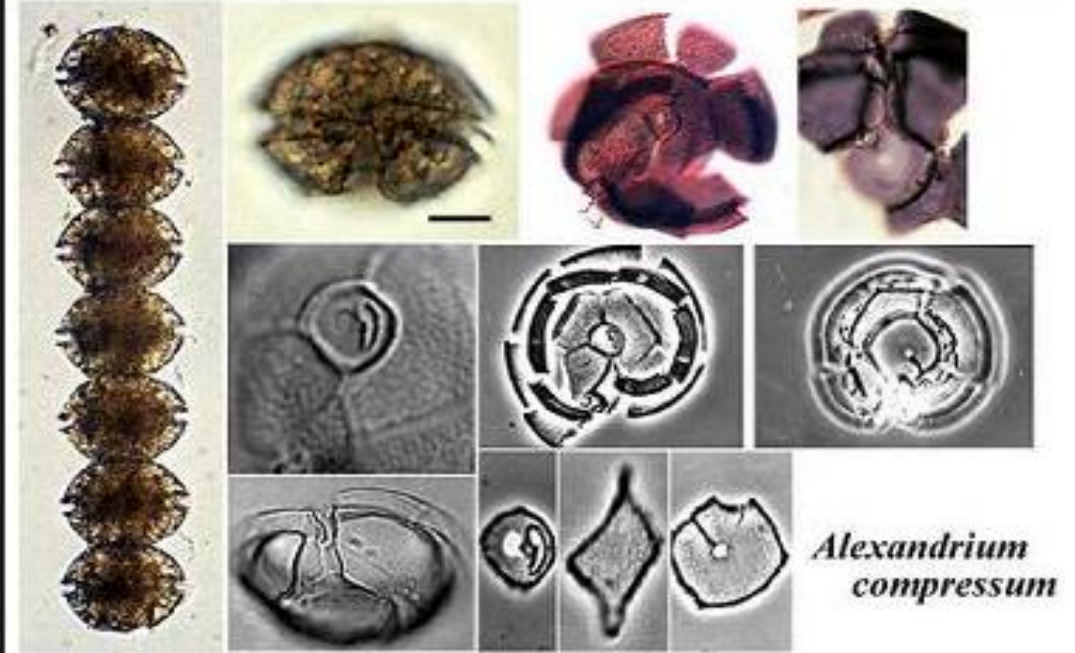
Alexandrium fraterculus



Alexandrium ostenfeldii



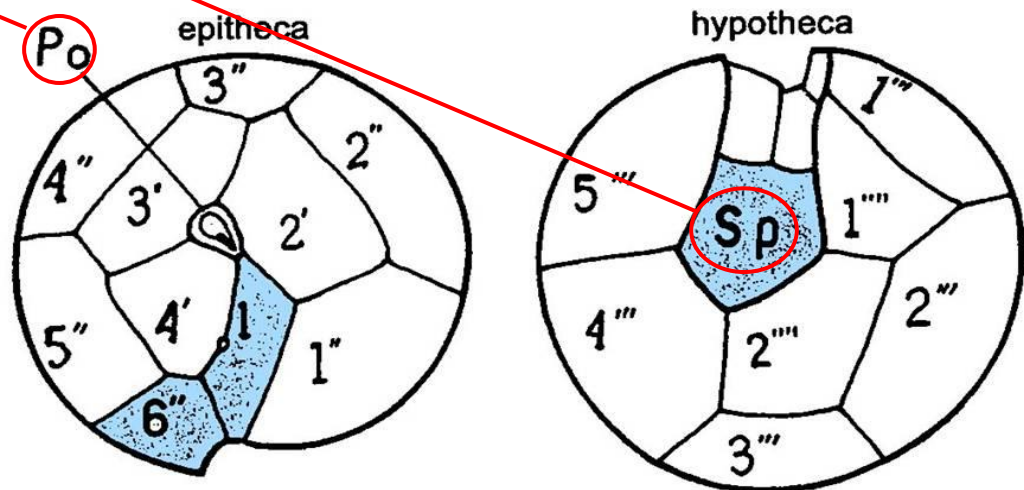
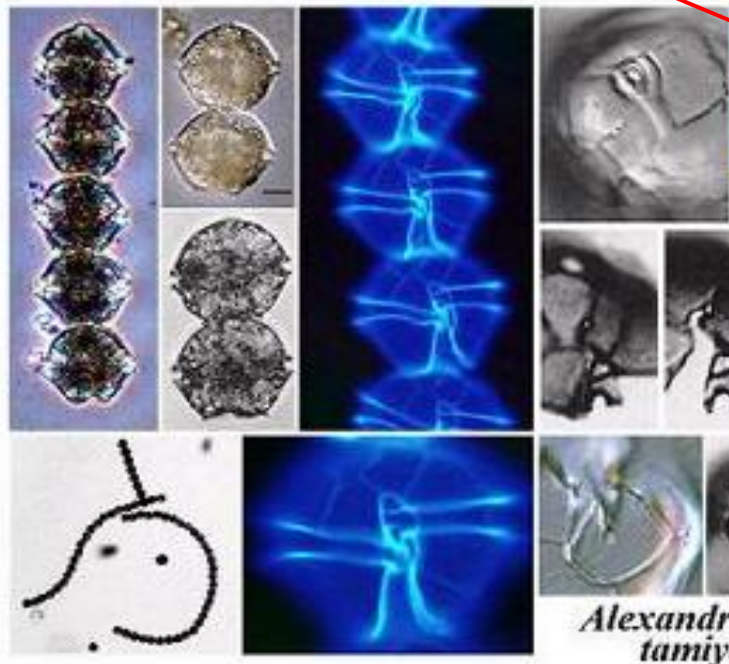
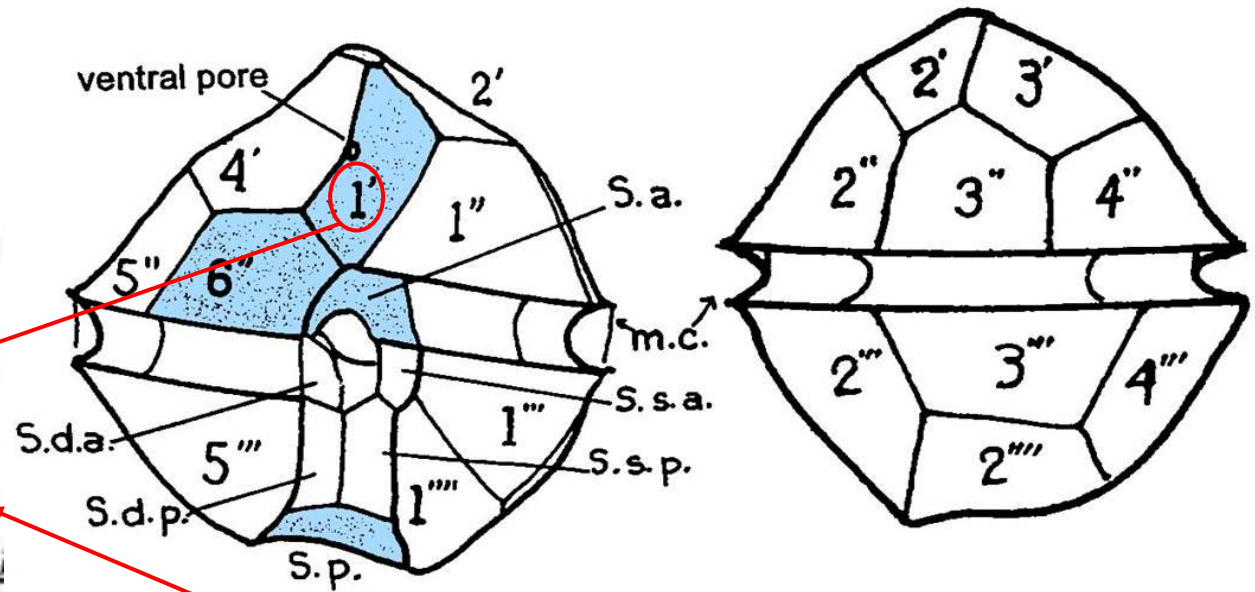
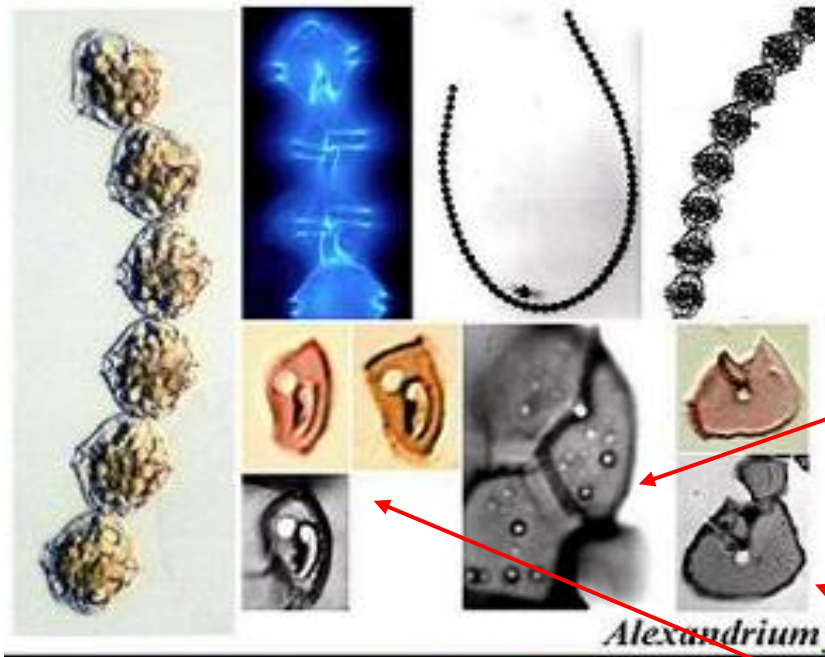
Alexandrium tamiyavanichii



Alexandrium compressum

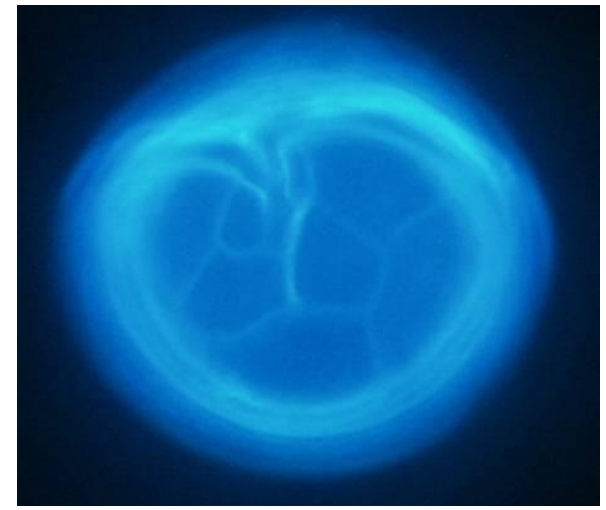
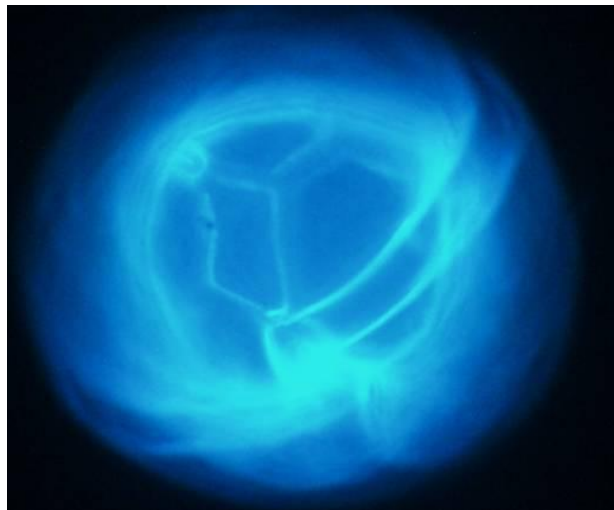
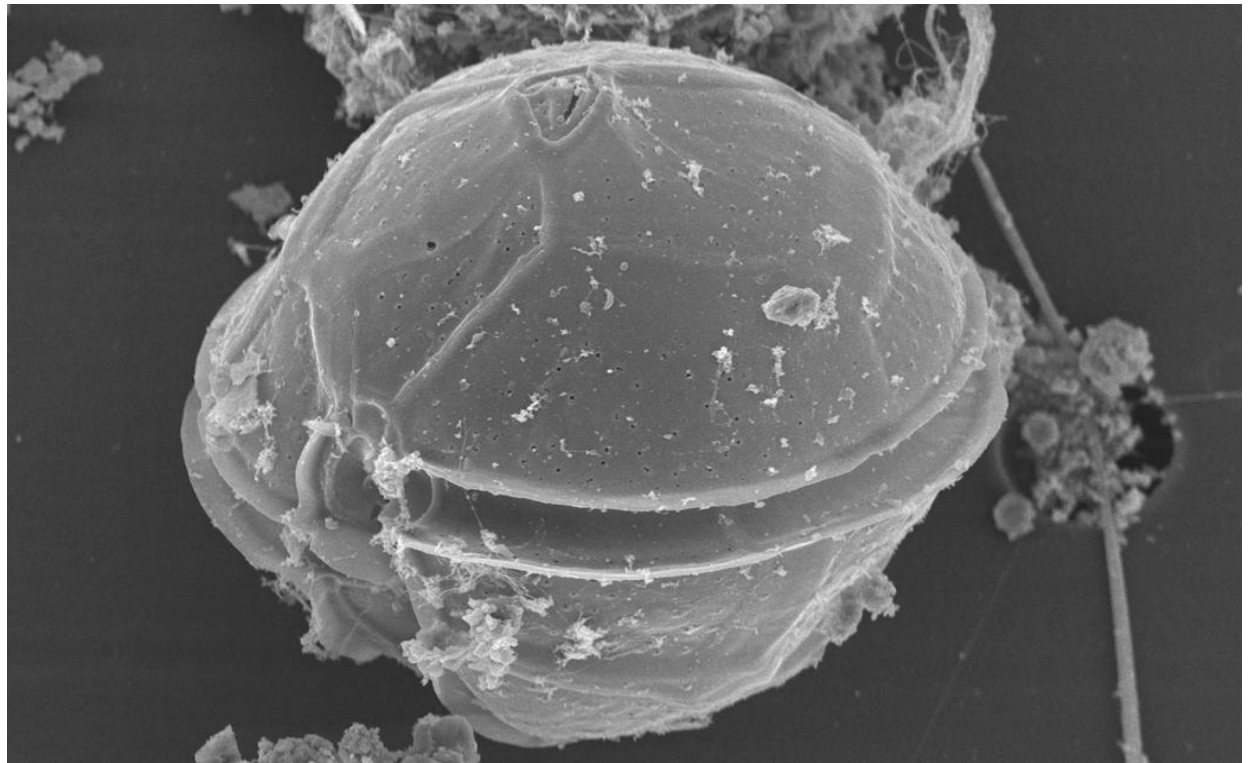
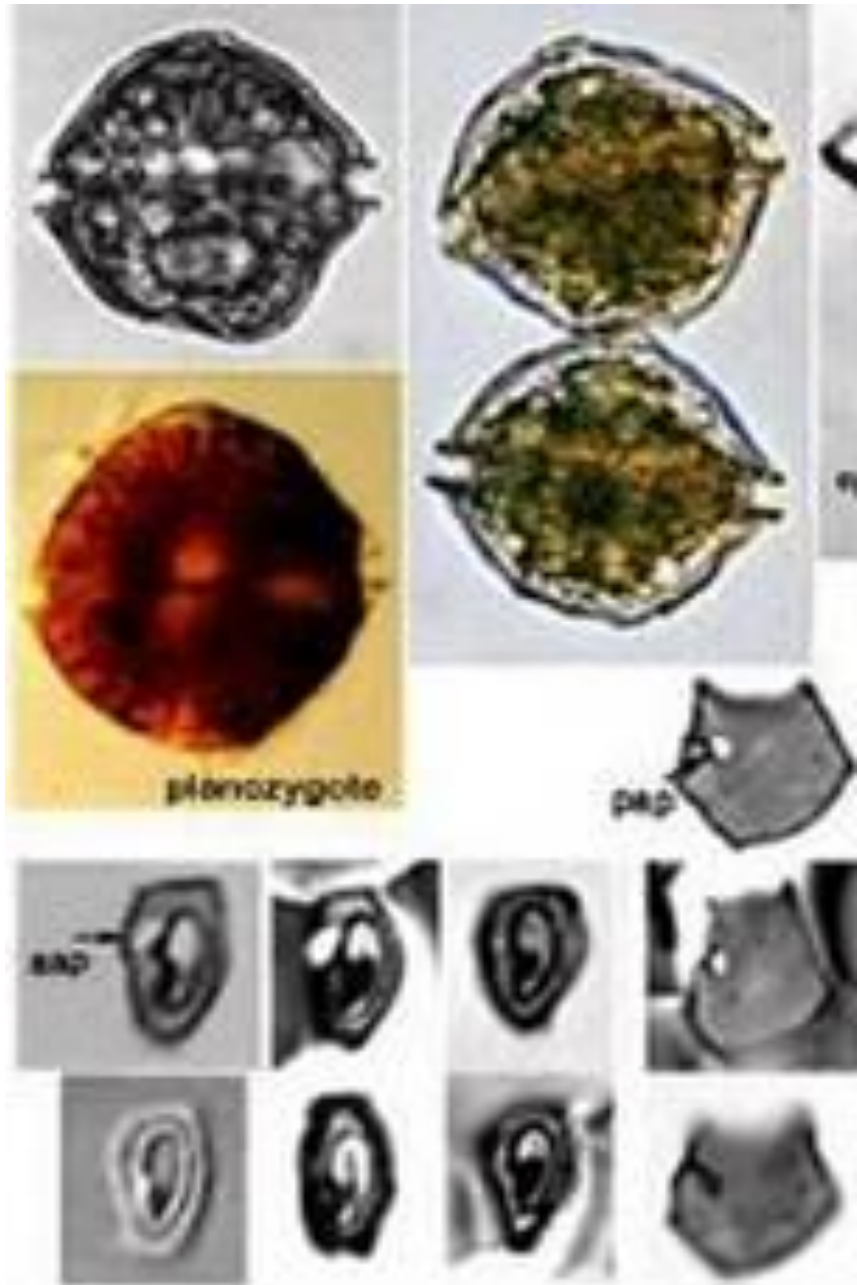
Alexandrium (M)

thin plates, pore at 1' plate, often filamentous



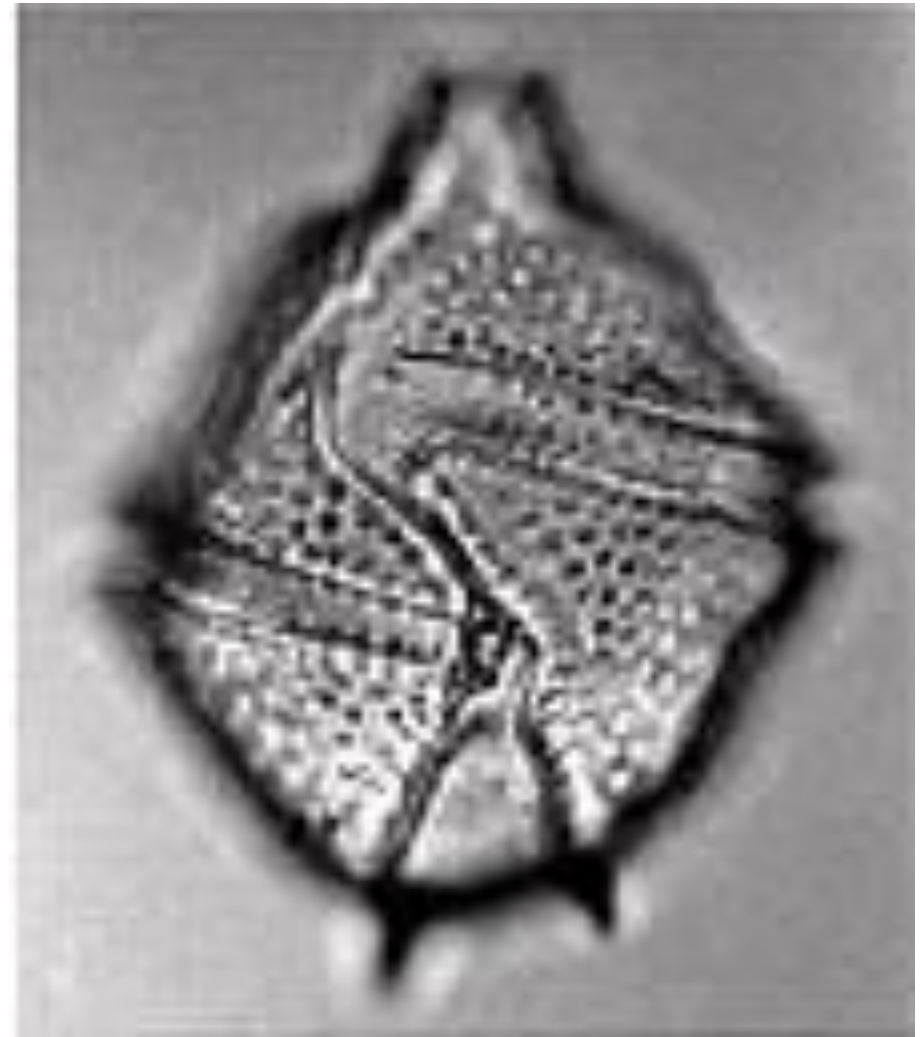
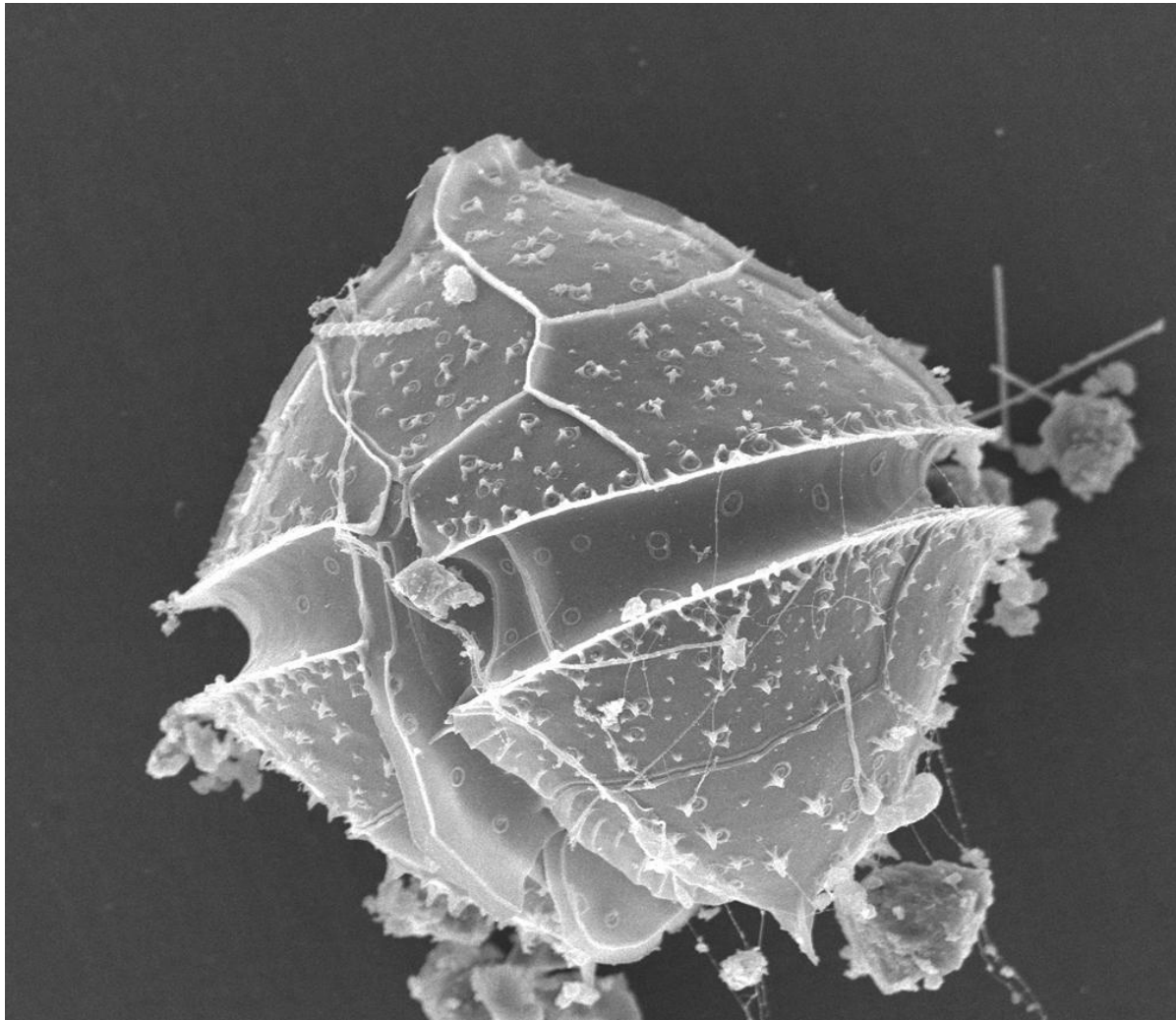
Alexandrium tamarense (M)

toxic species (PSP)



Peridinales

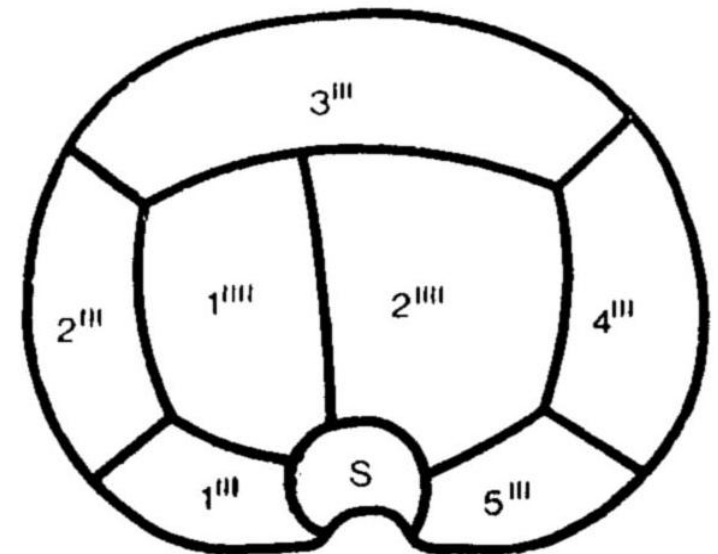
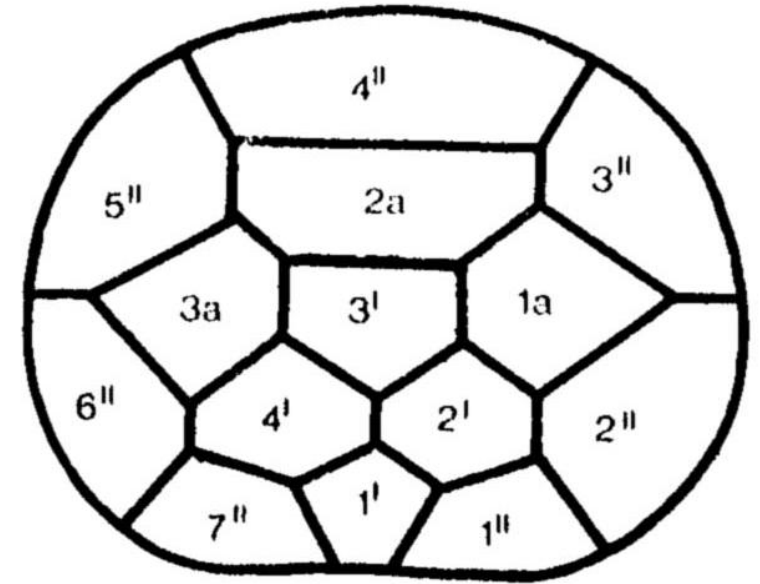
- flagellates, mostly dorsiventrally flattened cells
- polygonal plates, sulcus + cingulum
- marine and freshwater species



Peridinium (F)

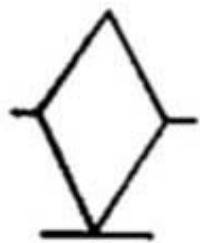
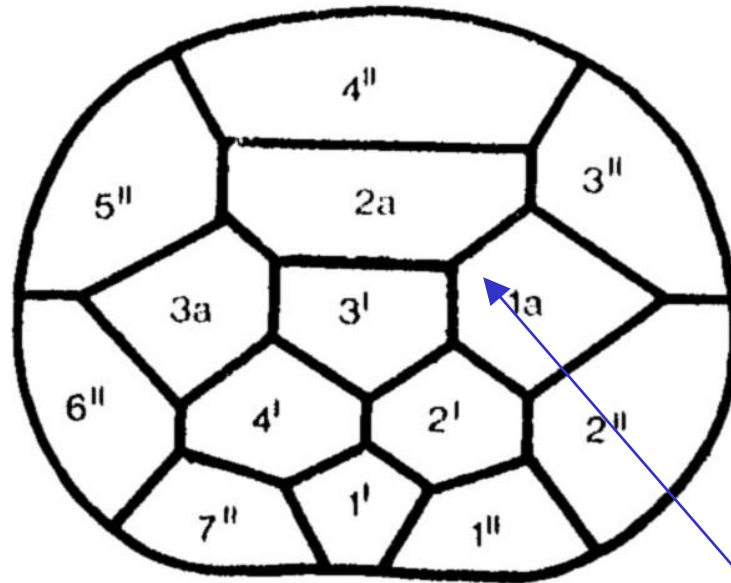
formula 4', 2a-3a, 7'', 5''', 2''''

- autotrophic, freshwater, 5-6 cingular plates

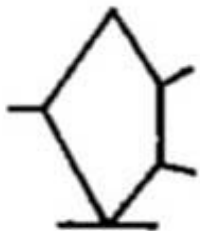


Peridinium (F)

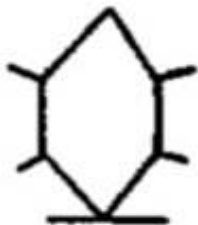
shapes of relevant plates



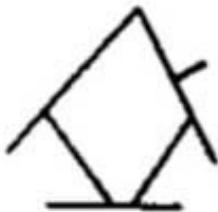
ortho



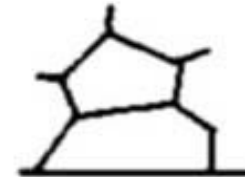
meta



para



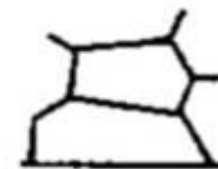
quadra



penta

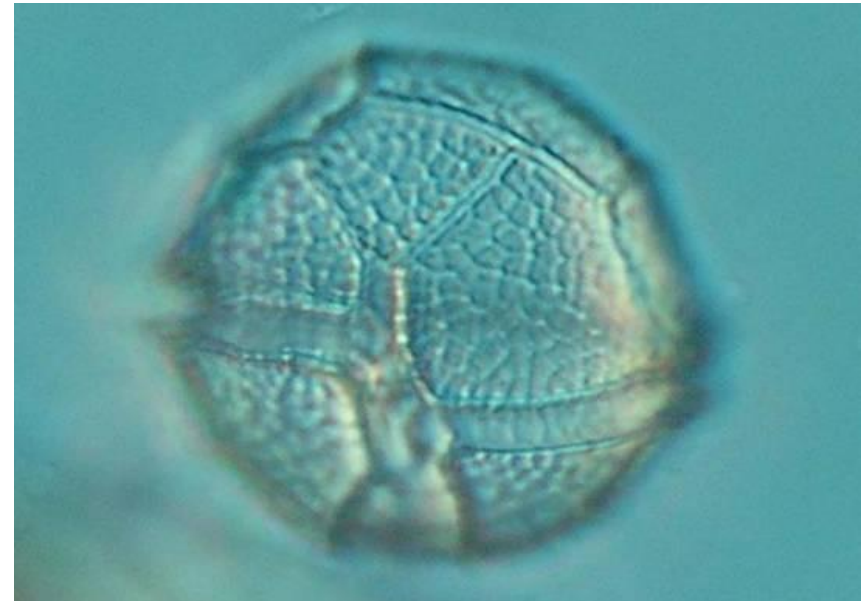
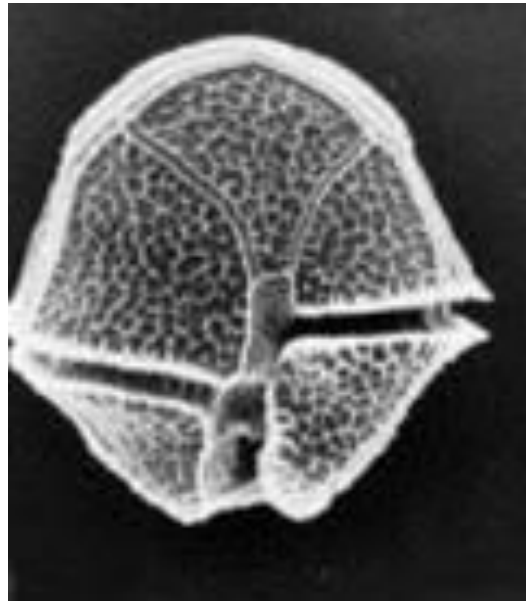
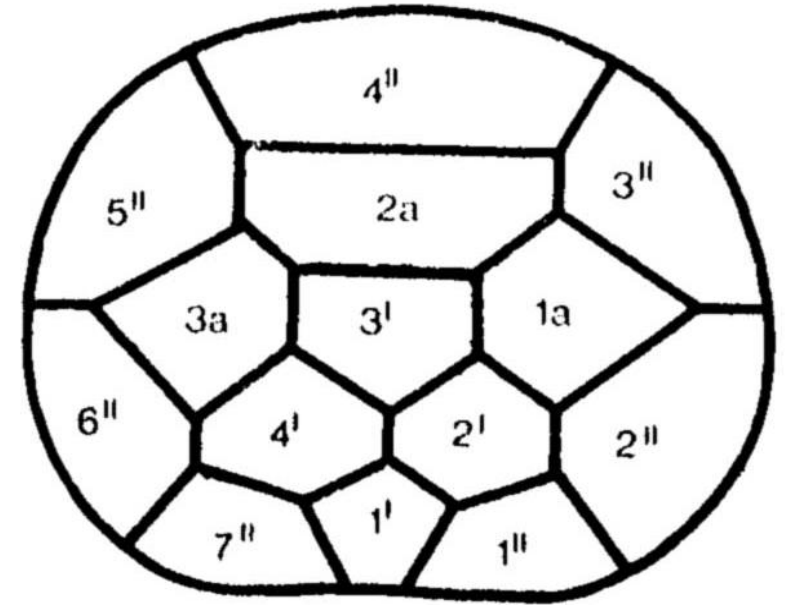


hexa



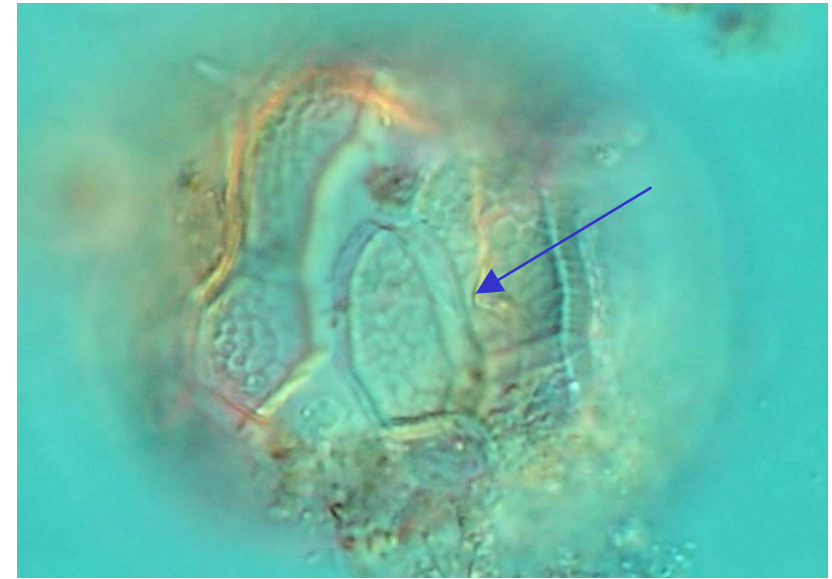
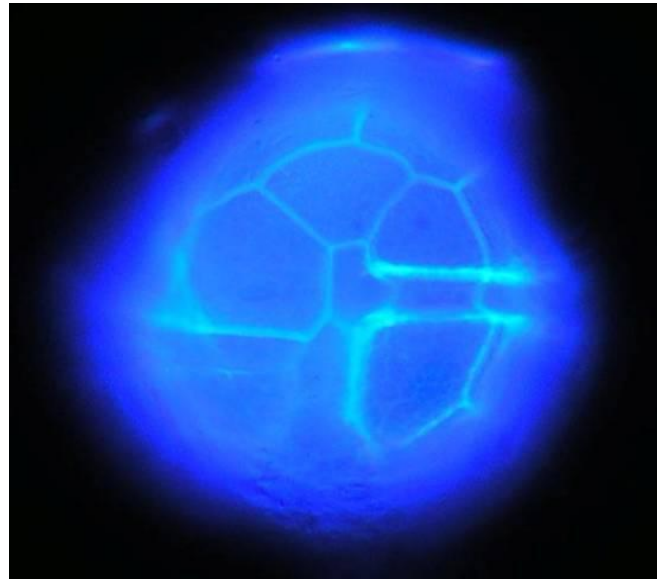
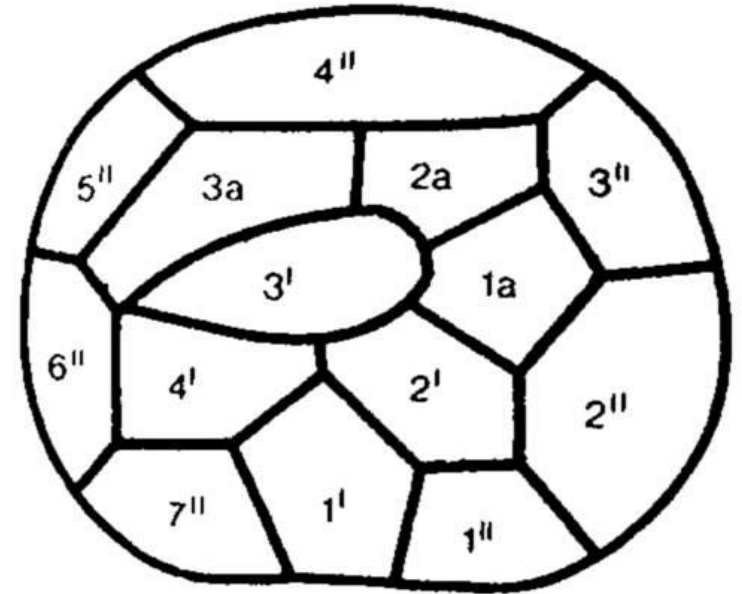
Peridinium (F)

Peridinium willei – no pore, symmetrical plates



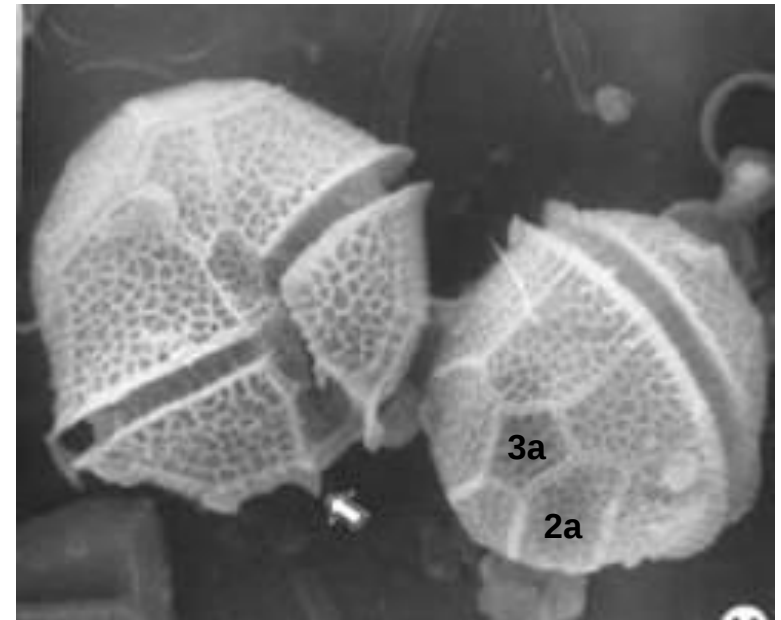
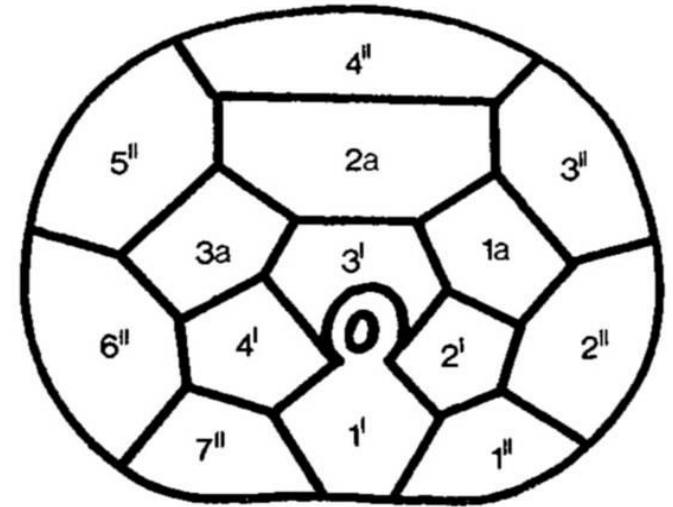
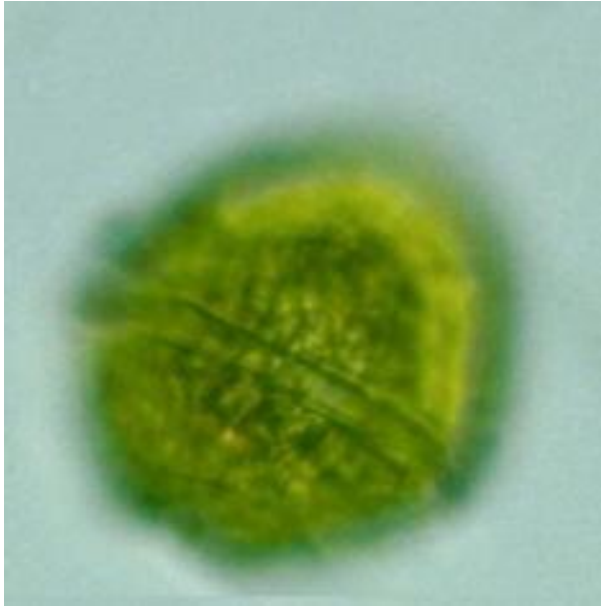
Peridinium ^(F)

Peridinium cinctum – typical shape of 3' plate



Peridinium (F)

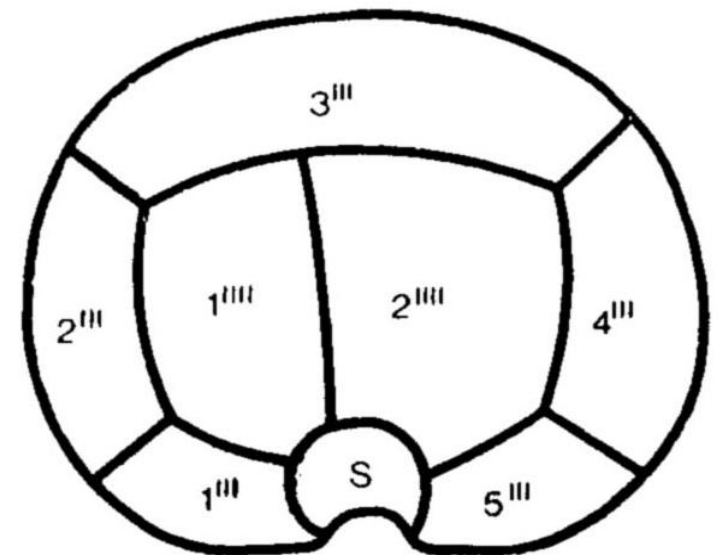
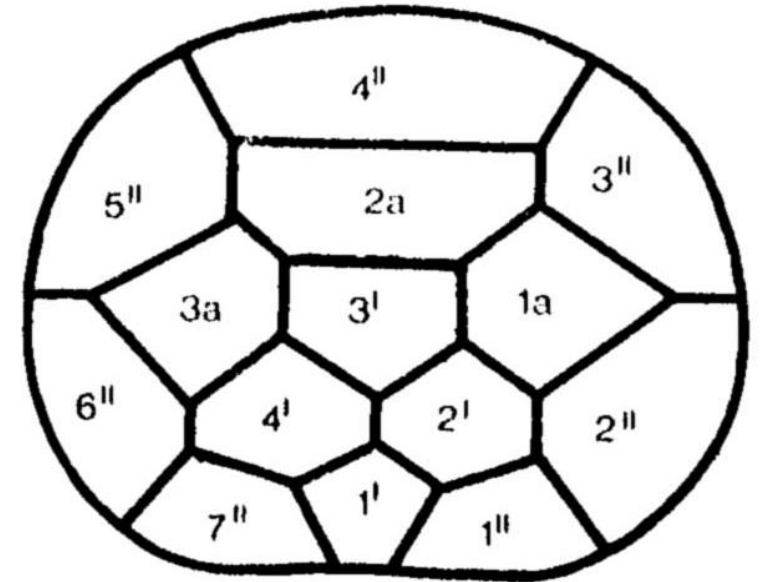
Peridinium bipes – pore, symmetrical plates



Protoperidinium ^(M)

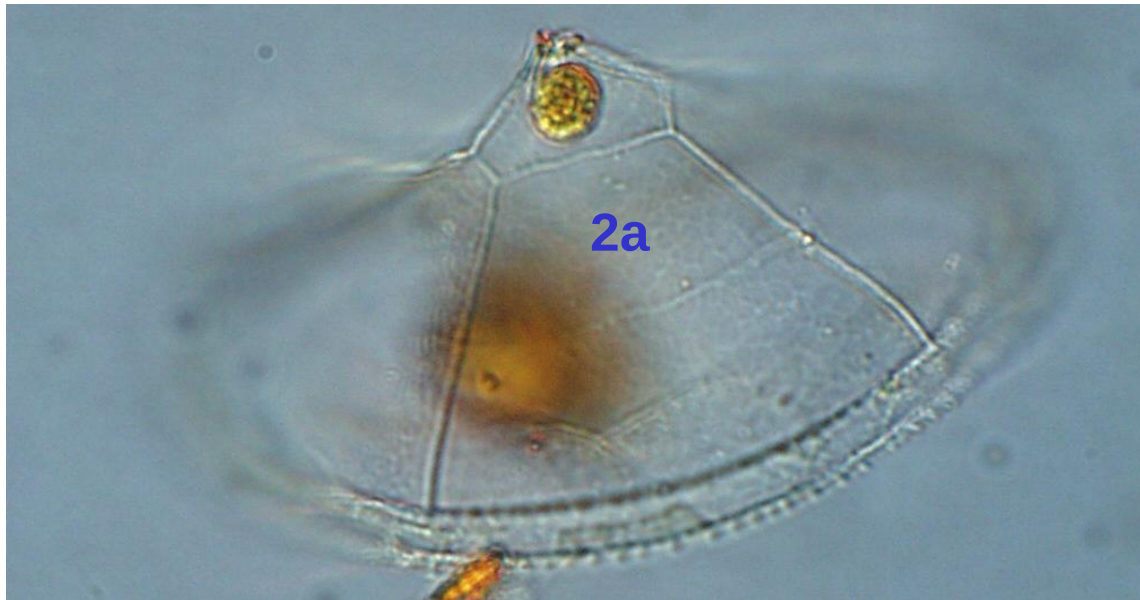
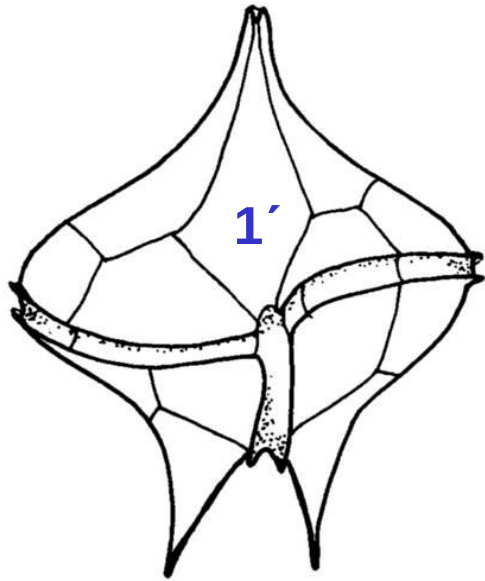
formula 4', 3a, 7'', 5''', 2''''

- heterotrophic, marine, only 3 cingular plates



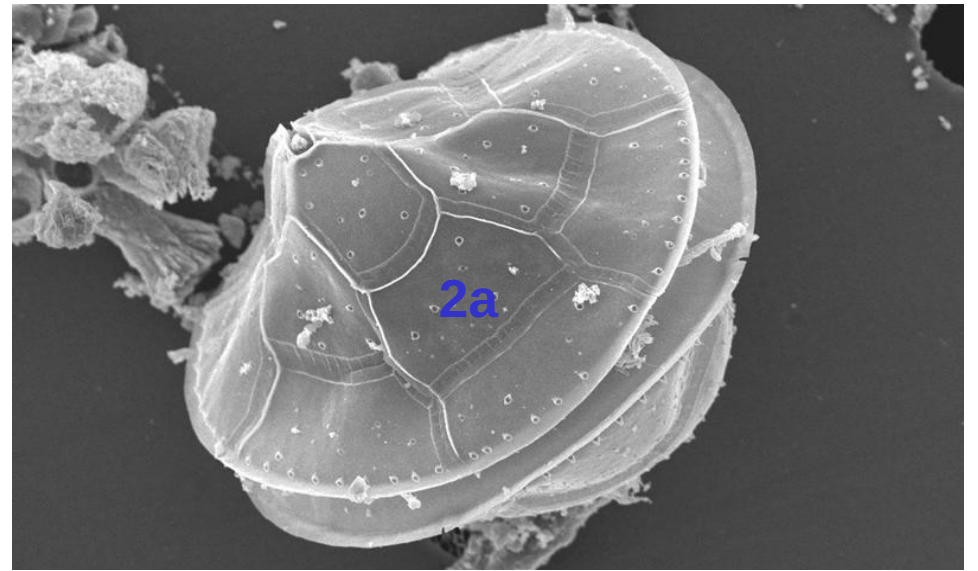
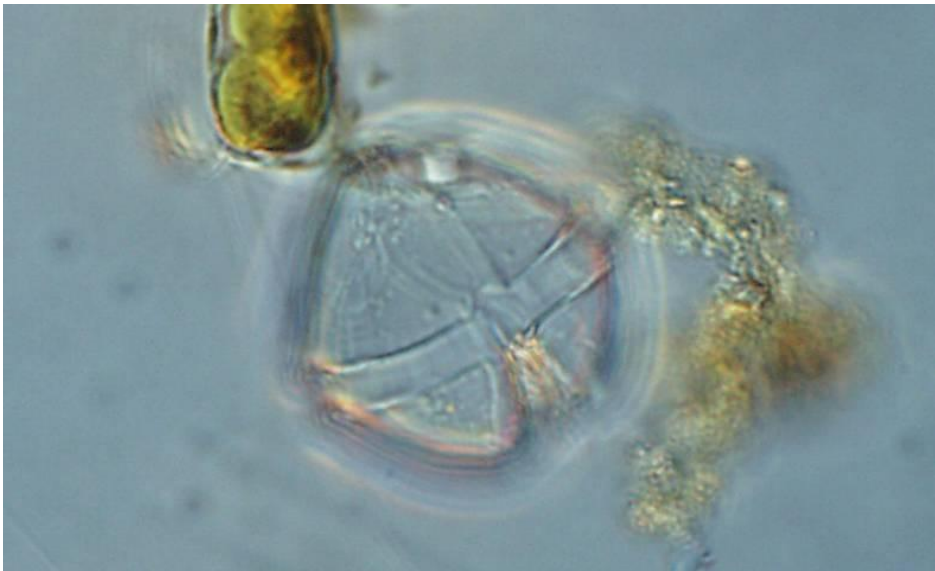
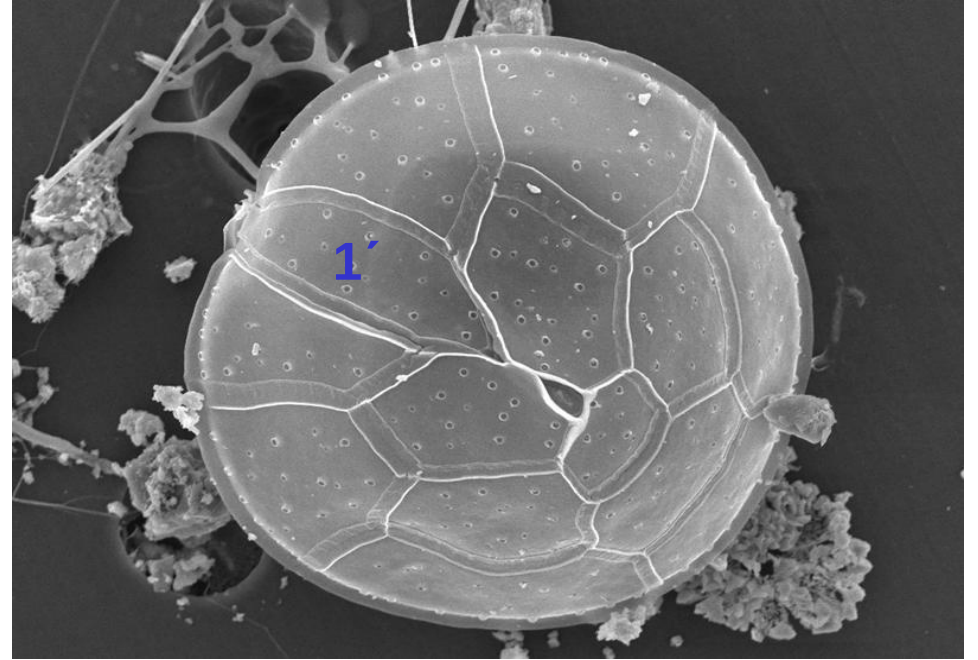
Protoperidinium (M)

Protoperidinium depressum – 1' ortho, 2a quadra



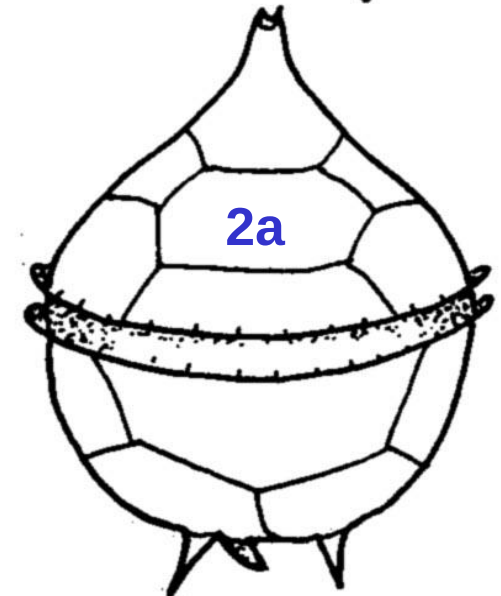
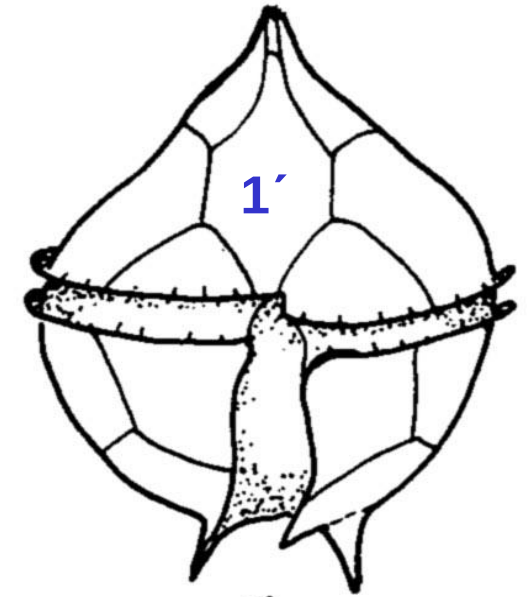
Protoperidinium ^(M)

Protoperidinium achromaticum – 1' ortho, 2a hexa



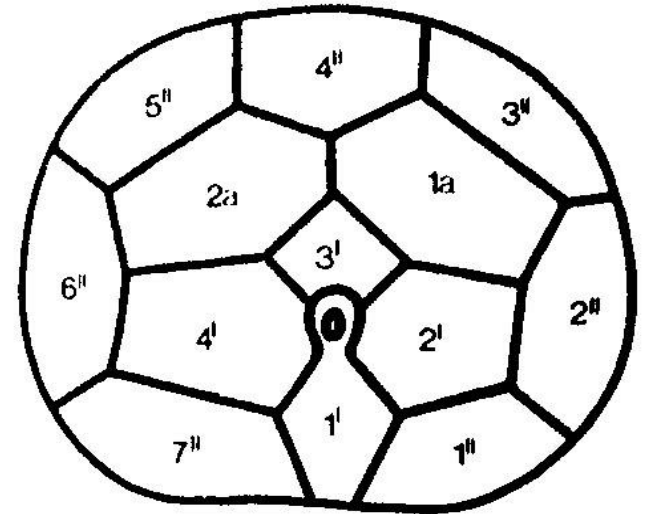
Protoperidinium ^(M)

Protoperidinium pellucidum – 1' para, 2a hexa

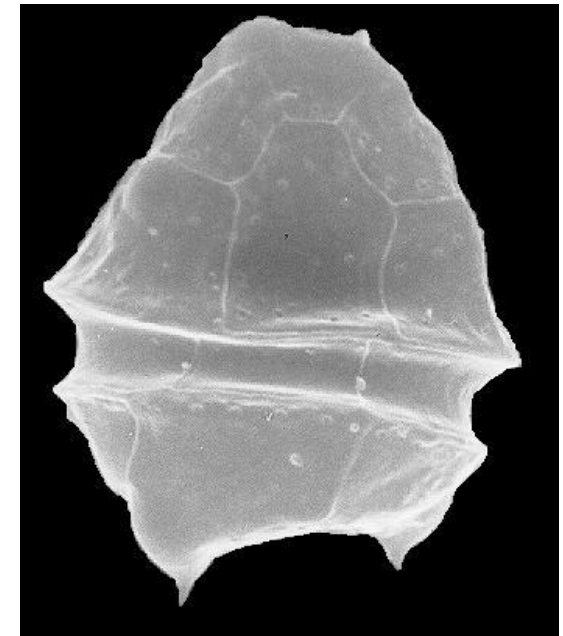
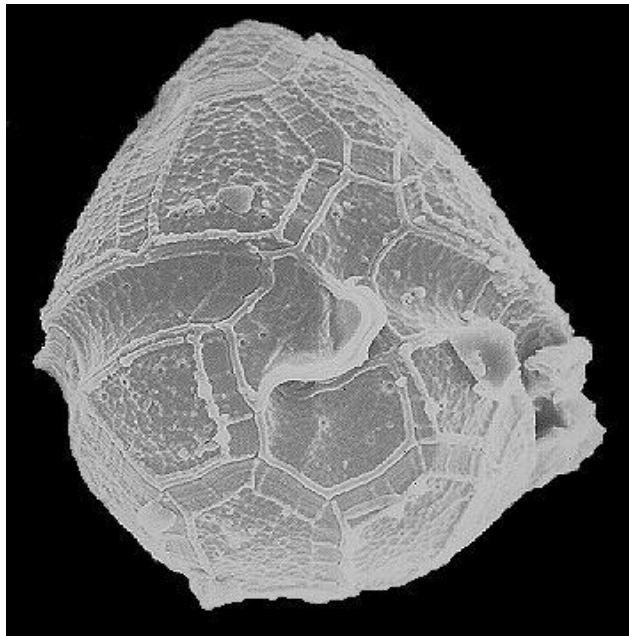


Parvodinium (F)

formula 4', 2a, 7'', 5''', 2''''', apical pore

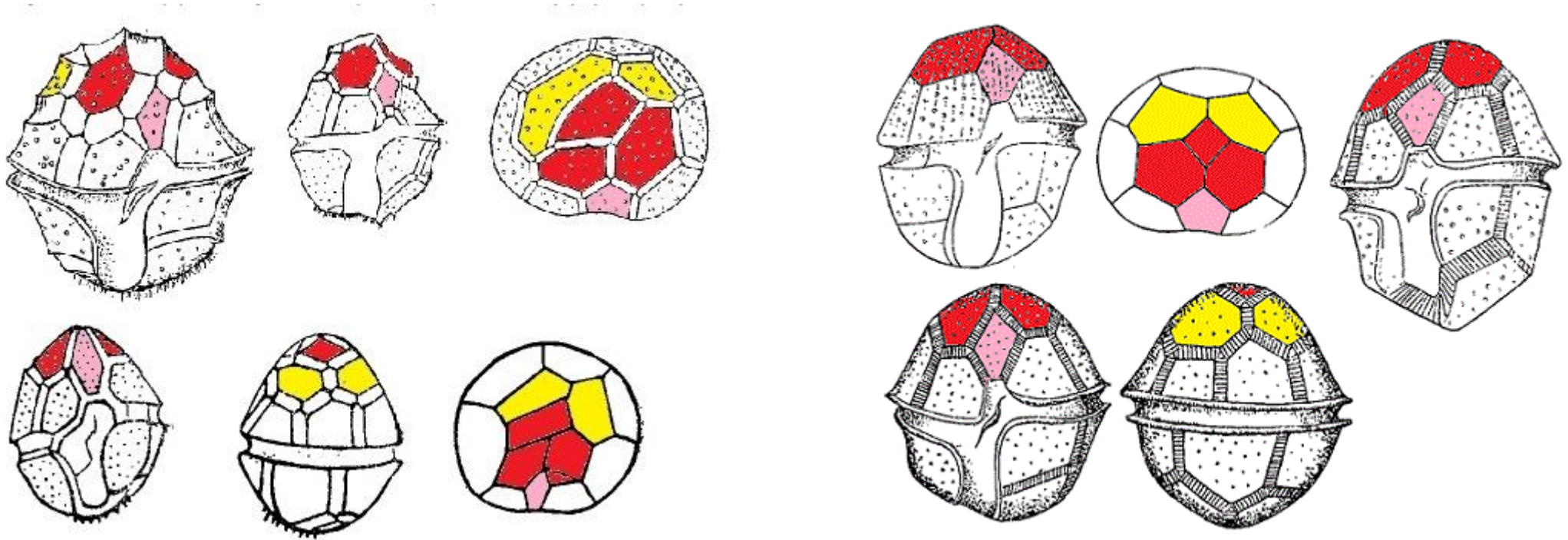


Parvodinium umbonatum



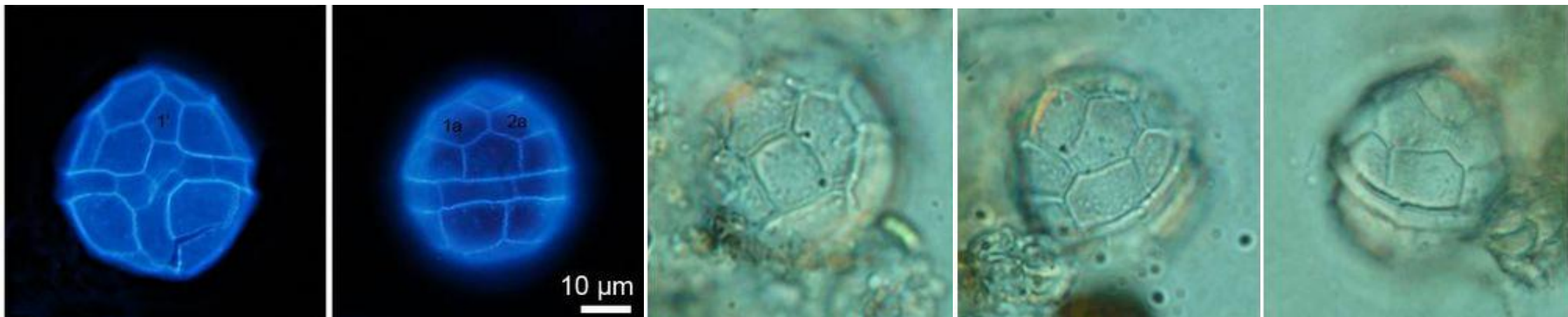
Palatinus (F)

formula 4', 2a, 7'', 5''', 2''''', no apical pore



Palatinus apiculatus

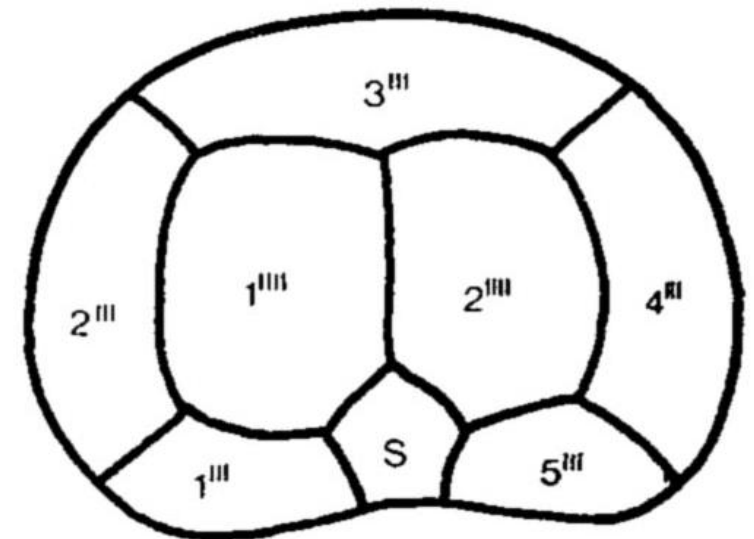
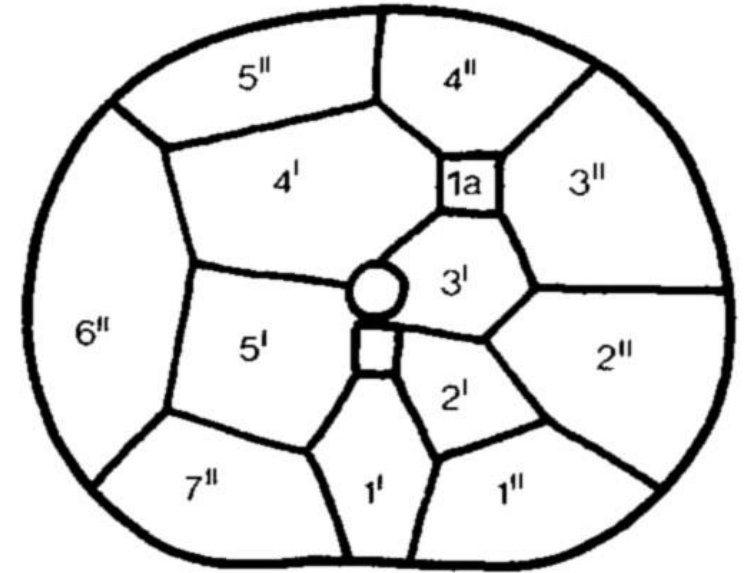
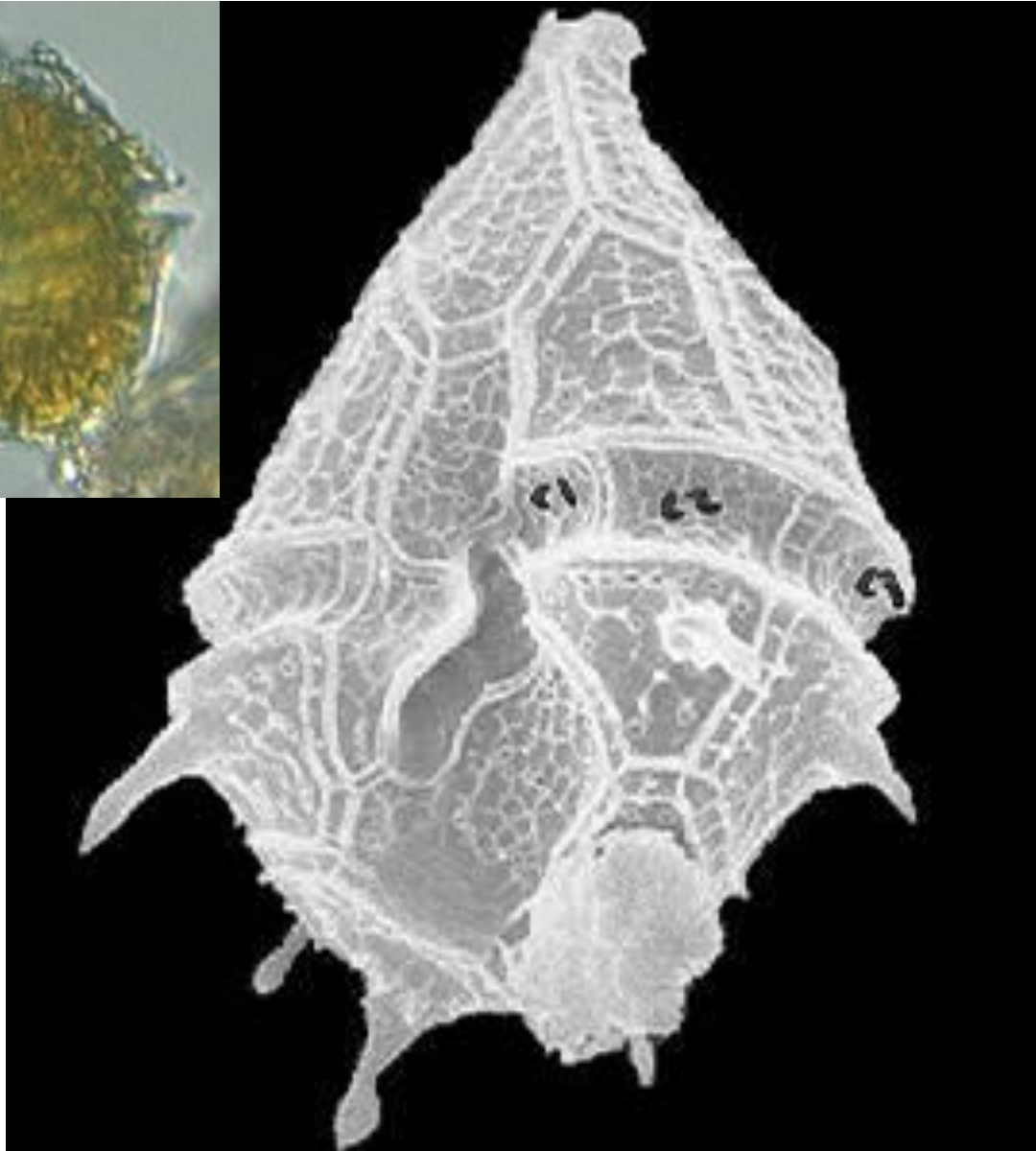
Palatinus pseudolaewis



Peridiniopsis (F)

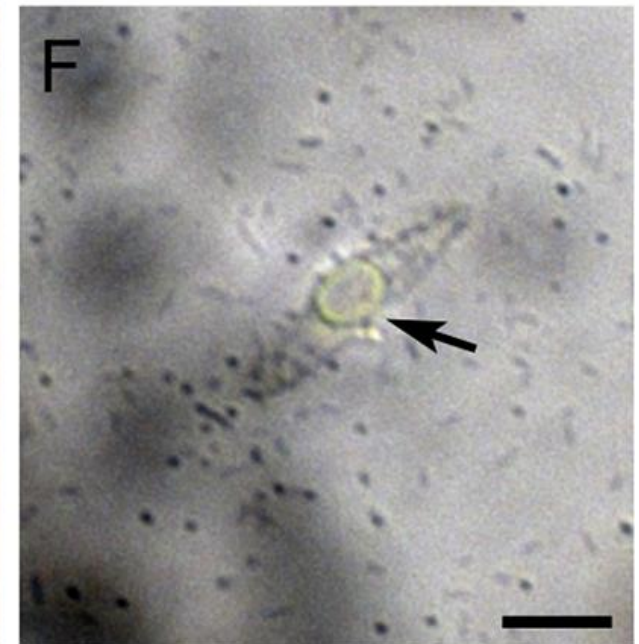
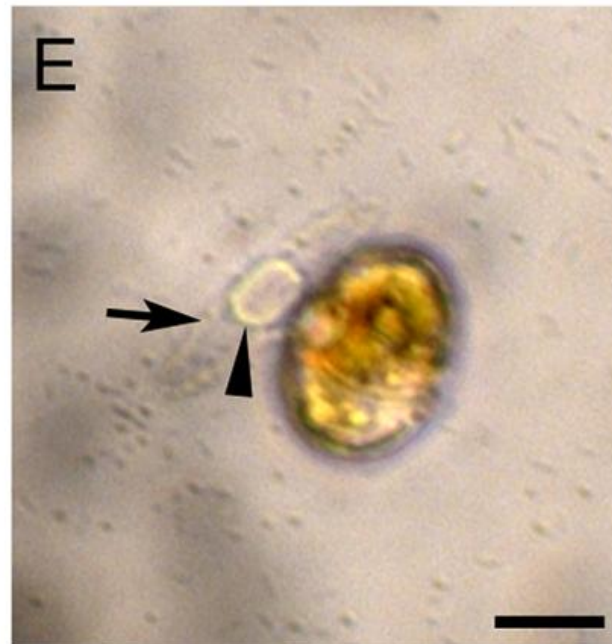
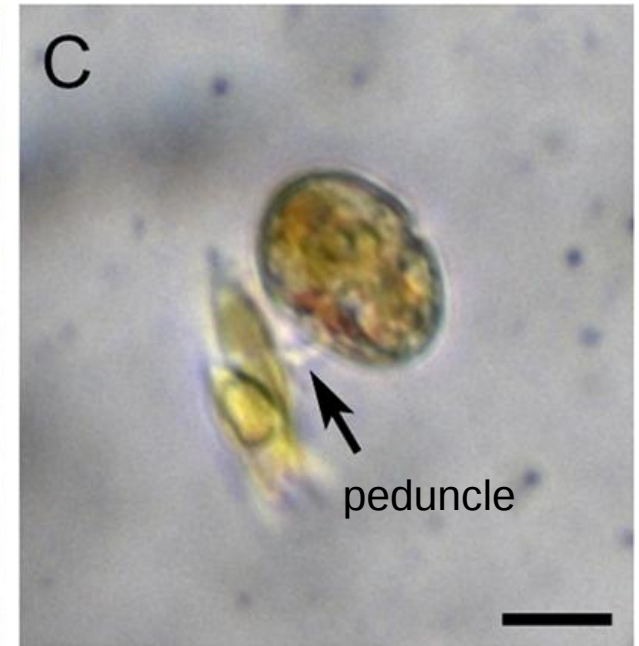
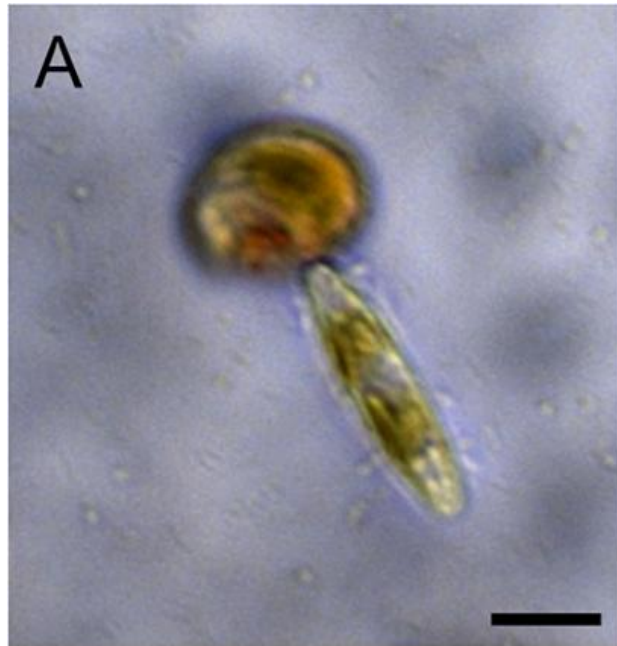
formula 3-5', 0a-1a, 6-8'', 5''', 2''''

- autotrophic, freshwater and brackish species



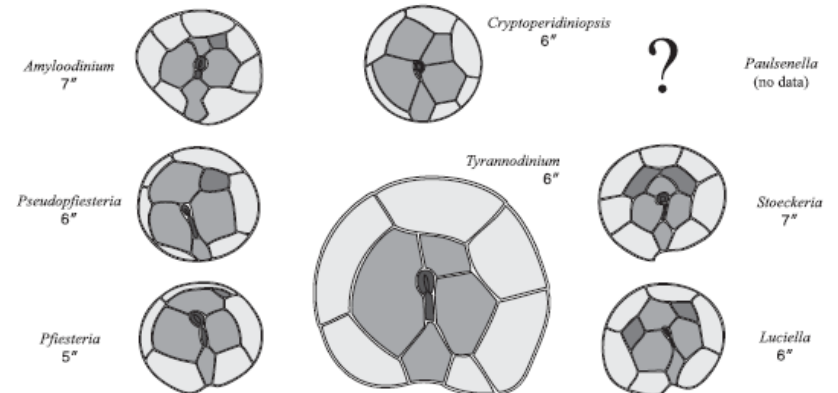
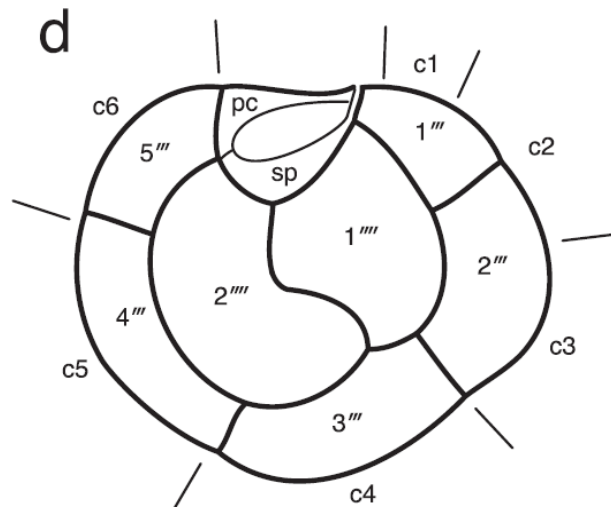
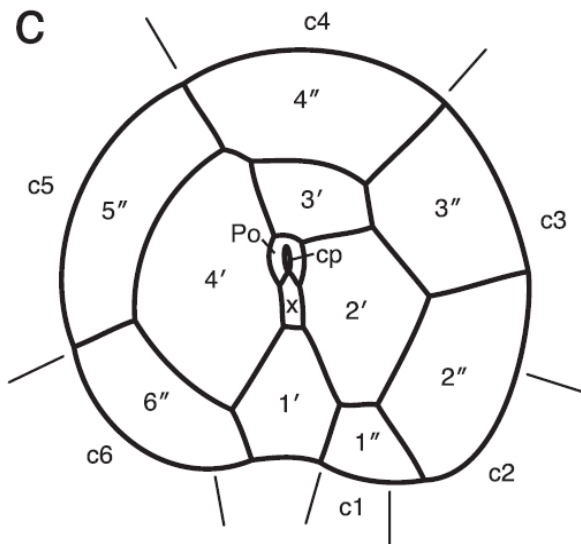
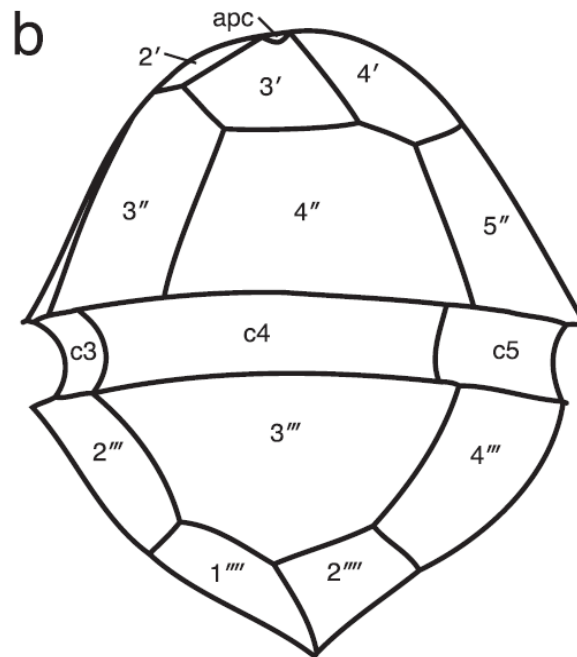
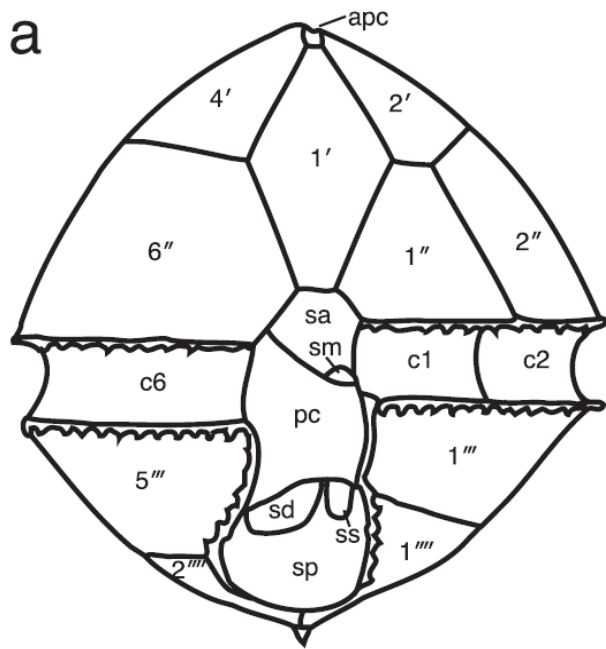
Unruhdinium, *Durinskia* (F,M)

chloroplast of diatom origin



Tyrannodinium (F)

freshwater, heterotrophic, with relatively thin theca

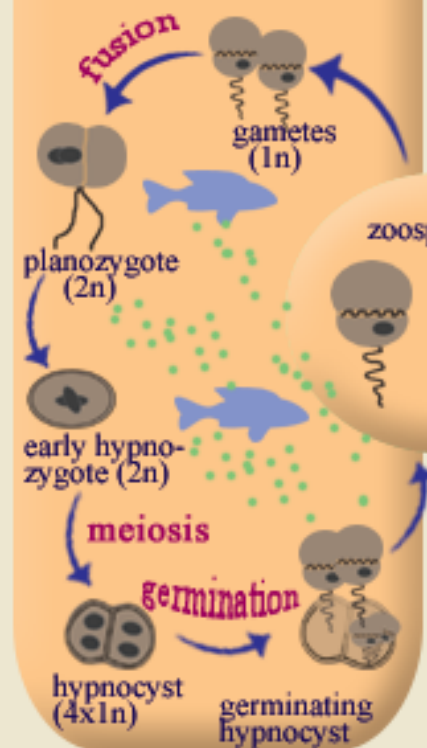


Pfiesteria piscicida (M)

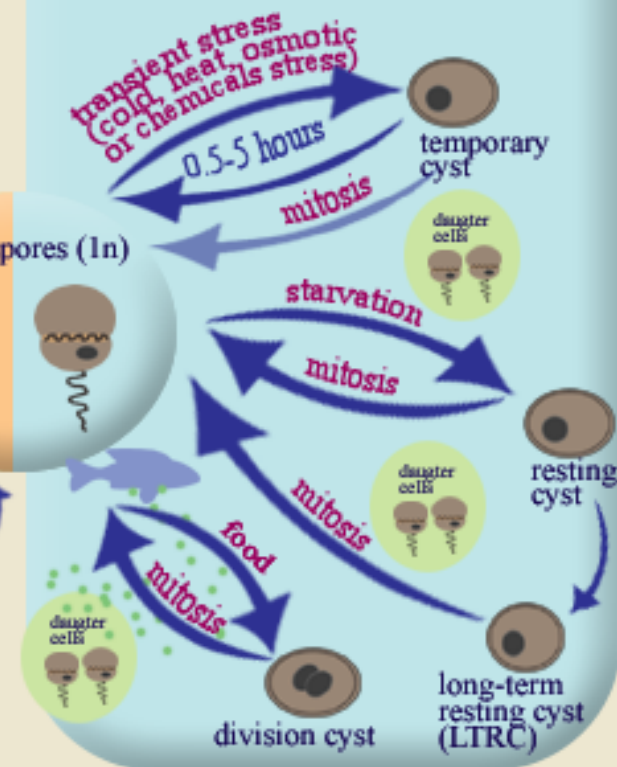
dangerous parasite of fish, toxin production

Reproduction of *Pfiesteria piscicida*

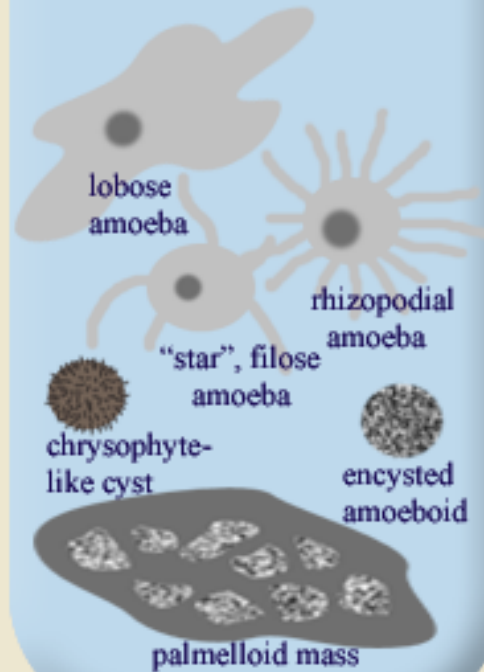
Sexual cycle



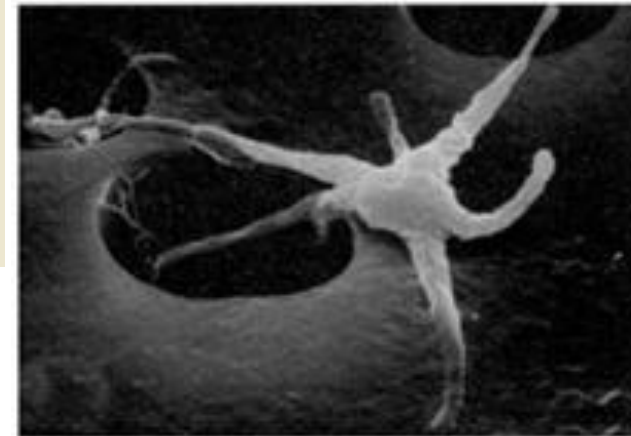
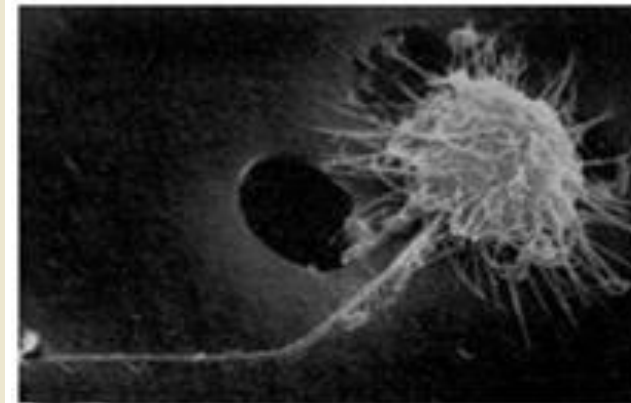
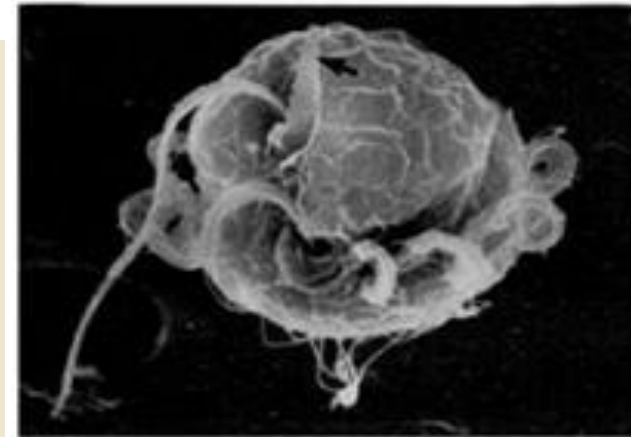
Asexual cycle



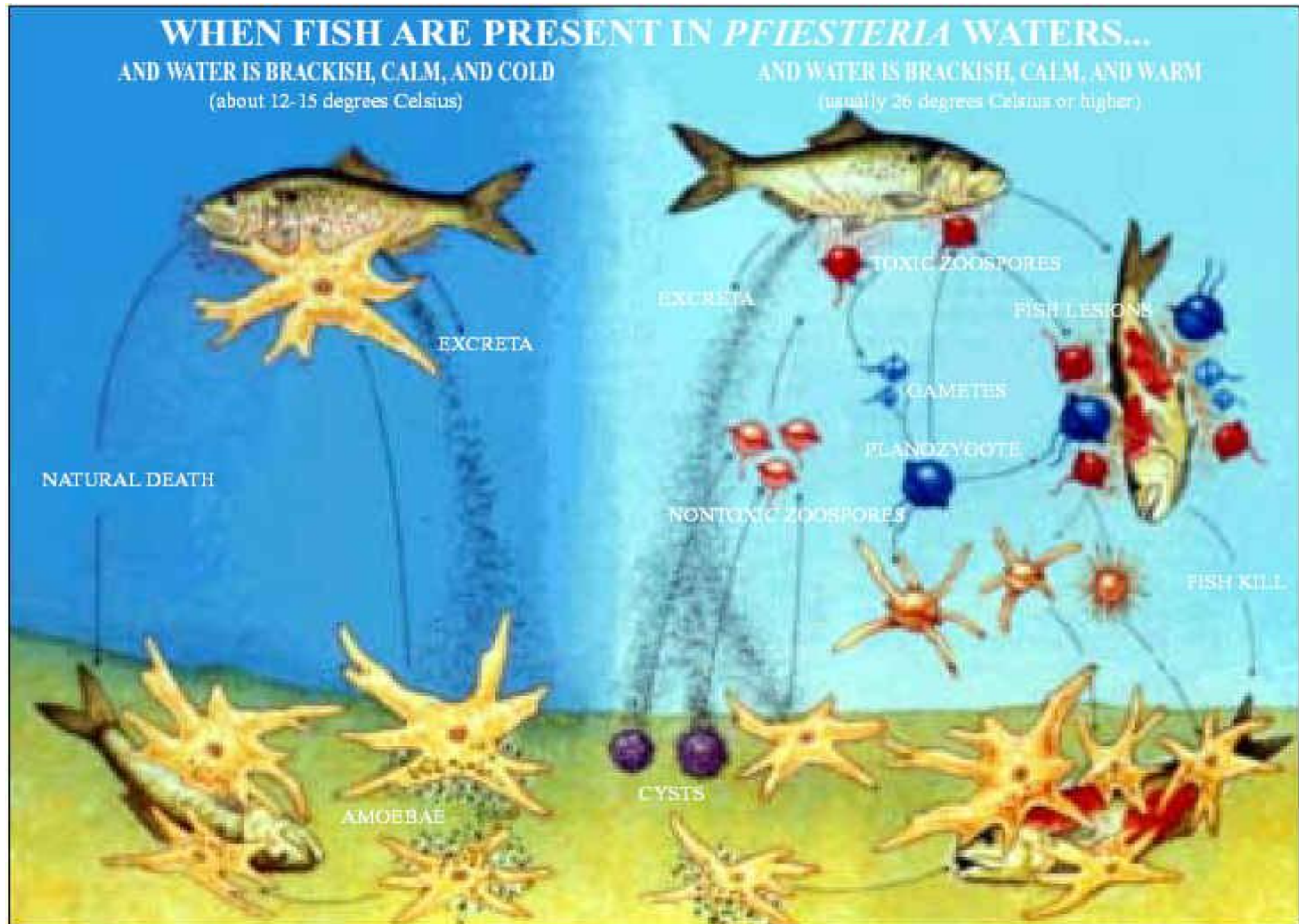
Some (not all) *Pfiesteria piscicida* (toxic strains) live forms postulated by Burkholder et al. (1997)



www.metapathogen.com



Pfisteria piscicida (M)



Pfisteria piscicida (M)

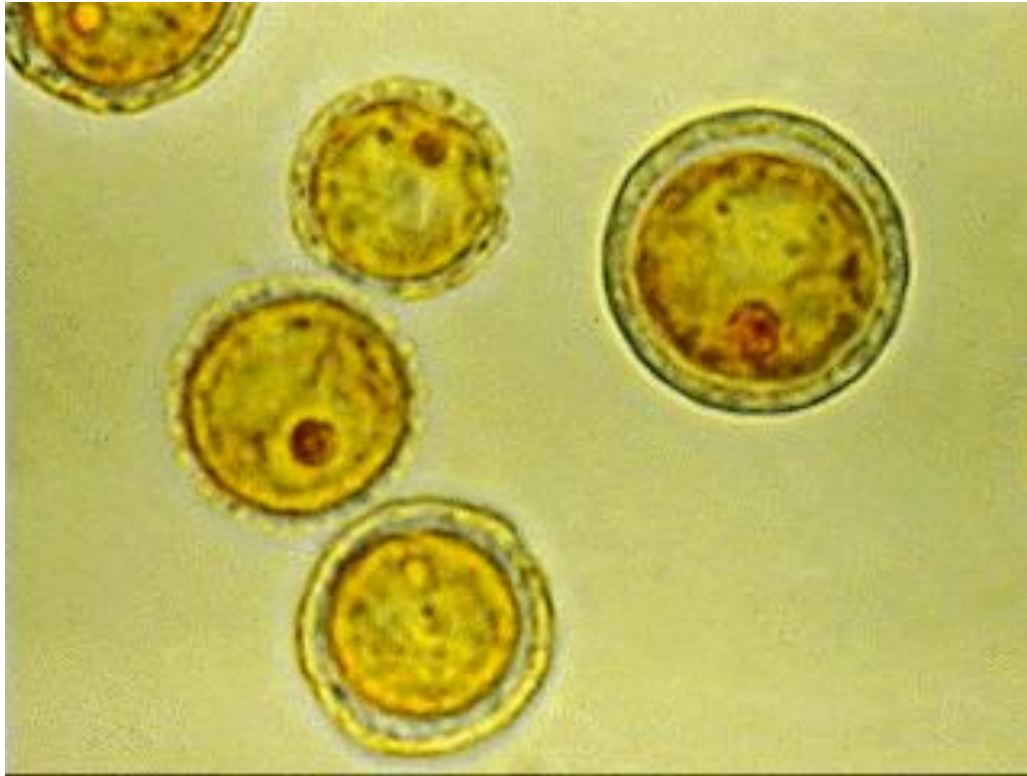


- blood lesions



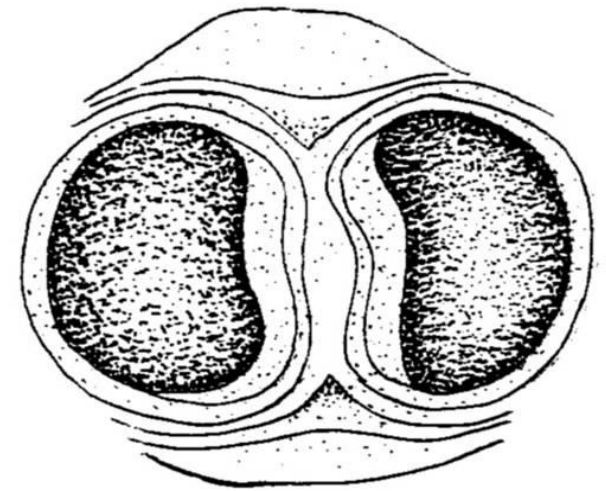
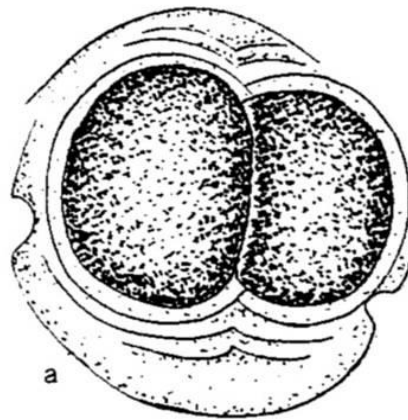
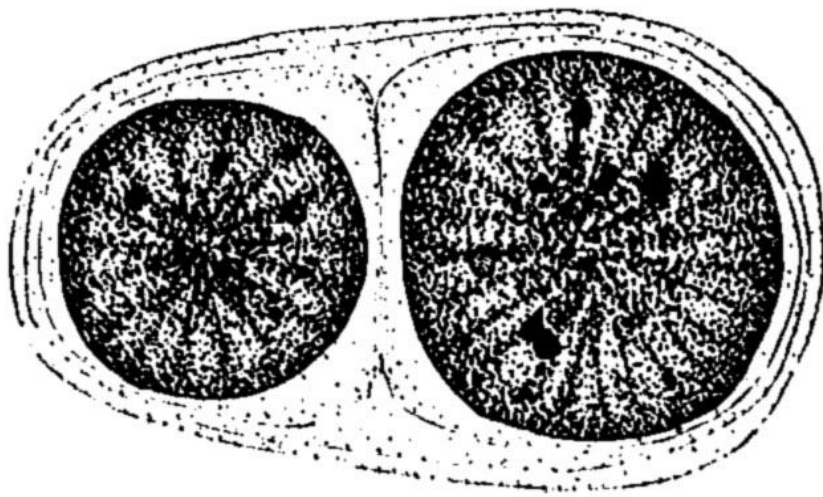
Thoracosphaera ^(M)

- coccoid dinoflagellate surrounded by a calcareous cell wall
- a number of fossil species



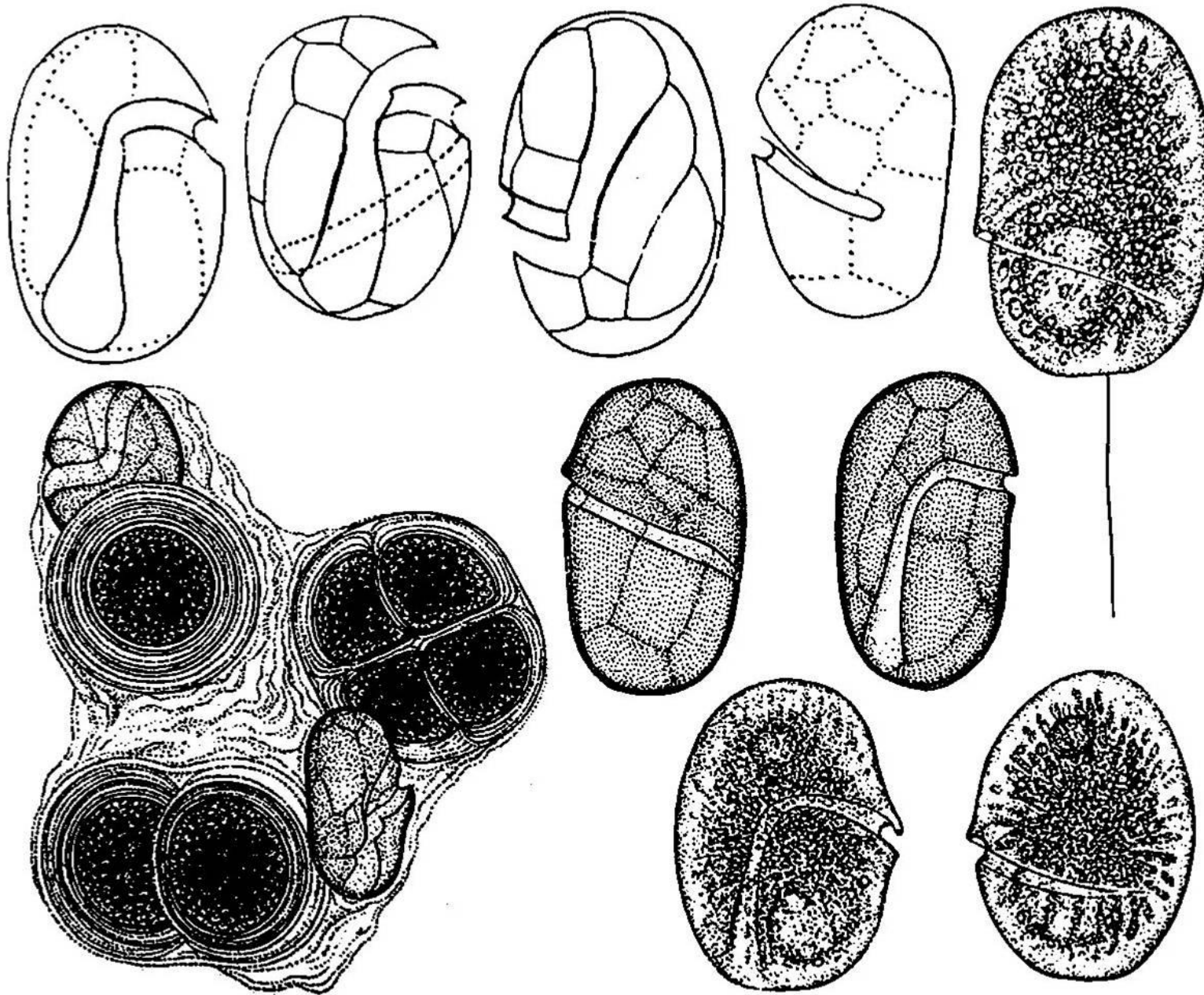
Gloeodiniales - *Gloeodinium montanum*

- capsal thallus
- peat bogs (N Europe, N America, New Zealand)

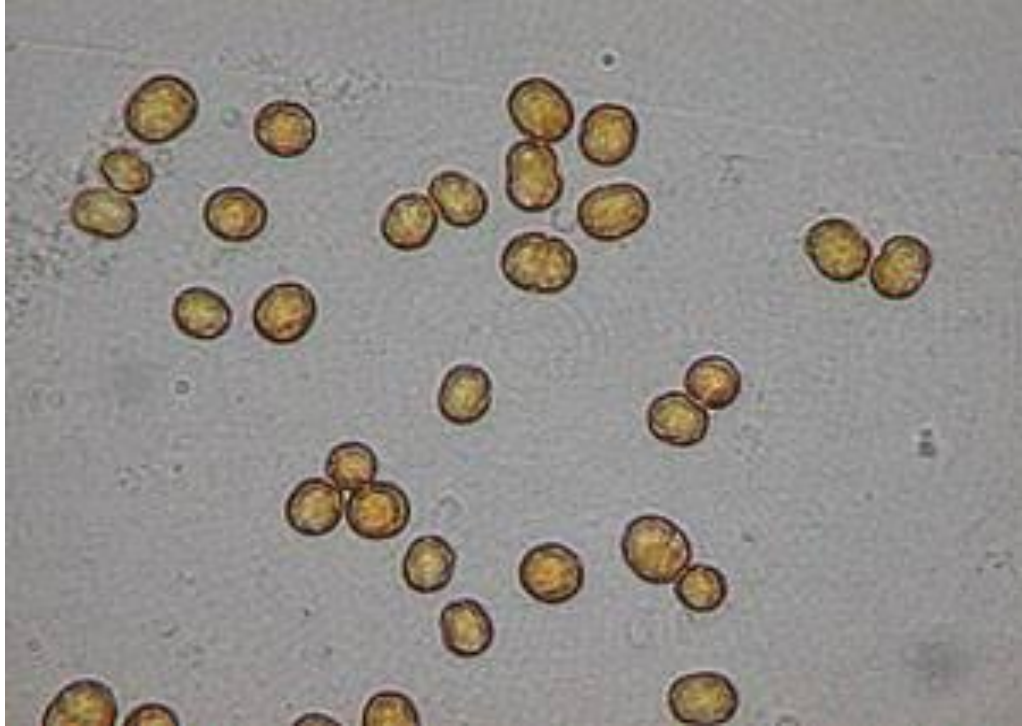


Suessiales - *Hemidinium* (F)

assymetric cells, incomplete cingulum



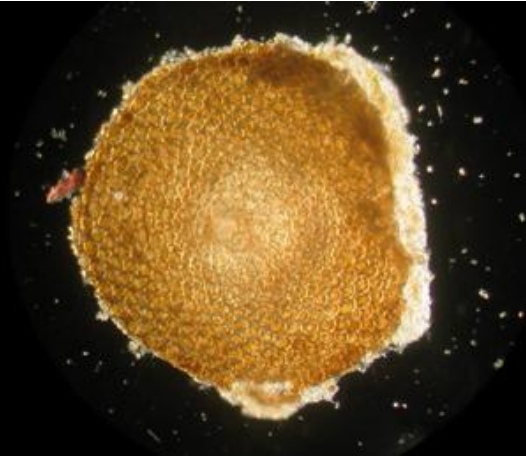
Suessiales - *Symbiodinium* ^(M)



http://www.youtube.com/watch?feature=player_detailpage&v=9Lm9hUj2h_0

Symbiodinium

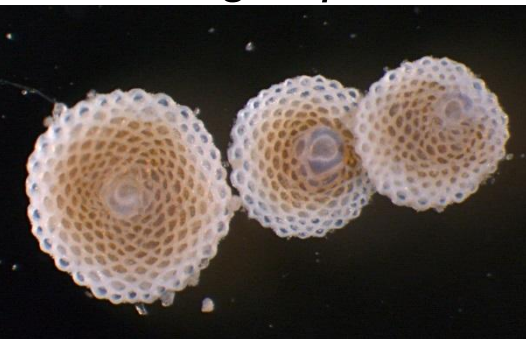
Pochon et al. 2006



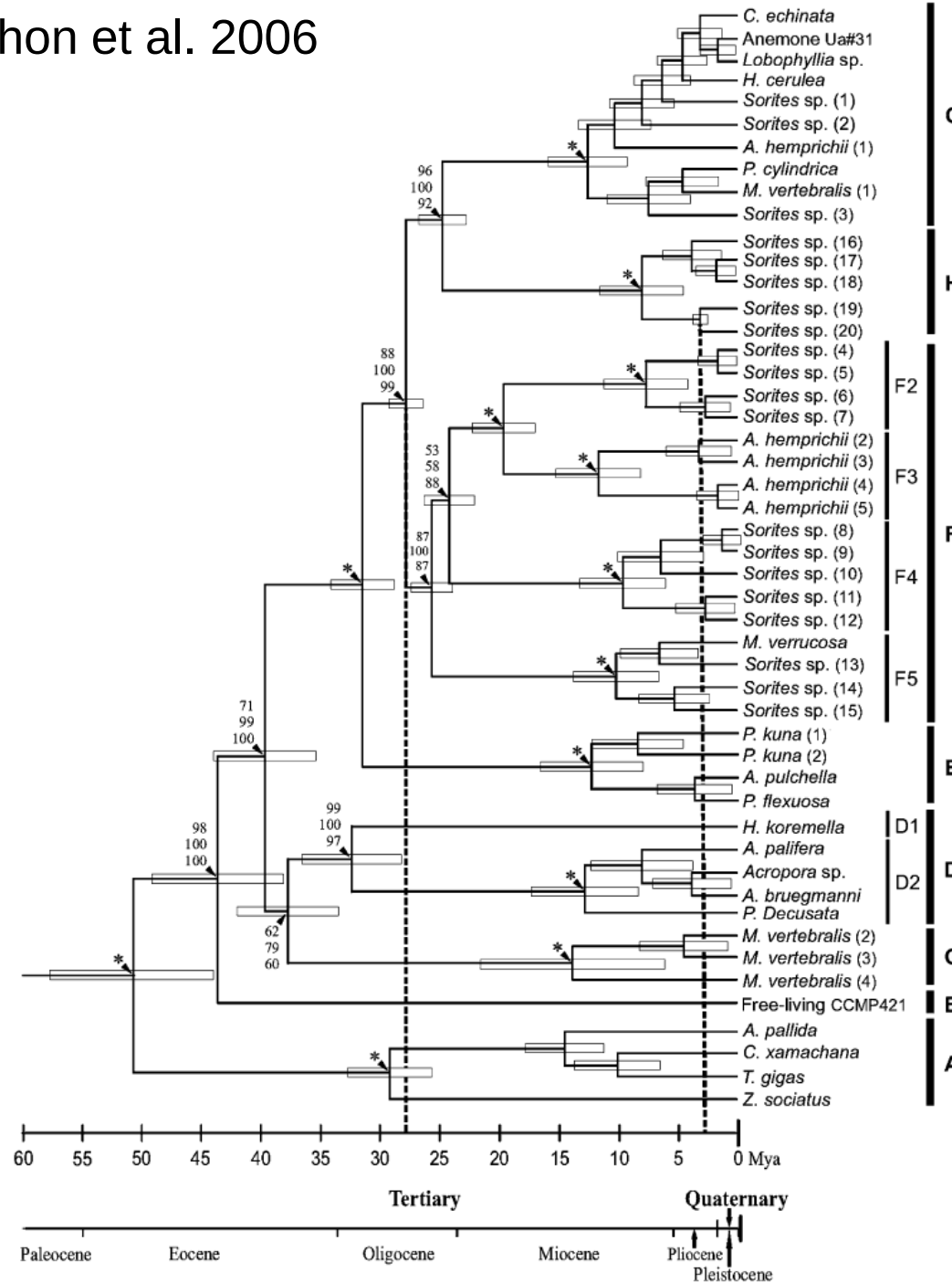
Sorites



Marginopora



Amphisorus



Acropora



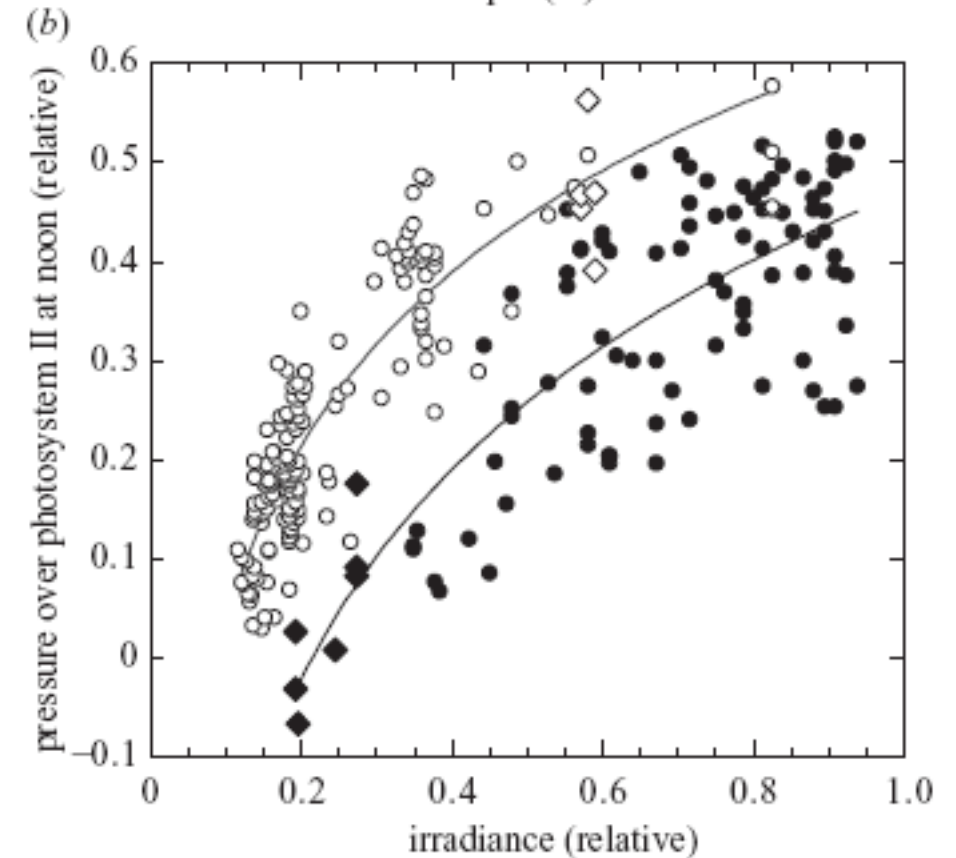
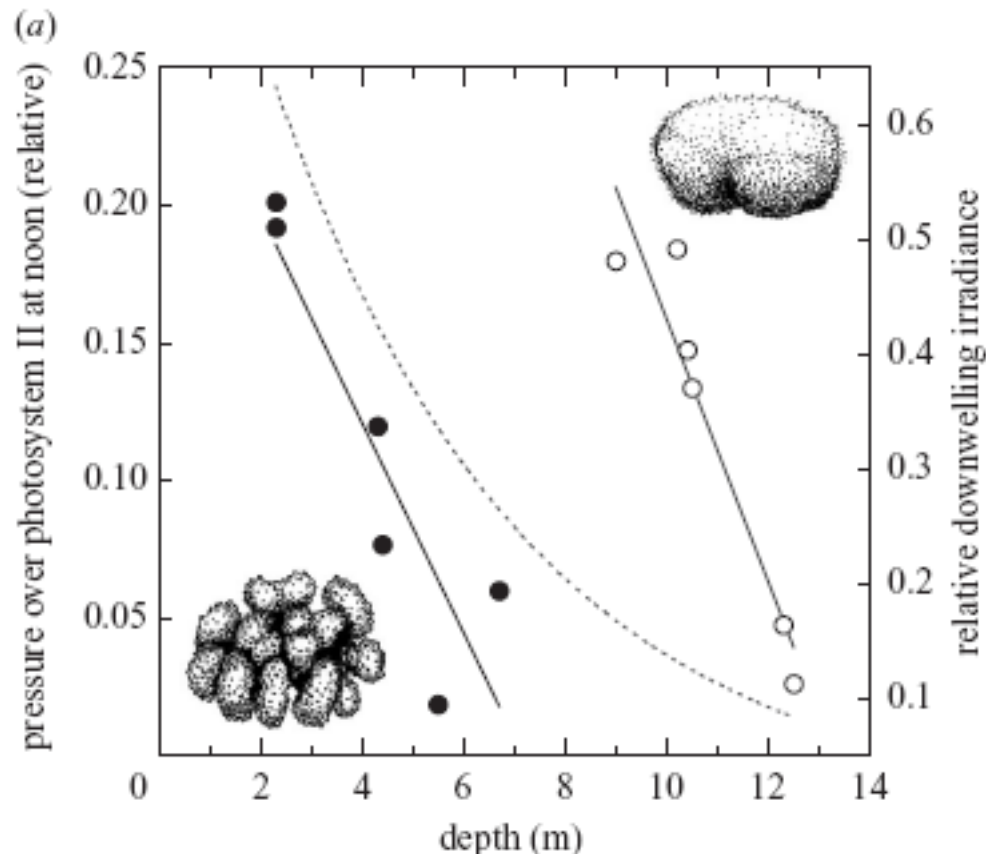
Plexaura



Zoanthus

Symbiodinium

- *Symbiodinium* lineages exhibit different physiologies in response to variations in light and temperature



Pocillopora

Pavona



Iglesias-Prieto et al. 2004

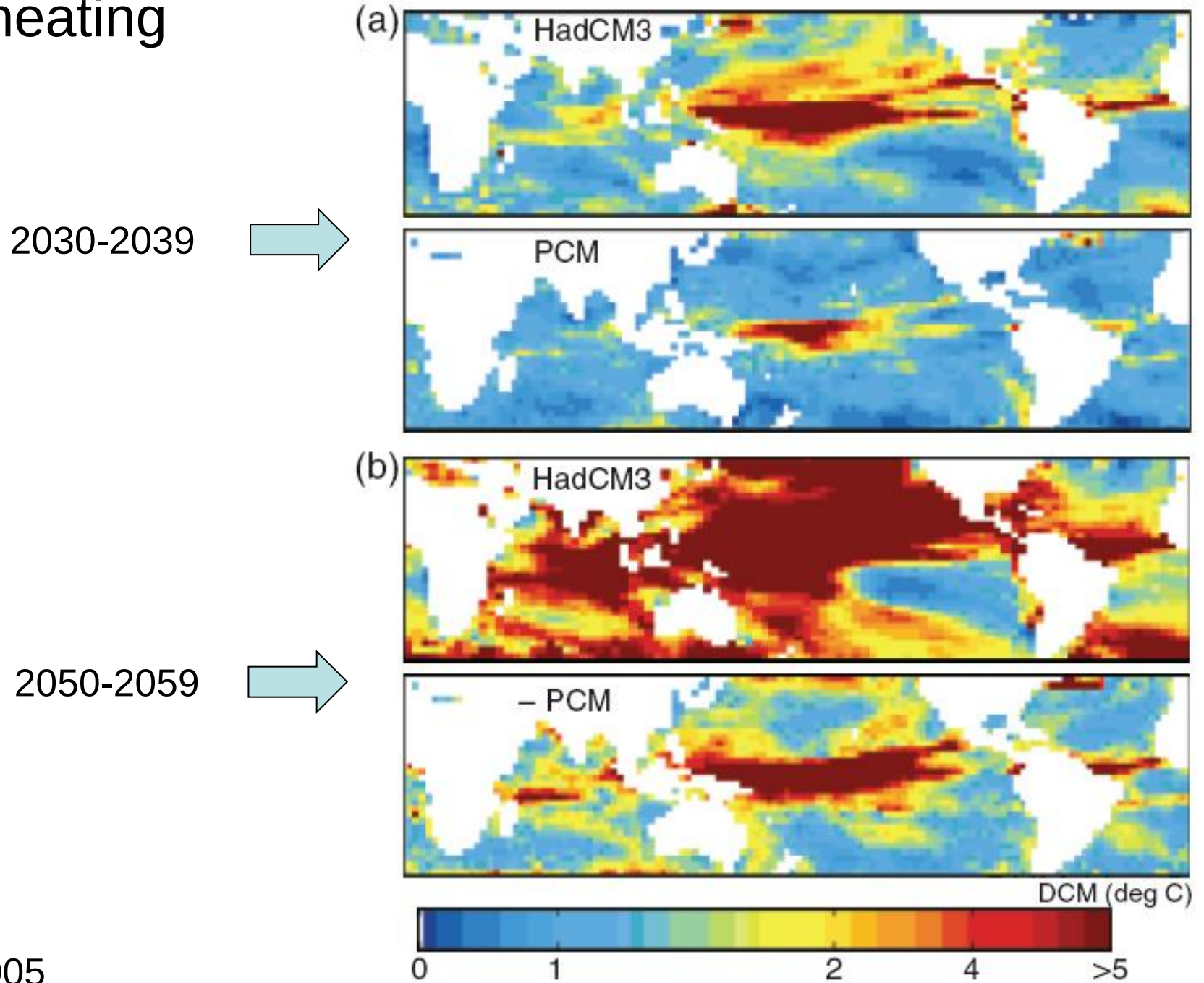
Symbiodinium

- Coral bleaching - the loss of intracellular endosymbionts
 - increase of temperature, solar radiation, acidification, ...



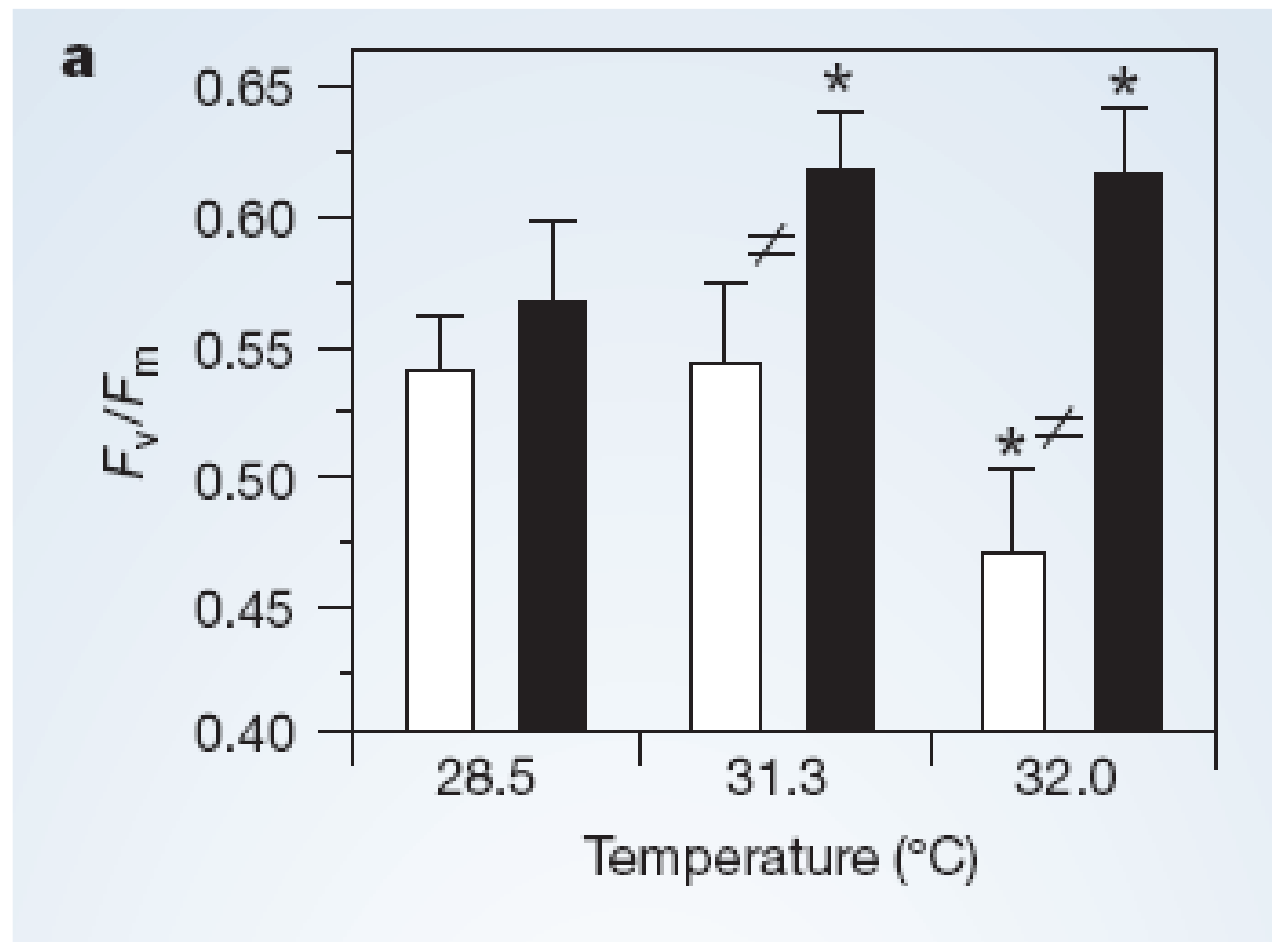
Symbiodinium

- Sea heating



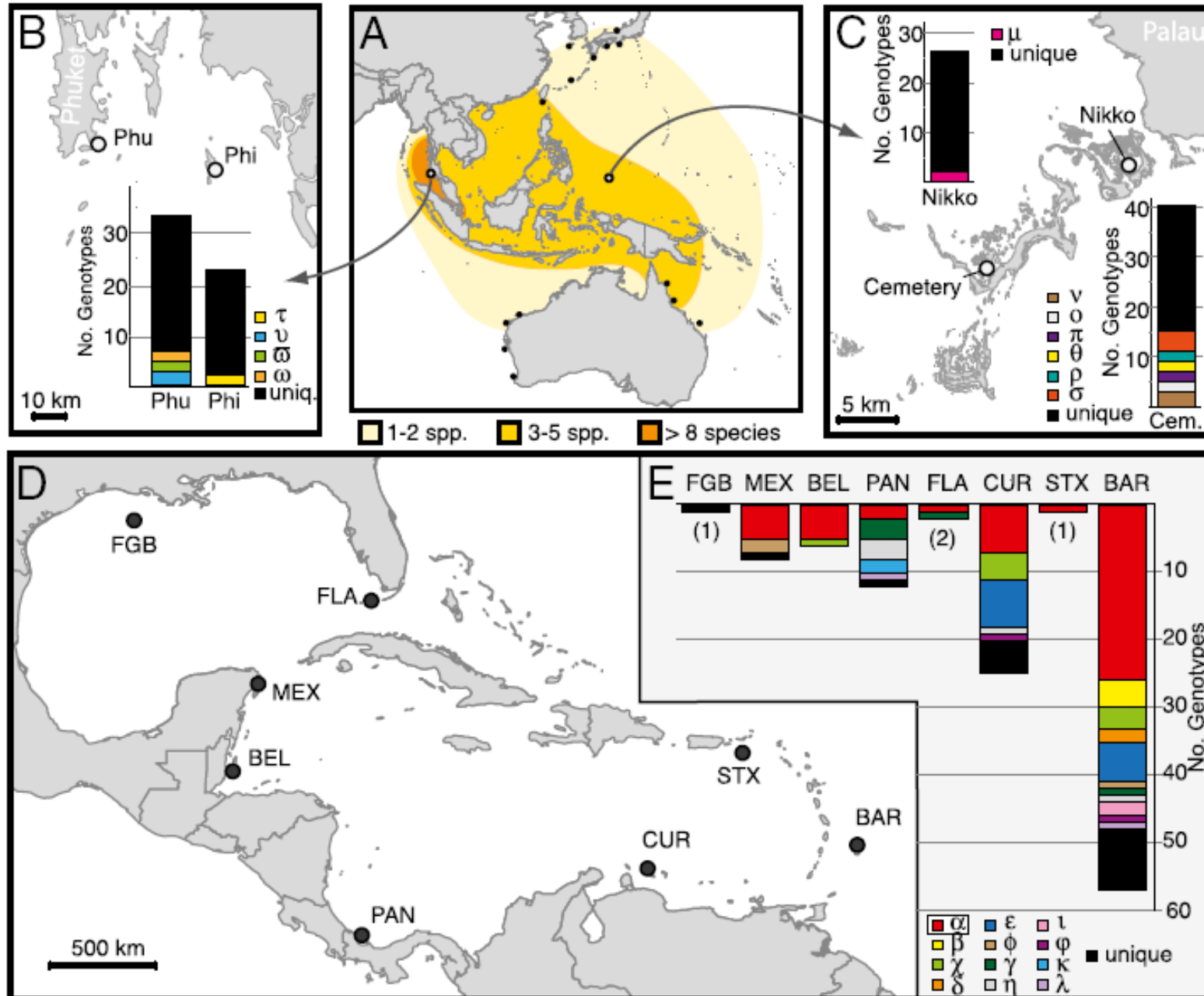
Symbiodinium

- To prevent bleaching, corals host specifically adapted *Symbiodinium*
 - clade C – sensitive to higher temperatures, PSII damage
 - clade D – tolerant to higher temp., photoprotection



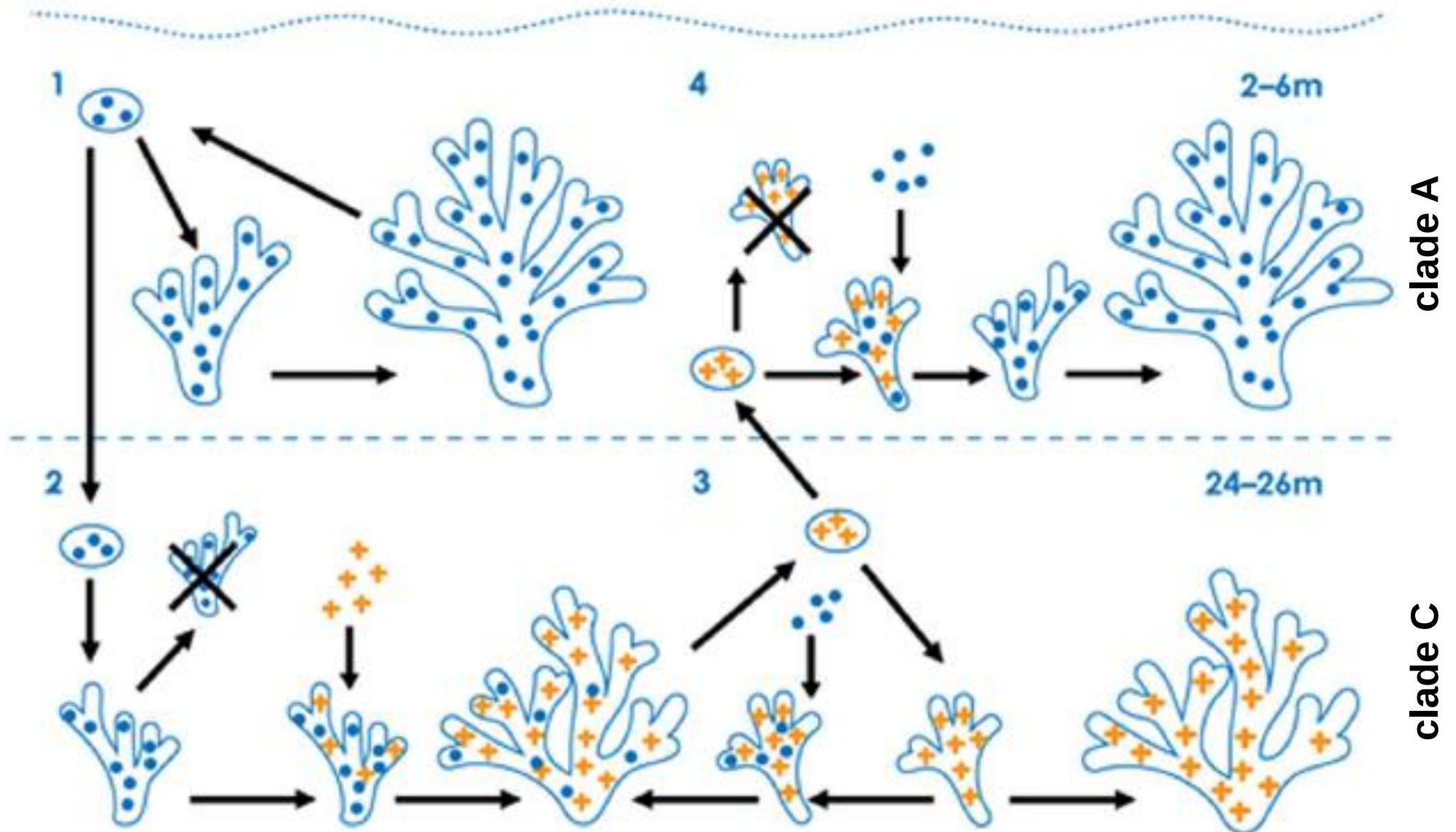
Symbiodinium

- S. trenchii*



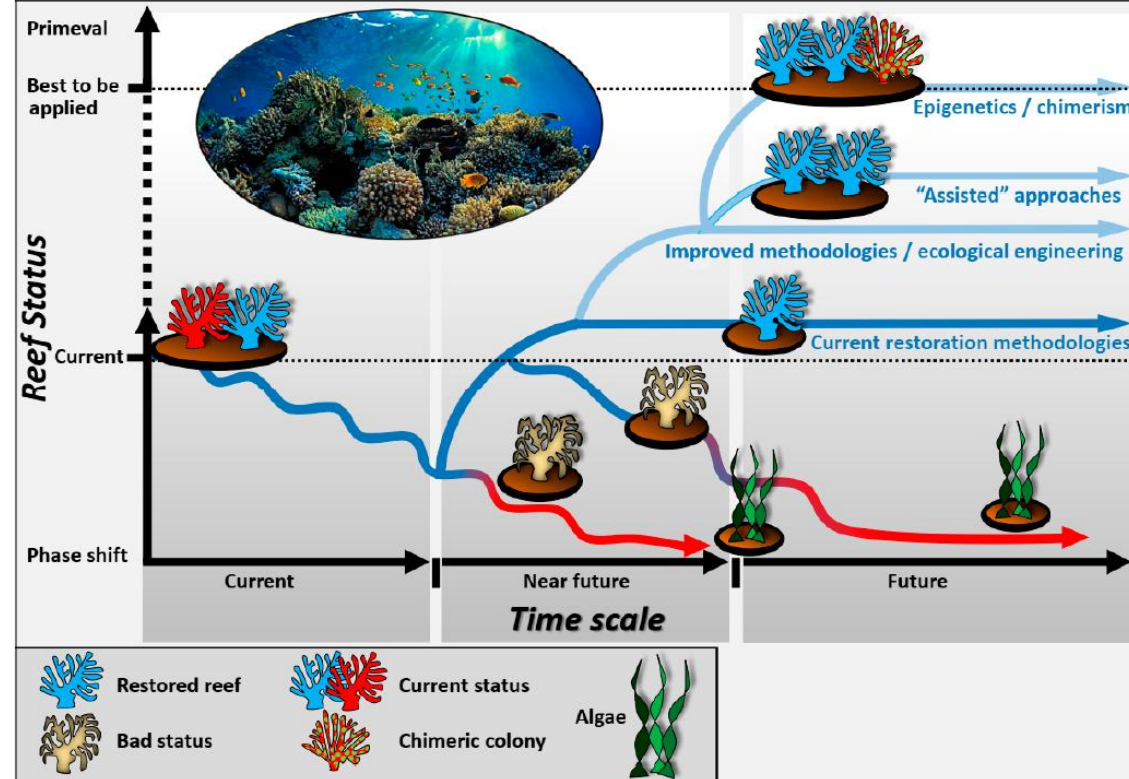
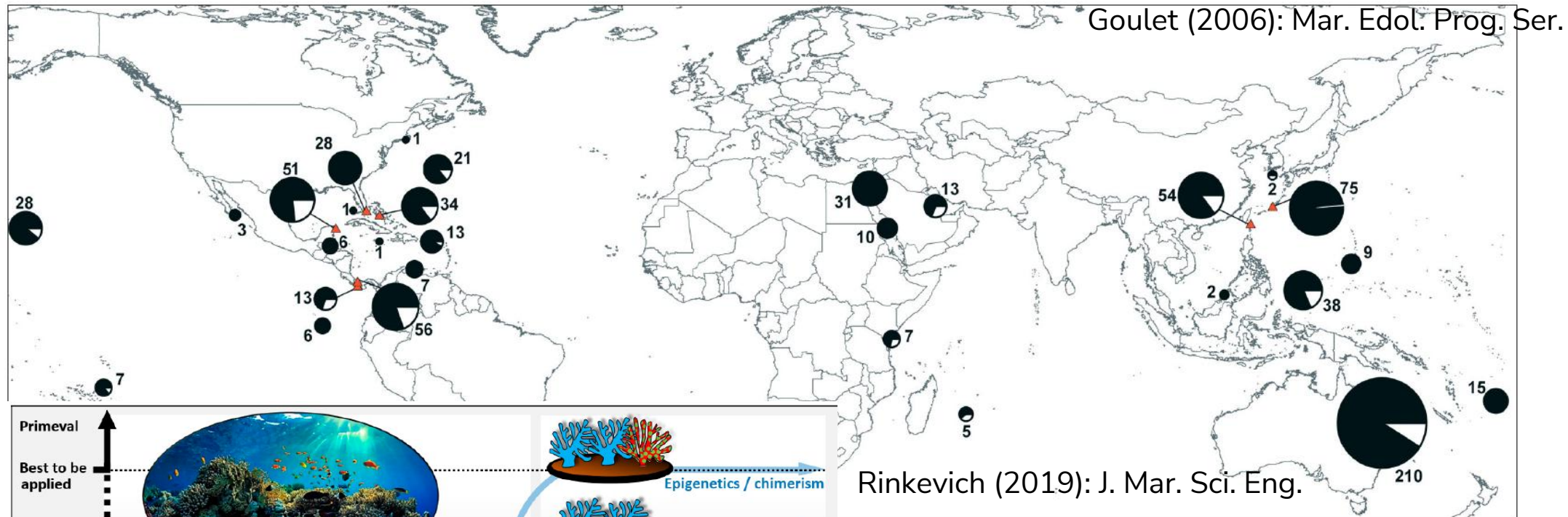
Symbiodinium

- Habitat adapted symbiosis



Habitat adapted symbiosis

- Only 23% of coral species host multiple symbions





Symbiodinium

LaJeunesse et al. 2011

- Enormous cryptic diversity
- Strong phylogeographic structure
- Host-specific lineages

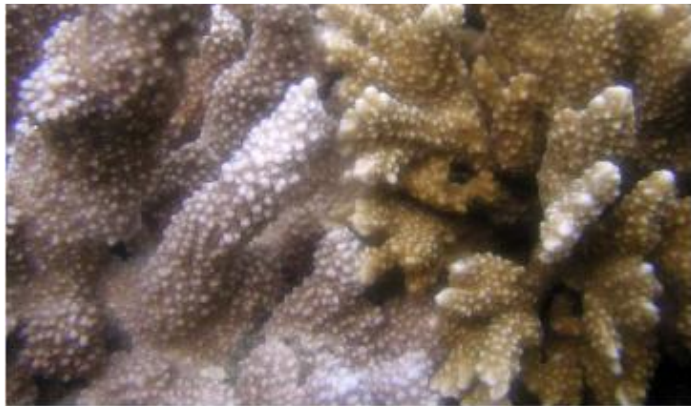
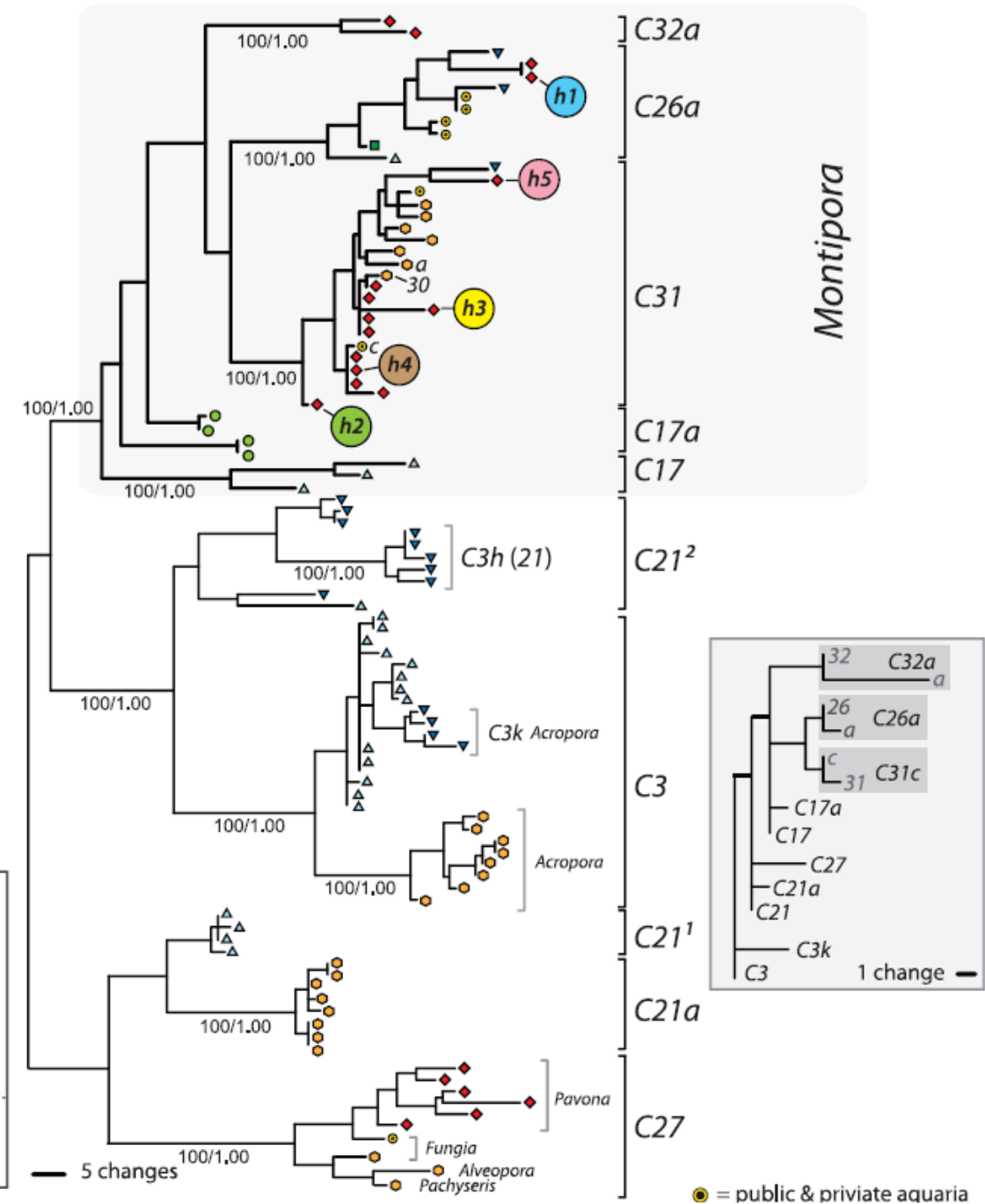


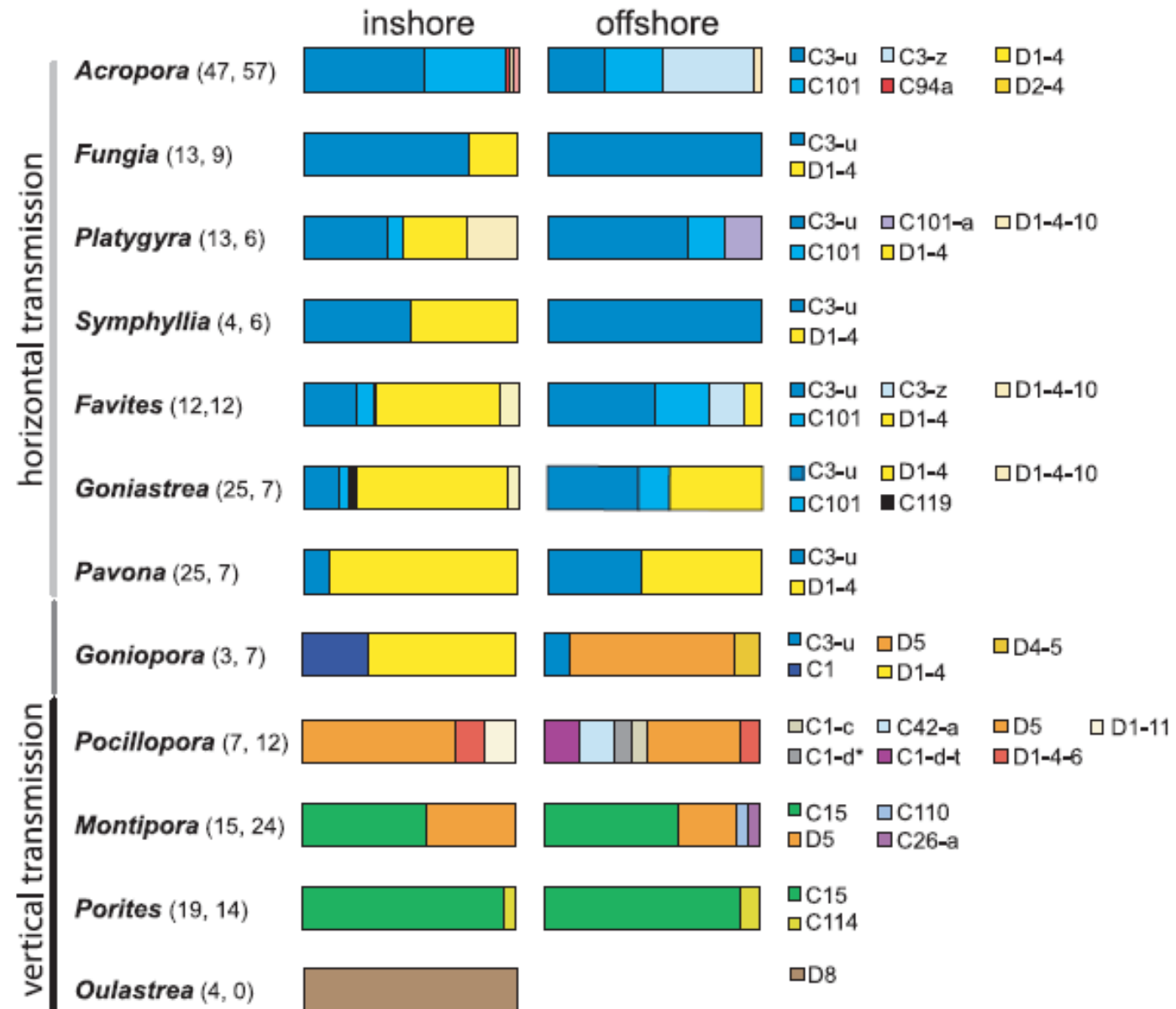
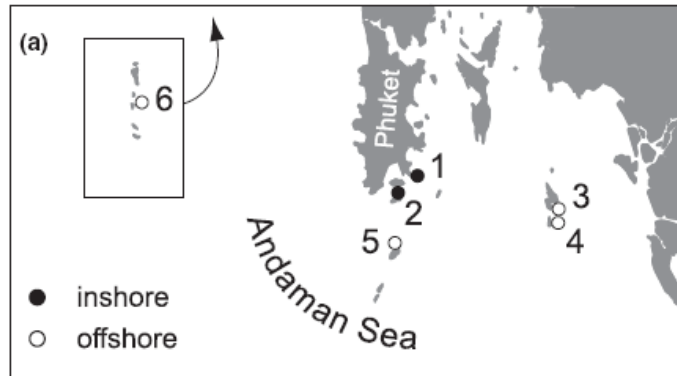
Figure 4. Color morphs of *Montipora capitata* are dominated by different species of *Symbiodinium*. The reddish brown colony on the left harbors the *Montipora*-specific symbiont C31/C31c, while the orangish-brown colony on the right harbors the Clade D symbiont, D1-4-6.



Symbiodinium

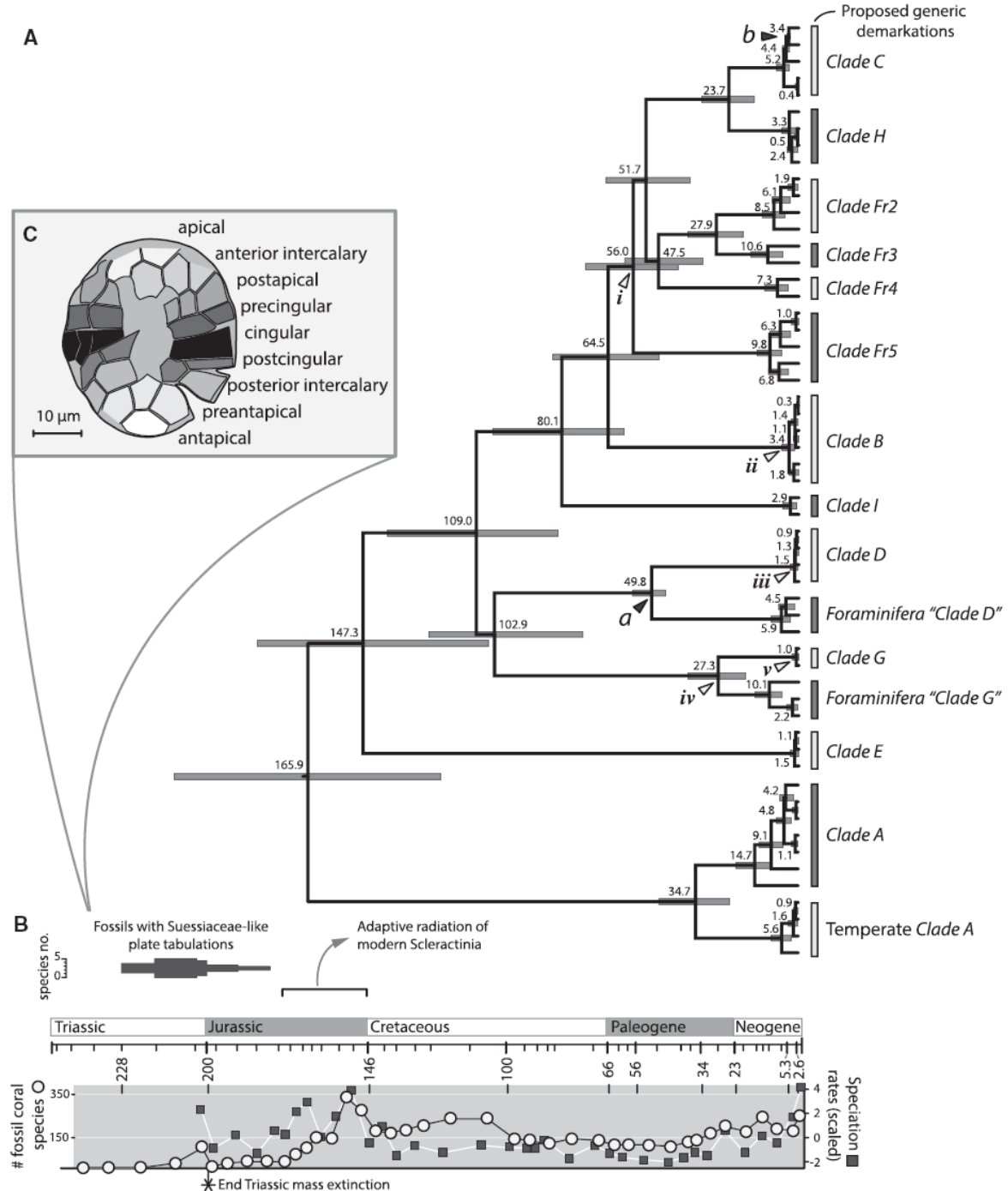
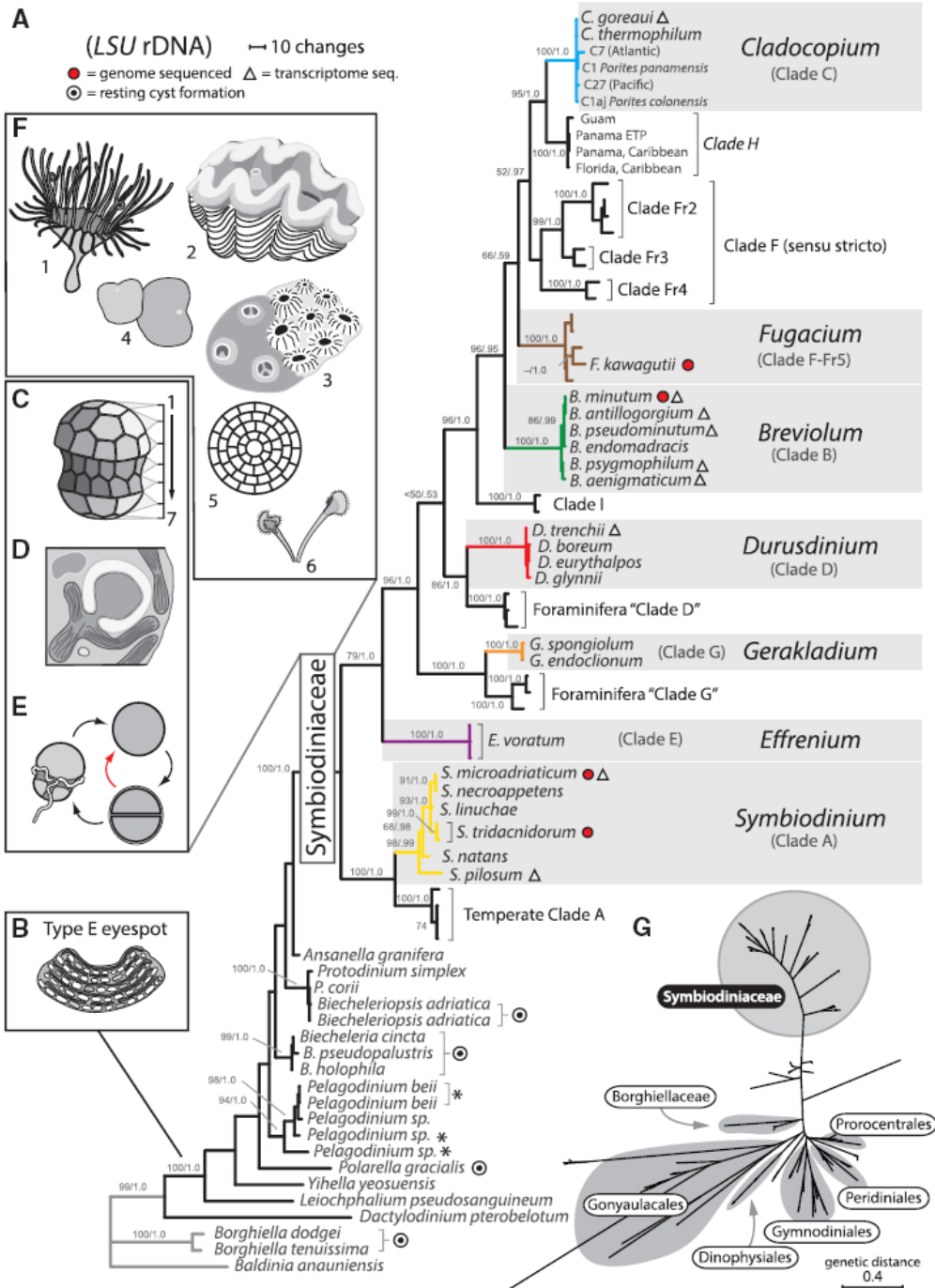
LaJeunesse et al. 2010

- Host-symbiont specificity, ecological differences
 - C3-z: offshore; C15: thermally tolerant



Symbiodinium

LaJeunesse et al. 2018



Symbiodinium

Mordret et al. 2016

- A symbiont of calcifying ciliate *Tiarina*

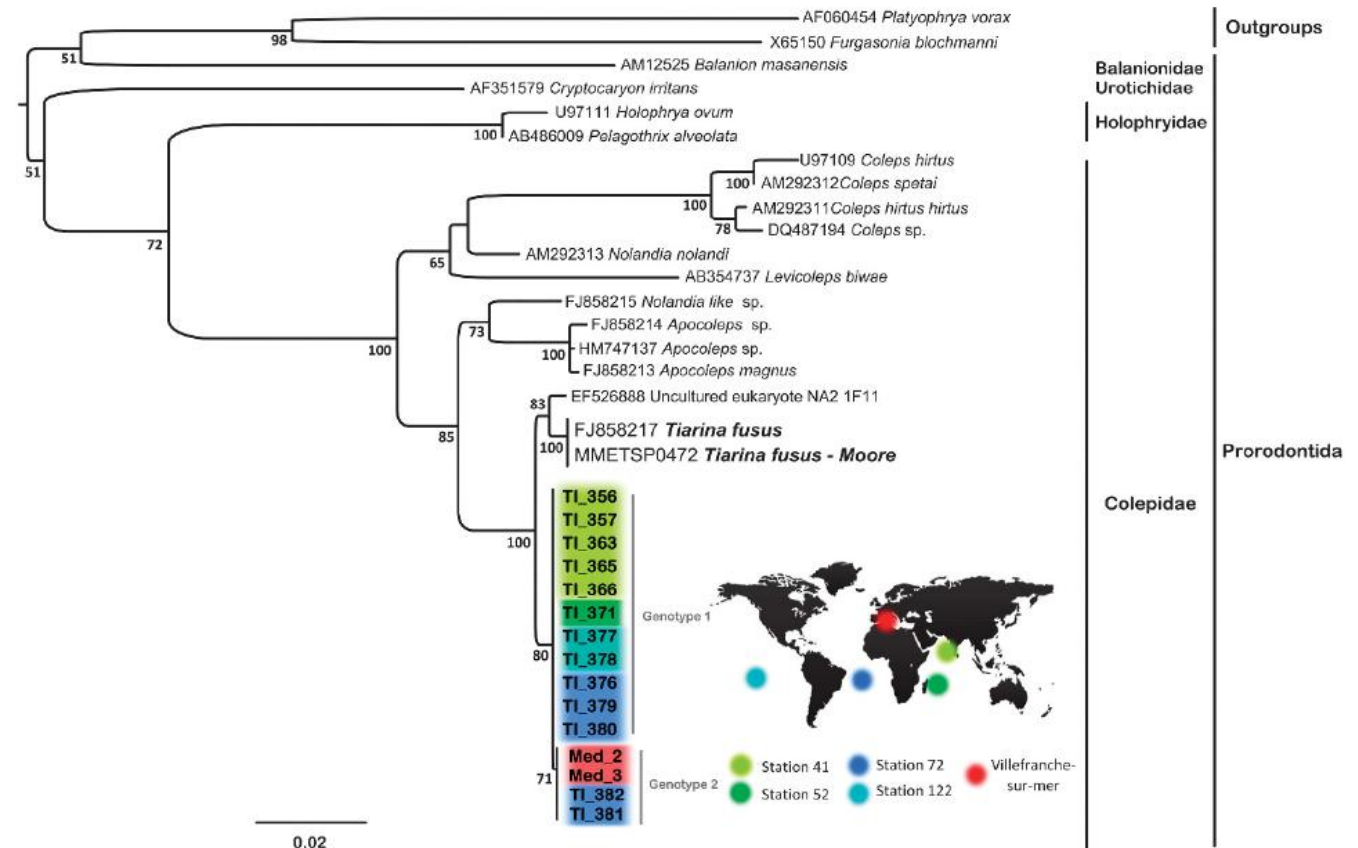
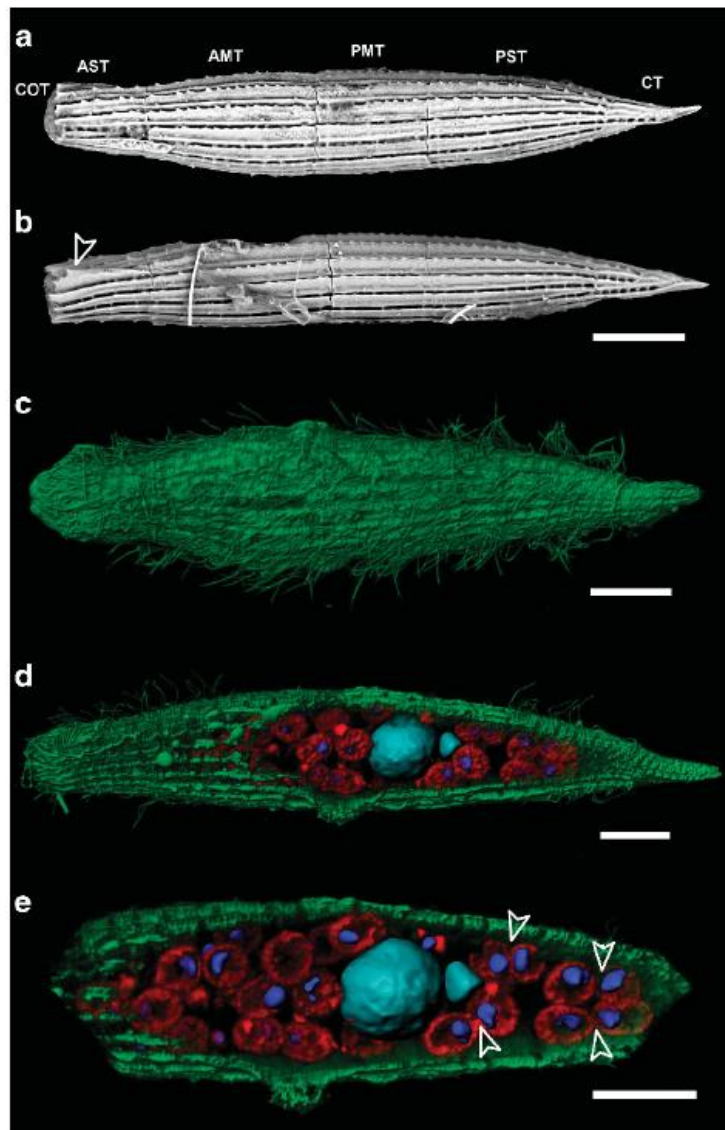
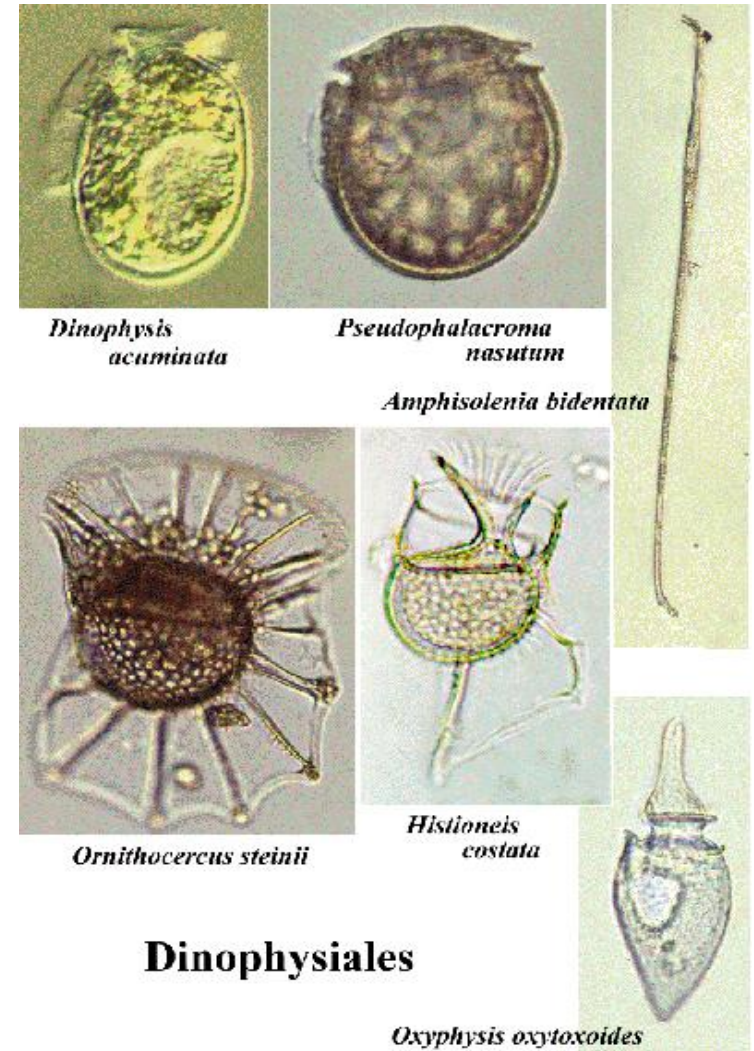
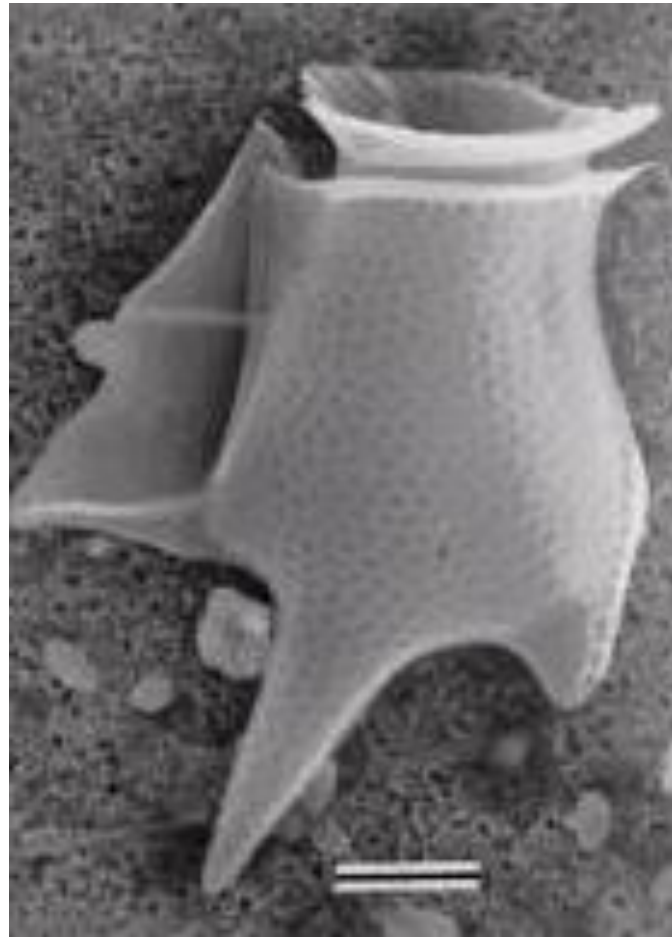


Figure 1 Microscopy images of the photosymbiosis between the ciliate *Tiarina* sp. (the host) and its intracellular symbiotic microalgae collected in surface oceanic waters. (a, b) Scanning electron microscopy images reveal the calcified skeleton of the ciliate composed of six different tiers: circumoral (COT), anterior

Dinophysiales

- flagellates, laterally flattened cells
- thecate, epitheca + hypotheca, left and right half of the cell separated by longitudinal suture
- only marine species



Dinophysis ^(M)

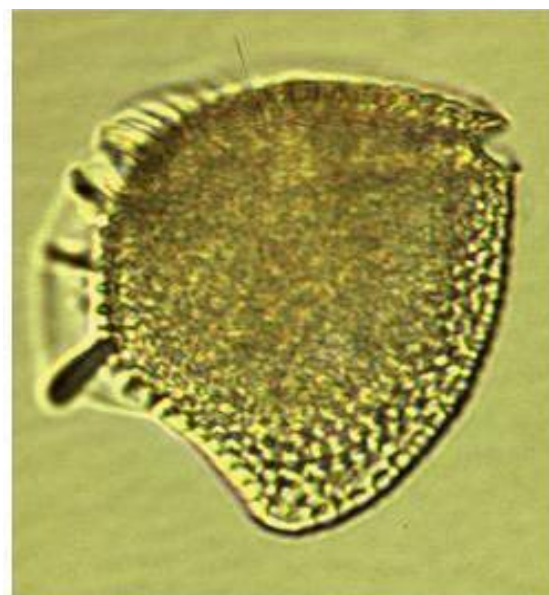
toxic species (DSP)



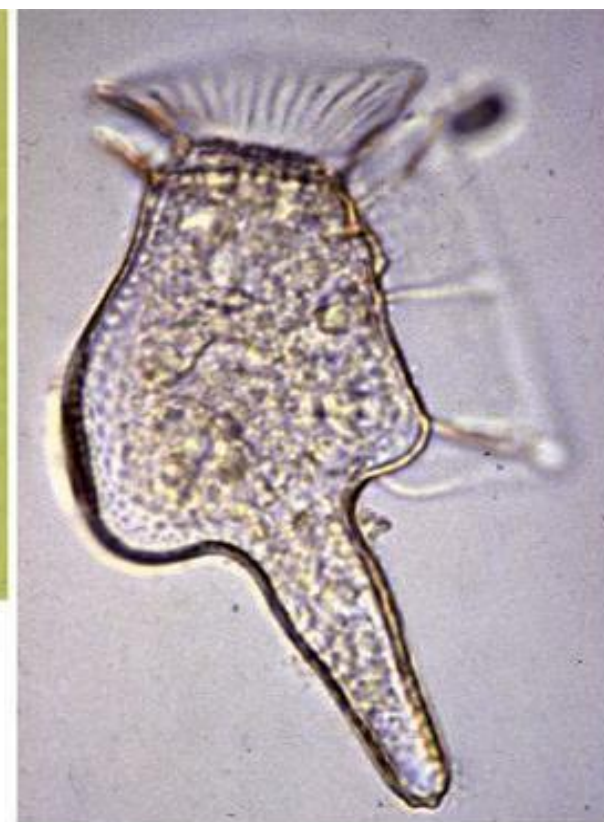
D. acuminata



D. fortii



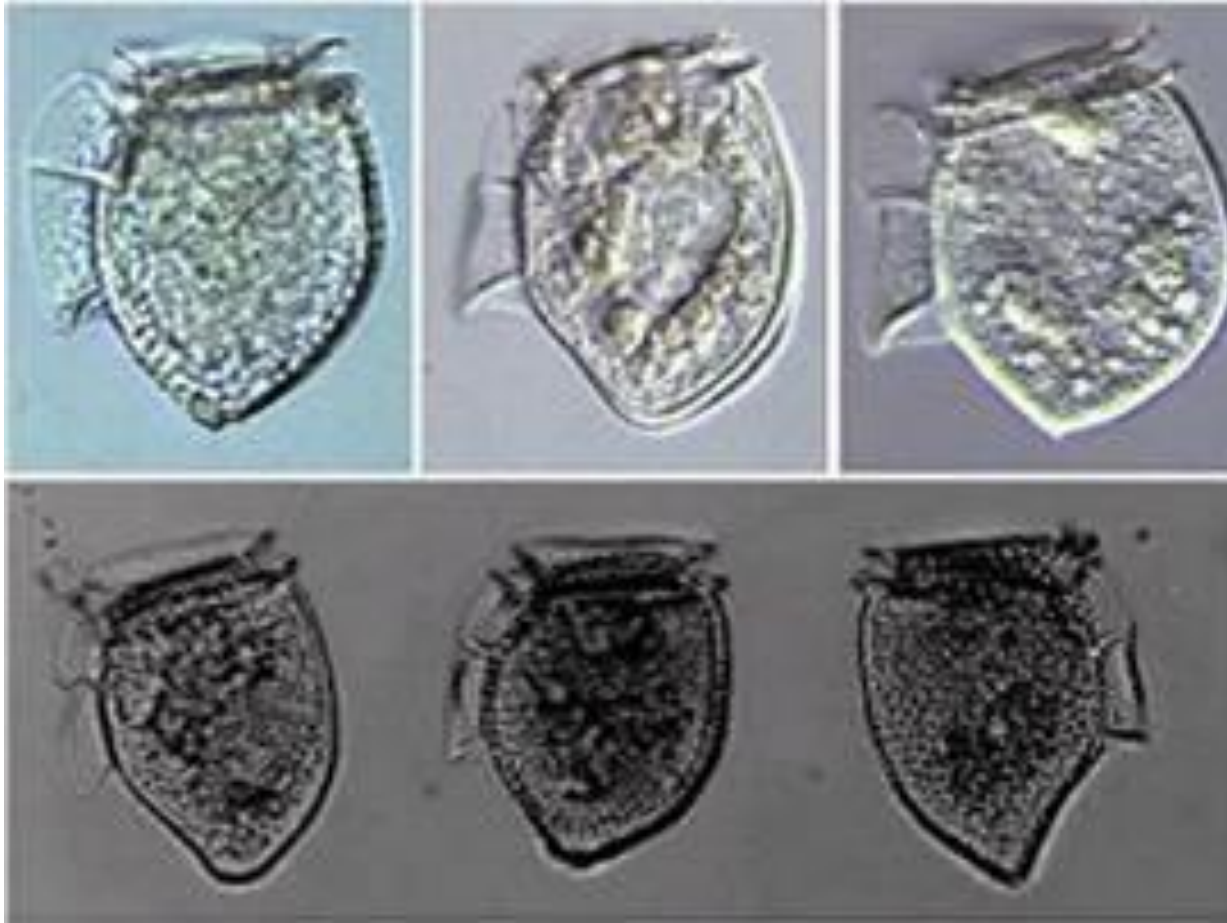
D. mitra



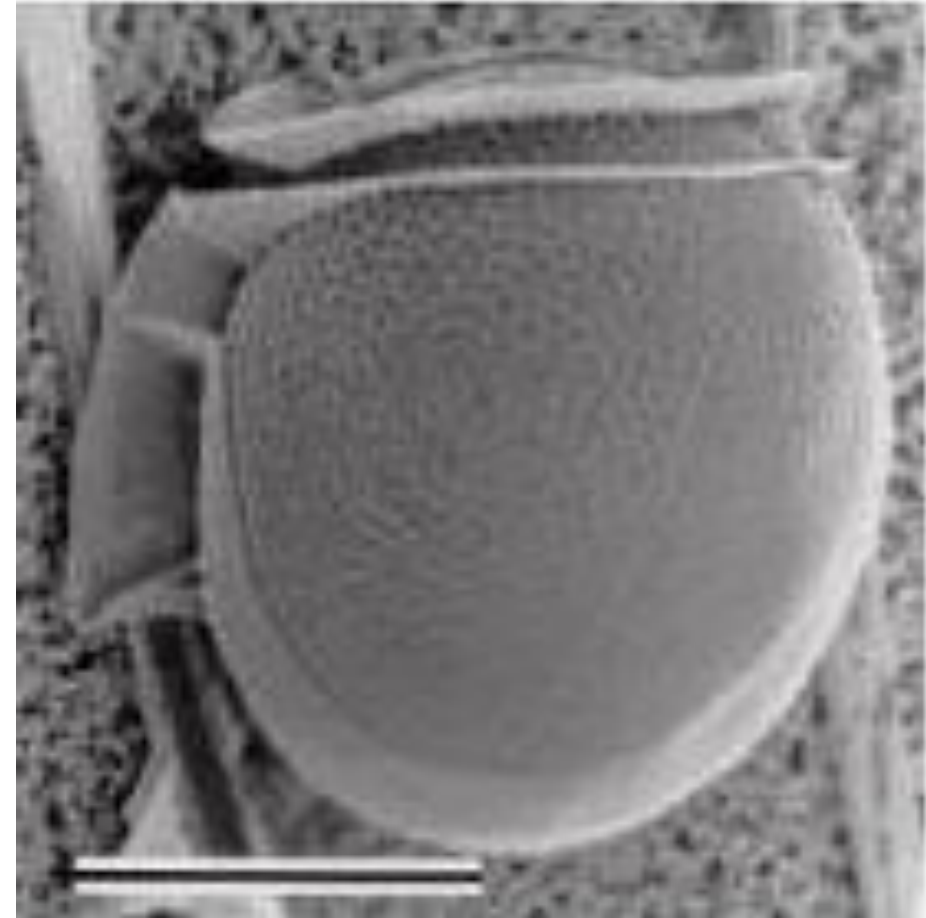
D. caudata

Dinophysis ^(M)

non-toxic species



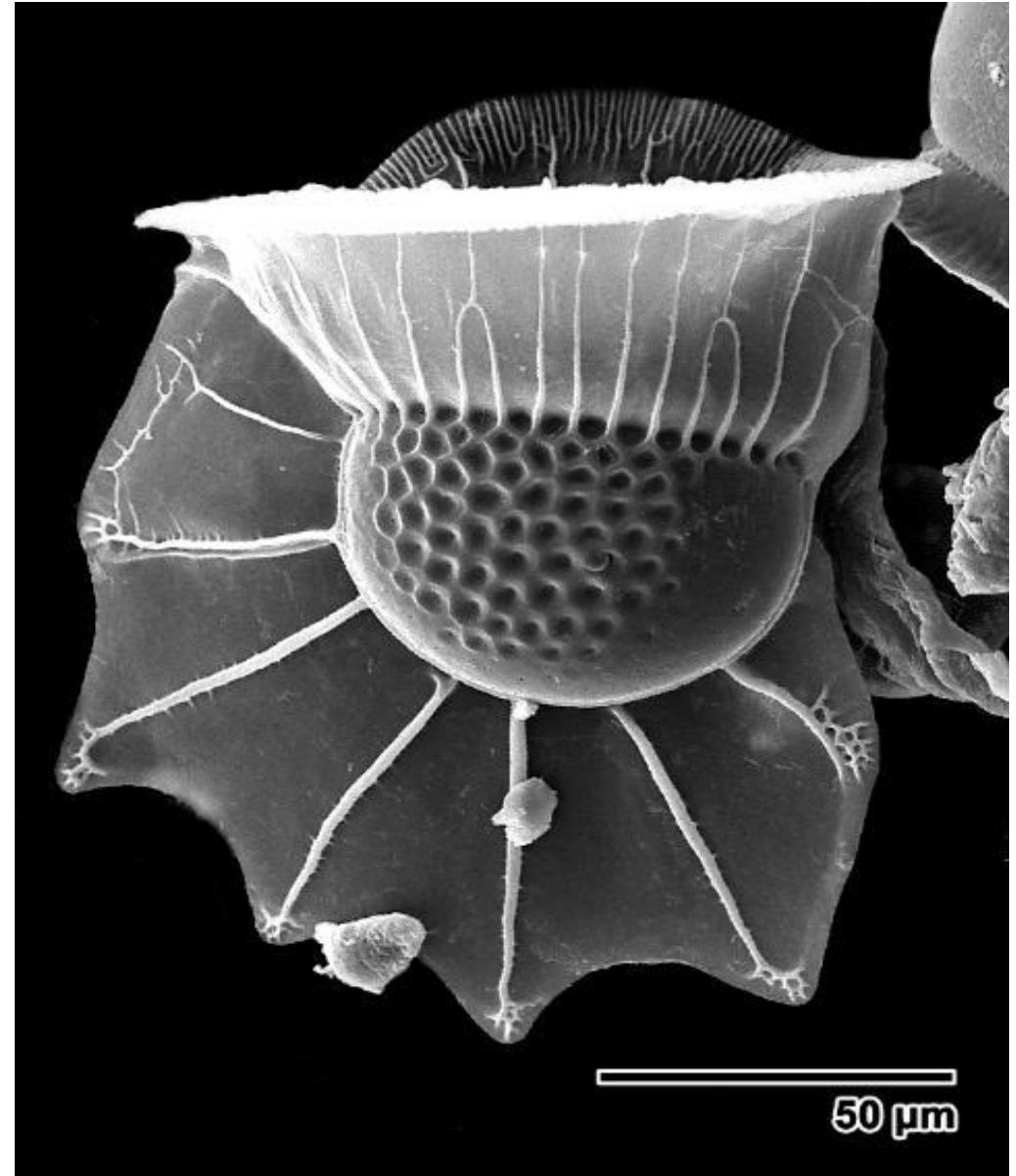
Dinophysis norvegica



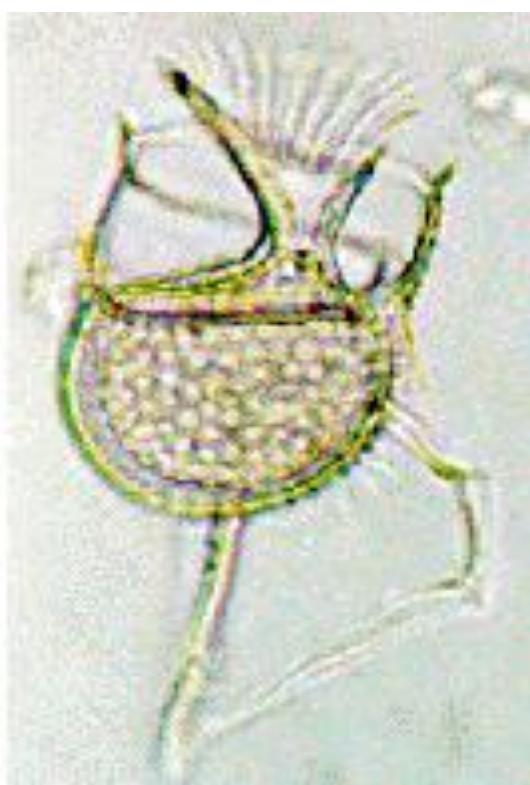
Dinophysis rotundata
(= *Phalacroma*)

Ornithocercus ^(M)

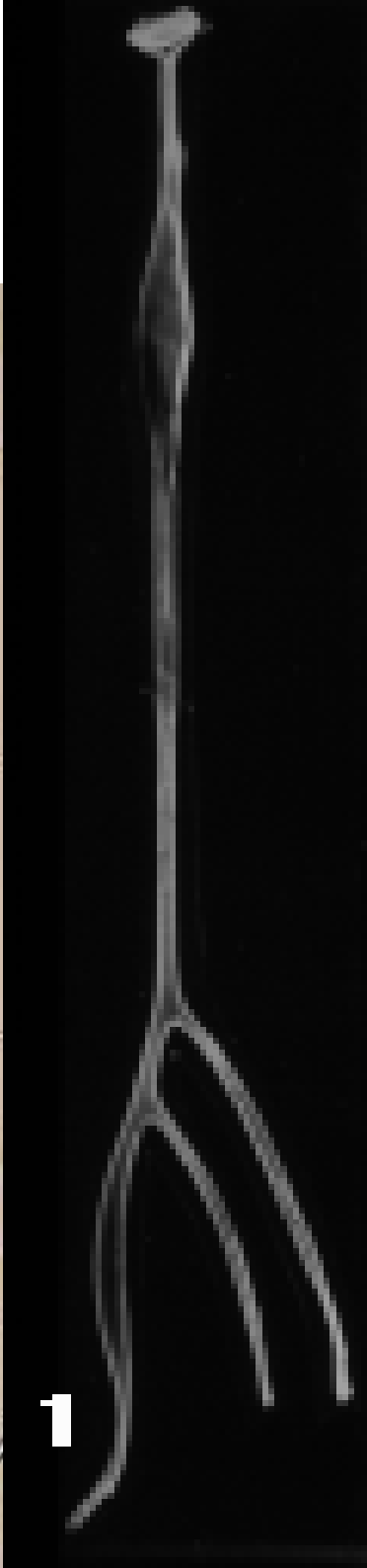
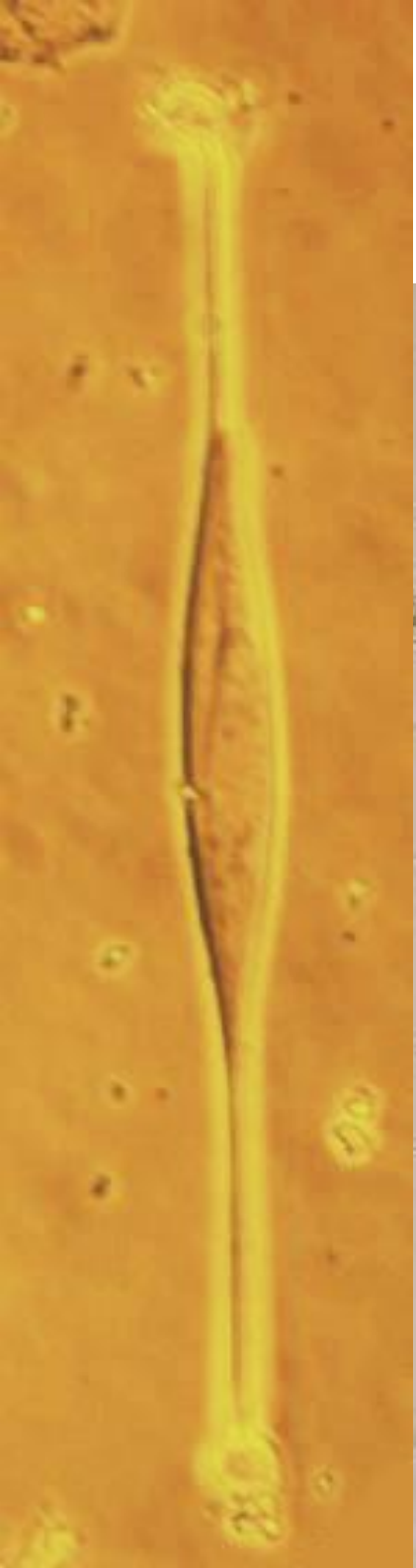
symbiotic heterocytous cyanobacteria instead of plastids (between two large wings)



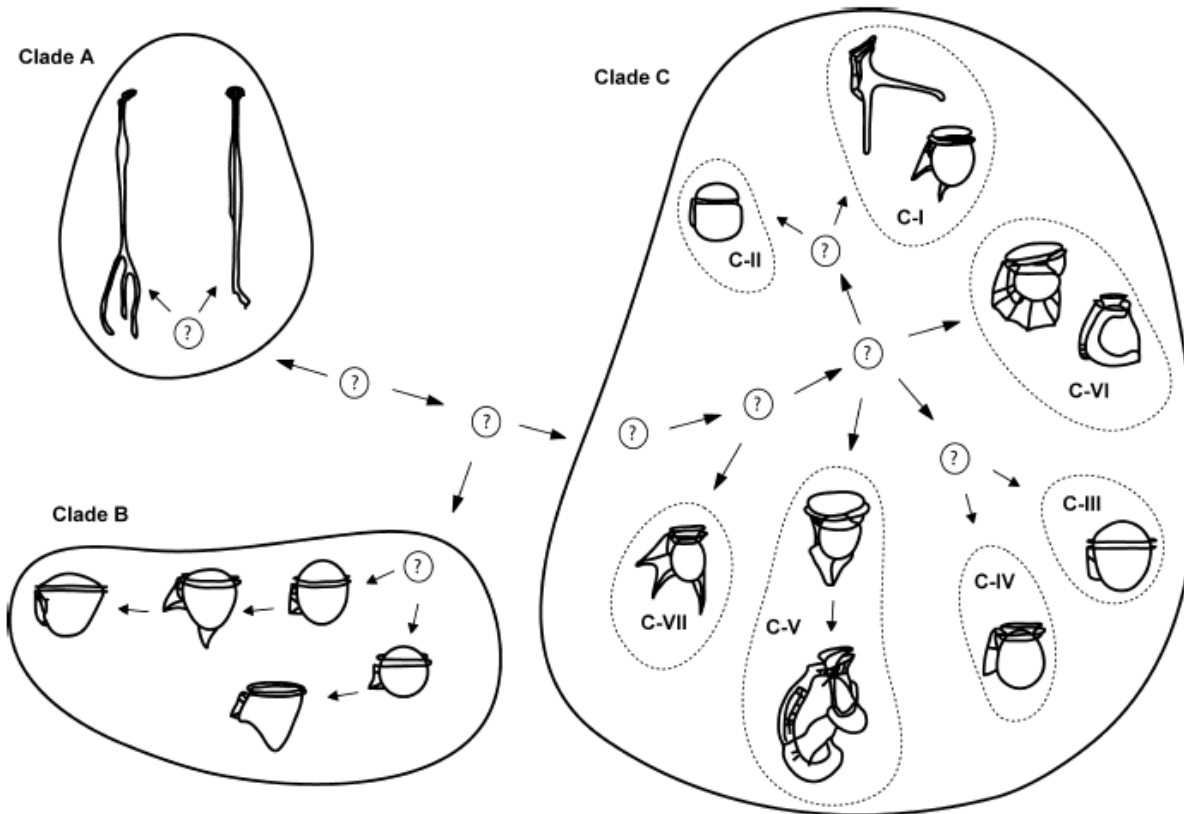
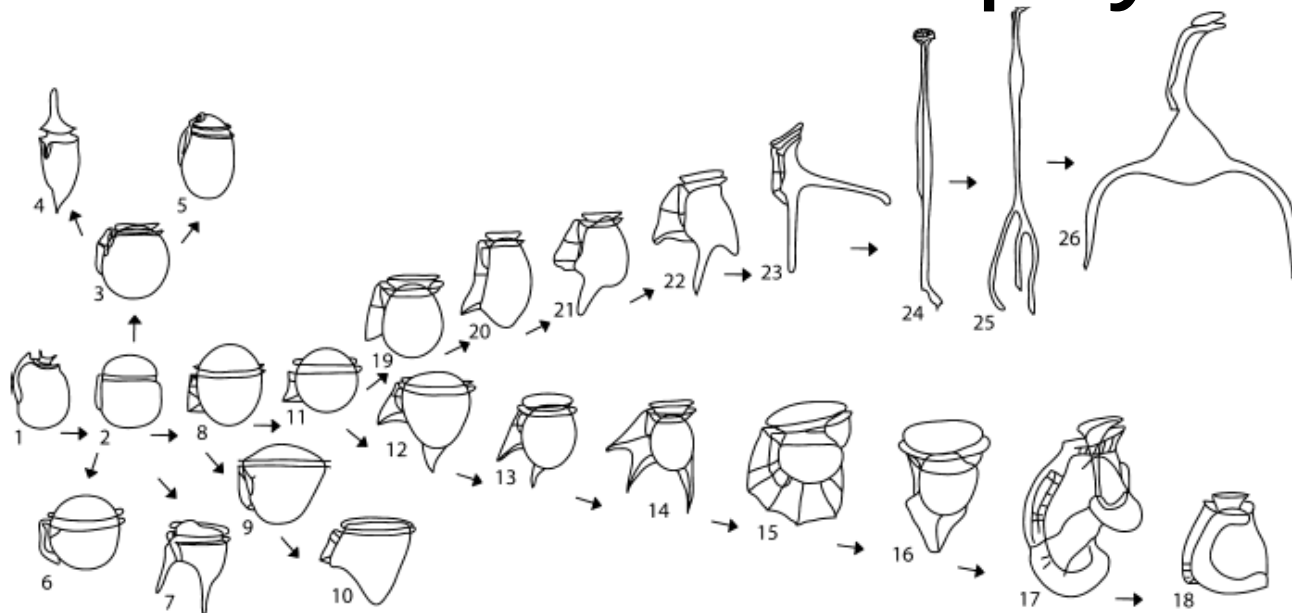
Histioneis ^(M)



Amphisolenia (M)



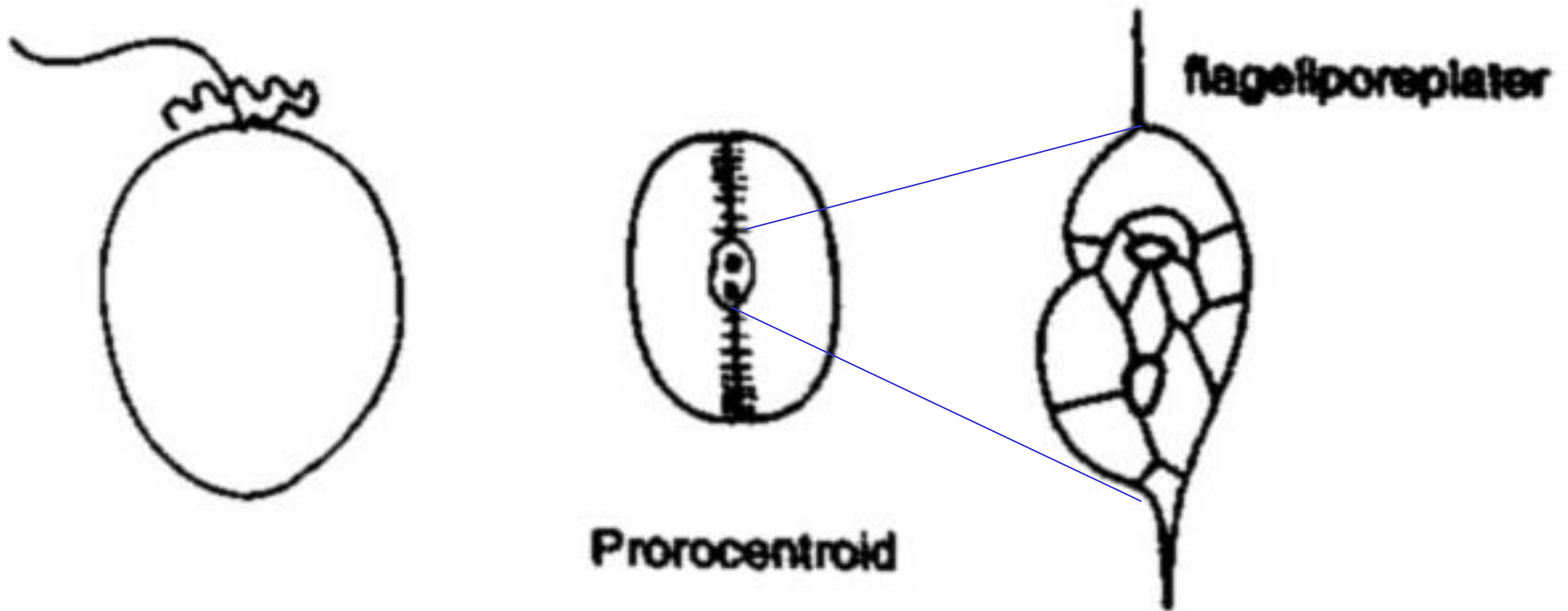
Dinophysiales



- comparison of traditional and modern evolutionary hypotheses
- A – *Amphisolenia*
B – *Phalacroma*
C – other genera
- convergent evolution of morphological attributes

Prorocentrales

- flagellates, laterally flattened cells
- thecate, 2 big plates separated by longitudinal suture + several minute plates near apical pores
- only marine species, autotrophic



Prorocentrum (M)



Prorocentrum lima (Ehrenberg) Dodge

Photomicrograph
by Yasuwo Fukuyo

WESTPAC-HAB
IOC Harmful Algal Bloom Programme

T0009



Prorocentrum sigmoides Böhm

WESTPAC-HAB

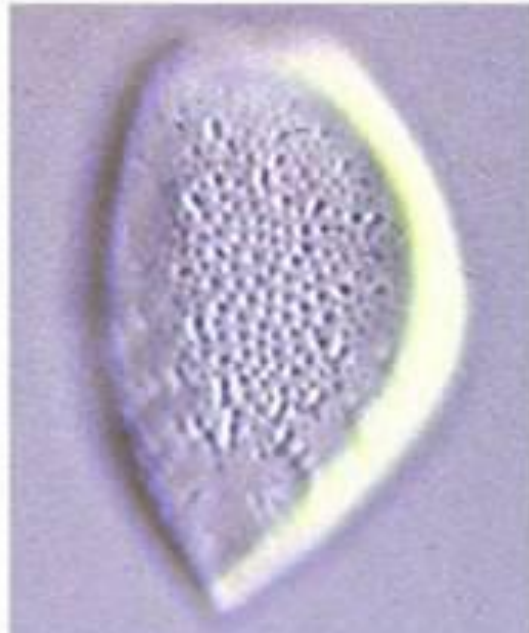


Prorocentrum mexicanum Tafall

Photomicrographs
by Yasuwo Fukuyo

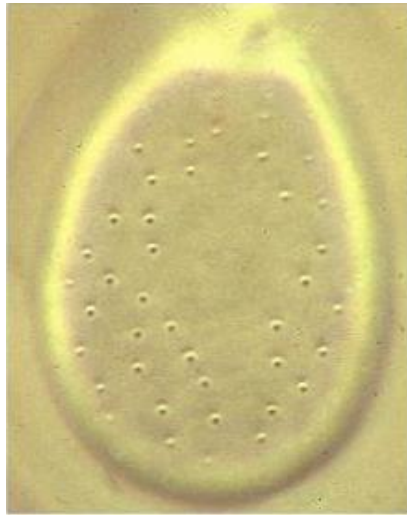
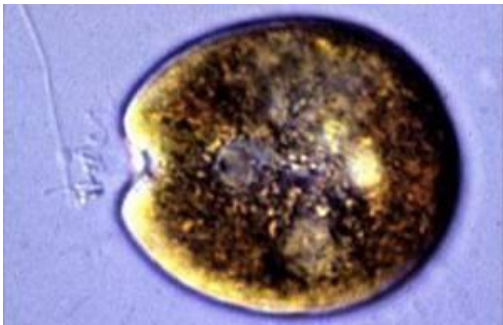
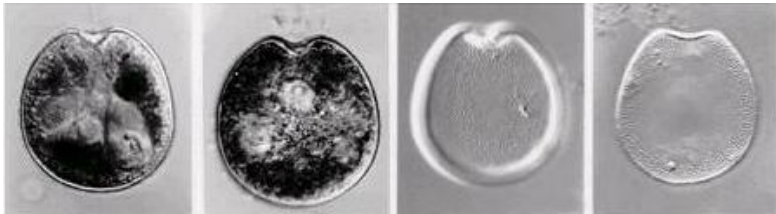
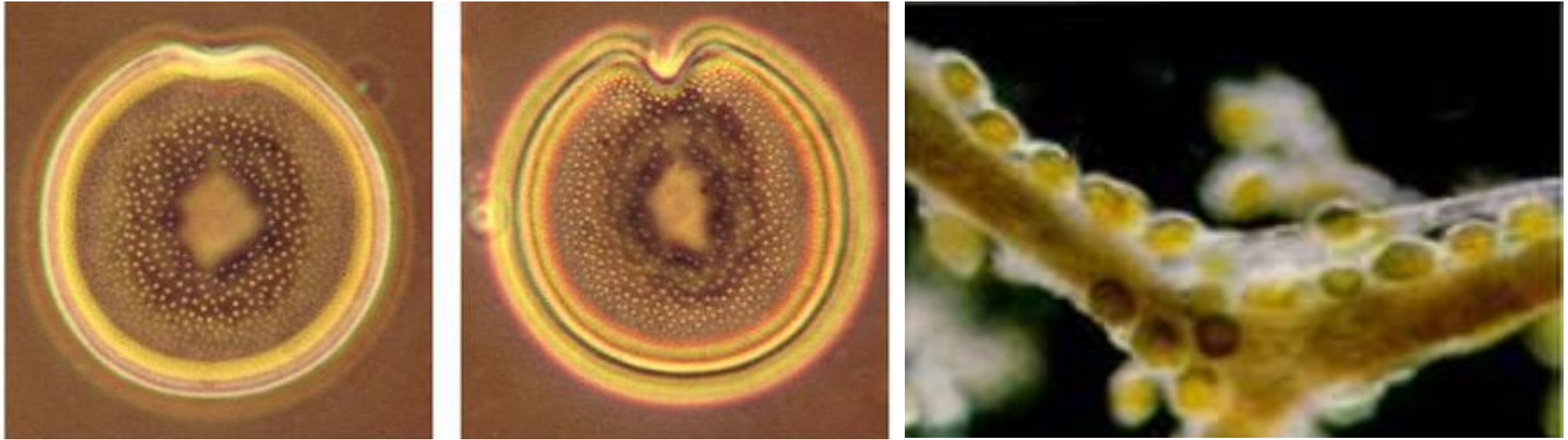
Prorocentrum micans (M)

planktonic species, red tides



Prorocentrum (M)

benthic species, CFP !



Prorocentrum concavum

Prorocentrum lima