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кафедра ботаніки

Sar: Alveolata & Rhizaria

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професор
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Херсон - 2020

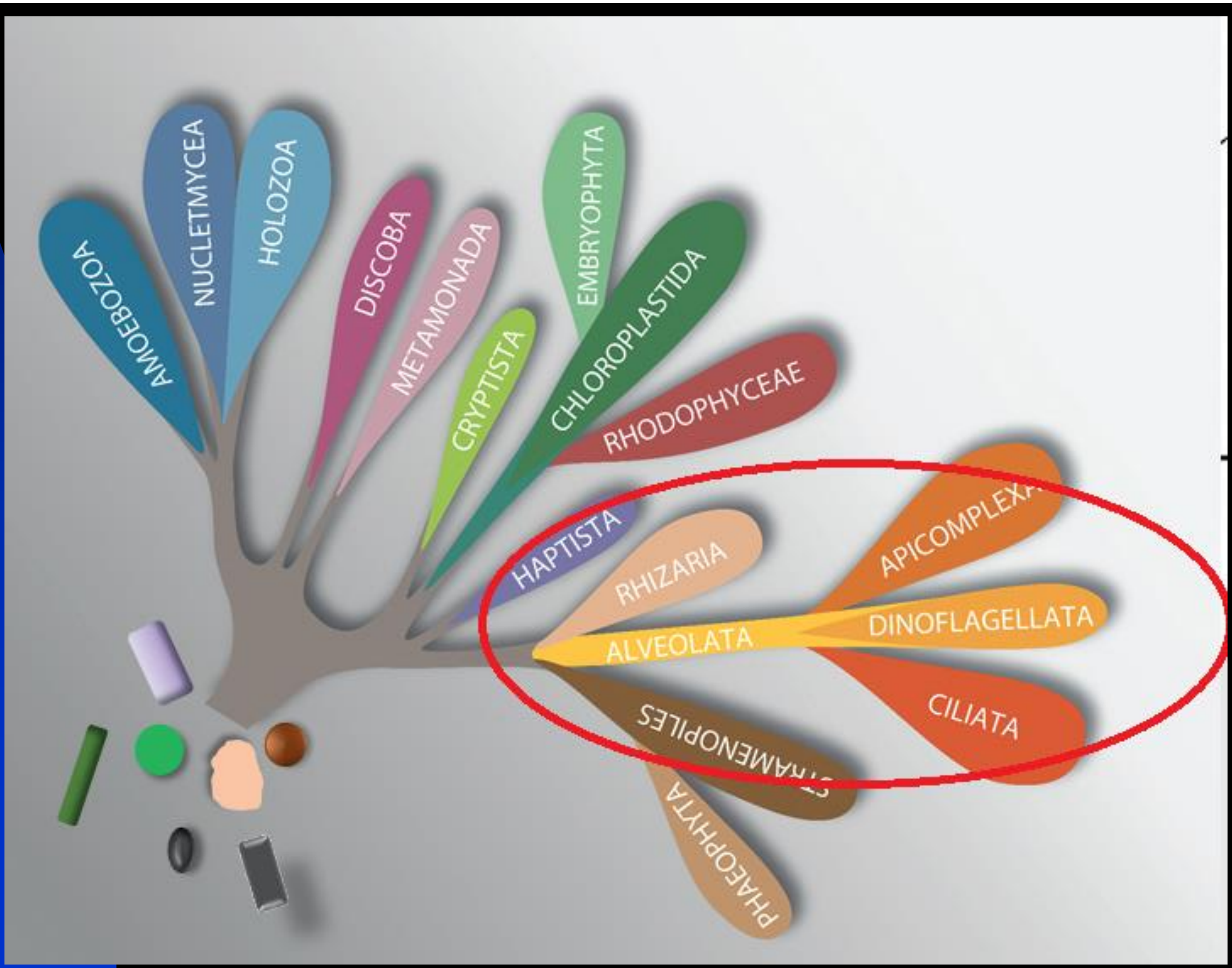
План лекції

1. Загальна характеристика Sar
2. Alveolata
3. Rizaria
4. Близькі до Sar клади першого рангу

1. Загальна характеристика

Sar Burki et al. 2008, emend. Adl et al. 2012

The least inclusive clade containing *Bigelowiella natans* Moestrup and Sengco 2001 (Rhizaria), *Tetrahymena thermophila* Nanney and McCoy 1976 (Alveolata), and *Thalassiosira pseudonana* Cleve 1873 (Stramenopiles). This is a node-based definition in which all of the specifiers are extant; it is intended to apply to a crown clade; qualifying clause—the name does not apply if any of the following fall within the specified clade—*Homo sapiens* Linnaeus 1758 (Opisthokonta), *Dictyostelium discoideum* Raper 1935 (Amoebozoa), *Arabidopsis thaliana* (Linnaeus) Heynhold 1842 (Archaeplastida), *Euglena gracilis* Klebs 1883 (Excavata), *Emiliania huxleyi* (Lohmann) Hay and Mohler in Hay et al. 1967 (Haptophyta). The name is derived from the acronym of the three groups united in this clade. The apparent composition of Sar is: Alveolata, Rhizaria and Stramenopiles, as defined in Adl et al. 2012. The primary reference phylogeny is Burki et al. (2008, Fig. 1).



2. Alveolata

*Alveolata Cavalier-Smith 1991

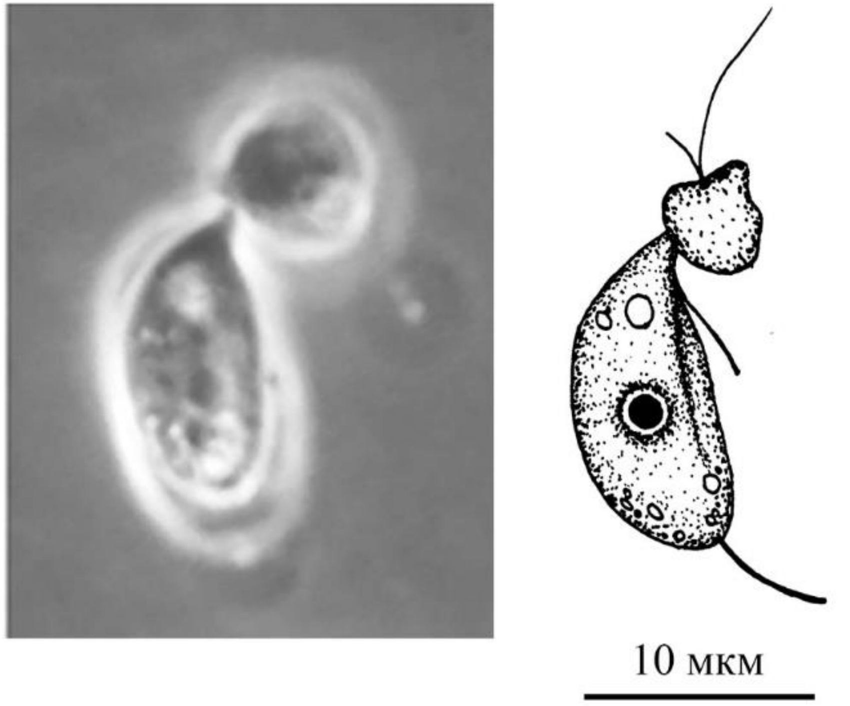
- **Alveolata** Cavalier-Smith 1991

Cortical alveolae, sometimes secondarily lost; with ciliary pit or micropore; mitochondrial cristae tubular or ampulliform.

**Colpodellida Cavalier-Smith 1993

●● Colpodellida Cavalier-Smith 1993, emend. Adl et al. 2005, 2019

Photosynthetic, or non-photosynthetic and predatory; complex plastids, when present bound by four membranes; mitochondrion with tubular cristae; highly flattened cortical alveoli; microtubules beneath alveolae; conoid-like structure with apical complex and rostrum; biciliate; micropore present; cysts at least in some species.



Colpodella edax (Klebs, 1892)

** Perkinsidae Lavine 1978

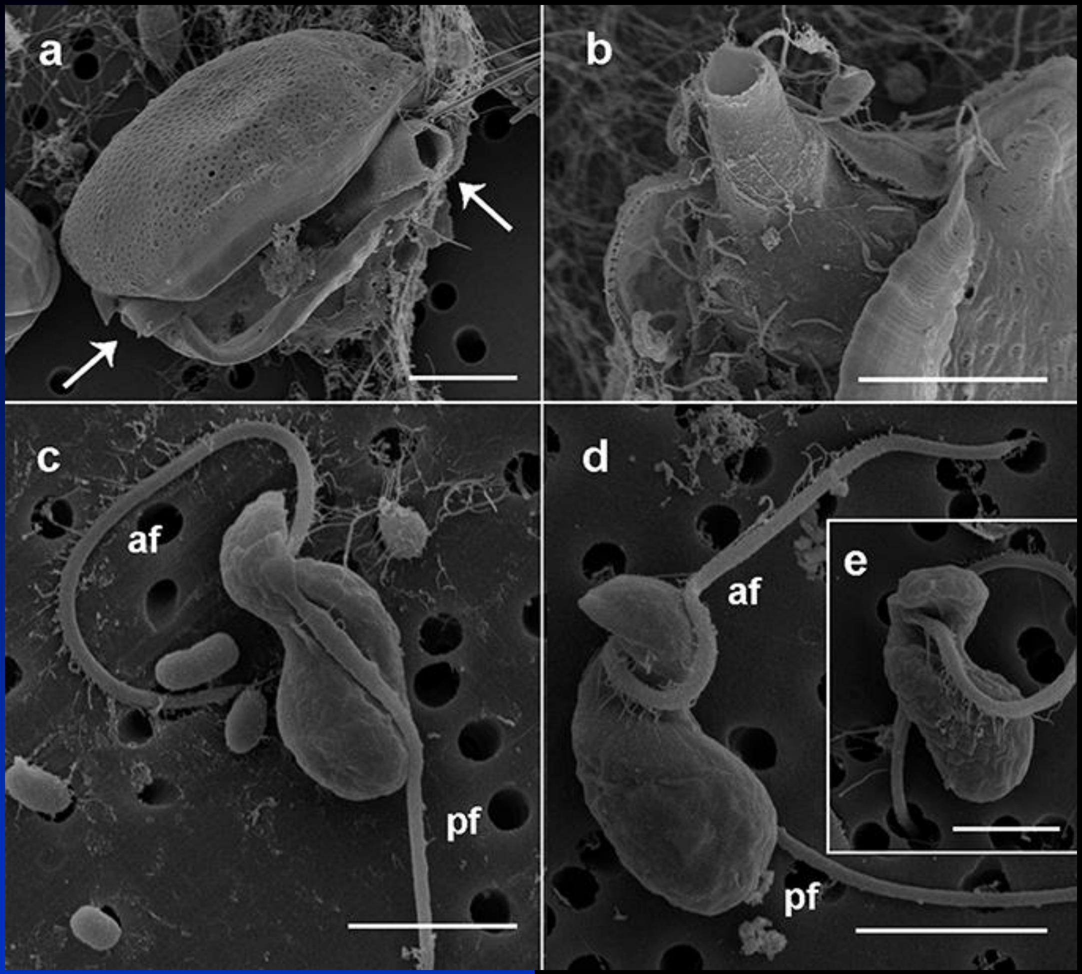
●● Perkinsidae Levine 1978, emend. Adl et al. 2005 [Perkinsozoa Moestrup & Rehnstam-Holm 1999; Perkinsozoa Norén & Moestrup 1999]
Trophozoites parasitic, dividing by successive binary fissions; released trophozoites (termed hypnospores) developing outside host to form zoospores via the formation of zoosporangia or morphologically undifferentiated mononucleate cells via a hypha-like tube; zoospores biciliate; apical organelles including an incomplete conoid (open along one side), rhoptries, micronemes and micropores, and a microtubular cytoskeleton with both an anterior and posterior polar ring. *Dinovorax, Snorkelia, Parvilucifera, Perkinsus, Rastrimonas,* X-cell parasites.

ORIGINAL RESEARCH ARTICLE
Front. Microbiol., 24 August 2017 | https://doi.org/10.3389/fmicb.2017.01594

Check for updates

Evolutionary Trends of Perkinsozoa (Alveolata) Characters Based on Observations of Two New Genera of Parasitoids of dinoflagellates, *Dinovorax* gen. nov. and *Snorkelia* gen. nov.

Albert Reñé*, Elisabet Alacid, Isabel Ferrera and Esther Garcés

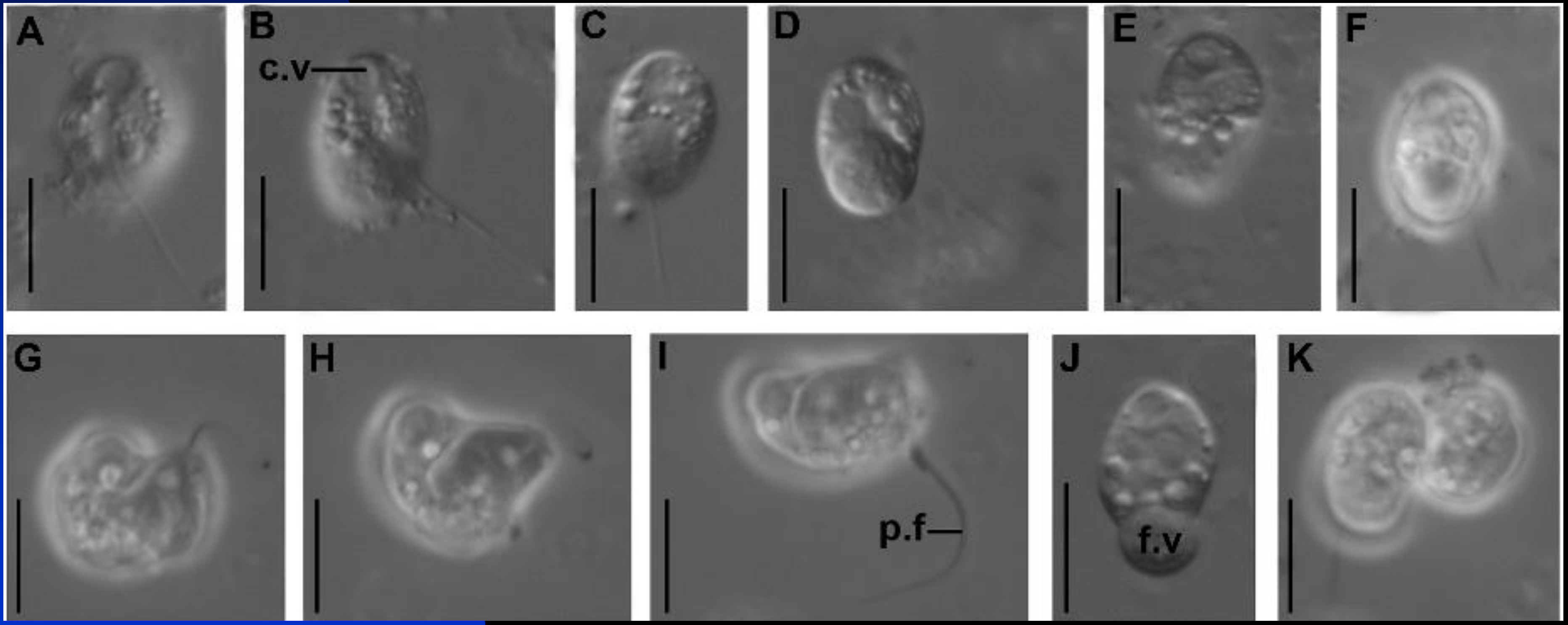


Scanning electron microscopy micrographs of the sporangia and zoospores of *Dinovorax pyriformis*

** Colponemida Cavalier-Smith 1993

●● Colponemida Cavalier-Smith 1993 emend. Adl et al. 2019 (P?)

Biciliate alveolates, typically cytotrophic predators, found in soil, freshwater and marine environments. These described genera are most probably multiple genera as DNA sequences obtained are divergent and many remain to be described. Poorly sampled due to cytotrophy, we expect better taxon sampling to improve the resolution of this node.



Colponema vietnamica

** Dinoflagellata Butschi 1885

●● Dinoflagellata Bütschli 1885, emend. Fensome et al. 1993, emend. Adl et al. 2005
Cells with two cilia in the motile stage—typically, one transverse cilium ribbon-like with multiple waves beating to the cell's left and longitudinal cilium beating posteriorly with only one or few waves; nucleus typically a dinokaryon with chromosomes remaining condensed during interphase and lacking typical eukaryotic histones and centrioles; dinoflagellate/viral nucleoproteins package chromatin; closed dinomitosis with extranuclear spindle.

***Noctilucales Haeckel 1894

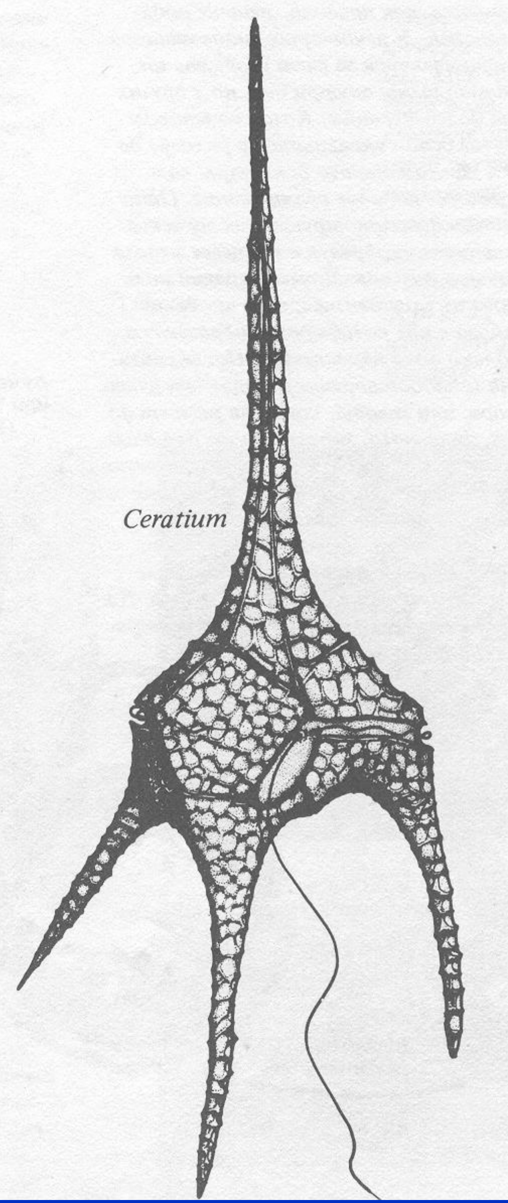
●●● Noctilucales Haeckel 1894 [Noctiluciphyceae Fensome et al. 1993]
Principal life cycle stage comprising a large free-living motile cell inflated by vacuoles; dinokaryon during part of life cycle only. Fossils unknown. *Abedinium, Cachonodinium, Craspedotella, Cymbodinium, Kofoidinium, Leptodiscus, Noctiluca, Petalodinium, Pomatodinium, Scaphodinium, Spatulodinium.*

Noctiluca

***Dinophyceae Pascher 1914

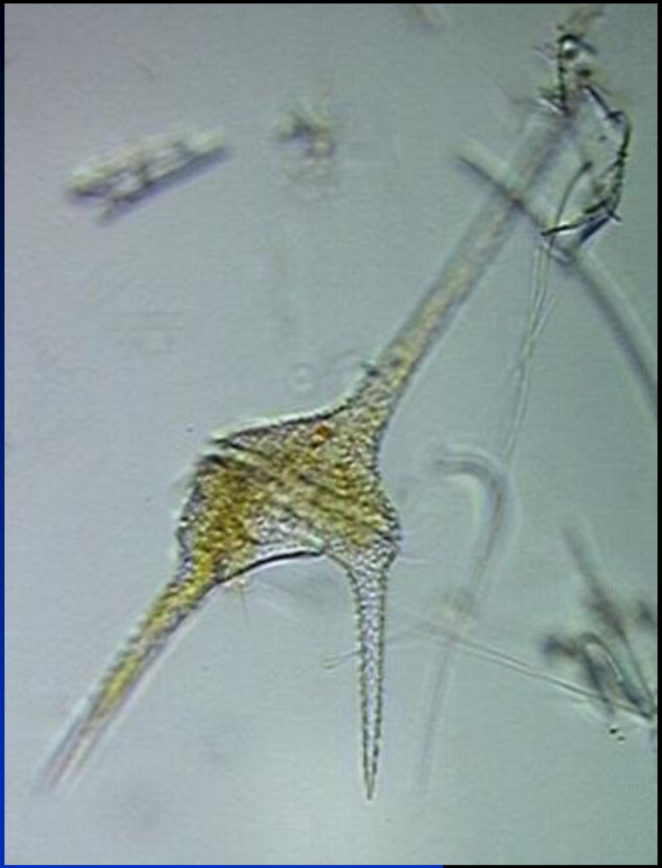
●●● Dinophyceae Pascher 1914

Cell cortex (amphiesma) containing alveolae (amphiesmal vesicles) that may or may not contain cellulosic thecal plates, the pattern (tabulation) thus formed being a crucial morphological criterion in recognizing affinities among dinophyceans; with a dinokaryon through the entire life cycle.

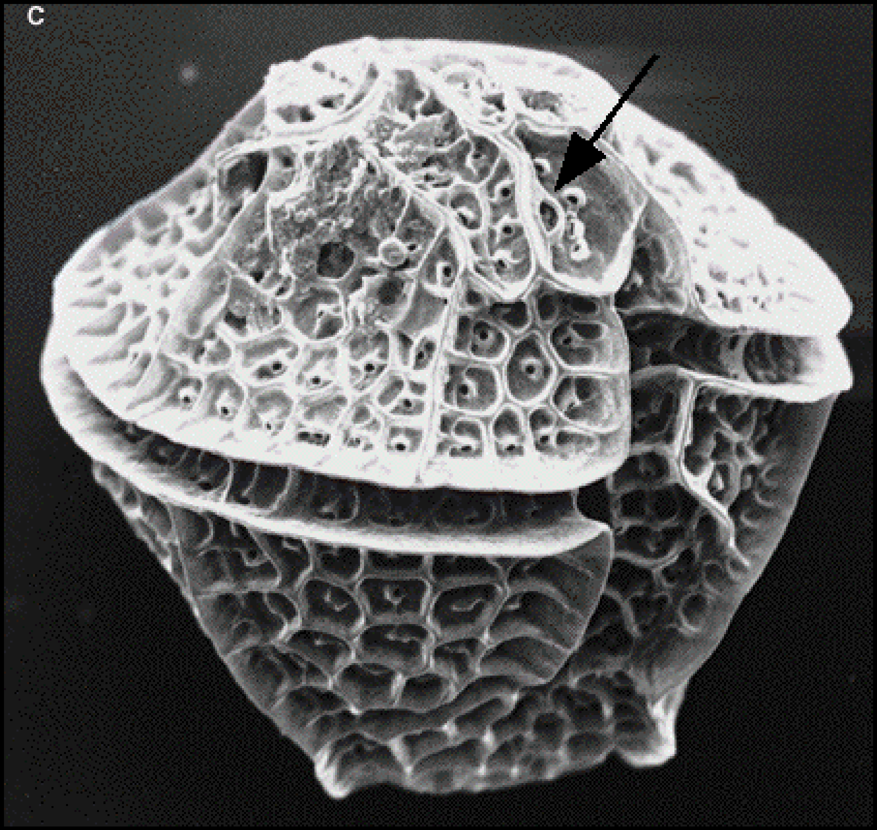


Ceratium sp.

1. **Клітини вкриті альвеольованою амфієсмою.**
2. Клітинні покриви з целюлозного панцира, або з органічних лусочок, клітинна оболонка целюлозно-пектинова.
3. Фоторецептор та стигма в цитоплазмі або в плазмалемі.
4. Тип пластид: вторинно-симбіотичні хлоропласти з 3 мембранами, вторинно-симбіотичні хлоропласти з 4 мембранами, пластидною ЕПС та нуклеоморфом, **третинно-симбіотичні родопласти з 5 мембранами та пластидною ЕПС.**
5. Пігменти: хлорофіл a + b, a + c, фікобіліни, фукоксантин, запасаюча речовина – хризоламінарин (цитоплазма), крохмаль (цитоплазма, перипластидний простір).
6. Морфологічні типи: монадний.



Ceratium



Goniaulax – альвеольована амфієсма

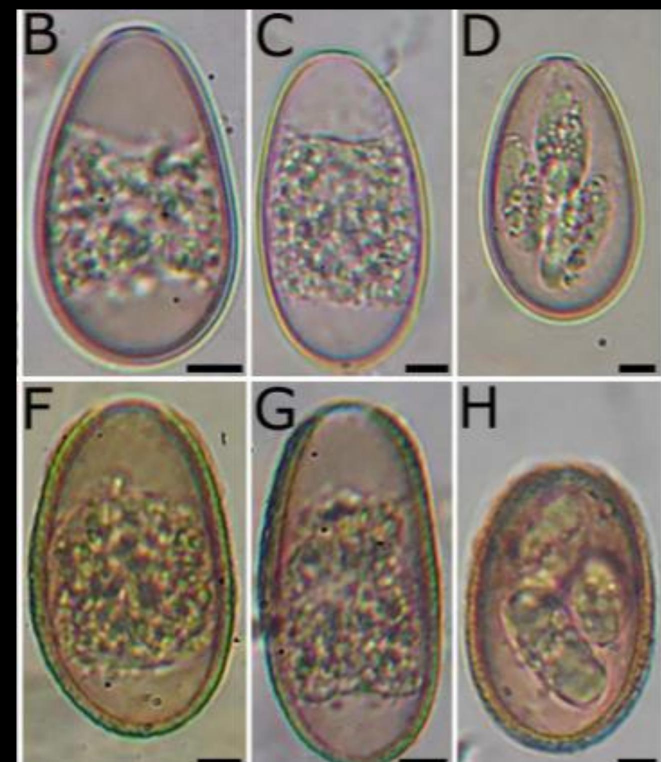
(Фото І.Ю. Костікова)

** Apicomplexa Levine 1980

●● Apicomplexa Levine 1980, emend. Adl et al. 2005

At least one stage of the life cycle with flattened subpellicular vesicles and an apical complex consisting of one or more polar rings, rhoptries, micronemes, conoid and subpellicular microtubules; sexuality, where known, by syngamy followed by immediate meiosis to produce haploid progeny; asexual reproduction of haploid stages occurring by binary fission, endodyogeny, endopolyogeny and/or schizogony/merogony; locomotion by gliding, body flexion, longitudinal ridges and/or cilia; mostly parasitic.

Plasmodium falciparum

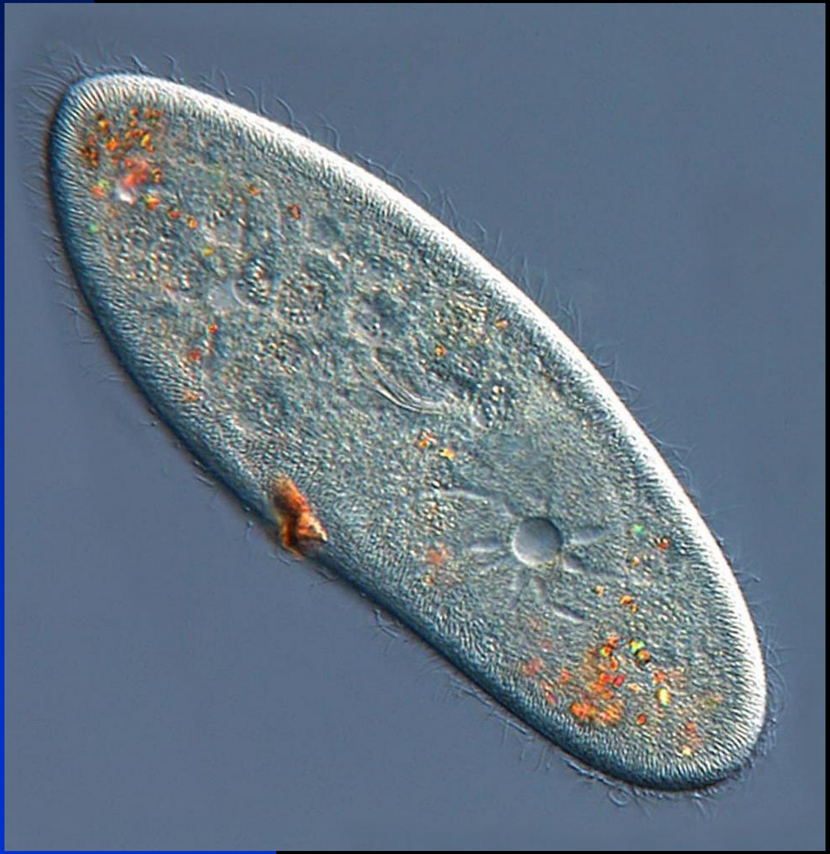


Eimeria sp.

**Ciliophora Dofien 1901

●● Ciliophora Doflein 1901 [Ciliata Perty 1852; Infusoria Bütschli 1887]

Cells with nuclear dimorphism, including a typically polygenomic macronucleus and at least one diploid micronucleus; somatic kinetids having a postciliary microtubular ribbon arising from triplet 9, a kinetodesmal fibril or striated rootlet homologue arising near triplets 5–8, and a transverse microtubular ribbon arising in the region of triplets 4–6; sexual reproduction, when present, by conjugation typically with mutual exchange of haploid gametic nuclei that fuse to form the synkaryon or zygotic nucleus.[35]



Paramecium caudatum

2. Rhizaria

*Rhizaria Cavalier-Smith 1902

● **Rhizaria** Cavalier-Smith 2002
With fine pseudopodia varying as simple, branching, or anastomosing patterns, often supported by microtubules in those groups examined by electron microscopy.

**Cercozoa Cavalier-Smith 1998

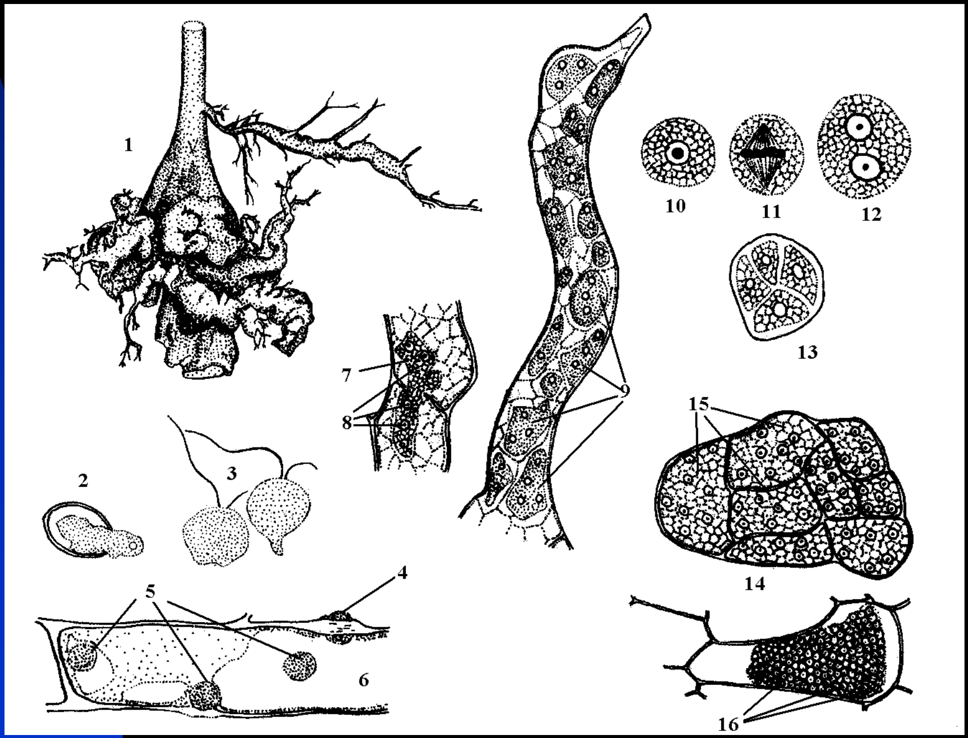
●● Cercozoa Cavalier-Smith 1998, emend. Adl et al. 2005; emend. Cavalier-Smith 2018
Diverse clade lacking distinctive morphological or behavioural characters; biciliated and/or amoeboid, usually with filopodia; most with tubular mitochondrial cristae; cysts common; kinetosomes connecting to nucleus with cytoskeleton; usually with microbodies and extrusomes.

Cercomonas sp.

**Endomyxa Cavalier-Smith 2002

●● Endomyxa Cavalier-Smith 2002, emend. Bass & Berney in Adl et al. 2019 (R)

This clade has varied somewhat in definition and composition but retains a core group of Rhizaria robustly distinct from Cercozoa and Retaria. Retaria as defined here is either a sister clade to Endomyxa, or branches within it. Numerous environmental lineages exist without morphological data. It is defined here as the least inclusive clade containing the last common ancestor of Vampyrellida, Phytomyxea, *Filoreta*, *Gromia*, Ascetosporea, and all its descendants.



Plasmodiophora brassicae

**Retaria Cavalier-Smith 2002

●● Retaria Cavalier-Smith 2002 (R)

Mainly marine heterotrophs, with reticulopodia or axopodia, and usually having various types of skeleton.

●●● Foraminifera d'Orbigny 1826

●●● Foraminifera d'Orbigny 1826

Filopodia with granular cytoplasm, forming branching and anastomosing network (reticulopodia); bidirectional rapid (10 mm/s) transport of intracellular granules and plasma membrane domains; tubular mitochondrial cristae; fuzzy-coated organelle of unknown function in reticulopodia; polymorphic assemblies of tubulin as (i) conventional microtubules singly or in loosely organized bundles, (ii) single helical filaments and (iii) helical filaments packed into paracrystalline arrays; majority of forms possess a test, which can be organic walled, agglutinated or calcareous; unusual characteristic beta-tubulin; wall structure in naked and single-chambered forms quite variable for "naked" athalamids, such as Reticulomyxa, thicker veins vested with an amorphous, mucoid material; for thecate (soft-walled) species, such as members of the genus *Allogromia*, proteinaceous with little or no foreign material; for agglutinated species, foreign materials bound with an amorphous or fibrous organic matrix; for multichambered (polythalamous) forms, walls containing agglutinated material or mineralized with calcite, aragonite, or silica; life cycle often comprising an alternation of asexually reproducing agamont and sexually reproducing gamont.

Elphidiella

Spirillina decorata

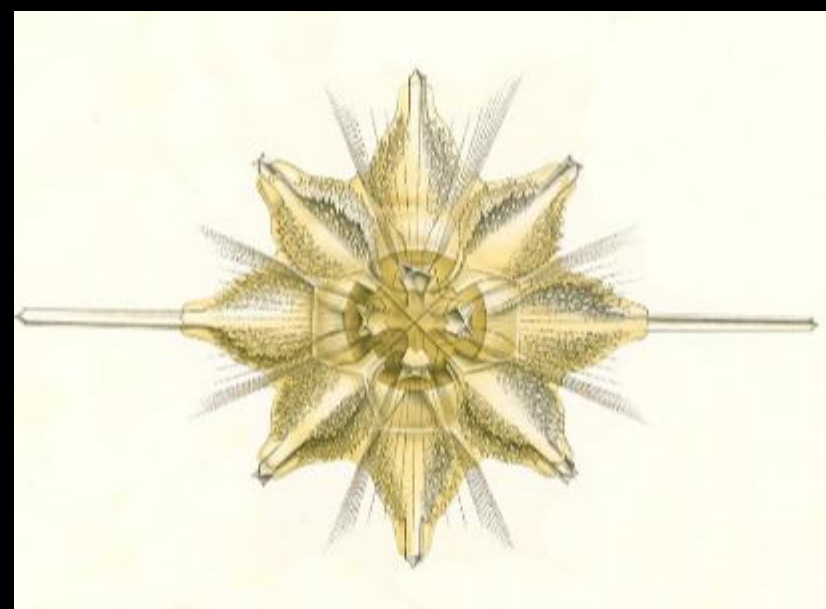
***Radiolaria Muller 1958

●●● Radiolaria Müller 1858, sensu Adl et al. 2005

Cells with distinctive organic, nonliving, porous capsular wall surrounding the intra-capsulum, which contains the nucleus or nuclei and cytoplasmic organelles; tubularcristae; axopodia supported by internal microtubules, extending distally through the capsular wall pores and connecting to a frothy external layer, the extracapsulum; extracapsulum containing digestive vacuoles and in some cases algal and/or cyanobacterial symbionts; skeletons, when present, of amorphous silica (opal) or strontiumsulphate (in Acantharia) and varying in shape from simple scattered spicules to highly ornate geometric-shaped shells, within and/or surrounding the central capsule; the siliceous skeleton is secreted within a specialized cytoplasmic envelope (cytokalymma) that dynamically determines the shape of the skeletal matter.

Anthocyrtium hispidum

Amphilithium clavarium



Acanthometra

**Aquavolonida Bass & Berney 2018

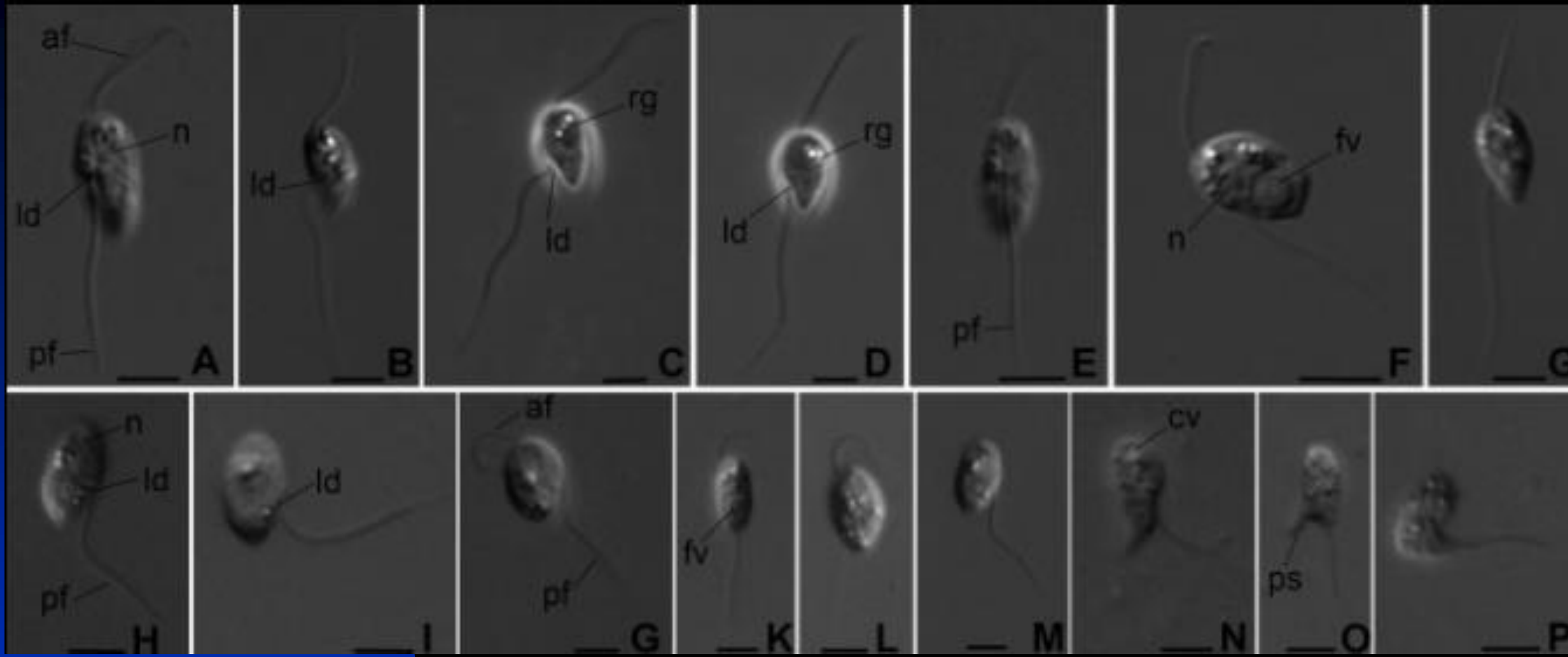
●● Aquavolonida Bass & Berney 2018

Defined as the least inclusive clade containing the last common ancestor of the rhizarian lineages sharing a unique combination of 18S rRNA sequence signatures consisting of two complementary substitutions from U-A to G-C and from G-C to C(U)-G(A) in helix 11, one complementary substitution from A-T to C(T)-G(A) in helix 48, and a specific motif of two adjacent substitutions (AU instead of YG) in a nonbinding part of the 3° stem of helix 25 and all their descendants.

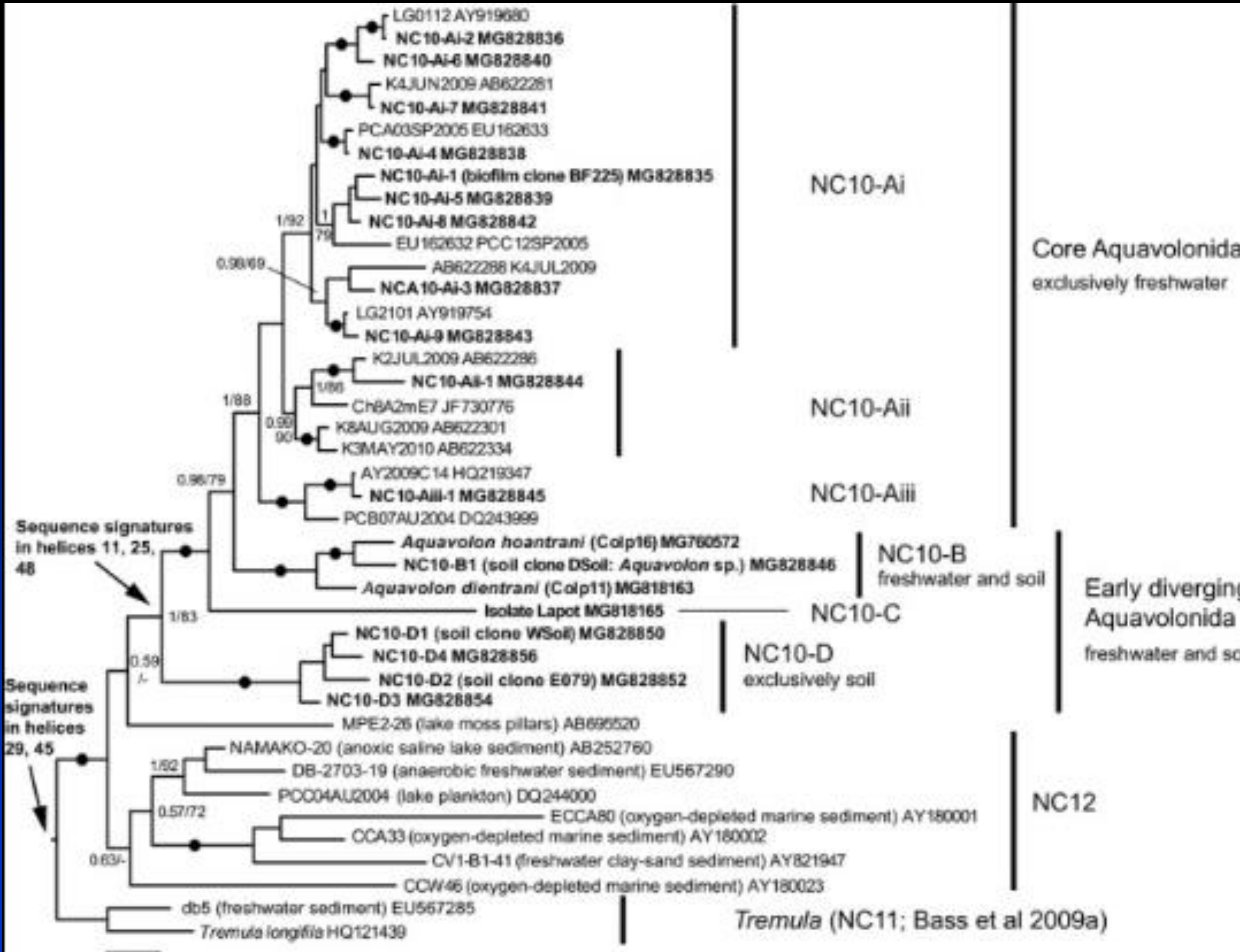
› J Eukaryot Microbiol. 2018 Nov;65(6):828-842. doi: 10.1111/jeu.12524. Epub 2018 May 14.

Rhizarian 'Novel Clade 10' Revealed as Abundant and Diverse Planktonic and Terrestrial Flagellates, Including Aquavolon N. Gen

David Bass [1] [2], Denis Victorovich Tikhonenkov [3] [4], Rachel Foster [1], Patricia Dyal [1], Jan Janouškovec [4] [5], Patrick J Keeling [4], Michelle Gardner [1], Sigrid Neuhauser [6], Hanna Hartikainen [1], Alexandre P Mylnikov [3], Cédric Berney [1]



Aquavolon hoantrani та *A. dientrani*


LG0112 AY919680
NC10-Ai-2 MG828836
NC10-Ai-6 MG828840
K4JUN2009 AB622281
NC10-Ai-7 MG828841
PCA03SP2005 EU162633
NC10-Ai-4 MG828838
NC10-Ai-1 (biofilm clone BF225) MG828835
NC10-Ai-5 MG828839
NC10-Ai-8 MG828842
EU162632 PCC12SP2005
AB622288 K4JUL2009
NCA10-Ai-3 MG828837
LG2101 AY919754
NC10-Ai-9 MG828843
K2JUL2009 AB622286
NC10-Aii-1 MG828844
Ch8A2mE7 JF730776
K8AUG2009 AB622301
K3MAY2010 AB622334
AY2009C14 HQ219347
NC10-Aiii-1 MG828845
PCB07AU2004 DQ243999
Aquavolon hoantrani (Colp16) MG760572
NC10-B1 (soil clone DSoil: Aquavolon sp.) MG828846
Aquavolon dientrani (Colp11) MG818163
Isolate Lapot MG818165
NC10-D1 (soil clone WSoil) MG828850
NC10-D4 MG828856
NC10-D2 (soil clone E079) MG828852
NC10-D3 MG828854
MPE2-26 (lake moss pillars) AB695520
NAMAKO-20 (anoxic saline lake sediment) AB252760
DB-2703-19 (anaerobic freshwater sediment) EU567290
PCC04AU2004 (lake plankton) DQ244000
ECCA80 (oxygen-depleted marine sediment) AY180001
CCA33 (oxygen-depleted marine sediment) AY180002
CV1-B1-41 (freshwater clay-sand sediment) AY821947
CCW46 (oxygen-depleted marine sediment) AY180023
db5 (freshwater sediment) EU567285
Tremula longifila HQ121439
1/92
0.98/69
1
79
1/88
1/86
0.99/90
0.98/79
1/83
0.59/-
1/92
0.57/72
0.63/-
Sequence signatures in helices 11, 25, 48
Sequence signatures in helices 29, 45
NC10-Ai
NC10-Aii
NC10-Aiii
NC10-B
freshwater and soil
NC10-C
NC10-D
exclusively soil
NC12
Tremula (NC11; Bass et al 2009a)
Core Aquavolonida
exclusively freshwater
Early diverging Aquavolonida
freshwater and soil

3. Близькі до Sar клади

*Haptista Cavalier-Smith 2003

- **Haptista** Cavalier-Smith 2003

Thin microtubule-based appendages (haptonema or axopodia) used for feeding; complex mineralized (siliceous or calcareous) scales.

**Haptophyta Hibberd 1976

●● Haptophyta Hibberd 1976, ex. Edvardsen & Eikrem 2000

Autotrophic, mixotrophic or heterotrophic single cells; some in colonies, or a few filamentous; motile cells mostly possessing a haptonema, a filiform appendage situated between one pair of cilia; characteristic cell covering of unmineralized and/or mineralized scales; motile cells with two cilia generally without appendages, inserted apically or subapically; usually one or two chloroplasts with thylakoids in groups of three and with no girdle lamella; chloroplasts with immersed or bulging pyrenoid; nucleus usually posterior or central; outer membrane of nuclear envelope continuous with outer chloroplast membrane; major pigments chlorophylls *a*, *c1*, and *c2* with *c3* in prymnesiophyceans, fucoxanthin (e.g. 19′ hexanoyloxyfucoxanthin, 19′butanoyloxyfucoxnthin), beta-carotene, diadinoxanthin and diatoxanthin; chrysolaminarin often the main storage product; eyespots recorded in a few genera (*Pavlova*, *Diacronema*); haplo-diploid life cycles including heteromorphic alternating stages; motile, ciliated stage may alternate with nonmotile palmelloid (colonial), single-celled or filamentous stages, or with motile, ciliated stages; sexual reproduction may be common in prymnesiophyceans; some species ichthyotoxic.

Відділ Haptophyta

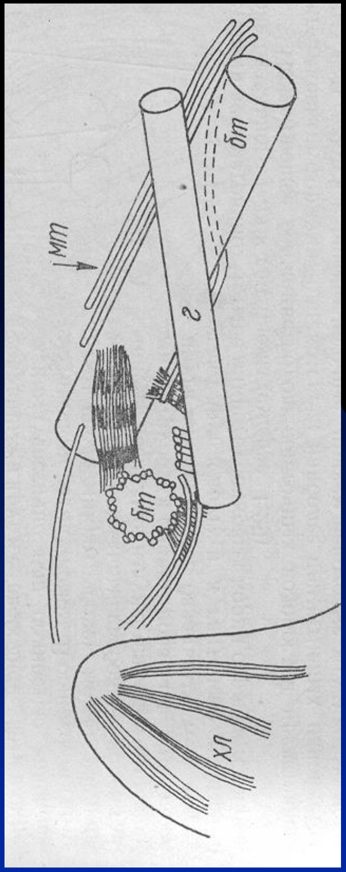


Схема джгутикового апарату Chrysochromulina aphles:
хл – хлоропласт,
бт – базальне тіло,
г – гаптонема,
мт – мікротрубочка.

300 видів

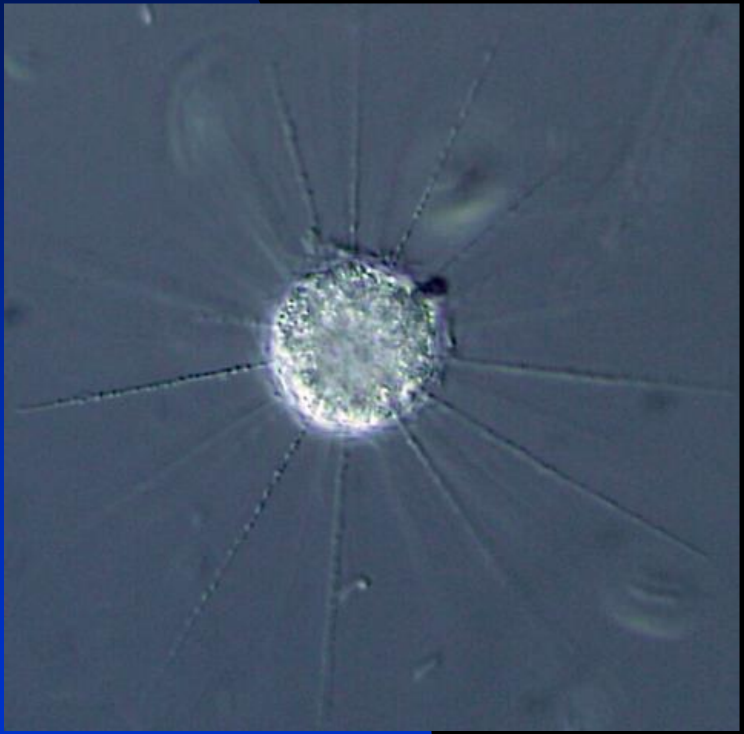
1. Джгутики – два ізоконтних, ізоморфних джгутиків, вкритих повстю з простих волосків чи дрібненькими лусочками (без ретронем).
2. Унікальною є нерухома нитковидна структура – **гаптонема,** що схожа на джгутик, але в ній відсутня центральна пара мікротрубочок, а периферичні мікротрубочки представлені меншою кількістю і не утворюють дублетів.
3. Поверхня клітин вкрита кокколітами (вапняковими чи мінералізованими лусочками), а з внутрішнього боку мембрани підстелена оперезуючою цистерною ендоплазматичної сітки.
4. Тип пластид: вторинно-симбіотичні родопласти з 4 мембранами, пластидною ЕПС, що переходить в ядерну оболонку.
5. Пігменти: хлорофіл а + с, фукоксантин, запасаюча речовина хризоламінарин та парамілон (в цитоплазмі).
6. Фоторецептор в цитоплазмі, стигма в пластиді.
7. Еджективні органели: мукоцисти.
8. Мітоз відкритий, центріолі відсутні.
9. Морфологічний тип: монадний.

Prymnesium

Emiliania

** Centroplasthelida Febvre-Chevalier 1984

●● Centroplasthelida Febvre-Chevalier & Febvre 1984[38] [Centrohelea Kühn 1926 sensu Cavalier-Smith in Yabuki et al. 2012; Centroheliozoa Dürrschmidt & Patterson 1987]
Without cilium; naked or covered with mucous, usually with organic or mineralized elements (scales) embedded in it; axopodia supported by microtubules forming hexagon-related pattern; ball-and-cone structure containing kinetocyst extrusomes along axopodia; centrosome as trilaminar disc with fibrous electron-dense cortex, flat mitochondrial cristae.



Raphidiophrys

*Cryptista Adl et al. 2019

- **Cryptista**[43] Adl et al. 2019 [Cavalier-Smith 1989, 2018] (R)

This is a node-based definition for the clade stemming from the most recent common ancestor of *Cryptomonas*, *Goniomonas*, *Kathablepharis*, and *Palpitomonas*. The name does not apply if any of the following fall within the specified clade: *Glaucocystis nostochinearum*, *Chlamydomonas reinhardtii*, *Telonema subtilis*, *Emiliana huxleyi*.

**Palpitomonas Yabuki & Ishida 2010

●● *Palpitomonas* Yabuki & Ishida 2010 (M)
Marine isolate, free-living heterotrophic, heterokont biciliate, with unilateral bipartite mastigonemes on anterior cilium; cilia emerge on left side with anterior cilium vigorous and trailing posterior cilium; when swimming, in slow gyromotion; one cilium can adhere to substratum; double-layered MLS-like structure on one ciliary root; vacuolated cytoplasm; phagotrophic on bacteria; without ejectisomes; flat mitochondrial cristae. *Palpitomonas bilix*.

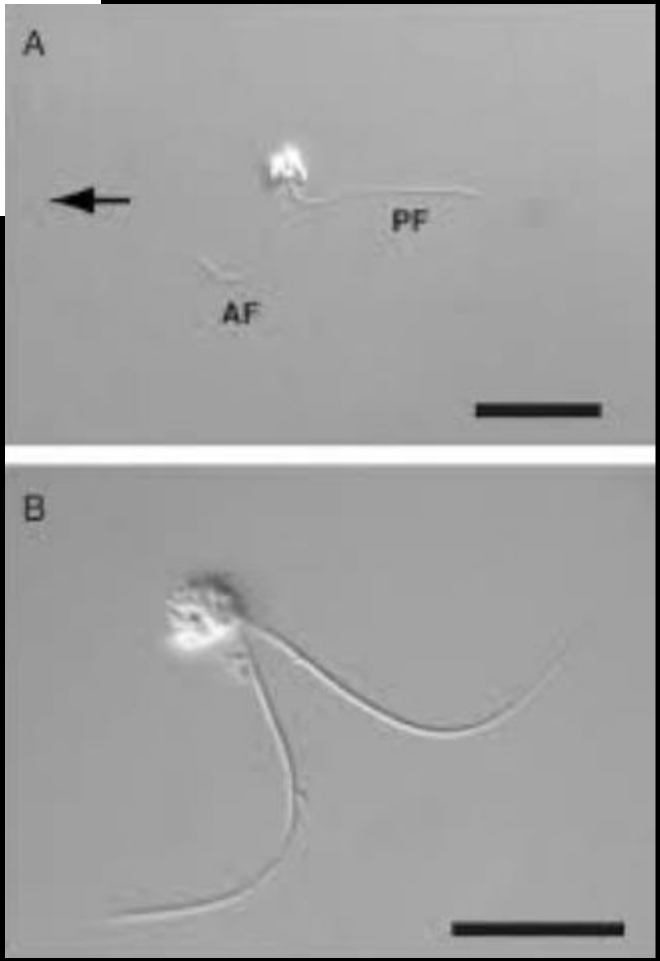
Protist

Volume 161, Issue 4, October 2010, Pages 523-538

ORIGINAL PAPER

Palpitomonas bilix gen. et sp. nov.: A Novel Deep-branching Heterotroph Possibly Related to Archaeplastida or Hacrobia

Akinori Yabuki [a], Yuji Inagaki [a,b], Ken-ichiro Ishida [a]



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Palpitomonas bilix represents a basal cryptist lineage: insight into the character evolution in Cryptista

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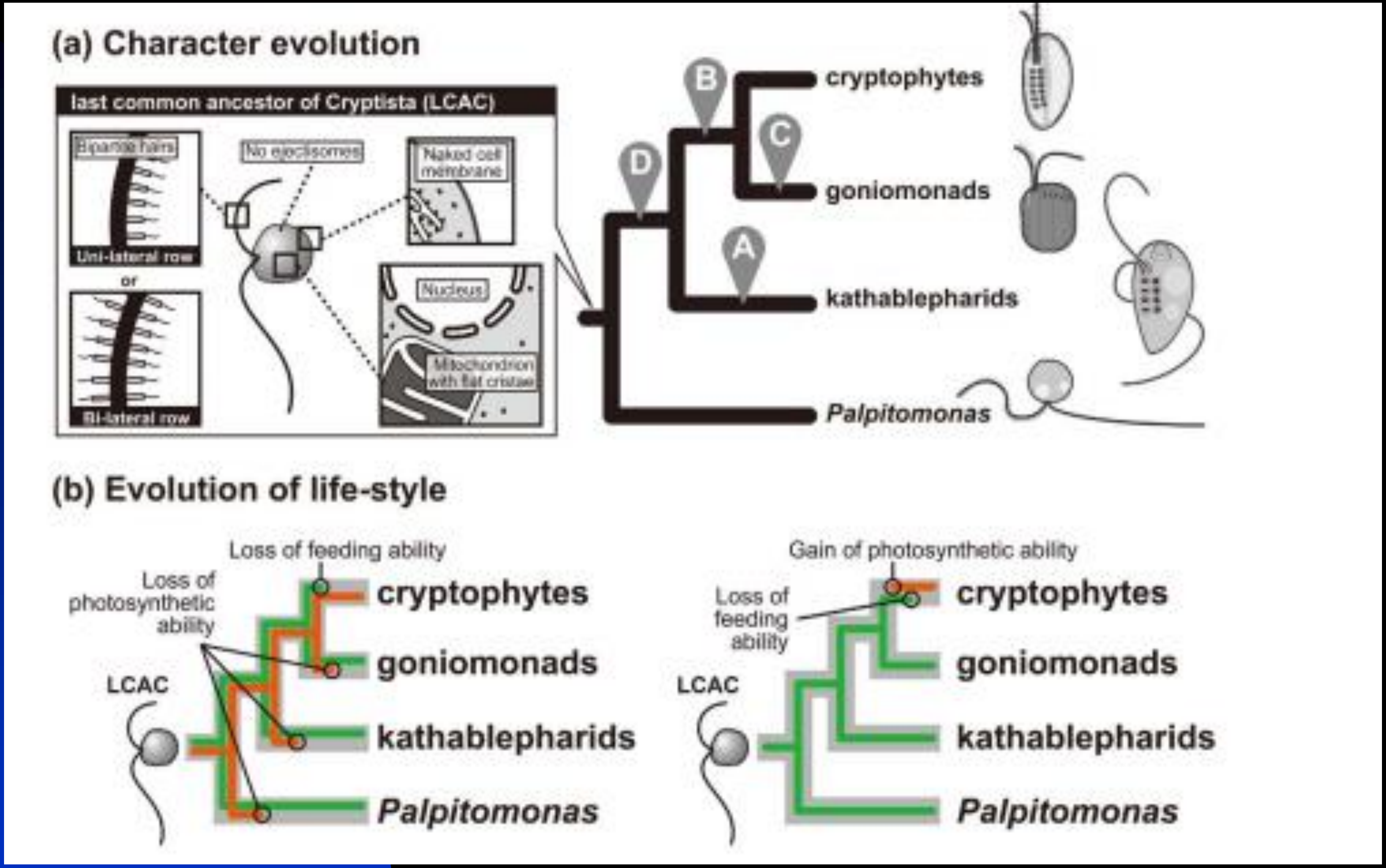
Phylogenetic position of the marine biflagellate *Palpitomonas bilix* is intriguing, since several ultrastructural characteristics implied its evolutionary connection to Archaeplastida or Hacrobia. The origin and early evolution of these two eukaryotic assemblages have yet to be fully elucidated, and *P. bilix* may be a key lineage in tracing those groups' early evolution. In the present study, we analyzed a 'phylogenomic' alignment of 157 genes to clarify the position of *P. bilix* in eukaryotic phylogeny. In the 157-gene phylogeny, *P. bilix* was found to be basal to a clade of cryptophytes, goniomonads and kathablepharids, collectively known as Cryptista, which is proposed to be a part of the larger taxonomic assemblage Hacrobia. We here discuss the taxonomic assignment of *P. bilix*, and character evolution in Cryptista.

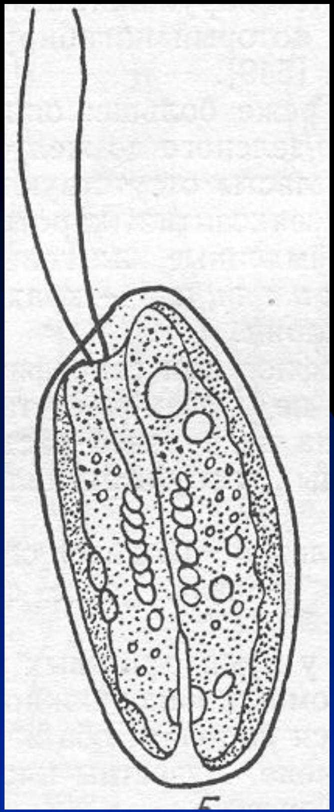


Філогенія Criptista

**Cryptophyceae Pascher 1913

●● Cryptophyceae Pascher 1913, emend. Schoenichen 1925, emend. Adl et al. 2012 [Cryptophyta Silva 1962; Cryptophyta Cavalier-Smith 1986]

Autotrophic, mixotrophic or heterotrophic with ejectisomes (trichocysts); mitochondrial cristae flat tubules; two cilia emerging subapically or dorsally from right side of an anterior depression (vestibulum); longitudinal grooves (furrows) and/or tubular channels (gullets) or a combination of both, extending posteriorly from the vestibublum on the ventral side; gullet/furrow complexes lined with large ejectisomes; with or without plastid nucleomorph complex; chloroplasts when present contain chlorophylls *a* and *c*2 and phycobiliproteins, located in thylakoid lumen; chloroplast covering comprised of inner and superficial periplast components (IPC and SPC respectively); includes heterotrophic species formerly known as *Chilomonas* and some genera diplomorphic such as *Cryptomonas* and *Proteomonas*.



Cryptomonas ovata

Відділ Cryptophyta

200 видів

Унікальним серед клітинних покривів є перипласт, а також целюлозно-пектинова клітинна оболонка, органічні лусочки.

- Джгутики: два гетероконтні, з простою або пірчастою мастигонемою з пірчастим або гребінчастим розташуванням.
- Мітоз закритий, центріолі відсутні.
- Фоторецептор та стигма в пластиді (не мають зв’язку з джгутиками).
- Тип пластиди: вторинно-симбіотичні родопласти з 4 мембранми, пластидною ЕПС, що переходить в ядерну оболонку та нуклеоморфом.
- Пігменти: хлорофіл а + с, фікобіліни, запасаюча речовина крохмаль (в перипластидному просторі).
- Еджектосоми.
- Морфологічний тип: монадний.

Cryptomonas

(Фото І.Ю. Костікова)

Рекомендована література:

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Питання для самостійної роботи:

1. Обсяг та характеристика Alveolata та Rhizaria, як груп першого рангу та положення представників групи в класичних таксономічних системах.
2. Особливе положення груп першого рангу Crypista та Haptista. Загальна характеристика, обсяг та місце в класичних таксономічних схемах.
3. Знайти оригінальні відомості в інтернет просторі про одного представника з наступних груп другого рангу: Colpodellida, Perkinsidae, Colponemida, Dinoflagellata, Apicomplexa, Ciliophora, Cercozoa, Endomyxa, Retaria, Aquavolonida, Haptophyta, Centroplasthelida, Palpitomonas, Cryptophyceae. На основі знайдених в інтернеті публікацій, з урахуванням філогенетичних та молекулярних даних, надати коротку характеристику, яка б включала: морфологічний тип, специфічні морфологічні або біохімічні особливості, екологічні особливості, місце в системі органічного світу та реальне або ймовірне використання.