Wolfgang Frey (Editor)

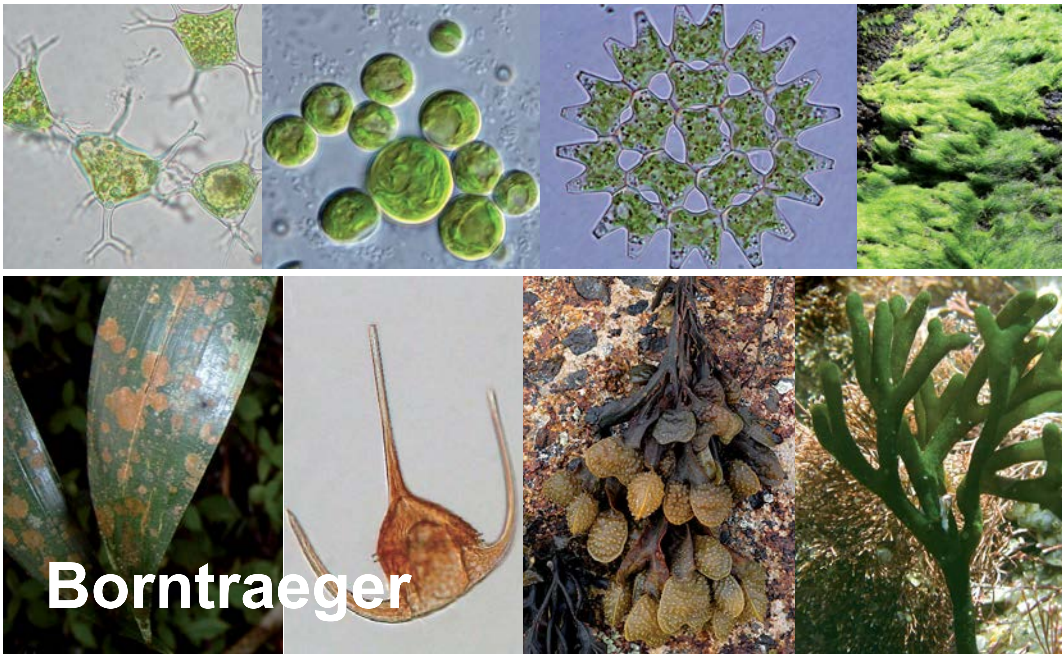
Syllabus of Plant Families

13th ed.

A. Engler's Syllabus der Pflanzenfamilien

2/1 **Photoautotrophic eukaryotic Algae**

Glaucocystophyta, Cryptophyta, Dinophyta/Dinozoa, Haptophyta, Heterokontophyta/Ochrophyta, Chlorarachniophyta/Cercozoa, Euglenophyta/Euglenozoa, Chlorophyta, Streptophyta p.p.



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Adolf Engler's Syllabus der Pflanzenfamilien

13th edition by Wolfgang Frey

Part 2/1 Photoautotrophic eukaryotic Algae

Glaucocystophyta, Cryptophyta, Dinophyta/Dinozoa, Haptophyta, Heterokontophyta/Ochrophyta, Chlorarachniophyta/Cercozoa, Euglenophyta/Euglenozoa, Chlorophyta, Streptophyta p.p.

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Pseudostaurastrum limneticum (Borge) Couté & G.Rousselin Photo: W.K. Hofbauer.
Dictyochloropsis spec. Unicellular coccoid microalgae with single reticulate chloroplast. Photo: J. Neustupa.
Pediastrum duplex Meyen Perforated coenobium. Photo: P. Škaloud.
Ulva spec. Thalli. Photo: F. Leliaert.
Phycopeltis treubii Karsten Epiphyllous disc-like thalli. Photo: F. Leliaert.
Ceratium tripos (O.F.Müller) Nitzsch Cell. Photo: H. Kawai & T. Nakayama.
Fucus guiryi G.I.Zardi, K.R.Nicastro, E.S.Serrão & al. Thallus. Conceptacles clustered as defined receptacles. Photo: B. de Reviers.
Codium duthieae P.C.Silva Siphonal thallus. Photo: O. De Clerck.

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Preface

Half a century ago, the 12th edition (vol. 1, 1954; vol. 2, 1964) of Adolf Engler's well-known "Syllabus der Pflanzenfamilien" ("Syllabus of Plant Families"), ed. by H. Melchior and E. Werdermann was published. Later, a revision of the mosses (13th ed., Kapitel V,2 Bryophytina) by K. Walther, followed in 1983.

The 13th edition will be published in five parts, starting in 2009 with **Part 3** "**Bryophytes and seedless Vascular Plants"**, followed in 2012 by **Part 1/1** "**Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p.**" and in 2015 by **Part 4** "**Pinopsida** (Gymnosperms), **Magnoliopsida** (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)]. Now **Part 2/1** "**Photoautotrophic eukaryotic Algae* Glaucocystophyta, Cryptophyta, Dinophyta, Haptophyta, Heterokontophyta, Chlorarachniophyta, Euglenophyta, Chlorophyta, Streptophyta p.p.**" follows. The **Rhodobionta** will be treated in Part 2/2.

As noted in **Part 3** "**Bryophytes and seedless Vascular Plants**", DNA sequencing and advances in phylogenetic analysis raised new interest in the relationships within and between Blue-green algae, Myxomycetes and Myxomycete-like organisms, heterotrophic Heterokontobionta, Algae, Fungi and Embryophytes. Now numerous molecular analyses led to new insights and a better understanding of the evolution and systematics of the lowermost groups. On the other hand, "classical" morphological and taxonomical expertise is in decline, especially for less showy groups of organisms. As also noted in Part 3, "we are convinced that in the 'molecular times' there is an indispensable need to preserve the knowledge of the whole diversity and biology of organisms for the next generations. Otherwise, we will not be able to educate experts in the future who will maintain our knowledge of the full range of the earth's biodiversity".

Following the tradition of Engler, and incorporating the latest results from molecular phylogenetics and phylogenomics, the editor and the authors hope to have created an up-to-date overview of families and genera that will serve as reference for a long time.

The authors and the editor are grateful to the publisher, Dr. A. Nägele, for realizing the basic and fundamental systematic treatment, the **Syllabus of Plant Families**.

Berlin, August 2014 W. Frey

Contents

Abbreviations/Symbols

acc.	according to
approx.	approximately
C	Central, central
c.	circa, about, approximately
cf.	confer, compare, see
cm	centimetre
comm.	communication
cosmopol.	cosmopolitan
CS	cross-section
diam.	diameter
distrib.	distribution
E	East
E N S W	East, North, South, West
e.g.	for example, exempli gratia
esp.	especially
et al.	"et alii" (masc.) bzw. "et aliae" (fem.), "and others".
excl.	excluding
ext.	extending
fam.	family, families
gen.	genus, genera
I., Is., is.	island, isle; islands, isles
i.e.	that is, id est
inc. sed.	incertae sedis, broader relationship to other taxa is unknown
incl.	including
ined.	inedited, not published
loc. cit.	locus cited, loco citato
LS	longitudinal section
Ma	million of years ago
medit., Medit.	mediterranean, Mediterranean region
N	North
N Africa	North Africa
nom. cons.	nomen conservandum , conserved name
nom. illeg.	nomen illegitimum, illegitimate name
nom. provis.	nomen provisorium, provisional name
occ.	occasional, occasionally
ord.	order, orders
orig.	originally, original
pers.	personal
p.p.	pro parte
predom.	predominant, predominantly
prob.	probably
resp.	respectively
S	South
s.ab.	see above
S Australia	South Australia
s.bl.	see below
s.l.	sensu lato

spec., sp.	species
spp.	species (plural)
s.str.	sensu stricto
subcl.	subclass
subfam.	subfamily, subfamilies
subtrop.	subtropical, subtropics
SW	South West
syn.	synonym, synonymous (not in all)
temp.	temperate, in temperate zones
trop., Trop.	tropical, tropics, Tropic (geo)element, Tropics
vs	versus
W	West
(5)	number of species
†	extinct
±	more or less
&	and

1 Introduction

The last three decades provided revolutionary new insights into the diversity and phylogeny of organisms on earth, not only in flowering plants, but also in lower plants and in the basal organisms on earth like the photoautotrophic eukaryotic Algae* (Glaucobionta, Rhodobionta, Cryptophyta, Dinophyta, Haptophyta, photoautotrophic Heterokontophyta, Chlorarachniophyta, Euglenophyta, Chlorophyta and Streptophyta p.p.). These groups of organisms, which are extremely diverse and which are the primary producers for all the oceans and seas, and in freshwater lakes, ponds and streams, have also been the focus of intensive research studies within the last three decades. The new molecular results allow now a new understanding of the relationships between the different phylogenetic lineages in algae. The relationships were dramatically revised and we have now a better understanding of the systematics of this phylogenetic assemblage [**Glaucobionta** (glaucophyte lineage), **Rhodobionta** (red algal lineage), **Cryptophyta, Dinophyta, Haptophyta, Heterokontophyta**) (chromophyte, dinophyte and cryptophyte lineage), **Chlorarachniophyta/Cercozoa** (chloroarachniophyte lineage), **Euglenophyta/Euglenozoa** (euglenophyte lineage), and **Chlorophyta, Streptophyta** p.p. (green algal lineage)] from the recent molecular phylogenies.

Part 2/1 of the 13th edition of “Engler’s Syllabus of Plant Families” gives an up-to-date review of the photoautotrophic eukaryotic Algae, except Rhodobionta, which will be treated in an own Part 2/2. The taxa are treated from subregnum to genus level, integrating morphological-anatomical and molecular data.

W. Frey

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* Included are heterotrophic genera, e.g., species of dinoflagellates and euglenids.

2 Photoautotrophic eukaryotic Algae*

Glaucocystophyta, Cryptophyta, Dinophyta/Dinozoa, Haptophyta, Heterokontophyta/ Ochrophyta, Chlorarachniophyta/Cercozoa, Euglenophyta/Euglenozoa, Chlorophyta, Streptophyta p.p

Algae s.str. Organisation type "Eukaryotic Algae", a polyphyletic assemblage of six distinct phylogenetic lineages: **Glaucobionta** (glaucophyte lineage), **Rhodobionta** (red algal lineage) (not treated in this volume), **Cryptophyta**, **Dinophyta**, **Haptophyta**, and **Hetero-kontophyta** (chromophyte, dinophyte and cryptophyte lineage), **Chlorarachniophyta/ Cercozoa** (chloroarachniophyte lineage), **Euglenophyta/Euglenozoa** (euglenophyte lineage), and **Chlorophyta**, **Streptophyta** p.p. (green algal lineage).

Algae are extremely diverse, ranging from amoeboid and unicellular species to multicellular forms and parenchymatic or plectenchymatic tissue thalli, lacking most tissue types of land plants (e.g., stomata, xylem, phloem). Most taxa are autotrophic with oxygene photosynthesis. Plastid types are "cyanelles", rhodo- and chloroplasts. Chlorophyll *a* is common to all groups, other types of photosynthetic pigments are chlorophyll *b* and *c* and known accessory pigments are carotenoids , xanthophylls, and phycobilins. 40% of global photosynthesis is contributed by algae. A wide range of reproductive strategies, ranging from simple asexual cell division to complex forms of sexual reproduction is known. C. 40 000 species, which are mostly adapted to water. Eukaryotic algae are primary producers in oceans and seas, occurring also in freshwater lakes, ponds and streams as well as on and in soil, rocks, ice, snow, and as symbiotic partners of plants, fungi and animals. Fossilized filamentous algae date back c. 1600 to 1700 Ma.

The **phylogenetic lineages** are characterized by the authors of this volume (cf. the different chapters, pers. comm.). "The **Glaucocystophyta** in the sense of Graham et al. (2009) form a distinctive monophyletic group of primary plastid bearing organisms, according to ultrastructural and molecular investigations and recent understanding. The photosynthetic organelles of this group of algae are distinct from the chloroplasts of other organisms because they possess a (rudimentary) peptidoglycan wall between their two membranes" (Hofbauer). The name **Heterokontobionta** (cf. Strasburger 36. Aufl., 2008) "is applied to those eukaryotes and their descendants producing heterokont flagellated cells, regardless of trophic modes, including four phylogenetically distinctive lineages and both autotrophic (mixotrophic) and heterotrophic members. Note that due "recent molecular data do not support

* Included are heterotrophic genera, e.g., species of dinoflagellates and euglenids.

the "Heterokontobionta" in this sense (Heterokontobionta s.l.). Stramenopiles (incl. Heterokontophyta/Ochrophyta) and Alveolata (incl. Dinophyta/Dinozoa) form a clade (SAR-clade or subkingdom Harosa) with Rhizaria (incl. chlorarachnids), and Cryptophyta and Haptophyta are prob. not closely related to this clade".

The diatoms are phylogenetically included in the Heterokontophyta lineage. Autotrophic heterokontobionta share the rhodophyte-derived chloroplasts by secondary endosymbiosis, although how many times they have been taken up by the host lineages is still controversial". "The **Cercozoa** is basically defined by molecular data, and it is impossible to describe common morphological features for this group. Cercozoans are mostly unicellular, flagellate or amoeboid (sometimes forming plasmodia). Only the **Chlorarachniophyceae** has been treated as algae and therefore described below." "Ultrastructural and molecular studies indicate that the Euglenophyceae is closely related to some groups of heterotrophic flagellates such as kinetoplastids, and now they are usually classified in the common phylum, **Euglenozoa**. Euglenozoans are prinicipally heterotrophic with the exception of a part of **Euglenophyceae**. Photosynthetic euglenids possess plastids derived from the secondary endosymbiosis with a green alga, and they are latecomers in the evolution of the Euglenozoa" (Kawai & Nakayama).

"The phylogenetic lineage of the **Chlorobionta** (Chlorophyta, Streptophyta; Viridiplantae, green plants) includes both micro- and macroscopic green plants, i.e., the green algae and the land plants (Leliaert et al. 2012). Given their phylogenetic, morphological and ecological diversity the Viridiplantae represent one of the most important eukaryotic groups with a key role in the global ecosystem. The evolutionary origins of the green plants trace back to the primary endosymbiosis of the ancient cyanobacterium by a primitive eukaryotic organism, possibly at c. 1750 Ma (Becker 2012)" (Neustupa).

References and further reading

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Strasburger (A. Bresinsky, C. Körner, J.W. Kadereit, G. Neuhaus, U. Sonnewald) 2002, 2008: Lehrbuch der Botanik 35., 36. Aufl. – Spektrum, Akad. Verlag; Heidelberg.

3 **Glaucobionta** Bresinsky & Kadereit

3.1 Division **Glaucocystophyta** Kies & Kremer (Glaucophyta Skuja)

Characterization and relationships

The **Glaucocystophyta** in the sense of Graham et al. (2009) form a distinctive monophyletic group of primary plastid bearing organisms, according to ultrastructural and molecular investigations and recent understanding (Bhattacharya et al. 1995, Price et al. 2012). The photosynthetic organelles are distinct from the chloroplasts of other organisms because they possess a (rudimentary) peptidoglycan wall between their two membranes. From their resemblance to Cyanoprokaryota, they have been termed as cyanelles (Pascher 1929). Furthermore the expression "cyanelles" may be ambiguous, because it has been used also for bluegreen photosynthetic organells of organisms different to the Glaucocystophyta (Kies 1992). In the following the term "cyanelle" will be uses synonymous to the terms "plastid" or "chloroplast". Formerly thought to be endosymbiontic cyanoprokaryota, the cyanelles of the Glaucocystophyta have been revealed to be true plastids (Herdmann & Stanier 1977). The genome bears only c. 10% of the DNA length of free-living cyanoprokaryotes and an organisation comparable to other plastids (Lambert et al. 1985, Kies 1992) and the cyanelles possess a homologous protein import function comparable to chloroplasts (Steiner et al. 2005). Glaucocystophyta cyanelles usually bear an electrondense crystalloid structure, centrally or apically. Recently this structure in the plastid stroma of the *Cyanophora*-cyanelle has been shown to possess characteristics of a bacterial carboxysome (Kies 1992, Fathinejad et al. 2008). Cyanelles are equipped with chlorophyll *a* only, and with phycobiliproteins arranged in phycobilisomes and further pigments. Starch kernels are produced in the cytosol and not in the cyanelles. The basis of the concept of the Glaucocystophyta is a biflagelled monadoid life form and thereof coccal and capsal life stages or forms are derived. Sexual reproduction is unknown.

It is often assumed that the Glaucocystophyta share a common ancestor with the Rhodobionta and Chlorobionta. Therefore they are often regarded as a basal division of algae (with primary endocytobiosis) and land plants (Palmer et al. 2004, Keeling et al. 2005, Keeling 2010). Adl et al. (2005) coined the expression Archaeplastida to form a supergroup comprising Glaucobionta, Rhodobionta and Chlorobionta/Chloroplastida, emphasizing a common ancestor going back to one early endosymbiontic event (Adl et al. 2012). Otherwise the Glaucocystophyta and the Rhodophyta are united in a sub-kingdom Biliphyta separated from the sub-kingdom Viridiplantae (Cavalier-Smith 1981) but whether the Glaucocystophyta or the Chlorobionta are more basal cannot be decided yet (Deschamps &

Moreira 2009). Furthermore the direct likeness of these three lineages is still a controversial matter (Stiller & Harrell 2005, Kim & Graham 2008, Nozaki et al. 2009). Also a completely independent evolution of Glaucocystophytes or affinities to the Euglenophyceae has been discussed (Kies 1989a). Due to unique features of their cellular organisation the Glaucocystophytes have a rather isolated phylogenetic position, but are of general importance because of their various implications for the endosymbiosis theory of cell evolution.

The separation of the main subgroups lies rather deep in the diverse phylogenetic trees; therefore the classification of the division into different orders, as proposed in Kies & Kremer (1986), is justified. The following synopsis is mainly based on the concept given in Kies & Kremer (1986). It has been supplemented by the incorporation of a range of recent results obtained by many renowned phycologists. The names of taxa were compared with and adjusted to the corresponding entries in AlgaeBase *(*Guiry & Guiry 2014*)* and Index Nominum Algarum *(2014)*, if possible. Fig. 3-1.1–6.
Distribution and fossil history. All known members of the Glaucocystophyta are recorded from limnic habitats with a scattered but cosmopolitan distribution. The author is not aware of any fossil record of this peculiar and phylogenetic old group of algae.

Systematic arrangement of taxa

Species numbers are provisional. Reliable taxonomic concepts until May 2014.

Class **Glaucocystophyceae** Kies & Kremer

Eukaryotic algae with plastids in form of cyanelles, enveloped by 2 layers of lipid membrane. Photosynthetic pigments of cyanelles comprising chlorophyll *a* together with phycobilisomes and carotenoids, but lacking echinenone and myxoxanthophyll. Cyanelles few to many, globose, slightly curved or curved-elongated and surrounded by a thin peptidoglycan cell wall. Unicellular or colonial with monadoid, capsalean or coccoid organisation. Cells usually uninucleate, may be naked or with a cell wall (cellulose). Pellicula usually present and composed of 1 layer of flat vesicles associated with microtubules. Cells immobile, with rudimentary flagella or without, or motile. Motile cells with 2 heterodynamic and unequal flagella in an apical groove. Both flagella mostly with non-tubular mastigonemata, rooted cruciate with 4 or 2 multi-layered structures (MLS). Dictyosomes mostly located parabasal. Contractile vacuoles often present. Mitochondria show flattened cristae. True starch grains produced freely in the cytosol. Centrioles and phycoblast absent. Asexual reproduction by binary fission, autospores or zoospores. Sexual reproduction unknown. 3 ord., 4 fam. (incl. Cyanoptychaceae nom prov.), 7 gen. (11–19).

1. Order **Glaucocystales** Bessey

Coccoid, unicellular or colonial, then retained in their common mother cell wall(s) and/or within common gelatinous layers. Rudimentary flagella and contractile vacuoles often present. Cyanelles are (globose to) slightly curved up to club-shaped (Scott et al. 1984). Asexual reproduction by autospores. 1 fam.

Fam. **Glaucocystaceae** G.S.West Cells ellipsoid to cylindro-ellipsoid. Contractile vacuoles not always visible (Gärtner & Ingolić 2001). Cell wall distinctive, containing cellulose; cells singular or up to several subgroups enveloped by the old mother cell walls within extensive common mucilage. Cyanelles numerous, club-shaped and with an apical thylakoid free region (crystalloid), typically arranged in 1 or 2 star-like patterns; in older cells may be arranged more irregularly (Fig. 3-1.1–2). Creeping motion was noticed (Skuja 1954). Vegetative cells usually thick walled with an equatorial ring. Zoospores not confirmed, but 2 rudimentary flagella within the cell wall are present (Schnepf et al. 1966), this being a very unique character for all coccal/capsalean organized algae known up to date. Asexual reproduction by autospores. 3 gen., incl. *Chalarodora* and *Glaucocystopsis* (4–11).

Glaucocystis Itzingsohn (2–9, depending on author).

Genera of uncertain affiliation

Chalarodora Pascher (1)

The occurrence of cyanelles was described also for the genus *Chalarodora* (Pascher 1929), but it is unclear if the further cytomorphological traits and genetics would show that the taxon belongs to the Glaucocystophyceae or represents an unusual Chlorophyte, or even something different; further studies are necessary. Recently the taxon has been refound in Slovakia (Hindák & Hindáková 2012, therein comprehensive discussion of literature data on this taxon).

Glaucocystopsis Bourelly (1)

Glaucocystopsis is rather poorly described. It differs from *Glaucocystis* by the number of only 4 cyanelles and by a pyrenoid, independently formed of the plastids (?), covered by starch plates. The latter character is unknown of any other Glaucocystophyte. Since then, the taxon has hardly been refound, apart from a few mentions (e.g., Bayly 1976). Also no cultures or detailed investigations exist, therefore it remains doubtful. It could also resemble a developing stage of a known form of *Glaucocystis*, or it could even be an analogous form of the Chlorophyceae.

Taxa to be excluded

Archaeopsis Skuja is an invalid name referring most prob. to a taxon (*Gloeocapsa monococca* Kützing) that is ascribed to the Cyanoprokaryota.

Pascher (1906) proposed a subgroup (“Reihe”) “Asterocystideae” as part of the Glaucocystaceae with the genera *Allogonium* Kützing and *Chroothece* Hansgirg in Wittrock & Nordstedt; this is obsolete because these forms are now integrated within the Rhodobionta.

2. Order **Cyanophorales** Kies & Kremer

Unicellular monadoid. Glaucocystophyta, monosymmetrically flattened, without a cell wall. 2 unequal, heterodynamic flagella arising from an apical groove. 1 to several disc-shaped cyanelles with a central electron dense body, for which recently further evidence was gained that it may be a carboxysome similar to that of bacteria (Burey et al. 2005, Löffelhardt 2007, Fathinejad et al. 2008). Asexual reproduction by binary fission.

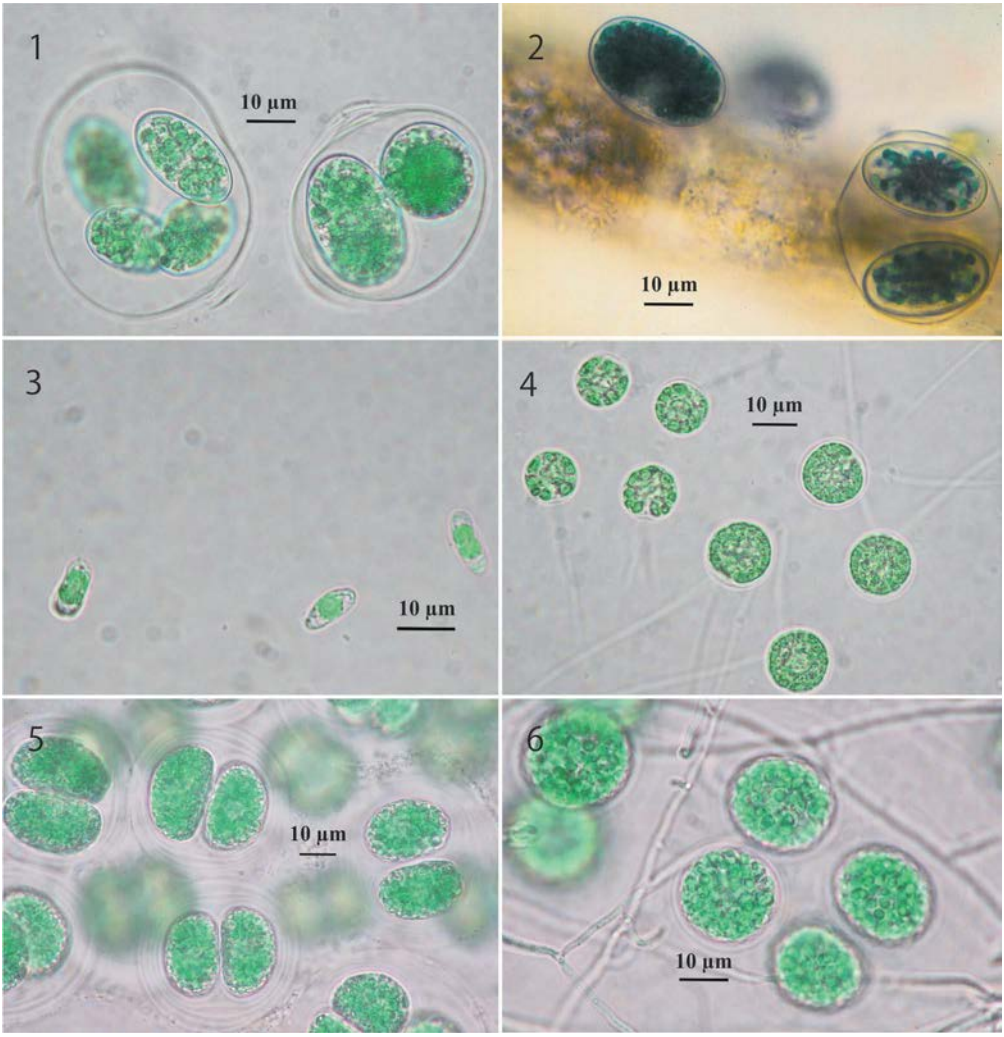

Fig. 3-1. Glaucocystophyta. 1–2. *Glaucocystis nostochinearum*. 1. Cultured material, colonies with 4, resp. 2 cells. Within the cells the club shaped cyanelles are masked by granular inclusions (storage material?). 2. Free living material attached to a trichome of an *Oedogonium* sp. Within the 2-celled colony enveloped by the mother cell wall, the star like arrangement of the club shaped cyanelles is visible (from Gärtner & Ingolić 2001, changed, with permission of the authors). **3. *Cyanophora paradoxa*.** Cultured material. The motlile cells showing an entire cyanelle or a situation of a cyanelle under division. **4. *Gloeochaete wittrockiana*.** Cultured material. Several cyanelles are leaving a central area where the nucleus is located; pseudoflagella visible. **5–6. *Cyanoptyche gloeocystis*.** 5. Cultured material. Colonies with laminated mucilaginous sheaths. 6. Cultured material. Young cells showing small, disc-shaped cyanelles. (Orig.)

Fam. **Cyanophoraceae** Kies & Kremer Cells naked with 2 heterodynamic unequal flagella. 1–4(–8) disc-shaped cyanelles (Fig. 3-1.3) with a central crystalloid structure which may represent a carboxysome. Reproduction by binary fission. 2 gen., incl. *Peliaina* Pascher (4) (s..bl.).

Cyanophora Korshikov (3).

Genera of uncertain affiliation

Peliaina Pascher (1)

Peliaina seems to be very similar to *Cyanophora*, but somewhat larger and bearing more cyanelles, but in order to verify this form as a Glaucocystophyte more detailed investigations would be necessary (cytomorphology, pigments, genetics).

Further poorly known monadoid genera which are described to possess cyanelles mentioned in Bourelly (1970), like *Cyanomonas* Oltmanns, *Cryptella* Pascher and *Skvortzoviella* Bourelly (*Lemmermanniella* Geitler), must remain doubtful until more data are available.

Taxa to be excluded

"Acc. to Schiller (1954) *Strobilomonas* Schiller is either a cryptomonad or a chloromonad. The author, however, made no mention of the reserve material or of the ejectosomes typical of cryptomonads." (Kies & Kremer 1986, p. 130).

3. Order **Gloeochaetales** Kies & Kremer

Capsal organized unicellular or colonial. Walled cells surrounded by a common mucilaginous sheath. Gelatinous hairs (= pseudoflagella), 1 or 2 per cell, divided or not divided, may be present. Asexual reproduction by bipartition, autospores or monosymmetrically flattened biflagellate zoospores. 2 fam. (incl. Cyanoptychaceae nom. prov.)

Fam. **Gloeochaetaceae** Skuja Cells globose or semiglobose without distinctive cell wall, solitary or colonial in mucilaginous pads attached to the substrate, each with 1 or 2 pseudoflagella (Fig. 3-1.4) Cyanelles numerous, oval or kidney shaped with a crystalloid inclusion in the central lumen (carboxysome?), thylacoids with phycobilisomes. Contractile vacuoles in young stages present. Motile cells rare, monosymmetricall flattened with 2 unequal flagella (Kies 1976). 1 gen. (2).

Gloeochaete Lagerheim (2)

Taxa of unclear family affiliation within the order Gloeochaetales

Glaucosphaeraceae Skuja defined by Skuja (1954) set into the order Gloeochaetales by Kies & Kremer (1986), containing also the genus *Cyanoptyche* Pascher, evidently belonging to the Glaucocystophyta, cannot be kept here because the name giving taxon has to be excluded. *Cyanoptyche* forms vegetative capsal colonies within layered mucilaginous sheaths (Fig. 3-1.5), with cells possessing numerous disc-shaped cyanelles (Fig. 3-1.6) with a central body (carboxysome?), free starch grains and contractile vacuoles. Asexual reproduction by autospores and biflagellated zoospores (Kies 1989b). Acc. to the deep phylogenetic split between *Gloeochaete* and *Cyanoptyche,* a new family should be erected (Cyanoptychaceae). 1 gen. (1–2).

Cyanoptyche Pascher (1–2).

Taxa to be excluded

Schrammia P.-A.Dangeard is regarded as synonymous to *Gloeochaete*.

Glaucosphaera vacuolata Korshikov, originally thought to be a Glaucocystophyte, was revealed to belong to the Rhodobionta (McCraken et al. 1980).

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Heterokontobionta p.p. (Autotrophic Heterokontobionta)

Introduction

The **Heterokontobionta** (informally stramenopiles Patterson, emend. Adl et al.) encompass eukaryotic organisms with a high diversity of autotrophic and mixotorophic organisms generally referred to as algae, and several heterotrophic lineages (Heterotrophic Heterokontobionta, cf. Part 1/1 of Syllabus).

Initially, Heterokontae Luther (Luther 1899) comprised only autotrophic raphidophytes and xanthophytes, but later broadened to include all protists with heterokont flagella (Leedale 1974). Heterokonta Cavalier-Smith (Cavalier-Smith 1986) was established for all eukaryotes bearing an anterior flagellum with tubular mastigonemes and a posterior smooth flagellum. Other common morphological features are mitochondria with tubular cristae and typically four microtubular flagellar roots.

The name **Heterokontobionta** (cf. Strasburger 36. Aufl., 2008) "is applied to those eukaryotes and their descendants producing heterokont flagellated cells, regardless of trophic modes, incl. four phylogenetically distinctive lineages and both autotrophic (mixotrophic) and heterotrophic members. Note that recent molecular data do not support the "Heterokontobionta" in this sense (Heterokontobionta s.l.). Stramenopiles (incl. Heterokontophyta/Ochrophyta) and Alveolata (incl. Dinophyta/Dinozoa) form a clade (SAR-clade or subkingdom Harosa) with Rhizaria (incl. chlorarachnids), and Cryptophyta and Haptophyta are prob. not closely related to this clade. Autotrophic heterokontobionta share the rhodophyte-derived chloroplasts by secondary endosymbiosis, although how many times they have been taken up by the host lineages is still controversial (Burki et al. 2012, Petersen et al. 2014).

The diatoms are phylogenetically included in the Heterokontophyta lineage based on molecular phylogenetic data (http://www.shigen.nig.ac.jp/algae_tree/HeterokontophytaE.html).

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Synopsis of classification of the Heterokontobionta p.p.

Division **Cryptophyta** Cavalier-Smith

Class **Cryptophyceae** F.E.Fritsch
Order **Cryptomonadales** Pascher
Cryptomonadaceae Ehrenberg,
Geminigeraceae B.L.Clay, P.Kugrens, & R.E. Lee,
Hemiselmidaceae Butcher ex P.C.Silva,
Pyrenomonadaceae G.Novarino & I.A.N.Lucas
Taxa incertae sedis
Class **Goniomonadea** Cavalier-Smith
Order **Goniomonadales** G.Navarino & I.A.N.Lucas
Goniomonadaceae D.R.A.Hill

Division **Dinophyta/Dinozoa** Cavalier-Smith / **Dinoflagellata** (Bütschli) R.A.Fensome, F.J.R.Taylor, G.Norris & al.

Class **Perkinsea** Levine
Order **Perkinsida** Levine
Perkinsidae Levine
Order **Rastrimonadida** Cavalier-Smith
Order **Phagodinida** Cavalier-Smith
Phagodinidae Cavalier-Smith
Class **Oxyrrhidophyceae** Cavalier-Smith
Order **Oxyrrhinales** Sournia
Oxyrrhinaceae Sournia
Taxa incertae sedis
Class **Ellobiophyceae** Loeblich III
Order **Thalassomycetales** Loeblich III
Ellobiopsidaceae Coutière
Class **Syndiniophyceae** Loeblich III
Order **Syndiniales** Loeblich III
Amoebophryaceae J.Cachon ex Loeblich III,
Sphaeriparaceae Loeblich III, **Syndiniaceae** Chatton
Order **Coccidiniales** Chatton
Coccidiniaceae Chatton & Biecheler
Taxa incertae sedis

Euduboscquellaceae D.W.Coats, T.R.Bachvaroff & C.F.Delwiche
Class **Noctiluciphyceae** R.A.Fensome, F.J.R.Taylor, G.Norris & al.
Order **Noctilucales** Haeckel
Kofoidiniaceae F.J.R.Taylor, **Leptodiscaceae** Kofoid,
Noctilucaceae W.S.Kent
Taxa incertae sedis
Protodiniferaceae Kofoid & Swezy
Class **Dinophyceae** F.E.Fritsch
Order **Gymnodiniales** Apstein
Actiniscaceae Kützing, **Amphilothaceae** Poche,
Brachidiniaceae Sournia, **Ceratoperidiniaceae** Loeblich III,
Chytriodiniaceae J.Cachon & M.Cachon,
Dicroerismataceae R.A.Fensome, F.J.R.Taylor, G.Norris & al.,
Gymnodiniaceae Lankester, **Warnowiaceae** Lindemann
Order **Haplozoonales** Poche
Haplozoonaceae Chatton
Order **Suessiales** R.A.Fensome, F.J.R.Taylor, G.Norris & al.
Borghiellaceae Moestrup, K.Lindberg & N.Daugbjerg,
Suessiaceae R.A.Fensome, F.J.R.Taylor, G.Norris & al.
Familia incertae sedis
Order **Peridiniales** Haeckel
Amphidiniopsidaceae J.D.Dodge nom. nud.,
Amphidomataceae Sournia, **Blastodiniaceae** Cavers,
Cladopyxidaceae Stein, **Crypthecodiniaceae** Biecheler,
Heterocapsaceae R.A.Fensome, F.J.R.Taylor, G.Norris & al.,
Heterodiniaceae Lindemann, **Kolkwitziellaceae** Lindemann,
Kryptoperidiniaceae Lindemann, **Oxytoxaceae** Lindemann,
Peridiniaceae Ehrenberg, **Podolampadaceae** Lindemann,
Protoperidiniaceae Balech, **Thoracosphaeraceae** Schiller,
Zooxanthellaceae R.Hovasse & G.Teissier
Familia incertae sedis
Order **Prorocentrales** Lemmermann
Prorocentraceae Stein
Order **Dinophysiales** Lindemann
Amphisoleniaceae Lindemann, **Dinophysaceae** Bütschli,
Oxyphysaceae Sournia
Familia incertae sedis
Order **Gonyaulacales** F.J.R.Taylor
Ceratiaceae Kofoid, **Gonyaulacaceae** Lindemann,
Heteraulacaceae Loeblich Jr. & W.S.Drugg,
Protoceratiaceae Lindemann, **Pyrocystaceae** (Schütt) Lemmermann,
Thecadiniaceae Balech
Taxa incertae sedis
Familia incertae sedis
Apodiniaceae Chatton, **Desmocapsaceae** Pascher,

Duboscquellaceae Chatton ex Loeblich III, **Oodiniaceae** Chatton,
Phytodiniaceae Klebs, **Ptychodiscaceae** Lemmermann,
Tovelliaceae Moestrup, K.Lindberg & N.Daugbjerg
Familia incertae sedis

Division **Haptophyta** D.J.Hibberd ex Edvardsen & Eikrem

Class **Pavlovophyceae** (Cavalier-Smith) J.C.Green & L.K.Medlin
Order **Pavlovales** J.C.Green
Pavlovaceae J.C.Green
Class **Coccolithophyceae** Rothmaler
Order **Phaeocystales** L.K.Medlin
Phaeocystaceae Lagerheim
Order **Prymnesiales** Papenfuss
Chrysochromulinaceae Edvardsen, Eikrem & L.K.Medin,
Prymnesiaceae Conrad ex O.C.Schmidt
Order **Isochrysidales** Pascher
Isochrysidaceae Bourrelly, **Noelaerhabdaceae** Jerkovic
Order **Coccolithales** Schwarz
Calcidiscaceae J.R.Young & P.R.Bown,
Coccolithaceae Poche nom. cons., **Hymenomonadaceae** Senn,
Pleurochrysidaceae J.Fresnel & C.Billard,
Reticulosphaeraceae Cavalier-Smith
Familia incertae sedis
Order **Zygodiscales** J.R.Young & P.R.Bown
Helicosphaeraceae M.Black, **Pontosphaeraceae** Lemmermann
Order **Syracosphaerales** W.W.Hay
Calciosoleniaceae Kamptner, **Rhabdosphaeraceae** Lemmermann,
Syracosphaeraceae (Lohmann) Lemmermann
Familia incertae sedis
Order incertae sedis
Alisphaeraceae J.R.Young, A.Kleijne & Cros,
Braarudosphaeraceae Deflandre,
"**Calyptrosphaeraceae** Boudreaux & W.W.Hay",
Ceratolithaceae R.E.Norris,
Chrysoculteraceae T.Nakayama, M.Yoshida, M.-H.Noël & al.,
Papposphaeraceae R.W.Jordan & R.R.Young,
Umbellosphaeraceae J.R.Young & A.Kleinje
Familia incertae sedis

Division **Heterokontophyta / Ochrophyta** Cavalier-Smith

Diatoms (Diatomeae, Bacillariophyceae s.l., Bacillariophyta)

Class **Coscinodiscophyceae** Round & Crawford
Subclass **Corethrophycidae** Round & Crawford

Order **Corethrales** Round & Crawford
Corethraceae Lebour
Subclass **Melosirophycidae** nom. prov.
Order **Melosirales** Crawford
Aulacoseiraceae Crawford, **Endictyaceae** Crawford,
Hyalodiscaceae Crawford, **Melosiraceae** Kützing emend. Crawford,
Orthoseiraceae Crawford, **Paraliaceae** Crawford,
Stephanopyxidaceae Nikolaev
Subclass **Coscinodiscophycidae** Round & Crawford
Order **Chrysanthemodiscales** Round
Chrysanthemodiscaceae Round
Order **Coscinodiscales** Round & Crawford
Aulacodiscaceae (Schütt) Lemmermann, **Coscinodiscaceae** Kützing,
Gossleriellaceae Round, **Hemidiscaceae** (Hendey) Simonsen,
Heliopeltaceae H.L.Smith, **Rocellaceae** Round & Crawford
Order **Ethmodiscales** Round
Ethmodiscaceae Round
Order **Stictocyclales** Round
Stictocyclaceae Round
Order **Asterolamprales** Round & Crawford
Asterolampraceae H.L.Smith
Order **Arachnoidiscales** Round
Arachnoidiscaceae Round
Order **Stictodiscales** Round & Crawford
Stictodiscaceae (Schütt) Simonsen
Order **Rhizosoleniales** P.C.Silva
Pyxillaceae (Schütt) Simonsen, **Rhizosoleniaceae** De Toni
Class **Mediophyceae** Medlin & Kaczmarska
Subclass **Biddulphiophycidae** Round & Crawford
Order **Biddulphiales** Krieger
Attheyaceae Round & Crawford, **Biddulphiaceae** Kützing
Order **Toxariales** Round
Ardissoneaceae Round, **Climacospheniaceae** Round,
Toxariaceae Round
Subclass **Cymatosirophycidae** Round & Crawford
Order **Cymatosirales** Round & Crawford
Cymatosiraceae Hasle, von Stosch & Syvertsen,
Rutilariaceae De Toni
Subclass **Chaetocerotophycidae** Round & Crawford
Order **Hemiaulales** Round & Crawford
Hemiaulaceae Heiberg, **Streptothecaceae** Crawford
Order **Anaulales** Round & Crawford
Anaulaceae (Schütt) Lemmermann
Order **Chaetocerotales** Round & Crawford
Acanthocerataceae Crawford, **Chaetocerotaceae** Ralfs

Subclass **Thalassiosirophycidae** Round & Crawford
Order **Eupodiscales** nom. prov.
Eupodiscaceae Simonsen
Order **Lithodesmiales** Round & Crawford
Bellerocheaceae Crawford, **Lithodesmiaceae** Round
Order **Leptocylindrales** Round & Crawford
Leptocylindraceae Lebour
Order **Thalassiosirales** Glezer & Makarova
Lauderiaceae (Schütt) Lemmermann, **Skeletonemataceae** Lebour, **Stephanodiscaceae** Glezer & Makarova, **Thalassiosiraceae** Lebour
Class **Fragilariophyceae** Round
Order **Plagiogrammales** nom. prov.
Plagiogrammaceae De Toni
Order **Raphoneidales** Round
Psammodiscaceae Round & D.G.Mann, **Rhaphoneidaceae** Forti
Order **Fragilariales** P.C.Silva
Fragilariaceae Greville
Order **Tabellariales** Round
Tabellariaceae Kützing
Order **Rhabdonematales** Round & Crawford
Grammatophoracae Lobban & Ashworth, **Rhabdonemataceae** Round & Crawford
Order **Cyclophorales** Round & Crawford
Cyclophoraceae Round & Crawford, **Entopylaceae** Grunow
Order **Licmophorales** Round emend.
Licmophoraceae Kützing, **Ulnariaceae** nom. prov.
Order **Striatellales** Round
Striatellaceae Kützing
Order **Thalassionematales** Round
Thalassionemataceae Round
Order **Protoraphidiales** Round
Protoraphidaceae Simonsen
Class **Bacillariophyceae** Haeckel
Subclass **Eunotiophycidae** D.G.Mann
Order **Eunotiales** P.C.Silva
Eunotiaceae Kützing, **Peroniaceae** (Karsten) Topachevs'kyj & Oksiyuk
Subclass **Bacillariophycidae** D.G.Mann
Order **Lyrellales** D.G.Mann
Lyrellaceae D.G.Mann
Order **Mastogloiales** D.G.Mann
Achnanthaceae Kützing emend. D.G.Mann, **Mastogloiaceae** Mereschkowsky emend.E.J.Cox
Order **Dictyoneidales** D.G.Mann
Dictyoneidaceae D.G.Mann
Order **Cymbellales** D.G.Mann

Anomoeoneidaceae D.G.Mann,
Cymbellaceae Greville emend. E.J.Cox,
Gomphonemataceae Kützing emend. E.J.Cox,
Rhoicospheniaceae Chen & Zhu

Order **Cocconeidales** nom. prov.
Achnanthidiaceae D.G.Mann, **Cocconeidaceae** Kützing

Order **Naviculales** Bessey
Suborder **Neidiineae** D.G.Mann
Amphipleuraceae Grunow, **Berkeleyaceae** D.G.Mann,
Brachysiraceae D.G.Mann, **Cavinulaceae** D.G.Mann,
Cosmioneidaceae D.G.Mann, **Diadesmidiaceae** D.G.Mann,
Neidiaceae Mereschkowsky, **Scolioneidaceae** D.G.Mann,
Scoliotropidaceae Mereschkowsky

Suborder **Sellaphorineae** D.G.Mann
Pinnulariaceae D.G.Mann, **Sellaphoraceae** Mereschkowsky

Suborder **Diploneidineae** D.G.Mann
Diploneidaceae D.G.Mann

Suborder **Naviculineae** Hendey
Naviculaceae Kützing, **Plagiotropidaceae** D.G.Mann,
Pleurosigmataceae Mereschkowsky, **Proschkiniaceae** D.G.Mann,
Stauroneidaceae D.G.Mann
Familia incertae sedis
Phaeodactylaceae J.Lewin

Order **Thalassiophysales** D.G.Mann
Catenulaceae Mereschkowsky, **Thalassiophysaceae** D.G.Mann

Order **Bacillariales** Hendey
Bacillariaceae Ehrenberg

Order **Rhopalodiales** D.G.Mann
Entomoneidaceae Reimer in Patrick & Reimer
Rhopalodiaceae (Karsten) Topachevs'kyj & Oksiyuk

Order **Surirellales** D.G.Mann
Auriculaceae Hendey, **Surirellaceae** Kützing

Other heterokontophytes

Class **Bolidophyceae** L.Guillou & M.-J.Chrétiennot-Dinet
Order **Bolidomonadales** L.Guillou & M.-J.Chrétiennot-Dinet
Bolidomonadaceae L.Guillou & M.-J.Chrétiennot-Dinet,
Pentalaminaceae H.J.Marchant,
Triparmaceae B.C.Booth & H.J.Marchant

Class **Dictyochophyceae** P.C.Silva
Order **Florenciellales** Eikrem, Evardsen & Throndsen
Order **Dictyochales** Haeckel
Dictyochaceae Lemmermann
Order **Rhizochromulinales** C.J.O'Kelly & D.E.Wujek

Ciliophryaceae Pouche,
Rhizochromulinaceae C.J.O'Kelly & D.E.Wujek
Order **Pedinellales** Zimmermann, Moestrup & Hällfors
Actinomonadaceae Kent
Class **Pelagophyceae** R.A.Andersen & G.W.Saunders
Order **Sarcinochrysidales** Gayral & Billard
Ankylochrysidaceae C.J.O'Kelly & Billard,
Nematochrysopsidaceae Gayral & Billard,
Sarcinochrysidaceae Gayral & Billard
Order **Pelagomonadales** R.A.Andersen & G.W.Saunders
Pelagomonadaceae R.A.Andersen & G.W.Saunders
Class **Pinguiophyceae** M.Kawachi, I.Inouye, C.J.O'Kelly & al.
Order **Pinguiochrysidales** M.Kawachi, I.Inouye, D.Honda & al.,
Pinguiochrysidaceae M.Kawachi, I.Inouye, D.Honda & al.
Class **Eustigmatophyceae** D.J.Hibberd & Leedale
Order **Eustigmatales** D.J.Hibberd
Chlorobotrydaceae Pascher, **Eustigmataceae** D.J.Hibberd,
Monodopsidaceae D.J.Hibberd,
Pseudocharaciopsidaceae K.W.Lee & Bold ex D.J.Hibberd
Order **Goniochloridales** nom. prov.
Goniochloridaceae nom. prov.
Class **Picophagea** Cavalier-Smith
Order **Picophagales** Cavalier-Smith
Picophagaceae Cavalier-Smith
Class **Synchromophyceae** S.Horn & C.Wilhelm
Order **Synchromales** Schnetter & K.Ehlers
Synchromaceae Schnetter & K.Ehlers
Order **Chlamydomyxales** Engler
Chlamydomyxaceae Engler
Order incertae sedis
Class **Chrysophyceae** Pascher
Order **Synurales** R.A.Andersen
Mallomonadaceae Diesing
Order **Paraphysomonadales** Cavalier-Smith, E.E.Chao, C.E. Thompson & al.
Paraphysomonadaceae Preisig & D.J.Hibberd
Order **Ochromonadales** Pascher
Chrysolepidomonadaceae M.C.Peters & R.A.Andersen,
Dinobryaceae Ehrenberg, **Ochromonadaceae** Lemmermann
Order **Chromulinales** Pascher
Chromulinaceae Engler, **Chrysamoebaceae** Bourrelly,
Chrysococcaceae Lemmermann
Order **Hibberdiales** R.A.Andersen
Chrysocapsaceae Pascher
Order **Chrysosaccales** Bourrelly
Chrysosaccaceae Bourrelly, **Stylococcaceae** Lemmermann,

Familia incertae sedis
Order **Phaeoplacales** Bourrelly
Chrysothallaceae Huber-Pestalozzi
Order **Hydrurales** Pascher
Hydruraceae Rostafinsky
Taxa incertae sedis
Aurosphaeraceae J.Schiller, **Chrysosphaeraceae** Pascher,
Nematochrysidaceae Pascher, **Thallochrysidaceae** W.Conrad
Familia incertae sedis
Class **Raphidophyceae** Chadefaud ex P.C.Silva
Order **Raphidomonadales** Chadefaud
Vacuolariaceae A.Luther
Class **Chrysomerophyceae** Cavalier-Smith
Order **Chrysomeridales** Cavalier-Smith
Chrysomeridaceae Bourrelly, **Phaeosacciaceae** J.Feldmann
Class **Aurearenophyceae** A.Kai, Y.Yoshii, T.Nakayama & al.
Order **Aurearenales** A.Kai, Y.Yoshii, T.Nakayama & al.
Aurearenaceae A.Kai, Y.Yoshii, T.Nakayama & al.
Class **Phaeothamniophyceae** R.A.Andersen & J.C.Bailey
Order **Phaeothamniales** Bourrelly
Phaeothamniaceae Hansgirg
Class **Xanthophyceae** Allorge ex F.E.Fritsch
Order **Pleurochloridellales** Ettl
Pleurochloridellaceae Ettl
Order **Chloramoebales** P.C.Silva
Chloramoebaceae A.Luther
Order **Rhizochloridales** Pascher
Myxochloridaceae Pascher, **Rhizochloridaceae** Pascher,
Stipitococcaceae Pascher ex G.M.Smith
Order **Heterogloeales** Fott ex P.C.Silva
Characidiopsidaceae Ettl, **Heterogloeaceae** Fott ex P.C.Silva,
Malleodendraceae Pascher
Order **Mischococcales** Fott ex P.C.Silva
Botryochloridaceae Pascher, **Botrydiopsidaceae** D.J.Hibberd,
Characiopsidaceae Pascher, **Chloropediaceae** Pascher,
Gloeobotrydaceae Pascher, **Gloeopodiaceae** Pascher,
Mischococcaceae Pascher, **Pleurochloridaceae** Pascher,
Sciadiaceae Gobi, **Trypanochloridaceae** Geitler ex Pascher
Order **Tribonematales** Pascher
Heterococcaceae P.C.Silva, **Heterodendraceae** Pascher
Neonemataceae Ettl, **Tribonemataceae** Pascher
Order **Botrydiales** J.H.Schaffner
Botrydiaceae Rabenhorst
Order **Vaucheriales** (Nägeli) Bohlin
Vaucheriaceae Dumortier