

Wolfgang Frey (Editor)

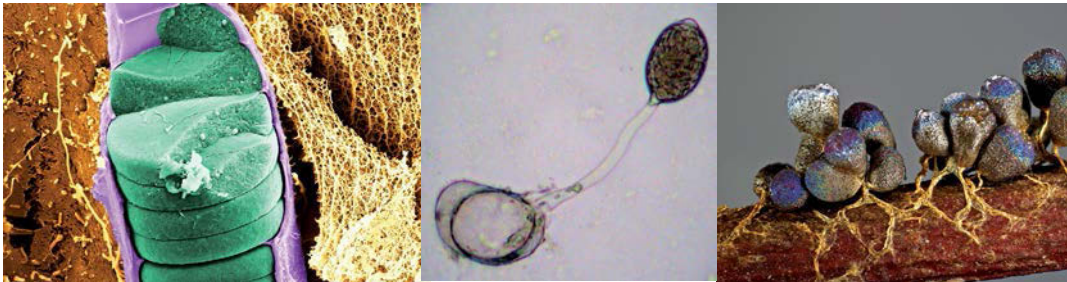
Syllabus of Plant Families

13th ed.

A. Engler's Syllabus der Pflanzenfamilien

1/1

Blue-green Algae, Myxomycetes and
Myxomycete-like organisms, Phytoparasitic protists,
Heterotrophic Heterokontobionta and Fungi p.p.



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Syllabus of Plant Families

Adolf Engler's Syllabus der Pflanzenfamilien

13th edition by Wolfgang Frey

Part 1/1 **Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Hetero- trophic Heterokontobionta and Fungi p.p.**

Burkhard Büdel,
Frank Kauff

Prokaryotic Algae, Blue-green Algae
(Cyanoprokaryota)

Martin Schnittler,
Yuri K. Novozhilov,
Maria Romeralo,
Matthew Brown,
Frederick W. Spiegel

Fruit body-forming protists: Myxomycetes and
Myxomycete-like organisms (Acrasia, Eumycetozoa)

Martin Kirchmair,
Sigrid Neuhauser

Phytoparasitic protists (Phytomyxea)

Angelika Preisfeld
Otmar Spring

Heterokontobionta p.p., Labyrinthulomycota
Oomycota

Kerstin Voigt
Dirk Redecker

Chytridiomycota, Zygomycota
Glomeromycota



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Scytonema spec. (Cyanoprokaryota). Broken turgescent trichome (−130 °C, Cryogenic SEM). Photo: B. Büdel, A. Donner, F. Kauff & L. Moosmann.

Plasmopara halstedii (Farl.) Berl. & de Toni (Oomycota). Oospore germination. Photo: O. Spring.

Physarum albescens D. Ellis ex T. Macbr. (Eumycetozoa, Physarales). Nivicolous myxomycete. Photo: M. Poulain.

Nostoc spec. (Cyanoprokaryota). Desert soil. Photo: B. Büdel.

Plasmodiophora brassicae Woronin (Phytophyta). Clubbed roots of Chinese cabbage. Resting spores in hypertrophied parenchyma cells of the cortex of the roots. Photo: M. Kirchmair, S. Neuhauser.

Wilsoniana bliti (Biv.) Thines (Oomycota). Oogonium with oospore. Photo: O. Spring.

Zygorhynchus moelleri (Zygomycota). Zygospore. SEM photo. Photo: K. Voigt.

Cribraria rubiginosa Fr. (Myxomycetes). Montane spruce-fir forests. Photo: M. Poulain.

Trichia varia (Pers.) Pers. (Myxomycetes). Common myxomycetes on decaying wood. Photo: M. Poulain.

Photos not according to the sequence of the systematic groups.

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Acrasia, Eumycetozoa

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Phytoparasitic protists

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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, only a revision of the mosses (13th ed., Kapitel V,2 Bryophytina), by K. Walther, followed in 1983.

The 13th edition is planned in five parts, starting in 2009 with Part 3 **Bryophytes and seedless Vascular Plants** and followed now with Part 1/1 Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p. of the Part 1 "Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Heterotrophic Heterokontobionta and Fungi". Due to the changes concerning article 59 of the nomenclatural rules Part 1/2 "Basidiomycota, Ascomycota, and Lichenized Fungi" will be edited after rearrangement of the nomenclature by leading experts. Therefore at present Part 1/1 **Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p.** of Part 1 is now published.

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 these lowermost groups. On the other hand, "classical" morphological and taxonomical expertise is in decline, especially for less showy groups of organisms. As 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".

The present volume provides a basic treatment of the world-wide morphological and molecular diversity of a part of "lower" organisms [Blue-green Algae, Myxomycetes and Myxomycete-like organisms (Acrasia, Eumycetozoa), Phytoparasitic protists (Phytomyxea), Heterotrophic Heterokontobionta (Labyrinthulomycota, Oomycota) and Fungi p.p. (Chytridiomycota, Zygomycota, Glomeromycota)]. 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.

We are grateful to the publisher, Dr. A. Nägele, for the understanding and cooperation and for realizing this volume.

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Abbreviations/Symbols

acc.	according to
appr.	circa, about
c.	circa, about, approximately
cf.	confer, compare
cool-temp.	cool-temperate
e.g.	for example, <i>exempli gratia</i>
esp.	especially
excl.	excluding
fam.	family, families
gen.	genus, genera
hrs.	hours
i.e.	that is, <i>id est</i>
l. c.	locus cited
lit.	literarily
LM	Light Microscop
MLC	microbody-lipid globule complex
Orig.	Original, originally
orth. bot.	orthographic botanical
p.p.	<i>pro parte</i>
prob.	probably
resp.	respectively
s.bl.	see below
SEM	Scanning Electron Microscop
s. l.	<i>sensu lato</i>
spec., sp.	species
spp.	species (plural)
s. str.	<i>sensu stricto</i>
syn.	synonym, synonymous
TEM	Transmission Electron Microscopy
Ø	diameter
* *	in the Northern and Southern Hemisphere
* *	in the Northern Hemisphere

Abbreviations of authors follow Brummit, R.K. & Powell, C.E. (1992): Authors of plant names. – Roy. Bot. Gard., Kew; International Plant Names Index (IPNO – <http://www.ipni.org>) and author's view of the respective contributions.

1 Introduction

The last two and a half decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth, not only in flowering plants, but also in lower plants and in the basal organisms on earth like Prokaryotic Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Lower Fungi. These groups of organisms have also been the focus of intensive research studies. The new molecular results allow a new understanding of the relationships between and within these groups. The relationships were considerably revised.

The most important insights from recent molecular phylogenies and phylogenomic evidence are: A better understanding of the systematics of the Cyanobacteria and the parallel evolution of their “morphotypes”, also the “beginning” of the understanding of the relationships in the Myxomycetes. Due to molecular results vampire amoebae (Vampyrellidae) are the closest relatives to the Phytomyxea (Plasmodiophoromycota). The Labyrinthulomycota are a clade of primarily marine protists separated from other Heterokontobionta and the Oomycota encompass a monophyletic group of fungus-like organisms, separated together with the Labyrinthulomycota from the Mycobionta. Recent phylogenomic studies provided evidence for the re-unification of the three phyla Chytridiomycota, Zygomycota and Glomeromycota into a phylogenetically coherent group named the Chytridiomycota s.l. for zoosporic fungi as a whole group, which share the formation of opisthokont flagellate spores as common morphological feature (see also Chapter 2 and the respective chapters).

This first volume of Part 1 (Part 1/1) of the 13th edition of “Engler’s Syllabus of Plant Families” gives an up-to-date review of basal groups of the Prokaryotic Algae (Cyanoprokaryota), Myxomycetes and Myxomycete-like organisms (Acrasia, Eumycetozoa), Phytoparasitic protists (Phytomyxea), Heterokontobionta p.p. (Labyrinthulomycota, Oomycota), Fungi p.p. (Chytridiomycota, Zygomycota, Glomeromycota) and the relationships on family and generic level, integrating morphological-anatomical and molecular data. Part 1/2 “Fungi p.p. (Ascomycota, Basidiomycota, Lichenized Fungi) will follow after resolving the nomenclatural problems.

W. Frey

2 Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p.

Part 1/1 of the “Syllabus of Plant Families” treats systematically not related groups, Blue-green Algae (Cyanoprokaryota), Fruit body-forming protists: Myxomycetes and Myxomycete-like organisms (Acrasia, Eumycetozoa), Phytoparasitic protists (Phytophyxa), Heterotrophic Heterokontobionta (Labyrinthulomycota, Oomycota) and Fungi p.p. (Chytridiomycota, Zygomycota, Glomeromycota). These groups are briefly introduced in this introductory chapter according to the view of the respective authors, including the new phylogenetic views based on investigations and results of gene sequencing. (The following text passages are from the respective chapters.)

“**Cyanobacteria** are an ancient group of prokaryotes, as can be inferred from morphological similarities of fossil records, which suggest an age of about 3.5 billion years (e.g. Schopf 2000). The taxonomy of Cyanobacteria, once based on mainly morphological and, at the species level also ecological features (e.g. Kondratieva 1975), clashed violently at higher hierarchical levels with the introduction of new taxonomic methods based on gene sequencing. In a recent review, Garcia-Pichel (2009) called the taxonomy of cyanobacteria either as a nightmare for newcomers, or a persistent headache for the initiated. These problems arose at least partly by the prokaryotic nature of the cyanobacteria. Molecular phylogenetics (16S rRNA) revealed, that in the cyanobacterial group Chroococcales, e.g. unicellular and filamentous types were developed independently. Even the “species-specific” colony morphology can vary in range, so that several species names can be applied to a set of strains, that are genetically identical on the basis of 16s rRNA. To date the majority of the genera and even more of the species are based on phenotype characterization (“morphotypes”) only and have not yet been verified by molecular taxonomic methods.

Under the heading **Fruit body-forming protists: “Myxomycetes and Myxomycete-like organisms”** several groups of a taxonomically heterogeneous ecological guild, called Myxomycetes and Myxomycete-like organisms (Schnittler et al. 2006) are treated. Unifying ecological traits for these organisms are (i) living as predators of other microorganisms, (ii) starting their life cycle as unicellular microorganisms from spore-like propagules, (iii) later combining their biomass by aggregation of cells or exclusively nuclear divisions (plasmodia of most Eumycetozoans) to finally (iv) convert it to typically stalked fruit bodies which (v) develop within hours not out of a true growth process but by rearrangement of the available biomass to (vi) release propagules for long-distance dispersal by air or, more rarely, animals.

Classical taxonomic treatments consider in particular fruit body morphology. Current knowledge does not allow arranging all myxomycete-like organisms in a natural system. Moreover, this guild includes only taxa developing fruit bodies. Here a classical system of arrangement of the taxa (cf. Olive 1975) is used.

The **Phytoparasitic protists** [Phytophyta (Plasmodiophoromycota)] are currently considered to be a monophyletic group of obligate biotrophic parasites of green plants and stramenopiles (heterokonts). Since their discovery the “true” taxonomic position of the Plasmodiophorids has been ambiguous: originally they were thought to be protists, later fungi, and now members of the protist supergroup Rhizaria. According to recent molecular studies their possible closest relatives are vampire amoebae (Vampyrellidae) or testate amoebae of the family Gromiidae.

Nowadays the **Heterokontobionta** are applied to those eukaryotes and their descendants producing heterokont zoospores, regardless of autotrophic or heterotrophic nutrition. The origin of the heterotrophic Heterokontobionta is still highly disputed. Since evidence for manifold loss of plastids in several lineages of Heterokontobionta has been supplied, a common photosynthetic origin is assumed by which plastids were gained via secondary endocytobiosis of rhodophyte plastids (e.g. Cavalier-Smith & Chao 2006). The heterotrophic Heterokontobionta outlined here include the **Labyrinthulomycota**, a clade of primarily marine protists separated from other Heterokontobionta, slime molds and true fungi by molecular data (Tsui et al. 2009), and the saprophytic or pathogenic **Oomycota**, which encompass a monophyletic group of fungus-like organisms, separated together with the Labyrinthulomycota from the Mycobionta. The reclassification of the Oomycota is supported by numerous biochemical peculiarities such as the dominance of cellulose (instead of chitin) combined with glycans and hydroxyproline (instead of proline) in the cell wall composition which contributed to the name “cellulosic fungi”. Hence, molecular genetic phylogeny in Oomycota started with a delay of almost a decade compared to vascular plants. Recent DNA sequence data brought tremendous changes to the interpretation of evolutionary relationships in every taxonomic rank and the process is far from finished.

The following phyla, **Chytridiomycota**, **Zygomycota** and **Glomeromycota**, belong to the kingdom of Fungi. Recent phylogenomic studies based on more than 100 genes provided evidence for the re-unification of those three phyla into a phylogenetically coherent group named the Chytridiomycota s.l. for zoosporic fungi as a whole group, which share the formation of opisthokont flagellate spores as common morphological feature (Ebersberger et al. 2009, 2011). The **Chytridiomycota** are retained as a group of zoosporic and chitinous fungi. Monophyly of this group, as currently delimited based on phylogenomic reconstructions, is not certain when just single or a few genes are used for phylogenetic analyses (e.g. Hibbett et al. 2007). The Chytridiomycota are osmotrophic in the major (vegetative) phases of their life cycle. Due to the potential of the Chytridiomycota to become phagotrophic during the short zoosporic phase, the Chytridiomycota can be considered as transitional link between fungal (excl. osmotrophic) and non-fungal (excl. phagotrophic) Opisthokonta. Traditionally, the **Zygomycota** are counted as the most basal terrestrial phylum of the kingdom of Fungi. The phylum formerly encompassed two classes, the Zygomycetes and the Trichomycetes, which differed by the ecological niches they inhabit. The Zygomycota are not accepted as a valid phylum (with five subphyla) because of a lacking resolution of basal fungal clades (James et al. 2006). However, based on the potential of all five subphyla to produce zygosporangia during

conjugation of two yoke-shaped gametangia it is referred to a phylogenetically coherent group. The **Glomeromycota**, are fungi-living mostly hypogeously, sometimes fruiting epigeously. As far as currently known, all members of the phylum are obligate symbionts, forming arbuscular mycorrhiza (Arbuscular mycorrhizal fungi, AMF) with vascular plants or mycorrhiza-like associations with non-vascular embryophytes, except for *Geosiphon pyriformis* F. Wettst., forming an endocytosis with cyanobacteria (Redecker & Raab 2006)".

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Blue-green Algae

3 Prokaryotic Algae, Blue-green Algae

The taxonomy of Cyanobacteria, once based on mainly morphological and, at the species level also ecological features (e.g. Geitler 1932, Fritsch 1945, Desikachary 1959, Bourelly 1970, Kondrateva 1975), clashed violently at higher hierarchical levels with the introduction of new taxonomic methods based on gene sequencing. In a recent review, Garcia-Pichel (2009) expressed the taxonomy of cyanobacteria either as a nightmare for newcomers, or a persistent headache for the initiated. These problems arose at least partly by the prokaryotic nature of the cyanobacteria. Since there is no sexual reproduction in bacteria, one cannot apply the biological species concept. Thus earlier cyanobacteriologists relied on features such as cell organization (filamentous, colonial, unicellular), ability and strategies of nitrogen fixation, and modes of propagation (e.g. baeocytes), which often do not reflect evolutionary relationships (Kauff & Büdel 2010). Molecular phylogenetics (16S rRNA) revealed, that in the cyanobacterial group Chroococcales for example, unicellular and filamentous types were developed independently. Even the “species-specific” colony morphology can vary in range, so that several species names can be applied to a set of strains, that are genetically identical on the basis of 16s rRNA (Palinska et al. 1996). The further treatment of cyanobacteria in both, the International Code of Nomenclature of Prokaryotes (ICNP) and the International Code of Botanical Nomenclature (ICBN) will be necessary as long as the majority of information from the botanical system is not fully integrated in the ICNP. An enumeration of this process, now lasting for 33 years, is presented by Oren (2011).

In this contribution we try to present the most recent view on the phylogenetics of Cyanobacteria, and also include new taxa described by several authors. Suggested recent reviews for further reading are Hoffmann et al. (2005), Komárek (2005), Garcia-Pichel (2009), and Kauff & Büdel (2010).

A most useful source of information is the “Database of cyanobacterial genera – Cyanodb” to be found in the internet at <http://www.cyanodb.cz> (© Komárek & Hauer 2011).

Characterization of the Cyanobacteria

Cyanobacteria are a monophyletic group of prokaryotes that perform oxygenic photosynthesis, possess photosystem I and II, and with few exceptions synthesize chlorophyll a as major photosynthetic pigment. Typically, phycobiliproteins serve as light harvesting pig-

ments. Their water-oxidizing, oxygen-evolving, plant-like photosynthesis (Garcia-Pichel 2009), together with the capability of many cyanobacteria to fix N_2 from the air, predestine them for life in harsh and often nutrient-poor environments. Consequently, they expose an “algal way of life” quite similar to that of eukaryotic algae (Wilmotte 1994).

Cyanobacteria are an ancient group of prokaryotes, as can be inferred from morphological similarities of fossil records, which suggest an age of about 3.5 billion years (Golubic & Seong-Joo 1999, Schopf 2000). It is strongly suggested by a study of Rasmussen et al. (2008), that they are the oldest microorganisms performing oxygenic photosynthesis on earth, which led to a sharp rise in atmospheric oxygen 2.45–2.32 billion years ago.

At present, about 230 genera with some 2250 species are known (Komárek & Hauer 2011). The majority of the genera and even more of the species are based on phenotype characterization (“morphotypes”) only and have not yet been verified by molecular taxonomic methods.

Cell types

Cyanobacterial cells range from 0.5 μm to 50–100 μm in width and thus are larger than those of most other bacteria and archaea. Some form macroscopic colonies, exhibiting sizes of a few μm to up to 30 cm. The heaviest macroscopic cyanobacterial colony reported is a ball-shaped *Nostoc pruniforme* Agardh ex Bornet & Flahault colony with a fresh weight of 3 kg (Dodds & Castenholz 1988).

Vegetative (normal) cell. Unicellular cyanobacteria usually have cells with a spherical, bacilloid, or fusiform shape, while the cells of filamentous types range from discoid to barrel-shaped. Some strains present pleiomorphisms, and even triradiate cells are realized (genus *Starrria* Lang; Fig. 3-11.2a–b). Not all filamentous forms necessarily imply a functional integration of cells into a truly multicellular organism. However, in the heterocytous group and some oscillatorians truly multicellular organisms with all attributes required for such a distinction are realized (Garcia-Pichel 2009). While the term “trichome” always refers to the filamentous cyanobacterial cell arrangement exclusively, the term “filament” describes the trichome plus the sheath envelope.

The cell wall outside the cell membrane is composed of a peptidoglycan layer with a thickness ranging from 10 nm in unicellular taxa, reaching 15 to 35 nm in filamentous species and more than 700 nm in large *Oscillatoria*-species (cf. Hoiczuk & Hansel 2000). Following the peptidoglycan layer, an outer membrane of the lipopolysaccharid-type, a common component of gram-negative cell walls, is inserted. Quite regularly, the cyanobacterial wall is completed by an S-layer, which is a two dimensional crystalline array formed by single species of (glyco-)protein and covering the entire surface of the cell (cf. Hoiczuk & Hansel 2000). Together with a specific pore complex, the S-layer provides the necessary structure for the gliding motility of filamentous cyanobacteria (Hoiczuk & Baumeister 1998). As a response to environmental factors, many cyanobacteria produce exopolysaccharides (EPS; Fig. 3-1.2–3) which sometimes contain visible and UV-light protecting pigments like scytonemin and mycosporine-amino acids [=MAAs] (Garcia-Pichel & Castenholz 1991, Böhm et al. 1995). These EPS are mainly composed of high-molecular-mass heteropolysaccharides. Their complexity in structure, their biosynthetic pathways, and the genes involved are reviewed in Pereira et al. (2009).

The cell content of cyanobacteria can be visibly separated in a region containing thylakoids, arranged either parallel to the cell membrane, radially, or in more or less coiled stacks in the cell periphery, and a region free of thylakoids: the nucleoplasm that hosts the cellular DNA (Fig. 3-1.1–3). Thylakoids carry the machinery of photosynthesis and consist of a double-unit membrane. Only the cells of the genus *Gloeobacter* Rippka, Waterbury et Cohen-Bazire have no thylakoids, and their photosynthetic apparatus is located in the plasma membrane. Phycobilisomes occur on the cytoplasmatic side of the thylakoids and function as light harvesting structures. They occur in most cyanobacteria, but are absent in chlorophyll b –containing taxa. Non-membrane bound granules occur in the cytoplasm and are polyphosphate bodies (poly- β -hydroxyalkanoates), lipid droplets, glycogen grana (reserve material), cyanophycin grana (multi-L-arginyl-poly(L-aspartic acid)), and carboxysomes, accumulations of the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (RUBISCO) (Fig. 3-1.2–3). In many planktonic species also gas vesicles occur: air-filled, cylindrical proteinaceous structures that provide buoyancy to the organisms.

Heterocytes (heterocysts). Cyanobacterial taxa with heterocytes form a monophyletic clade (Henson et al. 2004). Thus, the ability to develop heterocytes is phylogenetically seen a derived character and occurs without exception in the Nostocophycidae. Heterocytes develop in response to a lack of combined nitrogen in the environment (Garcia-Pichel 2009). They are morphologically distinct in being usually larger than vegetative cells, having thick cell walls and plug-like structures where they contact the neighbour cells (Fig. 3-4.1–3). Differentiation of heterocytes may occur from terminal or intercalary cells. They have successfully specialized in the fixation of di-nitrogen from air by providing a largely oxygen-free intracellular environment, thus avoiding nitrogenase inactivation by free oxygen. The oxygen releasing photosystem II (PSII) is absent from heterocytes, but a functional PSI provides ATP. They express *nif* (nitrogen fixation) genes and synthesize nitrogenase.

Akinetes. These are non-motile cells with a thick cell wall, larger than vegetative cells (Fig. 3-4.2) and containing high amounts of cyanophycin granules (nitrogen reserve). Akinetes are considered to be resting stages in the life cycle and occur exclusively in heterocytous cyanobacteria. They are resistant to unfavourable environmental conditions like desiccation, digestion in animal guts, and low temperatures, but they are not heat-resistant. Akinetes maintain a limited level of metabolic activities, including a residual photosynthetic activity. The ratio of PSI to PSII reaction centres is slightly higher than in vegetative cells (Sukenik et al. 2007).

Necridic cells. Necridic cells are apoptotic cells of filamentous cyanobacteria. They initiate the breaking of trichomes into hormogonia, shorter filaments or even false branching by a suicidal process that starts with loss of turgor, leakage of cell content, and finally shrinkage and separation from neighbouring cells. Finally, they will disintegrate, rupture, or last as a small vestigial remainder of the cell.

Cell division and reproductive modes

Basically, the mode of cell division is similar in all cyanobacteria: the cell membrane and the outer cell wall layers (peptidoglycan layer, outer membrane, S-layer) grow centripetally into the protoplast, finally dividing the mother cell into two new daughter cells (Fig. 3-1.1). Ap-

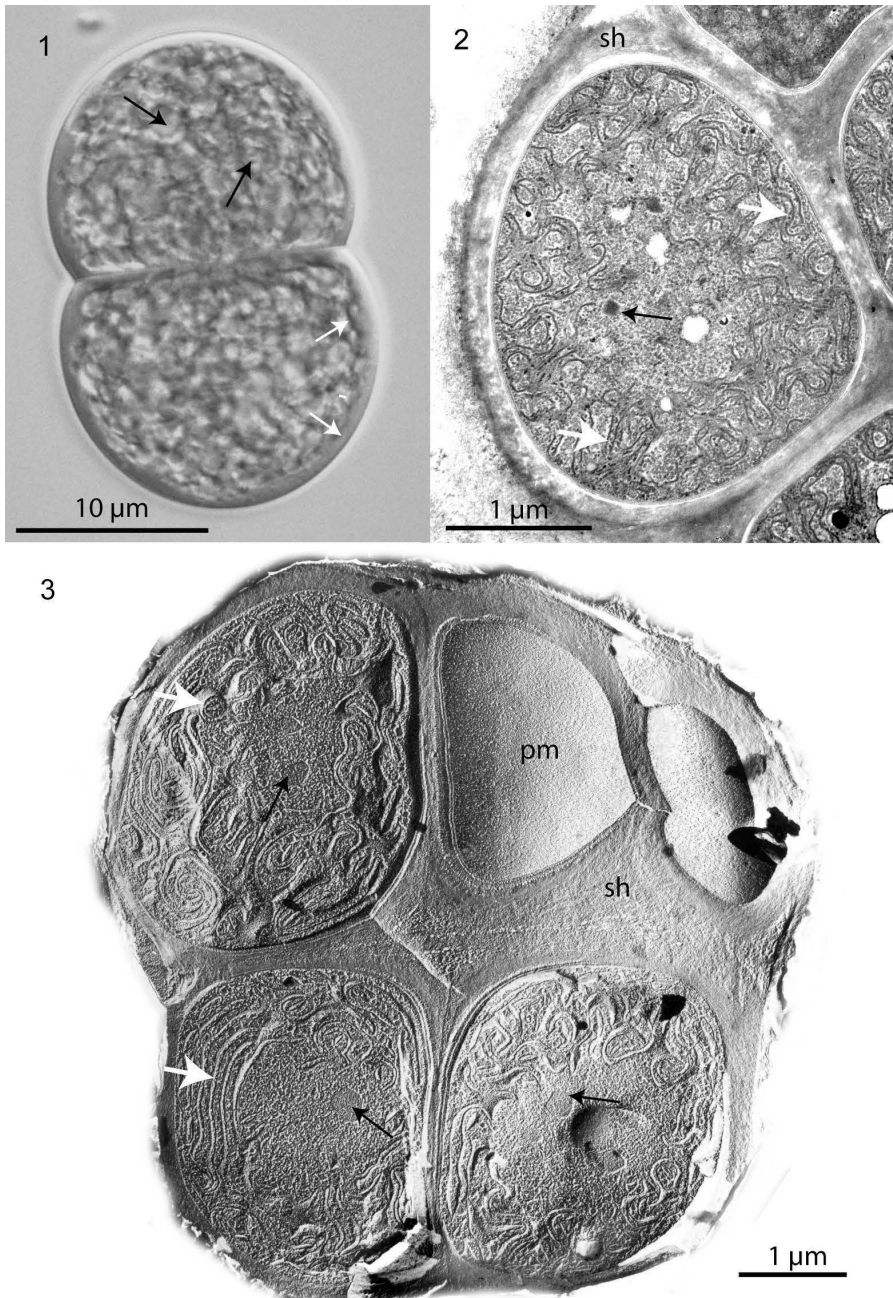


Fig. 3-1. Cyanobacterial cell. 1. *Cyanothece aeruginosa*. Cell in binary division, centripetally extending new cell wall; black arrows indicate DNA regions and white arrows thylakoids. 2. *Chroococciopsis* sp. TEM view of a cell; white arrows indicate thylakoids; black arrow indicates a carboxysome (localization of RUBISCO). 3. *Chroococciopsis* sp. Freeze etched TEM-view of a group of 5 cells in a common sheath envelope, black arrows point to carboxysomes, white arrows show thylakoids. (sh sheath, pm plasma membrane.) – Orig.