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Taxonomic review of cyanobacteria 2021/2022 according to polyphasic evaluation

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Abstract: The progress of the taxonomy of cyanobacteria should be realized from the synthesis of all data, obtained by any method or procedure. Such synthesis must be as complete as possible. Phylogenetic reconstructions exhibit often conflicts with morphological characters. Taxa above the genus level are often polyphyletic, which introduces confusion into the cyanobacterial taxonomic classification. This article attempts to synthesize results from available literature and to propose a novel view of the taxonomy of cyanobacteria on the level of families and orders.

Key words: cyanobacteria, taxonomic classification, polyphasic approach, traditional evaluation, cytomorphological characters, ecological markers, molecular sequencing

Introduction

The morphological taxonomy of cyanobacteria did not develop in the last decades (end of 20th and first decades of 21st centuries) quite in agreement with all discovered information and data (especially DNA sequences), in spite of the increasing importance of these organisms in numerous ecosystems of the Earth. However, with the enormous development of molecular methods in biological sciences in this period, many studies used molecular sequencing and reconstructed the phylogenetic history of various groups of cyanobacteria. Such studies yielded a lot of very important finding about the relationships between different groups within cyanobacteria, but unfortunately, the obtained data were only rarely and unsatisfactory compared with the traditional cytomorphological characters. It is also often impossible to use the new experimental data to the identification of the natural populations, which is important for ecological and biotechnological studies. Of course, the taxonomic review is quite inevitable for all applied disciplines, and the introduction of the results from all new molecular studies into a systematic classification is necessary and must be respected. This article is one of the first approaches to compare all cyanobacterial markers and characteristics, to find necessary coincidences and to elaborate ways for synthesis of all data.

Methods

The following sources were used:

1) Cytomorphological features important for taxonomic classification of cyanobacteria were selected from all available papers (e.g., the form of thallus and life form, structure of thallus, form and size of cells and filaments, type of false or true branching, presence and form of sheaths and envelopes, form and position of thylakoids within cells, inclusions and different types of granules, necridic and prominent cells – heterocytes or akinetes, etc.). The habitat preference was considered as an important ecological factor (aerophytic, water habitats – planktic, benthic, periphytic; extreme habitats – e.g. hot springs). Furthermore, geographic distribution of the species was included among the factors.

2) The traditional system of cyanobacteria, which was published in papers and summarised in the main following compendia: Tilden (1910), Geitler (1925), Geitler (1932), Huber–Pestalozzi (1938), Desikachary (1959), Komárek et Anagnostidis (1998, 2005), Komárek (2013).

3) The available papers from the period 1990–2021 which included the molecular sequencing of cultured, mostly monospecific, cyanobacterial populations and strains. From these results, the approximate scheme was constructed in Fig. S1 (the tree does not represent the phylogenetic reconstruction, the branches and nodes illustrate only the relatedness and represent the hand–drawn average of relations derived from cited literature). The relations following from the cited results were therefore transferred to hypothetic units in the same scale.

The first approach to the cyanobacterial systematic classification, based on combination of all available criteria is summarized in Table 1. The diacritical characters of orders are fully valid also for included families. The taxonomic status of various families corresponds more or less with their genetic position. In the table are included only the main cytomorphological and ecological diacritic characters. (The database of cyanobacteria up to species level see in Hauer & Komárek (2022): cyanodb.cz).

Results

My studies resulted following conclusions:

1) Genetic, cytological–ultrastructural and morphological data are more or less in a good coincidence (e.g., the size and form of filaments with organization and position of thylakoids, characteristic structure of cells of heterocytous types, true or false branching in various types of trichal genera, etc.).

2) The simple unicellular types without thylakoids in cells (Gloeobacterales) represent a clearly separate cluster according to molecular sequencing.

3) The coccoid (both unicellular and colonial) cyanobacteria with thylakoids in cells are divided in two main groups according to molecular criteria, which are separated also by cytological structure and type of cell division. Both these clusters (synechococcoid and chroococcoid) are not only distant by the structure of cells, but also phylogenetically (Synechococcales – Pseudanabaenales; Chroococcales – Oscillatoriales), and must be therefore classified in separate higher taxonomic units (orders).

4) The similar division into at least two groups must be applied to filamentous monoseriate types without heterocytes and akinetes (Pseudanabaenales and Oscillatoriales), differing by molecular position (they are evidently polyphyletic), as well as by their cell structure and several morphological details.

5) The types with the ability to reproduce by endogenic developing reproduction cells (endospores), or by asymmetrically separating cells (exospores) are concentrated in one special cluster, corresponding to the traditional order Pleurocapsales.

6) All the heterocytous, nostocalean and scytonematalean types, or types with heteropolar filaments (e.g. Rivulariaceae, Gloeotrichiaceae, etc.) are included in a large monophyletic clade. It is divided preliminary into several groups according to the published molecular and morphological criteria, but the definition of correct taxonomic units (orders, families, genera, species) is not yet quite clear and their delimitation and precision will be possible after more detailed and specialized studies.

The preliminary taxonomic review according to revised published parameters is proposed in Table 1. It is the first approach and therefore is constructed only on the level of orders and families. The exact classification of genera and species needs corrections in more detailed future analyses and studies. The most complete review of the up–to–now described cyanobacterial diversity (up to the species level) is included in: Hauer & Komárek (2022): cyanodb.cz, cyanobacterial genera.

Table 1. Review (2021) of cyanobacterial orders and families.

Diacritic cytomorphological characters of cyanobacterial orders and families – 2021

Gloeobacterales Cavalier–Smith 2002: unicells or irregular groups of cells; without thylakoids within cells.

Gloeobacteraceae Komárek et Anagnostidis 1995: unicells or groups of cells; without thylakoids within cells.

Synechococcales Komárek et al. 2014 (incl. Gloeomargaritales Moreira et al. 2017): unicells or groups of cells; the typical parietal position of few thylakoids.

Prochlorococcaceae Komárek et Strunecký 2020: small spheroidal to slightly elongated unicells, only a few μm in diameter; cell division in one direction; few simple parietal thylakoids; mostly planktic.

Synechococcaceae Komárek et Anagnostidis 1995 (incl. Gloeomargaritaceae Moreira et al. 2017, Thermosynechococcaceae Komárek et al. 2020, Thermostichaceae Komárek et Strunecký 2020): more or less spheroidal, oval, elongated up to rod–like cells, solitary, in mucilaginous colonies or agglomerations, or oriented in rows in pseudofilamentous formations; parietal thylakoids; cell division only crosswise; mucilage forms sometimes characteristic structural formations; planktic, periphytic, also in extreme habitats.

Chamaesiphonaceae (typical, sensu stricto) Borzì 1878: elongated, up to club–shaped or rod–like cells, mostly polarised and attached to any substrate by the help of mucilaginous discs or stalks; parietal thylakoids; cell division cross–wise, reproduction by typical exospores, separating in the upper (terminal) part of cells or by perpendicular or multidimensional fission.

Acaryochloridaceae (Komárek et al. 2014): spheroidal cells, usually agglomerated in irregular groups; parietal thylakoids in cells; cell division in one irregular plane.

Pseudanabaenales (unknown authority): simple, uniseriate and relatively thin trichomes and filaments, always less than 4 μm wide; without any true or false branching; cells more or less uniform, cylindrical (rarely shortened up to ± isodiametric or spheroidal); thylakoids only parietal; cell division only cross–wise in the trichome.

Romeriaceae Komárek et al. 2014: trichomes relatively short, wavy, disintegrating, solitary or gathered few in fine mucilaginous colonies, in which are trichomes organised usually irregularly to cells shortly cylindrical, all cells of the same morphology, dividing of cells cross–wise.

Pseudanabaenaceae Anagnostidis et Komárek 1988 (incl. Pseudonostocaceae Elenkin 1934): simple, straight or wavy, thin isopolar trichomes (less than 4 μm wide), usually without mucilaginous sheaths (rarely with diffluent and fine mucilaginous envelopes), without any branching; cells rarely spheroidal, mostly cylindrical up to long cylindrical, dividing only cross–wise, perpendicularly to the longer trichome axis; living solitary or in colonies, periphytic, benthic, subaerophytic, sometimes form large macroscopic formations.

Spirulinaceae (Gomont) Hoffmann et al. 2014: simple, thin, cylindrical trichomes, which are very regularly and sometimes tightly screw–like coiled, never branched, with the same morphology along the whole length; living solitary or in irregular agglomerations; division of cells only cross–wise, the walls between the cylindrical (sometimes short) cells sometimes indistinct in the optical microscope; reproduction by fragments of trichomes; (the family is clearly different cytomorphologically and genetically from the habitually apparent Arthrospiraceae).

Prochlorotrichaceae Burger–Wiersma et al. 1989: very thin, cylindrical trichomes without or with fine, mucilaginous sheaths; all cells of the same morphology, with parietal thylakoids, in several genera polar or central gas vesicles (aerotopes) in cells; filaments occur usually solitary, rarely in groups.

Leptolyngbyaceae Komárek et al. 2014: simple, thin, cylindrical trichomes along the whole length, without branching, obligatory in mucilaginous thin, firm sheaths or envelopes (which are only facultatively lacking, e.g. during reproduction); cells cylindrical, dividing only cross–wise; living in solitary filaments or in irregular fascicles, colonies or clusters; reproduction by fragments of trichomes and filaments; rich, widely distributed family.

Heteroleibleiniaceae Komárek et al. 2014: simple, thin, cylindrical and more or less heteropolar wavy trichomes, usually enveloped by thin sheaths and attenuated towards apical ends; the rounded bases usually attached to variable substrates; very rarely develop laterally filaments, falsely branched; thylakoids parietal, cell division cross–wise, reproduction by fragments of filaments; occurs solitary or in groups.

Schizotrichaceae Elenkin 1934: simple, thin, cylindrical trichomes, usually fasciculated together and enclosed in thin, firm or fine sheaths; cells morphologically uniform, divide only cross–wise, with parietal thylakoids; reproduction by fragments of trichomes and filaments.

Oculatellaceae Mai et Johansen in Mai et al. 2018: with similar features like Pseudanabaenaceae, only on average with slightly wider trichomes (0.2–4 μm wide); cells often only shortly cylindrical or ± isodiametric; this family is particularly supported by molecular sequencing.

Chroococcales Schaffner 1922: unicells, groups of cells or morphologically distinct, multidimensional colonies; thylakoids within cells irregular parietal, radial or irregular wavy, more or less over the cell volume; few families with gas vesicles; cells spherical, elongated, oval, club–shaped or irregular, sometimes attached to the substrate; commonly develop mucilaginous sheaths or envelopes, sometimes stratified; division of cells rarely in one, mainly in several planes.

Aphanothecaceae Komárek et al. 2014: cells elongated, cylindrical or oval, rarely fusiform, solitary or irregularly situated in mucilaginous colonies or agglomerations; sometimes oriented in short rows; thylakoids mainly irregular wavy, sometimes agglomerated in peripheral parts of cells; cells enveloped often by sheaths or by the firm or diffluent envelopes, enveloping mucilage sometimes lamellated; cell division only cross–wise, perpendicularly to the long axis of cells, sometimes a little irregular.

Cyanobacteriaceae Komárek et al. 2014: cells oval, rarely solitary, usually in irregular agglomerations; thylakoids mainly irregular, situated along the cell volume; division of cells mainly cross–wise; periphytic or attached to the substrate.

Coelosphaeriaceae Lemmermann 1933: cells usually spherical, sometimes a little elongated, rarely living solitary, usually in spheroidal mucilaginous colonies, in which are situated usually in peripheral parts; cells are sometimes attached radially at the ends of mucilaginous, sometimes pseudodichotomically divaricated stalks, composed from more dense slimy substance and radially developed from centers of colonies; thylakoids wavy – parietal; cell division mainly by two perpendicular planes, perpendicular to the surface of colonies; reproduction by fragmentation of old colonies.

Merismopediaceae Elenkin 1933: cells ± spherical, solitary or situated in spheroidal, irregular, plate–like or cubic mucilaginous colonies, sometimes in regular rows; cells with parietal–wavy thylakoids, very rarely with gas vesicles (planktic types); cell division in two or three perpendicular planes; grow in different types of periphyton, rarely in plankton.

Microcystidaceae Elenkin 1923: cells ± spherical, agglomerated in irregular, later macroscopic mucilaginous colonies; thyla-

koids irregular, in cells occur obligatorily gas vesicles; cell division in three perpendicular planes; mainly planktic types (particularly in freshwater reservoirs).

Gomphosphaeriaceae Elenkin 1933 (incl. Cyanothrichaceae Elenkin in Kiselev 1947): colonial types, cells a little distant one from another, not regularly rod–like or spherical, usually slightly elongated, club–shaped, or shortened and discoid; cells organized in ± spherical or elongated («pseudofilamentous») colonies, in which are oriented radially or in rows; thylakoids irregular, slightly wavy; cell division in one or two directions, perpendicularly to the long axis of cells or elongated colonies; in colonies occur sometimes necridic cells; usually periphytic genera; both synonymous families are morphologically different and joined taxonomically mainly on the basis of molecular relations.

Chroococcaceae Nägeli 1849: unicellular, mostly forming agglomerations and ± regular or irregular colonies; cells mainly irregularly spherical or hemispherical, usually agglomerated within irregular mucilaginous, sometimes coloured, lamellated and delimited envelopes; cell division in two, three or more perpendicular planes; thylakoids irregular wavy, often situated through the whole cell volume; mostly periphytic, benthic or metaphytic species.

Prochloraceae Lewin 1977: cells spherical or slightly irregular, living solitary or in small groups (agglomerations), enveloped by thin mucilaginous layer; thylakoids irregular; cells divide in irregular planes; living exclusively endobiotically.

Stichosiphonaceae Hoffmann et al. 2005: cells solitary or in groups, elongated, usually heteropolar, attached by one end to the substrates; thylakoids irregular, agglomerated usually near the periphery of cells, particularly near the apex; cell division cross–wise, perpendicular, sometimes in the upper part of the cell, later sometimes a little irregular; mostly periphytic or epiphytic.

Entophysalidaceae Geitler 1925 (incl. Chlorogloeaceae Geitler 1925, Siphononemataceae Geitler 1925): cells firstly spheroidal or slightly elongated, later irregular, agglomerated in sometimes rich, irregular colonies, usually attached to various substrates; thylakoids in cells irregular; cell division firstly cross–wise or in perpendicular planes, later irregularly; different genera form mucilaginous, sometimes large, periphytic colonies.

Pleurocapsales Geitler 1925: unicellular or in groups and agglomerations, usually attached to the substrate by some parts; cells irregular, sometimes bipolar, and sessile by the help of special mucilaginous discs or short stalks; slime envelopes usually thin, firm, or diffluent; thylakoids irregular, wavy; cell division sometimes in irregular planes, later obligatory by the formation of endospores and/or exospores after a rapid irregular division of some cells, or of upper parts of cells (formation of nanocytes); living usually attached to various substrates, or periphytic.

Chroococcidiopsidaceae Geitler ex Büdel et al. 2012: cells ± irregular spheroidal or in agglomerations, all divide in endospores.

Hydrococcaceae Kützing 1843: cells ± irregular, agglomerated in irregular or ± pseudofilamentous, sometimes divaricated, attached formations (± along the whole length or in any part of the colony); reproduction by cell division and by endospores, which are formed occasionally in few terminal cells.

Pleurocapsaceae Geitler 1925 (incl. Hyellaceae Ercegović 1932, Scopulonemataceae Ercegović 1932): cells solitary or in groups, mainly irregular, attached to the substrate (sometimes only partly, sometimes by special mucilaginous formations), colonies irregular; cell division combined, by irregular planes, or sometimes are formed exospores and endospores, which develop in upper parts of cells or from the whole volume of cells; the elongated colonies arise in several genera by the help of daughter cells, attached to the old basal mother cells; thylakoids irregular; mostly periphytic.

Dermocarpellaceae Ginsburg–Ardré ex Christiansen 1980 (Dermocarpaceae Geitler 1925 – invalid.): unicellular, spheroidal or ± pyriform, polarized cells, attenuated to one end and attached to the substrate, less frequently irregular, club–shaped form; division and reproduction exclusively by endospores, forming multidimensionally in the whole cell volume, or only from the upper part of cells; thylakoids irregular wavy; only periphytic species.

Xenococcaceae Ercegović 1932: unicellular, with spheroidal or irregular cells, living solitary or in irregular groups, free or more commonly attached to the substrate; cell division irregular or by endospores, developing usually only in a part of colony; thylakoids irregular; mostly periphytic.

Oscillatoriales Schaffner 1922: exclusively simple filaments, isopolar or rarely heteropolar, always without true branching, rarely falsely branched; trichomes sometimes enveloped by sheaths or gelatinous envelopes, ± straight, wavy or coiled, thin to thick (2–60 μm wide); always without heterocytes and/or akinetes; filaments live solitary, in fascicles and colonies (sometimes very large, flat), rarely attached to the substrate by one end; only one genus grows mainly in solitary cells (molecular similarity).

Cyanothecaceae Komárek et al. 2014: with one genus, exceptionally growing in large, solitary cells or their groups, occasiona-

lly joined in short, few–celled filamentous formations; cells usually widely oval to cylindrical, 6–60 μm long; thylakoids irregular lengthwise or ± radial and coiled, agglomerated usually near cell periphery; cell division cross–wise, usually perpendicularly to the long axis of cells.

Borziaceae Borzì 1914: exceptionally unicells, mostly relatively short isopolar trichomes, rarely enveloped by thin sheaths, never branched; cells spherical, oval to short cylindrical, ± isodiametric or slightly elongated, end cells sometimes slightly narrowed; cell division only in one perpendicular plane; thylakoids lengthwise, radial, wavy, sometimes more agglomerated in peripheral parts of cells; mainly periphytic.

Coleofasciculaceae Komárek et al. 2014 (incl. Desertifilaceae Hašler et al. 2017): simple, uniseriate, isopolar trichomes and filaments, sometimes with thin sheaths, without any branching; cells usually cylindrical, cell division only perpendicular; cells isodiametric or slightly shorter or longer than wide; thylakoids irregularly coiled, sometimes more agglomerated near the cell periphery; this family was defined mostly by the help of molecular sequencing.

Ammatoideaceae Elenkin 1939: trichomes mostly isopolar, uniseriate, enveloped by sheaths, which are sometimes layered and a little widened towards ends; common false branching; trichomes are narrowed towards ends and usually pointed in terminal parts; growth usually in clusters; cells ± cylindrical or barrel–shaped, isodiametric, shorter or longer than wide, but distinctly narrowed towards ends; thylakoids irregular, coiled; mainly periphytic.

Homoeotrichaceae Elenkin 1949: simple, uniseriate, heteropolar trichomes, usually with widened basis attached to the substrate and distinctly narrowed apical free ends; usually in sheaths; relatively common lateral false, «tolypothrichoid» branching; cells of different length, ± cylindrical, dividing only cross–wise; thylakoids mostly irregular, coiled; filaments usually attached to various substrates by basal parts.

Microcoleaceae Komárek et al. 2004 (syn. Phormidiaceae Anagnostidis et Komárek 1998 sine typo; incl. Laspinemaceae Zimba et al. 2021, Symplocaceae): simple isopolar, uniseriate, ± straight or wavy trichomes, mostly 2–10 μm wide; without or with sheaths, exceptionally with false branching; cells ± cylindrical, of different length, ± isodiametric, dividing only perpendicularly cross–wise, along the whole trichome length; very diverse family; thylakoids lengthwise, irregular, wavy; end cells usually rounded or conical–rounded; (to this family belongs the majority of traditionally and originally described „*Phormidium*“ and „*Symploca*“ – species).

Arthrospiraceae (provis., not yet validly described): relatively thin isopolar, uniseriate trichomes, usually enclosed in indistinct sheaths, in principal cylindrical, obligatory regularly screw–like coiled, with similar shape of cylindrical cells; cross–wise walls thin, sometimes indistinct; cell division only perpendicular; thylakoids radial or irregular, cells occasionally with gas vesicles; end cells rounded; grows mainly in clusters and colonies; (from the similar family Spirulinaceae differs clearly genetically, but also by a little larger trichomes and cytologically).

Gomontiellaceae Elenkin 1949 (incl. Crinaliaceae Elenkin 1949): simple isopolar, uniseriate trichomes or ensheated long filaments, ± cylindrical, but always with differently laterally complanate trichomes (not circular in cross–section); cells in principle ± cylindrical, ± isodiametric or slightly longer or shorter than wide, more or less uniform, dividing only cross–wise; thylakoids usually irregular, often agglomerated near the periphery of cells; living in irregular clusters.

Oscillatoriaceae (Gray) Kirchner 1898: simple, cylindrical trichomes, isopolar, without or with distinct sheaths, uniseriate, relatively wide (mostly 6–60 μm); mostly not branched, in ensheathed filaments occurs rarely false branching; cells short, almost all distinctly shorter than wide, discoid; division only perpendicular cross–wise, in filaments occur special meristematic zones and necridic cells; thylakoids short wavy, irregular, usually densely agglomerated near peripheries of cells or ± organised with the characteristic radial arrangement; common family, in various habitats.

Vermifilaceae Berthold et al. 2020: simple, cylindrical, uniseriate trichomes in sheaths, usually growing in fascicles, isopolar; cells ± isodiametric, often shorter than wide, dividing cross–wise; thylakoids irregular wavy; (the family was defined mostly according to molecular analyses and must be more studied).

Nostocales Borzì 1914 (incl. Stigonematales Geitler 1925, Scytonematales): filaments, sometimes short, isopolar or heteropolar, uni– to multiseriate, without branching, or falsely or true branched, sometimes with something diversified thallus; sometimes forming morphologically characteristic colonies; main diacritical feature of the order is the ability to produce heterocytes, which can lack only in clearly derived types; occasional is the presence of akinetes; division of cells perpendicularly to the cell/trichome axis, or in more planes, in several types occur multiseriate formations; thylakoids irregular, coiled; occur in various freshwater, marine and aerophytic ecosystems, sometimes forming mass populations (in the plankton of reservoirs, on rocky walls, in thermal habitats, etc.).

Chlorogloeopsidaceae Mitra et Pandey 1967: relatively short, irregular filaments, or agglomerated clusters of cells, especially in older stages ± multidimensional, multiseriate, and with occasionally developing basal, lateral, terminal, or intercalar heterocytes; cells often tightly agglomerated one to another; rarely developed akinetes.

Stigonemataceae Borzì 1925: filaments rarely uniseriate (young), mainly multiseriate, ± irregular, often with true branches, morphologically similar to the main multiseriate filaments; heterocytes develop in all parts of thallus; colonies sometimes polarised; cells arranged in pseudofilament within the colony; reproduction by fragments of colonies and by hormogonia.

Capsosiraceae Geitler 1925: ± uniseriate trichomes, composed from ± spheroidal cells, tightly gathered one to another and forming dense, usually multiseriate clusters from which grow lateral branches; usually polarised thallus; cells divide perpendicularly into one or more planes; reproduction sometimes by hormogonia, developing in terminal parts of branches, or by monocytes, liberating from various cells in trichomes; mostly periphytic among other plants.

Rhizonemataceae Büdel et Kauff ex Lücking et al. 2014: cylindrical trichomes, ± contorted, bipolar, uniseriate, true branched with the T–type, not constricted at cross–walls, with ± narrowed, yellowish terminal cells; grows in clusters endophytically in lichens (Asco– and Basidiomycetes); cells ± short, usually rectangular, with blue–green to olive–green pigmentation; gelatinous, hyaline, or brownish sheaths; branching rare, heterocytes frequent, intercalar; reproduction also by hormogonia and akinetes.

Symphyonemataceae Hoffmann et al. 2005: trichomes uniseriate, mostly isopolar, wavy, with sheaths; filaments specially Y–formed, true–branched, usually distinctly narrowed towards ends (namely branches); less frequently false scytonematoid branching; heterocytes intercalar, rarely terminal; filaments usually in slimy, sometimes lamellated envelopes; cells divide mostly perpendicularly by cross–wise section, reproduction by fragments of trichomes, by hormogonia and hormocysts; thylakoids irregular–wavy.

Hapalosiphonaceae Elenkin 1916 (incl. Fischerellaceae Anagnostidis et Komárek 1990, Loriellaceae Geitler 1925, Nostochopsidaceae Geitler 1925, Mastigocladaceae Geitler 1925): trichomes mainly uniseriate, less frequently polyseriate (esp. in main filaments and older parts), true branched, usually by branches perpendicularly growing from old filaments; rarely false branching; the ends of branches only slightly attenuated; terminal cells usually conical, not pointed; usually all trichomes in sheaths; heterocytes intercalar, less frequently lateral; cell division perpendicular, rarely in more planes (in old parts of trichomes), reproduction by fragments of filaments and terminal hormogonia.

Scytonemataceae Rabenhorst ex Bornet et Flahault 1888 (incl. Heteroscytonemataceae McGregor et Sendall 2018, ?Tildeniaceae Kosinskaja 1926): trichomes uniseriate, ± cylindric, in sheaths, narrow or wide, rarely surrounded by wide slimy and lamellated envelopes; common false binary, rarely simple branching, branches usually of the same morphology as main filaments, not attenuated; all cells of the same morphology, ± isodiametric or slightly shorter or longer than wide, divide cross–wise, terminal cells usually rounded, rarely with special morphological formations; heterocytes intercalar, they occur also necridic cells; growth in clusters or fascicles on the substrate; reproduction by hormogonia.

Borzinemataceae Geitler 1942 (syn.: Tolypothrichaceae Hauer et al. 2014, Dapisostemonaceae Hentschke et al. 2016, Godleyaceae Hauer et al. 2014, Microchaetaceae Lemmermann 1907): initially obligatory heteropolar; trichomes uniseriate, filaments usually with sheaths, more or less cylindrical, sometimes later slightly widened towards ends; heterocytes develop intercalary, but initially in basal position; common lateral false branching, the branches are of the same morphology as the main filaments and often grow in the same direction, as the original filament; cell division cross–wise, perpendicular to the trichome axis, terminal cells usually ± rounded; thylakoids irregular–wavy; reproduction by hormogonia, sometimes form akinetes; usually occur attached to substrates, with polarized thallus.

Rivulariaceae Rabenhorst ex Bornet et Flahault 1886 (incl. Gloeotrichiaceae Komárek et al. 2014, Cyanomargaritaceae Shalygin et al. 2019): trichomes uniseriate, always heteropolar, in sheaths, with widened basis and usually basal heterocyte and narrowed towards ends, sometimes ending by hair–like apex (exceptions exist only in few clearly derived types); polarized growth of filaments, sometimes in characteristical macroscopic colonies, occasionally spherical, sometimes encrusted by CaCO3; sheaths sometimes calyculate at the basis and striated; heterocytes develop also intercalary, in several species akinetes, arising rather in basal parts of trichomes; cells divide crosswise; thylakoids radial or irregular–wavy.

Leptobasaceae Elenkin 1916 (syn.: Fortieaceae Komárek et al. 2014): trichomes uniseriate, isopolar, cylindrical or with slightly widened both ends, within sheaths, forming filaments; heterocytes develop solitary or two together, intercalary; both ends of trichomes grow apically on both sides; cells divide cross–wise, perpendicularly to the trichome, terminal cell usually rounded; rarely scytonematoid false branching; thylakoids irregular coiled; reproduction mainly by hormogonia.

Aphanizomenonaceae Elenkin 1938: trichomes uniseriate, mostly isopolar, never branched, ± cylindrical and often distinctly narrowed toward both ends, sometimes enveloped by very indistinct, narrow slime envelope; cells ± cylindrical, almost isodiametric, always with aerotopes, often elongated and longer toward ends and ± pointed; rarely develop cylindrical akinetes; heterocytes develop mostly solitary, intercalary; division of cells only perpendicularly; thylakoids irregular, coiled; living in solitary trichomes or fasciculated in irregular colonies of filaments; occurs in the plankton of different water bodies, sometimes in masses; reproduction by hormogonia or fragments of trichomes and filaments.

Nostocaceae Agardh ex Kirchner 1890 (incl. Hydrocorynaceae Elenkin 1934): trichomes not very long, mostly with sheaths, rarely living ± solitary, usually aggregated in characteristical colonies, uniseriate, not branched, usually in principal cy-

lindrical without morphologically different ends; cells ± isodiametric or a little shorter or longer than wide, cylindrical, barrel–shaped up to almost spheroidal; cell division only cross–wise; heterocytes develop intercalary, solitary, or in several genera obligatory in terminal position; akinetes develop or ± solitary in special positions, or in rows (sometimes long); thylakoids irregular–wavy; usually not forming gas vesicles; it is a very rich and variable group, different species often form morphologically characteristic colonies; occur in freshwater, marine and also subaerophytic habitats, also in masses.

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Supplementary material

The following supplementary material is available for this article:

Fig. S1. The scheme is constructed mainly according to the synthesis of published molecular trees based on molecular sequencing, combined with traditional diacritical morphological criteria.

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

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