Chapter 2
Blue-Green Algae (Cyanobacteria) in Rivers

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Abstract This chapter presents some of the more commonly encountered lotic cyanobacterial taxa. The cyanobacteria are a group of oxygenic prokaryotes present in nearly all aquatic ecosystems. While the ecological importance of this lineage is well known, much confusion exists pertaining to their systematic and taxonomic status. In order to facilitate generic-level identification, we separate the cyanobacteria into four major groupings: the Chroococcales (coccoid cells often in a mucilaginous envelop), the Oscillatoriales (filamentous forms lacking specialized cells), the Nostocales (filamentous with inducible specialized cells), and the Stigonematales (filamentous, obligatory specialized cells coupled with cell division in multiple planes). We discuss the major genera found in each lineage, the current state of the systematics, and the broad ecological roles and niches of these taxa. Dichotomous keys and images are presented to facilitate generic identifications.

Keywords Cyanobacteria • Genus • Identification • Lotic • Morphology • River • Taxonomy

Introduction

The cyanobacteria (also known as blue-green algae, cyanophyta, cyanoprokaryotes) are a group of photo-oxygenic bacteria found in aquatic, aerophytic and terrestrial habitats, and from pole to pole. They are among the most ancient lineages of prokaryotes and are some of the most ubiquitous organisms on Earth (Falcon et al. 2010). The cyanobacteria are incredible ecosystem engineers, accounting for ca. 20–30 % of global oxygen production (Pisciotta et al. 2010) and have been credited with elevating the atmospheric oxygen levels ca. 2.5–2.2 bya (Schopf 2000). Cyanobacteria are also known to fix atmospheric nitrogen, contributing greatly to

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the global nitrogen budget (Karl et al. 2002), serve as the centerpiece of aquatic foodwebs (Scott and Marcarelli 2012), help to stabilize substrates, and are common photobionts.

Cyanobacteria are usually seen as harbingers of ecosystem degradation in lotic systems. Often the most visible components of freshwater harmful algal blooms (HABs), excessive cyanobacteria may lead to negative consequences such as light attenuation, biofouling, the accumulation of excess biomass and subsequent anoxia, and toxin production. Cyanobacterial blooms, typically in lentic ecosystems but also in lotic ones, are often triggered by anthropogenic factors, such as increased nitrogen and phosphorus loads related to land use (e.g., Beaver et al. 2014). Within lotic habitats, the presence of cyanobacteria are useful biomonitoring units (e.g., oligotrophic vs. eutrophic, Loza et al. 2013). Like their planktic counterparts, lotic cyanobacteria may be a source of cyanotoxins, but much less attention is paid to monitoring such benthic cyanobacteria (Seifert et al. 2007).

Given their vast preponderance, diversity, and ecosystem importance, cyanobacteria make excellent taxa for monitoring the health of aquatic ecosystems. However, two major impediments exist that preclude their usage to the wider aquatic community. First, the current state of cyanobacterial systematics is rather confusing. Second, many of the cyanobacteria are difficult to identify due to a limited amount of morphological characters, phenotypic plasticity, and small size.

Systematics and Taxonomy

Cyanobacteria have long been observed by phycologists in classic monographs (e.g., Agardh 1824; Kützing 1849; Nägeli 1849), but were first extensively documented by Bornet and Flahault (1886–1888) and later by Gomont (1892–1893). Their starting taxonomy was expanded by later researchers, most notably Geitler (1932), who helped revise many of the currently recognized genera familiar to most scientists. Recognizing the prokaryotic nature of the cyanobacteria, Stanier et al. (1978) advocated the transfer of the cyanobacteria from the *International Code of Botanical Nomenclature* (ICBN) to the *International Code of Nomenclature of Bacteria* (ICNB). While this appeal had much merit (after all, they are bacteria), it also meant that both codes could be utilized to name novel taxa, leading to an explosion of new names. The inclusion into the ICNB code allowed the cyanobacteria to be catalogued in the Bergey's Manual of Systemic Bacteriology, where Castenhoz (2001) broke them into five major lineages based, in part, on type of cell division and the presence of differentiated cells. While this was a major revision, many felt that this approach missed a tremendous amount of the actual biodiversity of this lineage. All of this began to change in the 1980s–1990s when Komárek and Anagnostidis began their revisionary work on the cyanobacteria as a whole (e.g., Anagnostidis and Komárek 1985). Eschewing the simplified version of systematics proposed by Castenhoz (2001), Komárek and Anagnostidis set about erecting smaller, monophyletic genera employing a polyphasic approach using a number of different characters including morphology, ecology, and genetic characters (most

notably the 16S rDNA sequence as proposed by the ICNB). Their work, along with that of colleagues, has greatly increased our knowledge of cyanobacterial diversity and evolutionary relationships (see references below).

Difficulties with Identifications

One of the main difficulties in identifying the cyanobacteria is the fact that they may exhibit a tremendous amount of environmentally or culturally induced phenotypic plasticity (Casamatta and Vis 2004). Conversely, other lineages are obligatorily very simple, and thus exhibit a limited range of morphologies that may mask a tremendous amount of genetic or cryptic diversity (Casamatta et al. 2003).

The other difficulty in identifying the cyanobacteria lies in the small size (filaments typically range from 1 to 10 µm) and lack of easily discernable morphological characters, as most cyanobacteria exist as simple coccoid or bacillus cells. Some lineages have evolved more complex structures, perhaps even being considered "multicellular" (Schirrmeister et al. 2011), including the "overwintering" akinete and the heterocyte (a common type of differentiated cell dedicated to nitrogen fixation), both of which are commonly employed in phylogenetic assessments. However, given the ancient history and ecological permissively of cyanobacteria, it is clear that the described diversity is not reflected in the current phylogenetic character sets.

Habitats

Lotic habitats are replete with cyanobacteria. Many taxa are strictly or predominantly benthic (e.g., *Phormidium*, *Geitlerinema*) and thus easily collected as mats or solitary filaments. Other taxa begin as benthic colonies before migrating to a more planktic habitat (e.g., *Merismopedia*, *Pseudanabaena*). Still others are may be epiphytic (*Chamaesiphon*, *Leibleinia*), endogloeic (*Pseudanabaena*, *Synechococcus*), or epilithic (*Homoeothrix*, *Pleurocapsa*, *Chamaesiphon*, *Calothrix*). In fast flowing waters, taxa with the ability to adhere to surfaces are common (*Lyngbya*), while stagnant waters, or even water margins, may select for forms with elaborate sheaths (*Microcoleus*). Myriad other microhabitats are excellent places for additional genera, but it should be noted that many cyanobacteria are quite capable of motility (*Geitlerinema*) or posses gas vacuoles for rapid movement throughout the water column (*Microcystis*). Thus, nearly every lotic ecosystem will have representative cyanobacteria if one merely looks.

We would be remiss if we did not point out that there exists tremendous variability among lotic ecosystems, with concurrent differences present in the cyanobacterial community. For example, first-order streams are often greatly influenced by allochothonous carbon inputs, and often contain more rocky substrates, favoring cyanobacteria capable of surviving periodic episodes of desiccation and benthic

growth habits (e.g., *Phormidium*). Further, differences in aspects such as substrates (e.g., limestone vs. muddy vs. sandy) may greatly impact the cyanobacterial community present. Additional factors, such as light levels, flow rates, the presence grazers, degree of disturbance, and anthropogenic impacts, just to name a few potential cofounding factors, all conspire to affect community composition. Conversely, the cyanobacterial community in higher order streams may appear more like their lentic counterparts, especially in deeper rivers with very slow flow, where planktic taxa frequently occur (e.g., *Microcystis*, *Woronichinia*, *Snowella*, *Anabaena*/*Dolichospermum*, *Planktothrix*; Hašler et al. 2008) and benthic species usually inhabit fine sediments such as mud or fine sand.

Another potential pitfall in crafting a guide to common cyanobacteria of lotic habitats concerns itself with the sometimes vast differences presented by geographic regions. The issue of endemism in cyanobacteria is one of great debate. Some taxa appear to be cosmopolitan (e.g., *Phormidium*, *Leptolyngbya*) within permissible habitats and appear in European and North American phycological keys. However, even wide-spread taxa may not actually represent the same organism, as many cyanobacteria are difficult to identify to species and may be masked by cryptic variation (e.g., *Phormidium retzii*, *sensu* Casamatta et al. 2003). In a recent survey, Sherwood et al. (2015) noted a large number of endemic cyanobacteria from Hawaii, indicating the need for more extensive sampling and descriptions to fully characterize the cyanobacteria. In addition, even within national boundaries there may exist vast habitat and concurrent cyanobacterial variability and heterogeneity (e.g., in the United States alone there would be alpine, desert, temperate, tropic, ephemeral, and other habitats). Thus, we caution that no guide will ever be able to encompass the tremendous amount of potential diversity, and thus we seek to present only some of the most common, ubiquitous members that one may encounter in a practical, brief, concise manner. For a more complete survey, we provide additional links to resources elsewhere.

Identification of Cyanobacteria

The current state of cyanobacterial systematics is in a state of some debate, but in order to facilitate identifications we have chosen to employ the scheme proposed by Anagnostidis and Komárek (1988, 1990), Komárek (2013), and Komárek and Anagnostidis (1986, 1989, 1998, 2005) (see Table 2.1).

Additional Keys and Resources

Alas, an exhaustive description of all common lotic cyanobacteria is not feasible, but fortunately many of the more "common" taxa have rather global distributions. There has been a flurry of new genera proposed over the last decade, representing an increase in types of habitats sampled and also more intensive scrutiny of less

Table 2.1 General orders of the cyanobacteria and main features (*sensu* references cited)

Order	Feature	Example genera
Chroococcales (Key 1)	Unicellular or colonial, never forming filaments (but rarely pseudofilamentous)	*Aphanocapsa*, *Chroococcus*, *Merismopedia*
Oscillatoriales (Key 2)	Filamentous, sometimes with false branching, no heterocytes, and akinetes	*Leptolyngbya*, *Lyngbya*, *Oscillatoria*, *Phormidium*
Heterocytous genera I (Key 3)	Filamentous, heterocytes and akinetes present (usually), sometimes with false branching	*Anabaena*, *Calothrix*, *Dichothrix*, *Nostoc*
Heterocytous genera II (Key 4)	Filamentous, division in multiple planes (true branching), heterocytes present	*Hapalosiphon*, *Nostochopsis*

esoteric habitats but with a more practiced eye for finely discernable genera. Many traditional "large" genera were found polyphyletic. Using a polyphasic approach many new monophyletic genera were established. For a more detailed listing of taxa, we recommend monographs from North America (e.g., Tilden 1910; Smith 1950; Prescott 1962; Whitford and Schumaker 1969; Komárek and Johansen 2015a, b) or Europe (Whitton 2005; Komárek and Anagnostidis 1998, 2005). While much of the taxonomy in these texts has changed, the works by Komárek and Anagnostidis (1998, 2005) and Komárek (2013) provide excellent starting points to the revised taxonomy and species identifications. The CyanoDB site (www.Cyanodb.cz, Komárek and Hauer 2015) is an excellent resource for approved cyanobacteria genera. For additional photomicrographs, we recommend the Hindák 2001 book.

Additional Lotic Cyanobacterial References

If describing cyanobacterial diversity in lotic ecosystems is challenging, understanding their ecology is even more difficult. Small, ephemeral, first-order streams through massive, ofttimes slow moving bodies of water all fall under the umbrella of lotic systems, with everything in between. The ecology of the constitutive cyanobacteria varies by surrounding land use, altitude, climate, flow rates, anthropogenic inputs, etc., just to name a few parameters. Thus, a comprehensive review of the ecological roles of cyanobacteria is beyond the purview of this chapter. In order to even partially ameliorate this shortcoming, we provide a list of references to further explore some of the vast ecological roles that cyanobacteria play in flowing waters: Sheath and Cole (1992), Steinman et al. (1992), Stevenson et al. (1996), Perona et al. (1998), Whitton and Potts (2000), Rott et al. (2006), Whitton (2012a, b), Loza et al. (2013), Manoylov (2014), and Stevenson (2014).

Key 1: Form-genera of the Chroococcales

1a	Cells not heteropolar	2
1b	Heteropolar cells or pseudofilaments divided into basal and apical end	9
2a	Flat, tabular-like colonies, cells spherical, or ovoid	*Merismopedia*
2b	Other than tabular-like colonies	3
3a	Spherical or hemispherical cells, irregularly arranged in diffluent mucilage	*Aphanocapsa*
3b	Cells and colonies otherwise	4
4a	Elliptical, oval to rod-like cells, irregularly in diffluent mucilage	*Aphanothece*
4b	Cells otherwise arranged (not in common mucilage)	5
5a	Cells solitary or in irregular clusters, but not mucilaginous colonies	*Synechococcus*
5b	Cells, mucilage, and colonies of different shape	6
6a	Cell spherical to hemispherical with distinct mucilaginous envelopes	7
6b	Cells of various shape, often irregular	8
7a	Spherical mature cells, daughter cells reach mother cell shape after division, layered mucilaginous envelopes, often colored	*Gloeocapsa*
7b	Spherical, hemispherical cells, do not reach cell shape after division	*Chroococcus*
8a	Mucilaginous colonies, spherical to irregular cells, often individually enveloped by distinct mucilage	*Chlorogloea*
8b	Usually pseudoparenchymatous colonies, pseudofilaments, irregular cells, produces baeocytes	*Pleurocapsa*
9a	Species does not form pseudofilaments	10
9b	Species forms pseudofilaments, cells spherical, cylindrical, or barrel shaped, exospores of different shape liberated separately	*Stichosiphon*
10a	Oval, elongated to rod-like cells, sheath (pseudovagina) not present, exospores produced at the upper part of mother cell	*Geitleribactron*
10b	Species enveloped by distinct sheath (pseudovagina)	11
11a	Cells oval, elongated, cylindrical, apically produced exospores	12
11b	Cells spherical, oval, club/pear like or irregular, produce baeocytes, mainly epiphytic	13
12a	One or more spherical or hemispherical exospores, epiphytic, or epilithic	*Chamaesiphon*
12b	Cells form gelatinous hairs at the apical part, one or more spherical to elongated exospores, epiphytic, or epilithic	*Clastidium*
13a	Cells usually live solitary or gathered in groups	*Cyanocystis*
13b	Cells usually form pseudoparenchymatous colonies	14
14a	Few cells enveloped by a common sheath	*Xenococcus*
14b	A common sheath envelopes the whole colony	*Xenotholos*

Aphanocapsa Nägeli (Fig. 2.1a)

Individuals are microscopic to macroscopic colonies, usually mucilaginous, spherical to irregular. Cells without individual gelatinous envelopes are spherical, temporarily hemispherical after division, irregularly arranged in homogenous colorless mucilage. Cells are usually green, blue-green, or olive-green. Cell content is homogenous or finely granulated, always without aerotopes. Binary fission in one
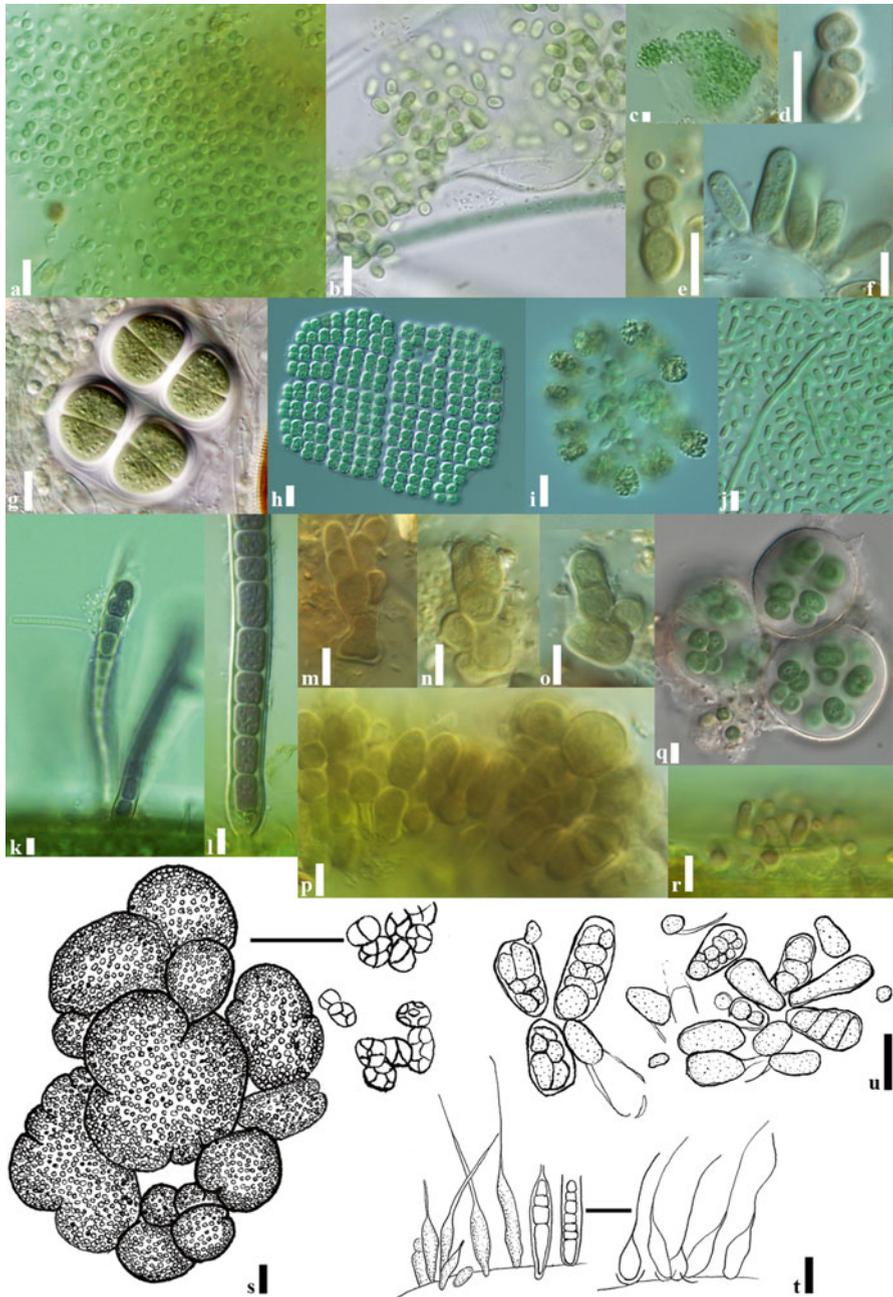
Fig. 2.1 (**a–u**) Examples of coccoid genera. (**a**) *Aphanocapsa*. (**b** and **c**) *Aphanothece*. (**d–f**) *Chamaesiphon*. (**g**) *Chroococcus*. (**h**) *Merismopedia*. (**i** and **j**) *Synechcoccus*: note the growth within the mucilage of other algae [endogloeic]. (**k** and **l**) *Stichosiphon*: note the pseudofilaments and pseudovaginal arrangement. (**m–p**) *Pleurocapsa*. (**q**) *Gloeocapsa*. (**r**) *Geitleribactron*. (**s**) *Chlorogloea*. (**t**) *Clastidium*. (**u**) *Cyanocystis*. Scale bars: (**a–c**, **g** and **h**, **k–q**) = 10 μm; (**d–f**, **i** and **j**, **r–u**) = 5 μm

or two perpendicular planes is typical for this genus. Cells after division can be gathered in small groups or subcolonies. Colonies of various species can differ in density of cells.

Occurrence: many species are epilithic on submerged stones or subaerophytic in spray and zones (*sensu* Rott et al. 2006) but may also be common as planktic members. Found extensively in lentic and lotic systems.

Expected taxa: *A. fonticola* Hansgirg, *A. grevillei* (Berkeley) Rabenhorst, *A. muscicola* (Meneghini) Wille, *A. rivularis* (Carmichael) Rabenhorst

Aphanothece Nägeli (Fig. 2.1b, c)

Individuals are microscopic (to macroscopic), usually consisting gelatinous colonies which can consist of small subcolonies. Cells are arranged within homogenous mucilage (usually colorless, sometimes yellowish, or brownish), occasionally slightly layered mucilage around cells, or small groups of cells can occur (e.g., *A. bullosa*). Cells divide into daughter cells by binary fission in one plane and after division grow into original cell shape (elongated, cylindrical to rod like) and size. Cell content is homogenous or slightly granulated, green, blue-green, violet, brownish, often with visible peripheral chromatoplasma.

Remarks: two major subgroups of *Aphanothece* differ in cell dimensions. The first is usually planktic and ≤1 µm wide, while the majority of benthic, metaphytic, or aerophytic species are in the second group (≥1 µm wide).

Occurrence: the majority of species is epilithic on submerged stones or subaerophytic in spray zones (*sensu* Rott et al. 2006), epipelic, epiphytic, metaphytic, in springs and streams.

Expected taxa: *A. stagnina* (Sprengel) A. Braun, *A. minutissima* (W. West) Komarková-Legnerová et Cronberg, *A. smithii* Komarková-Legnerová et Cronberg

Chamaesiphon A. Braun et Grunow in Rabenhorst (Fig. 2.1e, f)

Thallus formed by layered/shrub-like micro to macroscopic gelatinous colonies or can live solitary. Vegetative cells are variable in shape (spherical, elliptic, oval, pear like, or rod like) and can change during life cycle. Cell content is homogenous or finely granulated blue-green, olive-green, yellowish, reddish, pinkish, or violet, sometimes with visible peripheral chromatoplasma. Mother cells divide asymmetrically and form apically placed exocytes. Both mother cells and exocytes are surrounded by colorless or yellowish to brownish envelopes, which burst after exocytes liberation.

Remarks: species are differentiated by the shape and dimensions of cells.

Occurrence: mainly epilithic on submerged or wetted stones, epiphytic on filamentous algae or mosses, especially in unpolluted freshwaters, streams, and waterfalls.

Expected taxa: nearly all taxa (*sensu* Komárek and Anagnostidis 1998) can occur in streams and rivers, e.g., *C. minutus* (Rostafinski) Lemmermann, *C. incrustans* Grunow, *C. polymorphus* Geitler, *C. starmachii* Kann, *C. subglobosus* (Rostanfinski) Lemmermann.

Chroococcus **Nägeli (Fig. 2.1g)**

Solitary living cells in small groups (usually two to eight cells) or agglomerations of microscopic colonies. Spherical to hemispherical cells (1–50 μm) are surrounded by colorless to yellowish mucilaginous envelopes. The envelopes can be markedly distinct at margin, layered and wide or tightly attached to the cell surface. The genus was recently divided into two major lineages, with planktic species moved into *Limnococcus* and the remaining attached or metaphytic species remaining in *Chroococcus* (Komárková et al. 2010). Cell content is greenish, olive-green, reddish to violet, often granulated or divided into granulated centroplasma and homogenous or finely granulated peripheral chromatoplasma. Cell division depends on colony age; cells in young colonies divide by binary fission in three planes, in old colonies divide almost irregularly with respect to density of cells. Colonies reproduce by fragmentation into small parts or subcolonies.

Occurrence: mainly periphytic on stones and waterfalls or metaphytic, in cold to hot/thermal springs and streams.

Expected taxa: *C. tenax* (Kirchner) Hieronymous

Chlorogloea **Wille (Fig. 2.1s)**

Colonies are usually mucilaginous with markedly limited surface and variable in shape (spherical, hemispherical to irregular). Cells are variable in shape as well (spherical to almost irregular, 1–6 μm) usually irregularly arranged in colony, seldom at margin radial rows can occur. They are placed in individual colorless or greenish to reddish envelopes. Cell division in three perpendicular planes and reproduction by disintegration of colonies occur in this genus.

Occurrence: typically attached species on various substrates (stones, plants, and algae).

Expected taxa: *C. rivularis* (Hansgirg) Komárek et Anagnostidis, *C. microcystoides* Geitler

Clastidium **Kirchner (Fig. 2.1t)**

Cells live solitary or gathered in small groups. Cells are different in shape and size from spherical to oval/cylindrical or pear like (approximately 6–40 × 2–4 μm). Basal part of cell is oval while apical part is narrowed and can be extended into thin

hair-like gelatinous projection (up to 75 μm long). Cell content is yellowish, blue-green, olive-green, or gray-green. Mucilaginous envelope (pseudovagina) is usually thin and firm, occasionally can be slightly lamellate. Spherical exocytes are produced in apical part of cells, then released and attached on substrate.

Occurrence: epiphytic (on algae) or epilithic in clear streams.

Expected taxa: *C. rivulare* (Hansgirg) Hansgirg, *C. setigerum* Kirchner, *C. sicyoideum* Li.

Cyanocystis Borzi (Fig. 2.1u)

Cells live solitary or gathered in hemispherical to flatted groups attached to substrate. Cell shape varies from spherical, hemispherical, oval, broadly oval to club/pear like, or elongated, often obviously heteropolar, usually 10–30 μm long and 5–20 μm wide, seldom more or less. Cell content is homogenous or finely granulated, blue-green, olive-green, yellowish, and reddish to violet. Mucilaginous envelope (pseudovagina) is usually thin, colorless, firm, and disintegrates after baeocyte liberation, which grow to the mother cell size and shape before next reproduction.

Occurrence: common in mountain streams, cosmopolitan, mainly epiphytic species on filamentous cyanobacteria and algae, seldom epilithic.

Expected taxa: *C. aquae-dulcis* (Reinsch) Kann, *C. mexicana* Montejano et al., *C. versicolor* Borzi

Geitleribactron Komárek (Fig. 2.1r)

Solitary living heteropolar cells or groups of cells attached to the substrate. Cells are ovoid, cylindrical to rod like or club like, straight or slightly bent, usually with rounded apical part and narrowed basis, blue-green, pale blue-green, olive-green to grayish. Protoplast is homogenous or finely granulated, often with clearly visible peripheral chromatoplasma. Mucilaginous envelope is not present. Cells divide in the middle or asymmetrically in upper part. Daughter cells attach to the substrate by their ends after liberation and grow into original size.

Occurrence: epiphytic genus, usually on filamentous cyanobacteria and algae.

Expected taxa: *G. crissa* Gold-Morgan et al., *G. periphyticum* Komárek

Gloeocapsa Kützing (Fig. 2.1q)

Microscopic to macroscopic colonies, which can gather in gelatinous mats. Cells are irregularly arranged in colonies, spherical, hemispherical, oval to slightly elongated, with homogenous to finely granulated content, blue surrounded by individual mucilaginous envelopes, colorless or colored yellow, yellow-brown, reddish, and blue to violet. Structure of envelopes is dependent on life cycle and can be distinct and layered or gelatinous and diffluent. Cells divide by binary fission in three

perpendicular planes and then are irregularly arranged in the colony. Cells after division grow into original size and shape. In some, species was observed formation of resting spores (akinetes) surrounded by individual thick, firm, structured, and intensely colored envelopes. Nanocyte production was occasionally observed in several species.

Occurrence: mainly aerophytic and subaerophytic species, members of the genus can occur on walls of waterfalls, on wetted stones along banks.

Expected taxa: *G. aeruginosa* Kützing, *G. gelatinosa* (Meneghini) Kützing, *G. granosa* (Berkeley) Kützing, *G. punctata* Nägeli, *G. thermalis* Lemmermann.

Merismopedia Meyen (Fig. 2.1h)

Microscopic (occasionally large macroscopic), flat, tabular-like, large colonies often consist of small subcolonies. Cells are precisely oriented along two perpendicular planes in the colony. Cell density is variable from tightly to sparsely arranged cells. Cells are hemispherical, oval, usually with homogenous content, blue-green, olive-green to reddish. Mucilaginous envelopes vary from diffluent gelatinous to thin distinct layers. Cells divide by binary fission in two perpendicular planes and grow into original size before next division.

Occurrence: very common in metaphytic and benthic habitats, often becoming planktic.

Expected taxa: *M. convoluta* Brébisson, *M. elegans* A. Braun*, M. glauca* (Ehrenberg) Kützing

Pleurocapsa Thuret in Hauck (Fig. 2.1m–p)

Colonies are irregular, attached to stony substrates, pseudofilamentous, sometimes sarcinoid. Yellowish to brownish mucilaginous sheaths are thin and firm and cover cells or rows of cells or pseudofilaments. Cells are variable, ovoid, elongate, polygonal, or apically narrowed, 0.8–20 μm in diameter, homogenous or slightly granular, blue-green, gray-green, brownish, or violet. Cells divide irregularly in various planes. Reproduction by baeocytes was observed in several species.

Occurrence: typically epilithic, parts of colonies can be endolithic.

Expected taxa: *P. aurantiaca* Geitler, *P. concharum* Hansgirg, *P. minor* Hansgirg.

Stichosiphon Geitler (Fig. 2.1k, l)

Solitary or gathered in groups, single celled to heteropolar pseudofilamentous attached by narrowed basis (mucilaginous stalk) to the substrate. Mucilaginous sheath (pseudovagina) is colorless, firm, and distinct, opened at the apex. Cells are spherical, hemispherical, cylindrical, barrel shaped, or almost rectangular, homogenous to finely granulated, blue-green, olive-green to grayish. After repeated binary
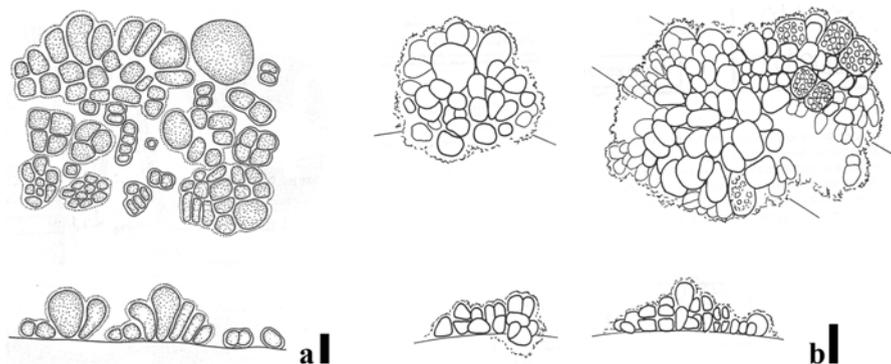
Fig. 2.2 (**a** and **b**) Examples of coccoid genera. (**a**) *Xenococcus*. (**b**) *Xenotholos*. Scale bars = 5 µm

fission exospores remain in the pseudovagina. Number of exospores is species dependent and ranges from 4 to more than 80, with shape a stable species level identifier (e.g., *S. filamentosus*, oblong exocytes; *S. gardneri*, narrowly oblong; *S. regularis*, widely ovate).

Occurrence: mainly epiphytic on submerged plants and cyanobacteria and algae (*Rhizoclonium*, *Cladophora*, *Oedogonium*, *Plectonema*, *Homoeothrix*), occasionally epilithic.

Expected taxa: *S. regularis* Geitler, *S. pseudopolymorphus* (Fritsch) Komárek, *S. filamentosus* (Ghose) Geitler

Synechcoccus Nägeli (Fig. 2.1i, j)

Cells cylindrical to oblong, elliptical, occasionally forming pseudofilaments (2–4, but up to 20 cells). Transverse cell division results in similar shaped or different daughter cells that may remain joined together. Cells typically small (0.5–6(11) µm wide), but may occasionally be much longer (1.5–20 µm long).

Occurrence: very common genus, may be planktic, occasionally associated with other algae, subaerial, or endogloeic.

Expected taxa: *S. elongates* (Nägeli) Nägeli, *S. nidulans* (Pringsheim) Komárek in Bourrelly

Xenococcus Thuret in Bornet et Thuret (Fig. 2.2a)

Sessile cells are solitary or gathered in monolayered groups of colonies, old colonies form irregular or pseudoparenchymatous mats. Colorless or yellowish, thin and firm sheath (envelope) covers small clusters including few cells (subcolonies). Cell shape varies from spherical or oval to irregular or pear shaped (1.5–5.5 µm in diameter, freshwater species), polarity of attached cells is possible to recognize. Cells

divide irregularly in multiple planes, usually in a perpendicular plane to substrate. Baeocytes (reproducing cells) are formed by multiple fission and subsequently liberates from mother cells. The members of the genus can be misidentified with members of the genus *Xenotholos* (see description below).

Occurrence*: freshwater species are usually epiphytic on filamentous algae such as *Cladophora* or *Tribonema*

Expected taxa*: *X. bicudoi* Montejano et al., *X. lamellosus* Gold-Morgan et al., *X. minimus* Geitler, *X. willei* Gardner

Xenotholos Gold-Morgan et al. (Fig. 2.2b)

Cells usually aggregated into globular, often multilayered, colonies. Old colonies form pseudoparenchymatous thallus. Single cells occur at the beginning of life cycle and subsequently divide, grow, and form new colonies. Sheath (envelope) is usually firm, thin, colorless, and overlaps the whole colony. Cell shape varies from spherical, oval to irregular, or pyriform (1–20 μm in diameter), polarity of attached cells is possible to recognize. Cells divide by binary fission in more planes, often with layered aggregations, division tend to be synchronized with pseudofilamnetous formation. Baeocytes (reproducing cells) are formed by multiple fission and subsequently liberation from mother cells. The identification of *Xenotholos* and *Xenococcus* requires a detailed study of colonies, arrangement of cells and mucilage sheath.

Occurrence*: mainly epiphytic, found on filamentous cyanobacteria and algae (e.g., *Blennothrix*, *Cladophora*, *Rhizoclonium*)

Expected taxa: *Xenotholos kerneri* Gold-Morgan et al., *Xenotholos caeruleus* Gold-Morgan et al., *Xenotholos amplus* Gold-Morgan et al.

Key 2: Form-genera of the Oscillatoriales

1a	Trichomes screw-like coiled	*Arthrospira*
1b	Trichomes straight	2
2a	Filaments attached as epiphytes (along the length)	3
2b	Filaments not attached	4
3a	Filaments attached along the entire length	*Leibleinia*
3b	Filaments attached at one end	*Heteroleibleinia*
4a	Multiple trichomes (2+) in a common sheath	*Microcoleus*
4b	Trichomes single (or rarely multiple)	5
5a	Trichomes attached at one end (epilithic, rarely endogloeic), heteropolar	*Homoeothrix*
5b	Trichomes otherwise	7
6a	Trichomes without sheaths (or, very fine), trichome straight (occasionally wavy), cells barrel shaped, typically narrow (1–3 μm)	8
6b	Trichomes otherwise	10
7a	Trichomes solitary (or in fine mats), short, cells cylindrical to barrel shaped, constricted (often markedly) at cross-walls	*Pseudanabaena*

7b	Trichomes otherwise	9
8a	Trichomes isopolar, in mats or clusters, rarely solitary, thin, fine, or firm sheath	*Leptolyngbya*
8b	Trichomes (very) motile, typically attenuated, typically distinctive apical cells	*Geitlerinema*
9a	Cells ± isodiametric, sheaths facultative, or obligatory	*Phormidium*
9b	Cells wider than long	11
10a	Trichomes in mats, sheaths absent (very rarely environmentally inducible)	*Oscillatoria*
10b	Sheathes thick, ± obligatory	*Lyngbya*

Arthrospira (Gomont) Stizenberger (Fig. 2.3a)

Individuals are typically encountered as solitary trichomes, often free floating in plankton, but occasionally as fine mats in the benthos. Trichomes are screw shaped or coiled, isopolar, and sheathes rare, but may be facultatively present (fine and thin). Cells are ± isodiametric with visible cross-walls. Morphologically similar to *Spirulina*, but with visible cross-walls (the separation between these genera has been conformed via molecular and morphological examination).

Remarks: many species have been recorded, but the intrageneric systematics is rather vague at this time. No known toxic forms and often employed in biotechnical applications (often incorrectly identified as "*Spirulina platensis*"). We also note that *Arthrospira* has been cited in the North American Water Quality Assessment and by researchers from California and Florida.

Occurrence: typically planktic, but often present in the benthos of a variety of aquatic habitats.

Expected taxa: *A. jenneri* (Gomont) Stizenbergeri, *A. platensis* Gomont

Geitlerinema (Anagnostidis et Komárek) Anagnostidis (Fig. 2.3m)

Trichomes thin (1–4 μm), straight (rarely bent or screw like), not (rarely) constricted, cells longer than wide, never posses aerotopes. End cells are often distinctive, being hooked, coiled, bent, typically acumate, or rounded. Highly motile with intensive gliding motility, but also rotation and waving. Thallus often vibrant blue-green, delicate, diffluent, thin mats, but sometimes individual trichomes. This genus is composed mostly of taxa formally members of *Oscillatoria*, but appears to be polyphyletic and in need of revision (Perkerson et al. 2010).

Occurrence: common in freshwaters, often forming thin, delicate, brightly colored mats in benthic habitats. Also an occasional epiphyte or present in subaerial habitats. Records concerning marine taxa probably correspond to a new, as of yet undescribed genus.
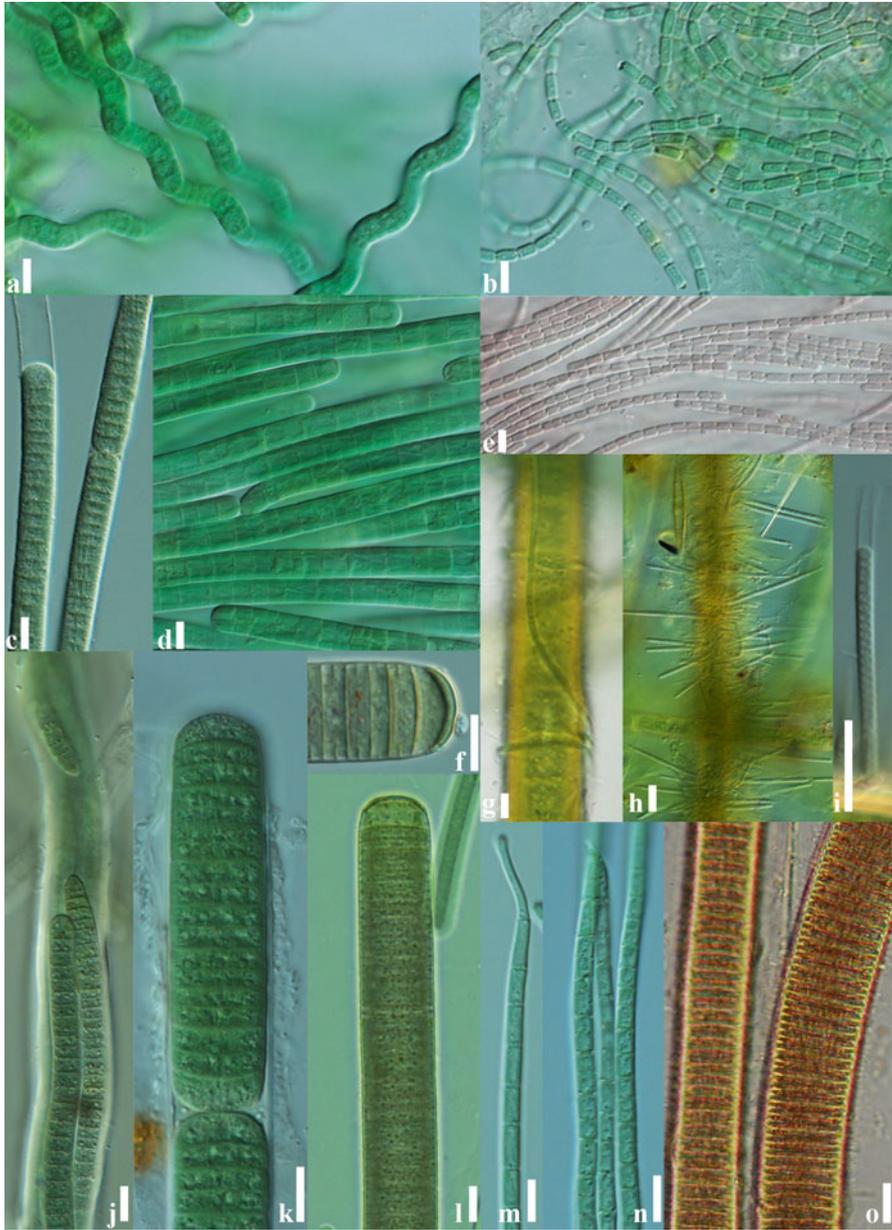
Fig. 2.3 (**a–o**) Examples of filamentous genera without heterocytes. (**a**) *Arthrospira*. (**b**) *Pseudanabaena*: note the isopolar nature. (**c**) *Phormidium*: note the difference between the filament and the trichome. (**d**) *Ammassolinea*. (**e**) *Pseudanabaena*. (**f**) *Oscillatoria*. (**g**) *Leibleinia*. (**h** and **i**) *Heteroleiblenia*: note the heteropolar tapering. (**j**) *Microcoleus*: note the copious mucilaginous sheath. (**k** and **l**) *Oscillatoria*: (**k**) note the fragmentation into hormogonia. (**m**) *Geitlerinema*. (**n**) *Leptolyngbya*. (**o**) *Lyngbya*: note the filament (cells with the sheath). Scale bars: (**a, f, j–l, o**) = 10 μm; (**b–e, g–i, m–n**) = 5 μm

Expected taxa: *G. amphibium* (Agardh ex Gomont) Anagnostidis, *G. splendidum* (Greville ex Gomont) Anagnostidis, *G. tenuis* (Stockmayer) Anagnostidis

Heteroleiblenia (Geitler) Hoffmann (Fig. 2.3h, i)

Heteropolar filaments attached at one end, at times forming tuft-like layers. Sheathes thin, colorless, firm. Cells ± isodiametric, with unornamented, obligatorily rounded end cells. Trichomes may be constricted or not at cross-walls. Resembles *Leibleinia*, but differs in mode of attachment (one end vs. the entire filament). Reproduction via trichome disintegration into hormocytes and hormogonia.

Occurrence: previously described as thin *Lyngbya* species, common, cosmopolitan components of both freshwater and marine habitats as epiphytes on other algae, plants, or inanimate substrates. Komárek and Anagnostidis (2005) caution that due to the paucity of molecular data the status of this genus remains open to debate.

Expected taxa: *H. kuetzingii* (Schmidle) Compere, *H. pusilla* (Hansgirg) Compere

Homoeothrix (Thuret) Kirchner (Fig. 2.5e)

Simple heteropolar filaments, rarely with false branching, appearing solitary, or occasionally in loose fascicles, but always attached basally to substrate. Sheathes typically thin, but may be firm, hyaline, or occasionally widened, often do not extend to the end of the filament. Trichomes 3–5 μm, tapering, typically to a thin, hair-like projection. Filaments constricted or not, cells ± isodiametric, blue-green to yellowish to grayish.

Occurrence: commonly attached to variable substrates in flowing and stagnant waters, may also be endogloeic (all taxa are attached, though). Colonies often have a collection of coccoid cells at the base (sometimes quite conspicuous). Some systematic confusion remains between *Tapinothrix* and *Homoeothrix*, so further investigation into the complex is warranted. Differs from *Heteroleibleinia* in polarity.

Expected taxa: *H. janthina* (Bornet et Flahault) Starmach, *H. varians* Geitler

Leibleinia (Gomont) Hoffmann (Fig. 2.3g)

Filaments solitary, attached along their length (or by a part in later stages, leaving free ends), always epiphytic. Obligatory sheathes thin, firm, colorless. Apical cells may be rounded, never with calyptra or thickened outer cell wall.

Remarks: it is a difficult genus to identify to species due to a paucity of morphological characters, many members of the genus were originally described as epiphytes of morphologically similar genera (e.g., typically *Lyngbya*, but also *Phormidium*). *Leibleinia* is a poorly understood genus, not yet studied in culture or
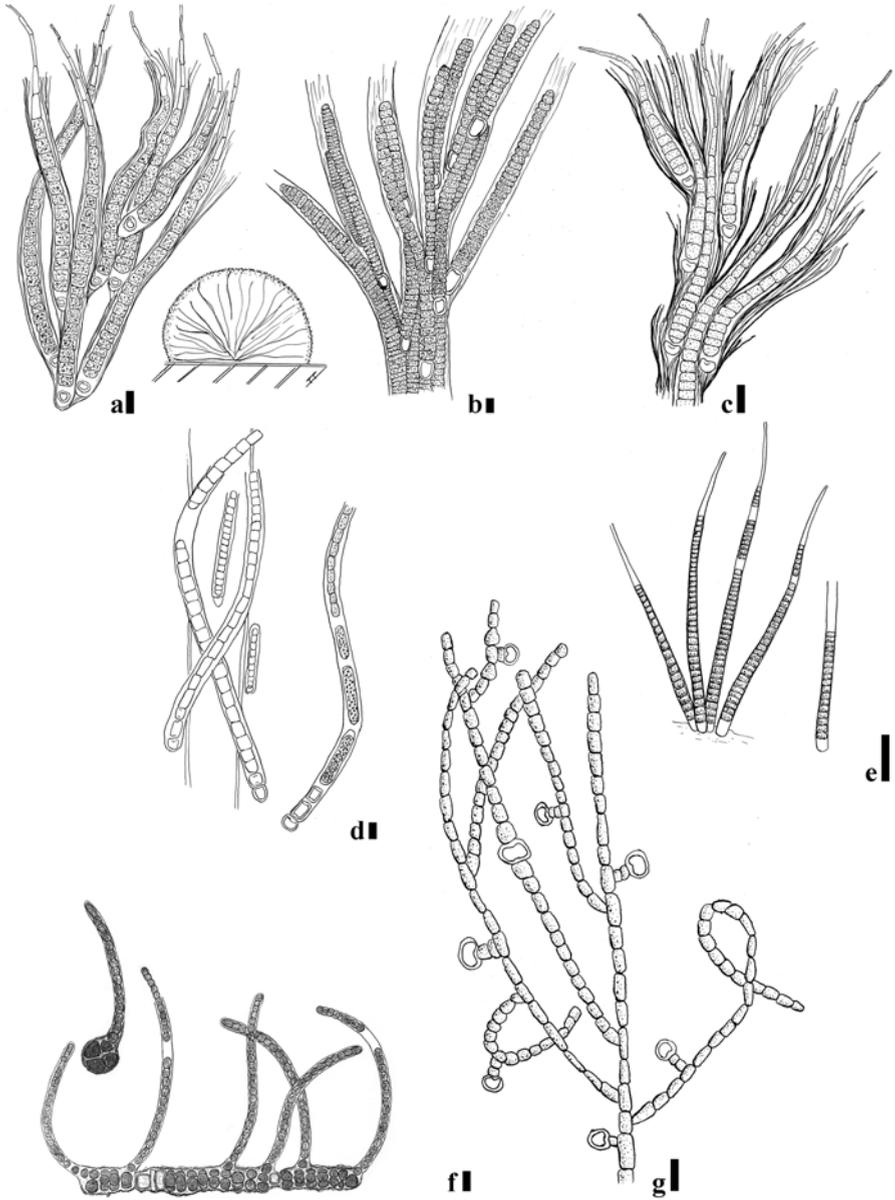
Fig. 2.5 (**a–g**) Examples of filamentous heterocytous genera. (**a**) *Rivularia*. (**b**) *Coleodesmium*. (**c**) *Dichothrix*. (**d**) *Microchaete*. (**e**) *Homoeothrix*. (**f**) *Fischerella*. (**g**) *Nostocopsis*. Scale bars = 10 µm

via molecular methods; Komárek and Anagnostidis (2005) advocated critical revisions in the future.

Occurrence: common in marine and freshwater habitats as epiphytes; it can be periodically common, but more common in less disturbed habitats.

Expected taxa: *L. epiphytica* (Hieronymous) Compere, *L. nordgaardii* (Wille) Anagnostidis et Komárek

Leptolyngbya Anagnostidis et Komárek (Fig. 2.3n)

Filaments typically forming mats or clusters, rarely solitary, occasionally solitary, free floating, or in fascicles. Filaments mostly straight, ± flexuous, wavy, curved, or rarely straight. Facultative thin, firm sheaths, with small trichomes (0.5–3.5 μm wide) and isodiametric, cylindrical cells, that may occasionally be shorter than wide. Peripheral thylakoids occasionally visible.

Occurrence: one of the most commonly encountered cyanobacterial genera, it is found in nearly all aquatic habitats, as well as subaerophytic and in soils, cosmopolitan taxa. One of the most specious genera, it is highly polyphyletic as currently described (Komárek and Anagnostidis 2005; Casamatta et al. 2005). Considered a highly "weedy" species, often associated with other cyanobacteria and algae. It is difficult to identify at species level due to lack of morphological characters and small size. Many species have been transferred from other genera (e.g., *Oscillatoria*, *Lyngbya*, *Phormidium*).

Expected taxa: *L. subtillissima* (Kützing ex Hansgirg) Komárek, *L. angustissima* (W. et G.S. West) Anagnostidis et Komárek, *L. valderiana* (Gomont) Anagnostidis et Komárek

Lyngbya (Gomont) C. Agardh (Fig. 2.3o)

Thallus often expansive, leathery, large, prostrate. Filaments straight or sometimes rarely wavy, rarely solitary. Obligatory sheathes that are firm, thin, or thick, may be lamellate, colorless to yellowish, or reddish, containing single motile trichome. Filaments rarely with false branching, typically ≥6.8 μm. Cells are discoid, always shorter than long (up to 1/15 as long as wide, but very rarely approaching isodiametric), only rarely with aerotopes. Apical cells usually with thickened outer cell or with a calyptra. Reproduction via trichome disintegration into short, motile hormogonia.

Occurrence: a specious genus with wide ecological tolerance (freshwater, marine, tropical to polar, etc.), many members are cosmopolitan marine taxa (e.g., *L. aestuarii*, *L. agardhii*). *Lyngbya* may be commonly encountered as benthic mats in lotic systems. Many species, especially planktic taxa, have been transferred into other genera (e.g., *Planktolyngbya* was erected to include small, planktic members).

Expected taxa: *L. martensiana* (Gomont) Meneghini, *L. maior* (Gomont) Meneghini

Microcoleus (Gomont) Desmazieres (Fig. 2.3j)

Thallus flat, prostrate on substrates. Sheathes usually colorless, firm, tapering, typically open at ends, containing multiple (often numerous) trichomes. Trichomes often densely aggregated, parallel in tight fascicles, may extend beyond the end of the sheathes. Without or slightly constricted, typically attenuated. Cells ± isodiametric, granular, with apical cells subconical to acutely conical.

Occurrence: a common genus, found in aquatic (freshwater and marine) and terrestrial habitats. Recently, some taxa have been transferred into new genera (e.g., *M. chthonoplastes* = *Coleofasciculus chthonoplastes sensu* Siegesmund et al. 2008).

Expected taxa: *M. lacustris* (Rabenhorst) Farlow, *M. subtorulosus* (Gomont) Gomont

Oscillatoria (Gomont) Vaucher (Fig. 2.3f, k, l)

Thallus flat, often conspicuous, smooth, often blackish blue-green, green to olive, thin. Trichomes often isopolar, straight, cylindrical, may be screw like or waved. Motile, with gliding, oscillation and rotation. Trichomes larger (typically ≥6.8 μm), constricted or not, cells discoid, always more than 2× shorter than wide (may be 3–11×), ± prominent granules, never with aerotopes. Sheathes absent, but rare under adverse conditions. Reproduction via trichome disintegration into short hormogonia, employing necridia.

Remarks: most members are benthic. *Oscillatoria* was previously perhaps the largest, most commonly encountered genus with many members have been transferred into new genera based on more narrowly defined requirements (e.g., presence of aerotopes, type of cell division, and cell dimensions) such as *Leptolyngbya*, *Limnothrix*, *Pseudanabaena*.

Occurrence: exceptionally common in lotic systems, often benthic, epipsammic, or epiphytic, but may become free floating after dislodging. Planctic isolates belong to other genera (e.g., *Planktothrix*). Widely reported in the literature, but many species have been transferred to other genera.

Expected taxa: *O. princeps* (Gomont) Vaucher, *O. simplicissima* Gomont, *O. tenuis* (Gomont) Agardh

Phormidium (Gomont) Kützing (Fig. 2.3c)

Thallus typically expanded, mucilaginous, often leathery, often conspicuous, often dark blue-green, but variable based on epiphtyes and habitat conditions. Sheathes often present, but highly environmentally plastic. Filaments straight or curved, but not with false branching (probably *Pseudophormidium*). Trichomes straight, flexed, curved, motile (often highly). Cells ± isodiametric, lacking aerotopes. End cells may be pointed, rounded, narrowed, with or without calyptra.

Occurrence: exceedingly common in flowing water; Sheath and Cole (1992) reported *P. retzii* as the most common macroalgal (forming macroscopic mats) taxon in North America. One of the largest genera of cyanobacteria in terms of species numbers, it is also perhaps the most problematic from a phylogenetic standpoint (Komárek and Anagnostidis 2005) and has been shown polyphyletic. Numerous species have been transferred to other genera based on molecular and morphological data (e.g., *P. autumnale* has been transferred to *Microcoleus autumnalis sensu* Strunecký et al. 2013, and some *Phormidium*-like taxa were described as new genus *Ammassolinea*, Fig. 2.2d, *sensu* Hašler et al. 2014). It resembles *Oscillatoria*, but is differentiated by types of trichome division and disintegration. It is found from pole to pole in all types of freshwaters, may also be subaerial.

Expected taxa: *P. retzii* (Gomont) Agardh, *P. nigrum* (Gomont) Anagnostidis et Komárek.

Pseudanabaena Lauterborn (Fig. 2.3b, e)

Trichomes typically solitary, occasionally in fine mats, sheathes rare, occasionally motile, rarely more than 30 cells. Cells typically cylindrical (rarely ± isodiametric), 1–3.5 μm wide, often barrel shaped, usually with conspicuous constrictions at crosswalls. End cells may be rounded or pointed, facultative aerotopes. Considered by some a weedy, junk genus composed of a polyphyletic assemblage of filaments with little morphological differentiation; recent molecular analyses have identified "true" *Pseudanabaena*, but a polyphyletic genus as a whole. Species rich yet poorly described from marine, freshwater, and subaerial habitats, many members were transferred into from other genera (most notably *Oscillatoria* and *Phormidium*). May possess aerotopes, but this may also be a similar genus (*Limnothrix*) and may necessitate taxonomic change. Superficially resembles *Komvophoron*, but differs in type of reproduction and cell dimensions.

Occurrence: very common in aquatic habitats in benthic and planktic habitats, also known as common endogloeic members.

Expected taxa: *P. catenata* Lauterborn, *P. galeata* Bocher, *P. mucicola* (Naumann et Huber-Pestalozzi) Schwabe

Key 3: Form-genera of the Nostocales

1a	Filaments heteropolar	2
1b	Filaments other than heteropolar	7
2a	Filaments form hairs at the apex	3
2b	Filaments do not form hairs at the apex	5
3a	Gelatinous spherical colonies, sometimes with internal cavity, filaments are radially arranged	*Rivularia*
3b	Species do not form gelatinous spherical colonies	4
4a	Single filaments, attached to the substrate by heterocyte, usually unbranched	*Calothrix*
4b	Single filaments, attached to the substrate by heterocyte, false branching	*Dichothrix*
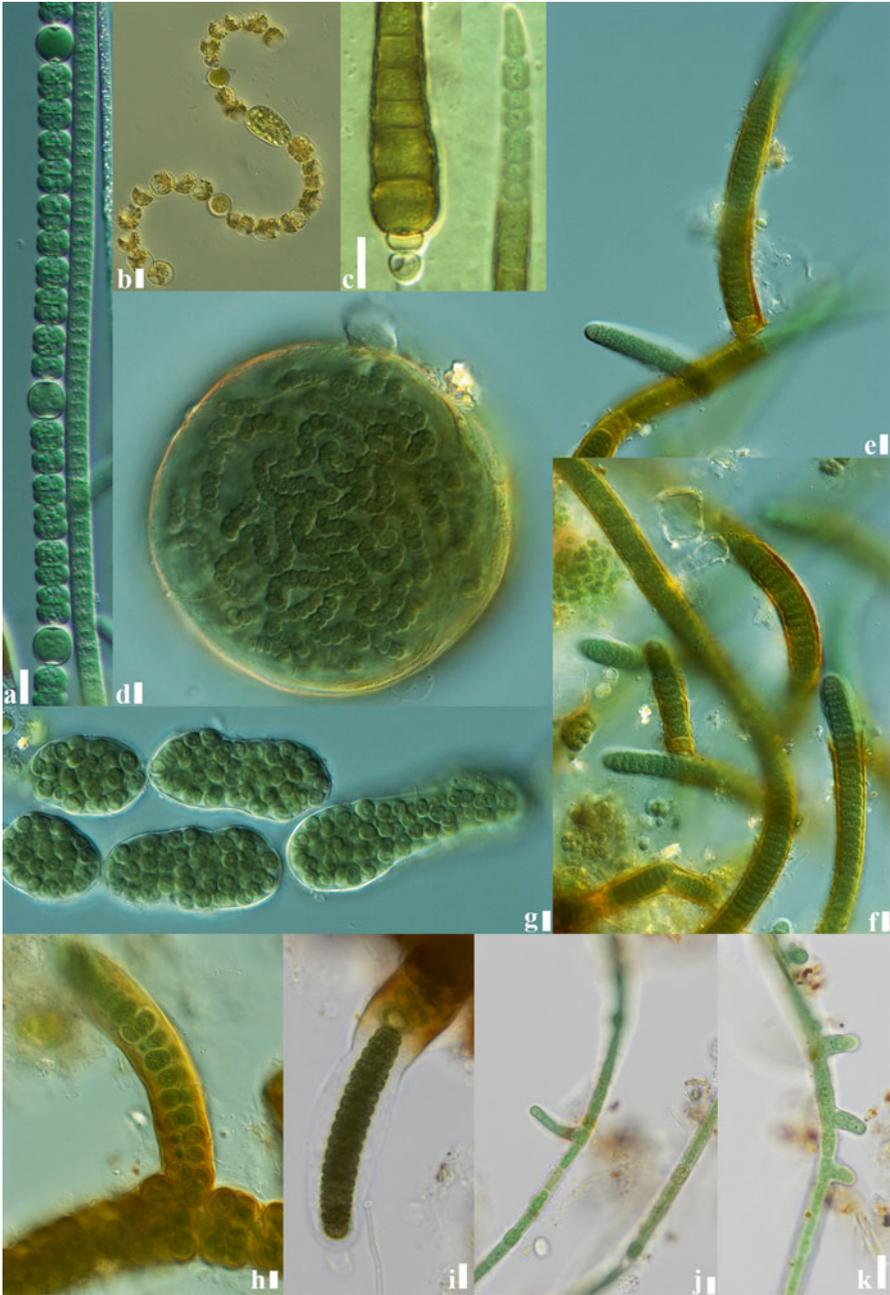
Fig. 2.4 (**a–k**) Examples of filamentous heterocytous genera. (**a** and **b**) *Anabaena*: (**a**) note the heterocytes and (**b**) overwintering akinetes. (**c**) *Calothrix* (**d** and **g**) *Nostoc*. (**e** and **f**) *Tolypothrix*: note the false branchings. (**h** and **i**) *Stigonema*. (**j** and **k**) *Hapalosiphon*. Scale bars: (**h** and **k**) = 10 μm; (**a–g**) = 5 μm

5a	Filaments usually without false branching, or occasionally false branched	*Microchaete*
5b	Filaments with frequently false branching	6
6a	More than one trichome within common sheath	*Coleodesmium*
6b	One trichome within sheath, common branching	*Tolypothrix*
7a	Paraheterocytic type of akinete development, akinete usually larger than vegetative cells, thin gelatinous mats, or single filaments	*Anabaena*
7b	Apoheterocytic type of akinete development, spherical to lobate microscopic, or macroscopic gelatinous colonies	*Nostoc*

Anabaena (Bornet et Flahault) Bory (Fig. 2.4a, b)

Single filaments, bundles, or micro- to macroscopic mats on submerged water plants. Trichomes are straight, bent or coiled, isopolar, paraheterocytic, constricted, or unconstricted at cross-walls. Sheath if present is usually diffluent and colorless. Cells are spherical, oval, barrel-like, cylindrical with homogenous to granular content, blue-green to greenish, planktic species contain gas vesicles. Heterocytes are intercalary, spherical, oval to cylindrical, homogenous, colorless to yellowish, with visibly thicken walls. Akinetes are intercalary and vary from almost spherical to, oval, reniform, cylindrical and grow solitary or in short chains (up to five). Cells divide perpendicularly to trichome axis. Trichomes reproduce by fragmentation and akinete germination in short parts (hormogonia).

Remarks: the genus was recently split into *Anabaena sensu stricto* (mainly periphytic species without gas vesicles), *Dolichospermum* (mainly planktic species with gas vesicles), and *Sphaerospermum* (planktic with gas vesicles). Depending on the order of the body of water, different genera may be present (e.g., higher order rivers or those with low flow rates may favor the occurrence of *Dolichospermum*, with low order streams containing *Anabaena*).

Occurrence: *Anabaena sensu stricto* occurs world wide, benthic or epiphytic, especially on submerged plants.

Expected taxa: *A. cylindrica* Lemmermann, *A. subcylindrica* Borge, *A. sphaerica* Bornet et Flahault, *A. oscillarioides* Bornet et Flahault.

Calothrix (Bornet et Flahault) Agardh (Fig. 2.4c)

Heteropolar filaments are attached to the substrate, living solitary, or occasionally false branched, in groups or mats. Basal parts of filaments are formed by heterocytes (seldom two), which can be spherical to elliptical or flattened. Occasional akinetes formed above the heterocyte. Vegetative cells above heterocytes are wider than at the apex where are narrowed continuing into hair-like gelatinous projection, unconstricted to slightly constricted at cross-walls. Cell content is homogenous to

finely granulated, blue-green, pale blue-green, greenish, brownish, yellowish. Sheath is usually distinct, thin, firm mono to occasionally multilayered, colorless to yellowish or brownish. Cells divide perpendicularly to filament axis, meristematic zones occurs below hair projections. Apical parts of filaments liberate short motile hormogonia by help of necridic cells. Hormogonia possess heteropolar development and growth.

Occurrence: a cosmopolitan genus, mainly periphytic, epilithic to epiphytic.

Expected taxa: *C. fusca* Bornet et Flahault, *C. parietina* (Bornet et Flahault) Thuret, *C. braunii* Bornet et Flahault, *C. elenkinii* Kosinskaja, *C. stellaris* Bornet et Flahault, *C. simplex* Gardner.

Rivularia (Bornet et Flahault) Roth (Fig. 2.5a)

Microscopic to macroscopic (several centimeters), hemispherical to irregular colonies attached to substrate, occasionally internal cavity occurs, colonies usually gelatinous, or in limestone habitats can be encrusted with $CaCO_3$. Filaments are radially oriented, false branched, and sometimes grow in layer-like structure. Sheath is thin to thick with conspicuously widened apical end. Trichomes are heteropolar, widen at the base, have a basal heterocyte, and apices narrow to hair-like end, which usually grows out of the sheath. Trichomes are constricted or unconstricted at the cross-walls, falsely branched at the intercalar heterocytes. Akinetes do not occur (typical feature differing *Rivularia* from *Gloeotrichia*). Cells are cylindrical, barrel shaped to wider than longer without any aerotopes. Reproduction via hormogonia from the apical parts of trichomes.

Occurrence: benthic, often epiphytic, occasionally epilithic in stagnant, or running waters.

Expected taxa: *R. aquatica* De-Wildeman, *R. minuta* (Bornet et Flahault) Kützing, *R. biasolettiana* (Bornet et Flahault) Meneghini, *R. dura* (Bornet et Flahault) Roth, *R. borealis* Richer.

Coleodesmium Borzi (Fig. 2.5b)

Heteropolar filaments are attached to the substrate, usually branched forming fascicles or coherent mats. One or more trichomes (9–10 µm wide) are placed within firm, colorless or yellowish to brownish and often layered sheath. In contrast to morphologically similar genera such as *Calothrix*, trichomes do not form apical hairs. Cells are short, barrel shaped, constricted at the cross-walls, blue-green, with finely granulated or homogenous content. Basally formed heterocytes are elliptical, akinetes occur occasionally, 8 µm wide, one or few in chain. Trichomes reproduce by hormogonia formation (with help of necridic cells).

Occurrence: mainly epiphytic or epilithic in cold mountain streams, a small genus in terms of species.

Expected taxa: *C. floccosum* Borzi, *C. wrangelii* (Geitler) Borzi.

Dichothrix (Bornet et Flahault) Zanardini (Fig. 2.5c)

Members of the genus usually form fasciculate colonies with falsely branched fila-
ments. Sheaths are thin, firm, lamellose, colorless, or yellowish. Trichomes in colo-
nies are fasciculate, heteropolar, and branched, 5–30 µm wide. Spherical to elliptical
heterocyte at the base of trichomes, which facilitates trichome branching. Apical
portion is narrowed or protrudes into thin hairs. Cells are variable from short to bar-
rel shaped to elongated or almost cylindrical with or without constrictions at the
cross-walls. Akinetes usually do not occur (described in *D. gelatinosa*). At the sub-
terminal part of the trichome is often a meristematic zone, with trichomes reproduc-
ing by formation of hormogonia using necridic cells.

Remarks: several *Dichothrix* stages can be similar to *Calothix* and false branch-
ing is an important diagnostic feature.

Occurrence: epilithic or epiphytic, often in cold clear streams

Expected taxa: *D. willei* Gardner, *D. olivacea* Bornet et Flahault, *D. sinensis* Jao.

Microchaete (Bornet et Flahault) Thuret (Fig. 2.5d)

Members of the genus live in single filaments or aggregated into small clusters
growing erect on substrates. Filaments are heteropolar, occasionally false branched
at heterocytes, constricted, or unconstricted at the cross-walls. Sheath is usually,
colorless, thin, and narrow. Heteropolar trichomes with spherical, hemispherical, or
oval heterocyte at the base. Basal part is not conspicuously widened, nor is the api-
cal portion conspicuously narrowed (which separates it from *Calothrix*). Intercalar,
isodiametric to cylindrical heterocytes occur often in pairs. Akinetes develop facul-
tatively, usually in basal part of the trichome. Cells are of various shapes from wider
than longer to cylindrical or barrel shaped. Apical parts of trichomes disintegrate
into short hormogonia, which subsequently germinate by formation of heterocytes
and possess a heteropolar mode of growth.

Occurrence: frequently epiphytic in freshwaters.

Expected taxa: *M. diplosiphon* Gomont ex (Bornet et Flahault), *M. tenera*
(Bornet et Flahault) Thuret, *M. brunnescens* Komárek, *M. robinsonii* Komárek.

Nostoc (Bornet et Flahault) Vaucher (Fig. 2.4d, g)

Usually found as gelatinous microscopic to macroscopic colonies (spherical, lobate,
irregular) of various colors (yellowish, green, olive-green, brownish). Filaments are
isopolar, metameric, usually surrounded by distinct or diffluent sheath. Mucilage of
old colonies sometime incorporates intensely colored pigments such scytomemin or
gloeocapsin. Isopolar trichomes are usually constricted or slightly constricted at the
cross-walls. Intercalar heterocytes are spherical, oval, rectangular, isodiametrical to

slightly cylindrical. Akinetes are spherical, oval or slightly elongated, and develop apoheterocyticaly, often in short chains. Cells are spherical to barrel shaped, often distinctly granulated. Life cycle is complicated and includes various stages of different morphology from unifilamentous stages to large macroscopic multifilamentous colonies. Hormogonia occur after trichomes disintegration into short parts and mainly during akinete germination.

Remarks: the taxonomy of this genus currently under revision, e.g., a new genus *Desmonostoc* was recently erected based on *Nostoc muscorum* (Hrouzek et al. 2013)

Occurrence: mainly periphytic species, on submerged stones or plants, occasionally planktic or tychoplanktic, subaerophytic on wetted stones along banks and waterfalls.

Expected taxa: *N. linckia* (Bornet et Flahault) Bornet, *N. paludosum* (Bornet et Flahault) Kützing, *N. sphaericum* (Bornet et Flahault) Vaucher, *N. parmeliodes* (Bornet et Flahault) Kützing.

Tolypothrix (Bornet et Flahault) Kützing (Fig. 2.4e, f)

Single filaments or densely aggregated filamentous mats. Heteropolar filaments are often multilaterally branched, unconstricted to constricted at the cross-walls. Sheathes can be thin to wide (up to two times wider than trichome), firm, uni- to multilayerd, often colorless to yellowish. Trichomes can be slightly narrowed at the end, but more frequently they are cylindrical or sometime widened. Hairs are lacking. Colonies are attached by basal spherical, hemispherical, or oval heterocytes to the substrate or to the other trichome. Akinetes occur occasionally. Cells are barrel shaped, isodiametrical, or slightly cylindrical, green, blue-green, yellowish, homogenous to slightly granulated. Hormogonia are liberated from the apical parts of trichomes and can germinate from one or both ends.

Occurrence: benthic on submerged plants and stones, often subaerophytic on wetted stones and bark of trees.

Expected taxa: *T. tenuis* Kützing (Bornet et Flahault), *T. distorta* (Bornet et Flahault) Kützing, *T. penicillata* (Bornet et Flahault) Thuret, *T. limbata* (Bornet et Flahault) Thuret, *Tolypothrix crassa* W. et G.S. West.

Key 4: Form-genera of the Stigonematales

1a	Filaments uniseriate (rarely biseriate) heterocytes	2
1b	Filaments biseriate	3
2a	Heterocytes terminal on short lateral branches	*Nostochopsis*
2b	Heterocytes intercalary, thin, firm, close sheath	*Hapalosiphon*
3a	Narrow, erect branches with hormogonia at the apices	*Fischerella*
3b	Wide branches (nearly as wide as the main filament), arising from all sides, not producing hormogonia in the branch apices	*Stigonema*

Fischerella (Bornet et Flahault) Gomont (Fig. 2.5f)

Thallus felt-like, prostrate, creeping, sometimes erect. Filaments biseriate, highly branched (true branching), sheathes thick, sometimes lamellate, colorless, or yellowish to brownish. Erect, true branches typically unilateral. Cells barrel shaped to round, heterocytes globose, barrel shaped or quadrate, intercalary in basal trichome, cylindrical in branches.

Occurrence: typically subaerial or on moist soil, also encountered in shallow waters at margins epiphytic, epidendric, or entangled with other aquatic plants. It is not found in running waters *per se*, but often associated with moist habitats in the immediate vicinity.

Expected taxa: *F. ambigua* (Kützing *ex* Bornet and Flahault) Gomont, *F. muscicola* (Thuret) Gomont

Hapalosiphon (Bornet et Flahault) Nägeli (Fig. 2.4j, k)

Thallus attached (but later may be free floating), creeping, coiled filaments. Filaments are uniseriate, copious unilateral, true branches that are often as thick as the main branch. Heterocytes may be oblong to quadrate to cylindrical, intercalary. Sheathes thin, firm, usually colorless.

Occurrence: a common epiphyte in the littoral region of lakes and ponds, commonly attached to plants, also present in streams (in similar habitats).

Expected taxa*: Hapalosiphon tenuis* Gardner, *H. intricatus* W. et G.S. West

Nostochopsis (Bornet et Flahault) Wood (Fig. 2.5g)

Thallus gelatinous, attached, expansive, mucilaginous, and typically smooth; large (>4 cm), yellowish to yellow-green to olive-green. Uniseriate trichomes with ± isodiametric to barrel shaped cells, but may occasionally be elongated and ballooned. Many true branches of the main axis, terminating in either rounded apical cells or on short branches ending with an apical heterocyte. Copious heterocytes may be terminal, intercalary, or lateral.

Occurrence: a monotypic genus (*N. lobata*), often encountered in clean and small order streams throughout temperate to tropical regions attached to substrates.

Expected taxa*: N. lobata* (Bornet et Flahault) Wood

Stigonema (Bornet et Flahault) Agardh (Fig. 2.4h, i)

Thallus cushion like, turf like (but may become free floating or even encountered scattered among other algae). Trichomes multiseriate (seldom uniseriate) true branches that may become "erect." Filaments enclosed by a yellow to yellow-brown sheath, thick or thin, may be lamellated. Cells often ± round to cylindrical to barrel

shaped may appear to not touch each other. Heterocytes mostly intercalary, but may be lateral. Hormogonia common under favorable conditions, often consisting of only a few (two) cells, morphologically dissimilar to the rest of the trichomes.

Occurrence: commonly reported from several biomes, most often in subaerial, humid, periodically wetted habitats, but also common from streams, seeps, waterfalls, and dripping walls. It has a worldwide distribution, being common in the tropics but also reported from alpine regions as well.

Expected taxa: *S. mamillosum* (Bornet et Flahault) Agardh, *S. minutum* (Bornet et Flahault) Hassall, *S. ocellatum* (Bornet et Flahault) Hassall

Cyanobacterial Terms

Akinete Thick-walled spore, often inducible, typically used to survive adverse environments. Frequently employed in species or generic identifications (e.g., *Anabaena*, Fig. 2.4a). May be apoheterocytic (develop from vegetative cells between heterocytes) or paraheterocytic (develop from vegetative cells outside of heterocytes).

Baeocytes Reproductive cells resulting from successive cell division within a mother cell without being liberated and enclosed by a sheath (e.g., *Pleurocapsa*, Fig. 2.1p).

Calyptra A thick covering at the tip of a trichome (e.g., *Phormidium*, Fig. 2.3c).

Endogloeic Growing within mucilage (typically of other algae, e.g., *Synechoccocus*, Fig. 2.1i).

Exocytes Reproductive cells released from apical portions of sessile, heteropolar cells (e.g., *Chaemosiphon*, Fig. 2.1e).

False branching A branch not formed as a result of cell division and does not result in multiple planes, leading to filaments which appear to pass each other (e.g., *Tolypothrix*, Fig. 2.4e).

Filament Linear arrangement of cells enveloped by a sheath (e.g., *Phormidium*, Fig. 2.3c).

Heterocyte A thick-walled cell, often inducible, used to fix atmospheric nitrogen. The size, shape, and placement are frequently employed in identifications (e.g., *Anabaena*, Fig. 2.4a).

Heteropolar Cyanobacterial "body plan" in which basal and apical regions (cells, filaments, trichomes) may be distinguished (e.g., *Heteroleibleinia*, Fig. 2.3h).

Hormogonia A desheathed, reproductive fragment of a trichome typically arising adjacent to necridic cells or heterocytes (e.g., *Oscillatoria*, Fig. 2.3k).

Isopolar Cyanobacterial "body plan" in which each end is identical (e.g., *Pseudanabaena*, Fig. 2.3b).

Pseudofilaments Row of cells incidentally arranged in a linear series, not a single physiological entity (e.g., *Stichosiphon*, Fig. 2.1k, l).

Pseudovagina Sheath for heteropolar cells or pseudofilaments open only at one apical end (e.g., *Stichosiphon*, Fig. 2.1k, l).

Sheath Mucilaginous layer that may surround trichomes or cells. Many varieties exist (e.g., thin, thick, and lamellate) and may be facultative based on environmental conditions (e.g., *Microcoleus*, Fig. 2.3j).

Trichome Filament excluding the sheath (e.g., *Arthrospira*, Fig. 2.3a).

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