Montogue

Quiz BI106

Biology of Algae

Lucas Monteiro Nogueira

PROBLEMS

Problem 1

Algae share some similarities with bryophytes or mosses. Which of the following is *not* one such similarity?

A) Both algae and mosses are usually autotrophic.
B) Both algae and mosses use starch as a reserve substance.
C) Neither algae colonies nor mosses have vascular tissues.
D) Both algae and mosses form an embryo after fertilization.

Problem 2

Consider the eukaryote algae phylla of green algae (Chlorophyta), yellow-green algae (Xanthophyta), euglenoid algae (Euglenophyta), and dinoflagellates (Dinophyta). Choose the alternative that correctly indicates the number of surrounding outer membranes in a chloroplast of a typical cell belonging to each of these phylla.

A) Chlorophyta: 2; Xanthophyta: 3; Euglenophyta: 4, Dinophyta: 3
B) Chlorophyta: 2; Xanthophyta: 4; Euglenophyta: 3, Dinophyta: 3
C) Chlorophyta: 2; Xanthophyta: 4; Euglenophyta: 2, Dinophyta: 2
D) Chlorophyta: 2; Xanthophyta: 3; Euglenophyta: 3, Dinophyta: 3
E) Chlorophyta: 3; Xanthophyta: 4; Euglenophyta: 2, Dinophyta: 2

Problem 3

Regarding various aspects of phycology, true or false?

1.( ) Photosynthetic algae have chlorophyll in their chloroplasts. The algae have four types of chlorophyll, namely *a*, *b*, *c*, and *d*. Chlorophyll *a* is the primary photosynthetic pigment in all autotrophic algae.

2.( ) Carotenoids are yellow, orange, or red pigments that occur in many algae, be it in the form of oxygen-free hydrocarbons, the *carotenes*, or their oxygenated derivatives, the *xanthophylls.* Like the chlorophylls, carotenoids are soluble in water, alcohols, benzene, and acetone.

3.( ) There are two types of light reactions in photosynthesis: *photosystem I* (PSI), which is associated with the reduction of NADP to NADPH, and *photosystem II* (PSII), which is responsible for the splitting of water and the consequent evolution of oxygen. Each photosystem consists of a reaction center, where a special core molecule of chlorophyll *a* mediates electron transfer, and an assembly of light-absorbing molecules function like antennae to absorb and funnel light to the reaction centers. Antenna pigments can be more chlorophyll *a* or a variety of *accessory* pigments, such as chlorophyll *b*, carotenoids, phycocyanins, and phycoerythrins, depending on the particular taxon of algae. Both photosystems, PSI and PSII, are necessary for carbon dioxide to be converted to sugar, and Kirk's rule dictates that an accessory pigment that enhances light gathering in one photosystem will necessarily also funnel light to the other.

4.( ) Some algae are constituted of large, multinucleate cells in which the protoplasm is not separated by cell walls because nuclear divisions are not followed by cytokinesis. One such structure is called a *syncytium*.

5.( ) A typical algae flagellum consists of an *axoneme* of nine doublet microtubules surrounding two central microtubules, with all of the microtubules encased in the plasma membrane.

6.( ) A pyrenoid is a differentiated region within the mitochondria of some algae that carries adenosine triphosphate (ADP) produced in cellular respiration. The size of the pyrenoid varies with ATP content, but may occupy as much as 25% of the mitochondrion intermembrane space.

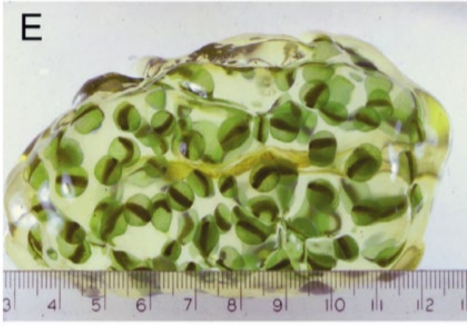
7.( ) In phototaxis, the orientation of an alga's movement is effected by the direction and intensity of light. This response is brought about by photoreceptor molecules such as *chlamyrhodopsin*, a short-chain aldehyde with an aromatic ring in its structure, which serves as the sensory light-sensitive molecule of *Chlamydomonas*.

8.( ) Although most algae use long starch polymers as storage products, some species rely on low-molecular-mass substances such as sucrose, trehalose, and even the alcohol mannitol as reserve substances.

9.( ) Algae that grow on the surface of sediments ranging from fine muds to coarse sands are said to be *epipelic*.

10.( ) Algal diversity in saline lakes varies inversely with salinity.

11.( ) Algae are known to form symbiotic associations with other organisms. There are also occurrences of parasitism. In the spring, green, baseball-sized gelatinous green masses can be seen in ponds and lake outflows, as shown in the photograph below; these are masses of amphibian eggs colonized by the green alga *Chlamydomonas amblystomatis*, which continuously harvests nitrogen-containing compounds from the egg until it is completely depleted. The algae, which are obligate parasites, must then find another host.



12.( ) Lichens are stable, self-supporting associations between mycobiont fungi and algae, usually a green alga or a cyanobacterium, but never both. The evolutionary benefit of these associations is attested by the fact that over 20% of all fungi, mostly among the Ascomycetes and the Basidiomycetes, are capable of forming lichens.

▶ Problem 4

Which of the following classes of green algae led to the development of land plants (embryophytes)?

A) Micromonadophyceae
B) Charophyceae
C) Ulvophyceae
D) Chlorophyceae

▶ Problem 5

Which of the following algae phylla include organisms capable of converting atmospheric nitrogen to ammonia?

A) Cyanobacteria only.
B) Cyanobacteria and green algae only.
C) Cyanobacteria, green algae, and yellow-green algae only.
D) Cyanobacteria, green algae, yellow-green algae, and red algae only.

▶ Problem 6

In mid to late summer, eutrophic temperate lakes frequently develop massive populations of colonial cyanobacteria, the so-called algae blooms. Populations of blue-green algae rise to the surface of the lake, forming a thick layer of algal biomass at the top of the water column, out-competing other algae and leading to major impacts on zooplankton and fish populations. The ability of cyanobacteria to out-compete other freshwater algae and form algal blooms is made possible by some specific characteristics of blue-green algae, which does *not* include:

A) Optimum growth at high temperatures.
B) Tolerance to low light.
C) Intolerance to low CO_2 concentrations.
D) Depth regulation by buoyancy.

▶ Problem 7

Regarding further aspects of phycology, true or false?

1.( ) Evidence for evolution of cyanobacteria as some of Earth's most ancient forms of life comes from layered, calcareous, approximately 2 billion-year-old structures known as stromatolites. These are very abundant in Precambrian deposits throughout the world and are commonly thought to have been produced by light-loving microorganisms such as cyanobacteria that trap sediments and deposit carbonates in layers. However, evidence for cyanobacteria as sources of stromatolites comes from the fossil record only, in that modern blue-green species are incapable of forming these structures.

2.( ) A typical blue-green such as *Synechocystis* sp. (shown below) has a peptidoglycan layer in which a polysaccharide composed of glucosamine, mannosamine, galactosamine, mannose, and glucose is directly linked to the muramic acid-6-phosphate of the peptidoglycan, forming a PG-PS complex rather typical of Gram-positive bacteria. However, other components typical of Gram-positive peptidoglycan layers, including teichoic acid and L-lysine, are not found in the cyanobacterial peptidoglycan.

3.( ) In cyanobacteria, carboxysomes are micro-compartments composed entirely of protein. These compartments encapsulate two enzymes, RuBisCO and carbonic anhydrase; co-localization of these enzymes enables cyanobacteria to generate high levels of CO_2, a substrate of RuBisCO, at the site of carbon fixation. This is advantageous because it drastically reduces the likelihood that RuBisCO will fix O_2 instead of CO_2, which generates 2-phosphoglycolate, a toxic byproduct.

4.( ) Many cyanobacteria are endowed with pili, proteinaceous appendages that project from the surface of the cell. One function of these structures seems to be associated with movement, as an alga can displace itself along a surface by continuously changing the configuration of the pili, a motion called *twitching*. The pili are usually constituted of 500 – 1000 units of the polypeptide oscilin.

5.( ) Cyanophycin is a biopolymer constituted of arginine and aspartate that serves as a nitrogen cellular reserve for most cyanobacteria. Biomarker experiments have shown that typical blue-greens can synthesize cyanophycin from both nitrate and ammonium, and from both external N sources as well as from N made available by degradation of cellular proteins.

6.( ) Circadian rhythms have been observed in eukaryote algae, including bioluminescent dinoflaggelates, but researchers have so far failed to identify biological-clock-oriented functioning in cyanobacteria.

7.( ) Cyanobacteria are capable of synthesizing potent hepatotoxins, such as the heptapeptide microcystin and the pentapeptide nodularin. Fortunately, conventional water treatment techniques such as activated charcoal can effectively minimize concentrations of these substances, and recent research has revealed that cyanobacterial toxins are not nearly as dangerous as initially thought, for they feature no tumor-promoting activity.

8.( ) Cyanobacterial akinetes are generally recognized by their larger size relative to vegetative cells and conspicuous granulation due to high concentrations of glycogen and cyanophycin. Akinetes are equivalent to endospores in Gram-positive bacteria and occur in all blue-green algae, including species not capable of producing heterocysts.

9.( ) In some filamentous strains of cyanobacteria, vegetative reproduction occurs by fragmentation of the trichome into short filaments called hormogonia. These are distinguishable from mature trichomes by cell size, cell shape, gas vacuolation, and, in an important limitation, absence of heterocysts. Blue-green hormogonia also do not fix nitrogen and synthesize no phycobiliproteins.

10.( ) A number of liverwort, hornwort, moss, fern, and angiosperm species are closely associated with cyanobacteria, usually *Nostoc* sp. (shown below: *Nostoc commune*). Photosynthesis is the role of the upper plant, which provides a supply of fixed carbon and in turn receives a steady supply of fixed nitrogen from the associated blue-greens.

11.( ) Green algae (Chlorophyta) can be distinguished on the basis of the enzymes involved in the oxidation of glycolate, the major substrate of photorespiration, which is metabolized in the peroxisomes. In the Chlorophyceae and the Ulvophyceae, the reaction is catalyzed by glycolate oxidase, while in the Charophyceae the reaction is catalyzed by glycolate dehydrogenase.

12.( ) Algal blooms are associated with excessive growth of blue-green algae and diatoms, but there are no reports of algal blooms precipitated by excessive growth of, say, green algae.

13.( ) Diatoms differ from other algae in that their cellular walls are composed of opaline silicon dioxide (silica) together with a small amount of organic coatings; that is, the cell wall of diatoms is almost entirely inorganic in composition. It has evolved as an energy-efficient structure, requiring significantly less energy to manufacture than the cellulose, protein, and mucopeptide cell walls of other algae. Other advantages inherent to diatoms' silica cell walls include the low density of silicon dioxide, which enables the algae to remain suspended in planktonic strata, and the ease with which silica can be distended and elongated during cell division.

14.( ) Like other algae, diatoms require a steady supply of light and nutrients. One major means by which they can attain favorable conditions for growth is to be adhered to living substrata, be it a plant/algae (epiphyte diatoms) or an animal (epizoic diatoms). Epizoic diatoms include species that develop in ciliates, copepods, krill, whales, and even diving birds.

15.( ) One remarkable trait of diatoms is that they seem to be impervious to viral infections. Indeed, as of the early 2000s, no virus or virus-like particle (VLP) capable of infecting diatoms has been reported. One reason for diatoms' resistance to infection may be attributed to the inherent toughness and selectivity of their silica cell walls.

16.( ) The valve faces of cylindrical centric diatoms can be described by Bessel functions.

17.( ) One remarkable feature of diatoms is kleptoplasty, a symbiotic phenomenon whereby the algae assimilate plastids from a food source and harness them to produce energy in the short term. The synergy between the stolen plastid and the alga is such that it is sometimes difficult to distinguish between these organelles and permanent plastids.

18.( ) Bioluminescence is not just a property of bacteria; some marine dinoflagellates also exhibit this phenomenon. Indeed, many marine dinoflagellates are capable of bioluminescence; the Dinophyceae are the main contributors to marine bioluminescence, emitting an instantaneous flash of blue-green light when stimulated.

19.( ) Red algae (Rhodophyta) and brown algae (Phaeophyta) are both predominantly marine groups of algae. They are distinguished from each other and other algae groups by their unusual plastid structures: red algae have unstacked thylakoids with no external endoplasmic reticulum, while brown algae exhibit triple thylakoids with an enclosing endoplasmic reticulum.

20.( ) Floridean starch is a storage product in red algae that bears resemblance to the amylopectin of higher plants. Like the starch of Chlorophyta, Floridean starch is produced in the chloroplast and stored in the same organelle, usually in the form of bowl-shaped grains no larger than 10 μm.

21.( ) Brown algae are capable of producing phlorotannins, special tannin molecules produced by Golgi in the perinuclear area of the cell. Numerous functions have been attributed to these substances, including protection against herbivory, as these molecules can inhibit the glycosidases of gastropods. Production of phlorotannins is an ‘induced’ defense mechanism, i.e., it is normally brought about by grazing, as opposed to a ‘constitutive’ defense mechanism, which would be the case if the phlorotannin concentrations were maintained at steady levels regardless of predation.

22.( ) Euglenoid algae comprise an almost entirely unicellular group of organisms, most of which inhabit freshwater. Only a fraction of euglenoids – about a third – are photosynthetic and conventionally classed among the algae.

23.( ) Euglenoids typically have an eyespot or *stigma*, a collection of orange-red lipid and pigment droplets. In most euglenoids the eyespot consists of 20 to 50 droplets. Eyespots are independent of the chloroplast, as suggested by the existence of colorless species with an eyespot but no plastids.

24.( ) Yellow-green algae (Xanthophyta) derive their name from the fact that their chloroplasts do not contain fucoxanthin, the pigment that confers the more intense coloration of brown algae. Yellow-green algae such as *Gloeobotrys* are some of the most successful groups of algae, having conquered water bodies large and small, fresh and marine, lentic and lotic; indeed, yellow-green algae may be considered second only to cyanobacteria in terms of evolutionary spread.

25.( ) The cryptomonads (Cryptophyta) constitute a relatively small group of algae, containing no more than 200 species of which half inhabit freshwater and half inhabit marine environments. These are planktonic algae, with no tolerance to light-deprived environments, and seemingly have a preference for cold waters.

26.( ) Algae are generally regarded as organisms that have plastids, which is why the Apicomplexa protozoans, being plast-less, are generally not included in the realm of phycology. However, in the 1990s it was revealed that at least two genera of apicomplexans, *Plasmodium* and *Toxoplasma*, include organisms endowed with small chloroplasts and hence capable of performing photosynthesis in a facultative fashion.

SOLUTIONS

P.1 ➡ *Solution*

After fertilization, algae do not form embryos. Other similarities and differences between algae and bryophytes are listed below.

Algae	Mosses
Has photosynthetic pigments and is usually autotrophic	Has photosynthetic pigments and is usually autotrophic
Some colonies have a thalloid shape	Some (Marchantiophyta, Anthocerotophyta) have a thalloid shape
Reserve substance is usually starch	Reserve substance is usually starch
Vascular tissues are absent	Vascular tissues are absent
Cell wall is often made of cellulose	Cell wall is made of cellulose

Male gametes are usually flagellated	Male gametes are usually flagellated
Requires water for fertilization	Requires water for fertilization
Aquatic, rarely terrestrial	Occurs in aquatic and humid terrestrial environments
Macroscopic forms have no stomata	Has stomata
Rhizoids, if present, are simple	Rhizoids are present in all members; they are generally simple, smoothwalled and tuberculated
Scales are absent	Scales are present in Hepaticeae
Each cell contains 1 – 2 chloroplasts and rarely many chromatophores	Each cell contains a large number of chloroplasts
Sexual reproduction is isogamous, anisogamous, or oogamous	Sexual reproduction is mainly oogamous

♦ The correct answer is **D**.

P.2 ➡ *Solution*

The number of outer membranes in chloroplasts of major algae phylla are listed below.

Algae phylum	Number of outer membranes in chloroplast
Green algae (Chlorophyta)	2
Red algae (Rhodophyta)	2
Euglenoid algae (Euglenophyta)	3
Dinoflagellates (Dinophyta)	3
Yellow-green algae (Xanthophyta)	4
Golden algae (Chrysophyta)	4
Cryptomonads (Chryptophyta)	4
Diatoms (Bacillariophyta)	4
Brown algae (Phaeophyta)	4

♦ The correct answer is **B**.

P.3 ➡ *Solution*

1. True. Indeed, chlorophyll *a* is the primary photosynthetic pigment (i.e., the light receptor in photosystem I of the light reaction) in all photosynthetic algae, and ranges from 0.3% to 3.0% of their dry weight.

2. False. Chlorophylls and carotenoids are both soluble in alcohols, benzene and acetone, but neither is soluble in water.

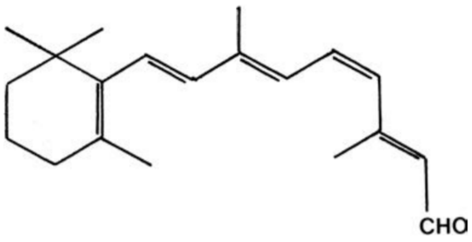
3. False. While it is true that both photosystems are needed to reduce CO_2 to hexose, PSI and PSII are physically distinct and have independent requirements for photons. What's more, accessory pigments can be involved in only one of the two PSs; for instance, in rhodophytes and cyanobacteria, the phycoerythrins appear to be connected primarily to PSI, while chlorophyll *a* molecules funnel energy to PSII reaction centers. This is further discussed in Kirk's *Light and Photosynthesis in Aquatic Ecosystems*; there is no such thing as 'Kirk's rule.'

4. False. A cell mass that fits the description provided in the statement is a *coenocyte*. A syncytium is a multinucleate cell derived from the fusion of many mononuclear cells followed by dissolution of their cellular membranes.

5. True. An axoneme consists of nine doublet microtubules surrounding two central microtubules, as illustrated below.

6. False. A pyrenoid is actually a differentiated region within the chloroplast that is denser than the surrounding stroma and may or may not be traversed by thylakoids. The pyrenoid is frequently associated with storage products, but also contains RuBisCO enzyme.

7. False. While it is true that chlamyrhodopsin serves as the photoreceptor of *Chlamydomonas*, the statement errs by saying that the molecule in question contains an aromatic ring in its structure; it actually includes a non-aromatic six-carbon ring, as illustrated below.



8. True. Chlorophyta and Euglenophyta algae harness sucrose as a reserve product; Cyanophyta and, to a lesser extent, Rhodophyta algae stock trehalose; mannitol occurs in Rhodophyta and Phaeophyceae, although it is also present in lower green algae, where it replaces sucrose as a photosynthetic product.

9. True. Epipelic algae include pennate diatoms, blue-greens, freshwater desmids, and motile members of other groups. Two common examples of epipelic algae are *Euglena* sp. and *Hantzschia virgate*, a diatom.

10. True. In mildly saline lakes (total salts 500 – 2000 mg/L), the algal flora is fairly rich and composed of a variety of diatoms (e.g., *Amphora, Campylodiscus, Cyclotella*), green algae (*Crucigenia*, *Pediastrum*, *Oocystis*), and cyanobacteria (*Anabaena*, *Aphanizomenon*, *Oscillatoria*). In more strongly saline conditions (2 – 20 g/L), many species are eliminated. At hypersaline levels (>20 – 600 g/L), algae diversity is low, including only select species of diatoms (e.g., *Anomoeoneis sphaerophora*), green algae (*Ctenocladus circinatus*), and cyanobacteria (*Nodularia spumigena*).

11. False. The ecological relations of *C. amblystomatis* and eggs of amphibians such as *Amblystoma* salamander are actually symbiotic in nature. The algae do extract nitrogen-containing compounds from the egg, but they also supply it with photosynthetic oxygen.

12. False. A lichen can, in fact, involve both a green alga and a cyanobacterium in the same association; about 4% of lichen "species" are constituted as such, and increasing research indicates that associations with a fungi and more than one type of alga may be more common than previously reported. In these lichens, the green algae provide a source of fixed carbon, while the cyanobacterial partner provides fixed nitrogen.

P.4 ➡ *Solution*

Charophyceae led to the development of land plants. The charophycean algae likely split from the rest of the Chlorophyta about 725 – 1200 million years ago. The terrestrial environment was colonized by these organisms about 500 mya. Molecular data suggests that the algae in the Zygnematales or Coleochaetales orders most likely evolved into the embryophytes. Charophyceae and land plants are sometimes gleaned in the so-called Streptophyta.

- ♦ The correct answer is **B**.

P.5 ➡ *Solution*

Besides blue-green algae, no other phylum of algae is capable of converting nitrogen gas to ammonia. The biogeochemical significance of cyanobacterial nitrogen fixation cannot be overstated.

- ♦ The correct answer is **A**.

P.6 ➡ *Solution*

Statement C is false. It is the tolerance of blue-greens to low CO_2 and high pH concentrations that allows continued growth of blue-greens, to the detriment of other algae, during bloom formation. The remaining alternatives are characteristics of cyanobacteria that favor bloom formation, namely, optimum growth at high temperatures (i.e., summer temperatures), tolerance to low light (important within the dense algal bloom, in that it enables algae to survive lower in the water column), and depth regulation by buoyancy (avoiding photoinhibition during the early phase of population increase, and allowing algae to obtain inorganic nutrients from the hypolimnion when the epilimnion becomes depleted in mid to late summer). According to Bellinger and Sigree, other traits of cyanobacteria that favor algal bloom include tolerance to low N/P ratios and resistance to zooplankton grazing.

- ♦ The correct answer is **C**.

P.7 ➡ *Solution*

1. False. There are in fact extant stromatolite cyanobacteria, but these are restricted to select sites in Australia, the US, and the Bahamas. The number of stromatolite types rose to a maximum some 700 – 800 million years ago, then declined precipitously. It has been suggested that this decrease was related to the evolution of numerous types of herbivorous gastropods, which grazed on microbial mats, thus preventing the buildup of stromatolites. Supporting this is the fact that modern stromatolites develop best in areas devoid of gastropods.

2. True. The PG-PS complex typical of Gram-positive bacteria is indeed present in blue-green algae. In addition, the degree of covalent crosslinks between peptidoglycan chains of cyanobacteria is described to be in the range of 60%, which exceeds the levels expected for Gram-negative bacteria (≈30%) and is more compatible with Gram-positive species. The similarities end, however, when we note that peptidoglycan layers such as teichoic acid and L-lysine are generally not encountered on the walls of cyanobacteria.

3. True. This is the opening paragraph of a recent update on carboxysome research by Cameron et al. (see reference below). The authors note that the carboxysome functions as the mainstay of the so-called CO_2 concentrating mechanism (CCM), a multicomponent system comprised of the carboxysome and a suite of inorganic carbon transporters that collectively enable cyanobacteria to proliferate under relatively low ambient atmospheric CO_2 and high O_2 levels. Ultimately, the CCM results in the accumulation of CO_2 at the site of RuBisCO within the carboxysome. This leads to increased levels of carboxylation of ribulose 1,5-biphosphate (RuBP) and formation of 3-phosphoglyerate (3-PGA). Moreover, by saturating RuBisCO with CO_2, the CCM also functions to limit the competing oxygenation reaction that functions in the production of 2-phosphoglycolate, a toxic metabolite. The overall effects of the CCM are achieved through the concerted functioning of multiple cellular components; the authors then point to a beautiful diagram illustrating the interrelationship of the CCM, the Calvin-Benson-Bassham cycle, and the light reactions of photosynthesis.

Reference: Cameron, J., Sutter, M. and Kerkeld, C. (2014). "The Carboxysome: Function, Structure and Cellular Dynamics," in: FLORES, E. and HERRERO, A. (Eds.). *The Cell Biology of Cyanobacteria*. Norfolk: Caister Academic Press.

4. False. The statement correctly defines pili and motion by twitching, but errs by saying that pili are made of oscilin; these are proteins of the outermost layer of some protists, and function by enabling the gliding motion of some cyanobacteria. The protein that constitutes pili, in actuality, is *pilin*, a protein composed of 145 to 170 amino acids that is closely related to oscilin in structural terms.

5. True. True. Indeed, use of $^{15}NO_3^-$ and $^{15}NH_4^+$ has revealed that cyanobacteria such as *Synechocystis* sp. can take up nitrogen from both sources, and can make use of external N sources or N stemming from inner metabolism. Both the rate and the extent of nitrogen incorporation into cyanophycin depend on the source of N (ammonium or nitrate) available and whether the cells have been starved of N.

Reference: Herrero, A. and Burnat, M. (2014). "Cyanophycin, a Cellular Nitrogen Reserve Material," in: FLORES, E. and HERRERO, A. (Eds.). *The Cell Biology of Cyanobacteria*. Norfolk: Caister Academic Press.

6. False. Although it was long thought that cyanobacteria lacked the complexity necessary for biological clocks, research has revealed that prokaryotic cyanobacteria such as *Synechococcus elongatus* are just as capable of maintaining circadian rhythms as higher algae. Algae have biological rhythms associated with taxes (phototaxis and chemotaxis), the timing of cell division, photosynthetic capacity, bioluminescence, and sensitivity to UV light.

7. False. Cyanobacterial hepatotoxins are remarkably potent; wild and domestic animals exposed to water contaminated with these substances can experience weakness, heavy breathing, pallor, cold extremities, vomiting, diarrhea, and may die within 2 – 24 h after contact. Human deaths and cases of illness have also been reported, and health experts are concerned that long-term ingestion of drinking water containing hepatotoxins may lead to increases in human liver cancer, as laboratory analyses indicate that hepatotoxins have tumor-promoting activity. Municipal water treatment plants remove variable amounts of microcystin from lake water, but substantial amounts can survive ozonation, treatment with activated charcoal, and chlorination.

Reference: GRAHAM, L. and WILCOX, L. (2000). *Algae.* Upper Saddle River: Prentice-Hall.

8. False. Akinetes can only be formed by algae that constitute heterocysts. Also disputable is the statement's classification of akinetes as "equivalent to endospores," in that, although akinetes feature a greater resistance to cold than vegetative cells, they exhibit neither the metabolic quiescence nor the environmental tolerance of bacterial spores.

9. True. Hormogonia offer the blue-greens an increased degree of motility, affording them the evolutionary advantage of conquering another environment, but formation of these structures comes at a cost. Hormogonia lack heterocysts and are unable to fix hydrogen; phycobiliprotein synthesis ceases, leading to attrition in light gathering; hormogonia cells continue to photosynthesize and assimilate exogenous ammonium, although the rates of CO_2 fixation and and NH_4^+ incorporation are reduced to about two-thirds of the values of vegetative cells.

Reference: LEE, R. (2018). *Phycology.* 5th edition. Cambridge: Cambridge University Press.

10. True. In the associations in question, the embryophyte provides the cyanobacteria with fixed carbon and, conversely, the blue-greens supply the plant with fixed nitrogen. The prevalence of cyanobacterial associates within ventral cavities of ancient plants such as liverworths and hornworths suggests that early land plants may also have relied upon such associations to obtain fixed nitrogen.

11. False. The attributions should have been swapped: glycolate dehydrogenase occurs in the Chlorophyceae and Ulvophyceae, while glycolate oxidase is the enzyme of choice among the Charophyceae.

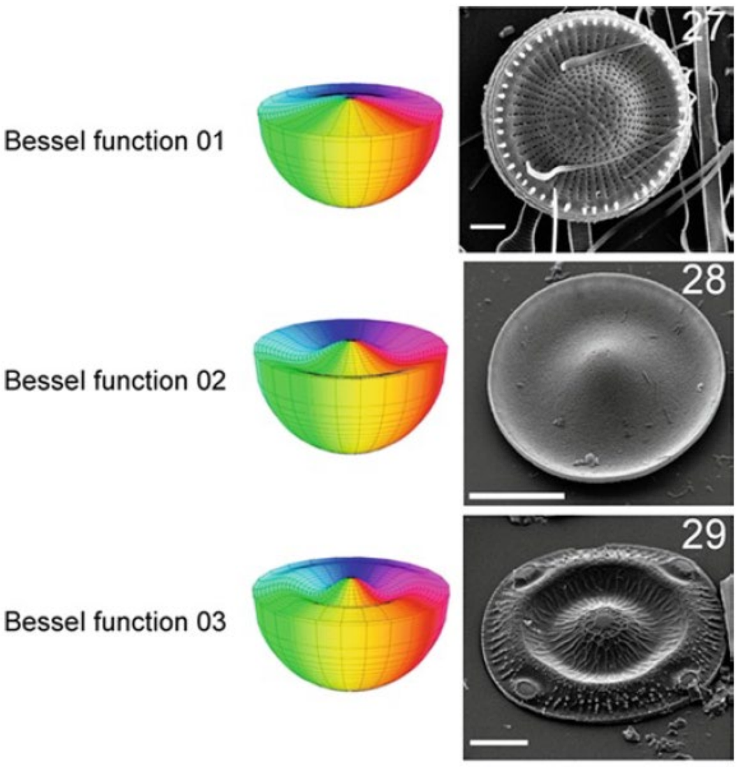
12. False. According to Bellinger and Sigee, while it is true that green algae in mesotrophic and eutrophic lakes do not normally produce the dense blooms seen with diatoms and blue-green algae, they do become dominant or co-dominant in early summer, between the clear-water phase and the mid-summer mixed algal bloom. When nutrient levels become very high, a switch may occur from colonial cyanobacteria to green algae as major bloom formers.

13. False. While it is true that silica cell walls usually require less energy to be formed than equivalent structures in other algae, the two supposed advantages of silicon walls offered at the end of the statement are false. For one, SiO_2 is quite dense, and for that reason planktonic diatoms can only develop efficiently in well-mixed unstratified waters. Further, silica is rigid and does not expand nearly as well as cellulose. This means that daughter cells are unable to enlarge and progressive cell divisions result in a gradual decrease in cell size. Ultimately, this decrease reaches a critical level, at which point sexual reproduction is required to completely shed the original cell wall and form new, large daughter cells. A third, more obvious disadvantage of SiO_2 cell walls is that formation of these structures requires an adequate supply of soluble silica in the surrounding water. The diatom spring bloom of temperate lakes strips out large quantities of silica from the water, reducing concentrations to a level that becomes limiting.

14. True. Diatoms are found attached to a number of diverse animal groups. A *Cocconeis*-like diatom was observed on the hairs of sei whales as long ago as 1934. In the 1980s, researchers reported the existence of diatom species that occur only on the skin of cetaceans such as killer whales and Dall's porpoises. Diving birds such as the red-throated loon, arctic loon, and common murre can also harbor dense populations of diatoms on their feathers; presumably, this allows the diatom to move from one body of water to another, thereby granting them the evolutionary advantage of colonizing different environments with ease.

15. False. The first diatom virus, a single-stranded RNA (ssRNA) virus infecting *Rhizosolenia setigera*, was reported by a Japanese group of researchers in 2004. In the ensuing years, further investigations led to the discovery of at least five other viruses, all of which are pathogens of *Chaetoceros* sp.

16. True. The complex mode of vibrations of a cylindrical centric diatom's valve face can be described by Bessel functions, much the way a function of one variable can be represented by a sum of sine waves. Gordon and Tiffany (see reference below) have associated the first Bessel functions to the surface of some diatoms, as illustrated below.



Reference: Gordon, R. and Tiffany, M. (2011). "Possible Buckling Phenomena in Diatom Morphogenesis," in SECKBACH, J. and KOCIOLEK, J. (Eds.). *The Diatom World.* Heidelberg: Springer.

17. False. Kleptoplasty is observed among dinoflagellates, not diatoms. To say the least, plastid dynamics in dinoflagellates is peculiar; for one, dinoflagellates have transferred most of the plastid genome to the nucleus of the cell, making them the only eukaryotes that encode the majority of the plastid genes in the nucleus. Having the genes for plastid targeted proteins may actually be an advantage, since it provides the cell with the freedom to replace the original plastid with a new one. The plastid genome of peridinin-containing dinoflagellates is reduced and broken up into mini-circles that encode only 16 proteins.

18. True. Bioluminescence does occur in marine dinoflagellates. There is evidence that bioluminescence in these species serves a defensive function. When the algae are agitated, they give off a flash of blue-green light that results from reaction of the substrate luciferin with the enzyme luciferase. In the case of dinoflagellates, bioluminescence appears to deter copepod predation. Two possible mechanisms have been suggested: a direct "startle" effect on the herbivores themselves and a more indirect effect – increased predation upon copepods that have fed upon glowing dinoflagellates increased the foraging efficiency of stickleback fish on copepods. This is viewed as an example of how prey (dinoflagellates) protect themselves by taking advantage of predation interactions at a higher trophic level.

19. True. Red algae and brown algae do exhibit the distinctive plastid structures mentioned in the statement.

20. False. In contrast to Chlorophyta starch, the Floridean starch of Rhodophyta algae is produced and stored *outside* of the chloroplast. This reserve substance is maintained in the form of bowl-shaped grains 0.5 to 25 µm in size. In spite of the differing locations of starch synthesis, the Rhodophyta and Chlorophyta use a common pathway for the synthesis of their respective storage products. Chlorophyta are in fact the only eukaryote algae in which the storage material occurs mainly within the chloroplast.

21. False. Phlorotannins are usually a constitutive defense mechanism in that they are always present in brown algae and seldom change with herbivory. What's more, phlorotannins are not normally secreted outside the cell; it is necessary for the cells to be damaged before they are released. Phlorotannins have also been associated with other functions, including absorption of ultraviolet radiation.

22. True. Only about a third of the 900 or so euglenoid species are photosynthetic and thus included among the algae; the others are colorless, being either heterotrophic or phagotrophic, and are conventionally included in the Protozoa. Some euglenoids (e.g., strains and species of *Euglena*) are facultative heterotrophs, able to carry out heterotrophic nutrition when photosynthesis is limiting or when surrounding concentrations of soluble organic materials are high. Autotrophic euglenoids are further characterized by use of chlorophylls *a* and *b*, one membrane of chloroplast endoplasmic reticulum, a mesokaryotic nucleus, flagella with fibrillary hairs in one row, no sexual reproduction, and use of paramylon or chrysolaminarin as storage products.

23. True. Indeed, there are colorless euglenoids that nonetheless exhibit eyespots. As mentioned in the statement, a stigma typically consists of up to 50 lipid droplets, but some species, such as *Eutreptia* and *Khawkinea*, may have only one or two large droplets. Several reports published since the 1960s have indicated the presence of a variety of pigments in euglenoid eyespots, including α-carotene, β-carotene, and seven types of xanthophyll.

24. False. Yellow-green algae actually occupy a relatively limited distribution of habitats, in that they tend to occur on damp mud (at the edge of ponds) and soil, but do not extensively occur in either lentic or lotic systems. Where planktonic forms do occur, they tend to be in ditches or small ponds. *Tribonema* sp. are often found as free-floating filaments in temporary waters, and *Botrydiopsis arrhiza* is found at the edge of ponds and in patches of water in sphagnum bogs, where it may form yellowish algal blooms. Even *Gloeobotrys limneticus*, which has widespread occurrence as mucilaginous colonies in lake plankton, never forms extensive or dominant populations (as seen, e.g., by blue-green algae).

25. False. While it is true that cryptomonads are especially prevalent in cold waters, the statement errs by saying that cryptomonads have no "tolerance to light-deprived environments"; in oligotrophic freshwater lakes, cryptomonads often form large populations about 15 – 20 m deep within a lake, where oxygenated surface waters interface with the anoxic lower part of the water column. In this location, these algae form deep-water accumulations of photosynthetic organisms referred to as *deep-chlorophyll maxima*. Studies on cultures of *Cryptomonas phaseolus* and *Cryptomonas undulata* isolated from deep chlorophyll maxima showed that these organisms had optimal growth under light-limiting conditions, suggesting photosynthetic adaptation to low light intensities.

26. False. What was revealed in the 1990s was not an incidental presence of fully-functioning chloroplasts in apicomplexans, but the existence of a reduced, colorless plastid known as an *apicoplast*. Molecular studies have shown that the apicoplast of some protozoans and dinoflagellate plastids are related and arose from red algae by a single endosymbiotic event that occurred relatively early in eukaryotic evolution.

ANSWER SUMMARY

Problem 1	D
Problem 2	B
Problem 3	T/F
Problem 4	B
Problem 5	A
Problem 6	C
Problem 7	T/F

REFERENCES

- BELLINGER, E. and SIGEE, D. (2015). *Freshwater Algae*. 2nd edition. Hoboken: John Wiley and Sons.
- FLORES, E. and HERRERO, A. (Eds.) (2014). *The Cell Biology of Cyanobacteria*. Norfolk: Caister Academic Press.
- GRAHAM, L. and WILCOX, L. (2000). *Algae.* Upper Saddle River: Prentice-Hall.
- LEE, R. (2018). *Phycology*. 5th edition. Cambridge: Cambridge University Press.
- SECKBACH, J. and KOCIOLEK, J. (Eds.) (2011). *The Diatom World*. Heidelberg: Springer.
- WEHR, J., SHEATH, R. and KOCIOLEK, J. (Eds.) (2015). *Freshwater Algae of North America*. Amsterdam: Elsevier.