ALGAE

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Contents

- 1. Introduction
- 2. Cyanobacteria
- 3. Glaucophyta
- 4. Rhodophyta
- 5. Chlorophyta
- 6. Heterokontophyta
- 7. Dinophyta
- 8. Haptophyta
- 9. Cryptophyta
- 10. Euglenophyta
- 11. Final Remarks
- Glossary
- Bibliography
- **Biographical Sketch**

Summary

This article represents an overview of the nine major groups that are considered part of the algae. These groups are very dissimilar, very diverse and have many peculiarities that make presentation and understanding of this complex assemblage of autotrophic, and some heterotrophic, organisms rather difficult. Special features and deeper knowledge can be found in the annotated Bibliography at the end of this contribution. Cyanophyta, which nowadays are considered as bacteria, are included in this presentation as prokaryotic photosynthetic members of the autotrophs (Cyanobacteria). A phylogenetic approach was taken in compiling the text and emphasis has been placed on some evolutionary explanations. The main reason for this is to reflect the evolutionary history of algae in the study of these living creatures. Besides, information about morphology, levels of organization, reproduction, fossil record, classification, habitats, and relative importance of the groups were included. Special emphasis was placed, in an introductory section, on the different kinds of tools used in algal classification through the years, from morphology to molecules. Life histories are discussed in detail due to their importance as mechanisms to preserve and improve genetic information, but also as examples of evolutionary trends in this particular phenomenon. Chloroplast origin is another topic included and reviewed in detail. Molecular biology has supported early ideas about the importance of chloroplast features in algal phylogeny. Endosymbiosis seems to be the key to understand origin and diversification among algae. These organisms are very important in our life not just because they give us a high percentage of the oxygen we breathe daily, but also because they are becoming increasingly important to our industry. As environmental indicators, algae are playing a remarkable role but, also as research tools, they are providing new insights in various fields of physiology, nutrition, biochemistry, ultrastructure, evolution and phylogeny. The improvement of strategies for their conservation is crucial.

1. Introduction

Algae do not represent a natural group: its creation as a taxon was an attempt to express the obsolete and inaccurate perception that relationships exist among members of the plants which do not have specialized structures such as roots, stem, leaves and flowers. In systematic biology we would call this an artificial group or a polyphyletic group, which means there is no single common ancestor for all the groups included in the Algae.

The best known algae are the common seaweeds which, as their name implies, are all marine and of a size easy to see and recognize. Among these are the brown algae (kelps), green algae (sea lettuce), and red algae (nori). Also well known are the prokaryotic organisms that form stromatolites (Cyanobacteria), which were in the past considered as members of this artificial group. Furthermore, algae include microscopic forms, unicellular or multi-cellular, which belong to the plankton (phytoplankton) and, from time to time, form extensive blooms, as in the case of red tides. Some of these microscopic organisms are heterotrophic, rather than autotrophic. Algae are mainly aquatic and their distribution is worldwide, from the poles to the equator. They also occur on land in all types of soil and on permanent ice or snowfields. They are the major and primary organic producers and their morphology goes from the microscopic phytoplankton to the macroscopic growths in the intertidal zones of all beaches.

The group named algae includes two main morphologically distinct patterns: prokaryotes (organisms without nuclei) and eukaryotes (organisms with nuclei). Although the former have been formally reclassified as bacteria, subkingdom Eubacteria, they are discussed here because, historically, they were included in the Cyanophyta group of algae. In this article they are referred to as Cyanobacteria.

The main and unique compound of the algae photosynthetic process, *chlorophyll a*, works together with various accessory pigments. These accessory pigments allow a differential response to light of various types and intensities. As a result, some reflect or absorb specific light wavelengths giving the characteristic colors that were the main reason for naming green algae, Chlorophyta, brown algae and their relatives, Phaeophyta and red algae, Rhodophyta. Furthermore, this feature has permitted a differential distribution of these organisms at different depths in aquatic ecosystems.

The study of this artificial group was carried out, through the years, utilizing the tools and techniques available at any given time. At the beginning of the 20th century, for instance, morphology was the key to classify and subdivide all organisms. Levels of organization, basic structural patterns or bauplans were explored and established as ground rules to understand algal biodiversity and evolution. Another important method was the use of evolutionary tendencies among living beings. Tendency to multicellularity, loss of motility, reduction of gametophyte phase, etc. were used to explain the progressive complexity from unicells to pseudoparenchymatous forms, the development of complicated life histories and several other biological phenomena present in extant forms. Within this framework, unicellular motile organisms were primitive and complex forms were considered advanced. Later on, biochemical characters such as pigments, reserve substances, cell wall components and many others, were introduced and used in combination with morphological and anatomical characters. More recently, data on ultrastructure gave an important impetus to the understanding of algae as different evolutionary groups. These studies focused chiefly on flagellar apparatus, their basal bodies, structure and orientation and cytokinesis during mitosis. These last studies, brought to light two different structural forms during the cell cleavage: the phycoplast, where microtubules are oriented perpendicularly to the plane of cytokinesis, and the phragmoplast in which the microtubules are parallel to the longitudinal axis of the spindle. Such data were determinant to establish a new hypothesis on the evolution of green algae.

Life histories and laboratory cultures generated new information about this group of organisms. Evolution of sexuality and its expression in the different types of algae, were considered of primary value to understand their taxonomic relationships because the transmission of reproductive features is, undoubtedly, crucial in ensuring a species survival in time and space. All characteristics related to this phenomenon, therefore, could be relevant.

As a brief summary, one can say that there are three types of life history or cycles, among algae. The one called haplontic or haplobiontic (Figure 1)



Figure 1. Haplobiontic life history.

in which an organism with a haploid chromosome number (n) gives, by mitosis, a number of cells, which will behave as gametes. These gametes will form a zygote, by syngamia, and meiosis will immediately occur resulting in haploid cells which germinate into a haploid phase similar, but not identical, to the first organism.

The second type is known as diplontic or diplobiontic (Figure 2). In this type the conspicuous thallus is diploid (2n) and, by meiosis, gives haploid cells acting as gametes, which fuse and form a zygote. This zygote germinates giving origin to a new diploid plant.



Figure 2. Diplobiontic life history, or diphasic life history.

The third kind is the haplodiplontic or diplohaplobiontic life history (Figure 3), also known as alternation of generations or diphasic life history. Sometimes confused as an alternation between asexual and sexual phases, alternation of generations is a true sexual life history differing from others in the timing of meiosis. This cycle starts with a conspicuous thallus with either a haploid or a diploid chromosome number. In the case of a diploid thallus (sporophyte), meiosis takes place and forms haploid cells. These haploid cells, however, do not act as gametes as in the diplontic life history mentioned above, they act as spores and sprout into a plant that has a haplontic condition and is known as gametophyte. The gametophyte generates gametes, by mitosis, which fuse into a zygote that, in turn, germinates into a sporophyte. This completes the life history. Hence, there are two different and independent thalli: a haploid thallus and a diploid one. Both thalli can be present simultaneously at the same time, or they can alternate

according with their evolutionary and ecological requirements. Also, they can be similar in form (isomorphic) or morphologically different (heteromorphic).



Figure 3. Haplodiplobiontic life history.

A variant of this life history is found among red algae and is called triphasic because on the gametophyte, the zygote develops in a carposporophyte phase, where a diploid group of cells is retained in a haploid plant. This structure forms carpospores, which start growing in a sporophyte thallus.

A very important contribution to algal systematics was the study of plastid diversity and its implications to a possible multiple origin of the algae, within the framework of the serial endosymbiosis theory. Chloroplasts are the most conspicuous organelles in the algal cell, and their shape, position and number have been used as criteria in the classification of algae: chiefly within green and brown algae. Three elements are relevant: organization of thylakoids, presence of pyrenoids inside the chloroplast and number of membranes surrounding the plast. Lately, this last feature has received much attention from the viewpoint of molecular biology: the most recent tool in the search of true evolutionary origin, history and relationships among algae. According to some authors, chloroplasts with more than two surrounding membranes originated from a eukaryotic symbiont rather than from a prokaryotic cyanobacterium. Those with three membranes came from isolated chloroplasts, whereas chloroplasts with four surrounding membranes were algal cells that were incorporated into a heterotrophic eukaryotic cell.

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Biographical Sketch

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Special interests in phycology: morphology, taxonomy, nomenclature, biogeography, evolution, molecular systematics, and conservation problems in tropical marine algae.