THE
FRESH-WATER ALGAE
OF
THE UNITED STATES

BY
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IV

PREFACE

The years since the appearance of the first edition have seen the addition of many genera and species to the known fresh-water algal flora of this country. For certain groups (Xanthophyceae, Chrysophyceae, Dinophyceae) the number of genera known to occur in the United States has been more than doubled. In addition, many genera known from but one or two localities in 1933 are now known to have a much wider distribution. The morphology and mode of reproduction of many of the genera described in the first edition are also more fully known than they were seventeen years ago, and this has necessitated a change in the systematic position of certain genera.

This edition follows the general plan of the first edition, except for treatment of the species in the various genera. In the first edition, where there were less than ten species in a genus, each was named and briefly characterized. In this edition the species of a genus are listed and references given to sources where a complete description of each of them can be found. Another change is the addition of a survey of the Charophyceae, Cryptophyceae, and Chloromonadales, groups that were not treated in the first edition.

The completeness of this edition has been greatly enhanced by the helpful cooperation of many phycologists. For supplying information or furnishing specimens I am indebted to Dr. Mary A. Pocock and to Professors L. H. Flint, D. L. Jacobs, C. E. Taft, E. N. Transeau, L. A. Whitford, and R. D. Wood. Special thanks are due Professors G. W. Prescott and R. H. Thompson for furnishing numerous original drawings and for permitting me to incorporate in this book their as yet unpublished additions to the algal flora of this country.

<div align="right">GILBERT M. SMITH</div>

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CHAPTER 1

NATURE, EVOLUTION, AND CLASSIFICATION OF THE ALGAE

Position of the Algae in a Natural System. The conception of the nature and systematic position of the group of plants known as the algae has been, and still is, continually changing. Although Linnaeus[1] gave the name *Algae* to one of his orders of plants, this cannot be considered the first recognition of them as a definite part of the plant kingdom, since the group that he called the algae consisted very largely of *Hepaticae*. The first delimitation of the Algae as we now interpret the term is that of A. L. de Jussieu,[2] but his characterization of the group is practically worthless since it is based entirely upon macroscopic features. Even when specialists began to devote their attention to this group of plants and had described many genera and species, there was for a long time but little knowledge of the cell structure and the methods of reproduction. Thus, we find C. A. Agardh,[3] the great pioneer in the study of algae, describing them as follows:

Plantae aquaticae acotyledoneae & agamae; gelatinosae, membranaceae vel coriaceae; filamentosae, laminosae vel tandem foliosae; colore virides, purpureae vel olivaceae; articulatae vel continuae; sporidia aut pericarpiis inclusa aut superficiei inspersa foventes.

Endlicher's[4] inclusion of algae, lichens, and fungi in an assemblage (kingdom) called the *Thallophyta* marks the recognition of a morphological distinction that is still followed today, especially in the widely used classification of Eichler,[5] that divides plants into *Thallophyta, Bryophyta, Pteridophyta*, and *Spermatophyta*. Endlicher separated the Thallophyta from other plants because of their lack of differentiation into stems and leaves. It is quite impossible to draw a sharp distinction between Thallophyta and Bryophyta on such a basis: certain algae, as the Laminariales, have a clear differentiation into stems and leaves; many liverworts have a plant body that is a simple thallus. It is possible, however, to base a clear-cut distinction between Thallophyta and other plants, on the structure of the gamete- and the spore-containing organs. In the Thallophyta the sex organs are one-celled; or when multicellular, as in certain Phaeophyceae,

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[1] LINNAEUS, 1754.   [2] DE JUSSIEU, A. L., 1789.   [3] AGARDH, 1824.
[4] ENDLICHER, 1836.   [5] EICHLER, 1886.

do not have the gametes surrounded by a layer of sterile cells. Bryophytes, and plants immediately above them in the evolutionary scale, have multi-cellular sex organs, in which there is an outer layer of sterile cells. Sporangia of Thallophyta are always one-celled: those of higher plants are always many-celled. Another distinction between the Thallophyta and other plants is the fact that the zygotes of Thallophyta never develop into multicellular embryos while still within the female sex organs.

Granting the distinctiveness of the assemblage of plants called the Thallophyta, there then arises the question: Is this a natural division of the plant kingdom that may, in turn, be divided into *Algae* and *Fungi?* To accept the Thallophyta as a natural division of the plant kingdom implies acceptance of the view that all algae are more or less closely related to one another. The question of the phylogenetic relationships between the algae rests, in turn, upon the discovery of an adequate basis for classifying them. The test of time has shown the inadequacy of taxonomic classifications of algae based either upon the organization of the plant body or upon the method of reproduction.

It has become increasingly clear during the past quarter century that the morphology and physiology of the individual cells are the fundamental basis upon which the algae must be classified. This evidence shows that there are several series among the algae, each of which has cells with certain distinctive morphological and physiological traits. Chief among the morphological characteristics is the structure of the motile cell, and for most of the series among the algae there is a striking constancy in its organization, especially with respect to the number, arrangement, and relative length of the flagella. On the physiological side there is, throughout each series, a constancy in the pigments present in the plastids (Table I), and a constancy in the chemical nature of the food reserves accumulating through photosynthetic activity. For example, the Chlorophyceae always have flagella of equal length, a predominance of green pigments in their plastids, and usually store photosynthetic reserves as starch. The Xanthophyceae on the other hand, always have flagella of unequal length, a predominance of yellow pigments in their plastids, no formation of starch, and usually store photosynthetic reserves as oils. This constancy with which the morphological and physiological cellular characteristics obtain in each series, and the marked differences between the various series (Chlorophyceae, Myxophyceae, Chrysophyceae, etc.) suggest very strongly that they have originated from pigmented ancestors quite different from one another.

Acceptance of the view that the various series among the algae are more or less independent of one another means that the Thallophyta cannot be considered a natural division of the plant kingdom. The *Algae,* likewise,

TABLE I. PRINCIPAL PIGMENTS OF THE DIFFERENT CLASSES OF ALGAE (BASED ON STRAIN, IN PRESS)

	Myxophyceae	Rhodophyceae	Xanthophyceae	Chrysophyceae	Bacillariophyceae	Phaeophyceae	Dinophyceae	Chlorophyceae	Euglenophyceae
Chlorophylls:									
Chlorophyll a....	+++	+++	+++	+++	+++	+++	+++	+++	+++
Chlorophyll b....	0	0	0	0	0	0	0	++	+
Chlorophyll c....	0	0	0	...	+	+	+	0	0
Chlorophyll d....	0	+	0	...	0	0	0	0	0
Chlorophyll e....	0	0	+	...	0	0	0	0	0
Carotenes:									
α-Carotene......	...	+	...	...	0	0	0	+	
β-Carotene......	+++	+++	+++	+++	+++	+++	+++	+++	+++
ε-Carotene......	...	...	...	...	+	0	...	0	
Flavicin.........	+	...	...	...	0	0	...	0	
Xanthophylls:									
Lutein..........	?	++	0	+	0	0	0	+++	?
Zeaxanthin......	?	...	0	...	0	0	0	+	
Violaxanthin.....	...	...	...	...	0	+	0	+	
Flavoxanthin....	...	...	...	...	0	+	...	?	
Neoxanthin.....	...	...	0	...	0	+	0	+	
Fucoxanthin.....	...	?	0	+	++	++	0	0	0
Neofucoxanthin A	...	...	0	...	+	+	0	0	0
Neofucoxanthin B	...	...	0	...	+	+	0	0	0
Diatoxanthin....	...	...	0	...	+	?	0	0	0
Diadinoxanthin..	...	...	0	...	+	?	+	0	0
Dinoxanthin.....	...	...	0	...	0	?	+	0	0
Neodinoxanthin..	...	...	0	...	0	0	+	0	0
Peridinin........	...	...	0	...	0	0	++	0	0
Myxoxanthin....	++	...	0	...	0	0	0	0	0
Myxoxanthophyll	++	...	0	...	0	0	0	0	0
Unnamed........	?	?	++	?		+			+
Phycobilins:									
r-Phycoerythrin..	0	+++	0	?	0	0	0	0	0
r-Phycocyanin...	0	+	0	?	0	0	0	0	0
c-Phycoerythrin	+	0	0	?	0	0	0	0	0
c-Phycocyanin...	+++	0	0	?	0	0	0	0	0

+++ indicates the principal pigment in each of the four groups of pigments.
++ indicates a pigment comprising less than half of the total pigments of the group.
+ indicates a pigment comprising a small fraction of the total pigments of the group.
? indicates small quantities of a pigment whose source or identification is uncertain.
0 indicates known absence of a pigment.
... indicates lack of knowledge concerning the presence of certain pigments in some classes of algae

cannot be regarded as a particular subdivision of the plant kingdom. This does not mean that the word "alga" must be abandoned, since it is still of great service as a descriptive term for designating simple plants with an autotrophic mode of nutrition.

Organisms to Be Placed among the Algae. Until the beginning of the twentieth century, it was customary to recognize the following four classes of algae: Chlorophyceae, Phaeophyceae, Rhodophyceae, and Myxophyceae (Cyanophyceae). Diatoms were universally included among the algae and placed either in the Phaeophyceae or in a class distinct from other classes.

During this time botanists rarely questioned the practice of protozo-ologists who placed all motile unicellular and colonial flagellated organisms in the class Mastigophora of the phylum Protozoa. An exception must be made in the case of the volvocine (*Chlamydomonas-Volvox*) series. Here, beginning nearly a century ago,[1] botanists began calling certain members of this series algae but made no attempt to assign them a definite place among the algae. This was first done by Rabenhorst (1863) who placed the *Chlamydomonas-Volvox* series in the group of grass-green algae to which he gave the name Chlorophyllaceae.

When, at the turn of the century, the Xanthophyceae (Heterokontae) were segregated[2] from the grass-green algae (Chlorophyceae), certain pig-mented flagellates were included in the series. Later the chrysomonads and the dinoflagellates each were shown to be related to organisms of an un-questionable algal nature. The euglenoids and cryptomonads are also related to organisms of an algal type, but types that are not so highly developed as in the case of the algal types related to the chrysomonad and the dinoflagellate series.

Thus, with the possible exception of the chloromonads, all the various groups (orders) of flagellates which protozoologists place in the subclass Phytomastigina of the class Mastigophora are phylogenetically connected to organisms of a truly algal nature. Disregarding, for the present, the interrelationships between them, these phylogenetic series (classes) may be briefly characterized as follows:

1. *Chlorophyceae,* in which the photosynthetic pigments are localized in chromatophores that are grass-green because of the predominance of chloro-phylls *a* and *b* over the carotenes and xanthophylls. Photosynthetic re-serves are usually stored as starch, and its formation is intimately asso-ciated with pyrenoids. Motile cells have flagella (generally two or four) of equal length and borne at the anterior end. Most members of the class reproduce sexually.

2. *Euglenophyceae,* in which the photosynthetic pigments are approxi-mately the same as in Chlorophyceae and are localized in grass-green

[1] BRAUN, 1851; COHN, 1853.   [2] LUTHER, 1899.

chromatophores. Paramylum, an insoluble carbohydrate, is the chief food reserve. Motile cells have either one or two flagella and have them inserted in a gullet at the anterior end of the cell.

3. *Xanthophyceae* (*Heterokontae*), in which the photosynthetic pigments are localized in chromatophores that are yellowish green because of a predominance of beta-carotene over chlorophylls *a* and *e*. Pyrenoids are usually lacking, and the reserve foods are stored as fats or as leucosin. The cell wall frequently consists of two overlapping halves and contains little, if any, cellulose. Motile cells have two flagella of unequal length at the anterior end.

4. *Chrysophyceae*, in which the photosynthetic pigments are localized in chromatophores that are usually golden brown because of a predominance of carotenes and xanthophylls over the chlorophyll. Oils are formed in abundance, and sometimes there is also a formation of leucosin. Motile cells may have a single anterior flagellum or two anterior flagella of unequal or of equal length. Members of this series have an endogenous formation of cysts surrounded by a two-parted silicified wall with a terminal pore. Sexual reproduction is of rare occurrence in this class.

5. *Bacillariophyceae* (*Bacillarieae*), in which the photosynthetic pigments are localized in chromatophores that are usually a deep golden brown because of a predominance of carotenes and xanthophylls (especially, fucoxanthin) over chlorophylls *a* and *c*. The cell wall regularly consists of two overlapping halves which are highly silicified. Reproduction by flagellated swarmers has been found in certain genera, but the precise nature of these motile bodies is unknown. Sexual reproduction is of widespread occurrence and is immediately preceded by meiosis.

6. *Phaeophyceae*, in which the photosynthetic pigments are localized in chromatophores that are olive yellow to deep brown because of a predominance of carotenes and a series of xanthophylls (notably, fucoxanthin) over chlorophylls *a* and *c*. The most abundant reserve product of photosynthesis is a polysaccharide, laminarin. All members of the class, of which there are numerous marine members, have a filamentous or a more elaborate organization. Motile reproductive cells are pyriform with two laterally inserted flagella. Sexual reproduction is found in most of the genera.

7. *Dinophyceae*, in which the photosynthetic pigments are localized in chromatophores that are yellowish green to deep golden brown because of a predominance of carotenes and a unique series of xanthophylls over chlorophylls *a* and *c*. Food reserves are stored as starch or as oil. Motile cells have a transverse furrow in which the two flagella are inserted. One flagellum encircles the cell transversely, the other extends vertically backward. Sexual reproduction is of rare occurrence in this class.

8. *Myxophyceae* (*Cyanophyceae*), in which the photosynthetic pigments

are not localized in chromatophores. In addition to chlorophyll *a*, beta-carotene, and two unique xanthophylls, the cells contain two phycobilin pigments c-phycocyanin and c-phycoerythrin. The cells do not have a definitely organized nucleus. The chief food reserve is a carbohydrate, cyanophycean starch. Sexual reproduction is unknown for this series and there is never a formation of flagellated reproductive cells.

9. *Rhodophyceae*, in which the photosynthetic pigments are localized in chromatophores that are usually reddish in color because of a predominance of r-phycoerythrin over the other pigments (r-phycocyanin, chlorophylls *a* and *d*, alpha- and beta-carotene, and the xanthophyll lutein). The chief food reserve is floridean starch, a carbohydrate intermediate between starch and dextrin. Motile reproductive cells are never found within this series. The sexual organs are of a unique type, and practically all members of the class reproduce sexually.

10. *Cryptophyceae*, in which the photosynthetic pigments are localized in variously colored chromatophores. Reserve foods are usually stored as starch or as starch-like compounds. Motile cells are compressed, biflagellate, and with a superficial curved furrow extending back from the terminal or lateral insertion of the flagella.

11. *Chloromonadales*, in which the photosynthetic pigments are localized in chromatophores of a distinctive green color. The chief food reserve is oil. Motile cells are biflagellate and with the flagella inserted in a reservoir at the anterior end. A majority of the genera have trichocysts within the cells.

Evolution of Plant-body Types among Algae. The modern conception of the nature of evolution of the thallus among algae originated from observations[1] which showed that there was a marked parallelism between the Chlorophyceae and the Xanthophyceae, and that practically all types of cellular or colonial organization among the Chlorophyceae have their counterparts among the Xanthophyceae. This was accepted as an interesting though not significant fact until it was shown that the types of plant-body construction found in the Chrysophyceae, Dinophyceae, and certain other series can also be homologized with those of the Xanthophyceae and Chlorophyceae.[2]

The explanation of this parallelism is based upon the hypothesis that only four basic types of body (thallus) construction can be evolved from a primitive motile unicellular ancestral form. This hypothesis also holds that the types of plant body evolved from the motile unicellular ancestor of one series are essentially like those evolved from the motile unicellular forms of other series. The idea of evolution in different directions from a motile unicellular ancestor was originally proposed to account for the

[1] PASCHER, 1913.   [2] PASCHER, 1914, 1925, 1927.

various types of body construction found in the Chlorophyceae.[1] Here it was postulated that there are three main evolutionary lines or tendencies from the motile unicell: (1) the *volvocine tendency*, in which the individual cells become organized into a colony but retain their vegetative motility; (2) the *tetrasporine tendency*, in which there is a loss of motility, except in reproductive stages, but a retention of the capacity for vegetative division; (3) the *chlorococcine (siphonaceous) tendency*, in which there is a loss of motility, except at the time of reproduction, and a loss of the ability to divide vegetatively. To these should be added (4) the *rhizopodal tendency*, in which there is evolution toward an amoeboid type of organization.

In its wider application[2] it is held that these tendencies are also found in phylogenetic series other than the Chlorophyceae, and that each of the algal series has repeated the same experiments in evolution of body types. Certain of these experiments were foredoomed to failure, since the potentialities are extremely limited. Thus, the volvocine tendency, or evolution of a volvocine colony, cannot develop a colony of any appreciable size and have the individual cells retain their motility. The siphonaceous tendency, with its abolition of vegetative cell division but retention of nuclear division, is also an experiment that was not particularly successful.

The tetrasporine experiment is along a line that results in a nonmotile holophytic organism capable of infinite variation. The beginnings of evolution along the tetrasporine line are found in those algae in which motile cells are imprisoned within a gelatinous sheath. Many of the Volvocales have temporary colonies of this nature, and certain of the lower Tetrasporales, as the Chlorangiaceae, have colonies in which motile cells are more or less permanently imprisoned within gelatinous sheaths. Colonies of the *Palmella* type are a step in advance of this. Here, the cells within the gelatinous matrix are without flagella but may develop them at any time and so return directly to a motile unicellular condition. Cells in colonies of the *Palmella* type have the capacity to divide vegetatively, and cell division may result in amorphous colonies of indefinite size or in colonies with a definite shape. The next step in the tetrasporine evolution is the loss of the cell's capacity to return directly to a motile condition. However, this is not accompanied by a loss of the capacity to divide vegetatively. When such cells divide vegetatively, the daughter cells may separate from each other or may remain united. Separation of daughter cells after cell division results in an immobile unicellular organism. Cohesion of the daughter cells, followed by further divisions in the same plane, results in an unbranched filament; the simplest of the filamentous types and the forerunner of the various branched types.

[1] BLACKMAN, 1900; WEST, G. S., 1904.
[2] FRITSCH, 1929, 1935; FRITSCH and WEST, 1927; PASCHER, 1914, 1925, 1927.

Evolution along the chlorococcine line (in which there is a loss of motility of the vegetative cells and a loss of the capacity to divide vegetatively) may begin with the primitive unicellular flagellate. It may also arise from unicellular members of the tetrasporine line by a loss of the capacity for vegetative division. The siphonaceous type is a modification of the chlorococcine type in which the nuclei retain their ability to divide and the cells develop the capacity to elongate indefinitely.

Evolution along the tetrasporine and the chlorococcine lines results in immobile organisms that are distinctly plant-like in organization. Evolution of the motile unicell along the rhizopodal line results in an organism with an amoeboid method of movement and nourishment. In certain series, as the Chlorophyceae, amoeboid stages are but temporary. These have been found in motile unicellular forms, such as *Chlamydomonas*,[1] and in gametes or zoospores of specialized filamentous forms, such as *Stigeoclonium*.[2] In other phylogenetic series, as the Chrysophyceae, Heterokontae, and the Dinophyceae, there has been a rhizopodal evolution to a state where the cells are in a more or less permanent amoeboid condition.[3]

The parallelism in the evolution of plant-body types among the various algal series with motile unicellular forms comes out most strikingly when the data are arranged in tabular form (Table II). Analysis of the data immediately brings out the fact that progressive evolution within the various series has not reached the same level: certain series have progressed but little beyond the motile unicell, others have advanced to the point where they have a complex plant body. The point which Table II does not bring out is the relative abundance of the different types in the various phylogenetic series. Some of them, as the Chrysophyceae and Dinophyceae, have but few advanced types; others, as the Chlorophyceae and Phaeophyceae, have many advanced types.

The preceding paragraphs have stressed the evolution of certain algal series from motile pigmented ancestors markedly different in their basic morphology and physiology. This postulation of the origin of certain series from motile unicells does not mean that all algal series have arisen in this fashion. The complete lack of flagellated vegetative and reproductive cells in the Myxophyceae suggests very strongly that motile cells have never been present in the myxophycean series. If the Myxophyceae have developed from a flagellated ancestor, one would expect to find flagellated reproductive cells somewhere among the many genera of this series.

The problem of determining the origin of Rhodophyceae and of Phaeophyceae is extremely difficult, since the simplest of them have a rather

[1] PASCHER, 1918.   [2] PASCHER, 1915.   [3] PASCHER, 1917.

TABLE II. THE PARALLELISM IN EVOLUTION OF PLANT-BODY TYPES AMONG THE CLASSES OF ALGAE WITH KNOWN FLAGELLATED UNICELLS

Unless otherwise noted, the examples cited are found in the fresh-water flora of the United States

Type of plant-body construction		Chlorophyceae	Xanthophyceae	Chrysophyceae	Dinophyceae	Euglenophyceae
Motile unicell		Chlamydomonadaceae, Sphaerellaceae, etc.	Heterochloridales	*Mallomonas, Chromulina*, etc.	*Glenodinium, Peridinium*, etc.	Euglenaceae, etc.
Palmelloid colony with imprisoned motile cells		Chlorangiaceae			....	*Colacium*
Palmelloid colony with nonflagellated vegetative cells		Palmellaceae, Tetrasporaceae, etc.	Chlorosaccaceae	*Chrysocapsa, Hydrurus*, etc.	*Gloeodinium*	
Simple filaments		Ulotrichaceae, etc.	Tribonemataceae	*Nematochrysis* (Pascher, 1925)		
Branched filaments		Chaetophoraceae, etc.	*Monocilia*	*Phaeothamnion*	*Dinothrix* (Pascher, 1914)	
Chlorococcoid cells		Chlorococcales	Heterococcales	*Chrysophora* (Pascher, 1925)	*Dinastridium* (Pascher, 1927)	
Siphonaceous cells		Siphonales	*Botrydium*			
Dendroid colonies		....	....	*Dinobryon*		
Globose colonies		Volvocaceae, etc.	....	*Chrysosphaerella, Syn-nura*, etc.		
Unicellular		Transitory stages only	*Myxochloris* (Pascher, 1930B)	*Chrysamoeba*	*Dinamoeba* (Pascher, 1915C)	
Plasmodial colonies		....	*Chlorarachnion* (Geitler, 1930)	*Chrysidiastrum*		

Tetrasporine tendency

Chloro-coccine tendency

Volvocine tendency

Rhizopodial tendency

complex organization, and all connecting links with hypothetical unicellular ancestors are unknown. One explanation for this absence of primitive Rhodophyceae and Phaeophyceae is that they developed in the ocean at a time when it was much less saline than at present, and that there was a dying off of the more primitive forms as the salinity of the ocean increased. There was, however, a survival of certain advanced types among the Rhodophyceae and Phaeophyceae, and these constituted a fresh starting point for the even more complex red and brown algae found in the present-day marine flora. The universal presence of motile zoospores and gametes throughout the phaeophycean series indicates that this series originated in a motile unicellular ancestor; the lack of motile reproductive cells in the rhodophycean series seems to show that, similar to the Myxophyceae, these algae have come from a nonflagellated unicellular ancestor.

Classification of the Algae. If the Thallophyta cannot be considered as constituting a natural division of the plant kingdom, how can the algae be brought into harmony with the International Botanical Code which says (Article 10), "every individual plant belongs to a species, every species to a genus, every genus to a family, every family to an order, every order to a class, and every class to a division"? It is clear that the algae must be separated into a number of divisions coordinate in rank with the Bryophyta, Pteridophyta, and Spermatophyta. Modern discussions on the phylogeny and classification of algae hold that certain of the classes noted above (see page 4), are sufficiently distinct to warrant recognition as divisions of the plant kingdom.[1] However, other classes have so many features in common that they are evidently related to one another. Thus, the number of divisions necessary for a complete classification of the algae is less than the number of classes. The first recognition of an affinity between classes was that which showed a relationship between the Xanthophyceae, Chrysophyceae, and Bacillariophyceae.[2] Features in common to these three classes include: cell walls composed of two overlapping halves, silicified cell walls, motile cells with similarities in flagellation, a distinct type of resting cell (cyst), and similarities in the nature of food reserves. Despite differences in the chlorophylls and xanthophylls (see Table I), there seems to be good ground for placing the three in a single division, the *Chrysophyta.* The golden-brown chromatophores of the Phaeophyceae resemble those of Chrysophyta, but there are some differences in the pigments causing the brown color. Since there are striking differences in the food reserves and in structure of motile reproductive cells, the Phaeophyceae should be placed in a separate division, the *Phaeophyta.* The Myxophyceae and Rhodophyceae are the only algae in which there are

[1] PASCHER, 1914, 1921, 1931.   [2] PASCHER, 1914.

phycobilin pigments, but these pigments are not identical in the two,[1] and the two classes differ in their chlorophylls and xanthophylls (see Table I). The differences in nuclear organization, localization or non-localization of pigments in chromatophores, and presence or absence of sexual reproduction are so striking that there does not seem to be a phylogenetic connection between the two classes. Thus the Rhodophyceae are to be placed in one division, the *Rhodophyta*, and the Myxophyceae in another, the *Cyanophyta*. The chlorophycean series is also so distinctive that it should be placed in a separate division, the *Chlorophyta*. Similarities in pigmentation and food reserves of Euglenophyceae and Chlorophyceae tempt one to place the Euglenophyceae in the Chlorophyta, but it seems better to place them in a separate division, the *Euglenophyta*. The Dinophyceae have sufficient distinctiveness to be placed in another division, the *Pyrrophyta*. Some phycologists[2] think that the Cryptophyceae should be included in the Pyrrophyta; others[3] think that they should not. For the present it seems better to consider the Cryptophyceae a class of uncertain systematic position and not to place them in any of the divisions mentioned above. The question of the proper disposition of the chloromonads is even more difficult, and in their case, also, it seems best to group them among algae of uncertain systematic position.

Relationship of Algae to Other Plants. According to the International Rules of Botanical Nomenclature the primary step in a classification of the plant kingdom is the establishment of *divisions*. The multicellular plant body in certain of the algal divisions, as the Cyanophyta, is merely an aggregation of individuals into a colony of simple construction. Other phylogenetic lines, as the Rhodophyta and Phaeophyta, include algae of large size, external complexity of form, and with some differentiation of tissues within the plant body. In reality, the six divisions listed above represent six kingdoms, all plant-like in nature. In five of these kingdoms there has not been an evolution of anything more complex than an algal type of organization. Thus these five kingdoms would have but one division each. The kingdom of the grass-green plants consists of a number of divisions of which the grass-green algae (Chlorophyta) are the most primitive and lead successively to the Bryophyta, Pteridophyta, and Spermatophyta.

[1] STRAIN (in press).   [2] PASCHER, 1914, 1927.   [3] GRAHAM (in press).

CHAPTER 2

THE DISTRIBUTION AND OCCURRENCE OF FRESH-WATER ALGAE

One ordinarily thinks of the fresh-water algae as plants largely restricted to standing and running waters and occasionally growing in other habitats. This is far from the truth. Algae are of widespread occurrence in moist situations (as tree trunks, walls, woodwork, rocks, and damp soil) where they frequently occur as an extended stratum consisting of either a single species or a mixture of species. There is, in addition, a rather long list of what may be called "algae of unusual habitats." These algae include those growing endophytic in other plants, leaf epiphytes, perforating algae of molluscs and calcareous rocks, snow algae, thermal algae, epizoic algae, and certain others.

Geographical Distribution of Algae. One of the striking features of the fresh-water algal flora is its cosmopolitanism. Many species are found in all parts of the world, from the tropics to the polar regions, and in a variety of habitats. Other species are restricted to particular habitats, but even these may be found at stations thousands of miles apart.

Some of the fresh-water algae, such as *Trentepohlia* and *Pithophora*, are more abundant in the tropics than in temperate regions, and a few of them appear to be limited by temperature. The best known of these are *Cephaleuros*, a green alga parasitic upon the leaves of several Angiosperms, and *Compsopogon*, a red alga found in the southern states of this country, the West Indies, and in Central America.

The only group of fresh-water algae in which there is any evidence of endemism is that of the Desmidiaceae. A specialist shown a collection rich in species of desmids, but not told the source of the collection, would be able to tell whether it came from Europe, Australia, the Indo-Malay region, or the Americas, but even in this family the majority of species are cosmopolitan.

Dispersal of Algae. The cosmopolitanism of most species, and the localism of others, are dependent upon the methods by which algae become distributed from one locality to another. All discussions of the means by which alga are dispersed[1] have been based upon general observations rather than detailed study, and it is not definitely known whether algae are trans-

[1] BORGE, 1897; STRÖM, 1926; WILLE, 1897.