

THE FINE STRUCTURE OF ALGAL CELLS

John D. Dodge



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Foreword

Part of the fascination that the algae have for researchers and students lies in their extraordinary diversity, both of morphology and cell chemistry. On the chemical side the various combinations of pigments, wall polysaccharides and storage materials have been discussed at great length and most of the phylogenetic schemes for the algae have been based mainly upon this information. On the structural side the gross morphological variations between the classes and cytology at the light microscopical level was concisely summarized by Fritsch (1935) long before the electron microscope had been used to examine algae. The present work is an attempt to bring together much of the information which has been gathered by electron microscopists over the past 20 years or so. This is a task which is becoming more and more difficult for, whereas there were perhaps two papers in this field published in 1952, there were 20 (+) in 1962 and 80 (+) in 1972 (with some 1972 journals not yet received). Altogether, just over 750 papers have been referred to and many other, mainly taxonomic papers, have not been included. This fine structural data is surely as important as the biochemical data for any consideration of the classification of algae and for attempting to analyse their phylogenetic relationships. However, it must be admitted that in some areas of algal ultrastructure very much more work is needed before any meaningful conclusions can be made.

It is impossible to write about algal fine structure without paying tribute to the hard work and inspiration which has been provided by Professor Irene Manton F.R.S., since the very beginning of the subject. Her first paper in this field in 1950 was about the male gamete of *Fucus* and since then, together with various colleagues, she has produced over 65 informative and beautifully illustrated papers on algal ultrastructure.

Fine structure is essentially a pictorial subject, a fact that many editors of scientific journals do not seem to understand, much to the anguish of the authors. In this book most of the main points have been illustrated but, as far as possible, the pictures have been assembled from micrographs taken at Birkbeck College. It is inevitable that they show a slight but I hope not too obvious bias towards the dinoflagellates. Perhaps at this point mention should be made of the main preparation methods which we have used. Apart from the direct preparations, which were mainly shadowed with gold/palladium alloy, the material was normally fixed in buffered glutaraldehyde, postfixed in osmic acid and embedded in Araldite or Spurr resin. All micrographs were taken on a Zeiss EM9A electron microscope. For much of the preparation and many of the pictures I am indebted to R. M. Crawford, B. S. C. Leadbeater, G. B. Lawes and B. T. Bibby. For the considerable amount of photographic work involved I am very grateful to P. Randall and D. Rogers. The research work, of which many of these micrographs formed a part, was generously supported by the Science Research Council, the Central Research Fund of London University, by Birkbeck College and in particular by C. T. Ingold, Emeritus Professor of Botany.

Many of the illustrations used in this book have already been published and I am grateful to the editors and publishers of the following journals for allowing me to

use them again: *Archiv. für Mikrobiologie*, *Botanical Journal of the Linnean Society*, *Botanical Review*, *British Phycological Journal*, *Journal of Cell Science*, *Journal of Phycology*, *New Phytologist*, *Nova Hedwigia*, *Protistologica* and *Protoplasma*.

I am very grateful to T. Bråten, R. M. Crawford, B. S. C. Leadbeater, M. Neushul, E. Swift, J. A. West and P. A. Walne for very kindly providing micrographs to illustrate specific points. Thanks are due to the various authors (named in the legends) who have allowed me to reproduce their figures and to the publishers of the following journals, in which the figures originally appeared: *Advances in Botanical Research*, *Archiv. für Mikrobiologie*, *Journal of Cell Biology*, *Journal of Cell Science*, *Journal of Phycology*, *Journal of Ultrastructure Research*, *Nature*, *Phycologia*, *Planta*, *Plant Physiology*, *Protistologica* and *Protoplasma*.

I would like to thank my colleagues at Birkbeck and elsewhere who, by their discussion and description of their discoveries, have helped me to form the views expressed in this book. I sincerely apologize to any authors who feel that I have misrepresented their findings. Lastly, my grateful thanks are due to Mrs Jill Smith for patiently typing the manuscript.

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JOHN D. DODGE

March 1973

Contents

Introduction	ix
1. A General Account of the Structure of Algal Cells	I
I. Bacillariophyceae (Diatoms)	I
II. Chloromonadophyceae (Raphidophyceae)	3
III. Chlorophyceae (Green Algae)	3
A. Zygnemaphyceae	3
B. Oedogoniophyceae	3
C. Bryopsidophyceae	4
D. Chlorophyceae (<i>sensu</i> Round)	4
IV. Chrysophyceae (Golden Algae)	6
V. Cryptophyceae	6
VI. Dinophyceae (Dinoflagellates)	8
VII. Euglenophyceae	11
VIII. Eustigmatophyceae	13
IX. Haptophyceae	13
X. Phaeophyceae (Brown Algae)	14
XI. Prasinophyceae	16
XII. Rhodophyceae (Red Algae)	16
XIII. Xanthophyceae (Yellow-Green Algae)	19
2. The Cell Covering	21
I. Naked membrane	21
II. Modifications within the Plasma-Membrane	21
A. Cryptophyceae—Periplast	21
B. Euglenophyceae—Pellicle	23
C. The Dinophyceae—Theca	25
III. Scaly Covering Outside Cell Membrane	30
A. Scales of Organic Material	30
B. Calcite Scales	30
C. Silica Scales	33
D. Scale Formation	33
IV. The Diatom Frustule	34
V. The Cell Wall	38
A. Incomplete Walls (such as the Lorica)	38
B. Complete Cell Walls	41
C. Calcified Algal Walls	52
D. Plasmodesmata in Algal Cell Walls	53
E. Cell Wall Formation	53

3. Flagella and Associated Structures	57
I. External Features	57
A. Smooth Flagella	57
B. Flagella with Single Row of Hairs (Stichonematic)	60
C. Flagella with Two Rows of Hairs (Pantonematic)	60
D. Flagella Bearing Spines	62
E. Scaly Flagella	62
II. Internal Structure of Flagella	65
A. The Free Part	65
B. The Transition Zone	69
C. The Flagellar Base, Basal Body or Kinetoplast	72
III. Flagellar Roots	72
IV. The Origin of Flagellar Hairs	74
V. Pseudocilia	76
VI. The Haptonema	76
4. Chloroplasts (Plastids)	81
I. Chloroplast Structure	81
A. Structure of the Thylakoid	81
B. Arrangement of the Thylakoids	86
C. The Chloroplast Stroma or Matrix	90
D. The Chloroplast Envelope and Endoplasmic Reticulum Sheath	95
II. Unusual Chloroplast Structure in Mutants, etc.	97
III. Chloroplast Development	98
IV. Chloroplast Division	101
V. Chloroplasts as Symbionts	102
5. The Pyrenoid	105
I. Types of Pyrenoid	105
A. Simple Internal Pyrenoid	105
B. Compound Internal Pyrenoid	107
C. Stalked Pyrenoids	109
D. Pyrenoid with Nuclear or Cytoplasmic Invaginations	113
E. Pyrenoid Entirely Embedded in a Starch-containing Chloroplast	116
II. The Pyrenoid Matrix	118
III. The Development of Pyrenoids	120
IV. Pyrenoids and Taxonomy	121
6. The Eyespot	125
I. The Types of Eyespot	125
II. The Development and Replication of Eyespots	136
III. Eyespot Structure and Taxonomy	136
IV. The Function of the Eyespot	137
7. The Nucleus and Nuclear Division	139
I. The Interphase Nucleus	139
A. Nuclear Envelope	139
B. Nucleolus	140
C. Chromatin	143

II. Nuclear Division—Mitosis	146
A. Chlorophyceae	148
B. Phaeophyceae	150
C. Chloromonadophyceae	150
D. Haptophyceae	150
E. Chrysophyceae	151
F. Bacillariophyceae	151
G. Xanthophyceae	152
H. Rhodophyceae	152
I. Euglenophyceae	153
J. Dinophyceae	154
K. Cryptophyceae	154
III. Nuclear Division—Meiosis	157
8. Cell Division (Cytokinesis)	159
I. Unicellular Algae	159
A. Flagellates	159
B. Desmids (Chlorophyceae)	160
C. Coccoid Algae (Chlorophyceae)	160
II. Multicellular Algae	162
A. Filaments	162
B. Parenchymatous Algae	166
9. Ejectile Organelles	167
I. Trichocysts in the Dinophyceae	167
II. Nematocysts (Cnidocysts) of Dinoflagellates	170
III. Ejectosomes of Cryptomonads	170
IV. Discobolocysts in the Chrysophyceae	174
V. Other Ejectile Organelles	175
10. Miscellaneous Organelles and Inclusions	177
I. Mitochondria	177
II. Golgi or Dictyosomes	179
III. The Contractile Vacuole	182
IV. The Pusule	185
V. Microbodies (Peroxisomes)	186
VI. Food Storage Materials	189
A. Polysaccharide	189
B. Lipids	190
C. Protein	190
VII. Polyphosphate Inclusions and Phosphatases	192
VIII. Virus-like Inclusions	192
IX. Membranous Extrusions and Inclusions, Digestion Vesicles	194
11. Reproductive Structures	195
I. Gamete Formation and Structure	195
A. Phaeophyceae	195
B. Bacillariophyceae	196
C. Xanthophyceae	197
D. Chlorophyceae	197

II. Gamete Fusion and Zygote Development	198
III. Spore Formation and Structure	203
IV. Encystment	208
12. Symbiosis	209
13. Experimental Ultrastructure Studies	215
I. Effects of Chemicals	215
II. Effects of Environmental Conditions	217
A. Nutrition	217
B. Light	220
C. Osmotic Potential	221
III. Senescence	221
14. Postscript: Fine Structure and Phylogeny	223
Tentative Conclusions	226
REVIEW ARTICLES AND BOOKS	227
REFERENCES	228
AUTHOR INDEX	245
SUBJECT INDEX	252

INTRODUCTION

In the past twenty or so years the electron microscope has added a completely new dimension to our knowledge of the algae. To some extent this has complemented the traditional disciplines of taxonomy, morphology and ecology but, as the intricacies of algal ultrastructure have unfolded, 'fine-structure' has come to have a place of its own and has provided us with many vital keys to the understanding of the inter-relationships and phylogeny of the algae. Whereas the first two decades of algal fine structure work have been essentially devoted to the descriptive approach, the trend is now towards use of electron microscopy to try to understand the functions of cells and organelles under both normal and experimental conditions. Clearly this is a trend that will continue, especially as the number of genera whose normal ultrastructure has not yet been described rapidly diminishes.

History

It is interesting to note the correlation between the bursts of fresh information on algal fine structure and the development of new techniques. The first such burst commenced in 1945 when Brown published what appear to have been the first algal electron micrographs. He used the recently developed shadow-casting technique to examine the flagella of various algae. This technique was perhaps most successfully applied in the early 1950s by Manton and her colleagues who investigated the structure of flagella in numerous algae and lower plants. During this period there was some descriptive work on algal cell walls and particularly on diatom frustules, which required no special preparation other than thorough cleaning.

The next burst of information came in the late 1950s when, with the development of methacrylate embedding and fairly reliable ultramicrotomes, some details of the internal structure of algal cells began to be revealed. Unfortunately polymerization of the embedding medium often caused much distortion of cell structure and in retrospect the work done during this period was only of limited value. However, a great improvement took place in the early sixties, first with the development of epoxy resins for embedding which resulted in improved stability of the tissue, and secondly with the introduction of aldehyde fixation which really stabilized most of the cell components. Now, with automatic ultra-microtomes and diamond knives generally available, the great period for fine structure began. Initially, this was almost entirely confined to unicellular organisms which could be fixed and embedded most readily. The revealing of the internal fine-structure of algal cells had now become limited less by technique and more by the availability of material and the inclination and time of the investigators.

The development of freeze-etching or freeze-fracturing during the mid sixties provided a technique which made it possible for the surfaces of cells, walls, membranes and organelles to be examined. Thus, we have now an increasing number of papers in which attempts are made to correlate the structure of membranes, etc., with their particular function in the cell.

The latest major development, scanning electron microscopy, has as yet made little general impact on our knowledge of algal ultrastructure. Certainly, it has already become a vital tool for diatom taxonomists and has been used for the study of the surfaces of desmids and dinoflagellates. As specimen preparation techniques

are developed and as the resolution of the microscopes improves SEM will no doubt become of more general use.

Of the other fine structure techniques, negative staining, which is so valuable for virus work, has been little used on algae although it has proved of value in studies of flagellar hairs. Electron microscopical autoradiography and other cyto-analytical techniques have not yet been much used with algae, but no doubt will be employed more in the future.

Scope of the book

The present survey excludes the blue-green algae (Cyanophyta) for these prokaryotic organisms are quite distinct from the true algae and they are, in any case, the subject of a recent review (Lang, 1969) and a number of books in preparation. At the other extreme the Charophyceae (stone worts) have not been considered in detail although they are occasionally referred to. The Craspedophyceae (Choanoflagellates) have also not been discussed in this book for their complete lack of chloroplasts seems to suggest that their affinities are more with the Protozoa than the algae.

The endeavour has been to provide a hybrid between a review and a comprehensive descriptive work. In other words to provide enough description of organelles, etc., to make it possible for the student to visualize and compare their structure and at the same time to provide enough references so that the research worker can enter the literature to find out more precise details from the original sources. The references given are not fully comprehensive but are intended to highlight the more important facts. It is hoped that the present work will complement the few specialized reviews of fine structure already published* and will perhaps make some of these known to a wider audience.

(* Euglenophyceae—Leedale, 1967; Eyespots—Dodge, 1969a; Chloroplasts—Gibbs, 1970; Pyrenoids—Griffiths, 1970; Nuclear division—Pickett-Heaps, 1969; Leedale, 1970; Pyrrophyta (= Dinophyceae)—Dodge, 1971.)

Classification of the algae

Almost every new algal text book that is published presents a revised system for the classification of these organisms. This has made for a situation, which must be highly confusing to the student and which makes teaching extremely difficult. In a work such as this it is essential to have some 'labels' at a higher level than that of the genus yet at the same time it is probably better to use a neutral classification scheme. Thus the largest units employed here are classes, most of which go back to Fritsch (1935, 1945), or earlier, and which, apart from the classes more recently designated (Prasinophyceae, Haptophyceae, Eustigmatophyceae) are the only stable feature which has persisted through the numerous classification schemes of the past few years. Phyletic terms such as 'Chlorophyta' will not normally be used in this book. The system, as used here, makes no implied allusions to the relationships between the classes although this subject is discussed in the text where appropriate and is summarized in Chapter 14.

The 13 classes covered in this book are as follows:

Chlorophyceae	Haptophyceae
Prasinophyceae	Bacillariophyceae
Chloromonadophyceae	Phaeophyceae
Euglenophyceae	Dinophyceae
Eustigmatophyceae	Cryptophyceae
Xanthophyceae	Rhodophyceae
Chrysophyceae	

1. *A General Account of the Structure of Algal Cells*

The object of this chapter is to give a brief description of the main structural features of the various classes and to note the organelles present in typical cells. For the smaller classes reference is made to all known papers describing general cell structure but for the larger classes only representative papers are noted. Later chapters should be consulted for detailed descriptions of, and references to, the organelles mentioned. The classes are here arranged in alphabetical order.

I. BACILLARIOPHYCEAE (DIATOMS)

This is a very distinctive and natural group of organisms, for the possession of a silica wall or frustule distinguishes the members of this class from all other algae. The frustule has been the subject of a great deal of work, including a wide ranging survey using transmission electron microscopy (Helmcke and Krieger, 1953–1966) and several more recent studies using scanning microscopy (e.g. Ross and Simms, 1970, 1971, 1972).

In general, diatoms are unicellular organisms, although they may become joined together to form filaments or colonies. Each cell contains two or more chloroplasts; a single nucleus; several mitochondria and Golgi bodies; endoplasmic reticulum and ribosomes (Fig. 1.1). Most of the detailed studies of fine structure have been concerned with pennate diatoms (i.e. those which do not have radial symmetry) e.g. Drum (1963), Drum and Pankratz (1964), Stoermer and Pankratz (1964), Stoermer *et al.* (1964, 1965), Lauretis *et al.* (1968), and Taylor (1972). As yet very little is known about centric diatoms except for details of the nuclear divisions (Manton, Kowallik and von Stosch, 1969a,b, 1970a,b), wall structure and formation after cell division (Round, 1971a; Crawford, 1971, 1973) and the structure of spermatozoids. These motile cells possess a single hairy flagellum with an atypical internal structure (Manton and von Stosch, 1966; Heath and Darley, 1972). Attempts have been made to study the structures involved in the gliding movement of pennate diatoms (Drum and Hopkins, 1966; Drum and Pankratz, 1965b) which is thought to be brought about by an expanding mucilaginous propellant. Colchicine-induced polyploids of *Navicula* have been studied by Coombs *et al.* (1968b).