Typical sheltered coast plants of *Hormosira banksii*.

Free-living *Hormosira banksii* plants in a mangrove swamp.

(*Photos, P. L. Bergquist*)

THE ALGAE

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PREFACE

THIS book has been prepared in response to many requests that I have received from colleagues. Although the present volume follows the general lay-out of my first book *An Introduction to the Study of Algae*, there has been so much rearrangement, the complete rewriting of many chapters and the addition of new ones, that it cannot be considered a second edition of the first book. I am particularly grateful to the Syndics of the Cambridge University Press for releasing the original copyright so that it has been possible to use some portions of the first book. In recent years considerable advances have been made in the study of the algae and this has affected, not only our knowledge of their life histories, but also our views on phylogeny. These new results have necessitated much rearrangement of material. There has also been extensive new work on the ecology of the algae, so that the chapters on marine algal ecology and ecological factors are more or less completely new. The same is true also of algal physiology. In order that the survey should be more complete there is a chapter briefly describing the historical aspect of the subject, and also a chapter on the economic uses of algae.

The purpose of the book remains the same as my first volume, namely to provide a general survey of all aspects of the algae such as may be required by a University undergraduate, with selected portions (marked by an asterisk) that can be used by first year students or which are suitable for use in schools at the sixth form level. The type method of instruction has again been employed because continued experience has not changed my belief in it. I still feel, however, that no study of the algae is complete without reference to the other aspects which have been included. I am aware that not everyone will agree with what has been included and material that has been excluded, nor with all the views expressed, but where there are divergencies of opinion, I have tried to see that the other view is also presented or made known. This is perhaps particularly true in the chapter on Evolution.

There are a number of excellent works available to advanced students and research workers, and the present volume is not intended to compete with them in any way. Apart from those works to which I expressed my indebtedness in the preface to *An Introduction to the Study of Algae*, there are some new books that have appeared since, and which have provided valuable reference material. I include here the second volume of Fritsch's *Structure and Reproduction of the Algae*, the *Manual of Phycology*, edited by the late Gilbert Smith, and the recent extensive work on the Rhodophyceae by the late Prof. Kylin. The sources of the new illustrations are acknowledged in the legends.

At the end of each chapter certain references are provided which can be consulted for further specific information. No attempt has been made to provide anything approaching a complete reference list and the choice of the various references is entirely my own. I am aware that this choice will not necessarily please everyone, but I hope it will prove useful.

I am grateful to my colleagues, Dr. J. A. Rattenbury for critical reading of the manuscript and to Dr. J. M. A. Brown for his reading and criticism of the two chapters on ecological factors and algal physiology. Dr. A. B. Cribb of the University of Brisbane has also read the proofs and made valuable suggestions for which I am most appreciative. My thanks go to Mrs. J. Rutherford for assistance in proof-reading.

V. J. CHAPMAN

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CONTENTS

CHAPTER PAGE

1. CLASSIFICATION 1

2. HISTORY 11

3. EUPHYCOPHYTA

Chlorophyceae:

General 16
Volvocales 20
Chlorococcales 39
Ulotrichales 49

4. EUPHYCOPHYTA

Chlorophyceae:

Oedogoniales 65
Chaetophorales 71
Siphonocladales 81
Dasycladales 91

5. EUPHYCOPHYTA

Chlorophyceae:

Siphonales 96
Conjugales 105
Charophyceae 115

6. EUPHYCOPHYTA

Phaeophyceae:

General 122
Ectocarpales 128
Sphacelariales 135
Tilopteridales 140
Cutleriales 142
Dictyotales 144
Chordariales 149
Sporochnales 160

7. EUPHYCOPHYTA

Phaeophyceae:

Dictyosiphonales 162
Desmarestiales 168

CHAPTER PAGE
Laminariales 170
Fucales 191

8. EUPHYCOPHYTA
Rhodophyceae:
General 216
Protoflorideae (Bangiales) 223
Euflorideae:
Nemalionales 227
Gelidiales 234
Cryptonemiales 235
Gigartinales 242
Rhodymeniales 246
Ceramiales 248

9. CHRYSOPHYCOPHYTA
Xanthophyceae 259
Bacillariophyceae 269
Chrysophyceae 273

PYRROPHYCOPHYTA
Cryptophyceae 275
Dinophyceae 275

10. MYXOPHYCOPHYTA 278

11. REPRODUCTION; EVOLUTION 294

12. ECOLOGY OF ROCKY COASTS 327

13. ECOLOGY OF SALT MARSHES 346

14. FRESH WATER ECOLOGY; SOIL ALGAE 358

15. ECOLOGICAL FACTORS 383

16. PHYSIOLOGY; SYMBIOSIS 412

17. GEOGRAPHICAL DISTRIBUTION; LIFE FORM 429

18. ALGAL UTILIZATION 444

INDEX 455

Chapter I

CLASSIFICATION

The general student is probably familiar with the seaweeds of the sea-shore and may even have observed green skeins in stagnant fresh-water ponds and pools. These plants, which are among the simplest in the plant kingdom, belong to the group known as algae.

However, there are many more representatives of this group than the seaweeds, and it is the purpose of this book to give some account of them. The first step is to consider how they are classified and the criteria upon which the classification is based.

In the older classifications the algae proper were divided simply into four principal groups, Chlorophyceae or green algae, Myxophyceae (Cyanophyceae) or blue-green algae, Phaeophyceae or brown algae and Rhodophyceae or red algae. However, now that more is known about the life history of many simpler organisms, which used not to be regarded as true algae, it has been realized that the old classification must be extended and the number of groups increased. This is because it has become evident that simple unicellular organisms, formerly often placed with flagellates, must properly be regarded as algae, even though of a very primitive kind. The reason for this change of view was that botanists began to realize, first in the case of the yellow-green algae (Xanthophyceae) and later with other primitive groups, that there were analogues with the Chlorophyceae (cf. p. 324), and also that there were a few additional 'algal' types even as defined according to the classical concept. In the present work the Euglenoids (*Euglena*) are regarded as true flagellates and not as algae even in the modern more extended usage of that word.

The principal criteria upon which the primary classification of the algae are based rest upon differences in pigmentation and other biochemical characteristics. Whilst there are one or two exceptions to the general basis of differentiation, these are so few (and even then somewhat uncertain) that they can be neglected. A study of Table 1, which summarizes the differences between the respective algal classes, indicates that there are also resemblances between

TABLE I

[1] *Biochemical and pigmentation differences within the different classes of algae (after Strain)*

	Chlorophyceae	*Siphonales*	*Phaeophyceae*	*Bacillariophyceae*	*Chrysophyceae*	*Xanthophyceae*	*Cryptophyceae*	*Dinophyceae*	*Rhodophyceae*	*Myxophyceae*
Chlorophylls										
Chlorophyll *a*	●	●	●	●	●	●	●	●	●	●
Chlorophyll *b*	◑	◑	—	—	—	◑	—	—	—	—
Chlorophyll *c*	—	—	○	○	·	—		○	—	—
Chlorophyll *d*	—	—	—	—	·	—		—	○	—
Chlorophyll *e*	—	—	—	—	·	○		—	—	—
Carotenes										
α Carotene	○	●	—		·	·		—	○	·
β Carotene	●	○	●	●	●	●		●	●	●
ϵ Carotene	—	○	—	○	·	·		·	·	·
Flavacin	—	—	—	—	·	·		·	·	○
Xanthophylls										
Lutein	●	○	—	—	○				◑	?
Zeaxanthin	○	·	—	—	·	—		—	·	?
Violaxanthin	○	○	○	—	·			—	·	·
Flavoxanthin	?	?	○	—	·	·		·	·	·
Neoxanthin	○	◑	○	—	·	—		—	·	·
Siphonein	—	○	—	—	·	—		—	·	·
Siphonoxanthin	(—)[2]	○	—	—	·	—		—	·	·
Fucoxanthin	(—)	—	◑	◑	○	—		—	(—)[3]	·
Neofucoxanthin	—	—	○	○	·	—		—	·	·
Diatoxanthin	—	—	?	○	·	—		—	·	·
Diadinoxanthin	—	—	?	○	·	—		○	·	·
Dinoxanthin	—	—	?	—	·	—		○	·	·
Neodinoxanthin	—	—	—	—	·	—		○	·	·
Peredinin	—	—	—	—	·	—		◑	·	·
Myxoxanthin	—	—	—	—	·	—		—	·	◑
Myxoxanthophyll	—	—	—	—	·	—		—	·	◑
Phycobilins										
r-Phycoerythrin	—	—	—	—	?	—		—	●	—
c-Phycoerythrin	—	—	—	—	?	—		—	—	○
r-Phycocyanin	—	—	—	—	?	—		—	○	—
c-Phycocyanin	—	—	—	—	?	—		—	—	●

---

[1] This table is only for advanced students.

[2] This record in *Rhizoclonium implexum* has not been confirmed.

[3] This record in *Polysiphonia* has not been confirmed.

	Chlorophyceae	*Siphonales*	*Phaeophyceae*	*Bacillariophyceae*	*Chrysophyceae*	*Xanthophyceae*	*Cryptophyceae*	*Dinophyceae*	*Rhodophyceae*	*Myxophyceae*
Reserve products										
Starch - - -	●	●	—	—	—	—	●	●	—	—
Fat or oils - -	○	○	—	●	○	●	—	○	—	—
Leucosin - -	—	—	—	○	●	—	—	—	—	—
Mannitol - -	—	—	●	—	—	—	—	—	—	—
Laminarin - -	—	—	○	—	—	—	—	—	—	—
Floridoside - -	—	—	—	—	—	—	—	—	●	—
Mannoglycerate -	—	—	—	—	—	—	—	—	○	—
Floridean starch -	—	—	—	—	—	—	—	—	●	—
Myxophycean starch	—	—	—	—	—	—	—	—	—	●
Cyanophycin -	—	—	—	—	—	—	—	—	—	○
Cell wall										
Cellulose - -	●	●	○	—	—	○	●?	●	●	◑
Pectin - - -	○	○	—	●	●	●	—	○	—	●
Silica - - -	—	—	—	○	○	○	—	—	—	—
Chitin (?) - -	○	○	—		—	○	—	—	—	—
Algin - - -	—	—	●	—	—	—	—	—	—	—
Fucoidin - -	—	—	○	—	—	—	—	—	—	—
Polygalactose Sulphate esters -	—	—	—	—	—	—	—	—	◑	—
Sterols										
Sitosterol - -	●	●	—	—	—	●	—	—	○	—
Fucosterol - -	○	○	●	●	●	—	—	—	●	—
Chondrillosterol -	○	○	—	—	—	—	—	—	—	—
Ergosterol - -	○	○	—	—	—	—	—	—	—	—
Unidentified sterols - -	—	—	—	○	○	—	—	—	○	—

● =Principal component.
◑ =Present in some quantity.
○ =Present but in small quantity.
(—) =Present in one or two species only: these may require confirmation.
· =Incompletely examined, but absent in those examined.
? =Uncertain.
— =Absent.

some groups, e.g. Chrysophyceae, Bacillariophyceae and Xanthophyceae, and between these as a whole and the Phaeophyceae; also between the Dinophyceae and Cryptophyceae, and the Rhodophyceae and Myxophyceae. These relationships are, however, discussed more fully later (see pp. 315, 321).

It should be noted that chlorophyll *a*, one of the components of the green pigment, is the most abundant chlorophyll in all types of algae, that β carotene is equally widely distributed, that starch is not a widely distributed food reserve outside the Chlorophyceae and that cellulose is not the universal wall constituent. There are a large number of xanthophylls and each algal class possesses its own characteristic members. The Siphonales, an order of the Chlorophyceae, is treated separately because of the carotinoid or yellow pigment differences. The phycobilins of the Rhodophyceae and Myxophyceae are not absolutely identical and hence are differentiated by the prefix r- and c- respectively. In several classes of algae, e.g. diatoms, Cryptophyceae, Chlorophyceae, colourless forms are known. Such organisms have to lead a saprophytic existence.

Using a combination of the pigment and biochemical differences, together with morphological differences, the algae as a group can be classified as follows:

- EUPHYCOPHYTA:
    - Charophyceae
    - Chlorophyceae
    - Phaeophyceae
    - Rhodophyceae
- MYXOPHYCOPHYTA:
    - Myxophyceae
- CHRYSOPHYCOPHYTA:
    - Chrysophyceae
    - Xanthophyceae
    - Bacillariophyceae
- PYRROPHYCOPHYTA:
    - Cryptophyceae
    - Dinophyceae

Some workers consider that the Chlorophyceae, Phaeophyceae and Rhodophyceae should have independent rank (e.g. Chlorophycophyta, Phaeophycophyta, Rhodophycophyta), and a few would also treat the Charophyceae in the same way. The present writer considers that phylogenetically these four classes are distantly related (see p. 309) and therefore groups them together. Ultimately the classification adopted must depend upon the view taken of the inter-relationships of these groups. A class of wholly fossil organisms, the Nematophyceae, is also included among the algae, but this is somewhat tentative as we have no means of knowing whether the plants, which only existed in the very earliest times, really were algae.

A brief summary of the principal characteristics of the different classes follows.

EUPHYCOPHYTA

(1) *Chlorophyceae*

This group used to comprise four great subclasses, the Isokontae (equal cilia), Stephanokontae (ringed cilia), Akontae (no cilia) and Heterokontae (unlike cilia). These subdivisions, as their names imply, were based upon the organs of locomotion of the motile reproductive bodies. The last subdivision has since been renamed the Xanthophyceae and, because of its relationships with the Bacillariophyceae and Chrysophyceae, has been transferred to the Chrysophycophyta (see below). The structure of the Chlorophyceae covers a great range from simple unicells to multicellular plants that are quite complex, though not as complex as those of the Phaeophyceae and Rhodophyceae. In the Chlorophyceae the chloroplasts vary considerably in shape and size whilst the final product of photosynthesis is mostly starch together with fat. Structures known as pyrenoids are often present and a starch sheath can generally be demonstrated around them. The motile cells of most members of the class are very similar and commonly possess either two or four equal flagellae, but in the Oedogoniales (the former Stephanokontae) there is a ring of cilia whilst in the Conjugales (the former Akontae) organs of locomotion are absent. Sexual reproduction is of common occurrence and ranges from isogamy to anisogamy and oogamy. Asexual reproduction normally takes place by means of motile zoospores, but a variety of non-motile spores (p. 19) may also be produced. The colour of the cells is usually grass green because the pigments are the same as those present in the higher plants and, furthermore, they are present in much the same proportions.

The Characeae comprise one predominantly fresh-water order, the Charales, which differ from other green algae (Chlorophyceae) because of their remarkable morphological and reproductive features. They are consistently uniform in structure with characteristic nodes and internodes and whorls of branches arising at the nodes. There is no asexual reproduction and the sexual reproductive organs present an elaborate oogamy. There is some evidence for believing that the plants may have a common ancestry with the Chaetophorales (see p. 115).

(2) *Phaeophyceae*

This group comprises the common brown algae of the seashore, and it is worth noting that the majority are wholly marine, predominantly of cold waters. There are a few, rare fresh-water species. The brown colour is due to the fucoxanthin pigment which masks chlorophyll *a* (see Table 1). The principal product of photosynthesis is a sugar alcohol, known as mannitol, together with the polysaccharide laminarin, whilst the cell walls not only contain cellulose but also specific materials such as algin and fucoidin (see p. 452). In some of the larger and more advanced brown algae these compounds are present in sufficient quantity to be of commercial importance (see p. 446). The class is further characterized by the fact that the sugar residues tend to have a 1 : 3 linkage instead of the more normal 1 : 4 linkage between the carbon atoms. The simplest forms are filamentous, and there are all stages of development and increasing differentiation up to the large seaweeds of the Pacific and Arctic shores with their great size and complex internal and external differentiation. There is also a number of greatly reduced parasitic and epiphytic forms. The pyriform, motile reproductive cells, which possess two flagella, one directed forwards and the other backwards, are commonly produced in special organs or sporangia that are either uni- or plurilocular. Some members possess non-motile, asexual reproductive spores (monospores and tetraspores). Sexual reproduction ranges from isogamy to oogamy, but in the latter case the ovum is liberated before fertilization. The life cycles are extremely diverse, and although alternation of generations does occur, it is an irregular rather than a regular process.

(3) *Rhodophyceae*

The members of this class form the red seaweeds, and although most of them are marine, nevertheless a few occur in fresh water. Their colour, red or bluish, is produced by the phycobilin pigments r-phycoerythrin and r-phycocyanin, whilst the products of photosynthesis are floridean starch, floridoside and a material known as mannoglycerate. This class, like the preceding one, differs from the other algal classes in that the sugar residues have a tendency to form 1:3 linkages. There is also a tendency to form polysaccharide sulphate esters (cf. p. 448). Reproductive stages with locomotor appendages are not known, even in the case of the male body or spermatium. Whilst most simple members are filamentous, all stages up to a complex thallus can be found, although there is not quite the same degree of complexity as in the Phaeophyceae. Despite variations in form there are only two basic types of thallus construction. Protoplasmic connections exist between the cells of all forms except most of those that comprise a small group, the Proto-florideae (cf. p. 223). Sexual reproduction is oogamous, the ovum being retained within the parent plant, and although the subsequent development of the zygote varies to a certain extent, it usually gives rise to filaments that bear special reproductive bodies known as carpospores; these latter are normally responsible for the production of a tetraspore-bearing diploid individual. There is a great uniformity in reproduction throughout the class, and most members also exhibit a regular alternation of generations.

MYXOPHYCOPHYTA

(4) *Myxophyceae*

The plants in this group show very little evidence of differentiation and the cells contain only a simple form of nuclear material. There is no true chromatophore, the pigments being distributed throughout the entire peripheral portion of the cytoplasm, nor are there any organs of locomotion, even among the reproductive bodies. The products of photosynthesis are a specialized polysaccharide, myxophycean starch, and a proteinaceous material, cyanophycin, present in granular form. The cell walls contain both pectin and cellulose, the former sometimes forming a gelatinous sheath. The colour of the cells is commonly blue-green, sometimes olive green, the colour being due to the varying proportions of chlorophyll *a*, c-phycoerythrin and c-phycocyanin. One interesting feature is the complete lack, so far as is known, of sterols in this class. There is no known sexual reproduction, propagation taking place by simple division, by non-motile gonidia, by spores or else by vegetative fragmentation. Members of the group are widely distributed in marine and fresh waters and also occur terrestrially. Some have the capacity to fix nitrogen from the atmosphere and others have the capacity to live in quite hot water.

CHRYSOPHYCOPHYTA

(5) *Chrysophyceae*

These form a primitive group, mostly of unicellular organisms, in which the brown or orange colour of the chloroplasts is determined by excess of the carotinoid pigments. Most of the forms have no cellulose cell wall and hence are 'flagellates' in the old sense of that term, but there are some members which do possess a cellulose wall and hence are 'algal' in the old sense of that term. Leucosin (a proteinaceous substance) and oils are the usual forms of food storage, whilst another marked feature is the silicified cysts or statospores, which generally have a small aperture that is closed by a special plug. The motile cells possess one, two or, more rarely, three equal flagella attached at the front end, but in one subsection the two flagella are unequal in length. The most advanced habit known is that of a branched algal filament, e.g. *Phaeothamnion* (cf. p. 273), whilst the palmelloid types attain to a higher state of differentiation, e.g. *Hydrurus* (cf. p. 273), than is commonly encountered in either the majority of the palmelloid Chlorophyceae or the Xanthophyceae. The occurrence of sexual reproduction is uncertain and such records as there are point to simple isogamy.

(6) *Xanthophyceae*

The plants in this group are usually of a simple nature, but their lines of morphological development frequently show an interesting parallel or homoplasy with those observed in the Chlorophyceae (cf. p. 325). The chloroplast is yellow-green in colour because of an excess of β-carotene, and starch is replaced by oil or leucosin as the normal food storage material. The cell wall is frequently composed of two equal or unequal halves overlapping one another. The motile cells possess two unequal flagella arising from the anterior end. Sometimes non-motile aplanospores are produced instead of zoospores. Sexual reproduction is rare and when present is isogamous, though in one genus (*Vaucheria*) there is a well-developed oogamy. This group is commonly regarded as having distinct affinities with the preceding group.

(7) *Bacillariophyceae* (*Diatoms*)

One of the characteristic features of these plants is their cell wall which is composed partly of silica and partly of pectin. The wall is always in two halves and frequently ornamented with delicate markings, which are so fine that microscope manufacturers make use of them in order to determine the resolving power of the lenses. Each cell contains one to many, variously shaped chromatophores, which are yellow or golden brown, containing accessory xanthophylls in addition to the usual chlorophyll *a*, and β-carotene. They are divided into two major groups, the representatives of one group being radially symmetrical, those of the other being bilaterally symmetrical. The presence of flagellate stages is highly probable in the former whilst there is a special type of sexual fusion in the latter group (cf. p. 272). The relationship of this group to the two preceding groups is not as distinct as it is between the Chrysophyceae and Xanthophyceae.

PYRROPHYCOPHYTA

(8) *Cryptophyceae*

Each cell commonly contains two large parietal chromatophores of diverse colour, though frequently of a brown shade, whilst the product of photosynthesis is starch. The motile cells have two unequal cilia and often possess a complex vacuolar system. Nearly all the members have a ‘flagellate’ organization and there are no true filamentous algal forms. One type (*Tetragonidium*) (cf. p. 275) has been described as having a tendency towards the coccoid (non-motile unicell with a cell wall) habit, but in general the class must be regarded as the least ‘algal’ like of all. Isogamy has been recorded for one species.

(9) *Dinophyceae*

Most of the members of this class are motile unicells, but there has been an evolutionary tendency towards a sedentary existence and the development of short algal filaments, e.g. *Dinothrix*, *Dinoclonium* (cf. p. 277). Many are surrounded by a cellulose wall bearing elaborate sculptured plates. Inside the cells there are dark yellow or brown discoid chromatophores which contain a number of xanthophylls not so far found in other algal classes. The products of photosynthesis are starch and fat. The motile cells normally possess two furrows, one transverse and one longitudinal, although these may be absent in some of the more primitive members. A transverse flagellum lies in the former, and the latter is the starting point for the second flagellum which points backwards. Sexual reproduction, if it occurs, is isogamous, but it has not been clearly established in the few cases reported. Characteristic resting cysts are also produced by many of the forms.

NEMATOPHYTALES

(10) *Nematophyceae*

This is a fossil group of which one genus has been known for a long time (*Nematophyton*), whilst the other (*Nematothallus*) has only been described more recently. There is still considerable doubt as to their true affinities, but it would seem that a place can best be found for them as a very highly developed type of alga. Their internal morphology suggests an alliance with more advanced members of either the Chlorophyceae or Phaeophyceae. The only reproduction so far recorded is that of spores which were developed in tetrads.

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Chapter II

HISTORY

The algae as such have a history that is as old as that of other plants. The first references to algae are to be found in early Chinese literature but there are also references in Roman and Greek literature. The Greek word for alga was *Phykos* whilst in Roman times they were called *Fucus* and were used by matrons for cosmetic purposes. The Roman writer Virgil apparently did not have much use for them as he writes of 'nihil vilior alga'. The Chinese regarded them aesthetically and this is signified in their name of *Tsao*. In the eighth century there are references to several kinds of Tsao. Algae have been known for a long time in Hawaii where they are used as a food and are called *Limu*.

In the early centuries writings about algae were restricted either to their use or else to their taxonomy. As with other plants no real progress was made in our scientific knowledge of the algae until the invention of the microscope. As early as the twelfth century, however, algae were being used for manurial purposes on the north coast of France. From here it seems that the practice spread to Great Britain, because in the sixteenth century there is reference to their use for the same purpose. This use of the algae for manure may have had something to do with the idea that they were 'bred of putrefaction' as described in 1583 by Cesalpino.

Up to about 1800 all algae were usually placed in one of four great genera, *Fucus*, *Ulva*, *Conferva* and *Corallina*. *Chara* (p. 121) was known but commonly grouped with the horsetails (*Equisetum*). Gerard's Herbal (1633) lists *Lichen*, *Quercus*, *Fucus*, *Chara*, *Conferva*, and sixty years later Ray gave an account of the characters of *Corallina*, *Fucus*, *Muscus* and *Lichen*. In the same century (seventeenth) the use of brown seaweeds for fertilizer in France had reached such a pitch that special decrees were passed in connexion with their collection. At the other end of the world the art of making agar permeated from China to Japan, and thus the foundation was laid for what was later to become a great industry.

During the eighteenth century the more observant workers began to query the unwieldy assemblages into which algae were then grouped. Dillenius in 1741 subdivided the group *Conferva* and Stackhouse in 1796 expressed his doubts about the assemblage of forms which Linnaeus had placed in the genus *Fucus*. Until the development of the microscope in the middle of the seventeenth century, algae were regarded as lacking sexuality. Even so, it was more than fifty years after the introduction of the microscope before R. Reaumour described the sex organs of *Fucus*, and another century elapsed before Turner, the author of the four great volumes on the Fuci, described fertilization in *Fucus*.

Towards the end of the eighteenth century, the burning of seaweed for the extraction of soda was reaching considerable proportions in France and was extending to Scotland, though here it did not reach its heyday until some way into the nineteenth century.

The beginning of the nineteenth century witnessed the appearance of Dillwyn's classical work on the *Confervae*. He lacked the courage to segregate the various entities even though his writings suggest he felt there was a need for division. It was also at this time that Vaucher published his *Histoire Confervae d'eau douce*, which represented a milestone, in that life history studies were first used as a basis for taxonomy. In this work confirmation was given of the reproductive process in *Spirogyra*.

The early years of the nineteenth century were distinguished by many great algologists. Not only were there Dillwyn and Vaucher, but also Roth, who named and described the genera *Hydrodictyon* (p. 44), *Batrachospermum* (p. 228) and *Rivularia* (p. 290). There were numerous workers in the marine algae, and actually the knowledge of these increased more rapidly than that of the fresh water algae. Between 1805 and 1816 Lamouroux described many new genera, including *Laminaria* (p. 172) and many of the tropical Chlorophyceae. In Great Britain and on the Continent marine algae were studied and described by Lyngbye, Bory and Greville, the last named first describing the well-known genera *Polysiphonia* (p. 249) and *Rhodymenia* (p. 246). In Sweden, C. Agardh established the importance of the cystocarp in Rhodophycean taxonomy and erected the divisions Diatomaceae, Nostochineae, Confervoideae, Ulvaceae, Florideae and Fucoideae. The Nostochineae included many Myxophyceae and the Confervoideae comprised the filamentous green algae. He was followed by J. Agardh, his son, who described new species and also studied reproduction in *Conferva*, *Bryopsis*, *Fucus* and *Griffithsia*.

In 1854–5 the great French algologist Thuret produced his wonderful monograph on fertilization in *Fucus*. He also puzzled over the problem of *Cutleria*, a plant in which apparently there were only sexual organs of reproduction. Although he realized that the life history of this plant offered a problem it did not fall to his lot to find the solution. About the middle of the nineteenth century W. H. Harvey in England produced a series of great marine algal floras: *Phycologia Britannica*, *Phycologia Australica* and the *Nereis Boreali Americana*; he also described algae from many other parts of the world, including New Zealand and Antarctica. In these classical works on marine algae the plants were divided into Chlorospermae, Rhodospermae and Melanospermae. During the same period Kützing (Kuetzing) in Germany was describing more new genera than anyone either before or after. These were published in a number of works: *Systema Algarum*, *Phycologia Generalis* and the *Tabulae Phycologicae*. At the same time Braun was studying reproduction in algae and he has since been remembered for his contributions to the sexual reproduction of the Charales. However, work on the algae was still largely restricted to taxonomy, very little having been done on life cycles and nothing on their ecology or physiology.

The discovery of salt deposits in the nineteenth century caused a major recession in the kelp trade in France and Scotland, but with the discovery of iodine, coupled with the fact that the marine algae were rich in it, the kelp trade received a new lease of life towards the end of the century. This was not long-lived because of the discovery of iodides from which iodine could be extracted more readily. By the turn of the century, therefore, the kelp trade was once more in the doldrums.

Towards the end of the nineteenth century a new group of workers came to the fore, Areschoug (1866–84) described new genera and species, but he also investigated zoospore and gamete formation in *Urospora* (p. 83) and *Cladophora* (p. 84) and carried out morphological studies in *Laminaria* (p. 172) and *Macrocystis* (p. 186). This period can best be regarded as one devoted to rearrangement of the existing algal classifications. The information that was accumulating, both about morphology and reproduction, forced workers to realize that the old classifications were thoroughly unsatisfactory. Between 1875 and 1900 Sirodot reorganized the Batrachospermaceae, Gomont the Myxophyceae, Phillips (1895–8) the Rhodymeniales and Schmitz laid the foundations for the modern arrangement of the Rhodophyceae. Kjellman added materially to our knowledge of the algae of cold waters in his studies of Arctic algae and algae of the Murman Sea. During these years too, De Toni started publishing his monumental *Sylloge Algarum* which was a conspectus of all known and described algal species.

Important life histories were worked out at the end of the nineteenth century. Williams described the complete life history of *Dictyota* (p. 145) in 1897–8 and in 1899 Sauvageau established the nature of the life cycle in *Cutleria* (p. 142) and *Aglaozonia*. Modern floristic studies also commenced about this time with the publication by Börgesen of his *Marine Algae of the Faeroes*. An indication of interest in algal physiology was foreshadowed by Berthold's study in 1882 of phototropism in *Bryopsis* and preliminary work on algal respiration by Bonnier and Mangin in 1894.

Taxonomic rearrangement was, however, still the order of the day. Wille in 1897 established the Protococcoideae, Confervoideae and Siphoneae, whilst a few years earlier Borzi had segregated off from the Chlorophyceae the yellow-green algae. In 1899 Luther established the Heterokontae and the nature of the cilia was then used by Blackman and Tansley in their classification of 1902. In 1900 Blackman postulated a flagellate ancestry for the algae and suggested that in the green algae three distinct tendencies, the Volvocine, Tetrasporine and Chlorococcine, could be recognized. In 1905 Oltmann's work on morphology, together with his contributions to life form, appeared.

The period 1910–15 saw the start of hitherto neglected aspects of phycology. In 1910 Pia commenced publishing his studies of fossil algae in Europe and he was followed by Walcott in the United States in 1914. It was in these years too that Pascher commenced his classical studies on the Protista and Flagellata, and from this work emerged our present modern concepts of the algae. Marine algal ecology received a tremendous stimulus by the work of Cotton in 1912 on the marine algae of Clare Island and the works of Setchell on geographical distribution in relation to temperature. The study and appreciation of the importance of soil algae came to the fore with the works of Fritsch and Salisbury and Brenchley (see p. 376). Fresh-water algal ecology also received a great impetus from the work of Transeau in the U.S.A. and first West and then Fritsch in England. Algal plant physiology and biochemistry made considerable advances with the work of Kylin, Kniep, Pantanelli and Harder, whilst important algal floras were being published by Jonsson, Börgesen, Collins and Skottsberg. The year 1915 also saw the establishment of the Laminarian life cycle.

The advent of the First World War naturally stopped further advances and subsequent major progress mainly dates from about 1930. Since then our knowledge of the algal cell, the cell wall and cell sap, nuclear division and the structure of flagella has greatly increased, especially with the introduction of new techniques from other disciplines, such as X-ray photography, the electron microscope and improved optical microscopes. Modern ideas on the classification of the Phaeophyceae and Rhodophyceae are based on the works of Kylin, Papenfuss, Feldmann and Svedelius and our modern knowledge of algal plastids and sexuality dates from around 1930. Since then, too, Pringsheim has demonstrated the importance of pure algal cultures as a means of establishing the taxonomic status of the smaller organisms.

Much, however, still remains to be discovered; how much is indicated to some extent in other parts of this book.

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Chapter III

EUPHYCOPHYTA

CHLOROPHYCEAE

VOLVOCALES, CHLOROCOCCALES, ULOTRICHALES

* Introduction

Cell structure within the Chlorophyceae is fairly characteristic, the protoplast commonly surrounding a large central vacuole, whilst in some of the simpler unicellular forms there may also be two or more small, contractile vacuoles, the function of which is the removal of surplus water and waste matter. The pigments, which are essentially identical with those of the higher plants, are contained in plastids: these vary from one to many per cell and in outline may be discoid, star-shaped, spiral, plate-like or reticulate. In certain primitive members plastids are lacking. There is some evidence to show that these plastids are capable of movement in response to light stimuli. The proportions of the pigments may change at the time of gamete formation, i.e. in *Ulva lobata* fertile female thalli are olive green and fertile male thalli brownish. Cells of fertile thalli contain much more carotene than those of vegetative thalli and a large proportion is the γ isomer.[1] Other colouring matter may also be present, e.g. euglenarhodone in *Sphaerella* and phycoporphyrin in some of the Zygnemales, whilst fucoxanthin (cf. p. 2) has been reported in *Zygnema pectinatum.*

The cells are commonly surrounded by a two-layered wall, the inner, which is often lamellate, being of cellulose (callose in certain Siphonales), and the outer of pectin, but in some forms the outer surface of this pectin sheath is dissolved as fast as it is being formed on the inner side. Some of the very primitive forms lack a cell wall but in such cases the exterior portion of the protoplasm still remains rigid. In a few species the outer layer of pectose becomes impregnated with an insoluble substance whilst in others the pectin layer gradually increases in thickness, and in at least three orders

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[1] Only a trace of this occurs normally.

(Siphonales, Dasycladales, Siphonocladales) lime may be deposited on the walls. In *Oedogonium* and *Cladophora* there is said to be a layer of chitin on the very outside. A study of the submicroscopic structure of filamentous species has shown (Nicolai and Preston, 1952) that there are at least three groups:

Group I:	The principal substance in the wall is crystalline natural cellulose. The wall structure in these algae resembles that of the higher plants.
Group II:	The principal wall material is similar to mercerized cellulose.[1]
Group III:	Neither of the above forms of cellulose. Later (see p. 308) the significance of these groups in relation to classification will need to be discussed.

The chloroplasts, irrespective of shape or number, normally contain rounded bodies, or pyrenoids, which are composed of a viscous mass of protein (the crystalloid) surrounded by a sheath of starch. The number of pyrenoids in each cell is commonly a constant specific character and can be used for taxonomic purposes. Very few families of Chlorophyceae lack this structure, those that do being the more highly evolved. In *Derbesia* the pyrenoids disappear when the alga is grown in diffused light, and in several genera they may disappear during zoospore formation. In such cases they must arise again *de novo*, but more commonly they are perpetuated by simple division at the time of mitosis. In those algae with pyrenoids the production of starch grains is associated with their presence.

Each cell usually contains one nucleus, but in certain orders a multinucleate condition is to be found, and in the Siphonales cell walls are only laid down at reproduction so that the vegetative plant is multinucleate. Each nucleus possesses a deeply staining body, the *nucleolus*, together with chromosomes which are usually small, short and few in number. At cell division, in those cases where there is but one plastid, the chloroplast divides into two daughter plastids. In many species there is a distinct diurnal periodicity in the time at which nuclear and cell division takes place. The flagella of the motile bodies are composed of an axial cytoplasmic filament or *axoneme* surrounded, except at the very apex, by a sheath which probably has the power of contraction. In *Chlamydomonas* the electron microscope has revealed that the axoneme

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[1] When cellulose is treated with strong alkali, changes take place, and it is then referred to as mercerized cellulose.

consists of 9–11 separate fibrils arranged in a ring. It is possible that this structure is general throughout the class. In the light of recent electron-microscope studies of the flagella of brown algae (cf. p. 125) and of *Chlamydomonas* (p. 21), it is possible that the structure of all of these will prove generally similar. In the motile forms the flagella are associated with other structures which are collectively known as the neuromotor apparatus. At the base of each flagellum is a granular *blepharoplast*. These are connected by a transverse fibre, or *paradesmose*, and this or one of the blepharoplasts is also connected to the intranuclear centrosome by a thin strand called the *rhizoplast*. The motile cells also possess a red eye-spot, the detailed structure of which is not yet elucidated in all the groups, although it appears to contain a primitive lens in the Volvocales. The mechanism is regarded as consisting of two parts: a light absorber near the flagellum base and a shading organ. Two or perhaps three red colouring pigments are sometimes present and are said to be due, at least in part, to the chromolipoid pigment haematochrome (cf. Fig. 1).

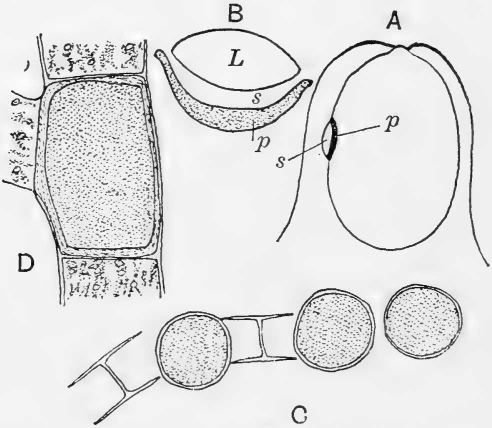

Fig. 1 A, diagram of eye-spot of *Chlamydomonas*. *p* = pigment cup, *s* = photosynthetic substance. B, diagram of cross-section of eye-spot of *Volvox*. *L* = lens, *p* = pigment cup, *s* = photosynthetic substance. C, aplanospores of *Microspora willeana* (× 600). D, akinete of *Pithophora oedogonia* (× 225). (After Smith.)

Vegetative reproduction takes place through fragmentation and ordinary cell division, though in the Chlorococcales and Siphonales cell division is unknown. Asexual reproduction is by means of bi- or quadriflagellate zoospores, except in the Oedogoniales where there is a ring of cilia, which are commonly produced in cells that do not differ from ordinary vegetative cells. These zoospores are often formed during the night and are then liberated in the morning: after liberation they may remain motile for as much as three days or for as short a time as three minutes. Their production can sometimes be induced artificially by altering the environmental conditions, e.g. removing the plant from flowing to still water (*Ulothrix*, *Oedogonium*), changing the illumination, or removing from water for twenty-four hours (*Ulva*, *Enteromorpha*). Each individual cell may produce one or more zoospores, the number varying with the different species. Liberation is secured by one of the following means: (*a*) lateral pores, (*b*) terminal pores, (*c*) gelatinization of the entire wall, (*d*) the wall dividing into two equal or unequal portions. In some species non-motile zoospores are formed which are called *aplanospores*, but if these should then secrete a thick wall they become known as *hypnospores*. Aplanospores which have the same shape as the parent cell are termed *autospores*. All these spores develop a new membrane when they are formed and hence differ from a purely resting vegetative cell or *akinete* (cf. Fig. 1).

Sexual reproduction is represented in all the orders and often there is a complete range from isogamy to oogamy, the ova sometimes being retained and fertilized on the parent thallus in the oogamous forms (e.g. *Volvox*, *Oedogonium*, *Coleochaete*, Charales). The isogamous forms are normally dioecious, the two sexes being termed + and −, because as plants and gametes are alike morphologically they can only be distinguished by the fact that the gametes can normally only fuse with gametes derived from another plant. In some cases (*Ulva*, *Enteromorpha*, *Chlamydomonas*) relative sexuality is known to occur, weak + or − strains fusing with strong + or − strains respectively (cf. p. 417). Segregation into + and − strains occurs during meiosis, a phenomenon which in many species takes place at the first division of the fertilized egg or zygote.

The isogametes and also the zoospores can be regarded as a temporary reversion to the primitive flagellate condition. In the case of algae with oogamy the gametangia (antheridia (male) and oogonia) are of distinctive shape. In some genera gametes are capable of developing parthenogenetically into new plants.

The occurrence of sexual reproduction in nature often marks the phase of maximum abundance when the climax of vegetative activity has just been passed. It can also be induced in culture by an abundance or deficiency of food material or by intense insolation. Interspecific hybrids have been recorded in *Spirogyra*, *Ulothrix*, *Stigeoclonium*, *Draparnaldia*, and *Chlamydomonas* (Fig. 2). Another striking fact is that characters which may develop in some species under the influences of the external environment are normally found 'fixed' in others. This not only indicates the plasticity of many members in the class, but the phenomenon may also be of importance phylogenetically.

As a group the Chlorophyceae are very widespread, occurring in all types of habitat, marine, fresh-water, soil and subaerial. Only about 10 per cent are marine and are mainly represented by the Ulvaceae, Siphonocladales, Dasycladales and Siphonales. Many of the marine species have a definite geographical distribution whereas most of the fresh-water and soil algae are cosmopolitan. A few genera, e.g. *Entocladia* (*Endoderma*), *Chlorochytrium*, *Cephaleuros*, *Phyllosiphon*, contain parasitic species, whilst species of other genera participate in symbiotic associations, e.g. *Carteria*, *Zoochlorella*, *Trebouxia* (cf. p. 427).

* VOLVOCALES

This order comprises the simplest members of the Chlorophyceae and is the only order of green algae (Chlorophyceae) with motile vegetative cells. It ranges from simple unicellular forms of a basic type, e.g. *Chlamydomonas*, to regular colonial aggregates of similar cells, e.g. *Volvox*, whilst in other cases the cells are aggregated in an irregular manner, e.g. *Tetraspora*, or in a dendroid form, e.g. *Prasinocladus*. Throughout the order the motile reproductive swarmer is very uniform in character and even when aggregated the individual cells commonly retain their power of locomotion.

* CHLAMYDOMONADACEAE: *Chlamydomonas* (*chlamydo*, cloak; *monas*, single). Fig. 2

The chlamydomonad type of cell characteristically possesses a single basin-shaped plastid, a red eye-spot, one pyrenoid and two flagella, and is often strongly attracted to light (phototactic). Variations in the structure of the cell occur throughout the genus, which contains about 325 species. Some species lack pyrenoids (*C.*

reticulata), some have one (*C. stellata*), or two (*C. de baryana*), or several (*C. gigantea*). The chloroplast may be reticulate (*C. reticulata*), or axile and stellate (*C. eradians*), or it may be situated laterally (*C. parietaria*). It has been said that under cultural conditions many of the characteristic features can be modified, and that therefore some of the species are not strictly species but are simply phases in the life cycles of other species.

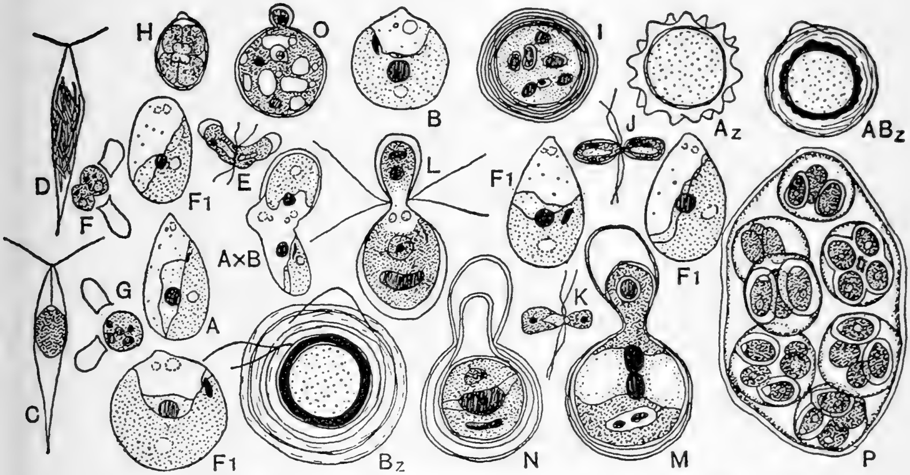

Fig. 2 *Chlamydomonas*. A, B, vegetative individuals of two parents. A_Z, B_Z, zygotes of parents. A × B, fusion between gametes of A and B. AB_Z, zygote of hybrid. F_1, four hybrid individuals obtained from germination of one heterozygote. C, *Chlorogonium ooganum*, female showing formation of ovum. D, *Chlorogonium ooganum*, male showing formation of antherozoids. E–G, stages in fusion of *C. media* (×400). H, vegetative division in *C. angulosa*. I, zygote of *C. coccifera*. J, conjugation in *C. longistigma* (×400). K, fusion of naked gametes of *C. pisiformis* (×400). L–N, stages in fusion of gametes of *C. braunii*. O, fusion of gametes in *C. coccifera*. P, *C. braunii*, palmelloid stage. (A–D, after Fritsch; E–K, after Scott; L–P, after Oltmanns.)

The motile cells are spherical, ellipsoid, or pyriform in shape with a thin wall which occasionally possesses an outer mucilage layer. The two flagella are situated anteriorly and either project through one aperture in the wall or else through two separate canals, but in either case at the point of origin of the flagella there are two basal granules or *blepharoplasts* (see p. 18). Each cell typically possesses two contractile vacuoles which have an excretory function.

At asexual reproduction the motile bodies come to rest and divide up into two, four, more rarely eight or sixteen, daughter cells. The first division at zoospore formation is normally longitudinal and all subsequent divisions are also longitudinal. The biciliate zoospores escape through gelatinization or rupture of the cell wall, but if this does not occur the colony then passes into the palmelloid state, which is usually of brief duration, though in *C. kleinii* it is the dominant phase in the life of the organism. *C. kleinii* may thus be regarded as forming a transition to the condition found in *Tetraspora* (cf. p. 34).

In sexual reproduction eight, sixteen or thirty-two biciliate gametes are formed in each cell. These are normally either + or − in character and fusion takes place between the strains. The development of motility, sexuality and power of fusion in at least one species appears to rest upon the development of certain sex hormones (see p. 417). In *C. agametos* an anticopulatory hormone is produced and so there is no fusion. In *C. longistigma* the gametes are naked (gymnogametes); in *C. media* they are enclosed in a cell wall and just emerge in order to fuse (calyptogametes); in *C. monoica* there is anisogamy as the naked contents of one gamete (male) pass into the envelope of the other; in *C. braunii* the anisogamy is more distinct, the female cell producing two or four macrogametes and the male cell eight or sixteen microgametes; in *C. suboogama* each cell gives rise to three macrogametes and an antheridial cell that produces four antherozoids; in *C. coccifera* there is oogamy, with the female cell producing one macrogamete enclosed in a wall whilst the male cell produces 16 or 32 spherical microgametes. In a related genus, *Chlorogonium oogamum*, one naked ovum is produced and numerous elongate antherozoids. The genus *Chlamydomonas* appears to be polyploid, the basic haploid chromosome number being 16–18.

The zygote is at first quadriflagellate but it soon loses the flagella and forms a smooth or spiny wall. It subsequently enlarges in most species and on germination generally gives rise to four swarmers. Since it has been demonstrated that meiosis occurs during this segmentation, the normal vegetative cells are haploid. In *C. pertusa* and *C. botryoides*, however, the zygote may remain motile for as long as ten days, and hence it may be considered that these two species exhibit the start of an alternation of generations. In *C. variabilis* the persistent 4-ciliate zygote has for long been known as

Carteria ovata (cf. also p. 427), but it has now been demonstrated that the two species represent the haploid and diploid somatic phases respectively of one species. Whether these examples represent a true alternation of generations or whether they must be regarded as possessing a special type of zygote will be considered later (see p. 312).

The genus is widespread, the various species occurring principally in small bodies of water, in sewage oxidation lakes (see p. 453) and in the soil.

Within the family Chlamydomonadaceae there is a considerable variety of forms. Among those which lack a true cell wall is the pear-shaped, 4-ciliate *Polyblepharides* and the biciliate *Dunaliella*. In *Phacotus* the chlamydomonad cell is surrounded by a special outsize hardened envelope which is flattened in side view. *Polytoma* is a colourless member of the family but nevertheless produces starch as its food reserve.

* SPHAERELLACEAE: *Sphaerella* (*sphaer*, ball; *ella*, diminutive of affection). Fig. 3

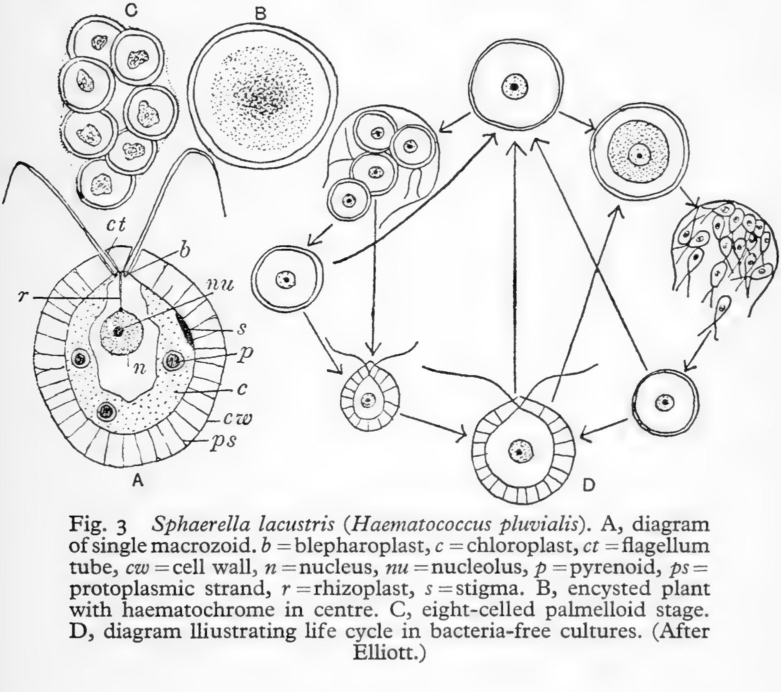

Fig. 3 *Sphaerella lacustris* (*Haematococcus pluvialis*). A, diagram of single macrozoid. *b* = blepharoplast, *c* = chloroplast, *ct* = flagellum tube, *cw* = cell wall, *n* = nucleus, *nu* = nucleolus, *p* = pyrenoid, *ps* = protoplasmic strand, *r* = rhizoplast, *s* = stigma. B, encysted plant with haematochrome in centre. C, eight-celled palmelloid stage. D, diagram illustrating life cycle in bacteria-free cultures. (After Elliott.)

A characteristic of this genus is the area between the protoplast, which is very similar to that of *Chlamydomonas*, and the cell wall; this region is filled by a watery jelly and is traversed by cytoplasmic threads passing from the central protoplast to the cell wall. The protoplast contains several contractile vacuoles and one or more pyrenoids, although two is the usual number. Movement is secured by means of two flagella as in *Chlamydomonas*. Asexual reproduction is by means of two or four zoospores, which may pass through an intermediate non-motile phase before maturing (see Fig. 3). The plants normally occur in ponds and when the water dries up the plant encysts and develops orange-coloured haematochrome. Later, when the ponds fill up again with water, these cysts give rise to isogametes or micro-zoospores. The cysts can be readily transported from pond to pond in mud attached to the feet of birds. Periodic drying appears to be an essential factor if the life cycle of the common species, *Sphaerella lacustris* is to be maintained. Eight-celled colonies, which behave just like *Pandorina* (see p. 25), are known in the related genus *Stephanosphaera*.

VOLVOCACEAE: *Gonium* (*gonium*, angle). Fig. 4

This genus represents one simple type of development within the colonial forms. The simplest type is probably represented by *Pascheriella* where three or four chlamydomonad cells are attached to each other laterally. The colony in the different species of *Gonium* is composed of four, eight or sixteen cells all lying in one plane and forming a flat quadrangular plate, but it has been suggested that the four and eight-celled colonies are merely degenerate forms of the principal species, *G. pectorale*, where there are four cells in the centre and twelve in the periphery, each cell being surrounded by a gelatinous wall and fused to the neighbouring cells by means of protrusions, whilst the protoplasts of the individual cells are also united by fine protoplasmic threads. The ovoid or pyriform cells contain contractile vacuoles and are provided with a pair of flagella. The centre of the colony is composed of mucus and there is also a firm outer gelatinous layer. The shape of the colony accounts for its mode of progression which is by means of a series of somersaults around the horizontal axis.

At asexual reproduction all the cells in a plate divide simultaneously to form daughter colonies. If cells should become isolated singly then after a time they will give rise either to a new daughter colony or to an akinete, or they will divide and pass into a temporary palmelloid state before becoming motile once more. Sexual reproduction is by means of naked isogametes, fusion occurring between gametes derived from separate colonies which must therefore represent + and – strains. The resulting quadriflagellate zygote soon comes to rest and subsequently germinates, when it gives rise to four biflagellate haploid cells which are liberated together as a small colony. When the later development of these cells is followed it is found that two of them give rise to + and two to – colonies, suggesting that meiosis must take place at germination of the zygote.

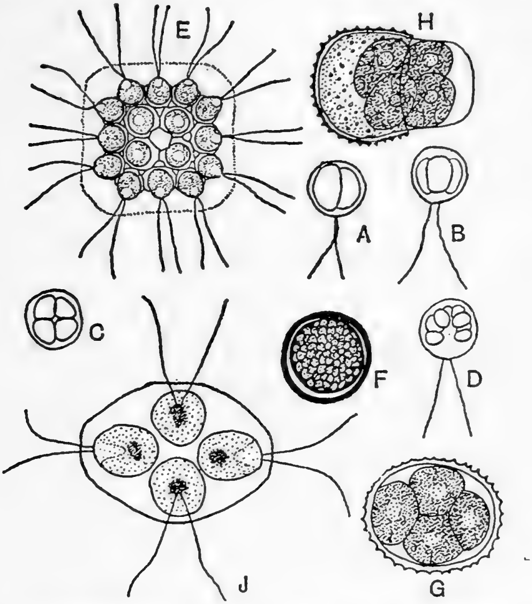

Fig. 4 *Gonium pectorale.* A–D, stages in the formation of a coenobium. E, colony (× 520). F, zygote. G, H, stages in germination of zygote. J, four-celled colony. (A–D, after Fritsch; E, after Smith; G–J, after Kniep.)

VOLVOCACEAE: *Pandorina* (after Pandora's box). Fig. 5

In this genus typical chlamydomonad cells are aggregated together to form oblong or spherical colonies. The number of cells in a colony ranges from four to eight, sixteen or thirty-two, sixteen being the normal number in the common species *P. morum*. In the species the cells are so compacted that they are flattened by mutual pressure. Each colony is enclosed in a gelatinous matrix with an outer watery sheath, and, together with the next two genera, exhibits some degree of polarity in its progression. In asexual reproduction the colony first ceases to be motile and sinks to the bottom of the pond. Then each cell gives rise by several divisions to a bowl-shaped daughter colony or *coenobium*. This becomes inverted and assumes a spherical shape after which each cell produces two flagella. The daughter colonies are ultimately liberated by disintegration of the parent envelope. In sexual reproduction there is a slight tendency to anisogamy, the male gametes being more active than the female. When the zygote germinates it produces one to three biflagellate swarmers, which, after a period of motility, come to rest and divide to give new colonies. Another simple colonial member like *Pandorina* is *Volvulina steinii* with 16 cells arranged in four tiers of four.

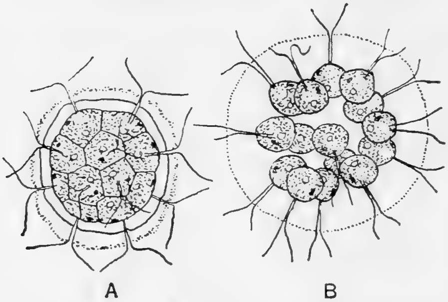

Fig. 5 *Pandorina morum*. A, vegetative colony (× 975). B, colony with female gametes (× 975). (After Smith.)

VOLVOCACEAE: *Eudorina* (*eu*, well; *dorina*, meaningless). Fig. 6

The colonies are spherical or ellipsoidal, the posterior end often being marked by mamillate projections. They contain sixteen, thirty-two (commonly) or sixty-four biflagellate cells, which are not closely packed and are sometimes arranged in transverse rows. The flagella of the individual cells emerge through funnel-shaped canals. Sometimes the coenobium becomes an amorphous palmelloid mass, and then when conditions once more become suitable individual cells break away and grow into new coenobia. In most species all the cells give rise to new daughter coenobia but in *E. illinoiensis* the four anterior cells are much smaller and do not reproduce. In *E. indica* the daughter colonies undergo inversion before liberation as in *Volvox*. This marks the first differentiation into a plant *soma* of purely vegetative cells, such cells dying once the colony has reproduced. It would be of considerable importance if the nature of the stimulus that induces some of the cells to lose their reproductive capacity could be determined.

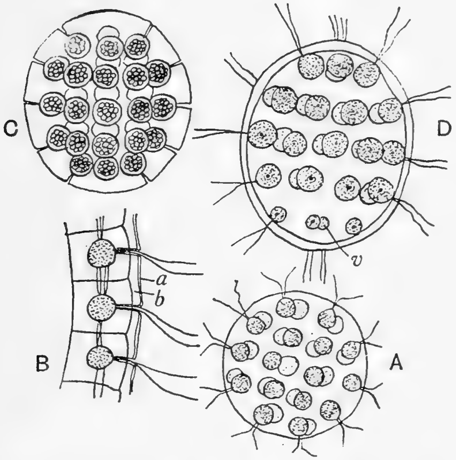

Fig. 6 *Eudorina elegans*. A, vegetative colony. B, transverse section showing structure and protoplasmic connections. *a* = outer layer, *b* = inner layer of mucilage. C, formation of daughter coenobia. D, *E. illinoiensis*, showing somatic cells, *v*. (After Fritsch.)

Sexual reproduction borders between anisogamy and oogamy, the species being either monoecious or dioecious: in the former case the anterior cells give rise to the antherozoids and the posterior form the ova. In the latter case antheridial plates or *plakea* containing sixty-four spindle-shaped antherozoids are liberated intact, and only break up after swimming to the female colony where the surrounding walls have already become gelatinous. The zygote remains within the parent colony until it disintegrates and when it germinates it gives rise to a single motile swarmer and what are probably two or three degenerate swarmers. The motile swarmer eventually comes to rest and divides to give a new coenobium.

VOLVOCACEAE: *Pleodorina* (*pleo*, more; *dorina*, meaningless). Fig. 7

This genus is very similar to the preceding one, but the somatic area is more highly differentiated as it occupies one-third to one-half of the colony, and the total number of cells is greater, 32, 64 or 128. The somatic cells are all aggregated into one area, either anterior or posterior, whereas in the next genus (*Volvox*) they are distributed indiscriminately. The number of somatic cells varies, between species: e.g. in *P. spherica* there is more sterilization than in *P. californica*. In the former species, which is dioecious, the egg cells still possess flagella at the time of fertilization so that sexual reproduction represents an extreme anisogamy rather than an oogamy. During the development of daughter colonies and antheridia inversions occur which are very similar to those of *Volvox*.

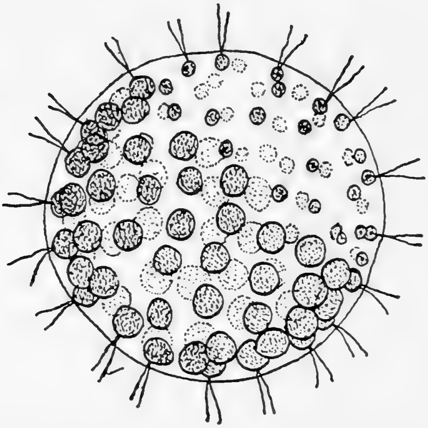

Fig. 7 *Pleodorina californica*. Colony of 120 cells (× 178). (After Shaw.)

Another genus comparable to *Pleodorina* is *Astrephomene* found in S. Africa, Australia and the U.S.A. The colony consists of sixty-four cells, the flagella of the two or four posterior cells forming a 'rudder'.

* VOLVOCACEAE: *Volvox* (*volvere*, to roll). Figs. 8–11

This genus represents the ultimate development that has been reached along this line of spherical colonies or *coenobia*, each of which behaves as a well-organized unit. Every colony is in the form of a sphere with 500–60,000 biflagellate cells set around the periphery, the flagellae emerging through canals. The actual number of cells in a colony varies from species to species. The interior of the colony is mucilaginous (e.g. *V. aureus*) or else merely contains water (e.g. *V. globator*), whilst the entire collection of generally ovoid cells is bounded on the outside by a firm mucilaginous wall. The individual cells, each containing two to five contractile vacuoles, in some species are surrounded by distinct individual sheaths, the middle lamellae of which form a polygonal pattern when stained with methylene blue. In some species too the cells are united by delicate cytoplasmic threads, or *plasmodesmae*. In *V. globator* and *V. rousseletii* the cells are 'sphaerelloid' in nature, each individual cell being enclosed in a separate envelope, whilst in *V. aureus* a number of individual chlamydomonad cells are enclosed in wedge-shaped prisms, which morphologically may be equivalent to an original mother cell. It has therefore been sug-

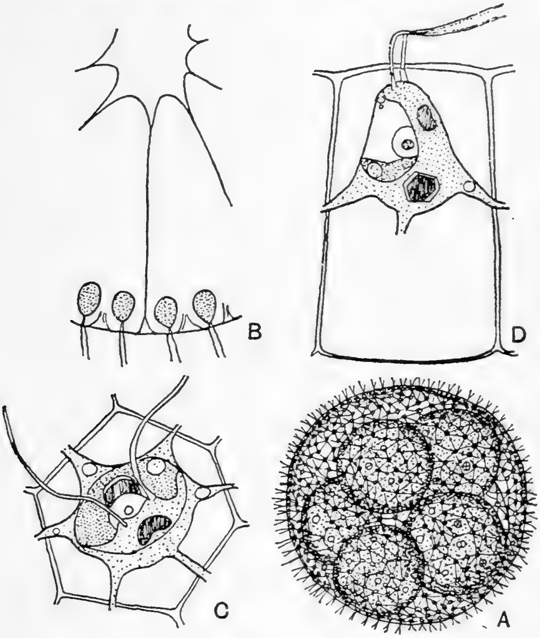

Fig. 8 *Volvox*. A, *V. aureus* with daughter colonies. B, structure of *V. aureus* as seen in section. C, surface view of single cell of *V. rousseletii* (× 2000). D, the same in side view (× 2000). (A, B, after Fritsch; C, D, after Pocock.)

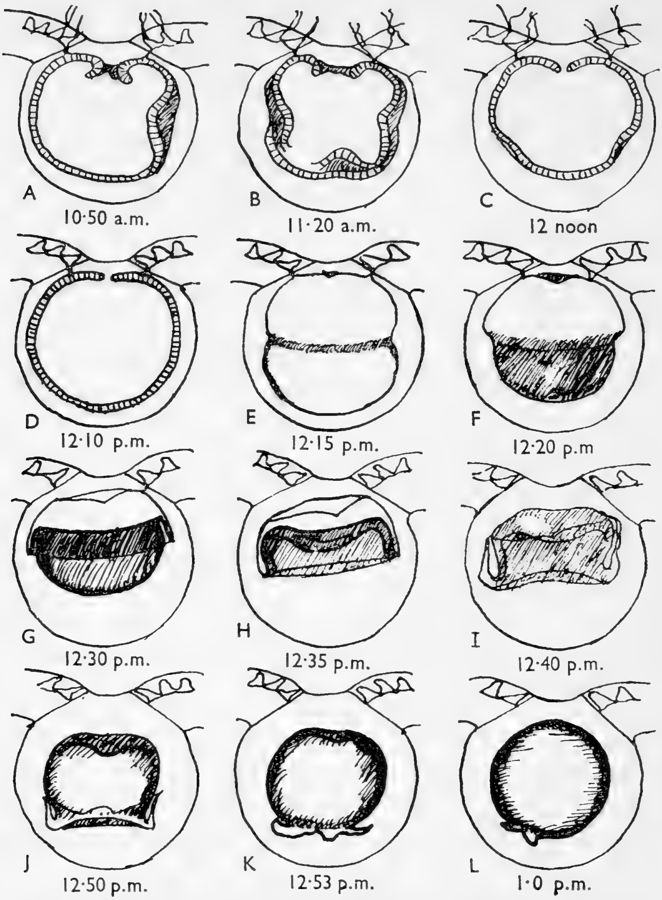

Fig. 9 *Volvox capensis* and *V. rousseletii*. A–J, stages in the inversion of a daughter colony. A, denting begins. C, dents smooth out. D, colony round again. E, 'hour-glass' stage. F, posterior half contracts. G, infolding begins. H, infolding complete. I, posterior half emerges through phialopore. J, flask stage begins. K, flask stage ends. L, inversion complete. (All × 150 approx.) (After Pocock.)

gested that the volvocine colony has arisen at least twice in the course of evolution, once from a *Sphaerella* and once from a *Chlamydomonas* ancestry. Some evidence in support of this view has recently come to hand from a study of chromosome numbers (see below). On the other hand, the great uniformity of their sexual reproduction can be employed as an argument against such a diphyletic origin.

The majority of the cells, including all those in the anterior quarter, are wholly somatic, and only a few are able to give rise to daughter colonies or gametes. As the plant matures some of the posterior cells enlarge and lose their flagellae. These are the potential reproductive cells. When daughter colonies are to be formed the enlarged gonidium divides longitudinally a number of times and a small hollow sphere is produced with a pore (*phialopore*) towards the outer edge. These coenobia, which hang down into the parent cavity, then invert, the process commencing opposite the phialopore. After inversion flagella are formed and the colonies may be liberated into the parental cavity or they may escape to the exterior (Fig. 9). If retained they remain until the parent tears open, in some species (*V. aureus*) at the adult phialopore, in other species (*V. globator*) at any place. In *V. africana* it is possible to see as many as four generations in the one original parent colony, because the original parent takes a long time before it breaks down.

In sexual reproduction the plants are either monoecious (*V. globator*) or dioecious (*V. aureus*). Cells becoming ova enlarge considerably but do not undergo division and the flagella disappear. Cells giving rise to antherozoids divide to give bowl-shaped or globose colonies containing 16, 32, 64, 128, 256 or 512 spindle-shaped, biflagellate antherozoids. Both bowls and spheres undergo inversion before maturation (cf. Fig. 10). The fertilization mechanism is not known for certain, but in the dioecious species the antherozoids are said to penetrate the female colony and then enter the ovum from the inner side. Zygotes do not germinate for a considerable time after liberation. The first division involves meiosis but the oospore produces a single swarmer that is liberated into a vesicle formed by extrusion of the inner oospore wall (endospore). This grows into a 'juvenile' plant of about 128 to 500 cells, which finally inverts. It subsequently reproduces by daughter colonies, each successive generation having an increased number of cells (see p. 44 for comparison with *Hydrodictyon*) until a fully developed colony is produced.

One of the features of this genus are the inversions that occur at different stages of the life-cycle, and it is difficult to see why they occur or what the conditions were under which they first developed. It may be associated with the fact that the new cells are formed with the eye-spot facing the interior, but even then the problem arises as to how the individual cells came to be arranged thus. Since the

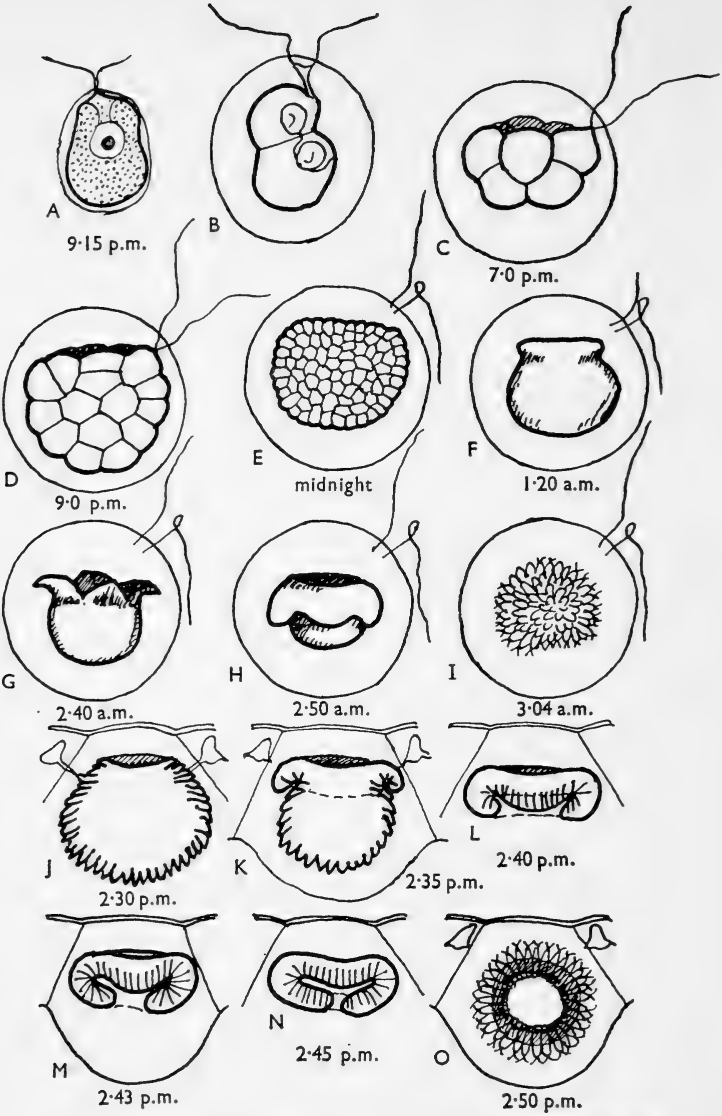

Fig. 10 *Volvox*. A–I, stages in the development of the oospore of *V. rousseletii*. A, zoospore just after escape. B, first division. F, preparation for inversion. G–I, inversion. (All ×375.) J–O, stages in the inversion of a sperm bundle of *V. capensis*. (All ×750.) (After Pocock.)

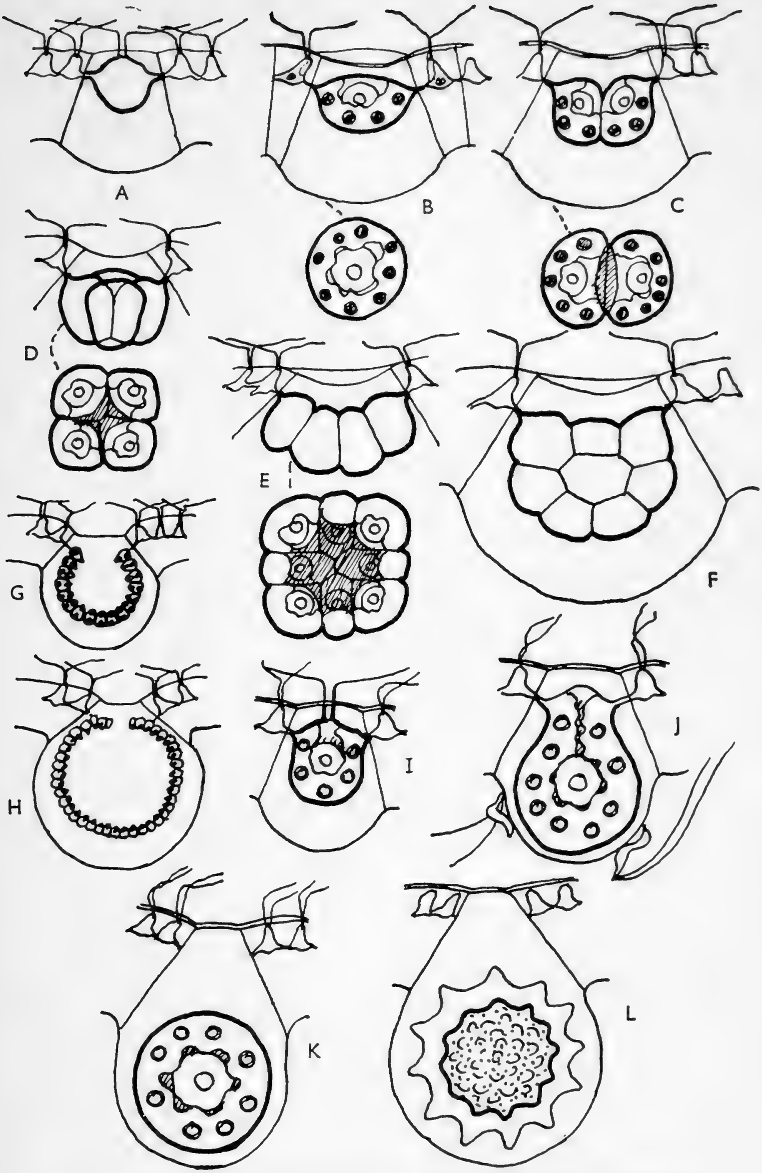

Fig. 11 *Volvox*. A–H, development of daughter colony (gonidium). C, two-celled stage. D, four-celled stage. E, eight-celled stage. F, sixteen-celled stage (all ×750). G, H, formation of phialopore (×225). I–L, development of oospore of *V. rousseletii* (×750). I, flagellar stage. J, mature. K, fertilized. L, exospore formation (After Pocock.)

eye-spot is photosensitive it is possible that light intensity determines this initial arrangement.

Recently some interesting information has come to light concerning the nuclear condition of the Volvocaceae (Cave and Pocock, 1951). *Gonium*, which would seem generally to be the most primitive member of the family, possesses the largest number of chromosomes ($n=17$). In *Volvox* the species regarded as primitive have more chromosomes ($n=14$ or 15) than species regarded as advanced ($n=5$). The facts may involve a re-interpretation of development within the family, *Gonium* being regarded as reduced rather than primitive, and similarly with the species of *Volvox*. In the genus *Astrephomene* colonies with 4, 6, 7 or 8 chromosomes occur. Polyploidy is suggested since clones with 4 chromosomes remain distinct from those with 6, 7 or 8.

TETRASPORACEAE: *Tetraspora* (*tetra*, four; *spora*, spores). Fig. 12

Members of this and allied families are placed by some workers in a separate order, the Tetrasporales. They are characterized by non-motile vegetative cells that may temporarily become motile. In so far as the cells are typically chlamydomonad-like, there seems no justification for placing the genera in a separate order. The species of *Tetraspora* form expanded or tubular, convoluted, light green macroscopic colonies. The colony in these palmelloid forms differs from the organized coenobium of the Volvocaceae because it is merely an unorganized loose assemblage of cells. The palmelloid condition, which occurs from time to time in members of the Chlamydomonadaceae, has in this and allied genera become the dominant phase, whilst the motile condition only occupies a brief period in the life cycle.

The colonies are most abundant in the spring when they are attached at first, although later they become free-floating. The spherical to ellipsoidal cells are embedded in the mucilage and are frequently arranged in groups of two or four, each group often being enclosed in a separate envelope. Two pseudocilia proceed from each cell to the surface of the main colonial envelope, each thread being surrounded by a sheath of denser mucilage. These structures cannot be organs of locomotion because there is no power of movement, but they either represent such organs which have lost their function or they are their precursors.

Vegetative reproduction takes place by fragmentation of the parent colony, whilst asexual reproduction is secured by means of biflagellate swarmers that may develop into a new colony or into a thick-walled resting spore that later gives rise to a new colony. The sexual colonies are monoecious or dioecious, depending on the species, and give rise to biflagellate isogametes. After fusion the zygote gives rise to four to eight aplanospores that are said to grow into new colonies. Recent work on *T. gelatinosa* suggests that the aplanospores are not always produced and that the zygote, after a resting period, can give rise directly to a new plant. In *T. gelatinosa* the new plant must be diploid and it gives rise to asexual swarmers. These develop into juvenile colonies that are capable of perpetuating themselves by biflagellate swarmers. Eventually swarmers are produced that give rise to an attached, pear-shaped colony. The swarmers from this colony give rise to the sexual plant so that in this species there is a definite alternation of morphological phases (Fig. 13). The place of meiosis does not yet appear to have been

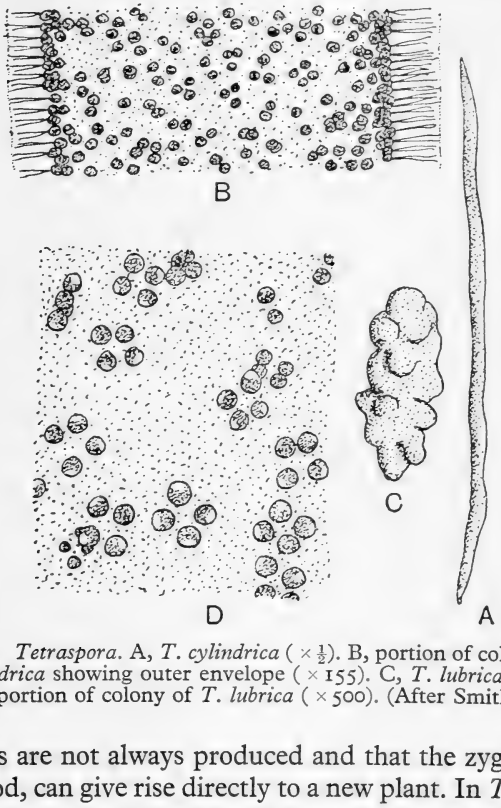

Fig. 12 *Tetraspora*. A, *T. cylindrica* (× ½). B, portion of colony of *T. cylindrica* showing outer envelope (× 155). C, *T. lubrica* (× ½). D, portion of colony of *T. lubrica* (× 500). (After Smith.)

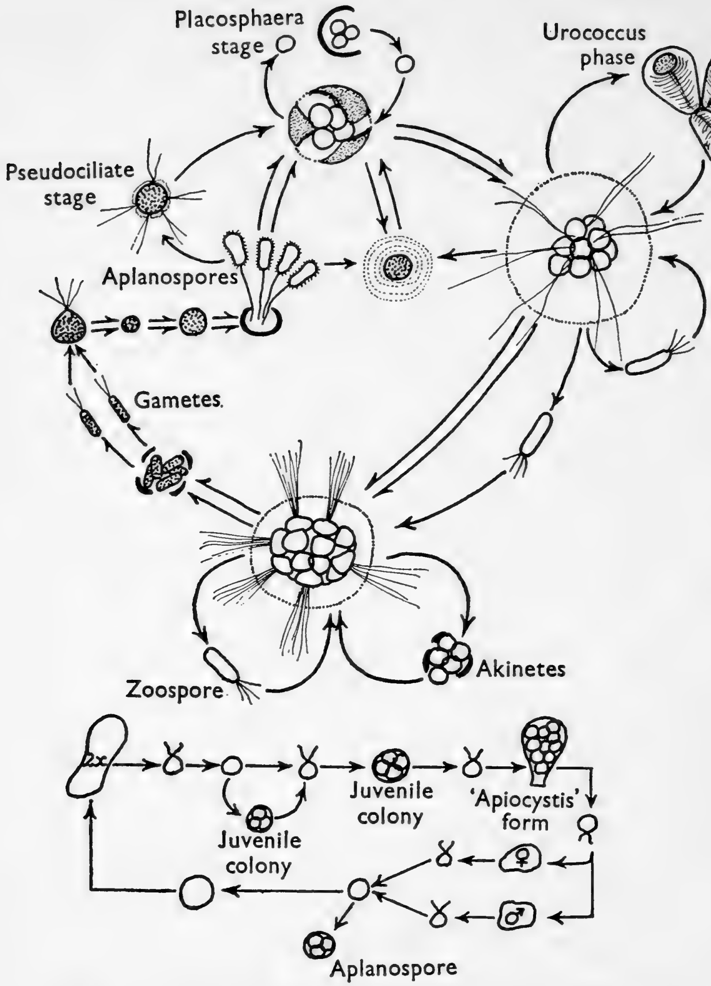

Fig. 13 Top: Life history of *Schizochlamys*. (After Thompson.) Bottom: Life history of *Tetraspora gelatinosa*. (After Hirose.)

established but may well take place at swarmer formation in the attached colonies.

In the allied genus *Schizodictyon* the gelatinous mass is fenestrated giving a net-like appearance. The net type of structure is a morphological development that has occurred separately in a number of different algal groups.

Apart from *Tetraspora gelatinosa*, another genus in which a life cycle has been fully worked out is *Schizochlamys* (Thompson, 1956). Here the adult can reproduce itself by akinetes, zoospores or gametes. The motile zygospore either gives rise to a pseudociliate stage or aplanospore, both of them ultimately developing to a colonial condition known as the *Placosphaera* stage (this stage was formerly placed in a separate genus, *Placosphaera*). Under conditions of drought the cells pass into what is known as the *Urococcus* phase, which suggests that species of the genus *Urococcus* are probably only stages in the life cycle of other palmelloid-like algae (Fig. 13).

CHLORODENDRACEAE: *Prasinocladus* (*prasino*, leek-like; *cladus*, short). Fig. 14

This is included here because it is an example of the tree-like or dendroid habit. The genus is found principally in marine aquaria

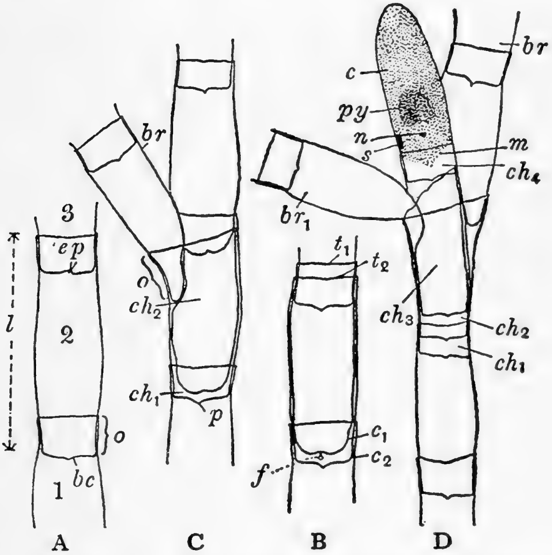

Fig 14 *Prasinocladus*. A, B, portion of plant showing cell structure. 1–3 = cells. C, portion of plant showing arrangement of cells at branching. D, portion of plant with branches and living cell. (All × 1600.) py = pyrenoid, n = nucleus, s = stigma, c = chloroplast, m = basal margin of terminal protoplast, br = first branch, br_1 = second branch, ch_1–ch_4 = short chambers behind terminal cell at times of division, ch_1 being the earliest, f = minute remnant of flagella, c_1, c_2 = bases of two cells, p = papilla, o = overlap of lateral wall, l = entire lateral extent of one chamber, ep = papilla pointing upwards, bc = basal cross wall, t_1, t_2 = tops of two cells. (After Lambert.)

where it starts life as a quadriflagellate swarmer of the chlamydomonad type. When the swarmer comes to rest with attachment papillae at the base, a new wall is formed. The apex of the old wall ruptures, the cell contents develop two flagella and the motile body moves up with its new wall until it becomes enclosed in the neck of the old one. The flagella are then lost for a time and then the process is repeated so that gradually a filament of dead envelopes is built up. An oblique division of the living cell results in branch formation, or after horizontal division the lower half may be left behind in the middle of the dead cells. It is evident that at each division a swarmer is formed that is not normally liberated. On the few occasions when it is liberated the species is perpetuated, but at present the conditions under which liberation occurs are not known.

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* CHLOROCOCCALES

This order contains a number of diverse forms, both in respect of their morphology and also of their reproduction. Nearly all are fresh-water or terrestrial. Some, because of their habit, e.g. *Chlorochytrium*, *Chlorococcum*, probably represent reduced forms. In structure the plants range from solitary, free-living or attached unicells to large coenobia (*Hydrodictyon*) up to 20 cm. long. A characteristic feature of the order is the lack of vegetative cell division, though this has not precluded nuclear division, so that cells in some species become multinucleate. In the various examples discussed below it will be noted that motility has been suppressed more than once in the class, a feature which, taken in conjunction with their diverse morphology, suggests that they may well be polyphyletic in origin. Some of the genera show indications of a relationship, but there are others whose relationships are extremely vague. Some forms (*Trebouxia*) have become associated with fungi and are an integral part of lichens. They were originally classed with *Chlorococcum* (*Cystococcus*) (see below and p. 427). Sexual reproduction when present is commonly by means of motile isogametes, but oogamy has been recorded for a species of *Dictyosphaerium*.

* CHLOROCOCCACEAE: *Chlorococcum* (*chloro*, green; *coccum*, berry). Fig. 15

Much confusion has existed over this genus, and many of the species formerly described are now known to be phases in the life cycles of species from other genera. The plants are represented by non-motile, spherical cells which vary much in size, occurring singly or else forming a stratum on or in the soil. *C. humicolum*, for example, is a very common soil species. There is no eye spot or contractile vacuole; the chloroplast is parietal with usually one pyrenoid. The cell walls are two-layered with a thin inner layer and an outer gelatinous one which is sometimes lamellose and irregularly thickened. The young cells with thin walls are uninucleate but the adult ones with thick walls are commonly multinucleate, and it is in this older condition that the protoplast divides and gives rise to 8, 16 or more biflagellate swarmers which are liberated all together in a vesicle, usually in the early hours of the morning. After a short motile phase the flagellae are withdrawn and a new vegetative phase commences.

Under dry conditions aplanospores are formed: when this occurs the parent cell gelatinizes and a 'palmella' stage results, the cells of which subsequently give rise to 2 or 4 biflagellate gametes. In culture solutions of low nutrient concentration reproduction takes place by means of zoospores, whilst in highly concentrated solutions they are replaced by aplanospores. The environment can therefore affect the type of reproductive body. The production of aplanospores suggests how the genus *Chlorella* may have arisen, whilst the multinucleate state indicates a transition to a coenocytic phase that is further developed in other genera (*Protosiphon*, *Hydrodictyon*).

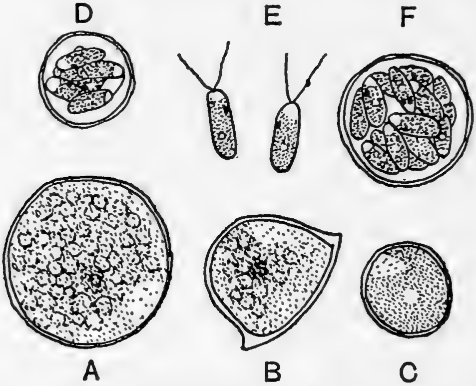

Fig. 15 *Chlorococcum humicolum*. A–C, vegetative cells. D–F, zoospore formation (× 800). (After Smith.)

Asexual reproduction is by zoospores or aplanospores and sexual reproduction by biflagellate iso- or anisogametes. There is no evidence of even a primitive oogamy such as is found in *Chlamydomonas*.

The allied genus *Trebouxia* (*Cystococcus*) forms the algal component in many lichens (see p. 427). The cells differ from those of *Chlorococcum* in lacking an irregularly thickened wall and the plastid is axile and not parietal.

CHARACIACEAE: *Characium* (a slip or cutting). Fig. 16

Each plant is a solitary unicell with a single parietal plastid, and motile only in the reproductive phase. It may be supposed that it has been derived from an ancestral motile organism that ceased to be motile and became attached. The ellipsoidal cells occur singly, or in aggregates on submerged plants or living aquatic larvae, being borne on a short stalk that emerges from a small basal disc. In most species the mature cells contain more than one nucleus. Asexual reproduction is by means of biflagellate zoospores which are liberated through a terminal or lateral aperture. Sexual reproduction is generally isogamous but some species exhibit anisogamy. In *C. saccatum* the + and − gametes are produced from separate plants. They fuse to give a zygote and this, on germination, divides to produce a number of zoospores. The allied marine algal endophyte genus *Codiolum* is interesting because one of the species, *C. petrocelidis* (found in the red encrusting alga *Petrocelis*) has recently been shown to be a phase in the life cycle of a larger green alga *Spongomorpha* (cf. p. 87). Another species, *C. kuckuckii* occurs in the brown alga *Splachnidium* and it remains to be seen whether this too is but a phase in the life cycle of another alga.

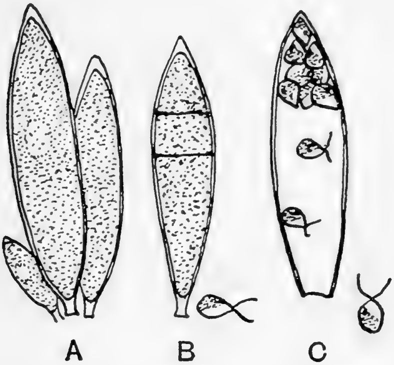

Fig. 16 *Characium angustatum.* A, vegetative cells (× 650). B, cell commencing zoospore formation (× 650). C, liberation of zoospores: the cell is probably broken accidentally (× 650). (After Smith.)

ENDOSPHAERACEAE: *Chlorochytrium* (*chloro*, green; *chytrium*, vessel). Fig. 17

The species grow endophytically in other plants such as mosses, angiosperms and red algae. The cells are spherical or ellipsoidal, the walls varying in thickness. Reproduction is by means of biflagellate gametes that normally fuse to give a motile zygote. This eventually settles on the leaf of a host plant and secretes a wall. Tubular prolongations grow out from these bodies and enter the host, either by way of the stomata or else between two epidermal cells. Subsequently the end of the tube swells out into an ellipsoidal or lobed structure into which the contents of the swarmer pass. In *Chlorochytrium lemnae*, which attacks duckweed (*Lemna*), the endoparasitic cells sink down in the old *Lemna* fronds to the bottom of the pond or stream and remain dormant until the next spring. There is evidence that reduction division takes place at gamete formation so that the vegetative phase must be diploid.

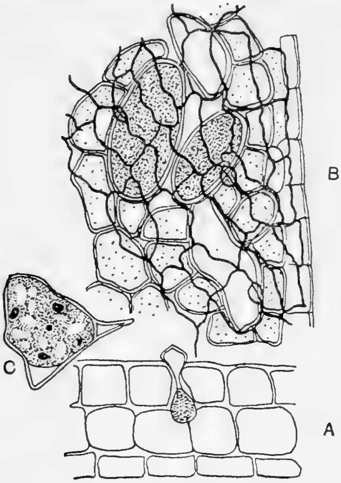

Fig. 17. *Chlorochytrium lemnae*. A, entrance of zygote into host. B, resting cells in leaf of *Lemna*. C, resting cell. (After Fritsch.)

Plants of the allied genus *Rhodochytrium* are colourless and hence it has been suggested that the simple fungi (*Chytridiales*) may have been derived from these algae.

CHLORELLACEAE: *Chlorella* (*chlor*, green; *ella*, diminutive of affection). Fig. 18

The globular cells are non-motile, solitary or aggregated into

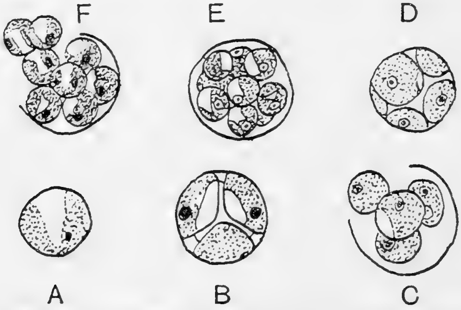

Fig. 18 *Chlorella vulgaris*. A, single cell. B, division into four. C, final stage of division into four daughter cells. D, first stage of division into eight. E, F, second and third stages of division into eight daughter cells. (After Grintzesco.)

groups, and usually lack pyrenoids. The species are not readily determined taxonomically but as many are kept in pure culture they are often given strain numbers. It seems that cells grown in the dark differ from those grown in the light. Quiescent dark cells are small and have a photosynthetic quotient (O_2/CO_2) of 1. They give rise to dividing dark cells which in turn give rise to 'light' cells in daylight. The light cells are larger, poorer in chloroplast material and less active photosynthetically (photosynthetic quotient = 3). During the course of development the amount of deoxyribonucleic acid increases. 'Light' cells give rise to a new generation of 'dark' cells in the dark. Reproduction is by means of division into 2, 4, 8 or 16 autospores. Several species form a symbiotic association with lower animals when they are known as *Zoochlorella* (cf. p. 427).

HYDRODICTYACEAE: *Pediastrum* (*pedi*, foot; *astrum*, star). Fig. 19

This alga occurs as a coenobium and it represents a more advanced stage of the simple condition seen in the fresh-water algae

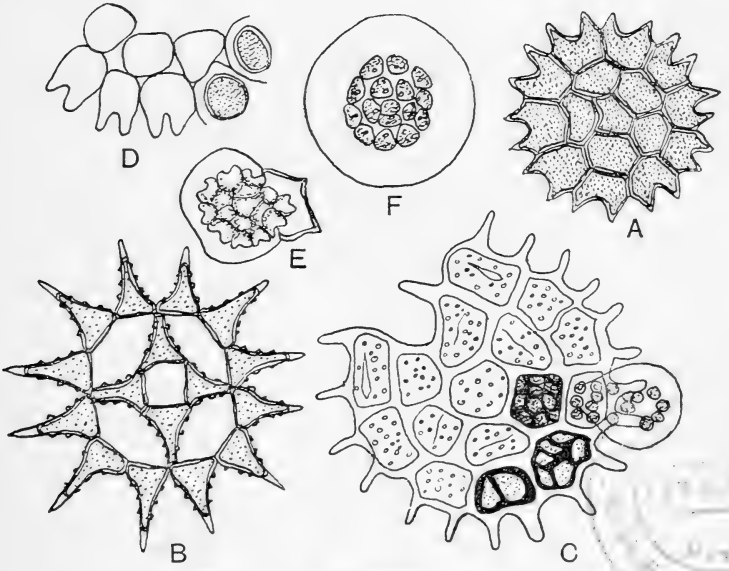

Fig. 19 *Pediastrum*. A, *P. boryanum* (× 333). B, *P. simplex* var. *duodeniarum* (× 333). C, *P. boryanum* var. *granulatum* showing liberation of zoospores. D, *P. duplex* with hypnospores. E, *P. boryanum* germination of tetrahedron. F, *P. boryanum* var. *granulatum*, formation of new plate. (A, B, after Smith; C–F, after Fritsch.)

Ankistrodesmus and *Selenastrum* where the sickle-shaped cells adhere together locally through mucilage. Species of *Pediastrum* are common components of fresh-water plankton. The cells are united into flat, disc-like coenobia with up to 128 cells, the number varying with the species. Experiments suggest that the shape of the cells is determined by heredity and mutual pressure, but the outermost cells commonly differ in shape from interior ones and possess 1–3 processes. Some species have tufts of gelatinous bristles. Young cells are uninucleate but mature cells may possess up to eight nuclei.

Asexual reproduction is by means of biflagellate zoospores which are usually liberated at daybreak from the parent cell into an external vesicle in which they move about for a time, but they become arranged into a new coenobium before the vesicle ruptures. In rare cases long-living aplanospores are produced from individual cells. Plants can also produce isogametes that fuse in pairs. The zygotes increase in size and eventually divide to give a number of zoospores. When these come to rest they develop into thick-walled polyhedral cells. These cells eventually produce zoospores that are liberated into a vesicle where they come together to form a new colony.

* HYDRODICTYACEAE: *Hydrodictyon* (*hydro*, water; *dictyon*, net), Fig. 20

The number of species are few, the commonest, *H. reticulatum*, having a world-wide distribution though it occurs but rarely in each locality. This appears to be due to the fact that its spread depends upon the germinating power of the zygotes and this only takes place under favourable conditions of water quality. It is a hollow, free-floating, cylindrical network closed at either end and up to 20 cm. in length. The individual coenocytic cells are multinucleate and are arranged in hexagons or pentagons to form the net. The chloroplast is reticulate with numerous pyrenoids, though in the young uninucleate cells there is but a simple parietal chloroplast which later becomes spiral and then reticulate. *H. africanum* and *H. patenaeforme* develop into saucer-shaped nets, the former with spherical cells up to 1 cm. diameter, which may become detached and lie on the substratum where they look like marbles. The latter species is composed of cells which may grow up to 4 cm. long by 2 mm. in diameter. Experiments have shown that 1000 lux represents optimum light conditions for growth of *H. reticulatum*, whilst the actual growing period depends upon light intensity, e.g. it is 3 weeks at 600–700 lux, 5½ weeks at 250 lux. Under normal conditions growth is periodic, increasing by day and decreasing at night. This is reflected in the oxygen balance between photosynthesis and respiration. Altering the length of the light period merely alters the degree of growth in the time. Under conditions of continuous light the periodicity is much reduced, though the effect is more marked with old cells. Light is essential for growth, as in continuous darkness the oxygen balance falls below the compensation point,

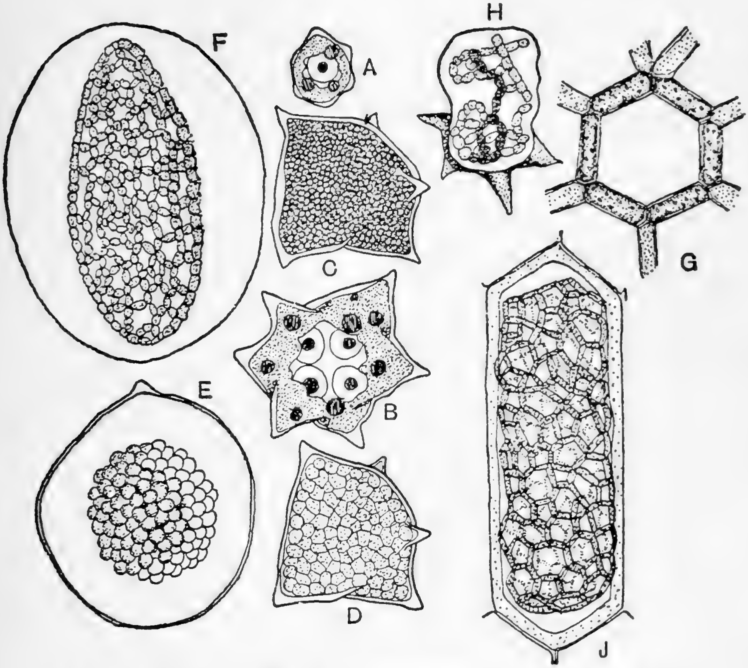

Fig. 20 *Hydrodictyon*. A–F, development of young net of *H. patenaeforme* from the zygote. A, young polyhedron. B, older polyhedron with four nuclei. C, protoplasm granular just before zoospore formation. D, 'pavement' stage. E, zoospores rounding off and wall of polyhedron expanding to form vesicle. F, fully formed net still enclosed in vesicle. (A–E ×250, F ×175.) G, portion of mature net of *H. reticulatum*. H, polyhedron and young net of *H. reticulatum*. J, *H. reticulatum*, formation of net in parent cell from zoospores. (A–F, after Pocock; G, H, after Oltmanns; J, after Fritsch.)

but a twelve hour period of darkness is necessary to get maximum photosynthesis on the following day.

Asexual reproduction in *H. reticulatum* is by means of numerous uninucleate zoospores, which swarm in the parent cell about daybreak and then come together to form a new coenobium which is subsequently liberated, further growth being brought about by elongation of the coenocytic cells. It has been found that zoospore production in this species depends not only upon light intensity but also upon its duration:

	2	4	6	8	10	hrs. of illumination
500 lux	0	0	6	88	100	of cells producing zoospores
4000 lux	11	87	100	100	100	

It is interesting to note that the arrangement of the daughter cells in the parent coenocyte conforms to the mechanical laws for obtaining the greatest rigidity with the maximum economy of space. Zoospore formation in the other species of *Hydrodictyon* does not appear to occur, or if it does it has not yet been observed.

Sexual reproduction in all three species is isogamous* and the plants are monoecious. In *H. patenaeforme* the zygote is motile for a short time, but in the other two species it is always non-motile. At germination the zygote enlarges and divides meiotically to give four* biflagellate swarmers which, after coming to rest, develop into polyhedral cells. These later divide to produce zoospores that are liberated into a vesicle in which, after a period of motility, they come together to form a new coenobium. Gamete and zoospore reproduction can be induced in *H. reticulatum* by varying the external conditions artificially. If plants are cultured in weak maltose solution in bright light or in the dark and are then transferred to distilled water, zoospores will develop from the light plants and gametes from the dark ones.

The vegetative plant must be regarded as haploid and its development is of considerable interest. Further increase in the size of the colony is probably impossible for purely mechanical reasons. *Hydrodictyon* is essentially a collection of a number of individual plants because it arises as the result of the fusion of a number of swarmers. *Volvox*, on the other hand, must be regarded as a single plant composed of many cells because it arises from a single zygote or gonidium.

* 4–8 swarmers or 1 if from an azygospore. Gametes are antiogamous in *H. africanum* (Pocock, 1960).

COELASTRACEAE: *Scenedesmus* (*scene*, rope; *desmus*, fetter). Fig. 21

The planktonic colonies are composed of four, eight, or more rarely, sixteen cells attached to each other at one point by mucilage pads. This type of colony has probably originated from that in which cells are attached at one point indiscriminately, as in *Ankistrodesmus*. The two end cells of the chain may differ in shape from the others and often have processes which are elaborations of the mucilaginous cell envelope: these processes are probably to be correlated with the planktonic mode of life, whilst tufts of bristles performing the same function and similar to those of *Pediastrum* are also recorded.

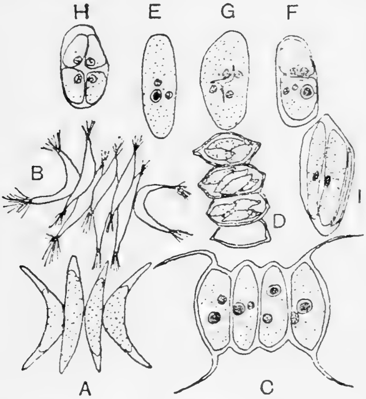

Fig. 21 *Scenedesmus*. A, *S. acuminatus*. B, *S. acuminatus* with mucilage bristles. C, *S. quadricauda*. D, *S. quadricauda* reproducing. E–I, stages in the formation of daughter coenobia in *S. quadricauda*. (After Fritsch.)

PROTOSIPHONACEAE: *Protosiphon* (*proto*, first; *siphon*, tube). Fig.22

This family has in the past been placed in the Siphonales (see p. 96) but in respect of that order it possesses several anomalous features, i.e. method of reproduction, haploid condition, type of environment, plastid, pigments, etc. and it has now been transferred to the Chlorococcales.

There is probably but a single species, *P. botryoides*, but it exists in a number of different strains, one from the deserts of Egypt tolerating temperatures up to 91° C and salt concentrations up to 1 per cent. It commonly grows associated with a very similar alga, *Botrydium*, in the damp mud at the edges of ponds. It contains starch whereas *Botrydium* (see p. 264) does not. The green aerial portion is more or less spherical, up to 100μ in diameter, grading into a colourless rhizoidal portion that may branch occasionally. The plastid, which contains numerous nuclei and pyrenoids, is parietal and reticulate. The shape and colour of the thallus can be modified by varying the external conditions; bright light and low moisture for example causes an old thallus to turn brick red. During dry weather the contents of the vesicle encyst to give large aplanospores or 'coenocysts'. When conditions are once more favourable these cysts either grow directly into vegetative cells or else produce biflagellate zoospores.

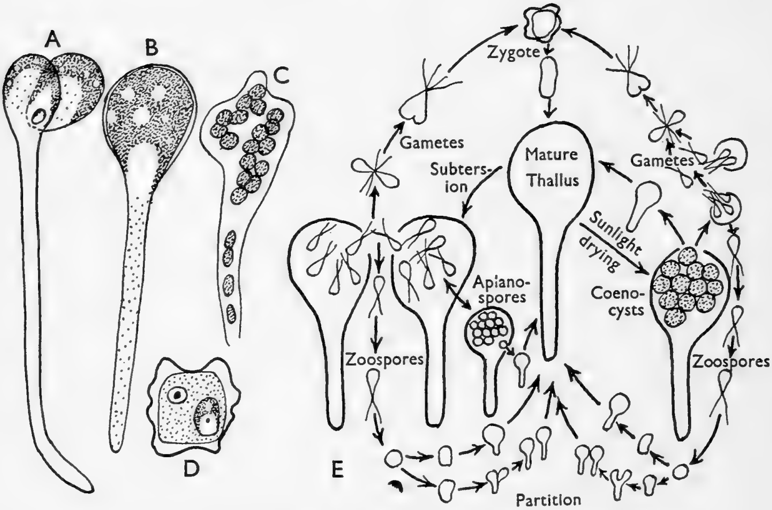

Fig. 22 *Protosiphon botryoides.* A, B, plants, one showing budding. C, cyst formation. D, zygote (× 1666). E, schematic diagram of life cycle. (A–C, after Fritsch; D, E, after Bold.)

Vegetative reproduction can take place by lateral buds which become cut off by cell walls. Flooding of plants on damp soil causes them to produce biflagellate swarmers which behave as isogametes though they can develop parthenogenetically. The zygote either germinates directly or may remain dormant for some time. The plant is probably haploid as there is evidence of meiosis at zygote germination. Morphologically it is of great interest as a possible source of origin for the Siphonales (see p. 310).

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* ULOTRICHALES

This order comprises filamentous and parenchymatous types which have clearly evolved from the filamentous form. There is little or no differentiation between base and apex in many of the forms though there is commonly a special attachment cell or pad of cells. In most genera all the cells except those for attachment are capable of producing reproductive bodies, but in two genera recently described from New Zealand (*Gemina*, *Lobata*) there appears to be a considerable degree of sterilization. Within the genus *Enteromorpha* there is also evidence of the development of heterotrichy or the condition in which the thallus possesses a prostrate adherent portion and an erect aerial portion.

In the past the treatment of the genera in this order has varied considerably. Some workers have divided the genera into three orders, Ulotrichales, Ulvales and Schizogoniales or Prasiolales. Others have recognized only the first and last of these orders, or else have regarded them as forming two suborders, the Ulotrichineae and Prasiolineae. Even when only one order is recognized some authorities accept only three families (Ulotrichaceae, Ulvaceae and Prasiolaceae) whereas others believe that there should be as many as eight families.

* ULOTRICHACEAE: *Ulothrix* (*ulo*, shaggy; *thrix*, hair). Figs. 23, 26

The unbranched filaments are attached to the substrate by means of a modified basal cell which frequently lacks chlorophyll, but even though attached at first, the plants may later become free-floating. Under unfavourable conditions, e.g. lack of nutrients,

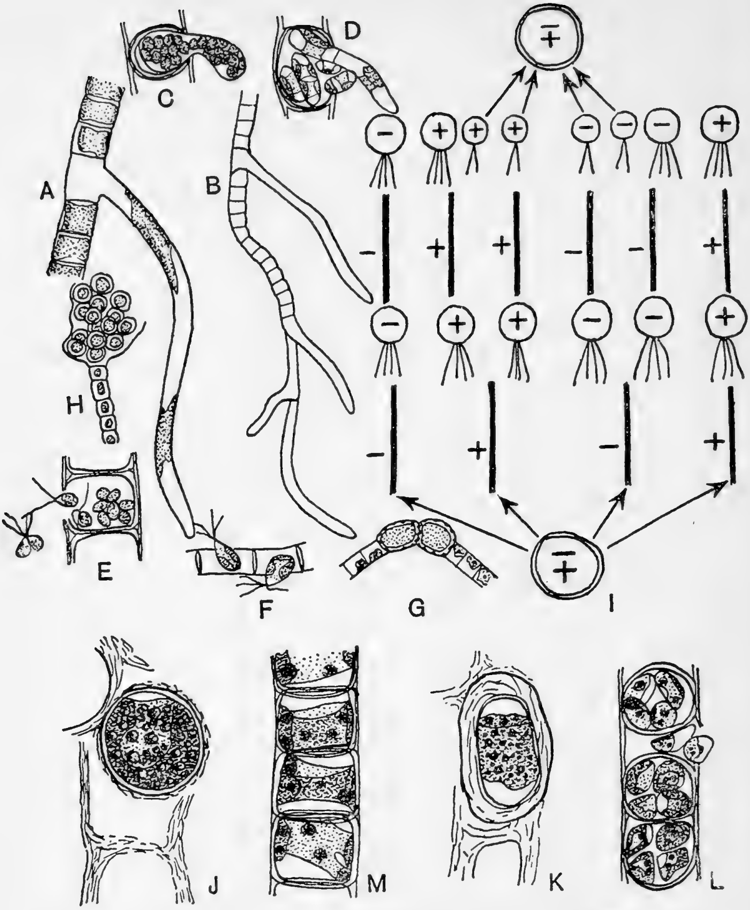

Fig. 23 *Ulothrix zonata.* A, B, rhizoid formation. C, liberation of swarmers into vesicle (×375). D, germination of aplanospores in the cell (×250). E, liberation of gametes (×375). F, escape of zoospores (×375). G, akinetes of *U. idiospora.* H, palmelloid condition. I, schema to illustrate the different types of filaments and swarmers. J, K, aplanospores (×400). L, zoospore formation (×400). M, banded chloroplasts in a portion of the vegetative filament (×400). (A, B, I, after Gross; C–F, J–M, after West; G, H, after Fritsch.)

rhizoids may grow out from the cells or else the filaments become branched. This suggests one way at least in which the branched habit may have evolved from the simple filament, in this case probably representing an attempt to increase the absorbing surface in order to counteract the deficiency of salts. The cells of the different species vary considerably in size, shape and wall thickness. When the walls are thick they are often lamellate. There is a single chloroplast which forms a characteristic circular band around the whole or most of the cell circumference. Vegetative reproduction can take place through fragmentation.

Swarmers are formed from all cells of the filament except the attachment cell, but they usually appear first in the apical cells and then in successive cells below. They are liberated through a hole in the side of the cell into a delicate vesicle, which subsequently bursts and liberates the swarmers. Asexual reproduction is by means of biflagellate zoospores, the numbers produced per cell depending on their width: wide cells give 2, 4, 8, 16 or 32 zoospores per cell, narrow cells 1, 2 or 4 per cell. These zoospores are quadriflagellate but in the larger species there are bi- or quadriflagellate microzoospores which only germinate at low temperatures. Undischarged zoospores turn into aplanospores and these may even germinate in situ before liberation.

Sexual reproduction is by means of biflagellate gametes of which 8, 16, 32 or 64 are produced per cell. The plants are dioecious with plus and minus strains. No parthenogenetic development of gametes has been recorded. The zygote germinates after 5–9 months giving rise to 4–16 bodies which function either as aplanospores or as zoospores. Since meiosis occurs at their formation the adult plant is haploid. The plants appear mostly in winter or spring and optimum conditions would seem to include low temperatures. The genus is well represented in both fresh and salt waters.

Genera closely allied to *Ulothrix* are *Schizomeris*, in which some of the cells may divide longitudinally and in which, so far, sexual reproduction has not been observed; *Hormidium*, the filaments of which have a strong tendency to fragment, and *Binuclearia* where the cells are in pairs in a gelatinous filament. *Hormidium flaccidum* is a widely distributed soil alga (see p. 380).

MICROSPORACEAE: *Microspora* (*micro*, small; *spora*, seed). Fig. 24

This genus is sufficiently distinct from the preceding one to warrant its inclusion in a separate family. The species are all freshwater and are free-floating, consisting of unbranched threads with walls of varying thickness, the thicker walls showing stratification. Each cell wall consists of two overlapping halves held in place by a delicate membrane. This structure arises from the fact that the filament is made up of a series of H pieces and as a result the filament readily fragments. At cell division a new H piece is introduced between the two daughter protoplasts. In young cells the parietal plastid is commonly reticulate but older cells are so filled with starch that plastid structure is difficult to see. There are no pyrenoids. Asexual reproduction is by means of biflagellate zoospores (quadriflagellate in one species), 1–16 being produced per cell and liberated by the thread fragmenting into H pieces or else by gelatinization of the cell walls. Any cell can produce single aplanospores instead of zoospores, and some species also produce multinucleate, thick-walled akinetes. These germinate directly to form a new filament or with later germination to give four protoplasts that then grow into new filaments.

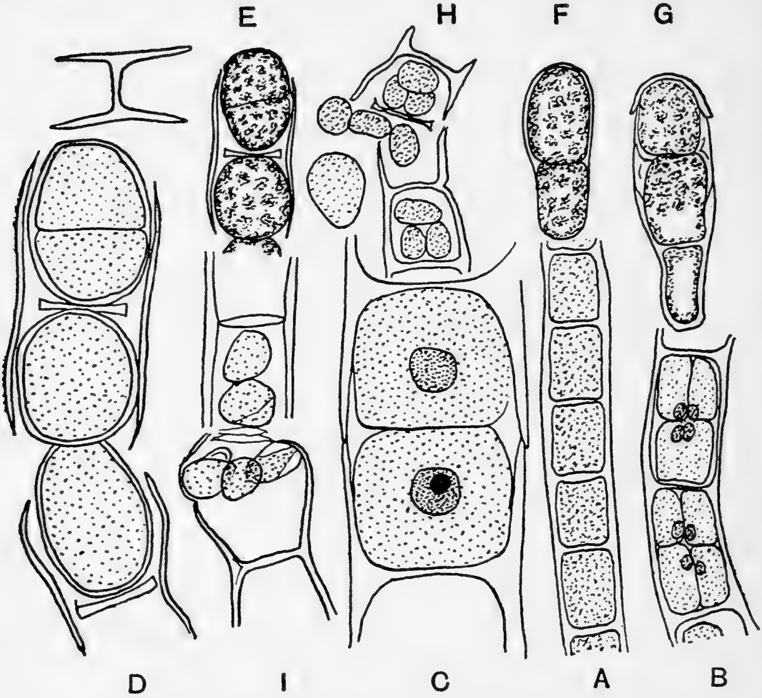

Fig. 24 *Microspora amoena.* A, portion of thread. B, early cleavage in swarmer formation. C, two young cells (× 745). D, akinete formation (× 550). E, formation of aplanospores. F, G, stages in germination of aplanospores. H, liberation of zoospores. I, zoospores (× 745). (C, D, I, after Meyer; rest after Fritsch.)

Microspora with its cell walls in two pieces has an analogue with *Tribonema* in the Xanthophyceae and it seems that this type of construction has arisen more than once in the course of evolution.

CYLINDROCAPSACEAE: *Cylindrocapsa* (*cylindro*, cylinder; *capsa*, box). Fig. 25

The single genus of the family is fresh-water and each plant consists of unbranched filaments attached at the base by means of a gelatinous holdfast. When young each thread is composed of a single row of elliptical cells with thick, stratified walls, the whole being enclosed in a tubular sheath. Each cell contains a stellate chloroplast and a single pyrenoid. In older filaments the cells divide longitudinally, usually in pairs, and this suggests how genera such as *Monostroma* may have evolved. Reproduction in this genus is more advanced than in allied genera because, apart from bi- or quadriflagellate zoospores, sexual reproduction is oogamous, the plants being monoecious or dioecious. Each antheridium gives rise to two biflagellate antherozoids and each oogonium to a single ovum.

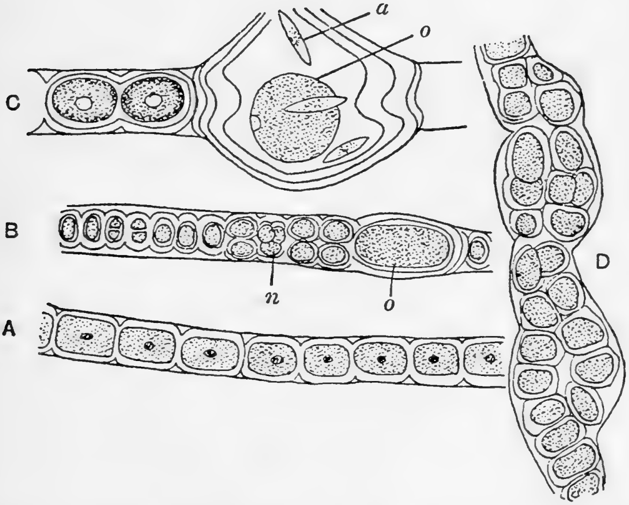

Fig. 25 *Cylindrocapsa*. A, vegetative filament. B, thread with young antheridia (*n*) and young oogonium (*o*). C, fusion of gametes. *a* = antherozoid, *o* = ovum. D, old mature filament. (After Fritsch.)

MONOSTROMACEAE: *Monostroma* (*mono*, single; *stroma*, layer). Figs. 26, 27

The thallus develops as a small sac, which in most species ruptures very early to give a plate of cells one layer in thickness, the cells often being arranged in groups of two or four. In *M. grevillei* the thallus ruptures only in the adult stage, whilst in *M. lindaueri* the sac frequently remains entire. Male and female gametes (+ and – strains) are produced from separate plants and several species exhibit anisogamy. The non-motile zygote increases in size and after some months undergoes meiosis and commonly forms thirty-two zoospores: in one species it has been shown that half of these give rise to male plants and half to female plants. The macro-

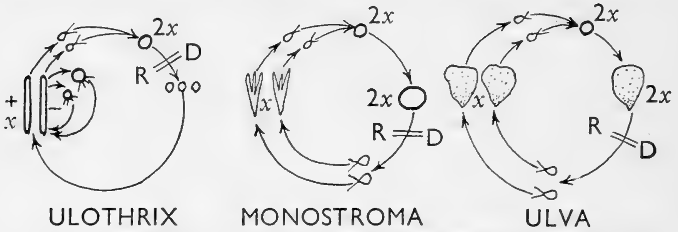

Fig. 26 Diagram to illustrate the three different types of life cycle found in the Ulotrichales. RD = place of reduction division in life cycle.

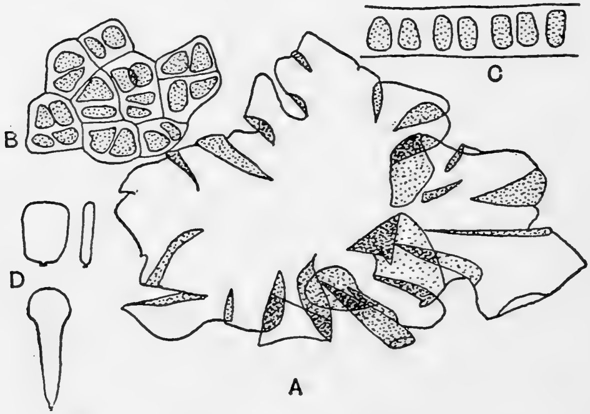

Fig. 27 *Monostroma crepidinum.* A, plant (× $\frac{2}{3}$). B, cells of thallus (× 200). C, transverse section of thallus (× 200). D, *M. lindaueri*, plants (× $\frac{2}{3}$). (After Chapman.)

scopic plants are thus all haploid and the diploid is only represented by the enlarged zygote. In this respect it is sharply differentiated from the genera *Ulva* and *Enteromorpha* (see below). Each zoospore from the zygote divides to give eight peripherally arranged cells with a central cavity and this then develops slowly into a sac. The genus is more widespread than is perhaps thought, frequenting both saline and fresh waters.

* ULVACEAE: *Ulva* (latin for a marsh plant). Figs. 26, 28

The thallus, which is composed of two layers, develops from a single uniseriate filament that subsequently expands by lateral divisions, but there is no hollow sac, though in *U. linza* and *U. rhacodes* the two layers may separate towards the margins or near the base. The plants are attached at first by a single cell, but later multinucleate rhizoids grow down from the lower cells and form a basal attachment disc that may persist throughout the winter, new plants arising from it in the spring. Detached fragments are another means of forming new thalli especially in stagnant-water forms, whilst normal asexual reproduction is by means of quadriflagellate zoospores.

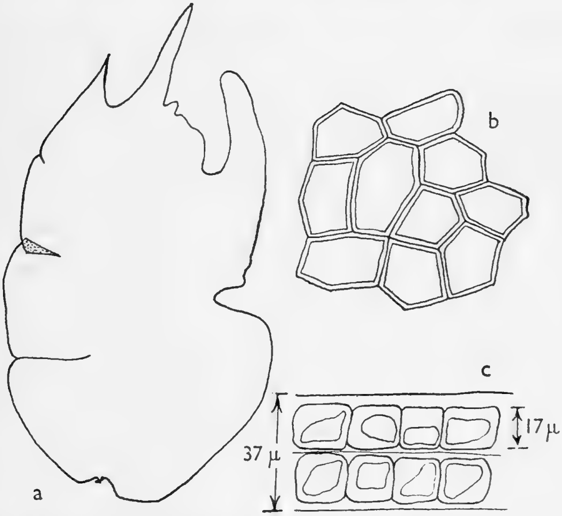

Fig. 28 *Ulva sorensenii.* A, plant. B, cells in surface view. C, transverse section of thallus. (After Chapman.)

In sexual reproduction, which occurs in plants other than those producing zoospores, fusion normally takes place between isogametes from separate plants (+ and −). Thirty-two or 64 gametes are produced per cell and in three species anisogamy is known to occur. In some species the gametes may fuse into clumps. In *U. lobata* two types of 'clump' reaction have been observed. In one type 10–20 gametes fuse together whereas in the other more than 100 are involved. At present there is no explanation of this difference. Whilst the gametes are positively phototactic before fusion, the zygote is negatively phototactic, and this change in behaviour causes it to descend on to a suitable substrate. It has been shown that in certain cases there may be relative sexuality among gametes from different plants, the sex of the older and weaker gametes becoming changed (see p. 19). Meiosis takes place at zoospore formation and, in all but one of the species investigated, there is a regular alternation of morphologically similar diploid and haploid generations (see Fig. 26). In *U. linza*, only the diploid generation is known and meiosis does not occur at zoospore formation. In *U. lobata* gamete liberation occurs with a fourteen-day periodicity, the periods of liberation being associated with spring tidal cycles (see p. 148).

The plants occur in saline or fresh water and become particularly abundant when the waters are polluted by organic matter or sewage.

In the allied sub-antarctic genus *Gemina* the plants resemble either *Ulva* or *Enteromorpha*. The cells are normally in pairs and apparently only some cells are capable of reproduction whereas in *Ulva* all cells of the thallus can give rise to swarmers (Fig. 32). The same is true also of the genus *Lobata*, the reproductive cells being restricted to the thickened central portion of the thallus.

ULVACEAE: *Enteromorpha* (*entero*, entrail; *morpha*, form). Fig. 29

The plants of this genus also commence life as uniseriate filaments which soon become multiseriate and tubular. Like *Ulva*, many of the species are attached by means of rhizoids and in *E. nana* (sometimes placed in a separate genus *Blidingia*), there is a basal prostrate portion, but there are also a number of forms, occurring especially on salt marshes (cf. p. 354), which are unattached for the whole or part of their life. Growth in length of the thallus is primarily intercalary though in the early stages it is also through

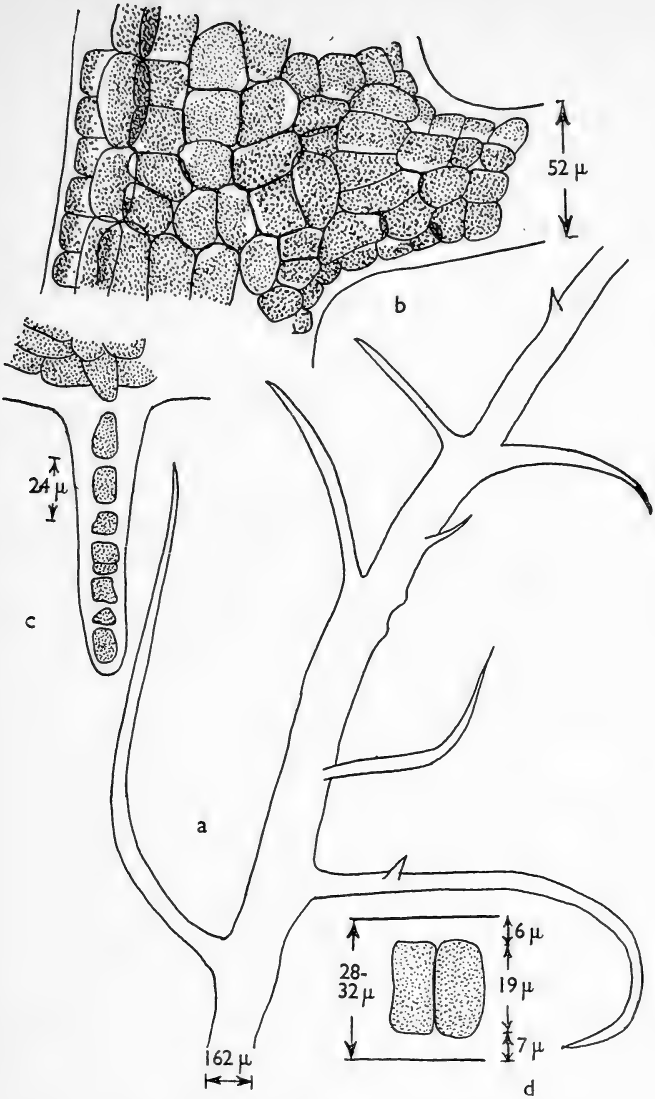

Fig. 29 *Enteromorpha intestinalis* f. *flagelliformis*. a, portion of plant. b, origin of branch of same showing basal constriction. c, d, e, transverse sections from near base, middle and apex of thallus. *o*=outside, *i*=inside of tube. f, g, cells of thallus. (Original.)

the divisions of an apical cell. In some species the plastids are said to exhibit polarity, occurring normally in the apical portion of the cell. Such polarity is apparently absent in *Ulva* and *Monostroma.* When the tubular thallus is damaged near the apex the wounded cells put out papillate outgrowths, but if the damage occurs near the base rhizoids are produced. Asexual reproduction is by means of zoospores, and as meiosis normally takes place at their formation the life cycle in these species is identical with that of *Ulva*, because morphologically similar haploid plants are known. The first division of the germinating zoospores is transverse, the lower segment forming an embryonic rhizoid.

The sexual haploid plants are dioecious, usually with isogamous reproduction, the gametes commonly being liberated around daybreak. Anisogamy occurs in *E. intestinalis* where the male gamete is small with but a rudimentary pyrenoid. The gametes may remain motile for twenty-four hours, whilst the zygote may retain motility for an hour, although the first division does not take place usually until after several days' dormancy. In *E. procera* and *E. nana* gametes are not known and the asexual swarmers are called neutrospores because meiosis does not occur prior to their formation. These two species are presumably diploid and the haploid generation has been lost (cf. *Ulva linza*). Parthenogenetic development of gametes has been recorded for some species, e.g. *E. clathrata*, and this presumably results in new sexual plants. In the reproductive areas some of the cells fail to divide. These are termed rest cells and later they may germinate and give rise to sporelings which eventually become separated from the parent thallus.

In the majority of species there appears to be a regular alternation of morphologically similar generations. In *E. prolifera*, however, there is alternation between heteromorphic generations, one being simple and the other much branched. Branching may not always be a good character because it appears to be dependant to some extent upon temperature and degree of salinity. Within the genus there are several lines of development including two probable lines of reduction in size. One such reduction series is represented by the sequence *E. clathrata* — *E. ralfsii* — *E. salina* — *E. percursa*, whilst *E. torta* may be a reduction form from *E. prolifera.* In the new genus *Feldmannodora* the individual cells are arranged in rows and are capsulated, groups of cells coming from a common parent cell.

PRASIOLACEAE: *Prasiola* (*prasio*, green). Figs. 30, 31

The young unbranched filament, which is known as the '*hormidium*' stage, consists of a single row of cylindrical cells with thick walls which frequently exhibit striations. Later on the cells divide longitudinally and produce a thin expanded thallus, known as the '*schizogonium*' stage which tapers to the base. The cells of the mature expanded thallus are often arranged in fours and possess axile, stellate chloroplasts, whilst in some species another feature is the presence of short rhizoids that occur in the stalk-like portion or else are produced from the marginal cells. In the juvenile filament reproduction takes place by means of fragmentation as a result of the death of isolated cells, whilst in the older, more leafy thallus, 'buds' can arise from the margin. Sometimes the cells pro-

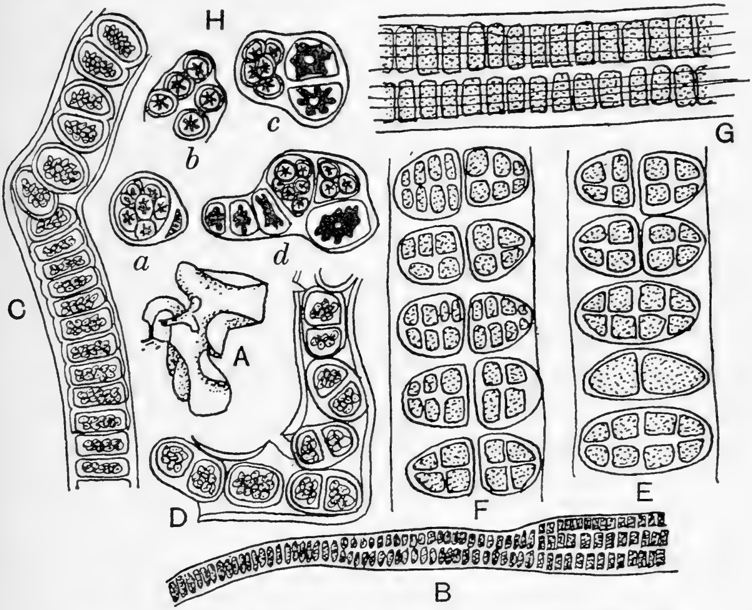

Fig. 30. *Prasiola*. A, plant of *P. crispa*. B, '*Schizogonium*' stage of *P. crispa* forma *muralis*. C, D, '*Hormidium*' stage of *P. crispa* f. *muralis* with akinetes. E, development of macrogametes in *P. japonica* (×665). F, development of microgametes in *P. japonica* (×665). G, *P. crispa*, membrane striations in '*Schizogonium*' stage (×650). H (*a–d*), formation of aplanospores in akinetes and young plants. (A, B, after Fritsch; C, D, H, after Oltmanns; E–G, after Knebel.)

duce large, thick-walled akinetes that germinate to form aplanospores from which new plants arise. In *P. japonica*, sexual reproduction is brought about by non-motile macro- (16 per cell) and motile micro-gametes (64 or 128 per cell) that are both produced from the same plant so that this species at least is monoecious and anisogamous. Despite the existence of sexual reproduction multiplication in this species is usually by asexual means. The plants are haploid (n=3), but in view of recent discoveries about *P. stipitata* it is desirable that *P. japonica* be restudied.

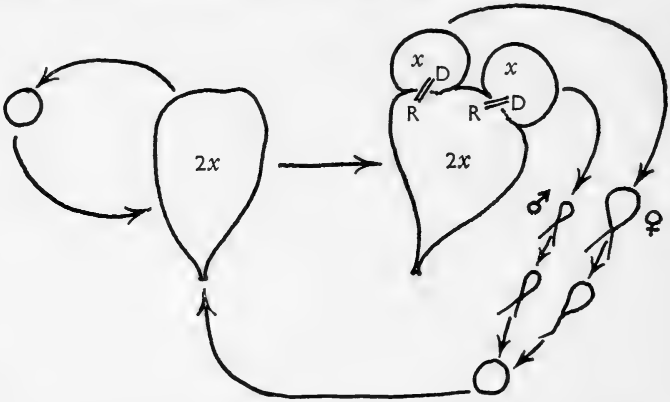

Fig. 31 Life cycle of *Prasida stipitata*. Meiosis (RD) occurs in peripheral cells of diploid thallus. (Modified from Friedmann.)

In *P. stipitata* the adult plant is diploid (n=12–14) and reproduces by aplanospores. Subsequently cells, termed *meiospores*, at the distal periphery undergo reduction division and give rise to leafy appendages, the cells of which are haploid. These appendages are monosexual and give rise to either male or female gametes that are anisogamous. The gametophyte plants are therefore attached to the diploid plant. It has been observed that wholly diploid plants occupy the upper levels of a *P. stipitata* zone and plants with gametophytes occur lower down.

The shape of the thallus in *P. crispa* varies considerably with the environment, the optimum conditions being where there is abundant nitrogen, such as may be found in areas occupied by bird colonies. The genus, which is generally absent from the tropics and sub-tropics, is represented by saline, fresh-water or terrestrial species, the last-named being tolerant towards considerable desiccation. This is attributable to the lack of vacuoles in the cells and also to the high viscosity of the protoplasm. Some authors believe that the genus should be separated from the Ulotrichales (see p. 49) but this hardly seems warranted (see p. 308).

CAPSOSIPHONACEAE: *Capsosiphon* (*capso*, box; *siphon*, small tube). Fig. 32

The original single species in this genus was at one time included in the genus *Enteromorpha*, but now two species are known and the characters justify segregation into a separate genus. The cells are arranged in horizontal and longitudinal rows but do not separate off into longitudinal areolae as in *Prasiola*. Sexual reproduction is unknown and the plants are probably diploid, reproducing only by

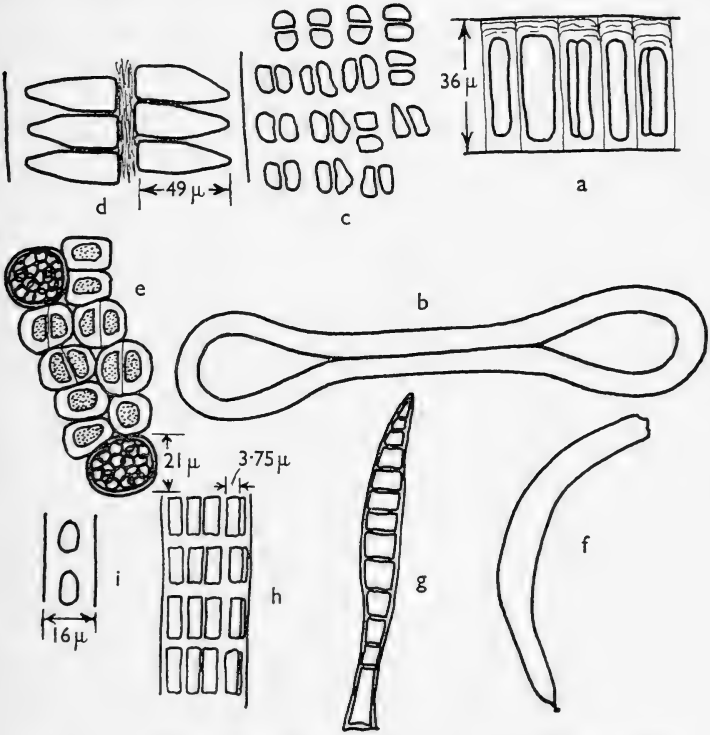

Fig. 32 *Gemina* and *Capsosiphon*. a = t.s. membrane of *Gemina enteromorphoidea*; b, t.s. thallus of *G. enteromorphoidea*; c, cells in surface view, *G. enteromorphoidea*; d, t.s. *G. linzoidea*; e, reproductive and vegetative cells of *G. linzoidea*; f, *Capsosiphon aurea* (× 2); g, *C. aurea* plantling; h, part of thallus of young plant of *C. aurea*; i, membrane of *C. aurea*. (After Chapman.)

akinetes. They are golden green in colour and both species frequent brackish ditches. Some authorities retain this genus in the Ulvaceae but the differences would appear to be sufficiently distinct to justify its removal to a separate family.

SPHAEROPLEACEAE: *Sphaeroplea* (*sphaero*, sphere; *plea*, full). Figs. 33, 34

This genus is widely distributed but is only frequent locally, being most abundant on ground that is periodically flooded by fresh water. The long, free, unbranched filaments consist of elongated coenocytic cells containing up to seventy annular parietal chloroplasts with pyrenoids. The plastids have denticulate margins and occupy the periphery of discs of cytoplasm, the discs being

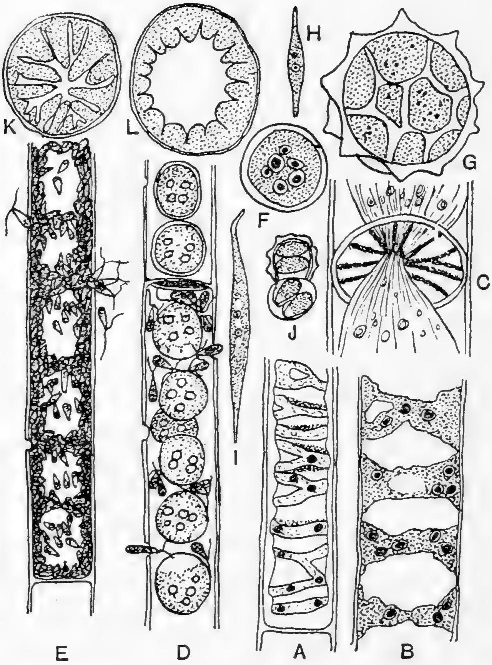

Fig. 33 *Sphaeroplea*. A, *S. annulina*, portion of thallus. B, *S. annulina* chloroplast. C, structure of septum in *S. africana* (× 375). D, female plant with ova and antherozoids. E, male plant. F, young zygote. G, zygote with thickened wall. H, I, young gametophytes. J, spores emerging from zygote. K, L, *S. africana*, transverse sections across the septa (× 375). (A–C, K, L, after Fritsch; D–J, after Oltmanns.)

separated from each other by vacuoles, although occasionally they may come together to form a diffuse net-work. Each disc normally possesses one or two nuclei. In most of the species the septa develop as ingrowths, though in *S. africana* they are replaced by a series of strands which sometimes fail to meet at the centre so that the coenocytes are continuous.

Vegetative reproduction is secured by means of fragmentation, and there is apparently no asexual reproduction though zoospores have been reported in *S. wilmani*: these may, however, be parthenogenetically developing ova. In sexual reproduction, although the cells do not change in shape, nevertheless both oogonia and antheridia are formed singly or in series, the species being either monoecious or dioecious. In the formation of oogonia the annular chloroplasts first become reticulate and then the ova are formed without any nuclear divisions being involved. In *S. annulina* the ova are non-motile, but in *S. cambrica* the large female gametes are biflagellate, thus representing an advanced anisogamy. In the antheridia the nuclei do undergo division and numerous, elongated, narrow antherozoids are formed which are liberated through small pores, subsequently penetrating the oogonial cells through similar perforations. The fertilized ovum (*oospore*) becomes surrounded by a hyaline membrane, and then inside this two new membranes are laid down, after which the first one disappears. The new external membrane is ornamented and the contents become a brick red. Germination stages are only known for some species and the oospores lie dormant for several months or even years. On germination 1–4 biflagellate swarmers (8 occasionally) are normally produced which come to rest and then grow into new plants. Sometimes the swarmers do not separate and so one gets a four- or eight-flagellate *synzoospore* depending on whether it comprises two or four zoids. These develop to a four-fold sporeling or sporeling with four claws. In some cases the swarmers from the oospore are completely suppressed and a new filament develops directly (cf. Fig. 34), this type of reproduction being known as *azoosporic*. In the most complete life cycle investigated the motile ova may also develop parthenogenetically after forming a short non-motile structure which divides to produce three new filaments. Various reduction stages from this life cycle can be noted among the different species (cf. Fig. 34). The adult plants are haploid because meiosis is known to take place at the segmentation of the oospore.

Primitive characters, which seem to be a feature of the genus, are the numerous ova, the entire lack of specialized organs for reproduction and a simple form of zygote germination. The plant must probably be regarded as an Ulotrichaceous filament which, whilst becoming non-septate, has still retained some primitive features. In *S. annulina* cells are frequently found with only one or two plastids thus showing a gradation towards *Ulothrix*. There would seem to be very little justification for following those authors who would place the family in the Siphonocladales (p. 81), though it must be admitted that *S. africana* does have some features characteristic of that order.

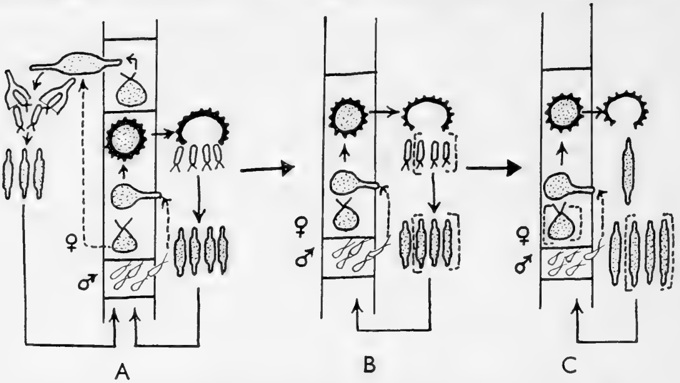

Fig 34 Evolutionary development of life cycles in the genus *Sphaeroplea*. A = *S. wilmani* type; B = *S. cambrica* type; C = *S. annulina* type. (After Rieth.)

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Chapter IV

EUPHYCOPHYTA

CHLOROPHYCEAE (*continued*)

OEDOGONIALES, CHAETOPHORALES, SIPHONOCLADALES, DASYCLADALES

* OEDOGONIALES

Three genera, *Oedogonium*, *Oedocladium* and *Bulbochaete* are comprised in this order. They are characterized by the presence of motile bodies with a ring of cilia around their anterior end. Because of this they were placed in earlier classifications in a special group called the Stephanokontae. The mode of ordinary cell division is also unique (see below). Sexual reproduction is by means of an advanced type of oogamy (see below) not found in any other order. These characters indicate that the order represents a specialized end line in the evolution of the green algae. The species are all fresh water and their taxonomy is difficult because it depends on a knowledge of the sexual plants and type of reproduction.

* *Oedogonium* (*oedo*, swelling; *gonium*, vessel). Figs. 35, 36

The three genera, *Oedogonium*, *Oedocladium* and *Bulbochaete*, which comprise this order were at one time classed as a separate group, the Stephanokontae. Under the new scheme of classification, however, they must be regarded, together with the other members of the old Isokontae, as forming the Chlorophyceae.

In *Oedogonium* the thallus consists of long unbranched threads which are attached when young, though later they become free-floating, whilst in the other two genera the filaments are commonly branched. Each cell possesses a single nucleus together with an elaborate reticulate chloroplast containing numerous pyrenoids. The cell wall contains, according to some workers, an outer layer of a chitinous material, and if they are correct this is of great interest because chitin is essentially an animal substance. The chromosomes of *Oedogonium* are especially interesting among those of the

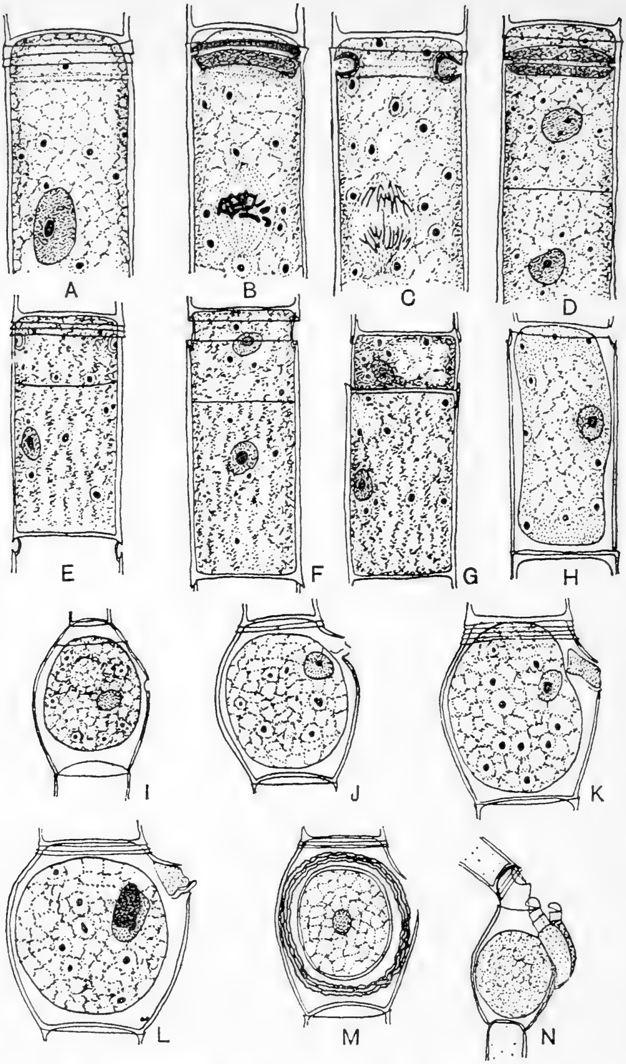

Fig. 35 *Oedogonium.* A–G, stages in cell division in *Oe. grande* (×526). B, C, formation of ring. F, G, expansion of ring to form new cell. H, formation of aplanospore in *Oe. nebraskense.* I, *Oe. ciliatum,* position of antherozoid 2 hours after entering egg. J–M, stages in fertilization of ovum of *Oe. americanum.* K, entrance of sperm. L, fusion of gamete nuclei. M, zygote. N, *Oe. kurzii,* dwarf male (×175). (A–M, after Ohashi; N, after Pringsheim.)

algae in that they have thickened segments at intervals along their length.

Vegetative cell division is so peculiar and characteristic that many accounts of the process have appeared. A thickened transverse ring, which develops near the upper end of the cell, first enlarges and then invaginates, the much thickened wall being pushed into the interior of the cell. Nuclear division now takes place near this end of the cell and a septum is laid down between the two daughter nuclei. Next, the outer parent cell wall breaks across at the ring and the newly formed membrane stretches rapidly now that the pressure is released — a matter of about fifteen minutes — so that a new cell is interposed between the two old portions. The new transverse septum becomes displaced by differential growth of the two daughter cells so that it finally comes to rest just below the fractured parent wall, and it is evident that the new longitudinal wall of the upper cell is almost entirely composed of the stretched membranous ring. The old walls form a cap at one end and a bottom sheath at the other, and as successive divisions always occur at the same place, a number of caps develop there and give a characteristic striated appearance to some of the cells. This method of growth in *Oedogonium* may be either terminal or intercalary, but in the other two genera, as each cell can only divide once, there is usually only a single cap. This peculiar mode of division is unique, and although there is no trace of its ancestry, its constancy suggests that the group terminates a line of evolutionary development.

Vegetative reproduction commonly occurs by means of fragmentation, whilst asexual reproduction is secured through akinetes or multiflagellate zoospores, the formation of the latter being said to depend on the presence of free carbon dioxide in the water. The flagella, which may have one or two rings of granular blepharoplasts at their base, form a circular ring around an anteriorly situated beak-like structure. This is the typical oedogonian swarmer, one of which is produced by each cell, and there are two theories that have been put forward to explain its origin:

(*a*) The group arose independently from flagellate organisms which possessed a ring of flagellae. If this is true then there could be no real connexion with the other members of the Chlorophyceae.

(*b*) Several divisions of the two original blepharoplasts and flagella took place, thus resulting in the ring structure. If this is correct then development might well have occurred from a Ulotrichalean type of swarmer.

When the zoospore is ripe the cell wall ruptures near the upper end and the swarmer is liberated into a delicate mucilaginous vesicle, but this soon disappears, thus allowing the zoospore to escape. After remaining motile for about an hour the anterior end becomes attached to some substrate and develops into a holdfast, or else the zoospore flattens to form an almost hemispherical basal cell. The type of holdfast depends on the species and the nature of the substrate, a smooth surface inducing a simple holdfast and a rough surface inducing the development of a branched holdfast. Development of the one-celled germling can proceed along one of two lines, depending on the species:

(*a*) The single cell divides near the apex by the normal method described above, in which case the basal daughter cell persists as the attachment organ and the upper cell goes on to form the new filament.

(*b*) The apex of the cell develops a cap and then a cylinder of protoplast grows out pushing it aside, and when the protoplast has reached a certain length a cross-wall is formed at the junction of the cylinder and the basal cell. The upper cell subsequently develops along the normal lines.

Sexual reproduction is by means of an advanced type of oogamy, the development of sex organs being assisted by an alkaline pH and some nitrogen deficiency. In some of the species the oogonia and antheridia are produced on the same plant (*monoecious* forms): in other species the oogonia and antheridia appear on different filaments which are morphologically alike (*dioecious homothallic* forms). The species belonging to both these groups are termed *macrandrous* because the male filament is normal in size. There is a third group of species in which the male filament is much reduced and forms dwarf male plants. Such species are *dioecious* and *heterothallic* and they form the *nannandrous* group. The dwarf males arise from motile *androspores* which are formed singly in flat discoid cells, the *androsporangia*, produced by repeated divisions of ordinary vegetative cells. The androspores may be formed either in the oogonial filament — *gynandrosporous* species — or on other filaments that do not bear oogonia — *idioandrosporous* species (Fig. 36). In shape and structure the androspores are small editions of the zoospores, and after swimming about they settle on the wall of the oogonium or on an adjacent cell and germinate into a small male plant which is composed of a rhizoidal holdfast with one or two flat antheridia above, though in some cases only one antheridial cell without any rhizoidal portion is formed. Usually two antherozoids are freed from each antheridium into a delicate vesicle which later dissolves.

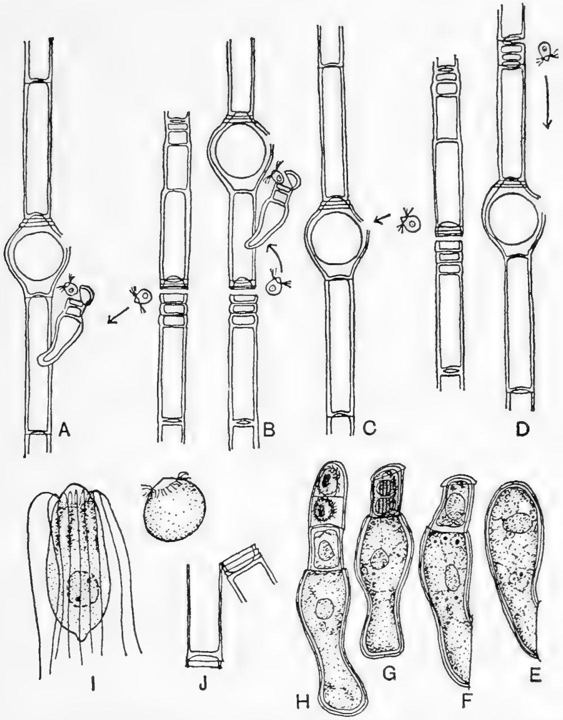

Fig. 36 *Oedogonium*. A, idioandrosporous nannandrous filament. B, gynandrosporous nannandrous filament. C, dioecious macrandrous filament. D, monoecious filament. E–H, stages in development of dwarf male plant (× 400). I, antherozoid (× 480). J, escape of zoospore (× 138). (A–D, after Mainx; E–I, after Ohashi; J, after West.)

The antherozoids are also like small zoospores, and if they fail to enter an ovum immediately they may remain motile for as long as thirteen hours. In the macrandrous monoecious species the antheridia are usually to be found immediately below the oogonia, where they arise by an ordinary vegetative division in which the upper cell subsequently continues to divide rapidly, thus producing a series of from two to forty antheridia. The antheridia frequently develop one day later than the oogonia, thus ensuring cross-fertilization.

The oogonia are enlarged spherical or ellipsoidal cells arising by one division in which the upper segment forms the oogonium and the lower a support cell, or else the latter subsequently divides to give antheridia. In some species the lower cell may also become an oogonium so that one can find a series of oogonia on one filament. Each oogonium contains one ovum with a colourless receptive spot situated opposite to the opening in the oogonium wall from which a small quantity of mucilage is extruded. The opening is either a very small pore, formed by gelatinization of a tiny papilla, or else a slit, but in either case there is an internal membrane forming a sort of conduit to the ovum. After fertilization the oospore often becomes reddish in colour and develops a thick membrane which is usually composed of three layers. The markings on the outer membrane are important taxonomically. At germination the protoplast divides into four segments, which may each develop flagella and escape as zoospores, or else they function as aplanospores that later give rise to zoospores. Meiosis takes place at the germination of the zygote so that the adult filaments are haploid. In one species it has been definitely established that two of the zygote segments ultimately develop into male plants and two into female plants. Zygote germination without meiosis is not uncommon, in which case it gives rise to what are presumably large diploid swarmers, and these develop into abnormally large threads that are always female. Oogonia appear on these diploid filaments and can be fertilized, but the fate of the zygote is unknown.

It remains to discuss the possible origin of the androspores, and there are two hypotheses that may be considered:

(*a*) The androspore is equivalent to a second and smaller type of asexual zoospore, such as the microzoospores found in some species of *Ulothrix*, but in the Oedogoniales they can no longer give rise to normal filaments. On this view the nannandrous forms are the more primitive, the macrandrous having been derived by the androsporangium acquiring the capacity to produce antheridia immediately and hence never appearing.

(*b*) The androspore is equivalent to a prematurely liberated antheridial mother cell which subsequently undergoes further development. On this view the macrandrous species are the more primitive. West (1912) considered that the dwarf males were to be regarded as reduced from normal male filaments, for in one species the male plants are intermediate in size. At present there does not appear to be any very convincing evidence in support of either theory.

* CHAETOPHORALES

A family in which the fundamental structure is the possession of both a basal and erect system of branched threads, this type of thallus being known as heterotrichous (cf. p. 312). Some authorities do not consider this character a sufficient distinction to warrant removal from the Ulotrichales (Fritsch). In some of the genera reduction has taken place and only the basal or erect system is now represented. Sexual reproduction is mostly isogamous but some species are anisogamous and a few oogamous.

* CHAETOPHORACEAE: *Stigeoclonium* (*stigeo*, sharp-pointed; *clonium*, branch). (*Myxonema*). Fig. 37

Many species are heterotrichous and the plants are frequently enclosed in a broad, watery gelatinous sheath. The chloroplast is band-like and often does not fill the entire cell, especially in the older parts of the thallus. The aerial part bears branches that terminate in a colourless hair, the degree and nature of the branching depending upon illumination, nutrition and the rate of water flow. There is no localized area for cell division in the aerial portion, but in the creeping system only the apical cells are meristematic. The prostrate system may be (*a*) loosely branched, (*b*) richly and compactly branched or (*c*) a compact disc, but the more developed the basal portion the less elaborate is the aerial and vice versa. Vegetative reproduction is by means of fragmentation, whilst sexual and asexual reproduction are the same as in *Draparnaldia* (see below), except that there is only one macrozoospore produced per cell. In two species, however, a third type of biflagellate swarmer is known, and hence reproduction in these species is comparable to that found in *Ulothrix* (cf. p. 51). These extra swarmers, which are probably the true gametes, are few in number but fusion between them is rare, probably because the plants are dioecious. In general the microswarmers seem to have taken over the function of the sexual biflagellate gametes. The zygote is said to germinate to zoospores, and these then give rise to the germlings in which the erect filament arises first and the prostrate portion subsequently or vice versa. By increasing the osmotic pressure or by adding toxic salts to the environment the thallus passes into a palmelloid state, whilst under other conditions akinetes can be formed. The plants are confined to well-aerated fresh water though they have also been found growing on fish living in stagnant water, but in these cases the movements of the fish presumably provide adequate aeration.

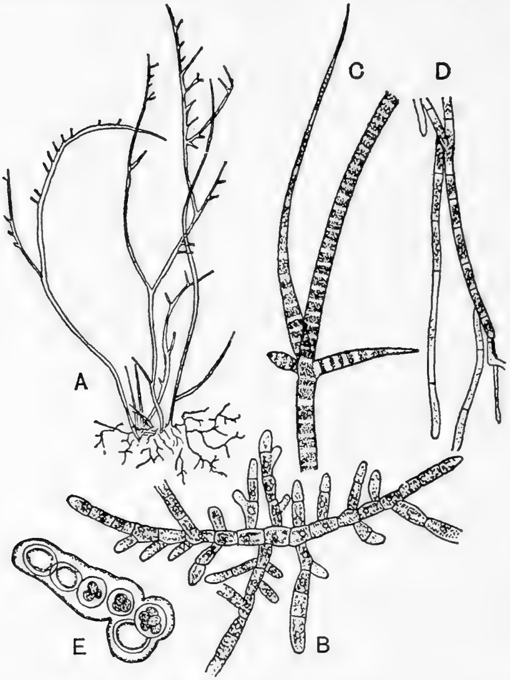

Fig. 37 *Stigeoclonium.* A, plant of *S. tenue.* B, basal portion of *S. lubricum.* C, aerial portion of *S. protensum.* D, rhizoids in *S. aestivale.* E, palmelloid state. (A–C, E, after Oltmanns; D, after Fritsch.)

CHAETOPHORACEAE: *Draparnaldia* (after J. P. R. Draparnaud). Fig. 38

The plants, which are confined wholly to fresh water, are represented principally by the aerial system, the prostrate system being entirely absent or else greatly reduced. The young plant is originally attached by means of a much reduced prostrate system together with rhizoids from one or two basal cells. The thallus, which is often invested by a gelatinous matrix of pectins, possesses a main axis composed of large barrel-shaped cells, each containing a small, entire or reticulate chloroplast and several pyrenoids. This axis is primarily for support, and it bears much branched laterals that normally grow out in tufts, the short cells composing the laterals being almost wholly filled by one entire chloroplast containing a single pyrenoid. The apices of these branches, which perform the functions of assimilation and reproduction, are often prolonged into a hair. In some species rhizoids develop at the base of the branches and grow downwards, thus clothing the main axis with a pseudo-cortex, but normal growth is generally restricted to a few cells of the thallus. When grown in culture with increased carbon dioxide or additional nitrate the plants take on a form very like that of *Stigeoclonium* (cf. above). Asexual reproduction is by

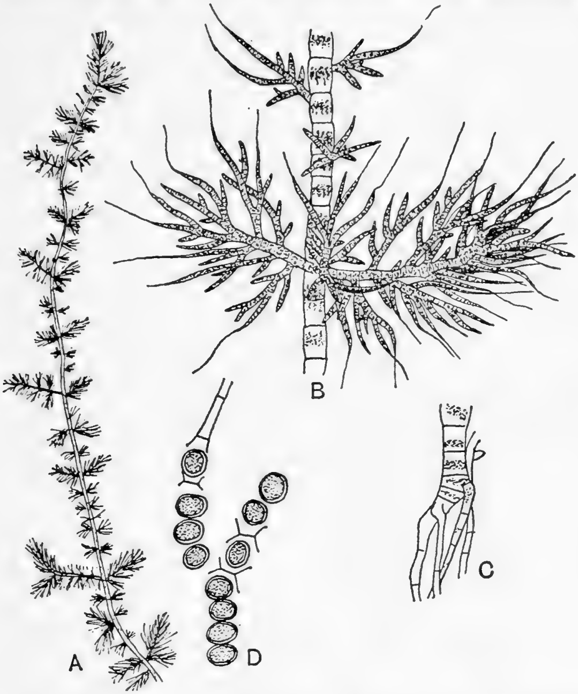

Fig. 38 *Draparnaldia.* A, portion of plant ($\times \frac{2}{3}$). B, same enlarged, C, rhizoids in *D. plumosa.* D, aplanospores of *D. glomerata.* (A, B, D, after Oltmanns; C, after Fritsch.)

means of quadriflagellate macrozoospores, one to four being produced in each cell. These, after swarming for a few minutes, settle, and germinate into a short filament which already possesses a hair at the four- or five-celled stage when it commences to put out rhizoids. Sexual reproduction is secured by means of quadriflagellate microswarmers or isogametes which fuse whilst in an amoeboid state, though these gametes may also develop parthenogenetically. The behaviour of the microswarmers demands further investigation as it does not seem to be clearly understood, nor has it been determined whether the plants are haploid or diploid. In *Draparnaldia glomerata* the nature of the swarmer is controlled by the pH of the medium, microswarmers being formed under alkaline conditions and macrozoospores under neutral or acid conditions.

Among the species and genera placed in the sub-family Erectae the species *Fritschiella tuberosa* is of more than passing interest. The plants possess four different vegetative systems: there is a prostrate system attached by a system of rhizoidal threads and giving rise to a primary erect system from which a secondary erect system arises. The prostrate system is perennial and also gives rise to the reproductive bodies.

Other genera exhibit signs of reduction, being represented by only the basal portion of the thallus. Such genera are the epiphytic disc-like *Chaetopeltis* (with emergent setae), the plate-like *Pseudendoclonium* and *Ulvella*, and the endophytic and endozoic *Entocladia* (*Endoderma*) consisting of branched threads ramifying in the host. This process of reduction has continued and reaches its climax in the next example.

* PLEUROCOCCACEAE: *Pleurococcus* (*pleuro*, box; *coccus*, berry). Fig. 39

The systematic position of this alga has varied considerably. By some authors it has been placed in the Chlorococcales whilst others have placed it in a special group, the Pleurococcales, but as the alga can occasionally develop branched threads there would seem to be evidence for regarding it as a much reduced member of the Chaetophorales. There are, it is true, almost equally sound arguments for the other systematic treatments of the genus, and its place at present must be largely a matter of opinion. *Pleurococcus* is terrestrial and forms a green coat on trees, rocks and soil, growing in situations where it may have to tolerate prolonged desiccation.

The cells, which are globose in shape and occasionally branched, are single, or else as many as four may be united into a group. Under certain cultural conditions branching may be copious. Each cell contains one chloroplast and there are no pyrenoids. The sole method of reproduction is through vegetative division in three planes when one may find up to fifty cells in a group. There is probably only one species, *P. naegelii*, all the other so-called species being reduced or modified forms of other algae. The resistance of the cells to desiccation is aided by a highly concentrated cell sap and a capacity to imbibe water directly from the air.

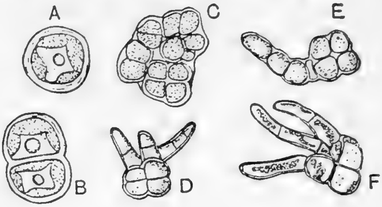

Fig 39 *Pleurococcus naegelii.* A, single cell. B, single-celled colony. C, normal colony. D–F, thread formation. (After Fritsch.)

TRENTEPOHLIACEAE: *Cephaleuros* (*cephal*, head; *euros*, broad). Fig. 40

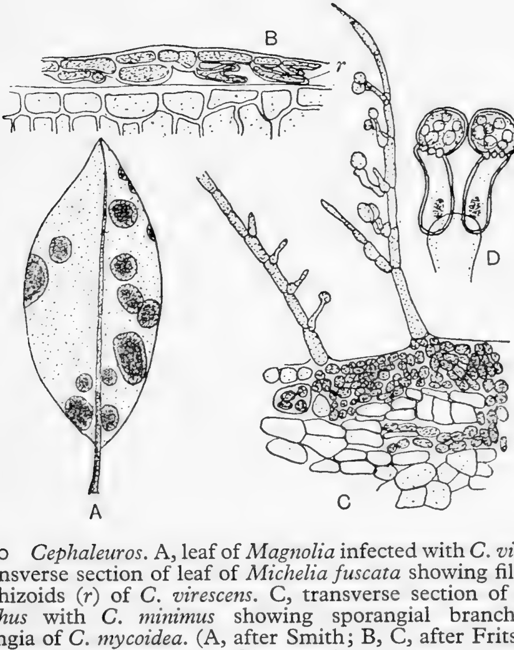

Fig. 40 *Cephaleuros.* A, leaf of *Magnolia* infected with *C. virescens.* B, transverse section of leaf of *Michelia fuscata* showing filaments and rhizoids (*r*) of *C. virescens.* C, transverse section of leaf of *Zizyphus* with *C. minimus* showing sporangial branches. D, sporangia of *C. mycoidea.* (A, after Smith; B, C, after Fritsch; D, after Oltmanns.)

These grow as epiphytes and parasites on and in the leaves of various phanerogams. The plants are composed of one or more branched interwoven threads from which vertical filaments arise that bear clusters of stalked sporangia very like those of *Trentepohlia*. Some species bear sterile erect filaments that terminate in hairs, whilst the parasitic species possess rhizoids which penetrate the cells of the host, although it has not been clearly established whether the host cells are killed before or after penetration. *Cephaleuros virescens* forms the red rust of the tea plant which may cause much economic damage, but the attack is only serious when the tea tree is growing slowly, because during periods of rapid growth the alga is continually being shed by exfoliation of the outer tissues. The disease cannot be controlled by spraying with poisons, but the bushes can be made less susceptible to attack by treating the soil with potash. Another species, *C. coffeae*, attacks the leaves of coffee plants. The genus is mostly confined to the tropics.

In recent years four species of this genus, including *C. virescens*, have been discovered in New Zealand growing under distinctly warm temperate conditions.

TRENTEPOHLIACEAE: *Trentepohlia* (after J. F. Trentepohl). (*Chroolepus*). Fig. 41

The species grow as epiphytes or on stones in damp tropical and sub-tropical regions, but they will also grow under temperate conditions if there is an adequate supply of moisture. The threads have a characteristic orange-red colouring due to the presence of β-carotene which is said to be a food reserve accumulated during periods of slow growth, but if this is so it would be expected that it should accumulate under favourable conditions of rapid growth and disappear under unfavourable conditions when growth is slow. This is a feature of its metabolism that would seem to require further investigation. The cells contain chloroplasts that are discoid or band-shaped and devoid of pyrenoids. Usually both prostrate and erect threads are present, though the latter are reduced in some species. Growth is apical, and the terminal cells often bear a pectose cap or series of caps which are periodically shed and replaced by new ones. The origin of the cap is not properly understood but it is thought to be due to a secretion, whilst its function may be either to reduce transpiration or else to act as a means of protection: alternatively, it may simply be a means of removing waste material. The cellulose walls are frequently thickened by parallel or divergent stratifications, whilst each septum between the cells may also have a single large pit which is penetrated by a protoplasmic strand. The cells are uninucleate when young and multinucleate when old, but the presence of the pigment makes the nuclei extremely difficult to distinguish. Vegetative reproduction is through fragmentation, whilst other means of reproduction are to be found in three different types of sporangia:

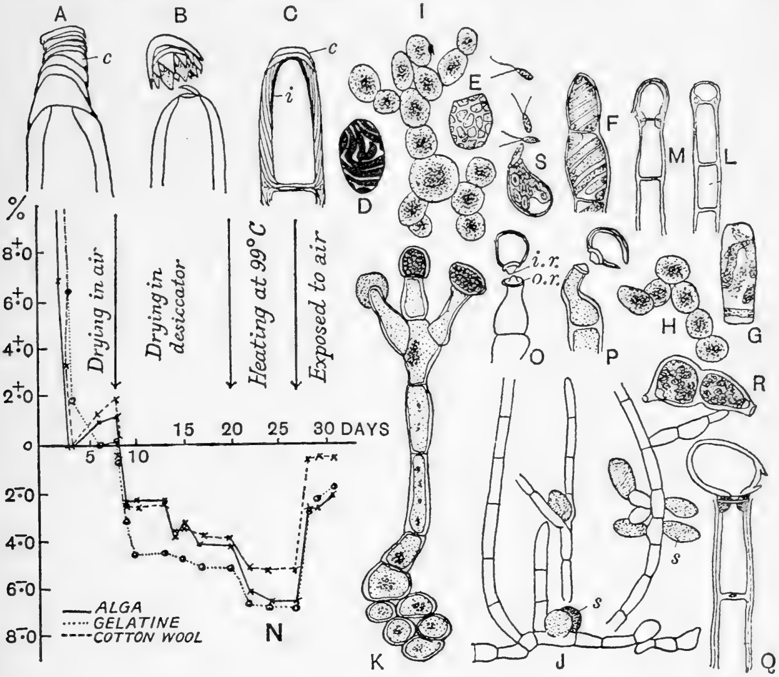

Fig. 41 *Trentepohlia*. A, B, *T. montis-tabulae* with pectin caps. C, *T. montis-tabulae*, cell structure. *c* = cap, *i* = innermost layer of cell wall. D–F, types of chloroplast. G, chloroplast in *T. iolithus*. H, I, *T. umbrina* fragmentation of prostrate system. J, threads of *T. aurea* bearing sporangia (*s*). K, *T. umbrina*, sporangia. L, M, two stages in the development of the 'funnel' sporangium in *T. annulata*. N, graph showing decreasing water contents of *Trentepohlia*, gelatin and cotton-wool on drying. O, P, *T. umbrina*, detachment of stalked sporangium. *i.r.* = inner, *o.r.* = outer thickening of sporangial septum. Q, mature 'funnel' sporangium, *T. annulata*. R, S, gametangia of *T. umbrina*. (A–G, J, L, M, O–Q, after Fritsch; H, I, K, R, S, after Oltmanns; N, after Howland.)

(*a*) *Sessile* sporangia that never become detached. These consist of enlarged cells which develop in almost any position and they produce biflagellate swarmers that may be isogametes.

(*b*) *Stalked* terminal or lateral sporangia that are cut off from an enlarged support cell which may give rise to several such bodies. The apical portion swells out to form the sporangium and cuts off a stalk cell underneath that frequently becomes bent. The dividing septum possesses two ring-shaped cellulose thickenings which may be connected with the detachment of the sporangium when it is mature. The detached sporangium is blown away and germinates under favourable conditions to give bi- or quadriflagellate swarmers.

(*c*) *Funnel*-shaped sporangia which are cut off at the apex of a cylindrical cell, the outer wall splitting later at the septum, thus liberating the sporangium, the subsequent fate of which is not definitely known. The sessile and stalked sporangia may occur on the same plant or else on separate plants. There has been no cytological work to show whether there is any alternation of generations and such an investigation would be highly desirable. In one species, on the other hand, reproduction is wholly by means of aplanospores.

Howland (1929) has investigated the physiology of the commonest species, *T. aurea*, in some detail and he found that:

(*a*) drought increases the resistance to plasmolysis;

(*b*) if the threads are dried first and then heated together with cotton-wool and gelatine, the results suggest that the threads hold water in a manner similar to that of cotton-wool, but that the loss of water on heating is comparable to that experienced by a colloid or gel under the same circumstances (cf. Fig. 41);

(*c*) in damp, warm weather only small cells are formed because cell division is relatively rapid;

(*d*) the threads can survive desiccation for at least six months;

(*e*) plasmolysis could only be produced in some of the cells by a 25 per cent solution of sea salt.

In many respects, e.g. the heterotrichous nature of the thallus, the different types of sporangia and the orange pigment, this alga is strongly suggestive of the more primitive brown algae. This feature, however, is discussed more fully in a later chapter (cf. p. 315).

Within the Trentepohliaceae there are several genera the species of which form a green discolouration on and in stones and shells of gastropods. Such genera are *Gongrosira* and *Gomontia*. These are very difficult to determine taxonomically. They are in need of study as some, at least, may represent stages in the life history of other algae. Recent work on *Gomontia polyrhiza* has shown that it has a life cycle of a large unicell alternating with a plate-like disc.

* COLEOCHAETACEAE: *Coleochaete* (*coleo*, sheath; *chaete*, hair). Fig. 42

Most of the species are fresh-water epiphytes attached to the host by small outgrowths from the basal walls, but there is one species that is endophytic in *Nitella*, one of the Charales (p. 115).

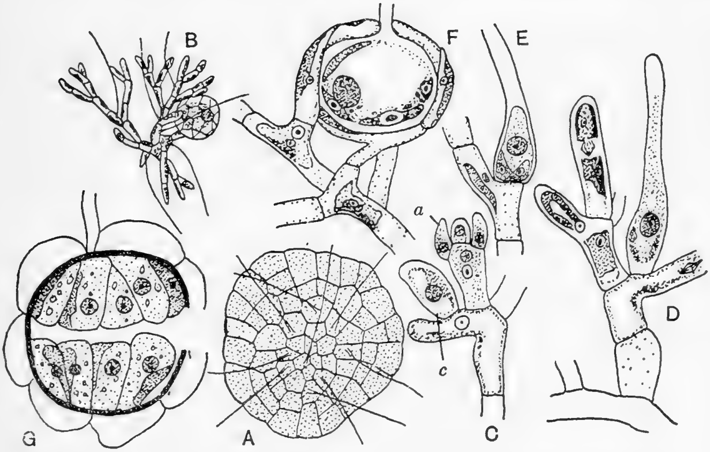

Fig. 42 *Coleochaete*. A, *C. scutata*, thallus with hairs (× 150). B, *C. pulvinata* with spermocarp (×45). C, *C. pulvinata* with antheridia (*a*) and young carpogonium (*c*). D, *C. pulvinata*, almost mature carpogonium. E, *C. pulvinata*, fertilized carpogonium, F, *C. pulvinata*, formation of envelope around fertilized carpogonium. G, *C. pulvinata*, mature spermocarp with carpospores. (A, B, after Smith; C–G, after Fritsch.)

Some of the species are truly heterotrichous whilst others only possess the prostrate basal portion, which is either composed of loosely branched threads or else is a compact disc. The growth of the erect filaments is by means of the apical cell whilst the basal cushion possesses a marginal meristem. Each cell contains one chloroplast with one or two pyrenoids, and although a characteristic sheathed bristle arises from each cell nevertheless in the old plants these may be broken off. These bristles develop above a pore in the cell wall through which the protoplast extrudes, whilst at the same time a membrane is secreted over the protruding bare protoplast. Asexual reproduction takes place in spring and early summer by means of biflagellate zoospores which have no eye-spot and are produced singly. After a motile phase the zoospore settles down and divides either (*a*) horizontally, when the upper segment develops into a hair and the lower forms the embryo disc, or (*b*) vertically, when each segment grows out laterally; in either case it will be noted that hair formation takes place at a very early stage.

Sexual reproduction is by means of a specialized oogamy, some of the species being dioecious and the remainder monoecious. The female organs, or *carpogonia*, are borne on short lateral branches and subsequently undergo displacement. Each carpogonium possesses a short neck or trichogyne (the long neck of *Coleochaete scutata* being an exception) the top of which bursts when the carpogonium is mature. In the disc forms the carpogonia originate as terminal bodies on the outside of the disc, but as the neighbouring cells continue growth they eventually become surrounded and appear to be in the older part of the thallus. The antheridia develop in clusters at the end of branches (*C. pulvinata*) or from prostrate cells. They finally appear as small outgrowths cut off from a mother cell with stages in their development that are strongly reminiscent of the Rhodophyceae (cf. p. 217). Each antheridium produces one biflagellate colourless antherozoid which has been contrasted with the non-motile rhodophycean spermatium.

After fertilization the neck of the carpogonium is cut off and the basal part enlarges; branches arise from the underlying cells and eventually surround the oospore where they form a red or reddish brown wall, though in the disc forms this wall is only formed on the side away from the substrate. At the same time the enclosed oospore develops a thick brown wall and the cells of the outer envelope then die. The oospore, or *spermocarp*, hibernates until spring when it becomes green and divides into sixteen or thirty-two cells, and these, when the wall bursts, each give rise to a single swarmer which must be regarded as a zoospore. Meiosis takes place at the segmentation of the zygote so that there is only the haploid generation. On the other hand, some observers have recorded the development of dwarf asexual plants before the reappearance of new sexual ones, but this is a phase of the life history that demands re-investigation, for if it is correct it may mean that there is an alternation of two unlike generations, an unusual phenomenon in the Chlorophyceae. Under certain conditions the cells will also produce aplanospores. The relation of this genus, with its advanced oogamy, to the other green algae is by no means clear, and although in many of its features the sexual reproduction is akin to that of the Rhodophyceae, it is commonly regarded as parallel evolution rather than as indicating a more direct relationship (cf. p. 326).

* SIPHONOCLADALES

Until 1935 this represented a well-established order, but in that year Fritsch placed most of the genera as septate members of the Siphonales but retained the Cladophoraceae as a separate order, the Cladophorales, with affinities to the Ulotrichales. In 1938 Feldmann re-established the order and suggested a relationship on the one hand with the Siphonales *via Valonia* and *Halicystis* and on the other hand with *Chaetophora* and *Ulothrix*. More recently Egerod (1952) has accepted the order but, unlike Feldmann, has continued to exclude the Cladophoraceae from it. There seems to be inadequate justification for this exclusion, and in fact the families in the order present a more or less orderly sequence of evolution, commencing from the Cladophoraceae. The members of the order are all septate at some stage of their existence, the cells or segments being multinucleate and possessing reticulate chloroplasts. Such plants are said to be partially coenocytic. A number of the more advanced genera have a specialized mode of cell division known as segregative cell division. In this process the contents of a single cell become separated by a number of cell walls so that one parent cell gives rise to a number of new cells which then enlarge.

Morphologically the order can be subdivided into the filamentous and vesicular forms. The former comprise genera such as *Lola*, *Rhizoclonium*, *Chaetomorpha*, *Cladophora* and *Microdictyon*, whilst the latter contains *Siphonocladus*, *Valonia*, *Boodlea* and *Dictyosphaeria*. It is the vesicular forms that mostly possess segregative cell division.

CLADOPHORACEAE: *Chaetomorpha* (*chaeto*, hair; *morpha*, structure-like). Fig. 43

The plants consist of simple unbranched filaments which are either attached or free-living. The multinucleate cells are large and usually barrel-shaped, and in some species, e.g. *C. darwinii*, are so large they can be seen by the naked eye. Reproduction can take place from all cells except the basal one and is by means of zoospores or gametes. In some species alternation of generations has been demonstrated and it probably occurs in most. The species occur in rock-pools and attached to rocks along the sea-shore.

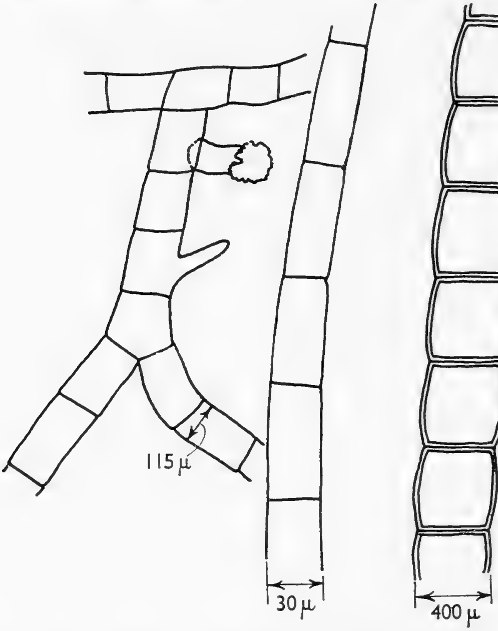

Fig. 43 Left to right: *Rama antarctica, Lola implexa, Chaetomorpha aerea.*

CLADOPHORACEAE: *Lola* (a thread). Fig. 43

This genus comprises fine, hair-like, unbranched filaments, usually free-living, that formerly were included in the genera *Chaetomorpha* and *Rhizoclonium*. The number of nuclei per cell are fewer than in the former genus (5–20), and the small rhizoidal branches of the latter genus are lacking. Most of the species occur on salt marsh muds.

CLADOPHORACEAE: *Rama* (a branch). Fig. 43

The species of this genus, mostly South Pacific, possess a few true branches such as are found in *Cladophora* (see below), but they also possess the short rhizoids characteristic of *Rhizoclonium*. The branches are each so long that they can also be mistaken for species of *Chaetomorpha*. On account of its characters this genus appears to occupy an important phylogenetic position (see p. 311).

CLADOPHORACEAE: *Rhizoclonium* (*rhizo*, root; *clonium*, branch). Fig. 44

The species are found in marine, brackish or fresh waters, several being very abundant on sand or mud flats. The uniseriate filaments possess occasional or numerous short septate or non-septate colourless rhizoidal branches. The number of nuclei per cell ranges from 1–4, the actual number being related to the volume of the cell, though it may also apparently be influenced by the presence of epiphytes. Asexual reproduction is by means of biflagellate zoospores which in some species are said to possess unequal flagella. Anisogamy similar to that of the related genus *Urospora* has been recorded for *R. lubricum*. *Urospora* is of interest because the zygote first produces a *Codiolum* stage (so called after the alga it resembles), which is considered to be diploid, and this gives rise to zoospores from which the normal filaments develop. If this interpretation is correct we have a rare example within the Chlorophyceae of alternation of morphologically dissimilar generations (see also below — *Spongomorpha* and *Halicystis* (p. 96)).

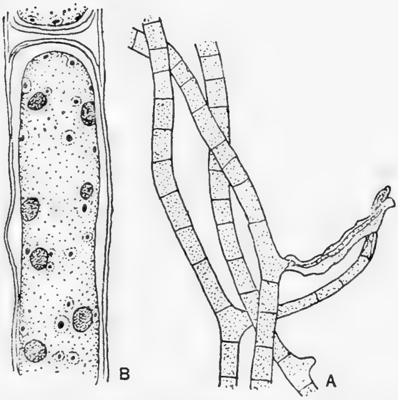

Fig. 44 *Rhizoclonium*. A, part of filaments of *R. riparium* (×90). B, cell of *R. hieroglyphicum* to show structure of chloroplast. (A, after Taylor; B, after Fritsch.)

* CLADOPHORACEAE: *Cladophora* (*clado*, branch; *phora*, bearing). Figs. 45, 46

This is a widespread genus that occurs in both fresh and saline waters. The sessile forms are attached by means of branched septate rhizoids, but some of them (e.g. *C. fracta*) may become free-living later, whilst there is one complete section (*Aegagropila*) which is wholly free-living, the species existing as ball-like growths. The *Cladophora* thallus is composed of branched septate filaments, each cell usually being multinucleate, though cells with one nucleus have been recorded. The elongate reticulate chloroplasts, containing numerous pyrenoids, are arranged parietally with processes projecting into the central vacuole, but under some conditions they break up into fragments. There would not appear to be much present support for the old view that the chloroplast of each cell is a complex of numerous disc chloroplasts. The cell walls exhibit stratification as they are composed of three layers, an inner zone, a median pectic zone, and an outer zone which is said to be chitinous. There is very little production of mucilage, and this probably accounts for the dense epiphytic flora that is frequently found associated with species of this genus. The branches arise towards the upper end of a cell and later on are frequently pushed farther up, a process known as *evection*, thus giving the appearance of a dichotomy. In *C. verticillata* branching is more or less restricted to the base and the branches are long and simple like a *Chaetomorpha* thread. All the cells are capable of growth and this is especially evident in cases of injury, but normally most of the plant growth is apical and in the section *Aegagropila* is wholly confined to the apex. At cell division the new septa arise from the outer layers and develop inwards, leaving in the process triangular-shaped spaces which later on may become filled with pectic substances or folded lamellae. Additional supporting rhizoids usually develop from the basal and subbasal cells of the lower branches.

In the *Aegagropila* group the species can exist as (*a*) threads, (*b*) cushions and (*c*) balls. The destruction of the old threads in the centre of the ball results in a cavity which may become filled with water, gas or mud. In Lake Söro the water in April and May is sufficiently free of diatoms for light to penetrate to such an extent that photosynthesis increases and so much gas collects in the centre of these balls that they float to the surface. Their characteristic

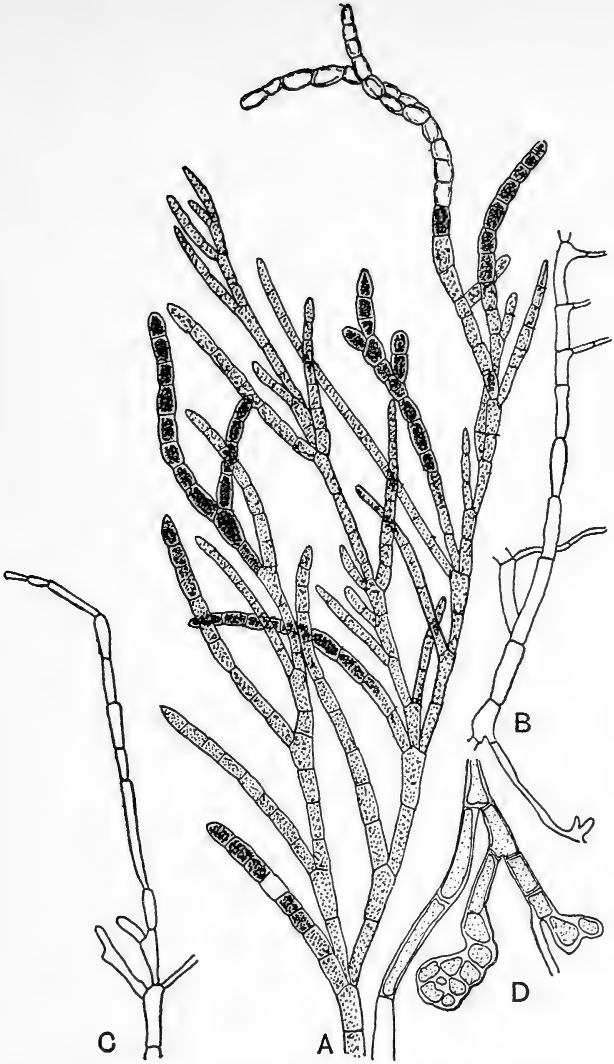

Fig. 45 *Cladophora*. A, plant with sporangia. B, shoot of *Aegagropila holsatica* bearing rhizoids. C, stolon of *Ae. holsatica*. D, rhizoids of *Spongomorpha vernalis* developing storage cells at the apices. (A, after Oltmanns; B, C, after Acton; D, after Fritsch.)

shape is brought about by a continual rolling motion over the soil surface under the influence of wave action, and hence the 'ball' forms are found near the shore whilst the 'thread' and 'cushion' forms are to be found farther out in deeper water where there is less motion. The harder the floor the more regular is the shape of the balls, but even so the ball structure would also appear to be inherent in the alga because 'balls' have been kept in a laboratory for eight years without losing their shape. The following types of branches have been recognized in the *Aegagropila* forms: (*a*) rhizoids; (*b*) cirrhoids, both these and the rhizoids being neutral or non-reproductive branches; (*c*) stolons or vegetative reproductive branches. Many of the species of *Cladophora* are perennial. In some of the fresh-water species certain cells may become swollen

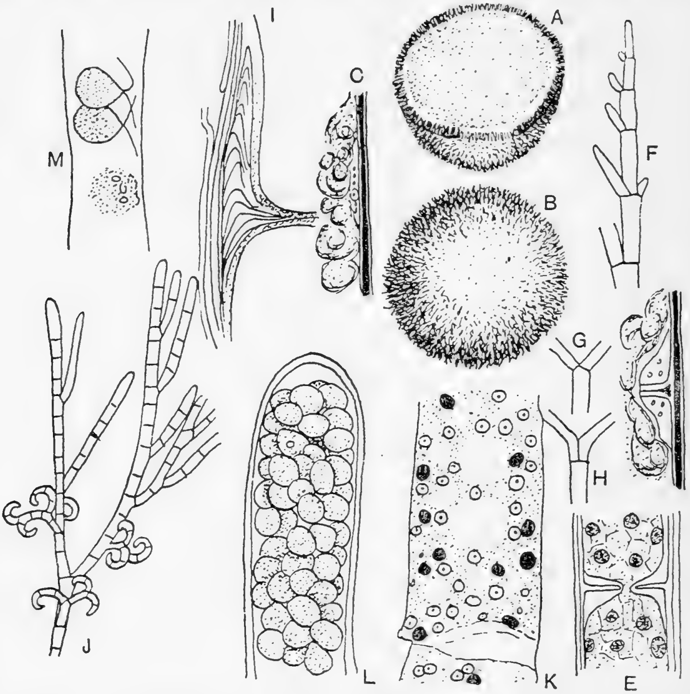

Fig. 46 *Cladophora*. A, ball of *Aegagropila holsatica* cut through and the dirt removed (× $\frac{3}{4}$). B, same before cutting (× $\frac{3}{4}$). C, *C. glomerata*, commencement of septum formation. D, *C. glomerata*, second stage in septum formation. E, *C. glomerata*, septum almost complete. F, diagram illustrating evection. G, H, types of branching. I, *C. glomerata*, structure of wall at a septum. J, *Spongomorpha coalita* with hook branches. K, *C. callicoma*, structure of chloroplast with nuclei and pyrenoids. L, *Ae. Sauteri*, zoospores in zoosporangium. M, *Ae. Sauteri*, zoospores. (A, B, after Acton; C–K, after Fritsch; L, M, after Nishimura and Kanno.)

to form akinetes in which the walls are thickened and food is stored.

In the section *Aegagropila* most of the species reproduce vegetatively, but biflagellate swarmers have been reported for one species, *Ae. Sauteri*, and these are interesting in that they may germinate whilst still within the sporangium (Fig. 46). Asexual reproduction in the other species, excluding the section *Aegagropila*, is by means of quadriflagellate zoospores (biflagellate in two species) which escape through a small pore in the cell wall. Biflagellate isogametes are the means of sexual reproduction, all the species so far investigated being dioecious. The zygote develops at once without a resting period. In a number of species alternation of two morphologically identical haploid and diploid generations has now been established with meiosis taking place at zoospore formation. In one or two cases, e.g. *Cladophora flavescens*, the zoospores sometimes fuse, and this irregular behaviour is very comparable to similar phenomena found in the more primitive brown algae (cf. p. 130).

In a few species there is an odd or heterochromosome, and in a cell the number of zoospores with the odd chromosome are equal to the number lacking it. Haploid plants of *C. suhriana* have six or seven chromosomes, whilst in *C. repens* the cells contain either four or five. In a fresh-water species, *C. glomerata*, a wholly different type of life cycle is known, and this difference may perhaps be compared with the various cycles found for *Ectocarpus siliculosus* under different conditions (cf. p. 131). Gametes and zoospores are both formed on diploid plants and meiosis takes place at gamete formation so that there is no haploid generation. Whilst zoospore formation takes place all the year round gametes only appear in the spring, but the reason for this seasonal restriction is not understood. Parthenogenetic development of gametes has also been recorded in a number of species. Of the species so far investigated the chromosomes appear to be present in multiples of 4, and this probably indicates polyploidy. The following diploid chromosome numbers have been recorded: *C. repens* 8 + 1, *C. suhriana* 12 + 1, *C. flavescens* 24, *C. flaccida* 24, *C. pellucida* 32, *C. glomerata* 92 + 4 (octoploid).

The subgenus *Spongomorpha*, in which the threads are held loosely together by rhizoids, but not so compactly as in *Aegagropila*, will have to be regarded as a separate genus, because recent work has shown that in one species, *S. coalita*, the asexual generation is the small endophyte *Codiolum petrocelidis* (Fan, 1959). Both this and *Acrosiphonia* differ from *Cladophora* in their cell wall material which is a further reason for treating them as separate genera.

ANADYOMENACEAE: *Microdictyon* (*micro*, small; *dictyon*, net). Fig. 47

Branching in these plants is usually multiple in one plane, and sooner or later cells of the branches become attached to those of other branches by means of special pads or *tenaculae*, so that a flat net-like thallus eventually results. *M. mutabile* from New Zealand can exist in a spongiose form with very few anastomoses so that it can easily be mistaken for a coarse species of *Cladophora*, but it also gives rise to the typical net thallus. In those species that have been investigated, sexual reproduction is isogamous and there is alternation of isomorphic generations. The same is also true of *Anadyomene stellata*.

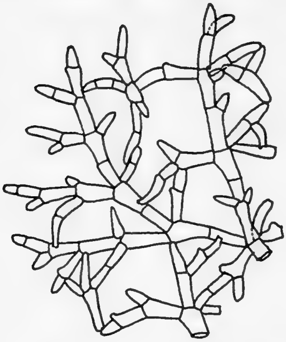

Fig. 47 Portion of net of *Microdictyon mutabile* (× 24). (After Dellow.)

SIPHONOCLADACEAE: *Cladophoropsis* (like *Cladophora*). Fig. 48

As the name implies, the species are very like those of *Cladophora* from which they differ, however, in the more or less general lack of a cell wall at the base of branches and also in possessing true segregative division within the cells, the contents of one cell rounding off into two or more portions which become cut off by new walls. In more advanced members of the family, e.g. *Siphonocladus*, the cell walls are even fewer.

* VALONIACEAE: *Valonia* (after the Valoni, an Italian race). 'Sea-bottle'. Fig. 49

In this genus, which is restricted to warm waters, the young coenocyte consists of one large vesicle whilst the old one becomes divided up into a number of multinucleate segments. It has been suggested (cf. p. 426) that it should really be regarded as a coenocytic wall enclosing a fluid, but this interpretation leads to difficulties. In some respects, therefore, the genus provides a link with the Siphonales. The macroscopic club-shaped vesicle is attached to the substrate by rhizoids of various types. There is a lobed chloroplast that congregates with the cytoplasm at certain points in the older plants and then each group is cut off by a membrane, thus producing a number of marginal cells. This type of division in which groups of cytoplasm are formed in the parent cell and then surrounded by new membranes is known as segregative cell division. The cells do not necessarily form a continuous layer and are frequently restricted to the basal region where they may develop rhizoids, whilst in other species they are nearer to the apex where they may give rise to proliferations. The lower cells can form short creeping branches, and as these bear more of the erect vesicles a tuft of plants is produced.

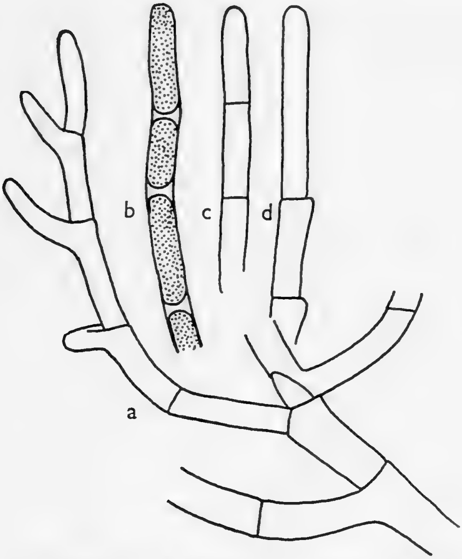

Fig. 48 *Cladophoropsis membranacea.* a, part of plant showing characteristic branching; b–d, stages in segregative cell division, wall formation and start of branching (b–d, after Börgesen) (all × 15).

Reproduction takes place by means of bi- or quadriflagellate swarmers, which are liberated from the cells through several pores, and although no sexual fusion has been seen as yet, nevertheless meiosis occurs in *V. utricularis* at swarmer formation. The plants are therefore presumably diploid, a condition that is also characteristic of most of the Siphonales. The reproductive cells may encyst themselves, and it has been suggested on this evidence that the plant is a colonial aggregate of coenocytic individuals resulting from the retention of cysts that have developed *in situ*. The correctness or otherwise of this interpretation can only be obtained through a better knowledge of their phylogenetic history and the reproductive processes of other members of the group.

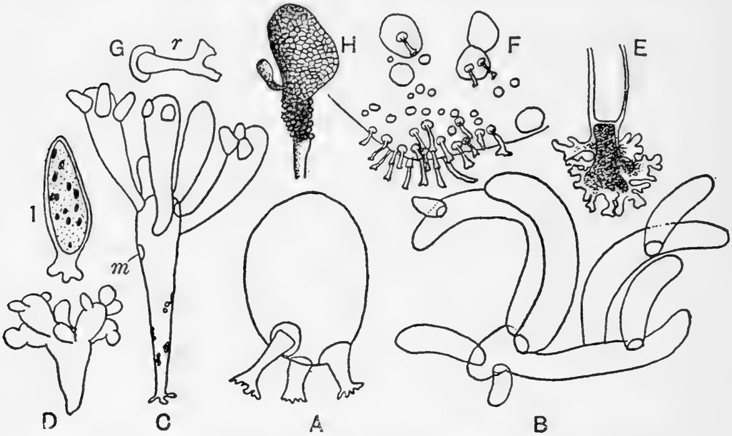

Fig. 49 *Valonia*. A, young plant of *V. ventricosa*. B, young plant of *V. ultricularis* (× 1·4). C, adult plant of same. *m* = marginal cell. D, plant of *V. macrophysa* (× 0·8). E, rhizoid of *V. utricularis*. F, rhizoids from marginal cells at base of vesicle of *V. ventricosa*. G, single marginal cell and rhizoid (*r*) of *V. ventricosa*. H, *V. utricularis* fruiting. I, *V. utricularis*, germinating swarmer. (B, D, after Taylor; rest after Fritsch.)

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DASYCLADALES

Formerly the members of this order were included in the Siphonocladales, but since they possess certain distinct characteristics they are best treated as a separate order. The thallus body is first characterized by the whorled (verticillate) arrangement of the lateral branches (in *Acetabularia* they are fused to form a disc), and secondly by the fact that the plastids are independent, disc-like, and not reticulate as in the Siphonocladales. In the species that have been investigated the vegetative thallus appears to be uninucleate. Prior to gamete formation the single primary nucleus fragments into smaller portions which may subsequently change shape in either the rhizoids or the main siphon. The small daughter nuclei eventually migrate into the gametangia. This peculiar nuclear behaviour has been established for *Acetabularia*, *Cymopolia* and *Neomeris* (Fig. 50). There is reason to believe that the adult plants are all diploid.

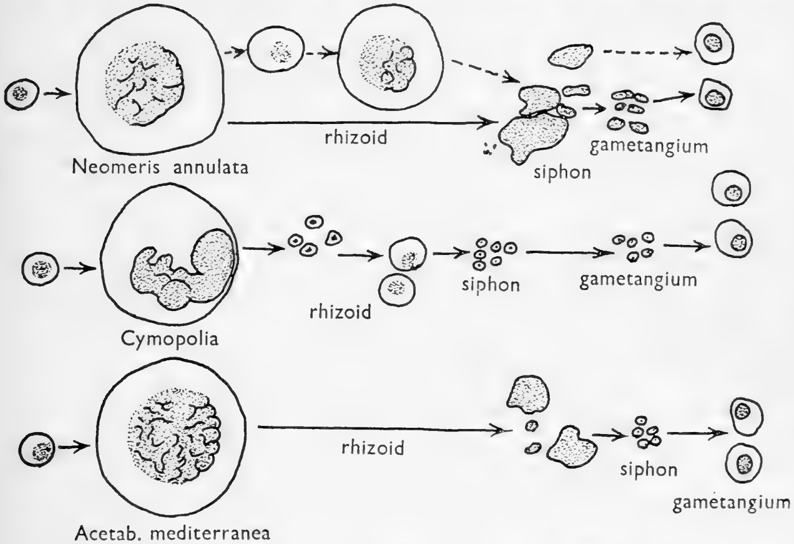

Fig. 50 Behaviour of the nucleus in certain members of the Dasycladales. Break-up of the large nucleus occurs in the rhizoid and the fragments, which may change shape, move up the siphon into the gametangia. (After Dao.)

In a number of genera the gametes are produced from special cysts (cf. *Acetabularia*). The order is very ancient and has apparently not changed very greatly: a large number of fossil forms are known (cf. pp. 297–30). The genera are primarily confined to warm waters and in many there is extensive calcification.

DASYCLADACEAE: *Dasycladus* (*dasy*, hairy; *cladus*, branch). Fig. 51

The family Dasycladaceae is very ancient and was formerly much more widely spread since sixty fossil genera are known whilst there are only ten living today (cf. p. 297). *Dasycladus* forms dense growths, up to 5 cm. in height, in shallow waters where the plants are anchored by means of richly branched non-septate rhizoids. The central axis bears dense whorls of profusely branched laterals which are arranged alternately above each other. The branches arise in whorls of four immediately below the apex of the parent cell, to which they are united by narrow constrictions, and although the rest of the main axis is impregnated with lime throughout there is none at the constrictions. If the axis of a branch is decapitated a new apex is regenerated, whilst if a rhizoid is cut off and inverted it develops a normal apical cell. Short-stalked spherical gametangia arise at the apices of the major branches in the upper half of the plant and are cut off by a septum. The plants are essentially dioecious and produce isogametes that sometimes exhibit relative sexuality.

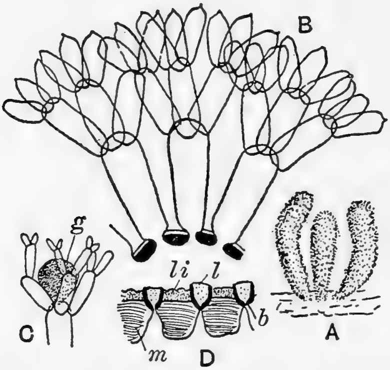

Fig. 51 *Dasycladus clavaeformis*. A, plants. B, assimilatory filaments showing mode of branching. C, gametangium (*g*). D, thickenings at base of assimilatory filaments. *b* = point of origin of branch, *l* = base of lateral, *li* = calcified wall, *m* thickened base of wall. (After Fritsch.)

Dasycladaceae: *Neomeris* (*neo*, new; *meris*, part). Fig. 52

This is a calcareous tropical genus which has been in existence from the Cretaceous era. The much calcified adult plants have the appearance of small worm-like masses with an apical tuft of hairs, whilst very young plants consist of an erect *Vaucheria*-like filament with a tuft of dichotomously branched filaments of the apex. In the adult plant the ultimate branches terminate in long deciduous hairs, whilst the apices of the next lower order of branches dilate and become pressed together, thus producing a compact surface with a pseudo-parenchymatous appearance (cf. Fig. 52E). Calcium

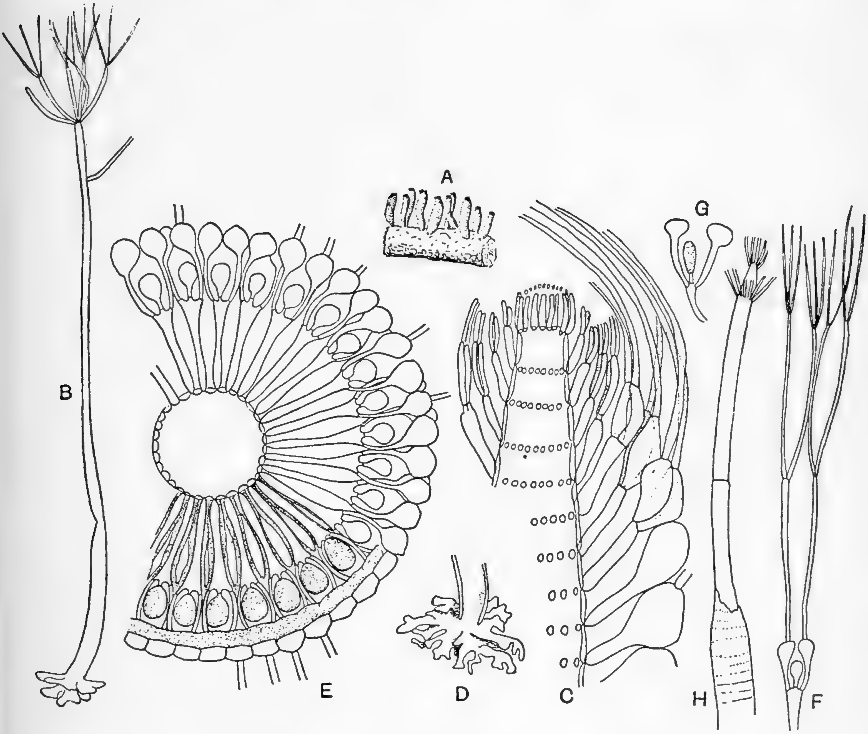

Fig. 52 *Neomeris*. A, plants of *N. annulata* (× ½). B, young plant of *N. dumetosa* (× ¼). C, longitudinal section through apex of *N. dumetosa* (× ⅓). D, rhizoid in *N. dumetosa* (× ¼). E, transverse section of thallus of *N. dumetosa* in middle of calcified area (× ⅓). F, *N. dumetosa*, assimilating filaments with sporangium (× ⅓). G, *N. annulata*, sporangium (× 33). H, regeneration of an injured axis (× ¼). (A, G, after Taylor; rest after Church.)

carbonate is deposited wherever there is a mucilage layer and an aggregation of the chloroplasts, but apparently both these conditions must be fulfilled before lime can be laid down. The principal interest of this form lies in its morphological resemblance to certain fossil genera (cf. p. 301). The species are dioecious and sexual reproduction is isogamous. In this genus the primary nucleus changes shape before fragmenting at gamete formation (Fig. 50).

DASYCLADACEAE: *Acetabularia* (*acetabula*, little cup; *aria*, derived from). Fig. 53

This is a lime-encrusted genus which is confined to warm waters, extending up as far as the Mediterranean in the northern hemisphere. The plants consist of an erect elongate axis bearing one or more whorls of branched sterile laterals with a single fertile whorl at the apex. The sterile whorl or whorls are frequently shed in the adult plant leaving a mark or annulus on the stem to show where they were formerly attached. The fertile whorl is composed of a series of long sac-like sporangia which are commonly fused, though they are sometimes separate: these are borne on short basal segments which are morphologically equivalent to the primary branches. The basal segments also bear on their upper surface small projections, with or without hairs, which form the *corona*, whilst in one section of the genus there is also an inferior corona on the lower surface. In *A. mediterranea* two or three years elapse before the plant attains to maturity. In the first year the branched holdfast produces an upright umbilical thread, together with a thin-walled, lobed outgrowth that penetrates the substrate in order to function as the perennating organ. The aerial part dies, and in the next year or years a new cylinder arises that bears one or more sterile whorls of branches, until in the third or even a later year, a shoot develops which produces one deciduous sterile whorl and a single fertile whorl or umbrella. Each sac-like sporangium, or umbrella lobe, gives rise to a number of multinucleate cysts which are eventually set free through disintegration of the anterior end of the sporangium. In the spring biflagellate isogametes are liberated from these cysts and fuse in pairs, or else develop parthenogenetically. Use has been made of the uninucleate condition to determine the effect on morphology of varying ratios of nuclei of different species. This is possible because part of one species can be grafted onto another. In particular *A. crenulata* and *A. mediter-*

ranea have been used with systems ranging from 4 cren. nuclei: 0 med. to 0 cren.: 4 med. nuclei. The morphological features of the discs exhibit a mixing effect but the form produced is not always strictly proportional to the number of nuclei of the two different species.

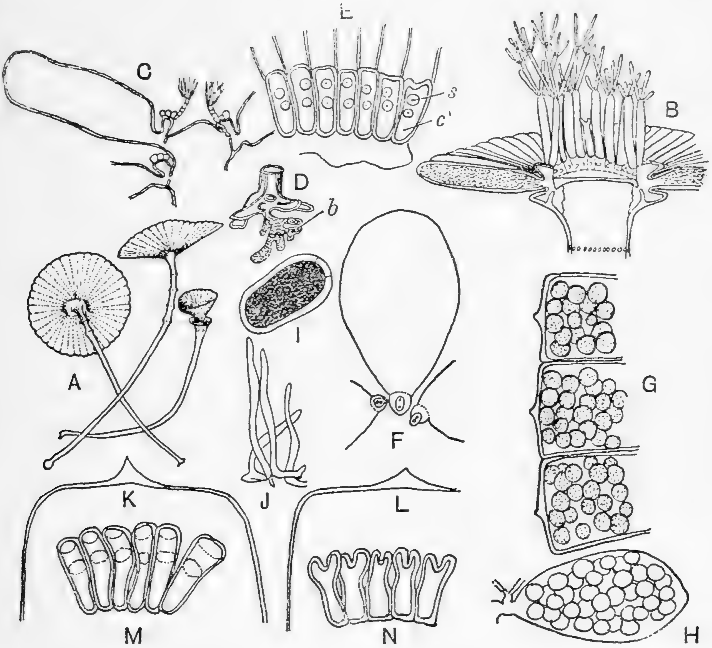

Fig. 53 *Acetabularia*. A, plant of *A. crenulata* (× 0·8). B, apex of *A. mediterranea* showing corona. C, apex of *A. moebii* showing two superposed fertile rhorls. D, *A. mediterranea*, attachment rhizoid and perennating vesicle (*b*). E, *A. crenulata*, cells near centre of thallus, showing superior corona (*c*) and leaf scars (*s*). F, *A. pusilla*, vegetative ray segment (× 44). G, fertile lobes of *A. schenkii* with cysts (× 44). H, cysts in *A. pusilla* in a single lobe of the umbrella (× 37). I, single cyst of *A. mediterranea*. J, young plant in first year. K, L. *A. crenulata*, apieces of ray segments (× 37). M, *A. crenulata*, superior corona (× 37). N, *A. crenulata*, inferior corona (× 37). (A, F–H, K–N, after Taylor; B–E, I, J, after Fritsch.)

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Chapter V

EUPHYCOPHYTA

CHLOROPHYCEAE (*continued*)

SIPHONALES, CONJUGALES, CHAROPHYCEAE

* SIPHONALES

This group is characterized primarily by possession of a coenocytic structure in which true septa are rare or absent, the coenocyte normally having a cytoplasmic lining surrounding a central vacuole and containing numerous disc-shaped chloroplasts. The order can be subdivided into two divisions, the Eusiphoneae (Halicystidaceae, Bryopsidaceae, Codiaceae) where the membrane contains mannan and there is only one type of plastid, and the Caulerpeae (Caulerpaceae, Udoteaceae) where the cellulose of the membrane is replaced by zylan and where the thallus contains photosynthetic chloroplasts and amylogenic leucoplasts. Some workers suggest that the difference is sufficient to justify the establishment of separate orders. The order may be polyphyletic in origin, and the fact that it reaches its maximum development in warm waters is possibly significant, not only in respect of the phylogeny of the group itself, but also in considering the evolution of the Chlorophyceae as a whole. Most of the genera possess the power of regeneration to a marked degree, but this can perhaps be regarded as a primitive character that has persisted throughout the course of time. In all cases so far studied the thallus is diploid and it seems that the function of the haploid generation (sexual reproduction) has been transferred to it. In those cases where it is known, sexual reproduction is anisogamous. In some of the tropical genera, e.g. *Halimeda*, there is intensive lime deposition. Representatives of the order are known to have existed from very early times (see p. 297).

HALICYSTIDACEAE: *Halicystis* (*hali*, salt; *cystis*, bladder) and *Derbesia* (after A. Derbes). Fig. 54

The gametophytic plants consist of an oval vesicle, up to 3 cm.

in diameter, arising from a slender branched tuberous rhizoid embedded in calcareous *Lithothamnion* (cf. p. 238) growing at or below low-tide mark. There are only a few species of *Halicystis*, one at least of which possesses pyrenoids, though all contain numerous nuclei in the peripheral cytoplasm. There does not appear to be any cellulose in the material composing the cell wall. Swarmers develope in the cytoplasm at the apex of the vesicle in an area which becomes cut off by a thin cytoplasmic membrane, the area thus cut off representing a gametangium. Macro- and microgametes are formed and forcibly discharged in the early hours of the morning through one or more pores. There are several crops of these swarmers produced by successive migrations of cytoplasm into the apical areas at bi-weekly intervals coincident with the spring tidal cycles. Fertilization occurs in the water, and the zygote in *H. ovalis* germinates into a branched protonemal thread that in three months has developed into a typical *Derbesia* plant with the erect aerial filaments arising from the basal rhizoidal portion.

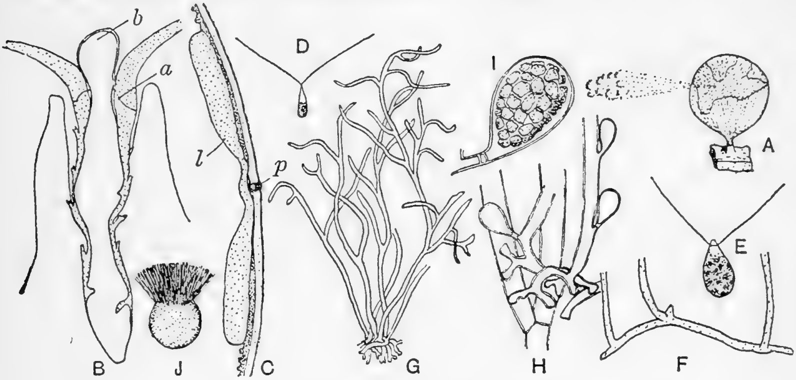


Fig. 54 *Halicystis ovalis* (and *Derbesia marina*). A, plant of *Halicystis* liberating gametes. B, rooting portion of *Halicystis* showing old rhizome and line of abscission (*a*) and new vesicle (*b*). C, gathering of protoplasm to form gametes. *l* = lining cytoplasm, *p* = pore of dehiscence. D, male gamete (× 600). E, female gamete (× 600). F, protonemal germling of *Halicystis*. G, *Derbesia* plant. H, *Derbesia*, with zoosporangia, growing on *Cladophora*. I, *Derbesia*, zoospore. (A–C, F–J, after Fritsch; D, E, after Kuckuck.)

It has been demonstrated only quite recently that both *Halicystis ovalis* and *Derbesia marina* are simply two stages in the life cycle of one alga, but in addition to the evidence from cultures the two species have the same geographical distribution. The mature *Der-*

besia threads produce zoospores that germinate into prostrate filaments, and these later give rise to slender branched rhizoids which, after eight months, produce the characteristic *Halicystis* bladder. Some weeks after its development the bladder becomes fertile and so the cycle starts once more. Although the cytology of the two plants has not yet been worked out, the *Derbesia* generation is presumably diploid and the *Halicystis* haploid. It also remains to be ascertained whether the other species of *Halicystis* have a similar life cycle. Since this first initial discovery some evidence has now been forthcoming to indicate that the same kind of life cycle holds for *Halicystis parvula* and *Derbesia tenuissima*. A species apparently belonging to the genus *Derbesia* occurs in New Zealand but no plants of *Halicystis* have ever been found. This species may therefore represent a final stage in evolution in which the sexual generation has been lost. Growth of the *Halicystis* vesicles is very slow and they become shed at the end of the growing season by abscission, new vesicles arising later from the perennating rhizoid, and in this manner regeneration may go on for several years. Some workers believe that this remarkable life cycle justifies the placing of the family in a new order, the Derbesiales.

* BRYOPSIDACEAE: *Bryopsis* (*bryo*, moss; *opsis*, an appearance). Fig. 55

Most of the species of this genus are restricted to warmer seas, though a few, of which *B. plumosa* is the commonest, occur in colder waters. The principal axis, which is often naked in its lower part, arises from an inconspicuous, filamentous, branched rhizome that creeps along the substrate and is attached to it by means of rhizoids. In one species the bases of the lower branches develop additional rhizoids that grow down and form a sheathing pseudocortex. The bi- or tripinnate fronds either have the branching confined to one plane or are radially branched, the branches being constricted at the point of origin, whilst the cell membrane is also thickened at such places. The cytoplasm in the main axis and branches frequently exhibits streaming movements. The function of the rhizome, especially in warmer waters, is probably that of a perennating organ, although vegetative multiplication can also occur through abstriction of the pinnae, which then develop rhizoids at their lower end. The only other known method of reproduction is sexual. The plants are dioecious and produce anisogametes which develop in gametangia that are cut off from the parent thallus by means of septa. Both types of gamete are biflagellate, but the microgametes differ from the macrogametes in that they lack pyrenoids. The gametes are liberated through gelatinization of the apex of the gametangium, and after fusion has taken place the zygote germinates at once into a new plant. The plants are diploid because meiosis takes place at gamete formation; there is therefore no haploid generation. The plants can behave like *Vaucheria* (cf. p. 265) in their response to certain environmental conditions; thus, gamete formation is hastened by transference of the plants from light to dark or by changing the concentration of the nutrient solution. Inversion of the thallus takes place under conditions of dull light or when it is planted upside down, and under these circumstances the apices of the pinnae develop rhizoids. This exhibition of polarity indicates clearly that the thallus is differentiated internally, but it is still a matter for speculation as to how such differentiation can occur in an organism which is to all intents and purposes one unit.

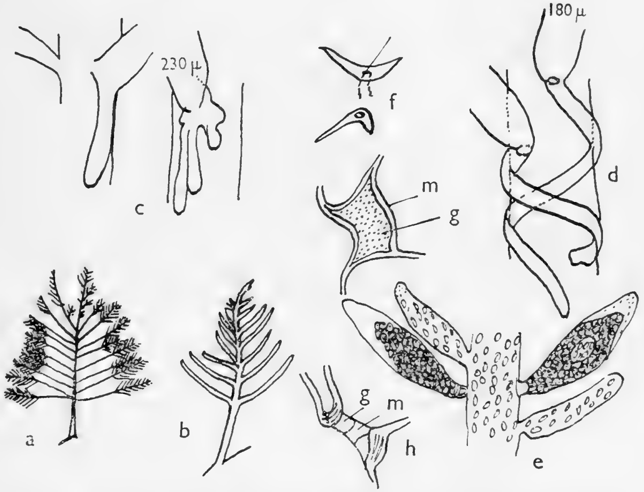
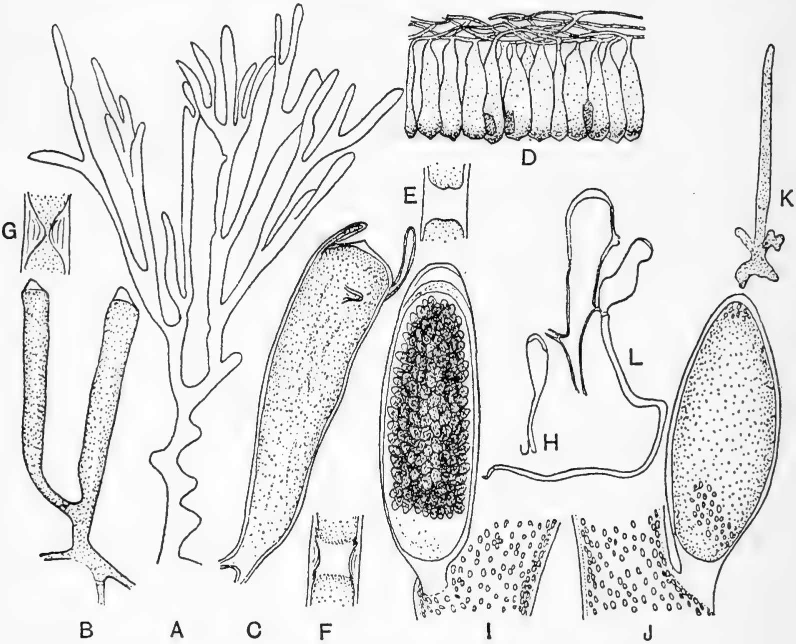


Fig. 55 *Bryopsis*. a, plant of *B. plumosa* (×0·6). b, portion of same (×7). c, *B. corticulans*, rhizoid formation from lower branches. d, the same, *B. scarfei*. e, *B. plumosa*, female gemetangia. f–h, stages in septum formation at base of gametangium. g = gelatinized material, m = membrane, r = ring of thickening initiating septum. (a, b, after Taylor; c, d, after Chapman; e–g, after Fritsch.)

* Codiaceae: *Codium* (fleece). Fig. 56

This is a widely distributed, non-calcareous genus with species living in the warm and cold oceans. The spongy thallus, which is anchored either by a basal disc or else by rhizoids, varies greatly in form and appears as erect, branched, worm-like threads (*C. tomentosum* group), flat cushions (*C. adhaerens* group), or as large round balls (*C. bursa* group). In *C. tomentosum* there is a central medulla of narrow forked threads and a peripheral cortex of club-shaped vesicles which are the swollen apices of the forked threads. Deciduous hairs may develop on the vesicles and scars are to be seen marking their point of attachment, whilst annular thickenings occur at the base of each vesicle and at the bases of the lateral



56 *Codium*. A, plant of *C. tomentosum*. B, *C. fragile*, utricles. C, *C. tomentosum*, single utricle with hairs. D, *C. tomentosum*, portion of thallus with medulla and cortical utricles. E–G, stages in formation of constriction at base of utricle. H, propagule of *C. isthmocladum*. I, *C. tomentosum*, female gametangium. J, *C. tomentosum*, male gametangium. K, *C. tomentosum*, juvenile thread. L, *C. isthmocladum*, utricle with propagule. (A, after Taylor; B, C, E–G, J, after Tilden; D, H, K, L, after Fritsch; I, after Oltmanns.)

branches, although a fine pore is left for intercommunication. The width of these pores in the case of *C. bursa* is said to vary with the season. Detachable propagules develop on the vesicles (Fig. 56L) and form a method of vegetative reproduction, whilst sexual reproduction is by means of gametes, which are produced in ovoid gametangia that arise from the vesicles as lateral outgrowths, each being cut off by a septum. The plants are anisogamous, the macrogametes being formed in green and the microgametes in yellow gametangia. Some of the species are dioecious whilst others are monoecious, and in two of the latter the male and female gametangia are borne on the same utricles. In *C. elongatum* it would appear that the determination of the sex may be a seasonal phenomenon, females appearing first, then hermaphrodites and finally males. The gametes fuse or else develop parthenogenetically, but in either case a single thread-like protonema develops which has a lobed basal portion, and it is from this that the adult develops through the growth of numerous ramifications of the one primary filament. Meiosis occurs at gametogenesis and the plants are therefore wholly diploid and comparable to *Fucus* (cf. p. 192). In *C. tomentosum* the 2n number of chrosomes is 20 whilst in *C. decorticatum* it appears to be 40 so that there is evidence of polyploidy.

CODIACEAE: *Halimeda* (daughter of Halimedon, King of the Sea). Fig. 57

The genus is known from Tertiary times onwards, and it has played a considerable part in the formation of coral reefs where the species are very abundant. The plants are borne on a short basal stalk that arises from a prostrate system of creeping rhizoids. The branched aerial thallus is composed of flat, cordate or reniform segments which are strongly calcified on the outside, the segments being separated from each other by non-calcified constrictions. Branching in some species is restricted to one plane and the size of the segments varies greatly from species to species. The segments are composed of interwoven threads with lateral branches that develop perpendicularly and produce a surface of hexagonal facets through fusion of the swollen ends. Sporangia develop at the ends of forked threads which vary greatly in their mode of branching: these threads, which are cut off from the parent thallus by basal plugs, arise from the surface of the segments or, more frequently, are confined to the edges. The sporangia produce biflagellate swarmers whose fate is not known although they are probably gametes.

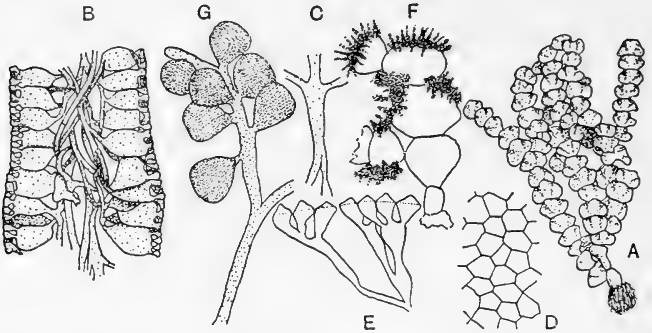


Fig. 57 *Halimeda.* A, plant of *H. simulans* (× 33). B, *H. discoidea*, longitudinal section showing structure (× 20). C. central filament: two fuse and subsequently divide into three (× 20). D, cuticle of *H. opuntia* (× 132·5). E, *H. scabra*, termination of filaments (× 100). F, fruiting plant. G, sporangia. (A, D, E, after Taylor; B, C, after Howe; F, G, after Oltmanns.)

* CAULERPACEAE: *Caulerpa* (*caul*, stem; *erpa*, creep). Fig. 58

Most of the species frequent the quiet shallow waters of the tropics where they are often rooted in sand or mud, but two have migrated to become denizens of the Mediterranean. The prostrate rhizome is attached by means of colourless rhizoids and gives rise to numerous, erect, upright assimilatory shoots with apical growth, the form and arrangement of which may vary very considerably (Fig. 58). Radial branching is regarded as primitive, whilst the more evolved forms of quieter waters possess a bilateral branching system. The genus has been divided by Börgesen into three groups:

(*a*) The species of this group, which grow where there is much mud, possess rhizomes that are vertical or oblique, thus enabling them to reach the surface even when covered successively by mud (e.g. *C. verticillata*).

(*b*) The rhizome in these species first branches at some distance from its point of origin and it possesses a pointed apex which aids in boring through sand or mud (e.g. *C. cupressoides*).

(*c*) The rhizome is richly branched immediately from its point of origin and the various species are principally to be found attached to rocks and coral reefs (e.g. *C. racemosa*).

It has also been shown that the form of the thallus in some of the species is largely dependent upon the conditions of the habitat, a feature particularly well illustrated by the plastic *C. cupressoides* and *C. racemosa*:

(i) In exposed situations the plants are small and stoutly built.
(ii) In more sheltered habitats the shoots are longer and more branched.
(iii) In deep water the plants are very large with richly branched flabellate shoots.

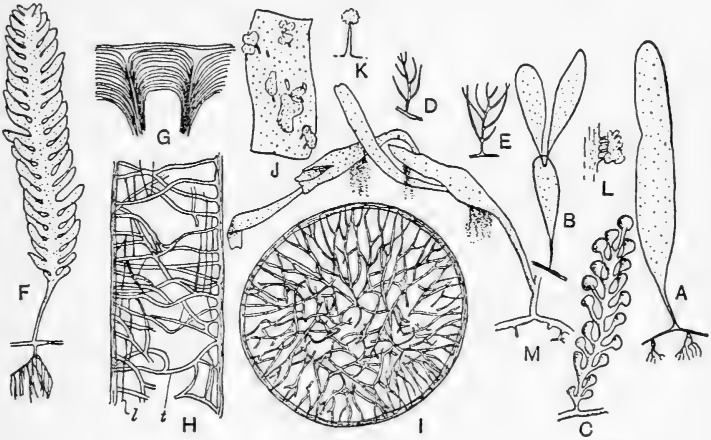


Fig. 58 *Caulerpa.* A, B, *C. prolifera* ($\times \frac{1}{2}$). C, *C. racemosa* f. *macrophysa* ($\times \frac{1}{2}$). D, E, *C. sertularioides*, side branches ($\times \frac{1}{2}$). F, *C. crassifolia* f. *mexicana* ($\times \frac{1}{2}$). G, structure of wall and two skeletal strands. H, longitudinal section of aerial portion showing longitudinal (*l*) and transverse (*t*) support strands. I, transverse section of rhizome with skeletal strands. J, K, L, *C. prolifera*, reproductive papillae ($\times 5$). M, *C. prolifera* with gametes being liberated. (A–F, after Taylor; G–I, after Fritsch; J–M, after Dostal.)

There is no septation, but the coenocyte is traversed instead by numerous cylindrical skeletal strands, or *trabeculae*, arranged perpendicularly to the surface and which are most highly developed in the rhizomes. They arise from rows of structures termed *microsomes*, and are at first either free in the interior of the coenocyte or else connected with the wall, although in the adult state they are always fused to the walls. The function of the trabeculae, which increase in thickness at the same time as the walls by successive deposition of callose, is extremely problematical and may be:

(*a*) mechanical; in this case they would presumably provide resistance to high turgor pressures, although the presence of high osmotic pressures in the cells has yet to be proved;
(*b*) to enlarge the protoplasmic surface;
(*c*) concerned with diffusion, because movement of mineral salts is more rapid through these strands than through the cytoplasm;
(*d*) lost or without any function.

In addition to the trabeculae there are also internal peg-like projections. Vegetative reproduction occurs through the dying away of portions of the old rhizome thus leaving a number of separate plants. The swarmers or gametes are formed in the aerial portions and are liberated through special papillae that develop on the frond. The sexual reproductive fronds have a variegated appearance caused by the massing of the biflagellate gametes at the different points, the swarmers in some species being separable into micro- and macrogametes. In certain species the whole plant can produce swarmers, whilst in others the reproductive area is limited, and in such cases the morphological identity and differentiation of the frond becomes of great interest. The thallus can be regarded as composed of a number of individual cells which only become evident at gametogenesis. Fusion between the swarmers has been observed in *C. racemosa*, and it is probable that in all the species the motile bodies are functional gametes and that the adult plants are diploid. The genus has been much employed in experiments on polarity because the structure of the thallus renders it extremely suitable.

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* CONJUGALES

The members of this order are somewhat distinct from the other members of the Chlorophyceae. The plants are either filamentous or else single cells with a wall of one or two parts. There is considerable variation in form of the plastids. The species are all characterized by a peculiar mode of sexual reproduction in which fusion takes place between masses of protoplasm which do not possess organs of locomotion. In the process cells come together in pairs and conjugate (see the different examples). Their peculiar reproduction suggests that they were evolved at a very early stage from one of the simpler orders, i.e. Ulotrichales. The order is subdivided into four major families, the Zygnemaceae, which are filamentous, the Gonatozygaceae which fragment into short lengths or single cells, and the Mesotaeniaceae and Desmidiaceae, most of which are single-celled. The Mesotaeniaceae are sometimes known as the saccoderm desmids and, together with the Zygnemaceae, are placed in the Euconjugatae. The Desmidiaceae are also sometimes known as the placoderm desmids. Both desmid families have probably been derived from filamentous ancestors by over-specialization of fragmentation.

* ZYGNEMACEAE: *Spirogyra* (*spiro*, coil; *gyra*, curved). Figs. 59, 60

The unbranched filaments are normally free-living although attached forms are known, e.g. *S. adnata*, and they form slimy threads which are known as 'Water-silk' or 'Mermaid's tresses'. They grow in stagnant water and are most abundant in either the spring or autumn, the latter phase being due to the germination of a percentage of the spring zygospores. Each cell contains one or more chloroplasts possessing either a smooth or serrate margin and arranged in a characteristic parietal spiral band. The single nucleus is suspended in the middle of the large central vacuole by means of protoplasmic threads that radiate out to the parietal protoplasm. The chloroplasts, which may occasionally be branched, are T- or U-shaped in cross-section and contain numerous pyrenoids which project into the vacuole on the inner side, the majority of the pyrenoids arising *de novo* at cell division. The cell wall is thin and composed, according to some investigators, of two cellulose layers, whilst others maintain that there is only an inner cellulose layer with an outer cuticle. The whole filament is enclosed in a mucilage sheath of pectose. Any cell is capable of division, and vegetative reproduction by fragmentation is exceedingly common, three methods having been described:

(*a*) The septum between two cells splits and a mucilaginous jelly develops in between, so that when one cell subsequently develops a high turgor pressure the cells become forced apart.

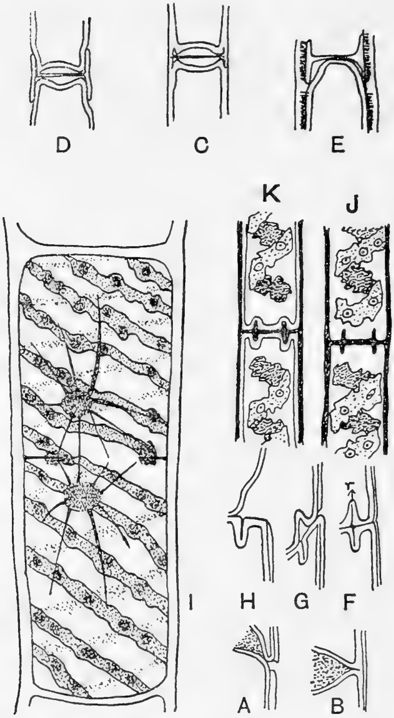

Fig. 59 *Spirogyra.* A, B, cell disjunction (diagrammatic). C–E, cell disjunction in *S. colligata.* F–H, *S. weberi*, cell disjunction by replicate fragmentation. *r* = replication of septum. I, vegetative structure and cell division, *S. nitida* (× 266). J, K, cell disjunction and development of replicate septa. (A–H, J, K, after Fritsch; I, after Scott.)

(*b*) Ring-like projections develop on both sides of a septum and the middle lamella dissolves. Then the rings of one cell evaginate and force the cells apart whilst the rings of the other cell evaginate after separation (*replicate fragmentation*) (cf. Fig. 59, F–H).

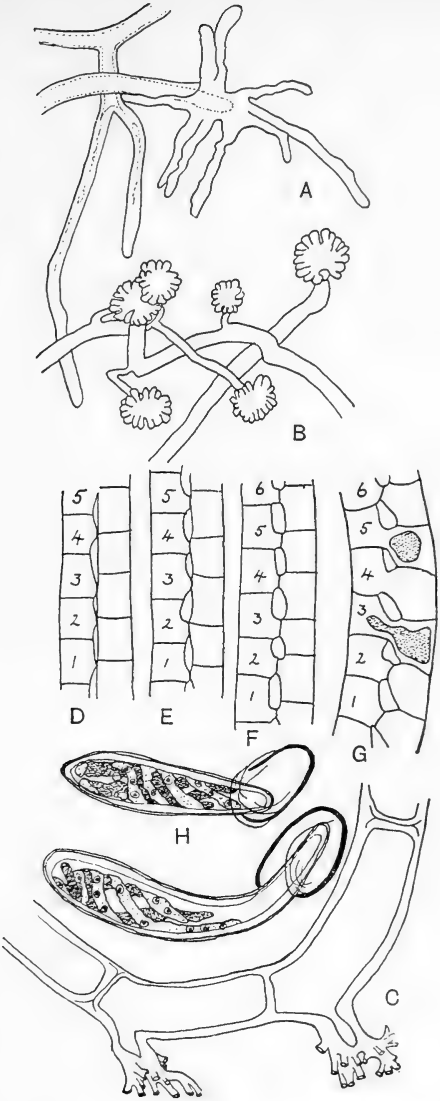

Fig. 60 *Spirogyra*. A, B, rhizoid formation in *S. fluviatilis*. C, rhizoids and haptophores of *S. adnata*. D–G, stages in conjugation, *S. varians*. H, germination of zygospore in *S. neglecta*. (A, B, after Czurda; C, after Delf; D–G, after Saunders; H, after Fritsch.)

(*c*) The septum develops an I piece and then when the wall inverts, due to increased turgor, the I piece is slipped off and the two cells come apart (cf. Fig. 59, C–E).

When two filaments touch they may form joints or *geniculations*, adhesion being brought about by a mucilaginous secretion produced by the stimulation of the contact. The formation of such geniculations, however, has no connexion with reproduction.

Sexual reproduction is secured by the process of conjugation, the onset of which is brought about by a combination of certain internal physiological factors combined with the pH of the external medium. It commonly takes place during the spring phase and then the threads come together in pairs, but either one or more than two filaments may also be involved. The threads first come together by slow movements, the mechanism of which may be connected with the secretion of mucilage; then they become glued together by their mucilage and later young and recently formed cells in both filaments put out papillae. These papillae meet almost immediately, elongate, and push the threads apart. Normally one of the threads produces male gametes and the other female, but occasionally the filaments may contain mixed cells. The papillae from male cells are usually longer and thinner than those from the female cells and so they can fit inside the latter. The conjugating cells accumulate much starch, the nuclei decrease in size and the wall separating the papillae breaks, thus forming a conjugation tube. The whole process so far described forms the *maturation phase* which is followed by the *phase of gametic union*. Contractile vacuoles, which make their appearance in the cytoplasmic lining, remove water from the central vacuole and so cause the protoplasm of the male cells to contract from the walls. The male cytoplasmic mass then migrates through the conjugation tube into the female cell where fusion of the two masses takes place and this is then followed by contraction of the female cytoplasm, though in the larger species it may contract before fusion. Fusion of the two nuclei may be delayed for some time, but in any case the male chloroplasts degenerate. The process described above is known as *scalariform* conjugation, and it includes certain abnormal cases where cells produce more than one papilla or where the papillae are crossed. In some monoecious species, however, *lateral* conjugation occurs, the processes being put out from adjoining cells on the same filament. More recently a species (*S. jogensis*) has been described in which contents of adjacent cells fuse, the contents of one cell passing through a pore in the intervening cell wall.

The last phase to be described is that of *zygotic contraction* which is brought on by further action of the contractile vacuoles, after which a thick three-layered wall develops around the zygote, the middle layer or mesospore frequently being highly sculptured. The zygospore occasionally germinates almost at once, thus producing plants that account for the autumn maximum, but it is usually dormant until the following spring. Meiosis takes place when the zygote germinates and four nuclei are formed of which three abort, the plants thus only exhibiting the haploid generation. A two-celled germling is formed, the lower cell being relatively

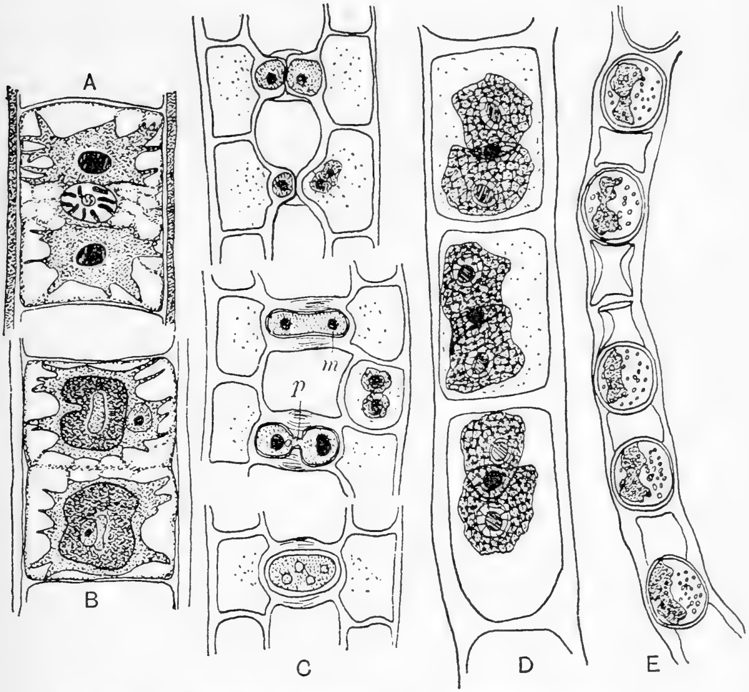

Fig. 61 *Zygogonium ericetorum*. A *Zygnema stellinum*, cell and nucleus before division (×500). B, the same, after division (×500). C, *Zygogonium*, stages in conjugation. *m* = male nucleus, *p* = conjugation process. D, terrestrial form (×1065). E, aplanospores formed from drying up of filament (×542). (A, B, after Cholnoky; C–E, after Fritsch.)

colourless and rhizoidal in character. Filaments of two different species have been known to fuse, the form of the hybrid zygospore being determined by the characters of the female thread. Azygospores, which have arisen parthenogenetically, and akinetes also form other means of reproduction.

ZYGNEMACEAE: *Zygogonium* (*zygo*, yoked; *gonium*, angle). Fig. 61

The commonest species of this genus, which is sometimes regarded as a subsection of the genus *Zygnema*, is the terrestrial *Z. ericetorum*. The cells of this species each contain a single axile chloroplast, whilst in *Zygnema*, of course, there is a pair of very characteristic stellate chloroplasts (Fig. 61, A). At low temperatures the walls develop a very thick cellulose layer, whilst the sap is coloured violet by a pigment (which is probably an iron-tannin), especially when the threads are subjected to strong light. Sexual reproduction is rare but when it does occur the gametes are formed from only a part of the protoplasm. In an Indian species azygospores are apparently the only means of reproduction and even these are scarce. Aplanospores and akinetes are commonly formed, and there is one abnormal form growing on Hindhead heath (England) which only exists in the akinete stage.

ZYGNEMACEAE: *Mougeotia* (after J. B. Mougeot, a French botanist). Fig. 62

The filaments of the different species are commonly unbranched, although they may occasionally possess short laterals. The chloroplast is a flat axile plate lying in the centre of the cell and orientated according to the light intensity, whilst the nucleus is to be found in the centre of the cell on one side of the chloroplast. Fragmentation takes place by method (*a*) as described for *Spirogyra* (cf. above), and knee joints or geniculations are also common. At conjugation the gametes are formed from only part of the cell protoplast, as in *Zygogonium*, fusion taking place either by way of papillae or through a geniculation. The zygote is cut off by new walls and so becomes surrounded by two or four sterile cells depending on where the zygospore has been formed. Most of the species are isogamous but anisogamy is known in *Mougeotia tenuis*. Reproduction by means of thick-walled akinetes and parthenospores occurs commonly, at least five species having only the latter mode of propagation.

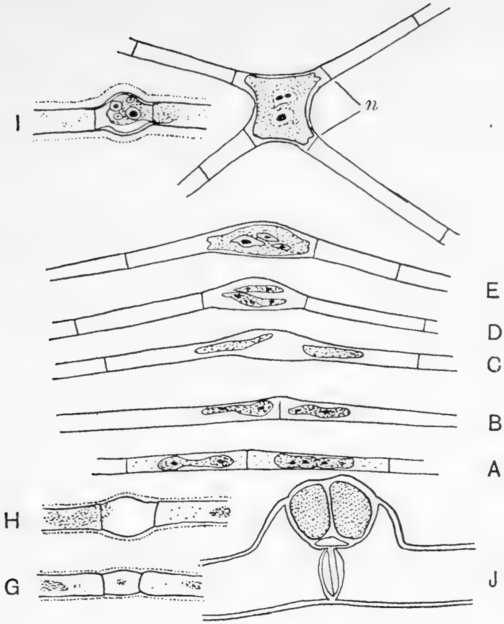

Fig. 62. *Mougeotia*. A–E, *M. mirabilis*, stages in conjugation through loss of cell wall. F, normal conjugation in *M. mirabilis*. *n* = new walls cutting off zygote. G–I, stages in lateral conjugation of *M. oedogonioides*. J, two azygotes in *M. mirabilis*. (A–F, after Czurda; G–I, after Fritsch; J, after Kniep.)

MESOTAENIACEAE: *Mesotaenium* (*meso*, middle; *taenium*, band). Fig. 63

This is an example of one of the *saccoderm* desmids, which as a group are characterized by a smooth wall in one complete piece and without any pores. The rod-shaped cells of *Mesotaenium* are single, have no median constriction, and are circular in transverse section. The chloroplast in this particular genus is a flat axile plate containing several pyrenoids, whilst in some species the presence of phycoporphyrin imparts a violet colour. The inner cell wall is composed of cellulose and the outer of pectose. Multiplication takes place by cell division, the daughter cells being liberated by dissolution of the middle lamella after a constriction has been formed, though in some cases this may not occur until a number of cells have been enclosed in a common mucilaginous envelope. Sexual reproduction is by means of conjugation, two processes being put out just as in the filamentous forms: these unite and then the middle septum breaks down so that the two protoplasts can meet in the centre, after which the conjugation tube may widen. The thick-walled zygote divides twice, the first division being heterotype, whilst in one species the divisions result in two macro- and two micronuclei. It is from these divisions that either two or four new individuals arise. The species are to be found in upland pools, peat bogs or on the soil.

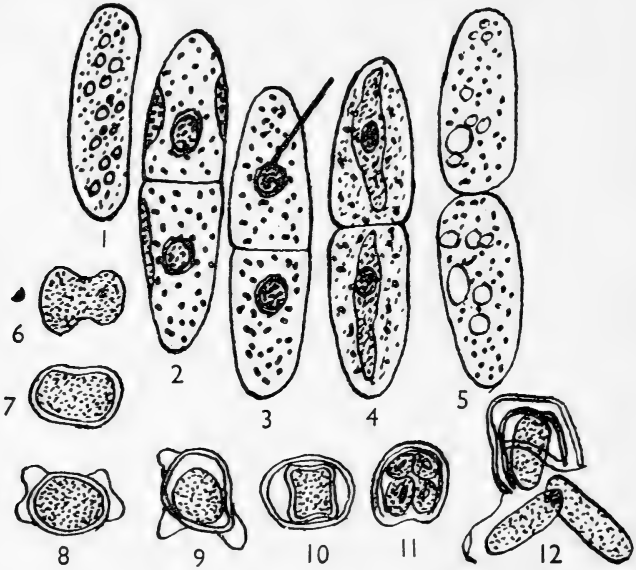

Fig. 63 *Mesotaenium*. 1–5, 6–12, conjugation of *Cylindrocystis brebissonii* and germination of zygospore. (After Fritsch.)

* Desmidiaceae: *Closterium* (enclosed space). Figs. 64, 65

This genus is an example of one of the *placoderm* desmids, a group that is commonly characterized by the highly perforated cell wall composed of two parts.

The curved cells have attenuated apices with a vacuole in each apex which contains crystals of gypsum that appear to have no physiological function and are probably purely excretory. The pores are arranged in rows in narrow grooves, cell movement being secured by the exudation of mucilage through large pores near the apices. Each semi-cell has one axile chloroplast which is in the form of a curved cone with ridges on it with one to several pyrenoids, whilst in transverse section the plastid has the appearance of a hub with radiating spokes or else looks like a coarsely cogged wheel. Cell division is peculiar and takes place by one of two methods producing either (*a*) connecting bands which appear as striae in the older semi-cells or (*b*) girdle bands (cf. Fig. 65). In small-celled species the process occupies about a day but a longer period is required with large-celled species. At conjugation, papillae from the two cells meet or else the naked amoeboid gametes fuse immediately outside the cells, whilst in *C. parvulum* there is some evidence

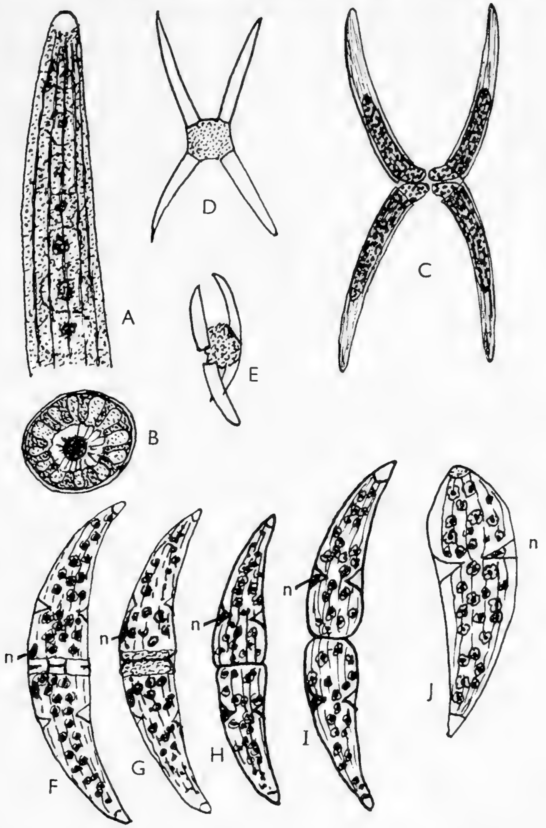

Fig. 64 *Closterium*. A, *C. lanceolatum*, chloroplast structure. B, *Closterium* sp., structure in transverse section. C, *C. lineatum*, first stage in conjugation. D, *C. rostratum* var. *brevirostratum*, zygospore formation, second stage. E. *C. calosporum*, mature zygospore. F–J. *C. ehrenbergii*, stages in cell division. n = nucleus. (E, after Smith; rest after Fritsch.)

of sexual differentiation. After the gametes have fused two of the chloroplasts degenerate and the zygospore on germination divides twice, during which meiosis takes place. Two daughter cells are then formed, each containing one chloroplast and two nuclei, but one of the latter subsequently degenerates. Under unfavourable conditions asexually produced chlamydospores have been observed in *C. moniliferum.*

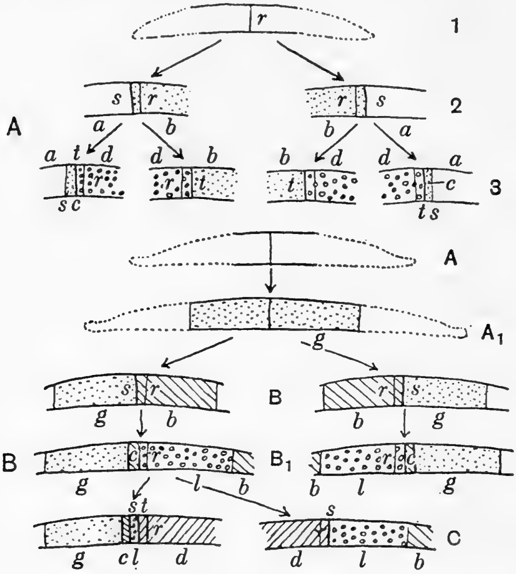

Fig. 65 *Closterium.* Diagrams to explain cell division in species of *Closterium* with (B) and without (A) girdle bands. The different segments of the wall are indicated by shading. 1, 2, 3, and A, B, C = the successive generations. The individuals in 1 and A have each arisen from a zygote and have not undergone division. *a*, *b*, *d* = semi-cells of various ages; *c* = the connecting band demarcated by the two sutures *s*, of the previous generation, and *t*, of the present; *g*, *l* = girdle bands developed before (*g*) and after division; *s* = suture between young and older semi-cells; *r* = the line of the next division. (After Fritsch.)

The genus is wholly fresh water and many species are planktonic and possess modifications, e.g. spines, which may be regarded as adaptations to this mode of existence. The group is extremely widespread but is scarce in waters containing much lime, the individual species thriving best in soft or peaty waters. The most favourable seasons for their development are the late spring and early summer, and their resistance in the vegetative state to adverse conditions would seem to be very great. The evidence suggests that, as a group, they have been evolved from filamentous ancestors, possibly by over-specialization of the process of fragmentation. Recent cytological work on Desmids has revealed great variation within clones of the same species. Thus, *Cosmarium cucumis* gave chromosome counts of 44 or 52, and *Netrium digitus* counts of 122, 172–82, and 592. Further counts and analyses of clones are obviously essential.

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CHAROPHYCEAE

The division comprises but a single order, the Charales. The plants represent a very highly specialized group that must have diverged very early in the course of evolution from the rest of the green algae, the intermediate forms subsequently being lost. There is a small amount of evidence which suggests that they may have originated in or along with the Chaetophorales, e.g. presence of nodes (*Draparnaldia*) and cortication in that order. There is no asexual reproduction but the process of sexual reproduction is very complex. The young plants develop from a protonemal stage, the erect plants having a structure which is more elaborate than any type so far described, whilst the thallus is sometimes lime encrusted (*Chara* spp.). The group is known to be very ancient because fossil members are found from almost the earliest strata. The living forms are widely distributed in quiet waters, fresh or brackish, where they may descend to considerable depths so long as the bottom is either sandy or muddy.

Nitella: (a little star). Figs. 66–9

The plants have the appearance of miniature horsetails (*Equisetum*) because they bear whorls of lateral branches arising from the nodes. The nodes are formed by a transverse layer of cells in contradistinction to the internodes, which consist of one large cell whose individual length may extend up to 25 cm. in *Nitella cernua*. The height of the different species varies up to 1 m., growth being brought about by an apical cell which cuts off successive segments parallel to the base. Each new segment divides transversely into two halves, the upper developing into a node and the lower into an internode (Fig. 67). Branches, both primary and secondary, are formed by the peripheral cells of the nodes protruding to form

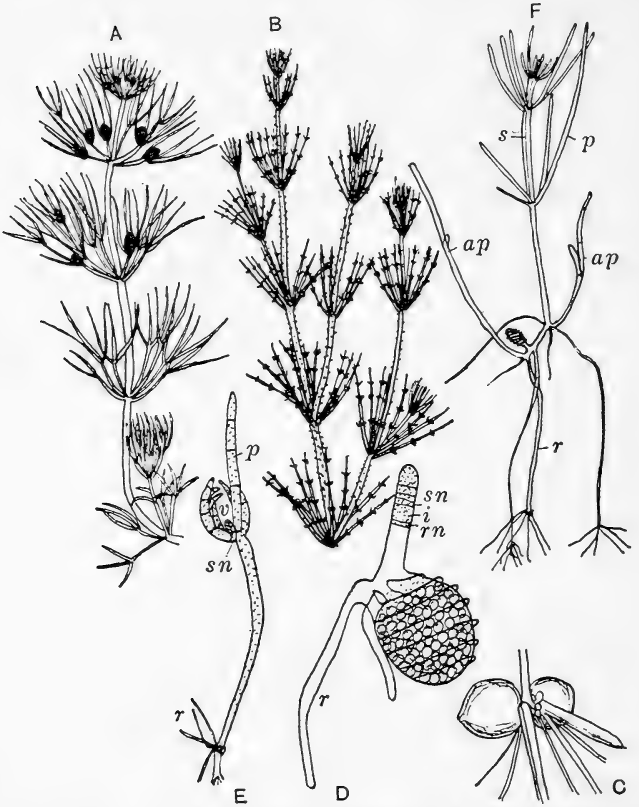

Fig. 66 Charales. A, *Nitella batrachosperma*. B, *Chara hispida*. C, underground bulbil of *C. aspera*. D, germinating oospore. E, protonema of *C. fragilis*. F, young plant of *C. crinita*. *ap* = accessory protonema, *i* = internode, *p* = protonema, *r* = rhizoids, *rn* = rhizoid node, *s* = shoot, *sn* = stem node, *v* = initial of young plant. (After Fritsch.)

new apical cells, but these soon cease to grow after the branch has reached a short length. At the basal node of the main plant branches of unlimited growth are produced: these arise on the inner side of the oldest lateral in the whorl, thus producing a fictitious appearance of axillary branching. Multicellular branched rhizoids with

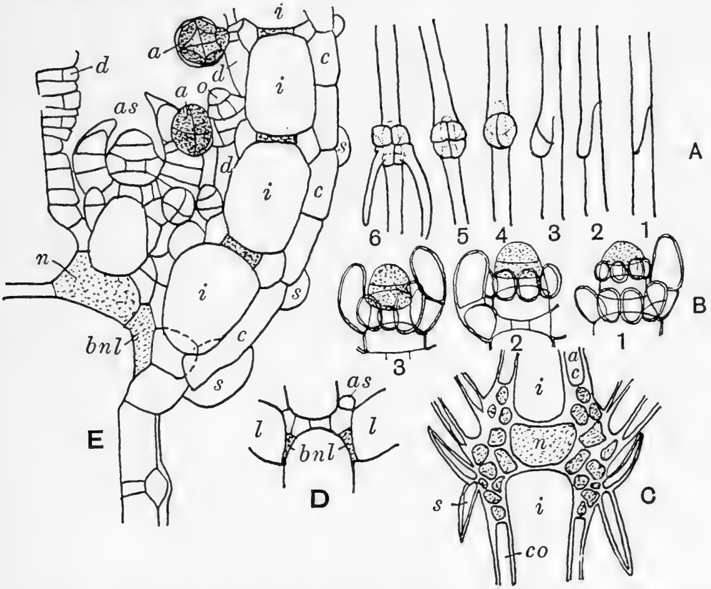

Fig. 67 Charales. A, 1–6, successive stages in development of root node of *Chara aspera*. A, double foot joint. 2, dilation of toe of upper foot. 3, toe portion cut off. 4, 5, subdivision of toe cell. 6, rhizoids growing out. B, 1–3, successive growth stages of apex of *Nitella*. In 1 apical cell is undivided, in 2 it has divided, in 3 the lower cell has divided into an upper node and a lower internode. C, *C. hispida*, node with stipules. D, *N. gracilis*, longitudinal section of node. E, *C. fragilis*, branch at node with axillary bud. *a* = antheridium, *ac* = ascending corticating cells, *as* = apex of side branch, *bnl* = basal node of branch (*l*), *c* and *co* = cortical cells, *d* = descending cortical cells, *i* = internodal cell, *n* = nodal cell, *o* = oogonium initial, s = stipule. (A, B, after Grove; C–E, after Fritsch.)

oblique septa function as absorption organs and also serve for anchorage. The rhizoids develop from the lowest node of the main axis, but every node is potentially capable of producing them though normally the presence of the stem apex inhibits their appearance, but if this is cut off they will then develop. This behaviour is very suggestive of an auxin control similar to that found in the higher plants. The cells, which have a cellulose membrane, contain discoid chloroplasts without any pyrenoids together with one nucleus. Cytoplasmic streaming is very readily observed, especially in the internodal cells. Sexual reproduction is by means of a characteristic oogamy where light intensity plays a part in determining the production of the sex organs. The species are either dioecious or monoecious, in which latter case the oogonia and antheridia are juxtaposed, the oogonia being directed upwards and the antheridia downwards, both organs usually appearing on secondary lateral branches of limited growth.

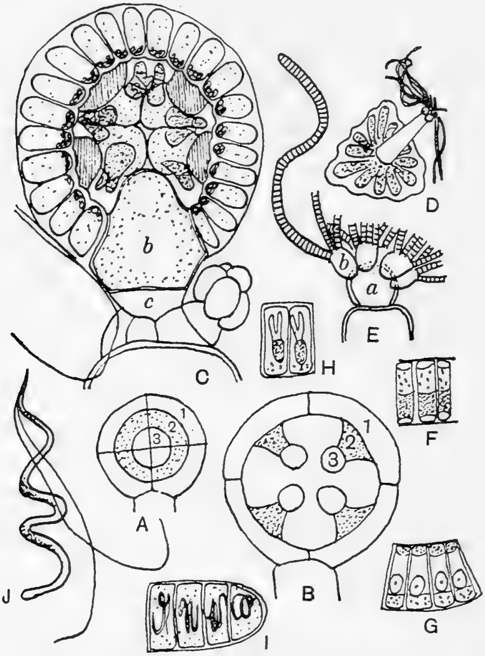

Fig. 68 Charales. A, B, stages in development of antheridium of *Chara*. 1–3, segments and cells to which they give rise. C, section of almost mature antheridium of *Nitella flexilis*. *b* = flask cell, *c* = extra basal cell. D, *C. tomentosa*, single plate with manubrium and spermatogenous threads. E, *C. tomentosa*, apex of manubrium with spermatogenous threads. *a* = primary head cell, *b* = secondary head cell. F–I, *C. foetida*, stages in formation of antherozoids in spermatogenous threads. J, mature antherozoid. (A, B, after Goebel; C–E, J, after Grove; F–I, after Fritsch.)

Antheridia. Fig. 68

The apical cell of the lateral branch cuts off one or two discoid cells at the base and then becomes spherical. The upper spherical cell divides into octants and this is followed by two periclinal divisions after which the whole enlarges and the eight peripheral cells develop carved plates (*shields*), thus giving the wall a pseudo-cellular appearance. At maturity these peripheral cells acquire brilliant orange contents. The uppermost discoid basal cell protrudes somewhat into the hollow structure formed as described above. The middle segment of each primary diagonal cell now develops into a rod-shaped structure, the *manubrium*, which bears at its distal end one or more small cells, the *capitula*; every one of these produces six secondary capitula from each of which arises a forked spermatogenous thread containing 100–200 cells. These antheridial cells each produce one antherozoid, an elongate body with two flagella situated just behind the apex. The complete structure has been regarded as one antheridium, whilst another view regards the octants as laterals, the manubrium as an internode, the capitula as a node and the spermatogenous threads as modified laterals, so that on this basis the antheridia are one-celled and conform to the normal structure of the majority of the antheridia in the green algae. This second interpretation, if it is correct, helps considerably in understanding this peculiar group.

Oogonia. Fig. 69

The apical cell of the lateral branch divides twice giving rise to a row of three cells, the uppermost cell developing into the oogonium whilst the lowest forms a short stalk. The middle cell cuts off five peripheral cells which grow up in a spiral fashion and invest the oogonium, each one finally cutting off two small *coronal* cells at the apex. The oogonial cell cuts off three cells at its base and it is maintained that these, together with the oogonium, represent four quadrants, only one of which develops to maturity. When mature, the investing threads part somewhat to form a neck, and the apex of the oogonium gelatinizes in order to permit the antherozoids to enter. After fertilization the zygote nucleus travels to the apex of the oospore and a coloured cellulose membrane is excreted around it, whilst the oogonium wall, together with inner walls of the investing threads, thicken and silicify. Four nuclei are formed by two successive divisions of the zygote nucleus, meiosis taking place during this process. One of these nuclei becomes cut off by a cell wall whilst the other three degenerate. The small cell so formed then divides and two threads grow out in opposite directions, one a rhizoid, the other a protonema. The cell next to the basal cell of the protonema divides into three cells, the upper and lower forming nodes which become separated by elongation of the middle cell (Fig. 66). The lower node develops rhizoids whilst the upper produces a whorl of laterals from all the peripheral cells except the oldest, which instead forms the apex of the new plant. The mature plant is therefore morphologically a branch of the protonema. Vegetative reproduction can take place from secondary protonemata which develop from the primary rhizoid ring or else from dormant apices.

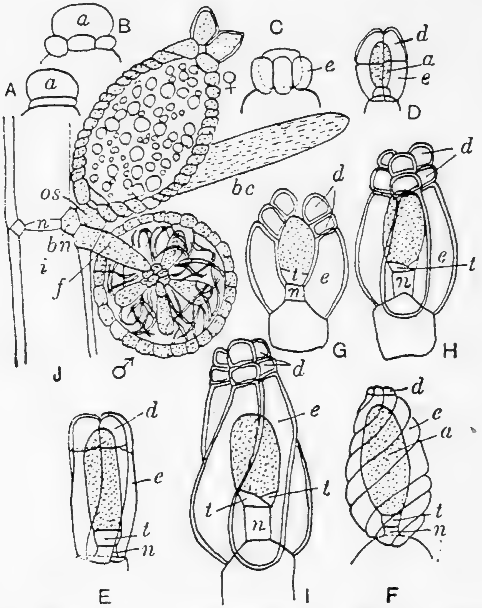

Fig. 69 Charales. A–F, *Chara vulgaris*, stages in formation of oogonium. A, first division. B, C, division of periphery to form envelope cells. D, coronal cells cut off. F, mature oogonium. G–I, *Nitella flexilis* stages in formation of oogonium. J, fertile branch of *C. fragilis*. *a* = oogonium, *bc* = bract cell, *bn* = branch nodal cell, *d* = coronal cells, *e* = envelope cells, *f* = flask cell, *i* = internode, *n* = nodal cell, *t* = turning cell, *os* = oogonium stalk cell. (After Grove.)

Chara (of a mountain stream). Figs. 66, 67

The genus is very similar to *Nitella* in its method of reproduction, but the plants are usually larger and coarser, often with lime encrustations. The stem is commonly corticated, the corticating cells arising from the basal nodes of the short laterals, one thread growing up and another down. Another characteristic feature is a single celled corona.

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Chapter VI

EUPHYCOPHYTA

PHAEOPHYCEAE

ECTOCARPALES, SPHACELARIALES, TILOPTERIDALES CUTLERIALES, DICTYOTALES, CHORDARIALES, SPOROCHNALES

* General

The algae composing this class range from minute discs to 100 metres or more in length and are characterized by the presence of the brown pigment, fucoxanthin, which masks the green chlorophyll that is also present. The class can be divided into a number of orders and families, which can be treated independently (Fritsch, 1945), or the families may be placed into three groups as proposed by Kylin (1933). These groups are based upon the type of alternation of generations, though the classification involves difficulties so far as one family (Cutleriaceae — see, however, p. 142) is concerned.

(*a*) *Isogeneratae:*

Plants with two morphologically similar but cytologically different generations in the life cycle (e.g. Ectocarpaceae, Sphacelariaceae, Dictyotaceae, Tilopteridaceae, Cutleriaceae).

(*b*) *Heterogeneratae:*

Plants with two morphologically and cytologically dissimilar generations in the life cycle:

- (i) Haplostichineae: Plants with branched threads, which are often interwoven, and usually with trichothallic growth (e.g. Chordariaceae, Mesogloiaceae, Elachistaceae, Spermatochnaceae, Sporochnaceae, Desmarestiaceae).
- (ii) Polystichineae: Plants built up by intercalary growth into a parenchymatous thallus (e.g. Punctariaceae, Dictyosiphonaceae, Laminariales).

(*c*) *Cyclosporeae:*

Plants possessing a diploid generation only, (e.g. Fucales).

In any consideration of phylogenetic problems there is really very little difference between the two methods of classification.

The Phaeophyceae are extremely widespread and are confined almost entirely to salt water, being most luxuriant in the colder waters, though the genera *Heribaudiella*, *Pleurocladia* and *Bodanella*, six species of *Ectocarpus* and *Sphacelaria fluviatilis* occur in fresh water. All of these except the *Sphacelaria* belong to the Ectocarpales and many of the records come only from China.

Some of the species of brown algae exhibit morphological variations and it has been shown that these may depend on (*a*) season of the year, and (*b*) nature of the locality. Church (1920) has given us an elaborate account of the morphology of the Phaeophyceae, and he suggested that if a brown flagellate came to rest it could develop in one of three directions to give:

(*a*) Uniseriate filaments which occupy a minimum area and obtain maximum light energy per unit of area, growth being either distal or intercalary.
(*b*) A mono- or polystromatic thallus which occupies a maximum area and obtains a minimum light energy per unit of area.
(*c*) Mass aggregation.

A morphological examination of the brown algae will show that development has taken place along each of these directions, often resulting in plant bodies of a complex construction, and the following types can be recognized among the various species:

(*a*) Simple filaments (e.g. *Acinetospora*).
(*b*) Branched filaments (e.g. *Pylaiella*).
(*c*) Erect filaments arising from a prostrate thallus (e.g. *Myrionema*).
(*d*) Interwoven central filaments (*cable* type, e.g. *Myriogloia*).
(*e*) Prostrate portion only (*reduced* filamentous or cable type, e.g. *Phaeostroma*).
(*f*) Filaments uniting to form a sphere (*hollow parenchymatous* or modified cable type, e.g. *Leathesia*).
(*g*) Multiseptation of primary cable type (e.g. *Chorda*).
(*h*) Erect filaments with cortication (*corticated* type, e.g. *Sphacelaria*).

(*i*) Simple or laminate *parenchymatous* thallus (e.g. *Punctaria*).
(*j*) *Improved parenchymatous* structure with internal differentiation of the tissues (e.g. Laminariales).

Many of the simpler types, whether reduced or not, exhibit the condition of heterotrichy similar to that found in the Chaetophorales, but this is a feature that will be discussed elsewhere (cf. p. 315). The thalli may also reach a relatively large size and under these circumstances additional support is obtained as follows:

1. Increase in wall thickness (*Stypocaulon*) or the production of a firmer cellulose material (*Sphacelaria*).
2. Twisting and rolling of the threads together.
3. Development of root branches or *haptera*.
4. The appearance of descending and ascending corticating filaments.
5. Multiseptation takes place in a longitudinal direction.
6. Development of internal hyphae.

The characteristic method of growth in the group is by means of an intercalary meristem at the base of a hair. This is termed trichothallic growth. In some of the more advanced orders trichothallic growth has been replaced by an apical cell or an apical or marginal group of cells. Branching may proceed from any cell, and it frequently takes the form of a regular or irregular dichotomy, though in the Fucales a spiral arrangement may be found. The cells vary greatly in size but they always have distinct walls, which are usually composed of cellulose on the inside and pectin outside, and although they are commonly uninucleate occasionally they become multinucleate. Plastids are also present and when the brown pigment has been removed by boiling, the thallus then becomes green. Usually each cell contains several plastids, which are usually parietal and discoid though there is some diversity of form. Although pyrenoids have been described for some species they do not appear to be wholly comparable with those in other algae. The pigments are not the same as those in the higher plants because chlorophyll *b* is replaced by chlorophyll *c* and there are a number of accessory xanthophylls (see p. 2). The products of assimilation are sugar, alcohols, fats and complex polysaccharides but not starch. A characteristic feature of the Phaeophyceae is the presence of colourless, highly refractive vesicles known as fucosan vesicles or physodes. These contain a material known as fucosan, and they are particularly abundant in tissues where active metabolism or division is taking place.

Hyaline hairs occur in many forms and their function has been variously ascribed as:

(1) shock absorbers,
(2) respiratory and absorptive organs,
(3) protection against intense illumination,
(4) protection against epiphytes,
(5) protection against covering by sand or silt,
(6) mucilage organs.

None of the evidence for any of these suggestions is entirely satisfactory, and the whole problem demands further investigation.

Vegetative reproduction may take place by splitting of the thallus or else by the development of special propagules (*Sphacelaria*). Asexual reproduction is commonly secured by means of uni- or biflagellate zoospores which are normally produced in specialized cells or sporangia. In one group (Dictyotales) tetraspores replace the zoospores, these bodies being produced in groups of four in each sporangium on plants that do not normally bear sexual organs. In yet another group (Tilopteridales) asexual reproduction is by means of uni- to quadrinucleate monospores. The homologies of these monospores have been subject to much speculation and they have been variously regarded as equivalent to

(*a*) propagules of *Sphacelaria*,
(*b*) simple forerunners of tetraspores,
(*c*) degenerate tetraspores,
(*d*) parthenogenetic ova.

The second suggestion is perhaps the most satisfactory in our present state of knowledge, especially when considered in relation to the vegetative characters. Sexual reproduction ranges from isogamy, with both gametes motile and *characteristically* bearing two flagellae *inserted laterally*, through a series in which differentiation first to anisogamy and finally to oogamy can be traced.

The ova are not normally retained on the parent plant so that fertilization takes place in the water, though the ovum may remain attached by a long mucilaginous stalk (cf. p. 193). The change from isogamy to anisogamy is also accompanied by a corresponding differentiation of the gametangia. Electron microscope studies of the antherozoids of several species (Manton, 1951, 1952) has revealed the fact that the long anterior flagellum is composed of eleven fibrils and the shorter posterior one of nine fibrils which seem to be of a rather different nature. Down the sides of the long flagellum can be found small hairs which presumably make it a more efficient locomotory organ.

Both unilocular and plurilocular sporangia are commonly found, but the fate of their products varies considerably. Plurilocular sporangia can be borne on both diploid and haploid plants, whereas unilocular sporangia are commonly confined to diploid plants. The plurilocular sporangia on the diploid plants represent an accessory means of reproduction, whilst those of the haploid generation are gametangia. In isogamous forms gametes are normally produced from plurilocular sporangia, so that in anisogamous forms the antheridia and oogonia must be regarded as modified plurilocular sporangia. On this basis the plants can be divided into two groups as in Table 2.

TABLE 2

Sporangia in Phaeophyceae

I. One kind of plurilocular sporangium.
    (i) Uni- and plurilocular sporangia on the same individuals, e.g. *Ectocarpus* spp.
    (ii) Uni- and plurilocular sporangia on different individuals, e.g. *Sphacelaria bipinnata, Cladostephus.*
II. Two kinds of plurilocular sporangia.
    (i) Meio- and megasporangia, e.g. *E. virescens* (see p. 130).
    (ii) Micro- and megasporangia:
        (*a*) Unilocular sporangia only on separate plants, e.g. *Sphacelaria hystrix, Halopteris filicina.*
        (*b*) Unilocular sporangia and both types of gametangia all on separate plants, e.g. *Sphacelaria harveyana.*
    (iii) Antheridia and oogonia:
        (*a*) Unilocular sporangia on separate plants, e.g. *Halopteris hordacea, Dictyota, Laminaria.*
        (*b*) Unilocular sporangia absent, e.g. *Fucales.*

In general the presence of a unilocular or tetrasporic sporangium indicates a diploid thallus, and as reduction division occurs in the formation of the contents the swarmers are invariably haploid. A haploid zooid, irrespective of whether it comes from a pluri- or unilocular sporangium can behave either as a gamete or as an asexual zooid. The chief evolutionary features to be observed in so far as reproduction is concerned within the Phaeophyceae are:

(1) The elimination of accessory reproduction (the plurilocular sporangia) in the sporophyte.

(2) A tendency to soral aggregation of sporangia on the sporophyte, e.g. Sphacelariales, Dictyotales.

(3) A tendency towards anisogamy and finally oogamy.

Most species show an alternation of generations, but this is by no means regular as there may be considerable modifications. Indeed, the alternation in the Ectocarpales and Dictyosiphonales is so irregular, that the phenomenon would be better termed a life cycle rather than an alternation of generations. Furthermore, the two generations are often not the same in size, and commencing from species with similar morphological generations one may have those in which either the sporophyte or gametophyte is dominant down to plants where only the gametophyte or sporophyte is known. A progression in anatomical development can be traced, but it seems almost impossible to do the same with the life histories or reproductive organs.

Within the Heterogeneratae, where the gametophyte is much reduced, the regular alternation may be masked by complications produced by such phenomena as parthenogenetic development of the ova. Those members of the Heterogeneratae (excluding the Laminariales) which exhibit this type of alternation have a fully developed diploid or *delophycée* form which is common in summer, and a much reduced haploid or diploid *adelophycée* stage which usually appears during the winter months in one of the following forms:

(*a*) In a *protonemal* stage which reproduces the large form by means of 'buds'.

(*b*) In a gametophytic *prothallial* stage which reproduces the large form by means of gametes from plurilocular sporangia.

(*c*) In a *plethysmothallial* stage which reproduces the large form by means of swarmers from either unilocular or plurilocular sporangia. Until recently these were regarded as arrested sporophytes in a juvenile condition.

Fritsch, however, has suggested (1939) that some of these plethysmothalli are really potential gametophytes (prothalli), especially those dwarf plants which perpetuate themselves by means of plurilocular sporangia. The term 'plethysmothallus' should be reserved for plants that are diploid and which have arisen from diploid swarmers produced in plurilocular sporangia on the macroscopic plants. Such plethysmothalli can then be regarded as diploid sporophytes which have been indefinitely arrested at the ectocarpoid stage. Since some of the so-called protonema may also bear plurilocular sporangia it would seem that the various categories cannot be sharply distinguished and their systematic usefulness, especially that of the protonema, is thereby diminished.

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* ECTOCARPALES

The members of this order, which are the least specialized of the Phaeophyceae, exhibit some range of form, but fundamentally they are of filamentous construction and basically are heterotrichous with prostrate and erect portions of the thallus, though one or other may subsequently become lost. A number represent forms that have become reduced as a result of either an epiphytic or parasitic habit.

* ECTOCARPACEAE: *Ectocarpus* (*ecto*, external; *carpus*, fruit). Fig. 70

The plants are composed of uniseriate filaments which are sparsely or profusely branched. The aerial portion is sometimes decumbent and arises from a rhizoidal base, which in some of the epiphytic species occasionally penetrates the host, and it is also possible that there may be one or two examples of mild parasitism. *E. fasciculatus* grows on the fins of certain fish in Sweden, but the nature of the relationship in this case is not clear. The branches of some species terminate in a colourless mucilage hair: in young plants of *E. siliculosus* these hairs are quite long, but later, with in-

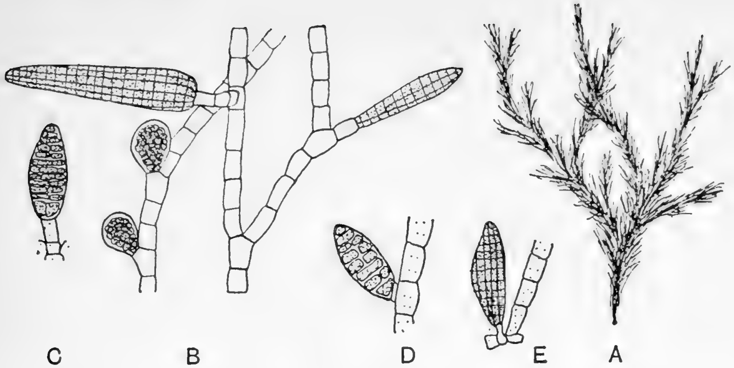

Fig. 70 *Ectocarpus.* A, *E. confervoides*, plant (×0·44) B, *E. tomentosus*, unilocular and plurilocular sporangia (×100). C, meisporangium, *E. virescens.* D, megasporangium, *E. virescens.* E, microsporangium, *E. virescens.* (A, B, original; C–E, after Kniep.)

creasing age, they become much shorter through truncation. The erect filaments of some species have an intercalary growing region, whilst in other species growth is diffuse, but the rhizoids increase in length by means of apical growth. Each cell, which contains one nucleus together with brown, disc or band-shaped chromatophores, possesses a wall that is composed of three pectic-cellulose layers. Generally two kinds of reproductive structures are present, the plurilocular and unilocular sporangia, but some species possess a third type, the meiosporangia. The unilocular sporangia always occur on diploid plants and they give rise, after meiosis, to numerous haploid zooids which may either function as gametes or else develop without undergoing a fusion. The sporangia are sessile or stalked and vary in shape from globose to ellipsoid, the mature ones dehiscing through the swelling up of the centre layer in the wall. The plurilocular sporangia, which are either sessile or stalked, range from ovate to siliquose in shape and are to be found on haploid or diploid thalli. In *E. siliculosus* they represent modified lateral branches and arise as side papillae from a vegetative cell in the filament. The plurilocular sporangia are divided up into a number of small cells, each one of which gives rise to a zooid and, when ripe, dehiscence takes place by means of a pore, the contents either germinating directly or else behaving as gametes. The gametes are usually alike in size but the sex function becomes weaker with age so that relative sexuality is induced, the older and weaker gamete behaving as the opposite sex towards the younger and stronger gamete.

In *Giffordia secunda* (*E. secundus*) there is well-marked anisogamy, as seen by the two types of plurilocular sporangia with large or small loculi that produce zooids which differ in size, the smaller gametangia being the antheridia and the larger, the oogonia. In addition, there is an accessory asexual plurilocular sporangium or meiosporangium. The contents of the oogonia are sometimes capable of parthenogenetic development. In *E. padinae* the unilocular sporangia are absent and there are three kinds of plurilocular sporangia. One type, which has very small loculi, represents the antheridia, whilst there are also medium-sized or meiosporangia, and large or megasporangia. The latter probably represent the female reproductive organs, but there is, at present, no definite proof for this hypothesis. It has been suggested that the meiosporangia may be haploid and the megasporangia diploid in character, but no cytological data appear to be available. In *E. virescens* unilocular sporangia are present together with meio- and megasporangia, both of which always occur on separate individuals. No fusion between zooids from the last two types of sporangia has been observed, but the zooids of the megasporangia are not very mobile and frequently germinate inside the sporangium. This may represent a case of apogamy in which sex has been lost, or it may represent parthenogenetic development of ova because the male organs (the meiosporangia) have ceased to function. In any case it must be regarded as a type in which some degeneration has occurred.

The life cycles of the species are full of interest, especially in view of what has been discovered for *E. siliculosus*. Knight (1929) found that the plants in the Isle of Man occurred in early spring and late autumn and were all diploid, the haploid generation being unknown. They bore unilocular and plurilocular sporangia, the former producing gametes after a reduction division whilst the latter gave rise to zoospores. In the Bay of Naples, on the other hand, the large plants were all haploid and only bore plurilocular sporangia. The zooids from these behaved as gametes, and after fusion meiosis commonly took place when the zygote commenced to germinate because it normally developed directly into a new haploid plant. Berthold recorded a microscopic form which has since been regarded as diploid because unilocular sporangia were found on it, but Knight was unable to find any such dwarf plants.

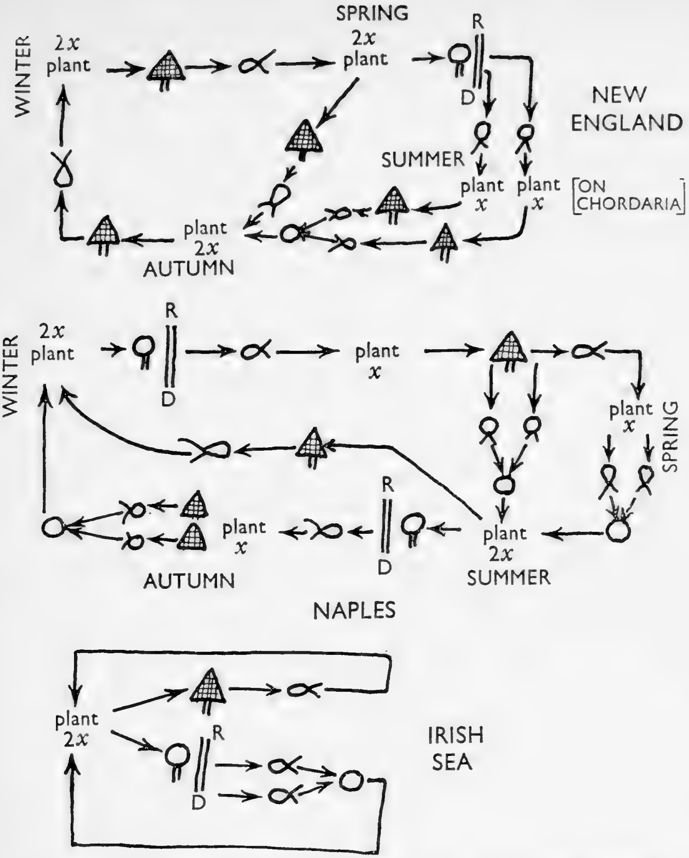

Fig. 71 Diagram to show different life cycles recorded for *Ectocarpus siliculosis* from different localities.

A schema of the Irish sea cycle is seen in Fig. 71. It has been suggested that the differences between the plants from the two localities are due to differences in the tides, light conditions or temperature, with perhaps more emphasis on the last. A further study of the Neapolitan form by Schussnig and Kothbauer (1934) has subsequently revealed the existence of unilocular sporangia, although the products from these did not undergo fusion. The results of this study do not fit in at all satisfactorily with those of Knight because it will be seen that there is a considerable seasonal variation. Yet another study of this species has also been carried out in America by Papenfuss (1935), and his conclusions agree fairly well with those of Schussnig and Kothbauer. This worker believes that in the Irish Sea the zoids from the unilocular sporangia probably do not fuse, as shown by Knight, but give rise instead to haploid plants (cf. Fig. 71). It would seem, therefore, that the somewhat complex schema of these later workers is probably the more correct, at any rate so far as the Neapolitan form is concerned. In America the diploid plants were found growing epiphytically on *Chorda* or *Spartina* and these either bore pluri- or unilocular sporangia independently, or else both could be found on the same thallus. The unilocular sporangia occurred only in summer, whilst the plurilocular were present throughout the whole year. Although the zooids from both types of sporangia acted as zoospores and germinated directly, nevertheless meiosis always took place in the unilocular sporangia, the zooids of which developed into the sexual plants that were found growing as obligate epiphytes on *Chordaria*, in some cases the nearest asexual plants being twenty miles distant. It is suggested, therefore, that dependence of the sexual generation upon a particular host may be rather more common than is perhaps suspected. The plants growing on *Chordaria* were dioecious and only bore plurilocular gametangia. It must also be borne in mind that the variations in the life cycles of the plants from these three localities may be due to genetic differences because, although the chromosome numbers may be identical, this would not exclude such a possibility. This extremely large genus is now subdivided, and recently a number of new genera have been established (Hamel, 1939).

ECTOCARPACEAE: *Pylaiella* (after de la Pylaie, a French botanist). Fig. 72

There are several species, one or two of which are widely distributed, e.g. *P.* (*Bachelotia*) *fulvescens*, *P. littoralis*, and although the latter is said to possess quite a number of varieties it is by no means certain that they may not be ecological or seasonal forms because it has been shown that the movement of the water can even affect the nature of the branches. In general appearance the plants are very like *Ectocarpus*, and for many years the species was included in that genus. The branching is opposite or alternate, but the branches do not end in a mucilage hair as they do in *Ectocarpus*. Attachment to the host plants or to the substrate is by means of rhizoidal filaments, and near the base the main filaments of the erect thallus are frequently coalesced into a rope-like structure as a result of wave action. In some places the plants appear to be confined principally to certain host plants whilst in other areas there may be no special hosts. In the Isle of Man, Knight (1923) has shown that in the spring the plants occur on *Ascophyllum nodosum*, in early summer they are to be found on *Fucus vesiculosus* and in late summer on *F. serratus*, yet in north Norfolk the species frequently grows on the stable mud banks of salt marsh creeks or else on *F. vesiculosus*. On the Swedish coast three forms have been noted, two of which are found on *Ascophyllum nodosum*, whilst the third, which is a vernal form that dies off at the end of June, occurs attached to stones. Of the two forms observed on *Ascophyllum* it is found that those directly attached to the host are the more numerous, and although they persist for the whole year, they are most fertile in winter when they produce unilocular sporangia. The other plants are really epizoic because they grow on the colonies of *Sertularia* (a hydroid) that are to be found on the *Ascophyllum*. These plants, which only bear plurilocular sporangia, are most vigorous during spring and early summer and are dead by the end of July.

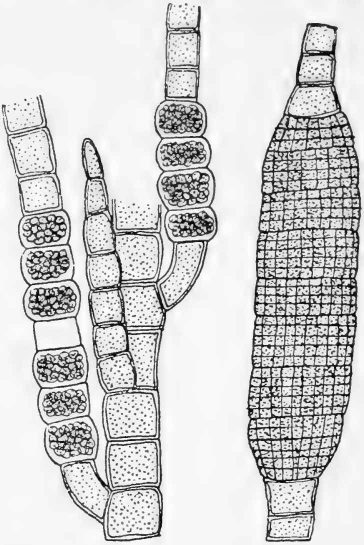

Fig. 72 *Pylaiella littoralis*. Portions of plant with plurilocular and unilocular sporangia (× 200). (Original.)

This genus is readily distinguished from *Ectocarpus* by the position of the sporangia because these bodies are nearly always intercalary, very rarely terminal, and when this latter is the case it is frequently due to the loss of the terminal vegetative portion. The unilocular sporangia are cask-shaped and open laterally, dehiscence of the sporangium being brought about by the swelling up of the middle layer of the wall, but this process is dependent on the temperature of the water when the plant is flooded by the incoming tide, high temperatures acting in an inhibitory manner. Meiosis

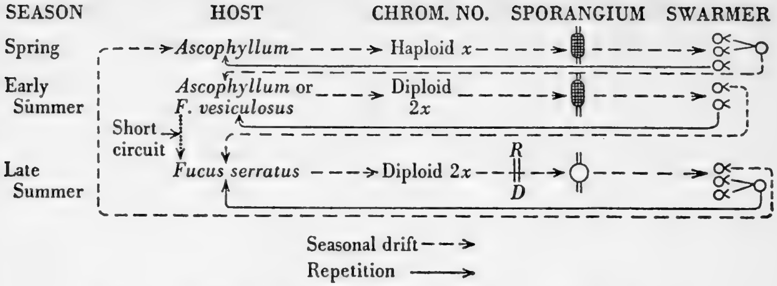

Fig. 73 *Pylaiella littoralis.* The life cycle according to Knight.

takes place in the unilocular sporangia, and each zoospore when it finally emerges possesses one nucleus, two plastids and flagellae and one eye-spot. After emergence the zoospores usually germinate singly but they have been known to fuse and thus restore the diploid condition. The plurilocular sporangia, which are produced on haploid or diploid plants, are oblong or irregularly cylindrical and also dehisce laterally, each cell producing one zooid which emerges singly. The zooids from these sporangia either fuse or else develop at once, the parthenogenetic zooids arising from diploid sporangia, principally during the summer in England and throughout the winter in Sweden, although isolated cases may occur at any time in the year. The other zooids, which function as gametes or which may occasionally develop parthenogenetically, arise from haploid sporangia and are most abundant in spring and early summer. Fig. 73 is a schema to illustrate the life cycle as found in English plants during the course of one year. In the related species *P. rupinicola*, only the diploid generation is known and the sexual haploid generation has apparently been lost. In *P.* (*Bachelotia*) *fulvescens* the sporangia may be borne in biseriate instead of uniseriate rows. For this reason the plants are commonly placed in a subgenus.

ECTOCARPACEAE: *Phaeostroma* (*phaeo*, brown; *stroma*, mattress). Fig. 74

This is cited as an example of a much reduced ectocarpoid form, which occurs as an epiphyte or partial parasite upon marine grasses, such as *Zostera*, or else upon other brown algae. The filaments, although creeping, are clearly ectocarpalean and in places may ter-

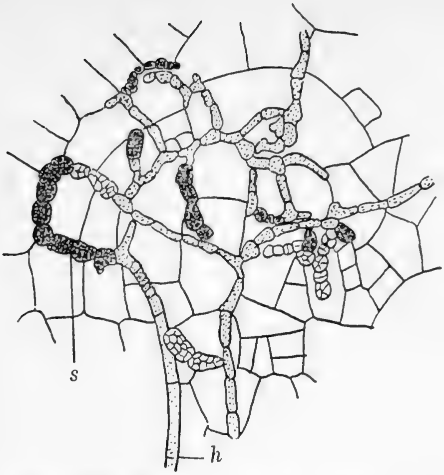

Fig. 74 *Phaeostroma bertholdi.* Thallus ramifying in *Scytosiphon* showing sporangia (*s*) and a hair (*h*). (After Oltmanns.)

minate in a typical hair. Plurilocular sporangia are produced, either in series or singly, in terminal or intercalary positions. There are numbers of these reduced forms and identification is impossible unless the reproductive organs are present.

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* SPHACELARIALES

The next three types belong to the Sphacelariales, an order frequently known as the 'Brenntalgen' because they possess a very characteristic large apical cell with dense brown, tanniferous contents, the detailed classification of the group being based primarily upon the behaviour of this apical cell at branch formation. The plants have regular branching and a bilateral symmetry, both of which form characteristic features. Structurally they can be regarded as strengthened multiseriate filaments, *Sphacella* perhaps being one of the more primitive members of the group with a noncorticate monosiphonous axis.

In most members of the order two types of lateral branch occur, those of limited and others of unlimited growth. The plants exhibit heterotrichy with a well-developed prostrate system, which is perennial and from which new erect systems can arise each season. In those cases where it has been studied there is an alternation of isomorphic generations. The order is most widely represented in the southern hemisphere, and it may well have originated in the Australasian region.

* SPHACELARIACEAE: *Sphacelaria* (gangrene). Fig. 75

The plants grow attached to stones or other algae by means of basal discs or rhizoids that have spread down from the lower cells of the axis. The basal disc may give rise to horizontal stolons and so enable the plant to spread.

The erect system is filamentous and the type of branching is termed *hemiblastic* in which the laterals, whether of definite or indefinite growth, arise from the whole height of a cell representing the upper segment derived from the division of a primary segment (Fig. 75, E). If the branching is pinnate practically every superior segment produces branch initials, though in some cases the initials may remain dormant and the branching is then less luxuriant. Branches of limited growth bear colourless hairs which are cut off as small cells to one side of the apical cell (Fig. 75, B–D). As the apical cell elongates the hair comes to occupy a lateral position. These hairs may disappear with age. This type of hair formation is regarded as sympodial, the hair initial being the true apical cell whilst the so-called branch axis is regarded as a subsidiary branch. Branching, which takes place in this way is said to be *holoblastic*.

Growth in length takes place by horizontal divisions of the apical cell, and when the basal cell so cut off (S in Fig. 75 E) has reached a certain length it divides into a superior and inferior segment. These segments exhibit no further enlargement, though they may divide by longitudinal and transverse walls to form a corticated thallus. This type of vegetative system is said to be *leptocaulous*.

Vegetative reproduction takes place in this genus by means of

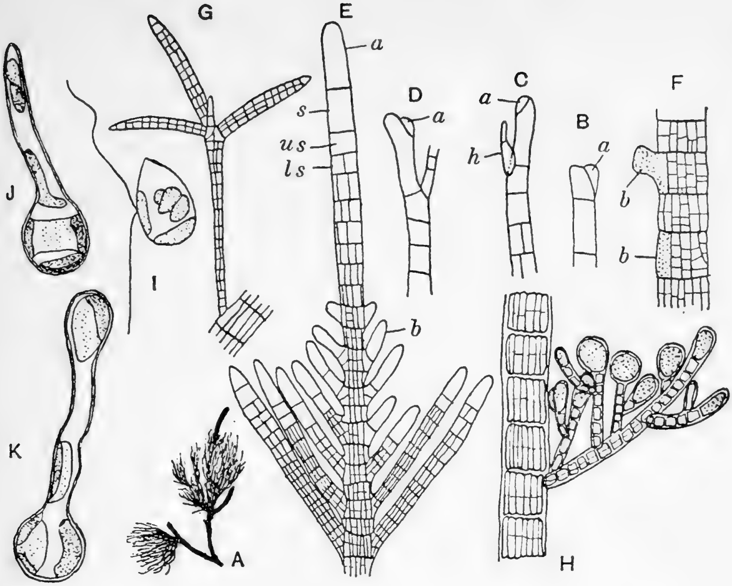

Fig. 75 *Sphacelaria*. A, plant of *S. cirrhosa* (× ½). B, apical cell (*a*) of *S. cirrhosa*. C, *S. cirrhosa*, origin of hair (*h*). *a* = apical cell. D, hair at older stage; *a* = apical cell. E, apex of thallus of *S. plumigera* showing branches, *b*; single segment (*s*), which later divides into upper (*us*) and lower (*ls*) segments; *a* = apical cell. F, origin of branch, *b*. G, bulbil of *S. cirrhosa* (× 52·5). H, unilocular sporangia, *S. racemosa*. I, zoospore of *S. bipinnata* (× 1200). J, K, germinating spore of *S. bipinnata* (× 1200). (A, original; B–G, after Oltmanns; H, after Taylor; I–K, after Papenfuss.)

modified branches or propagules which vary in shape from wedge-like to di- or triradiate with long or short pedicels. Unilocular and plurilocular sporangia are borne terminally or laterally on simple or branched laterals and are either sessile or shortly pedicellate. The life cycle of *Sphacelaria bipinnata* has been worked out in some detail and is probably typical of the genus.

The asexual generation bears both uni- and plurilocular sporangia. Zooids from the former fuse in clumps, but those from the latter germinate directly and represent a means of accessory reproduction. The cytology of the clumps has not been studied though meiosis occurs in the unilocular sporangia. These clumps must give rise to the isomorphic sexual generation which reproduces by means of isogametes liberated from plurilocular sporangia.

CLADOSTEPHACEAE: *Cladostephus* (*clado*, shoot; *stephus*, crown). Fig. 76

The plants, which are bushy in appearance, arise from well-developed holdfasts and are characterised by the ecorticate branches being arranged in whorls with tufts of hairs just below their apices. Cells just below the apex divide to give a number of branch segments, this type of branching being known as *polyblastic*. The first segment of these laterals of limited growth cuts off a cell or cells that form a cushion of tissue belonging to the main axis. Later the spaces between laterals may be filled by tissue so that the bases are completely enveloped. As a result of this septation the older branches, although originally hemiblastic in origin, appear to arise only from the tops of the original superior segments. The lower portions of the segments may later give rise to secondary whorls which are said to arise *meriblastically*. The main axis is corticate because both upper and lower primary segments undergo abundant division. In addition the cells so formed enlarge in width and length so that the axis increases in size from the apex downwards. Such a

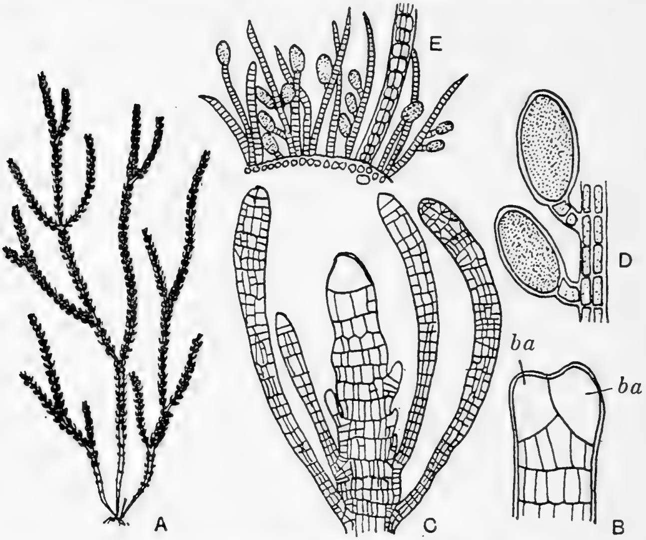

Fig. 76 *Cladostephus verticillatus*. A, plant (× ½). B, apex to show origin of branch. *ba* = branch apex. C, thallus showing cortication. D, unilocular sporangia (× 225). E, part of thallus with unilocular sporangia (× 45). (A, D, E after Newton; B, C, after Oltmanns.)

form of growth is termed *auxocaulous*. *Cladostephus* also forms long branches which arise in a hemiblastic manner. Since the initial does not undergo any anticlinal divisions (Fig. 76, B) it is equivalent to a number of initials representing laterals of limited growth.

There is no special means of vegetative reproduction. Both unilocular and plurilocular sporangia are formed on special branchlets or *stichidia*, which arise from the rhizoidal cortex in the internodes between the whorls of vegetative branches. The different types of sporangia occur on separate plants, the unilocular, which produce zoospores, on the diploid generation, and + and − plurilocular sporangia on separate gametophytic plants. The plurilocular sporangia give rise to isogametes.

STYPOCAULACEAE: *Halopteris* (*halo*, sea; *pteris*, fern). Fig. 77

The pinnate frond arises from a distinct basal pad, the plants in summer having the appearance of shaggy tufts, whilst in winter the branching appears more regular as surplus branchlets are shed. The inner cortex of the central axis is composed of a number of cubical cells whilst there is also an outer cortex of rhizoidal cells (pericysts), the whole forming a pseudo-parenchyma. Since there is no enlargement of the original cells *Halopteris* is leptocaulous. Pericysts are only found in the main axis and branches of unlimited growth. Branching in *Halopteris* is holoblastic (cf. hair production in *Sphacelaria*). At an early stage the branch initial cuts off a small upper axillary cell. This cell is regarded as the true apical cell so that the branch is really a lateral of a diminutive branch axis. In some species the axillary cell may later give rise to a tuft of hairs.

The sexual and asexual generations alternate, the former reproducing by means of antheridia and oogonia and the latter by unilocular sporangia and zooids. The reproductive organs are borne in the axils of laterals (when they must be regarded as terminal on axillary shoots) or on branchlets arising from pads derived from the axial initial. In *H. scoparia* the sori are united into spikelets, the lower laterals being sterile and only the upper being fertile. Many years ago an herbarium plant of *Halopteris* was reported with oogonia and antheridia but it was not until quite recently that the living material with these organs was found in New Zealand. A number of species are known, especially from the South Pacific, but their identification is not always easy.

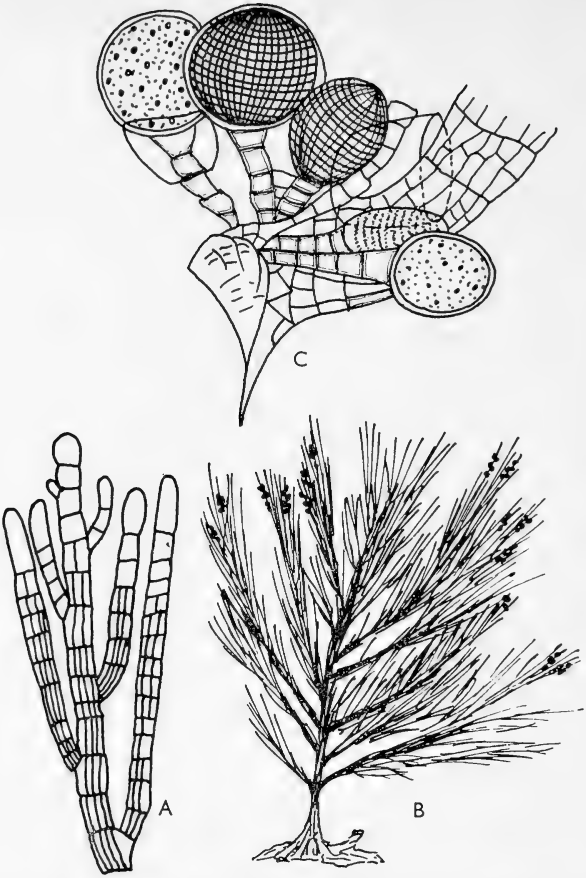

Fig. 77 *Halopteris*. A, apical portion of *H. funicularis* (× 180); B, fertile plant of *H. hordacea* (× 1); C, oogonia and antheridia of *H. hordacea* (× 126). (C, after Moore, A, B, after Lindauer.)

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TILOPTERIDALES

The members of this order comprise deep-water algae of Atlantic shores, the life cycles of which are somewhat incompletely known. They would appear to represent a transition from the Ectocarpalean type to the Dictyotalean type of reproduction, though retaining Ectocarpalean morphology. Asexual reproduction takes place by means of characteristic, large, motionless quadrinucleate monospores which almost certainly represent unsegmented or primitive tetraspores. Sexual fusion has not so far been reported within the order. Recent work (Kornmann, 1953) has shown that the genus *Acinetospora*, formerly placed in this order, is properly a member of the Ectocarpales.

TILOPTERIDACEAE: *Haplospora* (*haplo*, simple; *spora*, seed). Fig. 78

The plants, which arise from a basal disc, are filamentous, with irregular pinnate branching from the main axes. The lower portion becomes multiseriate by septation and then resembles *Sphacelaria* but the growth is always intercalary. The sexual plants develop intercalary, tubular, plurilocular gametangia which are produced by the transformation of one or more cells of the main filament.

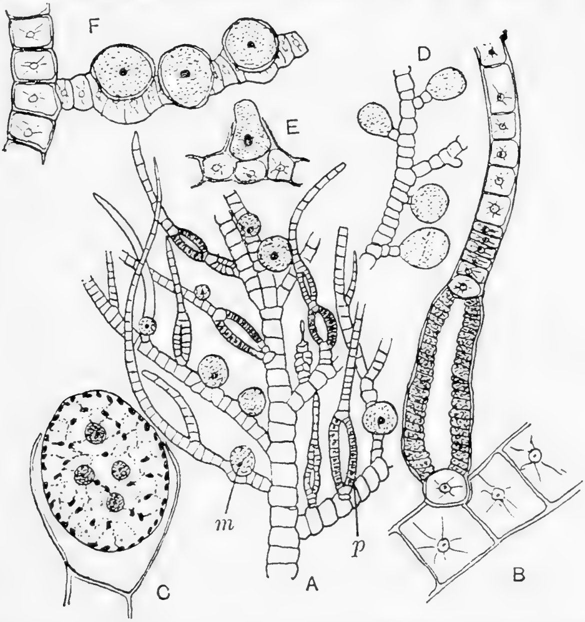

Fig. 78 *Haplospora globosa*. A, portion of plant with uninucleate sporangia, *m* (oogonia?), and plurilocular microgametangia, *p*. B, plurilocular microgametangium. C, monosporangium with quadrinucleate monospore. D, monosporangia. E, F, unilocular sporangia (oogonia?). (A–C, after Oltmanns, D–F, after Tilden.)

The swarmers from these gametangia are thought to be male gametes. Besides these organs there are larger and spherical uninucleate monosporangia borne on a stalk cell and partly immersed in the branches. These at one time were thought to be oogonia but at present they are regarded as an accessory means of reproducing the sexual generation. The asexual plant reproduces by means of quadrinucleate spores formed singly in stalked or sessile, terminal or intercalary, monosporangia. Meiosis has been reported as occurring in these sporangia and this would be expected if they were primitive tetraspores. It would seem that the plants known as *Haplospora globosa* and *Scaphospora speciosa* are simply alternate phases of one and the same species, the latter being the sexual generation. The whole life cycle, however, is in need of detailed study.

CUTLERIALES

This order is characterized by trichothallic growth, *regular* alternation of generations, and a well-marked anisogamy which in some respects approaches oogamy. They are generally placed in the Isogeneratae, even though this leads to a difficulty because in *Cutleria* the two generations are not equal morphologically although they are equal in *Zanardinia*. In *Microzonia* only the diploid generation is known at present. On this classification, therefore, *Cutleria* must be regarded as a modified member of the Isogeneratae or else it must be separated from *Zanardinia* and put in a separate family in the Heterogeneratae. A solution to this problem is to regard both types of alternation as having arisen from an ancestral form that was heterotrichous (see p. 316).

CUTLERIACEAE: *Cutleria* (after Miss Cutler). Fig. 79

The gametophyte and sporophyte generations are distinctly heteromorphic and also differ in their seasonal occurrence, the former being a summer annual whilst the latter is a perennial reaching its maximum vegetative phase in October and November with a peak fruiting period in March and April. The gametophyte is an erect, flattened thallus with irregular branching brought about by periodic failure of the marginal filaments to fuse together. In cross-section the plant consists of larger cells in the centre and smaller ones in the epidermis. The thallus and apices are clothed with

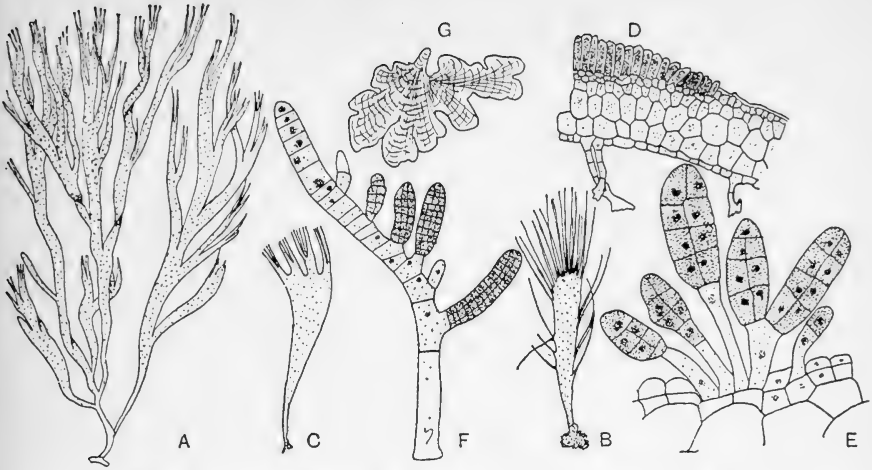

Fig. 79 *Cutleria multifida.* A, plant (× $\frac{1}{3}$). B, young plantling. C, plantling slightly older to show branching. D, transverse section of thallus with unilocular sporangia. E, female gametangia. F, male gametangia. G, '*Aglaozonia*' stage. (A, original; B–D, G, after Oltmanns; E, F, after Yamanouchi.)

tufts of hairs, each with a basal growing region, whilst the oogonia and antheridia, which are borne on separate plants, occur in sori on both sides of the thallus. The antheridia are borne normally on threads that are much branched. The mature plurilocular antheridium contains about 200 antherozoids, each of which possesses two chromatophores, and they are much smaller than the mature ova, each of which contains thirty or more chromatophores.

The oogonia, with which hairs are sometimes associated, are also formed from superficial cells which divide into a stalk cell and an oogonium initial. The ripe oogonium contains sixteen to fifty-six eggs which, after liberation, remain motile for a period of from 5 minutes to 2 hours, whilst the antherozoids can remain active for about 20 hours. Discharge of the gametes takes place at any time during the day but is at its best about 5 a.m., fertilization taking place in the water when the diploid number of chromosomes (48) is restored. No fertilization occurs whilst the ova are motile. Soon after they have become fixed they round off and then they attract large numbers of antherozoids chemotactically. With the passage of time this chemotactic power is lost and has gone completely within 3–4 hours. The chances of fertilization are correspondingly reduced with the lapse of time from loss of motility of the ovum. If sexual hormone production (see p. 415) is involved it must be assumed that it is only secreted for a relatively short period of time.

Upon germination a small columnar structure is first formed and then a flat basal expansion grows out from its base to form the adult sporophyte, which is a prostrate expanded thallus attached to the substrate by means of rhizoids. It differs so very much from the gametophyte that when first found it was thought to be a separate genus and was given the name of *Aglaozonia*. It sometimes happens that the ova do not become fertilized, and when this happens they germinate parthenogenetically to give haploid *Aglaozonia* plants, but these do not bear any reproductive organs. The sporophytic thallus is composed of large cells in the centre with superficial layers, both top and bottom, of small cells. The sessile unilocular sporangia, sometimes accompanied by deciduous hairs, are borne in palisade-like sori or else are scattered irregularly on the upper surface of the thallus. Each superficial cell first divides into a stalk cell and sporangium initial, then meiosis occurs and eventually eight to thirty-two zoospores are formed in each sporangium. The zoospores on germination give rise to new *Cutleria* plants. This life cycle was first worked out by Yamanouchi (1912) for the common species *Cutleria multifida* and its sporophyte *Aglaozonia reptans*.

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* DICTYOTALES

This order is characterized by species possessing a well-marked regular alternation of two identical generations. Morphologically the plants are parenchymatous and consist of one or more medullary layers of large cells and a cortical layer of small cells. The species are also characterized by apical growth and usually by dichotomous branching in one plane. In *Dictyota* there is a single apical cell but in other genera, e.g. *Padina*, *Taonia*, it is replaced by a marginal meristem. In the tropical genus *Padina* there may be considerable deposition of lime on the thallus. It is perhaps worth noting that lime deposition occurs with much greater frequency in the Chlorophyceae (pp. 92, 96) and Rhodophyceae (pp. 233, 238). Some of the genera, e.g. *Dictyopteris*, have a distinct mid-rib. Asexual reproduction is brought about by means of tetraspores produced in superficial tetrasporangia, whilst the sex organs are represented by antheridia and oogonia borne in sori on separate plants. All the organs of reproduction develop from surface cells which enlarge and protrude above the surface of the thallus. In some forms a stalk cell may be cut off. It seems that at meiosis in the tetrasporangia, segregation of the sexes takes place so that two of each group of four tetraspores will give rise to male plants and two to female. In certain genera, e.g. *Taonia*, *Padina*, the tetrasporangia and sex organs are borne in zonate bands across the thallus, and in some cases there is evidence of a correlation between their development and with diurnal tidal cycles (e.g. *Taonia*) or with spring tidal cycles, (e.g. *Padina*). It seems likely that light conditions are involved in the case where single tidal periods are involved. A period is evidently required between the initiation of each new crop, probably so that the plant can accumulate the necessary food material. In *Taonia* and *Dictyota* asexual plants are more abundant than the sexual, at least in some localities. This is partly accounted for by the persistence of a sporophytic rhizoidal portion that regenerates new plants, but more commonly the contents of the tetrasporangium fail to divide before they are liberated. These undivided contents give rise to new plants, which are more resistant and vigorous than plants produced from normal tetraspores, possibly because of the larger amount of food material available from a single sporangium. The order is primarily a tropical one but some species, e.g. *Dictyota dichotoma*, are widely distributed in temperate waters as well.

*DICTYOTACEAE: *Dictyota* (like a mat). Fig. 80

In the cosmopolitan species, *D. dichotoma*, the flattened thallus exhibits what is practically a perfect dichotomy because there is always a median septation of the apical cell. Viewed in transverse section the thallus is seen to be composed of three layers, a central one of large cells and an upper and lower epidermis of small assimilatory cells from which groups of mucilage hairs arise.

The male and female sex organs are borne in sori on separate plants, the male sorus being composed of as many as 300 plurilocular antheridia surrounded by an outer zone of sterile cells. At

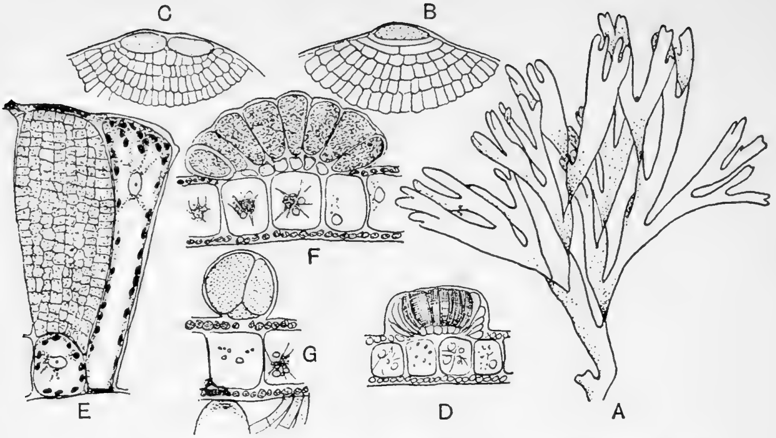

Fig. 80 *Dictyota dichotoma.* A, portion of plant showing regular dichotomy. B, apical cell. C, apical cell divided. D, group of antheridia surrounded by sterile cells. E, single antheridial cell and a sterile cell. F, sorus of oogonia. G, tetrasporangium. (A–D, F, G, after Oltmanns; E, after Williams.)

the formation of an antheridium a superficial cell divides into a stalk cell and an antheridium initial, the final partition of the antheridium initial into the individual antheridial mother cells taking place only a few days before the antherozoids are to be liberated. The mature antherozoid is pear-shaped with only one cilium, and as each plurilocular antheridium liberates about 1,500 antherozoids, a single sorus may generate as many as 450,000. The number of ova produced is not so numerous, and it has been estimated that there are about 6,000 antherozoids available for each ovum. The oogonial sorus is very similar to the antheridial sorus, the large fertile oogonia, twenty-five to fifty in number, being situated in the centre and surrounded by sterile cells on the outside. The oogonia likewise arise from superficial cells that divide into a stalk cell and oogonium initial, and each oogonium when ripe produces one ovum. Liberation of both kinds of gamete usually commences from the centre of a sorus and fertilization takes place in the water, but during the process the eggs are not caused to revolve by the activities of the antherozoids as they are in *Fucus* (cf. p. 202). If the process is followed under a microscope it can be noted that only some of the eggs appear capable of attracting antherozoids. Unfertilized ova may develop parthenogenetically; such plants, however, always die in culture, though it is possible that in nature they may persist. The sex organs are produced in regular crops, the new sori appearing between the scars of the old, and when the whole of the surface has been used up the plant dies.

After fertilization the zygote develops into a morphologically similar plant which reproduces by means of *tetraspores* that are formed in tetrads in superficial sporangia. At sporangium formation an epidermal cell swells up in all directions, and after a stalk cell has been cut off the sporangium initial divides twice to give the four tetraspores, during which the thirty-two diploid chromosomes are reduced to the haploid number of sixteen. A tetraspore at the time of liberation is an elongated body and grows at once into a new sexual plant. In some cases, however, the tetrasporangium fails to divide into four spores but germinates as a whole and this phenomenon probably explains the abundance of sporophytic plants in certain localities, although the conditions that cause this abnormality have not yet been discovered. Whilst the sex organs are produced in rhythmic crops there is no such periodicity in the case of the tetraspores, and here again there is scope for further research.

Three kinds of rhythmic periodicity for the sex organs of *Dictyota* have been described from different localities:

(*a*) In Wales the sori require 10 to 13 days to develop whilst in Naples 15 or 16 days are necessary, the gametes being liberated about once a fortnight in both areas.

(*b*) In North Carolina liberations occur once a month, at the alternate spring tidal cycles, although only 8 days are required for the development of the sex organs. This suggests that the plants are exhausted after each fruiting and a resting period is necessary in order to recuperate.

(*c*) In Jamaica the successive crops take a very long time to mature, e.g. very little change can be seen even after 22 days. This results in almost continuous fruiting with two successive crops overlapping. There is obviously a considerable difference in the behaviour of species of *Dictyota*. Further investigations would be desirable in order to ascertain whether one species can behave differently under different tidal regimes.

Wherever the plants occur, the bulk of the gametes (60–70 per cent) are usually liberated in a single hour at about daybreak. On the Welsh coast the gametes are set free just after each series of high spring tides during July to October, and it has been suggested that light plays the part of the determining factor during the intertidal periods. However, when plants were removed to the laboratory, it was found that the periodicity was maintained, so that it must be inherited, whilst plants from Carolina likewise retained their periodicity when transferred to the laboratory, the specimens fruiting at the same time as those living under natural conditions. The mean tidal differences vary considerably in the four localities, 11–18 ft. in England, 0.8 ft. at Naples, 3.0 ft. in North Carolina, and 0.8 ft. in Jamaica. These differences preclude either light or tidal rise from being the controlling factor because the English and Neapolitan plants behave similarly even though there is a great difference in the tides. Regularity of the tidal cycle, however, may modify the reproductive cycle, because where the tides are somewhat irregular, as in Jamaica, the reproductive rhythm is also irregular. This rhythmic behaviour is probably not due to any one factor but has been acquired over a long period of time as a response to the environment and is now inherited. The phenomenon is not confined to *Dictyota* because regular or irregular periodic cropping has been recorded for species of *Halicystis*, *Sargassum*, *Cystophyllum*, *Padina* and *Nemoderma*. Culture experiments are required in order to determine whether the habit persists in successive generations when they are grown under completely non-tidal conditions, but unfortunately *Dictyota* has not proved very amenable to cultural conditions. Finally, it can be argued that tides and light may have no control over this rhythm and that it may be associated instead with lunar periodicity, in which case even cultures will be of no avail. It has been observed that the plants in North Carolina always fruited at the time of full moon, and it is a well-known fact that a number of marine animals spawn regularly at such a period. The lunar explanation appears to have some satisfactory features, but even so produces difficulties when the behaviour of the species in Jamaica is considered.

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CHORDARIALES

This order is not recognized by Fritsch (1945), the members being placed in the Ectocarpales. The type of structure, though obviously derived from a branched filament, is so much more elaborate that segregation of the members appears justified. The basic construction in this order is the cable type, in which one or more erect parallel strands arise from a prostrate basal thallus. These give rise to interweaving lateral branches and the whole is often enclosed in a mucous matrix. In fully developed species there are three principal zones that can be recognized in the plant thallus:

(*a*) a *medulla* composed of one or more long threads accompanied by off-shoots of the first order;
(*b*) a *subcortex* composed of off-shoots from the medulla.
(*c*) a *cortex* of peripheral assimilatory filaments and colourless hairs;

Growth is commonly trichothallic but apical growth occurs in two families.

There is also a certain amount of seconardy tissue which in some parts may be rhizoidal in character. Degenerate or modified versions of this cable type of construction are to be found in some genera (*Leathesia*, *Elachista*), whilst in epiphytic forms (Myrionemataceae) there may be considerable reduction, though the structural pattern remains clear. In nearly all the species investigated the basic life cycle consists of a macroscopic diploid plant alternating with a microscopic gametophyte. In some cases the diploid plant arises as a lateral outgrowth from a microscopic plethysmothallus.

CHORDARIACEAE: *Mesogloia* (*meso*, middle; *gloia*, slime). Fig. 81

In this genus there is a *single* central strand terminating in a hair and having a distinct intercalary meristem just below the apex. The cortex is formed of short horizontal filaments with somewhat globose terminal cells that are packed in a gelatinous material. The hairs, which are frequently worn away in the older parts of the thallus, occupy a *lateral* position, but owing to inequalities of growth they may appear to be terminal. The unilocular sporangia are ovoid and are borne at the base of the cortical filaments, but the elongate plurilocular sporangia, which incidentally are only known for *M. levillei*, replace the terminal portion of the assimilatory hairs and hence are always stalked. Meiosis takes place in the

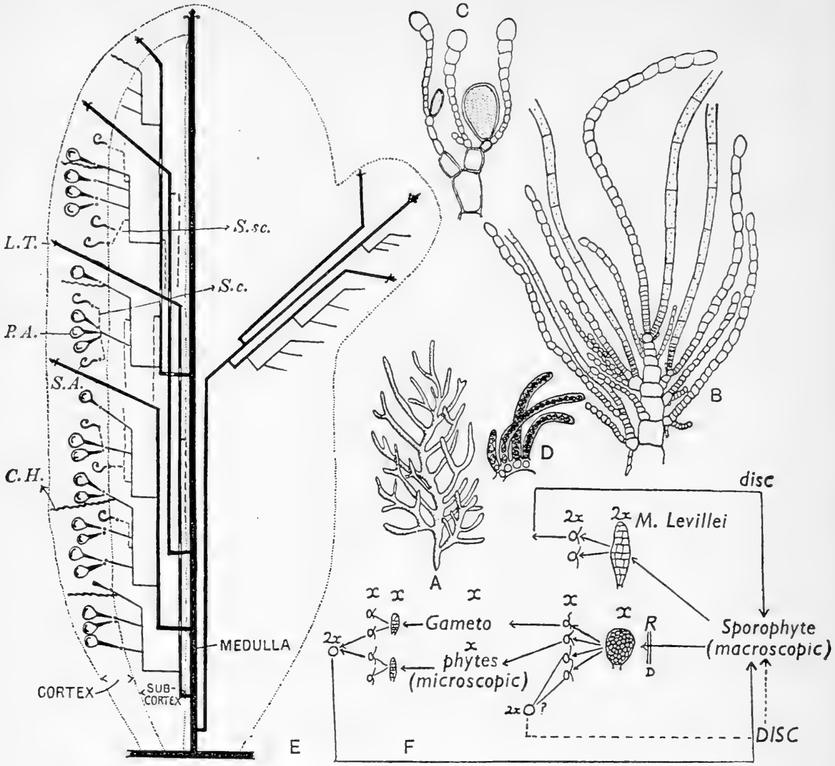

Fig. 81 *Mesogloia vermiculata*. A, plant (sporophyte). B, apex of filament with branches and beginning of cortication (× 135). C, unilocular sporangia. D, plurilocular gametangia on gametophyte. E, diagram to illustrate construction of thallus (cental thread type). *C.H.* = colourless hair, *L.T.* = leading thread with intercalary growth zone, *P.A.* = primary assimilator, *S.A.* = secondary assimilator, *S.c.* = secondary cortex, *S.sc.* = secondary sub-cortex. F, diagram to illustrate life cycle. (A, C, D, after Tilden; B, E. F, after Parke.)

unilocular sporangia during zoospore formation, and culture experiments on *M. vermiculata* carried out by Parke (1933) have demonstrated conclusively that the adult macroscopic plant of summer and autumn is diploid, the zooids from the unilocular sporangia germinating into a minute winter gametophyte (haploid *adelophycée* form) that bears plurilocular sporangia of an ectocarpoid type. The zooids from these sporangia fuse and the zygote develops into the characteristic basal disc from which the central erect filament of the macroscopic plant arises. There is thus an alternation of morphologically distinct generations in this species.

CHORDARIACEAE: *Eudesme* (well-binding). Fig. 82

This genus is very closely allied to *Castagnea* and by some workers the two genera are treated as one. The branched mucilaginous plants are densely hairy and differ from *Mesogloia* fundamentally in the presence of more than one central strand in the medulla, though there are other developmental differences as well. In the young plant the erect filaments arise from the centre of the

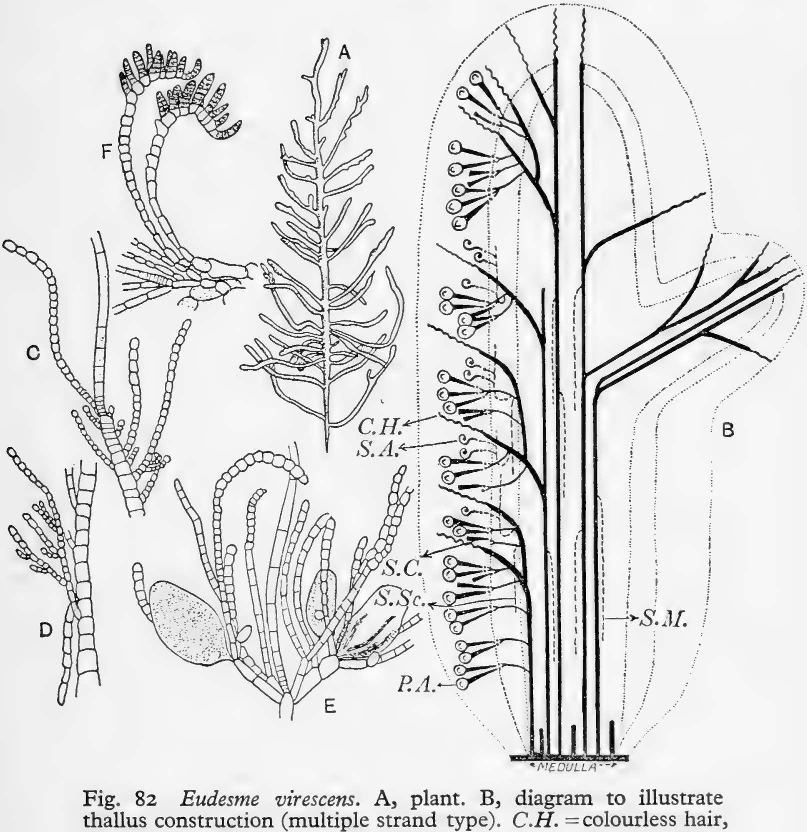

Fig. 82 *Eudesme virescens*. A, plant. B, diagram to illustrate thallus construction (multiple strand type). *C.H.* = colourless hair, *P.A.* = primary assimilator, *S.A.* = secondary assimilator, *S.C.* = secondary cortex, *S.Sc.* = secondary subcortex, *S.M.* = secondary medulla. C, apex (× 160). D, thallus with branch and corticating filament (× 75). E, unilocular sporangia. F, plurilocular sporangia. (A, E, F, after Oltmanns; B–D, after Parke.)

basal disc and are usually devoid of terminal hairs. There are also occasional sheathed hairs with a basal meristem and a terminal hair with the normal intercalary meristem. These also form medullary threads. Some of the upper cells become meristematic and produce lateral assimilators (Fig. 82D) and sheathed hairs. Further laterals are produced from growth of the cell beneath these hairs, one or other of the laterals assuming a terminal position. In this way the axial threads are built up of successive basal portions of laterals, the apical portions of which become the cortex and subcortex. This sympodial type of branching is in contrast to the monopodial branching of the axial thread of *Mesogloia*. Supplementary medullary threads, with secondary laterals, are formed by down-growing threads from the basal cells of the primary laterals. Branching hyphae may grow out from any cell.

The cortex is composed of club-shaped primary and secondary assimilatory hairs arranged either singly or in falcate tufts. The unilocular sporangia develop as outgrowths from the basal cells of the primary assimilatory filaments, whilst the plurilocular sporangia appear in secund rows on the outermost cells of the same type of filament. The zooids from the unilocular sporangia germinate immediately, or else some considerable time may elapse, perhaps as much as three years according to some observers, before any development takes place. They give rise to a microscopic plethysmothallus on which plurilocular gametangia similar to those of *Mesogloia* are to be found. After zooids have been liberated from the plurilocular sporangia of the plethysmothallus young macroscopic *Eudesme* plants appear, so that it may be assumed that there is a definite alternation of generations in which the small gametophyte forms the winter phase. Other genera with a similar structure include *Myriogloia* and *Tinocladia*.

CHORDARIACEAE: *Chordaria* (a small cord). Fig. 83

In *Mesogloia* there is a single central filament whilst in *Eudesme* there are several, but in *Chordaria* development has proceeded a stage farther and the branched cartilaginous fronds possess a firm, pseudo-parenchymatous medulla of closely packed cells that have become elongated in a longitudinal direction. The cortex is composed of crowded, radiating, assimilatory filaments, which are either simple or branched, the whole being embedded in a thick layer of jelly, thus giving the plant a slimy touch. This type of structure, even though the growth is still confined to the apex, marks the highest development of Church's consolidated or cable type of construction. The cells of the cortex are smaller than in other members of the family. The medulla comprises larger primary cells with smaller secondary hyphae interwoven among them. The end cells of the assimilators often have a much-thickened outermost wall. Branching of the axial threads is monopodial as in Mesogloia. The oblong unilocular sporangia are borne at the base of the assimilatory filaments, but plurilocular sporangia are un-

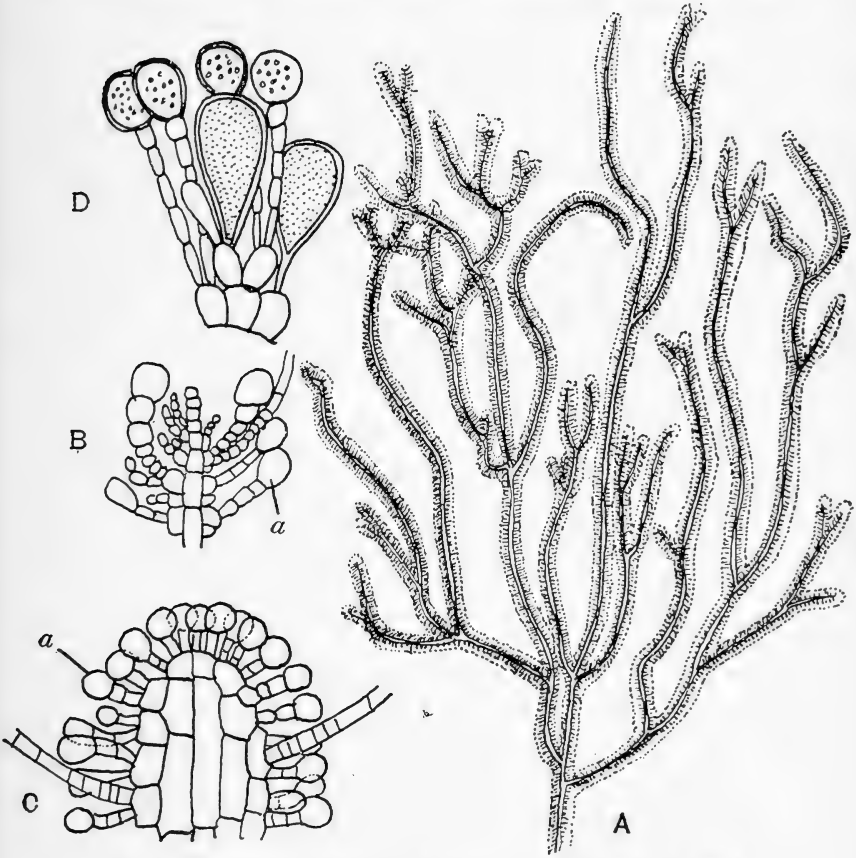

Fig. 83 *Chordaria divaricata.* A, plant (×$\frac{2}{3}$). B, apex of young plants showing commencement of cortication. C, apex of older plant of *C. flagelliformis* showing structure of thallus. a = assimilator. D, unilocular sporangia (×300). (A, D, after Newton; B, C, after Oltmanns.)

known. When this genus comes to be investigated it will probably be found to have a life history similar to that of the other Mesogloiaceae.

Corynophlaeaceae: *Leathesia* (after G. R. Leathes). Fig. 84

The present genus provides an example of degeneration in the cable type of construction. The young plant arises from a small, creeping, rhizomatous portion and is composed of a packed mass of radiating, dichotomously branched filaments which are sufficiently closely entwined to make the plant mass solid. From these medullary filaments there arises a cortex of densely packed assimilatory filaments from which occasional colourless hairs emerge. The young plants are subspherical at first, but with increasing age the central medullary filaments commence to disintegrate and as a result the mature thallus becomes hollow and irregularly lobed. Plurilocular and unilocular sporangia are known, the zoospores from the ovoid unilocular sporangia germinating to disc-like plantlets on which plurilocular gametangia ultimately appear. These plantlets either give rise to other similar plantlets or else to the adult thallus once more. By analogy with other species the

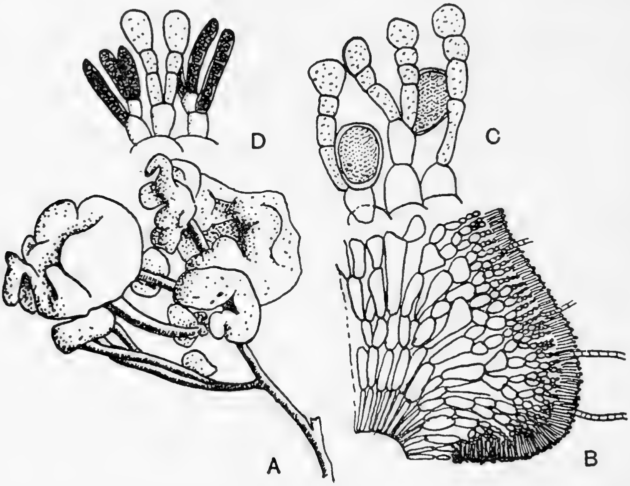

Fig. 84 *Leathesia difformis*. A, plants on *Furcellaria fastigiata*. B, transverse section to show thallus construction (× 24). C, unilocular sporangia (× 336). D, plurilocular sporangia (× 336). (A, after Oltmanns; B–D, after Newton.)

dwarf plantlets with the plurilocular sporangia may be regarded as haploid gametophytes.

The brown, flattened, spongy adherent plants of *Petrospongium* can be regarded as a still more reduced form of the spherical cushion.

ELACHISTACEAE: *Elachista* (very small). Fig. 85

Church (1920) regarded this genus as being explicable morphologically on the cable type of construction, although it must be regarded as a degenerate type in which the true structure is only seen in the sporeling. This possesses a horizontal portion from which a number of erect filaments arise, so that in the early stage it is comparable morphologically to *Eudesme*. In the older plant the erect filaments have developed to form a cushion composed of densely branched filaments matted together and only becoming free at the surface. The mature thallus comprises three distinct regions. In the dense central portion there is a mat of profusely

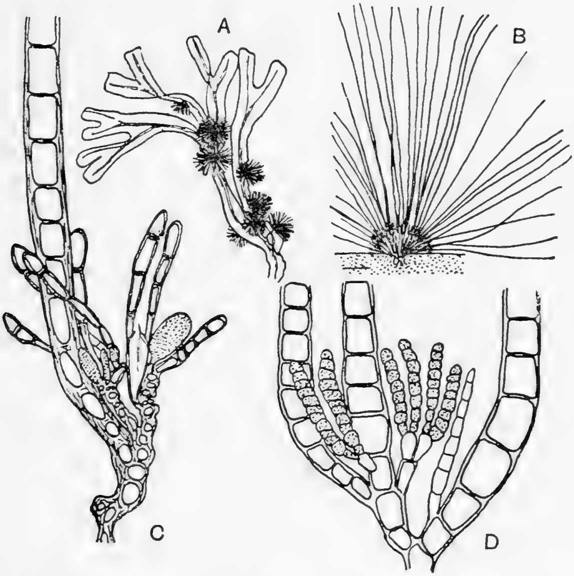

Fig. 85 *Elachista fucicola*. A, plants on *Fucus vesiculosus* (×0·36). B, single plant in section showing penetrating base, crowded sporangia, short paraphyses and long assimilators. C, unilocular sporangia (×120). D, plurilocular sporangia at base of assimilation thread (×220). (A–C, after Taylor; D, after Kylin.)

branched threads which gives way to a looser peripheral zone of assimilatory threads (paraphyses of some writers). Outside this is an outermost zone of free, long, assimilatory hairs with plastids.

The various species are epiphytic on other algae, *Elachista fucicola* being especially abundant on species of *Fucus*. Unilocular sporangia arise from the base of the assimilators, the distal portions being modified to form plurilocular sporangia. The zooids from the unilocular sporangia germinate in late autumn to give a branched, thread-like, microscopic gametophyte which persists throughout the winter. In late winter and spring plurilocular sporangia develop on the minute gametophytes, and when the zooids have been liberated they fuse and the zygote germinates into a new macroscopic *Elachista* plant.

Exceptions to the normal type of life cycle are found in *E. fucicola* and *E. stellaris*. Only unilocular sporangia are known and the zooids develop into protonemata that give rise to new sporophytes as lateral outgrowths. In these cases meiosis cannot take place. The species are epiphytic on other algae, the genus being represented in both hemispheres.

MYRIONEMATACEAE: *Myrionema* (*myrio*, numerous; *nema*, thread). Fig. 86

This represents one of the highly reduced species, but the fundamental basic cable construction of prostrate thallus and erect threads can be found, though the erect threads do not branch. The genus is of wide distribution, the commonest species being *M. strangulans* on species of *Ulva* and *Enteromorpha*. The various species form thin expansions or minute flattened cushions or discs that are very variable in shape and from which numerous, closely packed, erect filaments and hairs arise. The basal monostromatic portion of the thallus has a marginal growing region and is composed of crowded radiating filaments that may, on rare occasions, penetrate the host plant. The unilocular sporangia, which are not borne on the same plants with plurilocular sporangia, give rise to haploid zooids, and these develop into a thread-like gametophytic plant bearing long filaments, the possession of this type of gametophyte indicating that the genus is perhaps more closely allied to the Mesogloiaceae than to the Ectocarpaceae. Although *M. strangulans* possesses a life cycle typical of the Chordariales, it has been sug-

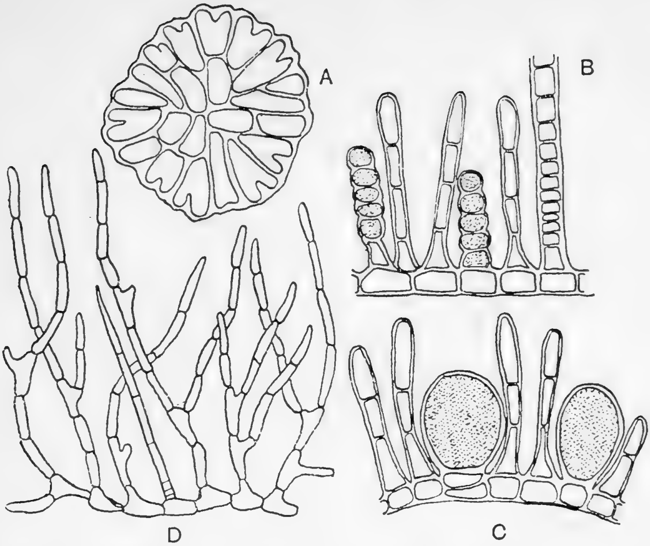

Fig. 86 *Myrionema strangulans.* A, young plant (× 640). B, plurilocular sporangia (× 340). C, unilocular sporangia (× 340). D, 11-day-old plant from zoid of unilocular sporangium (× 336). (After Kylin.)

gested that some of the other species placed in the genus or in allied genera may have isomorphic alternation in which case they may need to be removed to the Ectocarpales.

SPERMATOCHNACEAE: *Spermatochnus* (*sperma*, seed; *chnus*, fine down). Fig. 87

This is essentially one of the corticated types, the filamentous, cylindrical, branched thallus being derived from a central axis composed of a single filament with a definite apical cell. Each individual cell of this filament segments at one end and so definite nodes are formed. The corticating filaments arise from the nodes, and growth of the cortex is secured by tangential division of the primary corticating cells, though later more filaments may grow on top of them. The outermost layer of the cortex bears the assimilatory filaments and hairs. As the plants become older mucilage develops internally and forces the cortex away from the primary central filament although a connexion is maintained by the threads from each node. Unilocular sporangia, together with clavate paraphyses, develop in sori, the sporangia arising from the base of the sterile threads. The

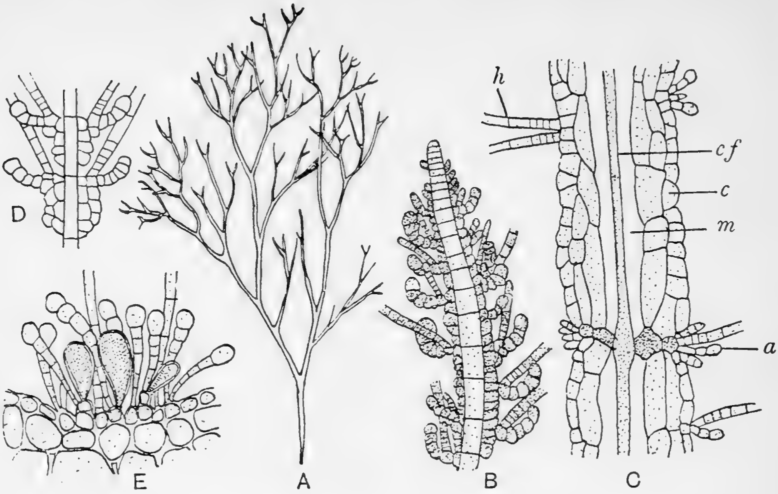

Fig. 87 *Spermatochnus paradoxus*. A, plant (×0·44). B, apex of young plant showing origin of cortication. C, portion of old thallus showing structure. *a* = assimilator, *c* = cortical cells, *cf* = central filament, *h* = hair, *m* = mucilage. D, portion of thallus showing cortication and pairs. E, paraphyses and unilocular sporangia (×200). (A, E, after Newton; B–D, after Oltmanns.)

life cycle has not yet been worked out, but if it is at all comparable with the other closely related genera then the zooids should give rise to a microscopic gametophyte generation.

NOTHEIACEAE: *Notheia* (a spurious thing). Fig. 88

The filiform sporophyte grows out parasitically from the base of conceptacles of the Fucalean *Hormosira banksii* (see p. 212) and on itself. There is an apical growing zone of three cells which give rise to filamentous rows of cells. Later divisions in different planes lead to a parenchymatous thallus in which epidermis, cortex and medullary tissue can be distinguished. The apical filamentous development is characteristically Chordalian and in its anatomy the plant has features reminiscent of both *Spermatochnus* (see above) and *Splachnidium*. True branching is rare, such branches being recognized by the lack of any basal constriction. Most of the apparent branches, which are constricted at the base, represent new plants that have developed from zygotes produced on a filamentous gametophyte that grows inside the conceptacle. In those portions of *Hormosira* that are attacked by the parasite the

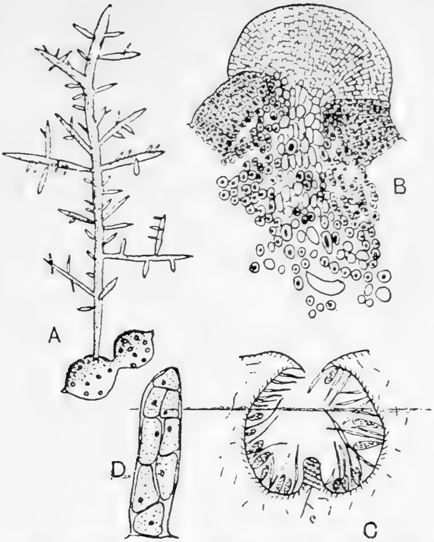

Fig. 88 *Notheia anomala.* A, plant growing out from *Hormosira.* B, point of entrance of parasite into host (× 40). C, conceptacle with megasporangia and branch shoot, *s* (× 40). D, mature megasporangia with eight ova (× 180). (A, after Oltmanns; B–D, after Williams.)

hollow of the vesicle-like internode becomes filled up by new tissue formed as a result of the stimulation, but the parasite is apparently unable to attack *Hormosira* unless the host is growing in areas where it is continuously submerged.

The fertile conceptacles contain either mega- or microsporangia, the former being much more frequent. Each megasporangium gives rise to eight pyriform zooids (originally believed to be non-motile ova) that germinate apparently in the conceptacle to a branched filamentous gametophyte with erect colourless hairs. Cells of erect branches can each produce a swarmer which is presumably a female gamete. It seems likely from the construction of the thallus that some of these germinate inside the conceptacle to give a new macroscopic plant. Others must escape and infect *Hormosira* plants. The microsporangia give rise each to 64 zooids the fate of which is not known. They could presumably either develop to a dwarf male gametophyte or else function as a male gamete. These features are of especial importance in considering the origin of the Fucales (see p. 317). The genus is monotypic and contains the one species, *Notheia anomala.*

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Notheiaceae

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SPOROCHNALES

This is a small order characterized ordinarily by the aggregation of the unilocular sporangia into swollen oval or elongate receptacles that bear a cluster of hairs at their apex. Structurally they are pseudo-parenchymatous with an intercalary, dome-shaped meristem lying beneath the group of hairs that terminates each growing branch. The gametophytes are microscopic plants which are believed to reproduce oogamously. In view of this uncertainty the life cycle obviously requires further study.

The chief centre of distribution is in the southern hemisphere where several species of *Sporochnus* occur together with the genera *Bellotia*, *Perithalia*, *Encyothalia* and *Pseudosporochnus*, which are confined to this region. All the species tend to grow in deep water and are only obtained in the castweed or else by dredging.

SPOROCHNACEAE: *Sporochnus* (*sporo*, offspring; *chnus*, fine down). Fig. 89

The plants are moderately large and the branches are terminated by a tuft of assimilatory hairs, each with a basal meristem. The mature thallus grows by means of a separate horizontal meristem that lies beneath the tuft of assimilatory hairs. Young plants consist of a simple erect thread anchored by rhizoids. The lower part represents a pedicel which plays no further part in development. The upper part forms the primary hair and the cell between the upper and lower parts is the archi-meristem from which the adult thallus is produced by longitudinal divisions in various planes. Down-growing threads are produced which coalesce to give the pseudo-parenchymatous body. The sporangia are borne laterally

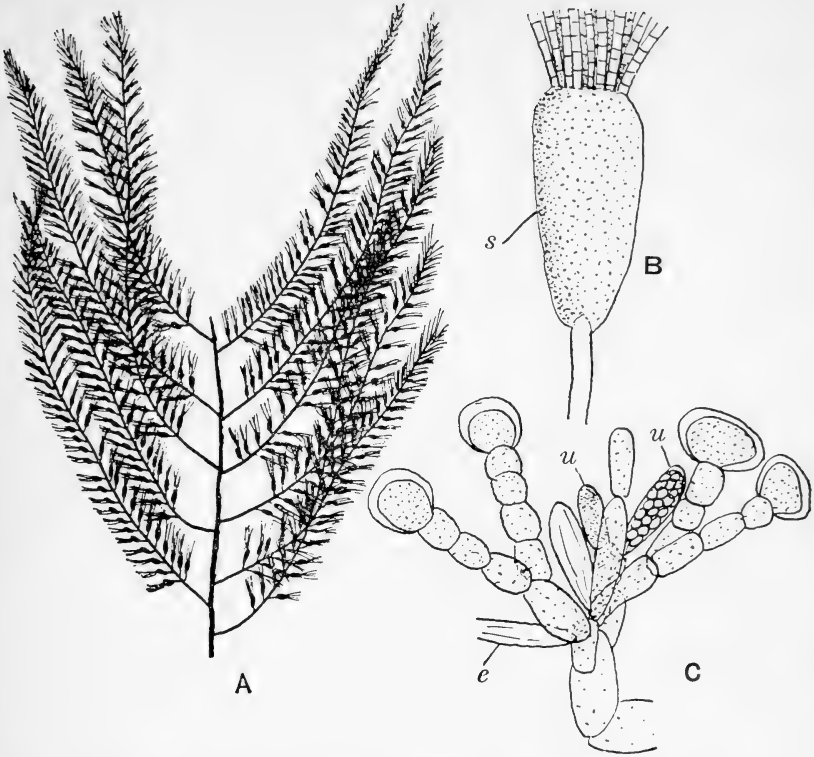

Fig. 89 *Sporochnus pedunculatus*. A, plant, B, fertile branch with receptacle. *s* = sorus. C, unilocular sporangia (*u*). *e* = empty sporangium. (After Oltmanns.)

on special branched fertile threads in the soral region. The gametophytes are ectocarpoid with small antheridia and swollen terminal cells that are believed to be oogonia. Fertilization has not been seen as yet.

Chapter VII

EUPHYCOPHYTA

PHAEOPHYCEAE (*continued*)

DICTYOSIPHONALES, DESMARESTIALES, LAMINARIALES, FUCALES

DICTYOSIPHONALES

The members of this order are fundamentally parenchymatous in construction, the thallus either being of a simple or branched radial habit or else a flattened leafy structure with intercalary growth. There is usually a medulla of large cells with a narrow cortical zone of smaller cells on which are borne the assimilatory hairs and sporangia. In some cases (*Asperococcus*, *Colpomenia*) there is subsequent degeneration of the large internal cells giving a tubular or saccate thallus. The members show heteromorphic alternation, the macroscopic plant being diploid, usually arising as a lateral outgrowth from a plethysmothallus.

PUNCTARIACEAE: *Petalonia* (*Phyllitis*, *Ilea*). Fig. 90

The unbranched fronds are expanded, membranous, leaf-like structures with an internal medulla composed of large, colourless cells interspersed with hyphae, and an outer layer of small, superficial, assimilatory cells. Unilocular sporangia are not known nor are there any paraphyses. The plurilocular sporangia, which are arranged at right angles to the surface, arise from the superficial cells and produce zooids that germinate to give a creeping basal thallus from which a new plant arises. It is therefore suggested that the plants are wholly diploid and that the haploid generation has been lost. Yendo (1919), however, has reported that these zooids can develop after a resting period into minute protonemal threads bearing antheridia and oogonia which presumably produced gametes, although no sign of fertilization was observed. If these observations are correct this genus must be regarded as anomalous,

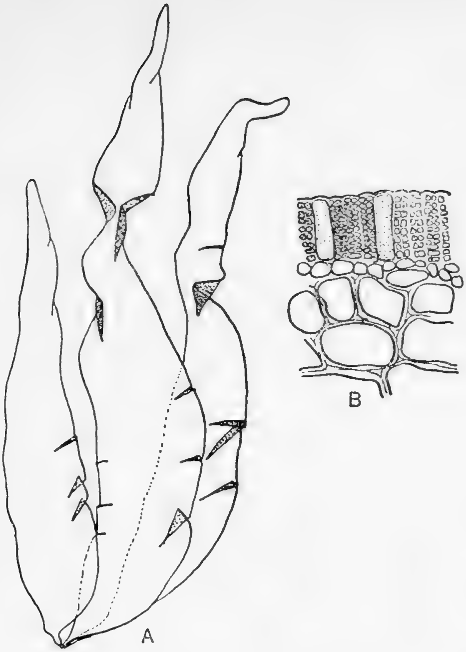

Fig. 90 *Petalonia fascia.* A, plant (× $\frac{2}{3}$). B, transverse section of thallus with plurilocular sporangia (× 375). (A, original; B, after Setchell and Gardner.)

because normally the gametophytic generation arises from the products of unilocular sporangia. It would therefore seem premature to accept this peculiar life cycle without further evidence, and at present it would be more in agreement with known life cycles if the plants are simply regarded as being wholly diploid and without a haploid generation.

In the related genus *Scytosiphon* it would also seem that only the diploid generation is present and that the reported protonemata are not gametophytic as has been suggested by some workers.

DICTYOSIPHONACEAE: *Dictyosiphon* (*dictyo*, net; *siphon*, tube). Fig. 91

The filamentous plants arise from small lobed discs and have either a few or many branches, the younger ones commonly being clothed with delicate hairs. In young plants there are the usual apical hairs with a basal meristem. Later the hairs are shed leaving

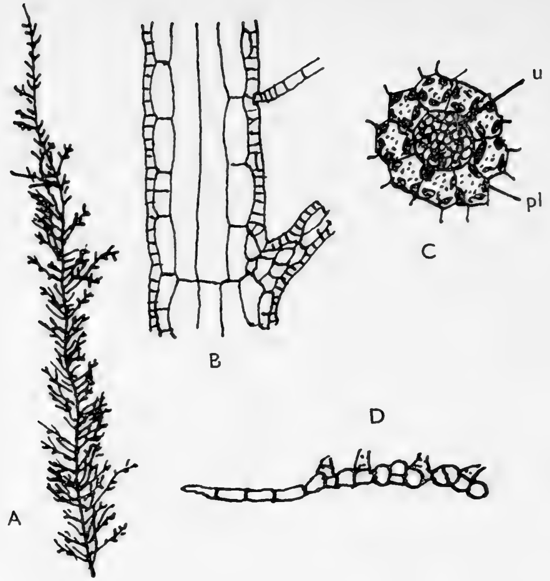

Fig. 91 *Dictyosiphon.* A, plant. B, longitudinal section of thallus. C, sporangium and thallus cells in surface view. D, gametophyte. (A, After Oltmanns; B,C, after Murbeck; D, after Sauvageau.)

four apical growing cells at the tip. There is a central medulla of four rows of large elongated cells which in parts may be penetrated by hyphae from the smaller cortical cells. In old plants the axial cells may rupture and separate so that the axis becomes partially hollow. There is a central medulla of large elongated cells and a cortex of small cells, but in old plants the medulla is often ruptured and the axis becomes partially hollow. On the macroscopic plants only unilocular sporangia are found, each of which is formed from a single subcortical cell. Meiosis takes place in these sporangia and the zooids germinate to form microscopic prothalli: these represent the gametophytic generation and reproduce by means of plurilocular gametangia. The gametes either develop parthenogenetically into a new protonema or else two of them coming from different gametangia, will fuse and the zygote develops into a small ectocarpoid plant. This may either reproduce itself by means of plurilocular zoosporangia or else it develops into a plantule from which the adult sporophyte arises. In *D. chordaria* meiosis appears to have been suppressed as the zooids give rise to a plethysmothallus that bears new sporophytes.

ASPEROCOCCACEAE: *Asperococcus* (*aspero*, rough; *coccus*, berry). Figs. 92, 93

The structure of the adult plant is essentially the same as that of the two preceding genera except that the central filaments degenerate and the centre becomes filled with a gas. The fronds are simple or branched and bear small superficial cells with sporangia and mucilage hairs scattered over the surface in sori. The plurilocular and unilocular sporangia occur on the same or on different plants, the sori with unilocular sporangia containing sterile paraphyses in addition. The principal interest of this genus is centred around the life histories which have been studied by several workers in considerable detail. In *A. compressus* the life cycle is simple, the zooids from the unilocular sporangia germinating directly into a protonemal phase that later turns into small plantules; these can reproduce themselves successively by means of zoospores from both pluri- and unilocular sporangia until the advent of favourable conditions

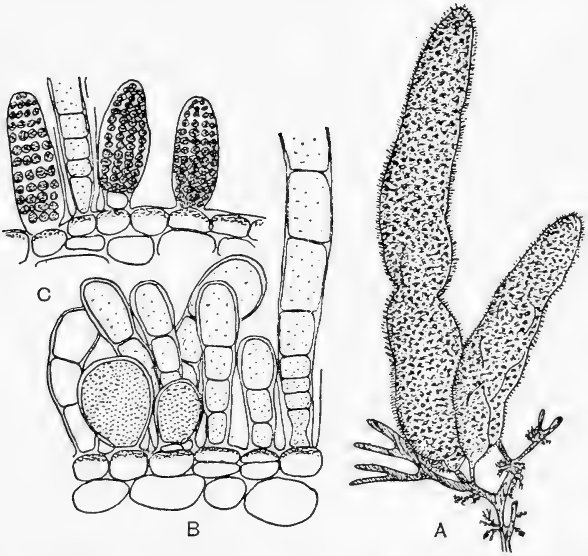

Fig. 92 *Asperococcus bullosus*. A, plant. B, unilocular sporangia (×225). C, plurilocular sporangia (×225). (A, after Oltmanns; B, C, after Newton.)

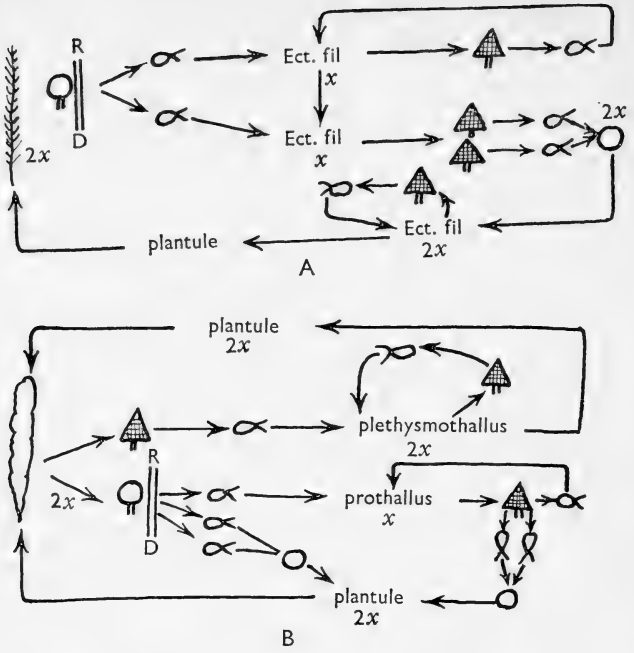

Fig. 93 Diagram of life cycles of *Dictyosiphon foeniculaceus* (A) and *Asperococcus bullosus* (B)

enables the development of the macroscopic phase to take place once more. There is no evidence of either meiosis or of gametic fusion. In *A. fistulosus* it would appear that the life cycle is dependent upon the behaviour of the zooids from the unilocular sporangia where meiosis has been shown to take place. If they fuse, the zygote develops first into a '*streblonema*' phase, so-called from the brown alga it resembles, and then into a plantule from which a new adult plant can arise. In this case there is no evidence for the existence of a gametophytic generation, nor has any evidence been obtained to show that such streblonemoid plants can reproduce themselves by means of sporangia. If no fusion of the zooids from the unilocular sporangia takes place the '*streblonema*' phase is again produced parthenogenetically, but under these circumstances plurilocular sporangia are formed which give rise to a new '*streblonema*' generation, nor has any investigator under such conditions succeeded in obtaining macroscopic plants again and so it has been suggested, therefore, that sex has been inhibited in these plants.

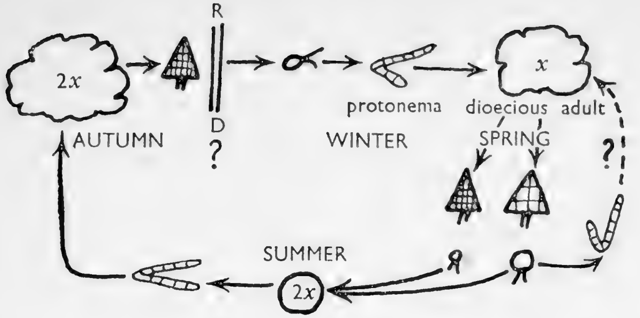

Fig. 94 Life cycle of *Colpomenia sinuosa*. RD = probable place of reduction division in life cycle. (Modified from Kunieda and Suto.)

In *A. bullosus* the zooids from the plurilocular sporangia on the macroscopic thallus do not fuse but germinate directly to give rise to a series of plethysmothalli bearing plurilocular sporangia: these tide over the winter season, and then in spring young *Asperococcus* plants develop in place of the sporangia on the ectocarpoid plantules. In the unilocular sporangia meiosis takes place and the zooids develop into minute gametophytic plants that produce plurilocular sporangia. If the gametes from these sporangia fuse the zygote develops into a plantule from which a new macroscopic plant arises, but if there is no fusion then they merely develop into a new gametophytic generation. Sauvageau also reported that the zooids from the unilocular sporangia may give rise to creeping filaments which later produce young plantules of *Asperococcus*. This direct reproduction of the macroscopic plants can only be explained by a premature abnormal fusion of some of the zooids from the unilocular sporangia. It will be evident that direct alternation of generations is obscured in this type through the number of possible independent circuits and 'short-cuts'. Recently the life cycle in *Colpomenia sinuosa*, a member of a closely allied genus, has been described in detail (cf. Fig. 94). The adult plants are like *Leathesia* in appearance, although they are essentially parenchymatous in structure. It will be seen, however, that there are two morphologically similar generations, the dioecious gametophytes appearing in spring and reproducing by means of anisogametes that are formed in dissimilar gametangia. The zygote gives rise to new adult asexual plants that reproduce by means of plurilocular sporangia in autumn. This life cycle is somewhat different from the others that have been described and a re-investigation would seem to be desirable.

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DESMARESTIALES

The plants belonging to this small order are often of large size with leaf-like lateral branches. The branches terminate in branched uniseriate filaments but these may also occur laterally in tufts along the branches. These filaments in *Desmarestia* and *Arthrocladia* are deciduous in the late growing season so that the plants have a definite summer and winter aspect. There is regular alternation of generations between the macroscopic diploid plant and microscopic gametophytes. The genus *Desmarestia* is interesting in that the cells readily liberate small quantities of free sulphuric acid on death and this causes damage to other plants that are adjacent. If collected they should always be kept separate from other material. The various species are restricted to the colder waters of the northern and southern hemispheres.

DESMARESTIACEAE: *Desmarestia* (after A. G. Desmarest). Fig. 95

The plants are bushy and usually of some size (2–3 ft.), especially the Pacific species. They sometimes bear gall-like swellings which are caused by a copepod. The erect, cylindrical or compressed thallus arises from a disc-like holdfast and exhibits regular pinnate branching, the branches either being elongate or else mere denticulations. The branches bear the deciduous filaments in the denticulations and at their apices. Morphologically the thallus is composed of a single prominent central row of large cells with an intercalary meristem at the base of the terminal hair. The large central cells, the transverse walls of which are pitted, are surrounded by cortical cells, the primary cortex being derived from the basal cells of the primary laterals. These divide periclinally to give a many-layered

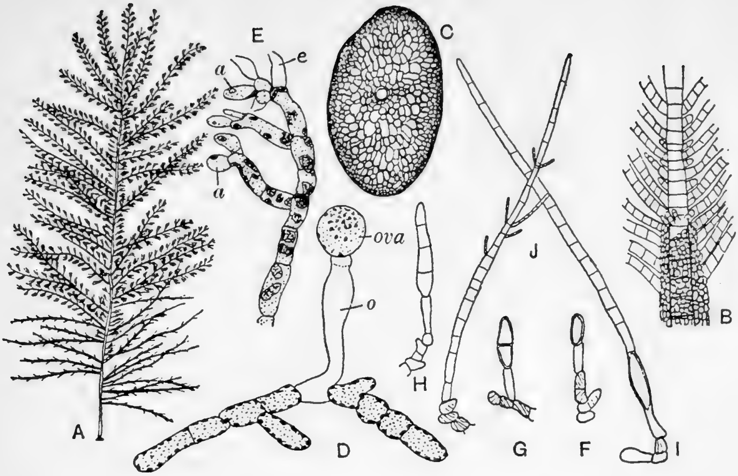

Fig. 95 *Desmarestia.* A, plant with summer and winter appearance ($\times \frac{1}{3}$). B, apex showing cortication. C, transverse section stipe. D, female gametophyte. *o* = oogonium. E, male gametophyte. *a* = antheridium, *e* = empty antheridium. F–J, stages in sporeling germination. (A, after Newton; B, C, after Oltmanns; D–J, after Schreiber.)

cortex, the cells of which become smaller toward the periphery. In the older parts, small hyphal cells are interspersed in the cortex: these originate as a result of secondary activity from the cortical cells. Large hyphae, which have originated from the axial cells, may form a system of veins within the cortex.

The unilocular sporangia are on slightly raised portions of the thallus and develop from cortical cells which undergo scarcely any modification. Meiosis takes place in the sporangium, and the ripe zoospores escape in a mass and germinate to give rise to dioecious filamentous gametophytes which are heterothallic. The smaller male plants produce terminal antheridia from each of which is liberated a single antherozoid, whilst the larger female plants produce the swollen oogonia. Each oogonium gives rise to a single ovum which escapes, but as fertilization and germination take place just outside the pore of the oogonium the young sporophyte develops as far as the monosiphonous stage whilst still possessing a primitive holdfast in the shape of the empty oogonium. Cortication, which is best observed near the apex of old plants, commences in the young plants after a few weeks, and further growth is maintained by an intercalary growing zone some way behind the apex. Since the establishment of the life history of the genus it has been removed from the Ectocarpales into a separate order.

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* LAMINARIALES

The Laminariales form an order which is principally temperate, the bulk of the species being confined to the colder waters of the earth, and there are, in particular, a number of monotypic genera confined to the Pacific coast of North America. The presence of such genera suggests that the original centre of distribution was in the Pacific waters that surround Japan and Alaska. The thallus, representing the large conspicuous sporophytic generation, is nearly always bilaterally symmetrical with an intercalary growing zone, whilst the gametophytes are microscopic. The sporophytes reproduce by means of unilocular zoosporangia, commonly formed in sori with paraphyses, whilst the gametophytes reproduce by means of ova and antherozoids that are borne on separate plants.

There is considerable variation in habit between the sporophytes of the different genera. They range from the long whip-like thallus of *Chorda* (Fig. 96) to the enormous giant *Macrocystis* (Fig. 106). In between these extremes are found the sea palm, *Postelsia* (Fig. 104), and the sea fern, *Thalassiophyllum* (Fig. 102). In the northern hemisphere *Laminaria* is a typical representative of the genus and *Ecklonia* in the southern whilst *Macrocystis* is a useful teaching representative in the Pacific and in South Africa.

The genera *Saccorhiza* and *Alaria* are of great interest because the fronds possess shallow conceptacles or cryptostomata that resemble those found in the Fucales, those in the first-named genus even possessing the typical tuft of hairs. This does not necessarily mean that either of these two genera could be a source of origin for the Fucales, and indeed it is likely that such conceptacles have arisen more than once in the course of evolution.

There are four families in the order:

(*a*) Chordaceae: this is monotypic.

(*b*) Laminariaceae: the species either possess a simple blade or one that is segmented longitudinally, but the splits do not extend into the transition zone so that there is only one intercalary meristem.

(*c*) Lessoniaceae: the splits of the primary blade extend into the transition zone so that each segment has a stalk and an intercalary meristem.

(*d*) Alariaceae: these have special lateral sporophylls.

CHORDACEAE: *Chorda* (a string). Fig. 96

The long whip-like thallus, which is clothed in summer with mucilage hairs, arises from a small basal disc with the growing region situated just above the holdfast. The hollow fronds are simple with diaphragms at intervals, the construction of the thallus being essentially that of a multiseptate cable derived from the

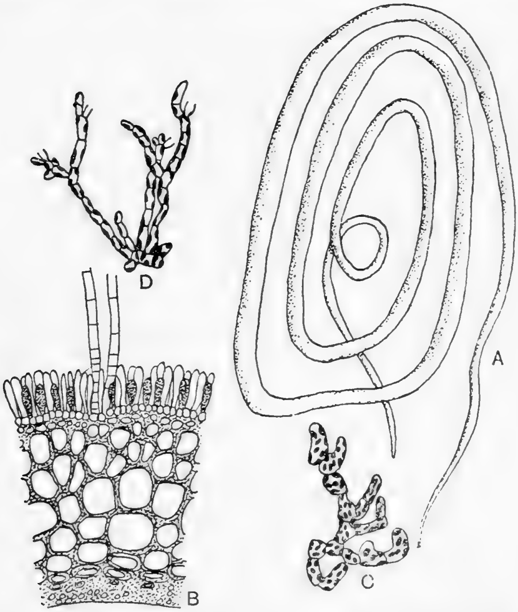

Fig. 96 *Chorda filum*. A, plant (× $\frac{1}{2}$). B, transverse section, high-power, with sporangia. C, female gametophyte (× 145). D, male gametophyte (× 175). (A, original; B, after Oltmanns; C, D, after Kylin.)

Eudesme type by further segmentation of descending hyphae to form a pseudo-parenchyma. The epidermal layer is ultimately clothed with sporangia, paraphyses and deciduous mucilage hairs, whilst the central cells become much elongated and support the filaments that go to form the diaphragm. The zoospores on germination give rise to small filamentous gametophytes, the male plants being composed of small cells, each with two to four chloroplasts, and the female of larger cells with more numerous chloroplasts. The gametangia are borne laterally or terminally on short branches, but the plants do not become fertile for at least three months after their formation and they usually require six months. After fertilization the oospore remains attached to the wall of the oogonium. The macroscopic plant is an annual.

* LAMINARIACEAE: *Laminaria* (a thin plate). Figs. 97–100

This genus has a very wide distribution in the waters of the north temperate and Arctic zones, and it is commonly studied because its morphology is characteristic of the group as a whole with the exception of *Chorda*. Moreover it was among the first genera in which the existence of a dwarf gametophyte was established, thus leading to a new orientation of ideas in the classification of the Phaeophyceae. The expanded lamina has no mid-rib and is borne on a stipe that arises from a basal holdfast which can vary greatly in form. The simplest transition area from stipe to lamina is quite plain, but one may also find folds, ribs or callosities in that position, which is also the region of intercalary growth. *Laminaria sinclairii* has been studied by Setchell (1905) in some detail in connexion with regeneration, a feature common throughout the genus. Three types of growth can be recognized, all of them confined to the stipe, whilst it is also possible to find all three processes taking place in one individual:

(1) The ordinary growth and extension of the blade during the growing season. This hardly merits the description of continuous physiological regeneration given to it by Setchell unless the concept of regeneration is to have a wider significance.

(2) Periodic physiological regeneration which represents the annual process whereby the new blade is formed. The transition area bulges, due to new growth in the medulla and inner cortex, and then ruptures from the pressure, thus leaving the

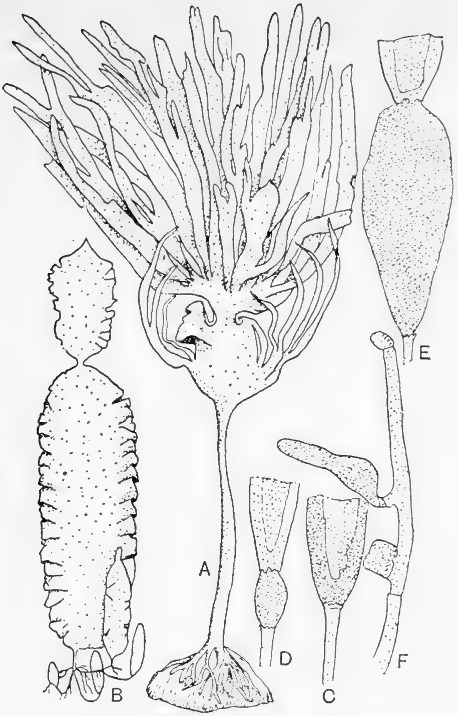

Fig. 97 *Laminaria.* A, *L. cloustoni.* B, *L. rodriguezii.* C–E, normal regeneration (× ½). C, rupture just commencing. D, E, the new tissues are more heavily shaded. F, wound regeneration (× ½). (A, B, after Oltmanns; C–F, after Setchell.)

frayed ends of the non-growing outer cortex forming collars, the upper one of which rapidly wears away. After the rupture the new cells of the medulla and inner cortex elongate rapidly. The failure of the outer cortex to grow is probably associated with the proximity of the inner cortical cells to the medullary hyphae where they can monopolize all the growing materials, thus cutting off any supply to the outer cortex, but there may, of course be other factors involved.

(3) Restorative regeneration whereby branches arise from wounded surfaces, the same tissues being involved as in process (2) (cf. Fig. 97).

A detailed study of growth in *L. saccharina* (by Parke, 1948) has shown that in this species the longevity and rate of growth of the sporophyte depend on season of zygote germination, depth in the sea and type of habitat. Thus winter sporophytes rarely attain maturity and the bulk of the populations in Great Britain originate in the spring, except on sheltered coasts where summer plants thrive equally well. The total life span of this species rarely exceeds three years but that of some others, e.g. *L. cloustoni*, may be longer. Growth is seasonal, more rapid growth occurring between January and June and slower growth afterwards. Latitude may exert an important influence here, because in the Barents Sea the blade of *L. digitata* only grows from spring to July whereas the stipe grows all the summer. The rhizoids or crampons, however, attain their maximum growth in the autumn. In *L. saccharina* and *L. cloustoni* the seasonal changes in growth rate are indicated in the stipe by alternate zones or 'rings' of lighter and darker tissue, the darker being formed during the periods of slow growth. In *L. saccharina* the maximum height and greatest growth is achieved during the second rapid growing season.

Many of the species are used as food by the Russians, Chinese and Japanese. The greatest number of species occur around Japan and from Alaska to California. Furthermore, these kelps, as they are called, are valuable as a source of iodine and as a potassic fertilizer (see pp. 445, 449).

The following brief notes concern a few species that are of more general interest:

L. cloustoni: The attachment crampons are arranged in four lateral rows and there is a long rough cylindrical stipe with an abrupt transition to the lamina. When bent, the frond and stipe tend to snap.

L. saccharina: The margin is thicker than the central part of the thallus and the wavy lamina is produced by continual growth of the central portion without any growth in the marginal areas. The stipe is short and the transition to frond is gradual.

L. digitata: In this species the transition from stipe to frond is gradual. In contrast with *L. cloustoni* the stipe is smooth and neither it nor the frond snap when bent over.

L. ephemera: A species closely allied to the above but differing from it in that there are no crampons but only a basal attachment disc.

Morphologically both lamina and stipe are divided into four regions. On the outside there is the actively dividing meristoderm or limiting layer, whilst inside there is first an outer and then an inner cortex and then a mass of interwoven threads that form the central medulla. The young sporeling is at first a uniseriate filament, but as a result of cell divisions it becomes a flat monostromatic plate. Rhizoids emerge from the basal cell and the thallus then becomes distromatic, the periclinal divisions that are responsible starting at the basal end. After the holdfast, stipe and blade have been differentiated, further growth is restricted to the intercalary meristem at the base of the blade. When a distromatic lamina has been produced a central group of cells, which form the primary tubes of the medulla, are cut off and separate the two outside layers. Whilst the origin of the medulla in the stipe is clear, it is not so for the lamina. It would seem though that in the lamina the medulla arises as an intrusion of medullary filaments from the stipe. The intercalary growing zone forms a ring around the base of the lamina, the central tissues not being meristematic.

Later the primary limiting layer in the stipe is replaced by a secondary meristem 4–8 cells deep in the cortex. This is responsible for the subsequent growth in thickness by the production of secondary cortical tissue. This meristem is persistent but its activity is seasonal and as a result in many species distinct growth rings can be seen.

The medulla consists of (*a*) primary medullary tubes, and (*b*) two types of lateral connecting branches, the connecting threads and the hyphae. The former arise first in the course of development as papilloid outgrowths from individual cells. They meet and fuse at their tips and so give rise to a system of cross connexions. With further growth the cells divide and elongate, but even when mature they are composed of relatively few cells. The hyphae, which arise later as branches of small cells cut off from the original vertical cells, remain free but may branch. Ultimately they contain numerous cells which subsequently elongate very considerably. One of the most characteristic features of the genus, and indeed of the order, is the presence in the medulla of 'trumpet-hyphae', which usually arise as modifications of some of the cells in the connecting threads, more rarely of the hyphae. At a transverse cell wall the ends of both cells swell out to form bulbs, the upper bulb always being larger, but so far no satisfactory explanation of this peculiarity has been advanced, though it may be due to purely mechanical requirements. The transverse wall is perforated to form a sieve plate and a callus

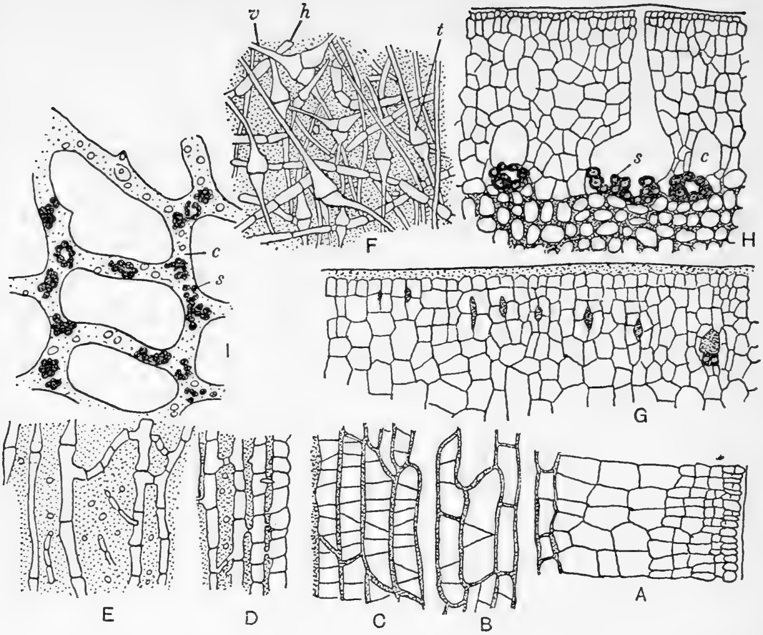

Fig. 98 Laminariaceae. A–F, portions of the stipe of *Macrocystis* passing successively from the epidermis, A, through the medulla, B–E, to the pith, F. *h* = hypha, *v* = connecting thread, *t* = 'trumpet' hyphae. G, stages in development of mucilage canals, *L. cloustoni*. H, mucilage canal of *L. cloustoni* in transverse section. *c* = canal, *s* = secretory cells. I, mucilage canal system in *L. Cloustoni*. *c* = canal, *s* = secretory cells. (After Oltmanns.)

develops on each side, both callus and sieve plate being traversed by protoplasmic strands. It will be seen that in many respects these trumpet hyphae resemble the sieve tubes of the flowering plants, but although the callus is said to be formed in land plants because of changes in pH, so far no evidence has been published to indicate whether this is also true for the Laminariaceae. Apart from the sieve plates the trumpet hyphae also possess spiral thickenings which appear as striations, and here again there is the problem of their interpretation (e.g. are they growth zones?), although it is possible that they have now lost any function they once possessed. The problem of these trumpet hyphae is still subject to considerable speculation: it has been suggested that they may be a storage or conducting tissue, whilst another suggested function is that of support, but as the plants are commonly submerged the water

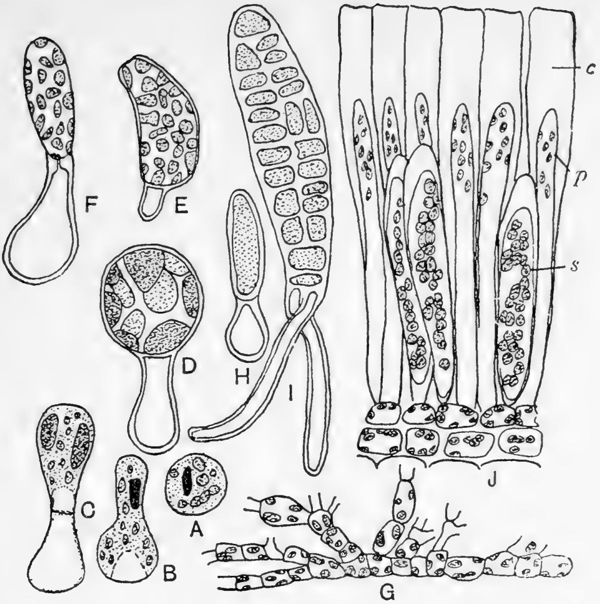

Fig. 99 *Laminaria.* A–F, stages in development of female gametophyte from a spore (A–D ×1333, E–F ×600). G, male gametophyte (×533). H, I, first two stages in development of young sporophyte. J, sporangia (*s*), paraphyses (*p*) and mucilage caps (*c*). (A–I, after Kylin; J, after Oltmanns.)

would seem to fulfil this requirement. In some species many of the other cells also contain pits with a thin membrane across the opening and these presumably facilitate the diffusion of food materials.

Most of the genera possess systems of anastomosing mucilage ducts. In *L. cloustoni* these are confined to the stipe and in *L. digitata* (and *Nereocystis*) to the frond, but in *L. saccharina* they occur in both organs. In the genus *Egregia* they are absent. When mature there are periodic openings from these ducts to the exterior and their bases are lined with secretory cells. They arise lysigenously through an internal splitting of the thallus due to cell disintegration: this is followed by a differential growth so that the canals become more and more submerged in the thallus. The attachment organs or crampons, which are positively geotropic, have an apical growth and differ from the rest of the thallus in that there are no connecting hyphae nor is there any pith. The amount of conduction necessary in these plants would be expected to be small, but even so the degree of differentiation is remarkable. So far as the lamina is concerned the group is usually regarded as primitive because the new portions do not originate separately but by intercalary growth from an existing portion (cf. Fig. 97).

The sporangia and paraphyses are borne in irregular or more or less regular sori on both sides of the lamina. They arise from superficial cells that grow out from the surface. These divide tangentially into a basal cell and paraphysis initial, and later from the basal cell a sporangium is cut off. In *L. saccharina* the sporophytes only reach maturity at the end of their second year, and for sori to develop the distal tissue of the frond must be in at least the sixth month of growth. The actual number of reproducing plants and the duration of the reproductive period in a population depend largely on the numbers of the different season and age groups making up the population. In general *L. saccharina* in Great Britain fruits in summer, *L. cloustoni* in winter, and *L. digitata* from April to November with maxima in spring and autumn.

The unilocular sporangia usually each give rise to thirty-two zoospores, meiosis taking place in the process. It is probable that the zoospores possess an eye spot, but it must be very small because in the three species where it has been recorded it was very difficult to distinguish. The zoospores, which in one or two cases are reported to be of two sizes, germinate to form minute gametophytes, but on germination they first put out a tube that terminates in a bulbous enlargement into which the contents of the zoospore migrate. There the nucleus divides and one daughter nucleus passes into the tube whilst the other degenerates, but at present the sigficance of this phenomenon is obscure: it would hardly seem to be associated with meiosis because this process takes place in the zoosporangium. Both kinds of gametophyte show much variation in shape and size, the male gametophyte being the smaller throughout as it is built of smaller cells that contain dense chromatophores.

The gametophytes can be cultivated in the laboratory, but for successful cultivation the water must be sterilized and the cultures placed close to a north window in winter and 2 or 3 m. distant in summer. Reproductive organs are only formed at low temperatures, 2–6° C., whilst above 12–16° they are rarely produced, this fact perhaps accounting for their temperate and arctic distribution (cf. Fig. 100). It is also known that the eggs may develop parthenogenetically to give a haploid sporophyte which has an irregular shape, whilst attempts to produce hybrids by artificial fertilization have so far met with no success. Schreiber (1930) found that the ratio of male to female gametophytes was always 1 : 1, and he subsequently showed that of the thirty-two zoospores produced in each sporangium, sixteen gave male and the other sixteen female gametophytes. The male gametophyte of *L. religiosa* is reported to bear unilocular and plurilocular sporangia, but this is so abnormal and has never been confirmed or reported for any other species, that it can hardly be accepted without further evidence. The ova of *L. saccharina* are reported to be capable of producing dwarf filamentous diploid plants which reproduce by means of unilocular sporangia. If this is confirmed it may be that here we have an example of a reversion to a primitive filamentous diploid progenitor, a feature which might help considerably in indicating their ancestry.

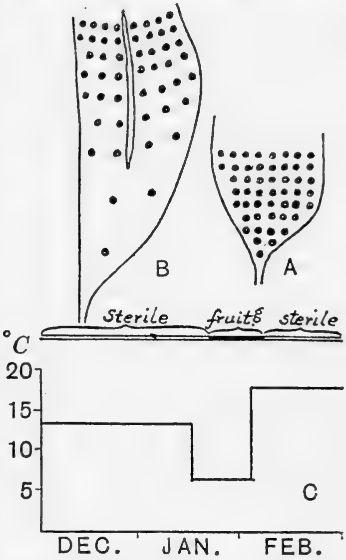

Fig. 100 *Laminaria.* A, *L. digitata*, marked thallus before growth in summer. B, *L. digitata*, marked thallus after growth in summer. C, effect of temperature on fruiting of gametophytes in *L. digitata.* After Schreiber.)

The most important characteristics of the gametophytic generation are:

(1) The male gametophyte always has smaller cells.

(2) The male gametophyte always consists of more than three cells whereas the female may consist of only one cell, the oogonium. Under good nutrient conditions both become much branched.

(3) The antheridia are unicellular and produce only one antherozoid.

(4) Any cell of the female gametophyte may function as an oogonium.

(5) The male gametophyte degenerates after the gametes are shed whereas the female gametophyte persists.

The young sporophyte first produces numerous rhizoids of limited growth, but these are later covered by a disc-shaped expansion. In older plants this disc is replaced by the haptera or crampons which arise as papillate outgrowths from the stipe.

LAMINARIACEAE: *Saccorhiza* (*sacco*, sack; *rhiza*, root). Fig. 101

S. polyschides used to be known as *Laminaria bulbosa*, but for some time it has been removed to a separate genus because it differs from the other species of *Laminaria* in several important respects. The persistent lamina arises from a flat compressed stipe with wavy edges which is twisted through 180° near the base as a result of unequal growth, this twisting being regarded as a mechanical device to facilitate swaying. The young sporophyte is attached at first by a small cushion-like disc, but later a warty expansion, the *rhizogen*, develops above it and forms a bulbous outgrowth which bends over and attaches itself to the substrate by means of descending crampons. As a result of the development of this adult holdfast the juvenile disc may be lifted completely off the sub-

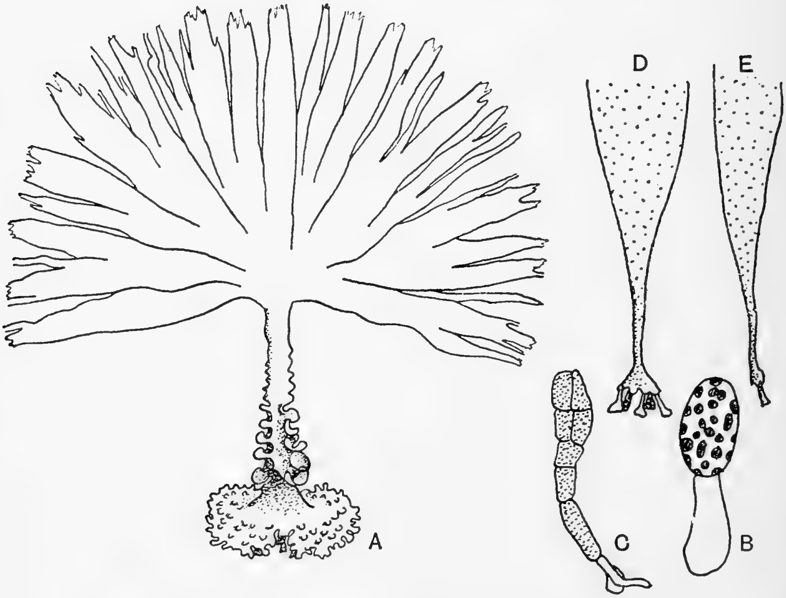

Fig. 101 *Saccorhiza polyschides*. A, plant (× $\frac{1}{3}$). B, female gametophyte. C, young sporophyte. D, E, young plants of *S. dermatodea* to show origin of bulb. (A, after Tilden; B, C, after Kniep; D, E, after Oltmanns.)

stratum. Subsequent growth of the stipe takes place in the outer layer of the medulla, and in the adult organ five regions can be recognized:

(1) Primary fixing organ.
(2) The bulb.
(3) A flattened twisted area said to provide additional rigidity.
(4) A portion with flounced edges.
(5) A flat straight portion that passes into the lamina.

The existence of these structures is supposed to be correlated with the large lamina which is cleft into many linear segments.

If, as sometimes happens, the whole of the plant is torn away with the exception of the bulb, this organ is still capable of reproduction and assimilation. The advanced external differentiation of the stipe is not reflected in its histology where the differentiation is poor because there is no secondary growing region, no mucilage ducts, and trumpet hyphae are not conspicuous.

The male gametophyte is filamentous whilst the female frequently consists of only one cell which functions as the oogonium. After fertilization has taken place the development of the sporophyte to maturity in both species requires only one year so that the plants are true annuals. *Saccorhiza polyschides* is found on the Atlantic coasts of North and West Europe whereas the other species, *S. dermatodea*, is circumpolar and is possibly the parent species from which the other developed, a speculation which is further supported by the fact that *S. dermatodea* is more primitive because the stipe is not twisted nor are the edges so wavy. The young sporophyte first develops a juvenile blade which does not bear sporangia and then a new and thicker basal fertile blade is intercalated, but it is only the juvenile blade that bears the cryptostomata.

LAMINARIACEAE: *Thalassiophyllum* (*thalassio*, sea; *phyllum*, leaf). Fig. 102

The perennial sporophyte is apparently composed of a spirally twisted, fan-shaped lamina unrolling from a one-sided scroll without any mid-rib. A study of the embryonal stages, however, shows that the young plant is flat and bilaterally symmetrical. The two edges then curl up and the plant tears down the centre giving rise to two lateral scrolls each unrolling from a thickened outer margin, but as one of the scrolls soon ceases to develop the mature plant

Fig. 102 *Thalassiophyllum clathrus.* A–F, developmental stages to show the origin of the single scroll (× $\frac{2}{3}$). G, adult plant. (After Setchell.)

only possesses one scroll borne on a solid bifid stipe with the vesitgial scroll on one of the branches. It is evident from this description that any branches found on the adult plant are false and represent adventitious outgrowths from the base of the blade. Growth in thickness takes place as a result of the development of a secondary meristoderm as in *Laminaria.* Slitting is represented by rows of small holes which commence to develop after the first tear has taken place.

LESSONIACEAE: *Lessonia* (after R. P. Lesson). Fig. 103

The plants grow erect and form 'forests' in relatively deep waters off the shores bounding the southern Pacific, reminding one in appearance of some of the fossil vegetation of the Carboniferous,

Fig. 103 *Lessonia.* A, adult plants of *L. flavicans.* B, C, sporeling stages in *L. nigrescens.* (After Oltmanns.)

although, of course, there is no connexion. The stipe of *L. flavicans* is extremely stout and rigid, 5–10 ft. long and sometimes as thick as a human thigh, the additional growth being due to a deeper seated secondary cortical meristem. It appears to be more or less regularly branched in a dichotomous fashion, a feature which is brought about by the lamina being slit down successively to the intercalary growing region, each successive segment developing into a new lamina with its own portion of stipe. Dried parts of the stipe, which can easily be taken for pieces of driftwood, are used by natives to make knife handles. This method of causing splitting should be compared with the other processes found in *Nereocystis, Macrocystis* and *Postelsia* (cf. below).

LESSONIACEAE: *Postelsia* (after A. Postels). Fig. 104

This is a monotypic genus, often known as the 'sea palm', that is confined to the Pacific coast of North America where it grows between Vancouver Island and central California on rocks which are exposed to heavy surf. The smooth, glossy, cylindrical stipe is thick but not very long, up to 1 m. in height. It is erect and hollow within and bears at its apex a number of short, solid, dichotomously branched structures from each of which hang 100–150 laminae that bear sporangia in longitudinal folds when they are mature. Apart from the cryptostomata of *Saccorhiza* and *Alaria* it has also been suggested that the occurrence of these sporangia in folds may illustrate how the fertile fucalean conceptacle may have arisen. Such a change would necessitate the development of wedges of sterile tissue in order to divide up the folds, but whether such a change could occur in a relatively differentiated thallus is a matter for speculation.

The numerous laminae are formed by a splitting process in which a portion of the lamina fails to continue growth whilst the rest goes on growing, and in this manner a weak area is formed from which a split commences.

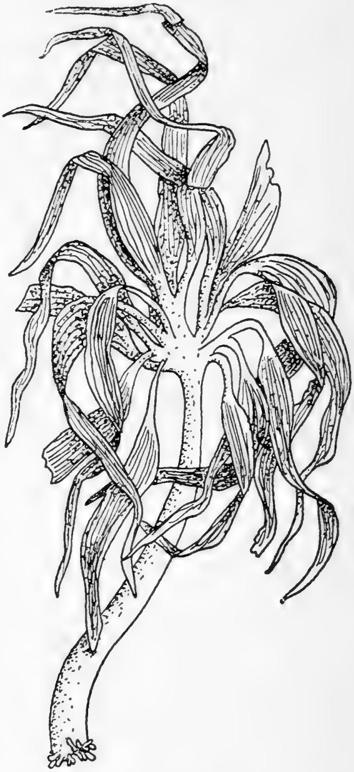

Fig. 104 *Postelsia palmaeformis*. (After Oltmanns.)

LESSONIACEAE: *Nereocystis* (*nereo*, Nereis, daughter of Nereus; *cystis*, bladder). Fig. 105

The plants, which from the recorded observations appear to be annuals, may attain a maximum length of 90 m., but 50 m. is more usual. This bears a bladder up to 2–3 m. in length[1] which has a capacity of several litres. The long, slender stipe is solid and cylindrical below but swollen and hollow above, finally contracting just below the terminal spherical bladder which bears a row of short, dichotomous branches, each giving rise to a number of long, thin laminae. The plant commences with only one blade which divides twice in a dichotomous fashion, thus producing four blades, and these form the centre of activity for the remainder through a process of slitting. The splitting of these four fronds is preceded by

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[1] Generally much smaller.

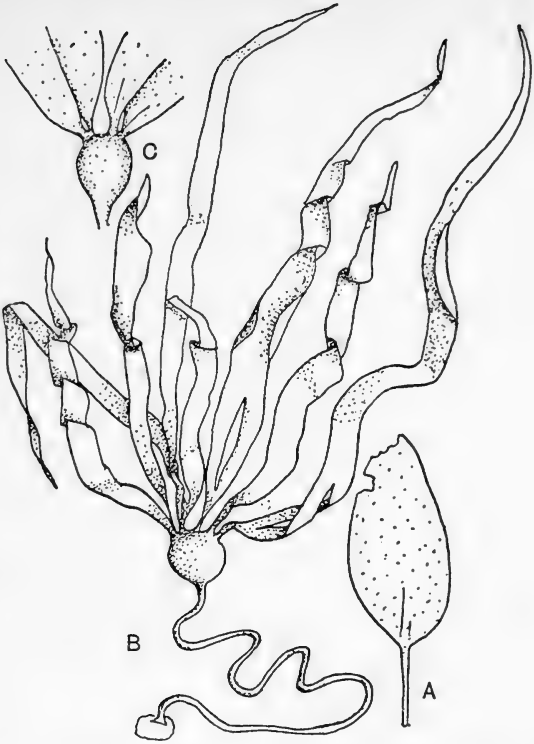

Fig. 105 *Nereocystis luetkeana.* A, young plant. B, mature plant. C, branching from bladder. (After Oltmanns.)

the development of a distinct line along the path of the future slit, the line representing new tissue, which has in consequence very little strength, thus forming an area of weakness along which the slit commences. The plant is found at a depth of from 5 to 25 m. between Alaska and Los Angeles. Besides being a good source of potash salts, as the ash contains 27–35 per cent potassium chloride, the stalk and vesicle can be treated to yield a candied edible product called 'Seatron'. Locally it is called by a number of names, bull kelp, bladder kelp, ribbon kelp and sea-otter's cabbage.

In the closely related genus *Pelagophycus* the spores are said to be non-motile, not even possessing cilia. Further confirmation of this fact is much to be desired because not only is it an unique state in the family but it also renders comparison with *Nematophyton* (cf. p. 305) of great interest. Local names employed for *Pelagophycus* are elk kelp, sea pumpkin and sea orange.

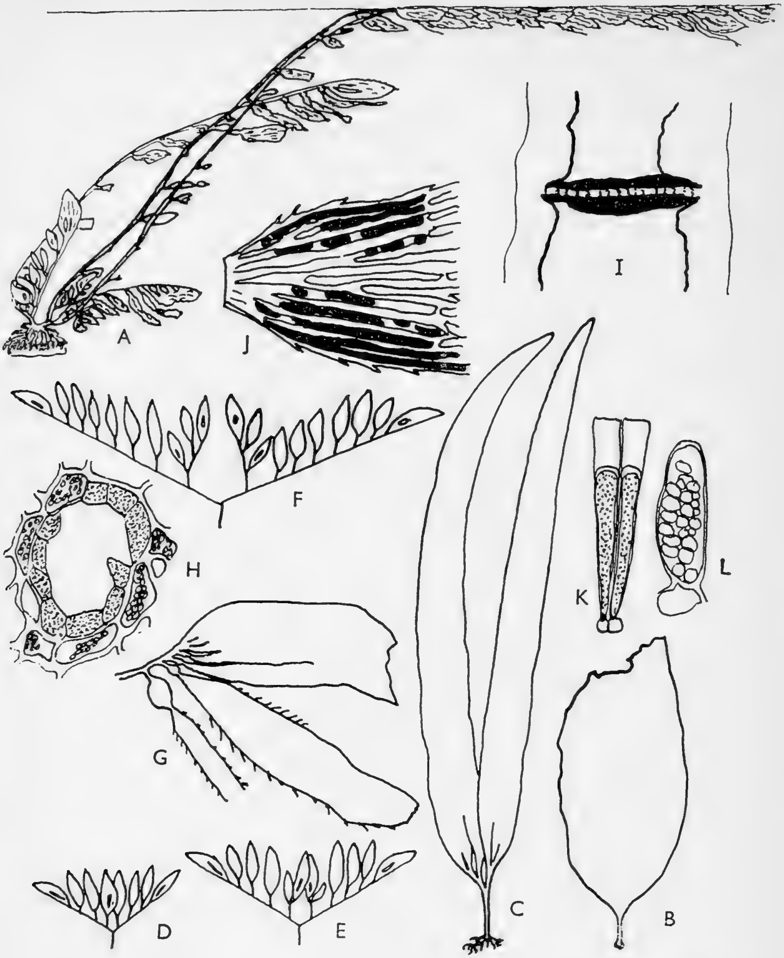

Fig. 106 *Macrocystis pyrifera.* A, entire plant ($\frac{1}{150}$). B, young plant ($\times \frac{1}{2}$). C, slightly older plant with primary slit and two secondaries ($\times \frac{1}{8}$). D–F, schematic drawings showing branching. G, shoot apex ($\times \frac{1}{3}$). H, mucilage duct (× 200). I, 'sieve tube' and plate with callus (× 290). J, part of fertile blade (sori black) ($\times \frac{1}{4}$). K, two paraphyses (× 140). L, unilocular sporangium (× 290), (A, B, D–L, after Skottsberg; C, after Oltmanns).

LESSONIACEAE: *Macrocystis* (*macro*, large; *cystis*, bladder). Fig. 106

The perennial fronds of this giant of the ocean may reach 200 ft. in length, the alga growing at a depth of 20–30 m. in the North and

South Pacific Ocean and near the Cape of Good Hope, all being regions where the temperature of the water ranges between 0 and 20° C. The upper part of the plant floats on the water surface, kept there by the basal bladders of the leaves. In the juvenile plant the stipe is simple and solid, but later on it branches one to three times in a dichotomous fashion, although ultimately the branching becomes unilateral and sympodial. The growing region on each branch is ventrally situated in the terminal blade, and it is here that splitting takes place to form the individual laminae. The splitting is brought about by local gelatinization of the inner and middle cortex together with a cessation of growth in the epidermal area; this forces the adjacent tissues into the gelatinized areas until finally the epidermis is ruptured. Of the two segments formed in this splitting process, one remains arrested, whilst the other, the outer, continues growth. The internal structure of the stipe and fronds is typical of the order as described under *Laminaria* (see p. 175). The rate of growth, during the growing season, of this plant is quite spectacular. On the Pacific coast of North America it has been found to be of the order of 7·1 cm. ± 4·3 per day, which works out at about $1\frac{1}{4}$ blades daily. The amount of organic matter accumulated in the growing tip is equivalent to that produced and exported from 35 blades immediately below. There are very many more blades than this in the plant during most of its life, so that the remaining surplus of photosynthesis over respiration must presumably be translocated to the stipe and haptera and stored as reserve.

Macrocystis (and also *Nereocystis*) is interesting in that in the cortex there are sieve tubes as well as trumpet hyphae in the medulla. Neighbouring tubes are connected to each other by lateral filaments, the cross walls of which are also perforated. Reproduction is by means of zoospores produced on sporophylls, generally dichotomously branched and with or without a bulb, near the base of the plant. Although two kinds of zoospore have been recorded, recent work has failed to substantiate the statement. Enormous numbers of zoospores are produced, the actual number being related to the size of the frond. Each sporangium produces thirty-two swarmers and on a large frond as many as 693,760 zoospores may be liberated per square millimetre of frond (both surfaces). On germination the zoospores give rise to the characteristic laminarian gametophytes, which are relatively long-lived (six months or more). Their form is determined by nutrient supply, bacterial growth, temperature, etc., leading to presence or absence of sex organs, extreme branching or very compact branching. The ova are normally fertilized in the sea, and though occasionally a single ovum may be fertilized whilst still in the oogonium, this can only be regarded as an abnormality.

ECKLONIACEAE: *Ecklonia* (after Ecklon). Fig. 107

This is a southern hemisphere genus. There is a short, solid unbranched stipe which is attached to the rocks by means of the usual rhizoids. In the young plant the stipe expands into a flatenned frond which is initially dentate. Later the terminal portion disappears and the basal portion produces numerous lateral outgrowths (sporophylls). In its internal morphology the structure is comparable to that described for *Laminaria*.

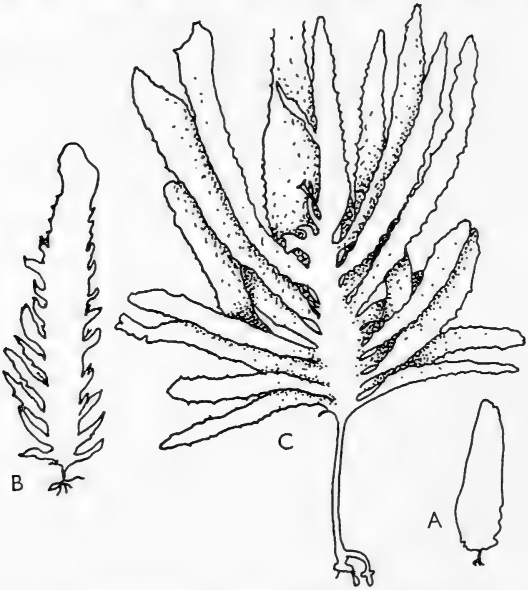

Fig. 107 *Ecklonia radiata*, young, juvenile and adult plants (× ¼). (After Bergquist.)

ALARIACEAE: *Alaria* (*ala*, wing). Fig. 108

This genus is widely distributed throughout the northern hemisphere, the common species being *A. esculenta*. There is a short,

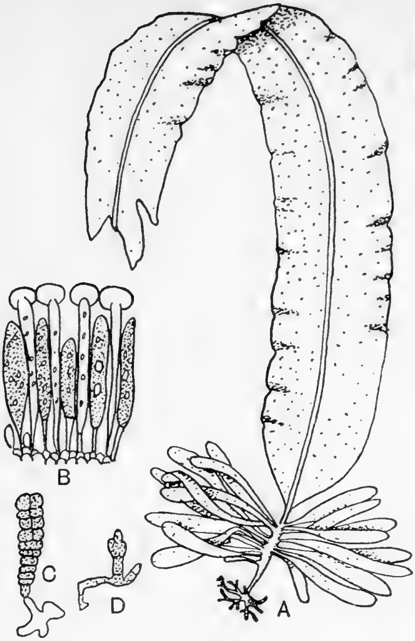

Fig. 108 *Alaria esculenta*. A, plant of *A. oblonga* with sporophylls. B, sporangia and paraphyses (× 200). C, germling sporophyte (× 100). D, female gametophyte (× 80). (A, after Oltmanns; B–D, after Newton.)

solid, unbranched stipe which is attached to the substrate by means of small, branched rhizoids. It is naked below with an intercalary growing zone that allows for continual renewal, whilst above the growing region the stipe expands into a flattened rachis which bears each year a fresh crop of marginal rows of sporophylls. The frond finally terminates in an expanded sterile lamina with a well-marked mid-rib, which is also an annual production. In addition to the intercalary growth there is also a marginal growth that imparts a wavy appearance to the terminal frond. This bears the so-called cryptostomata, although these are barely more than tufts of hairs arising in slight depressions. The sporangia are produced on the lower blades mixed up with unicellular paraphyses. The gametophytes are protonemal in form, simple or sparingly branched, the male, as usual, being composed of smaller cells with terminal, intercalary, or lateral antheridia, whilst the oogonia on the female gametophyte are usually terminal. The ovum is fertilized on emergence from the pore of the oogonium and the young sporophyte develops *in situ* without the characteristic early appearance of a holdfast.

ALARIACEAE: *Egregia* (outstanding). Fig. 109

This genus is composed of at least two, and probably more, species, one of the major species having a more northern distribution than the other, though the genus is confined to the waters of the Pacific between Vancouver Island and lower California. The whole plant can be regarded as an extension of the *Alaria* type in

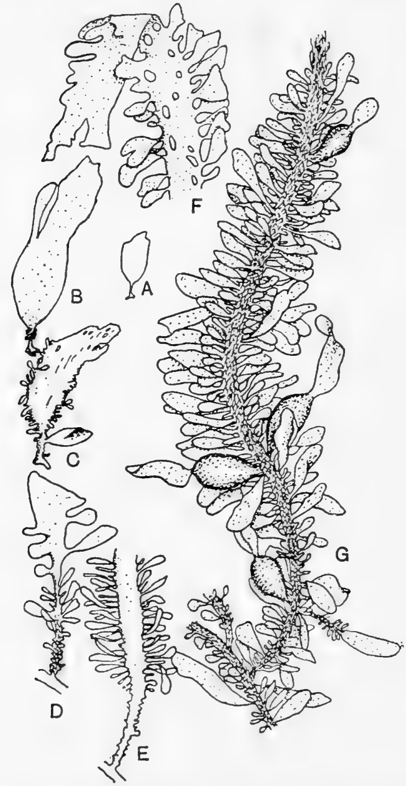

Fig. 109 *Egregia menziesii.* A–C, stages in growth of young sporophytes (× $\frac{5}{12}$). D, young frond. E, base of mature frond. F, apex of mature frond. G, mature plant. (A–C, after Griggs; D–G, after Oltmanns.)

which each branch becomes strap-shaped and bears three types of outgrowth:

(*a*) Ligulate sterile outgrowths.
(*b*) Small fertile outgrowths.
(*c*) Conspicuous stipitate bladders.

Recent work has shown that in deep-water plants most of the bladders contain liquid rather than air and therefore cannot function as flotation organs. The shape of the lower bladders is related to the depth of water in which the plant is growing.

The female gametophyte is composed of one or two large cells whilst the male plant is composed of numerous smaller ones, both plants reaching maturity in from nineteen days to four weeks depending on the season of the year, e.g. the length of daylight. Maturity is most rapidly reached at a temperature of 10–16° C., and although at 16–20° C. gamete development takes place nevertheless the antherozoids are unable to leave the antheridia.

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* FUCALES

The sporophytic plants are even more dominant in the life cycle than in the Laminariales, but although diploid there is no apparent asexual reproduction, the plants always reproducing by means of ova and antherozoids. In most genera it is likely that the plants exist over more than one season: this has been clearly established for species of *Fucus*, *Ascophyllum*, *Durvillea* and *Marginariella urvilliana*. There is considerable tissue differentiation, and in their external features the plants exhibit much more variation than is to be found in the Laminariales. The thallus is normally differentiated into a discoid holdfast, stipe and frond, and in all genera except *Durvillea*, growth in length is due to the activity of one or more apical cells. The genus *Bifurcaria* is anomalous in that the discoid holdfast is replaced by a basal rhizome. Morphologically an external meristoderm, cortex and inner medulla can be recognized. In the genera commonly occurring in the inter-tidal regions the walls of the central or medullary cells become abundantly gelatinized whilst there is a greater profusion of longitudinally running hyphae, though *Hormosira* is an apparent exception to this in that the swollen segments become hollow. In the genus *Halidrys*, sieve plates occur on the walls of the medullary cells and there is an indication of similar plates in the lateral medullary connections of *Bifurcaria*. Reproduction is by means of oogonia and antheridia borne in conceptacles which, in all but *Durvillea*, are localized in regions known as receptacles. Some workers consider that the structures called oogonia and antheridia are really macro- and microsporangia producing mega- and microspores which germinate before they are liberated from the sporangium, so that while the reproductive bodies have their origin as spores, nevertheless the liberated products are gametes. This view is discussed more fully later (cf. p. 317). In the primitive condition eight ova are produced in each oogonium and sixty-four antherozoids in each antheridium. Meiosis takes place during the first two divisions in the formation of microspores, and as there is often a pause after the second division the first four nuclei have been regarded as the functional microspores, each of which subsequently undergoes four mitoses so that they can be said to germinate to a sixteen-celled gametophyte where each cell functions as an antherozoid. In the macrosporangium the first four nuclei formed have been regarded as the functional megaspores, and each of these is considered to germinate subsequently to a two-celled female gametophyte where each cell functions as an ovum. In those species where less than eight mature ova are produced it must be assumed that some of the megaspores undergo abortion or else do not develop.

If the above is to be the correct interpretation, and it would seem to be more satisfactory than any other theory in comparison with other members of the Phaeophyceae, then we can say that not only is there a cytological alternation of generations but there is also a morphological alternation, although the sexual generation is even further reduced from the state found in the Laminariales. This would really form a basis for placing the Fucales in the Heterogeneratae. The alternative interpretation is that the sexual generation has been completely suppressed and is solely represented by the gametes, so that whilst there is a cytological alternation of generations there is only one morphological generation (cf. also Chapter IX). Recent cytological work has revealed that the 2n number of chromosomes is 64 except for *Sargassum horneri* where it is 32, *Halidrys siliquosa* (55–60) and *Pelvetia canaliculata* (22). It seems not unlikely, therefore, that the Fucales represent a polyploid series. The sex organs are borne in flask-shaped depressions of the thallus called conceptacles, each of which is lined with paraphyses and opens to the surface by means of an ostiole. The plants of the different species may be dioecious, monoecious or hermaphrodite. In a number of the fucoids the ova, when they are extruded through the ostiole, remain attached by means of a thin gelatinous stalk. These stalk-forming fucoids, e.g. *Scytothalia*, *Marginariella*, *Sargassum*, *Bifurcaria*, etc., have been studied in some detail and they possess certain features in common:

(1) The stalk is formed from the mesochiton or middle wall of the oogonium (see p. 202).
(2) They are inhabitants of deep water or in pools near low water springs (*Bifurcaria brassicaeformis* of South Africa is an exception here).
(3) The conceptacles are unisexual.
(4) They have only one oosphere per oogonium (*B. laevigata* is an exception).
(5) Maturation takes place at a late stage.
(6) The fertilized ovum begins development within the jelly of the attachment stalk.

In addition, those belonging to the family Fucaceae (*Bifurcaria*, *Marginariella*) have:

(7) Conceptacles borne on specialized laterals.
(8) The gelatinous stalks are hollow.
(9) They are specialized endemic genera or species.

It would seem from the above that the possession of this stalk-forming characteristic is probably an advanced feature phylogenetically.

The number of primary rhizoids in the embryo depends first upon the species and also upon the size of the rhizoidal cell, which in turn bears a relation first to the size of the egg, and secondly to the complexity of the thallus. On this basis a series of increasing embryonal complexity may be traced, e.g. *Fucus—Ascophyllum—Pelvetia—Cystoseira—Sargassum.*

Geographically the original centre of distribution was undoubtedly the southern Pacific in the waters of Australia and New Zealand where the greatest number of species are now to be found. This makes an interesting comparison with the preceding order whose original centre of distribution was the northern Pacific in the waters around Japan and Alaska. The Fucales are classified into five groups, the classification being based primarily upon the structure of the apical growing cell or cells:

(1) *Durvilleae.* A group comprising two genera, *Durvillea* and *Sarcophycus*, from Australia and Patagonia, both without any means of apical growth.

(2) *Fuco-Ascophyllae.* Growth is determined in the adult stage by *one four-sided* apical cell. Recently it has been found that in *Marginariella urvilliana* the apical growing cell is three-sided in the adult condition. The apical growing cell of the salt marsh fucoids (see p. 349) has also been shown to persist in the three-sided condition. Despite these exceptions, however, the basis of the classification remains very useful.

(3) *Loriformes.* Growth is due to *one three-sided* apical cell which gives rise to a long whip-like thallus.

(4) *Cystoseiro-Sargassaceae.* The apical cell is again *three-sided* but there is copious branching which results in bilateral, radial and bilaterally radial thalli.

(5) *Anomalae*, composed of one genus, *Hormosira*, confined to the Antipodes. Growth is brought about by a group of cells instead of a single cell.

In most of the Fucales the apical cell is sunk in an apical pit or groove. In the Fucaceae proper, this groove is usually parallel to the plane of flattening of the thallus, but in *Halidrys* and *Himanthalia* it is at right angles to it. In the adult the hairs in the young apical pit are deciduous, but in *Himanthalia*, *Bifurcaria* and *Xiphophora* hairs can be found growing out from the apical groove of mature plants.

Durvilleae

Durvilleaceae: *Durvillea* (after J. D. D'Urville). Fig. 110

The sporophyte is a dark olive brown or black in colour and

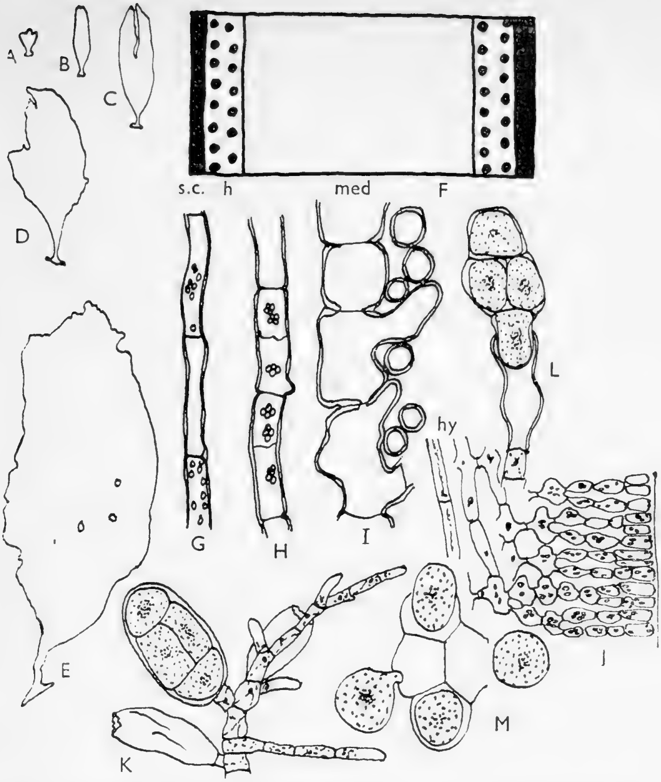

Fig. 110 *Durvillea antarctica.* A–E, young plants ($\times 1\frac{4}{5}$), F, diagram of tissues, black = secondary cortex; dots = unswollen hyphae; plain = medulla. G–I, stages in swelling of longitudinal hyphae (G, H × 260; I × 160). J. R.L.S. of meristoderm and cortex (hy = hypha) (× 170). K, oogonium L, M, oogonium liberating ova (× 180). (After Naylor.)

possesses very much the appearance of a *Laminaria*. This applies to all four species (five if one includes *Sarcophycus potatorum* of Tasmania). The large solid stipe arises from a scutate holdfast and very soon passes into a flat, expanded, fan-shaped lamina, which later becomes split into segments although no definite appendages are produced from this frond. The New Zealand *D. willana* is characterized, however, by lateral fronds proliferating from the stout stipe. The attachment disc bears a resemblance to the primary disc found in some members of the Laminariales, and it is formed in much the same way by tangential divisions of the outer layer or meristoderm. The growing region is the margin. Internally the thallus possesses small hyphae which anastomose and fuse with each other just as in the medulla of *Laminaria* (see p. 175). These hyphae extend right up to the apex, thus differing from genera such as *Fucus*. There is also a mechanism involved in thallus splitting in much the same way as there are thallus-splitting mechanisms in the Laminariales. Prior to splitting, new cortical tissue is formed.

In the most widespread species, *D. antarctica*, the adult lamina is characterized by large internal air spaces separated from each other by septa. These air spaces are considered to arise as a result of an active internal splitting process which may or may not be associated with degeneration of the tissues. In this genus, growth is localized to the tips of the laminae, the surface layer forming the primary meristematic layer.

The ends of the older laminae become frayed and broken off by wave action, whilst the holdfast may attain a diameter of 2 ft. through the addition of new tissue annually. If this secondary growth did not occur the plant would soon be torn from its moorings because the holdfast is continually becoming riddled with holes made by boring molluscs. The oogonia and antheridia, which are borne in conceptacles on different plants, as the genus is dioecious, occur over the whole of the lamina, this condition being regarded as the primitive state for the Fucales. The oogonia (macrosporangia) are usually borne on branched hairs, whereas in all other genera they are borne directly on the wall. This condition in *Durvillea* is comparable to the antheridial structure generally in the Fucales and must be regarded as the primitive condition. The ripe oogonium contains four ova. The plant is known as the ‘bull kelp’ and forms submarine forests in deep waters off New Zealand, the Antarctic islands and the southern part of South America.

FUCO-ASCOPHYLLEAE

* FUCACEAE: *Fucus* (a seaweed). Figs. 111–13

This genus contains a number of species that are widely scattered over the world with the majority in the northern hemisphere, many of them exhibiting a wide range of form with numerous so-called varieties. When two or more species occur in the same area they are generally present in different zones on the shore, probably dependent upon the degree of desiccation that they can tolerate (cf. p. 387). The plants are attached by means of a basal disc and there is usually a short stalk, which continues on to form the mid-rib of the frond in those regions where the expanded wings

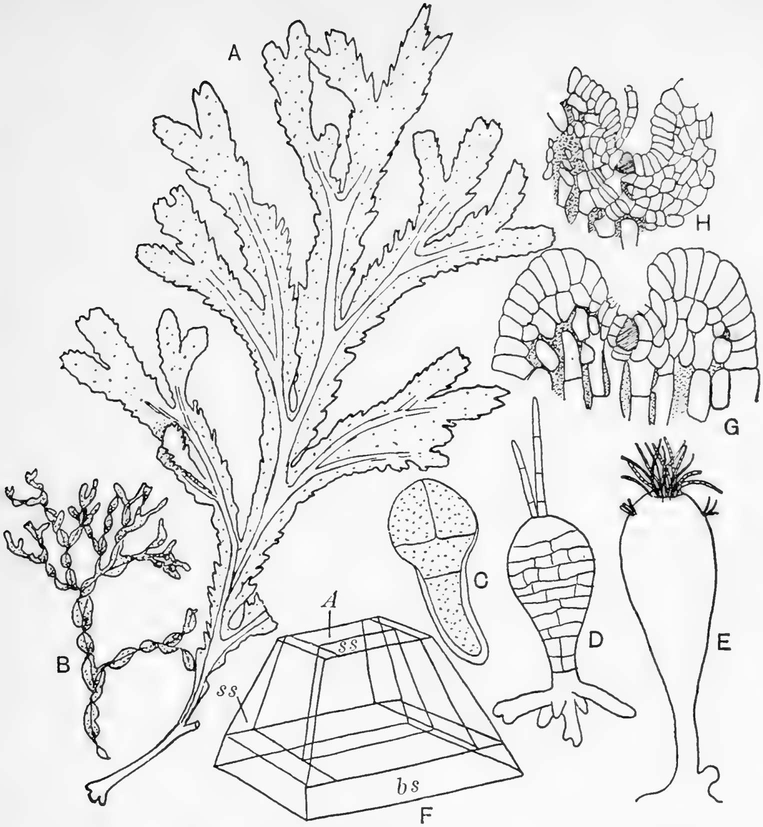

Fig. 111 *Fucus.* A, adult plant of *F. serratus* (× 0·30). B, a marsh form of *F. vesiculosus* (× 0·30). C–E, seedling stages of *F. vesiculosus* showing origin of rhizoids and apical tuft of hairs. F, diagram to show method of segmentation of apical cell, *A. bs* = basal segment, *ss* = side segments. G, apical cell of young thallus. H, apical cell of old thallus. (A, B, after Taylor; C–H, after Oltmanns.)

or *alae* are developed, these latter being of varying width with either entire or serrate margins. Branching, although apparently dichotomous, is in fact monopodial, the degree of branching increasing as the rate of growth decreases. In many species the branches bear swollen vesicles or pneumatocysts. In at least one species, *F. vesiculosus*, these are known to be seasonal in formation, but the nature of the habitat is also involved because more are produced in quiet than in rough waters. Their production appears to be linked with high photosynthetic activity in the spring and summer, the proportions of contained oxygen and nitrogen varying accordingly: carbon dioxide appears to be absent. Sometimes whole portions of the frond may be inflated in an irregular manner, but the factors causing this phenomenon are not known, although it is possible that contact with rock or soil provides the necessary stimulus. In at least one species, *F. serratus*, the overall growth rate not only varies with season but also with the degree of shelter.

With increasing age the lower portions of the alae may be frayed off by wave action, leaving only the mid-rib, which then has the appearance of a stipe. The whole of the expanded thallus is covered with sterile pits or cryptostomata similar to those of *Saccorhiza*, but in fruiting plants it is only the ends of the branches that become swollen and studded with the fertile conceptacles. In *F. spiralis* these conceptacles are hermaphrodite, containing both oogonia and antheridia; in *F. vesiculosus* and *F. serratus* the plants are dioecious, the two types of sex organs occurring on separate plants, whilst in *F. ceranoides* either state may be found.

In the two species that have been studied, *F. vesiculosus* and *F. serratus*, the peak of reproduction in the former occurs in spring and summer and in the latter in autumn and winter. This may possibly be related to differences in germination time and survival of plants as in *Laminaria* (see p. 178), though no such evidence has been reported. The mortality rate of sporelings is extremely high in the early stages of growth (this also may possibly be seasonal), the principal offenders being limpets. A number of very peculiar forms have been found which commonly occur on salt marshes: these rarely fruit, reproduction being secured principally by means of vegetative proliferations (cf. p. 349). The age of *Fucus* plants has not been studied in much detail but the following figures (Table 3) may be cited from the results of tagging plants.

TABLE 3

Age of Fucoids

Species	*F. spiralis*	*F. serratus*	*F. vesiculosus*	*Ascophyllum nodosum*
Max. age (yrs.)	4	4	2½	19
Av. age (yrs.)	1½	2	1	3–4

Recent work from Russia suggests that the maximum age of *Fucus* plants may be rather greater than that given above. In the

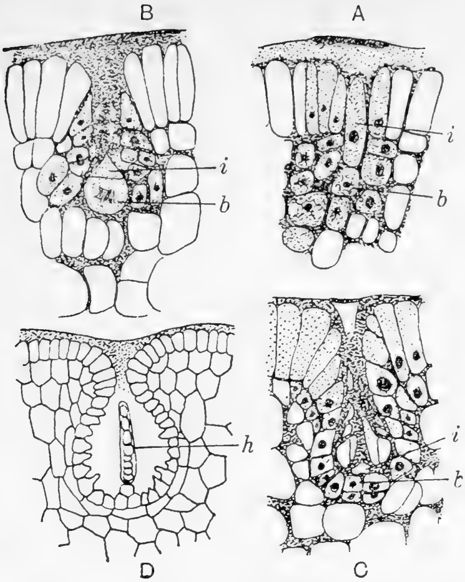

Fig. 112 *Fucus.* A–C, origin of conceptacles in *F. serratus*. *b* = basal cell, *i* = initial. D, juvenile conceptacle of *Cystoseira*. *h* = hair. (After Oltmanns.)

Barents Sea *F. vesiculosus* plants reach their maximum size at the greatest depth for the species (300 cm.).

Morphologically the primary thallus is built up by the activity of the apical growing cell (see below) and by the surface layer of cells, the *limiting layer* or meristoderm. Below the limiting layer is a cortex composed of several layers of parenchymatous cells which become more and more elongate and mucilaginous towards the centre, and these probably form the storage system. In the very centre the cells are extended into hyphae which are interwoven into a loose tangled web, but they do not extend right up to the apex. This central tissue is called the *medulla* and probably acts as a conducting system, because the transverse walls of the hyphae are frequently perforated with the same type of pit that is to be found in some of the Laminariaceae. The primary medullary hyphae are relatively thin-walled, but when secondary growth of the thallus takes place the new hyphae which result from this process are very thick-walled and so are probably mainly mechanical in function. Secondary growth is due to the activity of the limiting layer and the inner cells of the cortex, the latter tissue being responsible for the formation of the secondary hyphae (cf. Fig. 113) which penetrate between the primary medullary hyphae and finally outnumber them. There is a greater development of secondary thickening in the stipe and mid-rib than there is in the frond, whilst in very old parts of the thallus the limiting layer may die off and then the underlying cortical cells take over its function. Development of secondary hyphae is most pronounced near the basal disc, which ultimately consists of a mass of hyphae.

Growth in length takes place by means of an apical cell which lies at the bottom of a slit-like depression that has resulted from the more rapid growth of the surrounding limiting layer. The apical cell is three-sided in young plants whilst in the adult thallus it becomes four-sided, the new segments being cut off successively from the base and four sides, after which they develop into the various tissues (Fig. 111). Injury, and also the stimulus provided when the thallus lies on marsh soil, induces new growth in the neighbouring cells, and in this manner proliferations are formed which may also serve for vegetative propagation. Both cryptostomata and conceptacles arise as depressions in the surface of the thallus, and it is now known that they can arise in one of two ways (Fig. 112):

(1) A linear series of two or more cells is formed, but their horizontal activity then ceases, thus leaving a terminal initial cell which becomes sunk in a depression as the surrounding tissues grow up. In this type the sides of the conceptacle are derived from the limiting layer and underlying cortex, e.g. *Fucus*, though in *Himanthalia* only the limiting layer is involved. *Pelvetia canaliculata* forms an exception in that the first division is vertical and not horizontal. The floor of the conceptacle, however, is derived by division of the original basal cell of the linear series. Finally, around the remnants of the one or more initial cells, a central mucilaginous column is formed, stretching to the neck of the conceptacle and connected to the walls by thin strings of mucilage, which are later ruptured.

(2) The conceptacle develops from a single initial that divides transversely into two unequal cells, the upper or tongue cell degenerating, whilst the lower one gives rise to the walls of the conceptacle by lateral divisions except at the very top

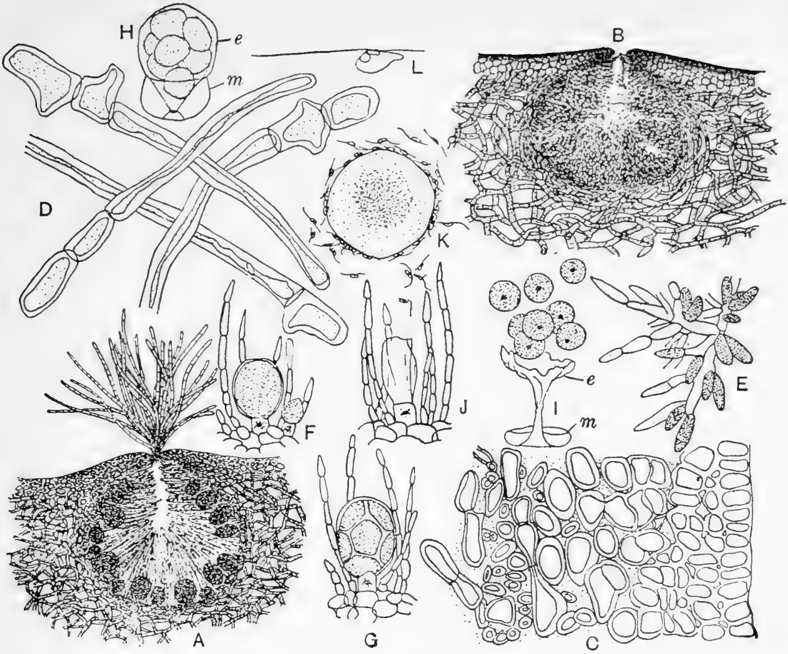

Fig. 113 *Fucus*. A, transverse section 'female' conceptacle of *F. spiralis* var. *platycarpus*. B, transverse section 'male' conceptacle of *F. vesiculosus*. C, portion of thallus of *F. spiralis* to show structure (× 125). D, origin of hyphae 1 cm. below apex, *F. spiralis* (× 235). E, antheridia (microsporangia). F, young, and G, old oogonium (megasporangium). H, liberated ova. *e* = endochiton, *m* = mesochiton. I, ova being liberated. *e* = endochiton, *m* = mesochiton. J, empty sporangium showing torn exochiton. K, ovum being fertilized. L, antherozoid. (C, D, after Pennington; rest after Oltmanns.)

where they come from adjacent tissue. This method of formation occurs in *Sargassum*, *Bifurcaria*, etc. The tongue cell and apical cell of the linear series are regarded as vestigial hairs so that the conceptacles really originate from the basal cell of a hair.

The cryptostomata or hair pits are regarded as a juvenile stage of the fertile conceptacle, because sporangia are frequently associated with the hairs, or else hairs occur in the same cavity after the sporangia have been lost. It has also been suggested in the past that the cryptostomata may represent abortive sexual conceptacles which fail to develop, or alternatively that they are structures which have no relation to the sexual conceptacles but have developed with them in a parallel manner. On the whole the available evidence supports the first hypothesis, and on this basis the following morphological series can be arranged:

(*a*) Plants with a continuous patch of hairs and reproductive bodies, e.g. *Laminaria* (see p. 178).
(*b*) Plants with cryptostomata and continuous patches of hairs and unilocular sporangia, cf. *Alaria* (see p. 189).
(*c*) Plants with cryptostomata containing hairs and sporangia, e.g. *Splachnidium rugosum*, *Ascoseira mirabilis* (see p. 318).
(*d*) Plants with hairs and reproductive bodies in scattered conceptacles, e.g. *Durvillea*.
(*e*) Plants with hairs and reproductive bodies in conceptacles which are confined to special positions (receptacles), e.g. *Fucus*.

In the mature fruiting conceptacles there are branched hairs or paraphyses with the antheridia borne terminally on the branches near the base, or else the paraphyses are unbranched and associated with the oogonia, which are either sessile or else borne on a single stalk cell, each oogonium characteristically containing eight ova when mature. In those species where the conceptacles are hermaphrodite all these structures occur together. The wall of the oogonium (macrosporangium) is three-layered (see p. 193) but that of the antheridium is two-layered. The explusion of the gametes normally takes place whilst the tide is out because the conceptacle is then full of mucilage and the loss of water causes the thallus to shrink, thus forcing the ripe ova and antherozoids in their envelopes through the ostiole to the surface. When the tide returns the inner wall bursts and so liberates the antherozoids. Each oogonium wall has three layers which are called the endochiton, mesochiton and exochiton. Normally when the ova are ripe the outer exochiton ruptures and liberates the eggs enclosed in the meso- and endochiton. Next the mesochiton ruptures and inverts itself, thus exposing the endochiton which is finally dissolved and the eggs set free into the water where fertilization takes place, the antherozoids clustering around the ova and causing them to rotate, until eventually one penetrates and fertilizes the ovum. A fertilization membrane is then produced. The entire process can usually be demonstrated in the laboratory.

The fertilized zygote divides at first by three transverse walls and becomes club-shaped. The lowest cell at the narrow end elongates to form the first rhizoid whilst the cell at the other end divides twice by two longitudinal walls at right angles to give a quadrant. Further divisions result in the development of a central group of cells, the primary medulla, with the cortex outside. Additional rhizoids are produced and the apex of the embryo becomes flattened and one cell produces a hair with a basal intercalary meristem. Excessive growth of neighbouring cells results in the formation of a terminal depression and additional hairs are produced. Next all the cells of the first hair, except the basal one, disappear and the basal cell becomes the three-sided apical cell. In those Fucales, e.g. *Fucus*, where the adult condition of the apical cell is four-sided, this change in the apical cell takes place quite early, the new four-sided cell being cut off from the original three-sided one. The peculiar salt marsh fucoids (see p. 349) are interesting in that the juvenile three-sided apical cell persists throughout life.

FUCACEAE: *Pelvetia* (after the French botanist, Dr. Pelvet). Fig. 114

The fronds in this genus have no mid-rib and are linear, compressed or cylindrical with irregular dichotomous branching. Air

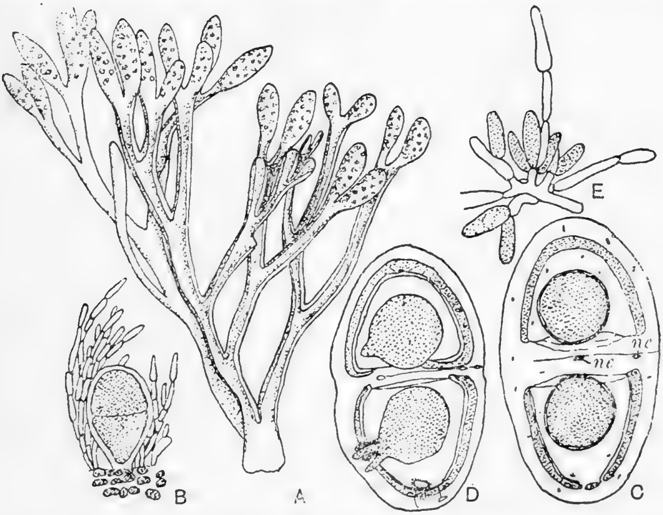

Fig. 114 *Pelvetia canaliculata*. A, plant ($\times \frac{3}{5}$). B, megasporangium (× 60). C, mature fertilized sporangium (× 72). *ne* = rejected nuclei. D, germinating oospores (× 72). E, microsporangia (× 156). (A, original; B–E, after Scott.)

vesicles may be present in some species but normally they are absent, especially in the European *P. canaliculata*, which grows on rocky shores forming a zone near high-water mark or even above, so long as it is reached by the spray.[1] The thallus of this species is said always to be occupied by an Ascomycete, *Mycosphaerella pelvetiae*. Modified salt-marsh forms derived from *P. canaliculata* are also recorded but these are confined to Great Britain (cf. p. 348); like the marsh forms of *Fucus* they are characterized by the general absence of fruiting receptacles, reproduction being primarily vegetative. The structure of the thallus is essentially similar to that of *Fucus*, but the Californian *Pelvetia fastigiata* also possesses a few cryptostomata which are otherwise absent from the genus. The oogonia are similar to those of *Fucus* except that normally only two ova mature, the remaining six nuclei being extruded from the cytoplasm into the wall, though in *Pelvetia fastigiata* one may occasionally find four ripe ova or else ova that contain two nuclei. In *P. canaliculata* the two mature eggs are arranged one above the other, whilst in the Japanese species. *P. wrightii*, they are placed side by side. This difference is probably dependent upon the relative position of the two megaspores which germinate. In the former species gametes are liberated at spring tide periods.

FUCACEAE: *Ascophyllum* (*asco*, wine-skin; *phyllum*, leaf). Fig. 115

The plants of this genus are large, often attaining several feet in length, and are commonly to be found on sheltered coasts at about mean sea-level. The thallus of the common species, *A. nodosum*, which sometimes bears nodular galls caused by the eel-worm *Tylenchus fucicola*, is more or less perennial, and regenerates each year from a persistent base or from the denuded branches. As in the two previous genera free-living or embedded forms have evolved in salt-marsh areas (cf. p. 349), and these differ considerably from the common parent species, *Ascophyllum nodosum*, not only vegetatively but also in the absence of sporangia. The normal fronds have a serrated margin but no mid-rib and commonly bear vesicles which are known as *pneumatocysts*, but when the vesicles are borne on the little side branches they are termed *pneumatophores*. Recent work has shown that in some regions at least one pneumatocyst and its associated piece of axis is produced annually,

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[1] The mean growth rate of this species is 3·2 cm. per year, and plants live for 4–5 years (Subrahmanyan, 1960).

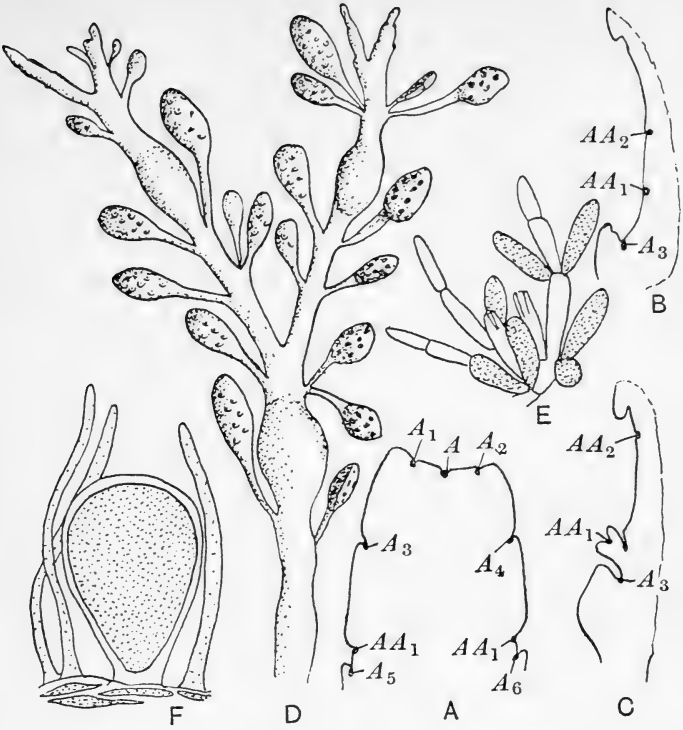

Fig. 115 *Ascophyllum nodosum*. A–C, diagram showing method of branching. A, apical cell. A_1–A_6, secondary initials in order of development. AA_1, AA_2, tertiary and quaternary initials. D, plant (×½). E, microsporangia (×225). F, megasporangium (×2·25). (A–C, after Oltmanns; D–F, after Newton.)

so the number of pneumatocysts may indicate the age of the plant. The axis is beset by simple, clavate, compressed branchlets that arise singly or in groups in the axils of the serrations. These are later converted into or are replaced by short-stalked, yellow, fertile branches which fall off after the gametes have been liberated from their conceptacles. The macrosporangia each give rise to four ova, the remaining four nuclei degenerating.

The method of branching is perhaps best understood from an inspection of Fig. 115. In spring the main branches divide dichotomously as in *Fucus*, after which opposite pairs of fertile receptacles or sterile tufts of hairs are produced in notches that are formed as follows on both sides of the thallus. The apical cell (A) cuts off another apical cell (A_1) that remains dormant for a time, during which period it is carried up the edge of the groove to the side of the thallus by the activity of the primary apical cell. The limiting layer immediately around A_1 does not undergo further growth and so it also comes to lie in a groove. Later on, tertiary (AA_1) and quaternary (AA_2) apical cells are cut off from A_1, the tertiary cell becoming the apical cell of a sterile or fertile branch.

The free-living salt marsh forms of *Ascophyllum nodosum* apparently arise as a result of alternating high and low salinities such as one finds in estuaries. Ecad *scorpioides* requires long periods of low salinity and ecad *mackaii* short, frequent periods. The same interpretation may apply to var. *minor* but, since it is turf-living, there is only rain water to lower the salinity. In ecad *mackaii* cessation of bladder formation is brought on by continuous submergence (though it does not survive if the salinity is below 2 per cent), lack of light, development of apical receptacles and reduced salinity.

HIMANTHALIACEAE: *Himanthalia* (*himant*, thong; *halia*, of the sea). Fig. 116

The short, perennial frond or button arises from a small disc-like holdfast, the shape of the button being dependent upon level because it is short and stumpy when it grows exposed at high levels, whilst it is more elongate at the lower levels where the plants are submerged for longer periods. From March to July of each year new receptacles grow out from the centre of the buttons and form very long strap-shaped and repeatedly forked structures filled with mucus. Although the button is regarded as the frond and the thong as the receptacle, it is possible to regard the button as part of the stipe and the thong as frond plus receptacle, as in *Durvillea*. In support of the second interpretation it should be mentioned that the receptacle contains horizontally running hyphae which have so far only been found in *Durvillea* in receptacular regions. In the receptacles these horizontal hyphae appear to be associated with the formation of air spaces. Growth curves show that the greatest length is attained by these annual thongs on plants growing in the lowest part of a dense zone, and that the shortest occur in the highest. This can be correlated with (*a*) the greater degree of desiccation at the higher levels, and (*b*) the less frequent flooding reducing the supply of nutrient salts. The apical groove, containing the apical cell and hairs, is perpendicular to the plane of flattening and not parallel. Internally it has been found (Naylor, 1951) that

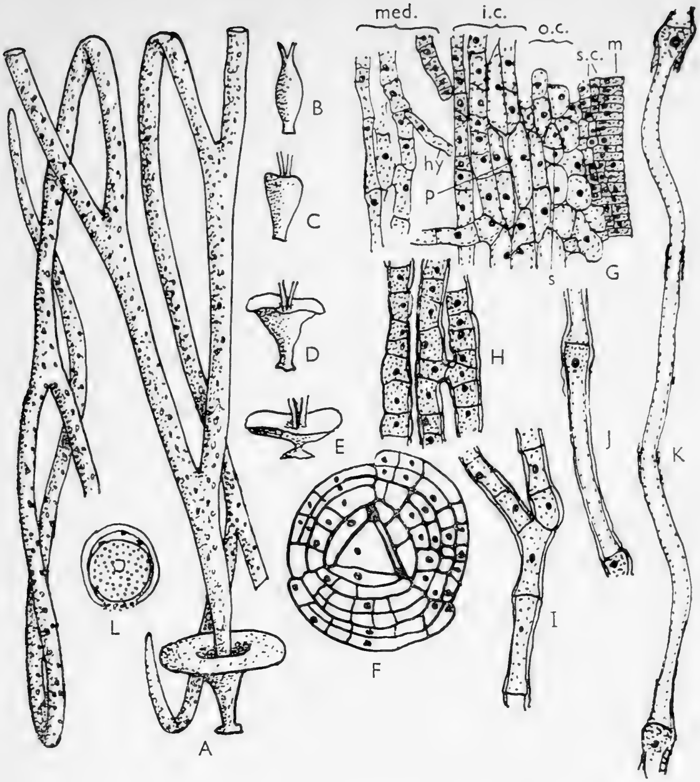

Fig. 116 *Himanthalia lorea.* A, fertile plant. B, C, abnormal buttons. D, button from bottom of dense zone. E, button from top of dense zone. F, T.S. apical cell. G, L.S. behind apex of young receptacle. m = meristoderm; s.c. = cells recently cut off from it; o.c. = outer cortex; i.c. = inner cortex; m = medulla; p = pit. H–K, stages in elongation of medullary cells (× 125). L, mature megasporangium (oogonium). (A–E, I, after Gibb; F–H, after Naylor.)

the extremely elongated cells of the medulla may take on an appearance resembling the trumpet hyphae of *Laminaria*. This may be a case of parallel development, but in view of other similarities to *Durvillea* it may be suggested that *Himanthalia* represents a primitive though somewhat specialized member of the Fucales. Reduction has proceeded so far in this genus that only one ovum matures in the ripe oogonium (macrosporangium). Liberation of gametes is controlled by the tides and exposure, and there is a definite periodicity related to these two factors.

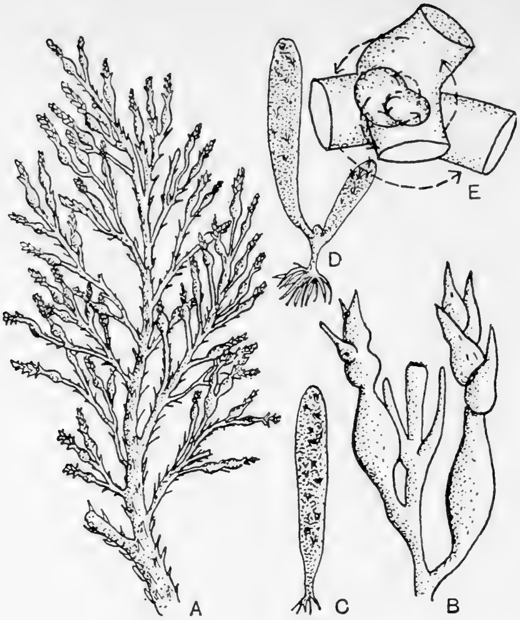

Fig. 117 *Cystoseira.* A, *C. ericoides* plant (× ½). B, portion of same enlarged (× 4·5). C, germling. D, same, rather older. E, diagram to show nature of branching in *C. abrotanifolia.* (A, B, after Newton; C–E, after Oltmanns.)

CYSTOSEIRO-SARGASSACEAE

SARGASSACEAE: *Cystoseira* (*cysto*, bladder; *seira*, chain). Fig. 117

The much-branched perennial thallus is either cylindrical or compressed and arises from a fibrous woody holdfast which has more or less the structure of a conical cavern. The primary branches arise from the main stipe towards the base and divide above into filiform branches and branchlets, but when the latter do not develop very far one gets what is known as the '*erica*' and '*lycopodium*' types, so called because of their resemblance to members of those genera. Seriate rows of small air vesicles may be inserted in the branches, and when this occurs the row of vesicles must be regarded as a modified branch. On the approach of the dormant season some species shed a considerable proportion of the branch system so that the plant may appear very different. The plants are monoecious or dioecious, the conceptacles being borne in terminal or intercalary positions on the ramuli, and, as in some of the other genera, only one ovum develops in each megasporangium, the remaining seven nuclei degenerating. In the sporeling the main shoot is very short and soon stops growth, and a new apical cell arises near its base (Fig. 117 D). This new apical cell gives rise to the adult axis which is therefore a branch of the sporeling. The later laterals develop monopodially and in succession. The first two shoots arise opposite each other but the remainder have a divergence of 2/5. The genus is principally confined to the warm sub-tropical and temperate waters of the globe.

* SARGASSACEAE: *Sargassum* (*sargasso*, Spanish for seaweed). Fig. 118

In the simplest forms branching is distichous but in the great majority it is radial with a divergence of 2/5. Like *Cystoseira* the main axis is usually very short and the thallus is primarily composed of richly branched, long laterals. Basically the leafy short laterals borne on the long laterals are built up as follows: the primary branch is a sterile phylloclade which bears cryptostomata, whilst the secondary branch is also sterile and is commonly reduced to an air bladder. In the simpler forms the subsequent branches are fertile and finger-like in appearance. In more advanced forms there may be further sterile phylloclades which may subtend axillary branch systems. In branching the main apical cell (a), (Fig. 117 E) cuts off a secondary initial (a_1) and this latter, as soon as it has emerged from the apical pit, cuts off another initial (a_2) on the distal side. This last initial divides more rapidly than the other and grows out into the subtending leaf, which is therefore a lateral that has pushed aside the parent axis. Later the parent initial (a_1) produces further initials on a 2/5 divergence. The plants are attached by means of a more or less irregular, warty, solid, parenchymatous base or else numerous stolon-like structures grow out from the main axis and anchor the plant. The genus, which is principally confined to tropical waters, is a very large one with about 150 species, some being dioecious whilst others are monoecious. Morphologically the structure of the species is similar to that for *Fucus* though there is little or no medullary material, and when present it is not gelatinized. In the ripe oogonium (megasporangium) only one ovum will normally reach maturity, though occasionally

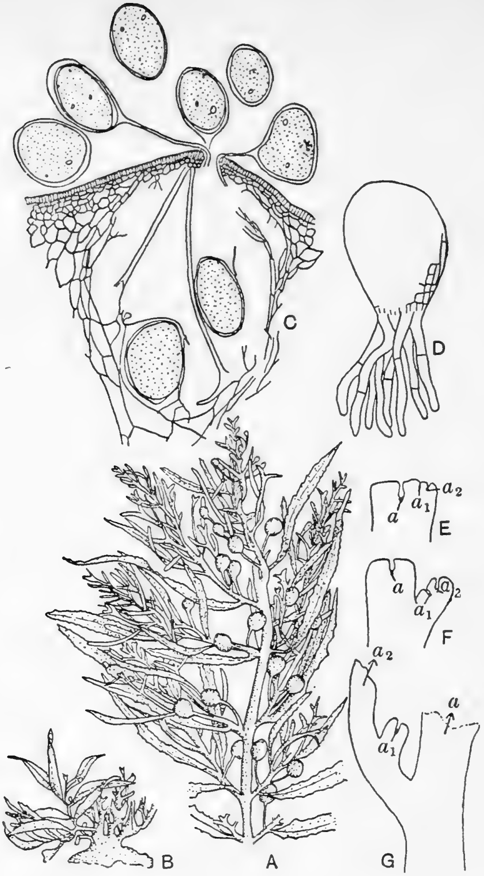

Fig. 118 *Sargassum*. A, *S. filipendula* (×0·45). B, base of plant. C, escape of sporangia each with eight nuclei (×40). D, seedling at rhizoid stage (×105). E–G, stages in branching, *S. thunbergii* (×0·22). a = main initial, a_1 = branch initial, a_2 = secondary branch initial. (A, B, after Taylor; C, after Kunieda; D, after Tahara; E–G, after Oltmanns.)

eight eggs may develop. In the former case the single ovum contains all eight nuclei, but only one of these grows larger and is actually fertilized. This state of affairs can be interpreted as a failure on the part of the megaspores and gametophytes to form cell walls, and is a secondary condition due to still further reduction. In *S. filipendula* there is no stalk to the young megasporangium and so it is embedded in the wall of the conceptacle. When ripe the

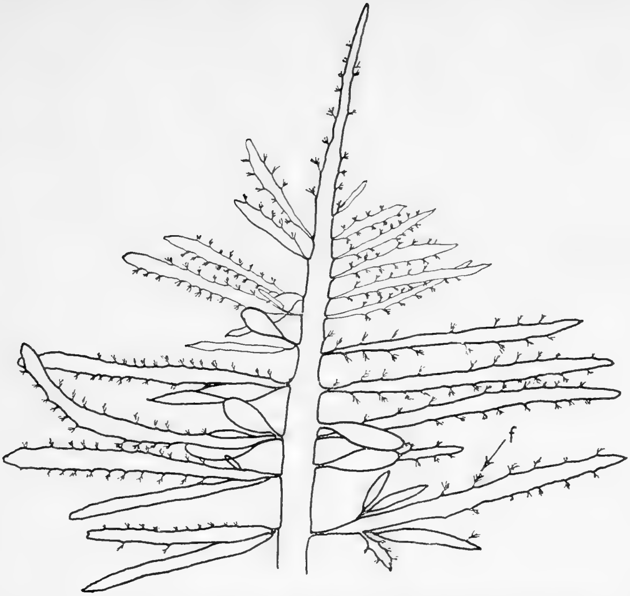

Fig. 119 Portion of fertile plant of *Carpophyllum flexuosum* (× 1).

whole megasporangium, not merely the inner wall and its contents, is discharged and remains just outside the ostiole attached to the conceptacle wall by a long mucilaginous stalk which is a secondary development. In one subsection of the genus the ostiole of the female conceptacle is closed by a disc-shaped gelatinous stopper, which disappears when the oogonia are ripe.

After fertilization the first divisions take place whilst the zygote is still attached to the parent plant by this long stalk. In *S. filipendula* fertile or degenerate reproductive organs are found in some of the cryptostomata, and this fact has been taken to signify that these sterile pits are abortive or juvenile conceptacles. The genus is especially abundant in Australian waters, and one species, *S. enerve*, is employed in Japan as a decoration for New Year's Day because, when dried, it turns green. Various species are also used in the same country for food, but the chief claim to notoriety in this genus is probably associated with *S. natans*, the so-called Sargasso weed, which from time immemorial has been found as large floating masses in the Sargasso Sea near the West Indies, frequent references to it being recorded in the stories of early travellers to that region. At one time it was thought that plants of *S. natans*, together with one or two other species that behave similarly, were attached in the early stages, but there would now seem to be good evidence that they remain floating throughout the whole of their life cycle. Börgesen suggests that these perennial pelagic species originally arose from attached forms such as *S. vulgare*, *S. filipendula* and *S. hystrix*.

SARGASSACEAE: *Carpophyllum* (*carpo*, fruit; *phyllum*, leaf). Fig. 119

This genus, confined to south temperate oceans, consists of a number of species. The plants are bushy and from the main axis arise pinnately a number of leafy appendages. The fertile receptacles arise later in the axils of these leafy appendages though in at least one species the subtending leaf is absent. The plants grow at or below low water-mark and are highly compressed with no gelatinization of the internal tissue. Most of the tissue consists of meristoderm and cortex with little or no medulla.

ANOMALAE

HORMOSIRACEAE: *Hormosira* (*hormo* necklace; *sira* chain). Fig. 120

The sporophyte, which has the appearance of a bead necklace, is composed of a chain of swollen vesicles (internodes) connected by narrow connectives (nodes). Growth takes place by means of a group of four apical cells, and these give off branches alternately in a dichotomous manner, the branches usually arising at the internodes, but apart from the discoid holdfast, there is no differentiation into appendages comparable to those of the other Fucaceae. The basal internode is solid but all the remainder are hollow: the nodes are also solid because they are composed solely of epidermis and cortex. The sporophytes are dioecious, the conceptacles being borne on the periphery of the inflated nodes. Although eight ova are originally formed in the oogonium only four attain to maturity, but in this genus, however, it is a case of degeneration of eggs and not merely of nuclei. When the ova are released from the oogonium they are still surrounded by the endochiton. This soon ruptures and releases the mature ova. After fertilization has taken place a special fertilization membrane is produced, which is composed of two layers, the inner one being of cellulose. Another interesting feature of this genus is its capacity to form and shed a

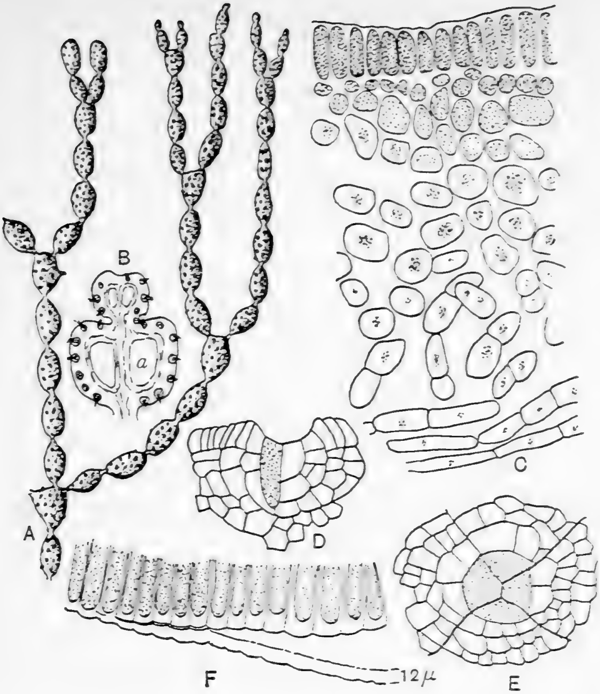

Fig. 120 *Hormosira banksii*. A, portion of plant ($\times\frac{3}{5}$). B, longitudinal section of apex of plant. a = air-filled space. C, transverse section of thallus at internode ($\times$ 150). D, longitudinal section of apex. E, transverse section of apex. F, cuticle being shed (semi-diagrammatic). (A, C, after Getman; B, D, E, after Oltmanns; F, original.)

cuticle that bears the impressions of the cell outlines, this feature perhaps being of significance when the problems concerning the Nematophyceae are considered (cf. p. 302). The genus is monotypic, the single species, *H. banksii*, being confined to Australia and New Zealand where it grows on rocks and in tide pools of the littoral belt in positions that are always exposed to the spray. Although several varieties have been described, it has recently been shown that these are merely rather more distinct representatives of a range of ecological forms. Use of a statistical technique, the discriminant function,[1] has enabled these various ecological forms to be differentiated (see also p. 410) (Fig. 121).

[1] This was based upon two measurements, bladder diameter and connective length.

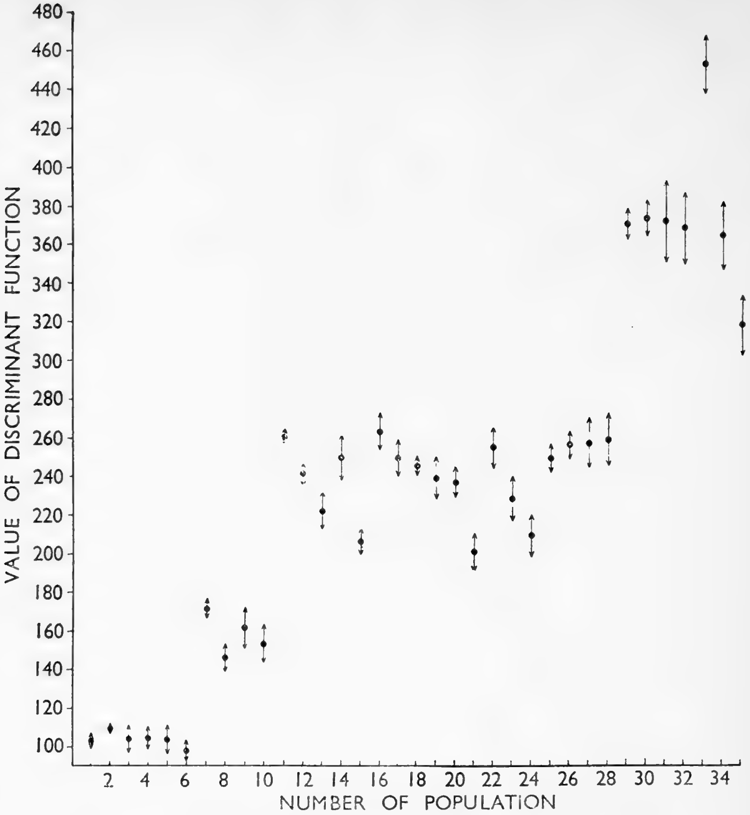

Fig. 121 Separation of exposed rocky coast populations of *Hormosira banksii* by use of the discriminant function. This is based upon diameter of bladder and length of connective. Group of most exposed plants on the left, successive groups of decreasing exposure to group of least exposed plants on the right. (After Bergquist.)

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Chapter VIII

EUPHYCOPHYTA

* RHODOPHYCEAE

Systematically these form a large but very uniform group in so far as their reproductive processes are concerned. Morphologically they appear to vary widely in the construction of the vegetative thallus, but actually in all cases the thallus is fundamentally filamentous and there is no true parenchymatous construction. There are unicellular and colonial forms in the primitive Protoflorideae. The basic filamentous thallus is built up essentially on one of two plans:

(*a*) Central filament (uniaxial) type in which there is a central corticated or uncorticated main axis bearing the branches.

(*b*) Fountain (multiaxial) type in which there is a mass of central filaments (rather like the cable type in the Phaeophyceae, see p. 123) which lead out like a spray to the surface. The central filaments either occupy the centre of the thallus or else they form a ring around a central hollow.

Growth of the thallus is nearly always apical (except in the Protoflorideae), though intercalary growth is known in the Corallinaceae (p. 240) and Delesseriaceae (p. 253). Heterotrichy is a feature in many young stages and may persist in the less specialized genera. Branching is nearly always monopodial and this uniformity in morphology and reproduction is indicative of a monophyletic origin. The cells composing the plants are frequently multinucleate and contain, in addition to the components of chlorophyll, the red pigment phycoerythrin together with phycocyanin in some cases, whilst *Polysiphonia* (p. 249) is interesting in that one species has been reported as containing fucoxanthin. The plastids are commonly band-shaped, and axile, though in some of the primitive Nemalionales they are stellate. In the more primitive forms there is often only one plastid per cell. Some of the primitive members may also have pyrenoid-like bodies in their cells, though these differ from the Chlorophycean pyrenoids. The cells are generally uninucleate but in some species a multinucleate condition is found: this is climaxed in *Griffithsia* where each cell contains several thousand nuclei. The cell wall is double, the inner wall consisting of cellulose and the outer of pectic materials. Except for most members of the first subdivision (the Protoflorideae) the cells remain united to each other by means of thin protoplasmic threads or *plasmodesmae*, which may be very conspicuous in the region of the fusion cell (cf. below), where their thickness can perhaps be associated with the need for the transmission of nutritive material. So far it has not been possible to establish with certainty that the protoplasmic strands actually penetrate the cell walls. Some species contain special small vesicular cells rich in iodine, but the function of these cells is not known. Iridescence caused by special bodies within the cells is a feature of a few species, e.g. *Chylocladia reflexa*, *Chondria coerulescens*.

The reproductive bodies are very characteristic, usually being found on separate plants, but the two sex organs may occur on the same plant, and certain abnormal cases are also known where sexual and asexual organs are present on the same thallus (see p. 256). The sexual plants are usually identical, but in *Martensia fragilis* and *Caloglossa leprieurii* the male plants are smaller than the female. The male organs, which are probably best termed antheridia although they have been given other names, each give rise to a non-motile body, or *spermatium*, which is carried by the water to the elongated tip (*trichogyne*) of the *carpogonium* or female organ. In this respect it will be seen that the Rhodophyceae are very distinct from the other algal groups.

The carpogonium with its trichogyne is usually borne on a special lateral branch (except in the Gelidiales) which consists of a varying number of cells, the parent mother cell being known as the *support cell*. Often associated with this branch, or in some cases forming a part of it, is a special cell, the *auxiliary cell*, into which the fertilized carpogonial nucleus passes. The carpogonial branch plus the associated auxiliary cell or cells is termed the procarp. Apart from receiving the fertilized nucleus, in some of the more primitive genera the auxiliary cell may also have a nutritive function. Some workers argue that such cells are not truly auxiliary cells and indeed cannot be strictly auxiliary cells unless receiving the fertilized carpogonial nucleus. This view may seem to be too extreme because it is evident that in these primitive genera we are dealing with an auxiliary cell in just the same sense as there are haploid carpospores in such genera. Carpospores are normally formed from a peculiar diploid generation that develops parasitically on the female plant. They are produced in sporangia that terminate filaments that arise usually from the auxiliary cell or fertilized carpogonium. These filaments are known as the gonimoblasts. In the primitive genera, e.g. of Nemalionales, where reduction division occurs at germination of the zygote the carposporophyte is haploid, but in all the others it is a parasitic diploid plant growing on the parent haploid plant. On germination the diploid carpospores give rise to a new independent asexual diploid generation, which reproduces by means of *tetraspores* formed in sporangia borne externally or else sunk into the thallus (Figs. 141, 145). In the majority of species where there are two separate diploid generations the plants can be termed morphologically triphasic but cytologically diphasic.

A common feature of the group that further emphasizes their uniformity is a tendency for the 2n number of chromosomes to be 40. The Rhodophyceae may be regarded as a classical example of plants in which meiosis occurs at different phases in the life cycle, for it may either occur immediately on germination of the zygote or at some later period. When meiosis is delayed there is either a carposporophyte (*Liagora tetrasporifera*, *Helminthocladia*) or carposporophyte and tetrasporophyte alternating with the sexual generation.

The classification of the Rhodophyceae is based primarily upon the structure of the female reproductive apparatus. After the Protoflorideae, which mostly lack pit connexions and have a single axile plastid in each cell, have been segregated, the remainder of the red algae, or Euflorideae, are classified as follows:

(1) *Nemalionales:*

Construction fountain type or central filamentous. Carpogonia occur singly, and the so-called auxiliary cell, if present, is formed from a carpogonial branch cell or its derivative and is nutritive. Reduction division normally occurs immediately after fertilization but exceptions are known (*Galaxaura*). When present the tetrasporangia are cruciate.

(2) *Gelidiales:*

Central filament type of construction. The sessile carpogonia are aggregated and true auxiliary cells are lacking, the adjacent cells being only nutritive. Reduction division is delayed so that the plants are morphologically triphasic and cytologically diphasic. The tetrasporangia are cruciate, more rarely tetrahedral.

(3) *Cryptonemiales:*

Both types of thallus construction. The carpogonia are borne on special accessory branches and may be aggregated into sori, nemathecia or in conceptacles. The auxiliary cell is borne on separate accessory branches *before* fertilization and is actively concerned in the post-fertilization processes. The tetrasporangia are cruciate or zonate.

(4) *Gigartinales:*

Both types of thallus construction. The support cell or a normal intercalary cell of the mother plant is set aside as an auxiliary cell *before* fertilization. The tetrasporangia are cruciate or zonate.

(5) *Rhodymeniales:*

Central filament type of construction only. The small auxiliary cells are derived from a branch formed from the support cell. They are cut off before fertilization but only develop after that process has taken place. The tetrasporangia are cruciate or tetrahedral.

(6) *Ceramiales:*

Only the central filament type of construction. The auxiliary cell or cells are cut off from the support cell or from an homologous pericentral cell *after* fertilization and as a direct consequence of the process. The tetraspores are usually arranged in a tetrahedral fashion, more rarely in a cruciate manner.

Some authors consider that a further two orders should be recognized, the Sphaerococcales and Nemastomales, and there is some evidence in support of this procedure. However, in this volume the genera of these two orders are retained in the existing orders (above) to which they have belonged in the past.

The antheridial plants, which are often paler in colour and more gelatinous, were first mentioned in a letter to Linnaeus in 1767.

The antheridia are either borne scattered over the whole surface (Nemalionales), or else in localized sori. These sori are reticulate in *Rhodymenia*, band-like in *Griffithsia*, borne on special branches in *Polysiphonia*, sunk in conceptacles in the Corallinaceae, and occur on the tips of the thallus on *Chondrus*. Very little is known about the seasonal periodicity of the male plants, which are often less frequent than either the female or tetrasporic plants, but this may be due purely to lack of observation, although it is also possible that the male plants are gradually becoming functionless. The antheridia often appear in an orderly sequence, being cut off usually as subterminal or lateral outgrowths from the antheridial mother cell. If they have been borne on a special part of the thallus (e.g. *Delesseria*) this may fall off or die away after fruiting is completed, whilst in other cases the mother cells simply revert to a normal vegetative state. The different types of male plant have been classified by Grubb (1925) as follows:

- (*a*) The antheridial mother cell does not differ from the vegetative cells either in form or content, nor are the antheridia covered by a continuous outer envelope, e.g. *Nemalion*, *Batrachospermum*.
- (*b*) The antheridial mother cells are differentiated from the vegetative cells, and the antheridia are surrounded by a common outer sheath, which is later pierced by holes or else gelatinizes in order to allow the ripe spermatia to escape:

(1) The antheridia develop terminally, e.g. *Melobesia*, *Holmsella*.
(2) The antheridia develop subterminally:
  - (*a*) Two primary antheridia, e.g. *Delesseria sanguinea*, *Chondrus crispus*.
  - (*b*) Two or three primary antheridia, e.g. *Scinaia furcellata*, *Lomentaria clavellosa*.
  - (*c*) Three primary antheridia, e.g. *Ceramium rubrum*, *Griffithsia corallina*.
  - (*d*) Four primary antheridia, e.g. *Polysiphonia violacea*, *Callithamnion roseum*.

The primary antheridia are commonly succeeded by a second crop which arises within the sheaths of the first, but a third crop only occurs in a few genera.

In all red algae the nucleus of the spermatium is in late prophase when liberated but normally no division takes place. In *Batrachospermum* and *Nemalion*, however, a division does occur but only one of the daughter nuclei acts as the fertilizing agent: this feature has led to the suggestion that in the more advanced red algae the contents of the antheridium are equivalent to a body which formerly did divide.

The carposporophyte is the generation that arises normally after fertilization and is parasitic upon the female plants. Cytologically it is haploid in the primitive members and diploid in the remaining members of the Rhodophyceae. Morphologically it comprises all the structures arising from the fertilized carpogonium, fusion cell or cells and gonimoblasts. In more advanced forms it is often protected by a wall of gametophytic tissue. The carposporophyte and the wall is termed the *Cystocarp* or *Gonimocarp*. The following types of carposporophyte have been recognized:

(i) Gonimoblasts arise from carpogonium without any prior fusion with a gametophyte cell.
(ii) Gonimoblasts arise from carpogonium after fusion with a gametophyte cell but without transfer of diploid nucleus.
(iii) Primary gonimoblasts transfer diploid nucleus to gametophyte cells from which secondary gonimoblasts then arise.
(iv) Gonimoblasts arise from fusion cell, the diploid nucleus having passed into a gametophyte cell.
    (*a*) The gametophyte cell is a cell or cells of the carpogonial branch.
    (*b*) The gametophyte cell is the support cell of the carpogonial branch or a true auxiliary cell cut off before or after fertilization.

The tetraspores are formed either in superficial tetrasporangia that terminate assimilatory filaments or short laterals, or in sporangia and short laterals that are sunk into the thallus, in which case the fertile branch often becomes swollen and irregular in outline. In some cases, e.g. *Plocamium*, *Dasya*, they are borne on special lateral branches or *stichidia*. The division of the sporangia is cruciate, zonate or tetrahedral. In some cases only two spores (bispores) are formed, e.g. Corallinaceae, Ceramiaceae. Meiosis normally occurs at the formation of the tetraspores, but when the spores develop on sexual haploid plants, as sometimes happens, there is no meiotic division and the products function as *monospores*. In *Agardhiella tenera* apospory is sometimes found and again there is no meiosis so that a succession of asexual plants can occur. In the

Nemalionales reproduction by means of monospores is quite common though the homologies of these bodies are somewhat uncertain. In some of the Euflorideae (*Plumaria*, *Spermothamnion*) polyspores or paraspores develop on the diploid plants, but it has recently been shown that these are in some cases morphologically equivalent to tetraspores, whilst in others, e.g. *Plumaria*, they form the reproductive organs of a triploid generation (cf. p. 256). Experimental cultures made on oyster shells have demonstrated that there are good grounds for believing that of the four spores in a tetrad, two will give rise to female plants and two to male plants. Observations have been published showing that monospores, carpospores and tetraspores of some Rhodophyceae appear capable of a small degree of motion, the spores of the Bangiaceae being the most active among those investigated. The mechanism of this movement is not understood, and it is doubtful whether it is sufficient to give it any significance in the reproductive processes of the plants.

Whilst there are apparently very few truly parasitic species among the Chlorophyceae and Phaeophyceae, nevertheless in the present group there are some very definite partial or total parasites. *Ceramium codicola* occurs on a Californian species of *Codium* and is said to be a partial parasite; *Ricardia montagnei* is probably a total parasite at some stage of its existence, and the members of the two genera, *Janczewskia* and *Peyssonnelliopsis*, are probably entirely parasitic. In European waters *Choreonema*, *Schmitziella*, *Choreocolax*, *Harveyella* and *Holmsella* are all to be regarded as partial or total parasites, and to this list *Polysiphonia fastigiata* should perhaps be added, since it is always found on one particular host, *Ascophyllum*.[1]

The division is principally marine, but there are a few fresh water genera, comprising in all about 200 species. The most important fresh-water genus is *Batrachospermum* with many species in Australasia, and others are *Lemanea* and *Hildenbrandtia*. They nearly all frequent fast-flowing streams where there is an abundance of aeration.

As in the Chlorophyceae there is one section, the Corallinaceae, that is characterized by lime encrustation. These algae have played a great part during past geological ages in the building up of rocks and coral reefs (cf. p. 238), a process which can still be seen going on in tropical seas today.

[1] A number of very interesting parasites have been recorded from S. Africa.

PROTOFLORIDEAE

This subdivision is sometimes known as the Bangioideae. The plants are simple, unicellular, filamentous or membranous forms. The cells contain a single axile chromatoplast. Growth of the thallus is diffuse and not apical, and plasmodesmae between cells are commonly lacking.[1] Sexual reproduction is known for a number of genera, but the carpogonium exhibits very little specialization. The spermatia are formed by repeated divisions inside the mother cell (e.g. *Porphyra*) or within special spermatangia (*Erythrotrichia*). After fertilization reduction division takes place and the zygote gives rise to haploid carpospores. Monospores form another means of reproduction, being produced in one of three different ways:

(i) Those formed from differentiated sporangia, e.g. *Erythrotrichia, Erythrocladia.*
(ii) Those formed from undifferentiated cells, e.g. *Bangia.*
(iii) Those formed by successive divisions of a mother cell, e.g. *Porphyra.*

BANGIACEAE: *Porphyridium cruentum* (*porphyridium*, diminutive of purple dye; *cruentum*, blood red). Fig. 122

This alga has had an extremely varied history, having been placed at various times in both the Palmellaceae and Schizogoniaceae of the Chlorophyceae, near to *Aphanocapsa* in the Myxophyceae, and among the Bangiaceae in the Rhodophyceae where it finds a home at present. The single cells are united into a one-layered, gelatinous colony of a blood-red colour which is found on the soil. Cell divisions take place in all directions, and when a cell divides the sheath elongates to form a kind of stalk which eventually ruptures. Monospores are produced as the only known means of reproduction other than vegetative division. The cell contents round off and escape from the cell envelope. So far no form of sexual reproduction has been observed. In each cell there is one large chromatophore with cyanophycin granules around the periphery and also a central nuclear-like body, composed largely of anabaenin, which undergoes a primitive form of mitosis at cell division. Whether this alga represents a primitive form or else is a much-reduced type cannot at present be determined. The principal argument in support of

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[1] Recently the existence of plasmodesmae in some species has been reported, so that this feature, formerly regarded as a major distinction, no longer exists.

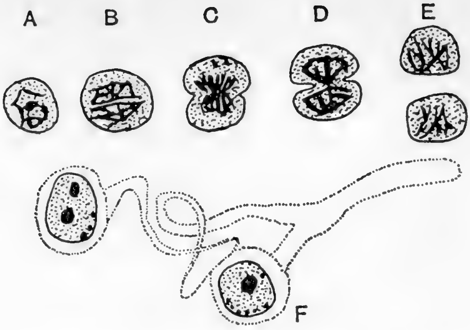

Fig. 122 *Porphyridium cruentum*. A–E, stages in nuclear and cell division (× 1280). F, cells connected by stalks after division (× 1280). (After Zirkle and Lewis.)

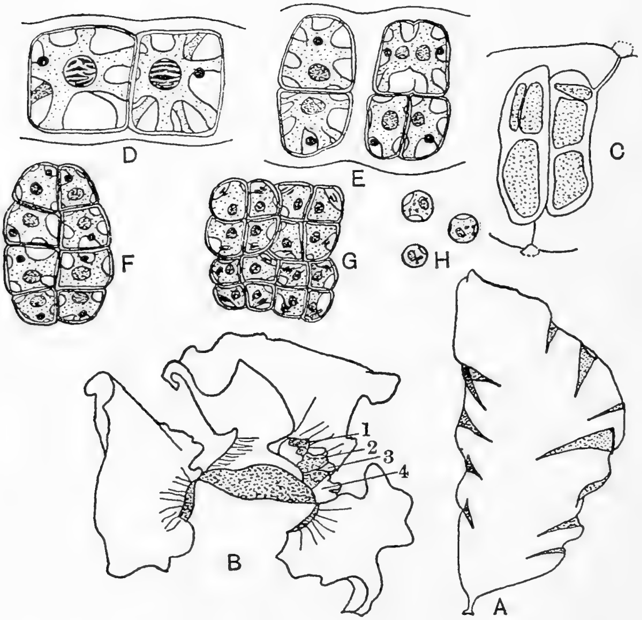

Fig. 123 *Porphyra*. A, thallus (× $\frac{1}{3}$). B, attachment disk with three primary blades and four (1–4) secondary. C, formation of carpospores. D–H, formation of spermatia in *P. tenera*. (A, D–H, after Ishikawa; B, C, after Grubb.)

the second hypothesis is the fact that *Porphyridium* is essentially a soil alga, where it may occur in sufficient quantities to give a blood-red colouring to the ground.

* BANGIACEAE: *Porphyra* (purple dye). Fig. 123

This is a genus which has a very wide range as it extends in the northern hemisphere from 15° to 71° N. and in the southern from the Cape of Good Hope to 60° S. It has a variable seasonal periodicity in English waters where its presence is determined by the amount of water available, e.g. whether the site is subject to spray, together with the intensity of light and shade. The plant is flat and membranous, whilst in the common species, *P. umbilicalis*, there are a number of growth forms, the shape, width and length of the various forms being determined by the age of the plant, the height above mean sea-level and the type of locality. The plants are attached by means of a minute adhesive disc which is capable of producing lateral extensions from which new fronds may be proliferated. The disc is composed of long slender filaments together with some short stout ones, those near to or in actual contact with the substrate swelling up, branching and producing suckers or haptera which are apparently capable of penetrating dead wood or the tissue of brown fucoids. In the latter case there is evidently a capacity for epiphytism once contact is secured, and there is even some evidence of partial parasitism. In California, *Smithora* (formerly *Porphyra*) *naiadum* is an obligate epiphyte on *Phyllospadix* and *Zostera*, two marine phanerogams.

The gelatinous fronds of *Porphyra*, which are normally monostromatic although they become distromatic during reproduction, are composed of cells that possess stellate chromatophores with a pyrenoid, the process of nuclear division being intermediate between mitosis and amitosis. Reproduction is by means of monospores, carpogonia, which have rudimentary trichogynes, and antheridia, the carpogonial areas occupying a marginal position on the thallus.

In the Japanese *P. tenera* monospores are shed in considerable numbers, 10,000 spores being produced from 1 sq. cm. of thallus. These become attached to the substrate in a short space of time and commence germination to a new plant one to two days after fertilization. In sexual reproduction all the frond, except the basal region, can produce antheridia. The species are dioecious or mono-

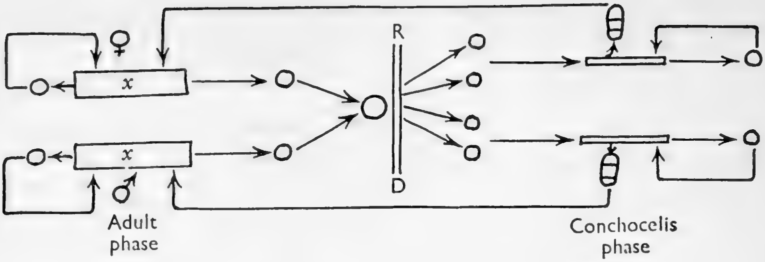

Fig. 124 Diagram of life cycle of *Porphyra umbilicalis.*

ecious, but in either case the male thalli or portions of the thalli are commonly paler in colour than the female. Each antheridial mother cell gives rise to 64 or 128 antheridial cells, each of which produces one spermatium. The fertilized (?) carpogonium divides into four or eight cells that represent primitive carpospores; in this plant these are haploid (though in most Rhodophyceae they are diploid) because meiosis occurs at germination of the zygote. Fertilization has never actually been observed although there is strong evidence which suggests that it does take place. The carpospores germinate and in the case of *P. umbilicalis* produce a prostrate, creeping filament (usually in shells) that has been identified with the algal species *Conchocelis rosea*. In the case of *P. tenera* of Japan, penetration of shells takes place within three days. This dwarf phase bears sporangia that produce monospores,[1] and these on germination are thought to give rise to a new adult plant, though some workers consider that they only reduplicate the *Conchocelis* phase. New adult plants of *P. umbilicalis* and *P. perforata* are said to arise from spores (*conchospores*) liberated from short swollen branches (fertile cell rows) or to arise as vegetative buds. At present there is no evidence that this dwarf phase is diploid. Production of the phase is apparently not universal because in New Zealand plants from the north produce the *Conchocelis* phase but similar plants from the south do not. It is clear that further work on the life history of species of *Porphyra* may well produce interesting results. Japanese workers consistently report monospores from the *Conchocelis* phase of *P. tenera*, whereas in the case of *P. umbilicalis* only conchospores and buds are reported. In the American *Smithora naiadum* the carpospores give rise to a prostrate cushion

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[1] These only mature under short day conditions, the spores being liberated from late September to mid December.

from which the adult plant grows. The full life cycle of *P. umbilicalis* can be represented as in fig. 124.

The genus, which goes under a variety of different common names in the various countries, is much used as a food (see p. 450). The plants normally occur on rocky coasts towards high-water mark. Haploid chromosome numbers of 2, 3 and 4 have been reported and further counts are clearly required.

Eufloridéae

The plants consist of branched filaments, or are compact pseudoparenchymatous or membranous thalli with the uniaxial or fountain type of construction. Fundamentally they are heterotrichous though this condition is lacking in many. Growth is normally from one or more apical cells and plasmodesmae are present. The carpogonium is usually highly specialized and only one spermatium is produced from each antheridium. The zygote nucleus commonly passes into the special auxiliary cell and after fertilization there is produced a parasitic phase, the carposporophyte, producing carpospores. This is nearly always diploid and then the carpospores give rise to an asexual generation reproducing by means of tetraspores.

Nemalionales

A primitive order in which the vegetative structure is both uni- and multiaxial. There are no true auxiliary cells in many genera (*Batrachospermum*, *Nemalion*) whilst in others the so-called auxiliary cell may be largely nutritive (*Galaxaura*). In the majority of the genera only haploid plants are represented in the life cycle, but in the genus *Galaxaura* there is distinct alternation of generations, and in the Bonnemaisoniaceae some extremely peculiar life cycles[1] have been recorded.

There are eight families in the order and as we come to know more about them it may become desirable to split the order. The Chantransiaceae, Batrachospermaceae, Lemaneaceae, Naccariaceae and Bonnemaisoniaceae are all uniaxial. The last-named family differs from the others in respect of some remarkable life cycles (see under *Asparagopsis*, p. 230), and also in possessing cystocarps of distinct shape with gametophytic walls. The Thoreaceae, Helminthocladiaceae and Chaetangiaceae are of multiaxial construc-

[1] Magne (1961) has recorded one also for *Nemalion helminthoides*.

tion. The last-named family differs from the other two in that some members at least possess a regular alternation of generations and there are differences in respect of the gonimoblasts and cystocarps.

In the uncorticated uniaxial Chantransiaceae the genus *Acrochaetium* is extremely widespread. Many of the species of *Chantransia* are now known to be phases in the life cycle of *Batrachospermum* species (see below). The marine *Chantransia violacea* and *C. efflorescens* are said to have alternation of haploid and diploid generations. In the genus *Rhodochorton* only the tetrasporic generation is known. Study of life cycles may assist in solving some problems and it is not unlikely that there are also problems of synonymy.

* BATRACHOSPERMACEAE: *Batrachospermum* (*batracho*, frog; *spermum*, seed). Fig. 125

Two genera commonly found in fresh waters, *Batrachospermum* and *Lemanea*, belong to the Nemalionales. *B. moniliforme*, which is a very variable species, is found attached to stones in swift-flowing waters of the tropics and temperate regions. The thallus, which is violet or blue-green in colour, is soft, thick and gelatinous, the primary axis, which grows from an apical cell, being formed of a

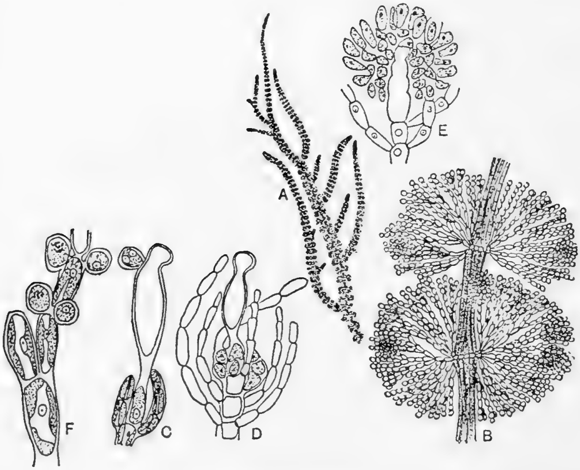

Fig. 125 *Batrachospermum moniliforme*. A, plant. B, portion of plant. C, carpogonial branch (× 480). D, fertilized carpogonium (× 360). E, mature cystocarp (× 240). F, antheridia (× 640). (A, B, after Oltmanns; C–F, after Kylin.)

row of large cells. Numerous branches of limited growth arise in whorls from the nodes and often bear long hairs at the ends. The basal cell of such a branch can give rise to a branch of unlimited growth or else to corticating cells that grow downward and invest the main axis. The cells of the thallus are uninucleate and contain only one pyrenoid. Reproduction takes place by means of monospores (though these are restricted to the juvenile phase), carpogonia and antheridia. The last-named arise as small, round, colourless cells at the apices of short, clustered, lateral branches. The carpogonia are also terminal and possess a non-nucleate trichogyne, separated by a constriction from the rest of the organ. The trichogyne shrivels away after fertilization. The nucleus of the zygote divides twice, giving rise to four nuclei; these pass into protuberances that form from the carpogonium and branch to give a mass of gonimoblast filaments. Each branch terminates in a sporangium that produces a single naked carpospore. This secretes a wall soon after liberation. On germination this gives rise to a microscopic branched filamentous stage, which, on account of earlier confusions is now known as the 'Chantransia' stage. Practically all fresh-water species of *Chantransia* represent a phase in the life cycle of a species of *Batrachospermum.* The 'Chantransia' phase can reproduce itself indefinitely, but eventually a new adult *Batrachospermum* plant arises as a vegetative lateral branch of the 'Chantransia' filament. The 'Chantransia' stage corresponds to the 'Conchocelis' phase in *Porphyra* and both represent the prostrate portion of the heterotrichous thallus.

The fresh-water *Lemanea* (Lemaniaceae) has a more compact, pseudo-parenchymatous thallus and much the same kind of structure is found in the marine Naccariaceae. The carpogonial branches are borne on special, little short shoots. The fertilized nucleus passes from the carpogonium into the hypogenous cell below and a wall of vegetative cells is formed around the gonimoblasts.

BONNEMAISONIACEAE: *Asparagopsis* (like asparagus fern). Fig. 126

The erect shoots arise from a perennial creeping thallus. This prostrate thallus possesses vesicular or iodine-containing cells and modified branches act as attachment organs. In the erect thallus primary and secondary laterals form a cortex which is often separated from the original axis by a space. In all Bonnemaison-

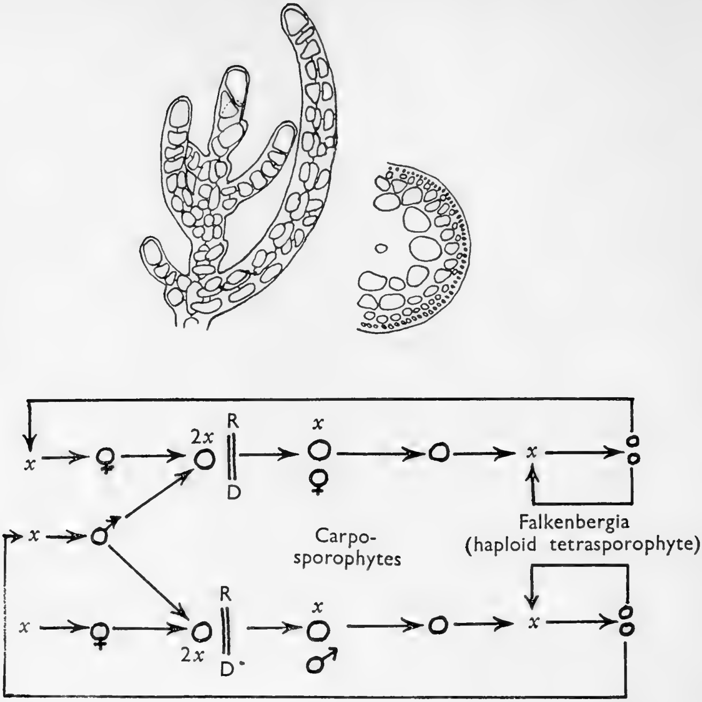

Fig. 126 *Asparagopsis armata.* Top left, apical portion of thallus; right, transverse section showing original main axis in centre (after Kylin): diagram of life cycle of *Asparagopsis armata.*

iaceae except *Asparagopsis*, the thallus is flattened and the appendages are arranged in two rows. The principal interest of this genus lies in its remarkable life history. In *A. armata* reduction division appears to take place at germination of the zygote and the haploid carpospores which result give rise to an entirely different generation that has formerly been known as *Falkenbergia rufo-lanosa.* Although the *Falkenbergia* plants are haploid they give rise to tetraspores but without meiosis taking place. From these tetraspores new plants of *A. armata* are presumably produced. At the first divison of the zygote two nuclei of the tetrad formed degenerate and the remaining two are of the same sex. There must therefore genetically be at least two types of female plant. The life cycle is represented in Fig. 126, and the situation must be regarded as quite atypical, though similar life cycles appear to exist in *Bonnemaisonia asparagoides* and its small asexual plant, *Hymenoclonium* *serpens*,[1] and the Japanese species *B. hamifera* and *Trailliella intricata*. Other representatives may be strictly diplobiontic (see p. 314) since tetraspores have been reported in *Delisea pulchra* and *D. suhrii*.

HELMINTHOCLADIACEAE: *Liagora* (after one of the Nereids). Fig. 127

The axial portion of the thallus contains large cells with which are intermingled narrower rhizoidal cells. Chalk is deposited to a greater or lesser extent on the outside of the thallus so that the plants are whitish in appearance. The principal interest of the genus is that in four species the carpospores divide to give four spores which must presumably be regarded as tetraspores. Although no cytological evidence is available it is presumed that meiosis is delayed to the time when the carpospores divide. There is thus no independent tetrasporic diploid generation. This feature was first discovered in *L. tetrasporifera*, an inhabitant of the Canary Islands. A similar state of affairs has more recently been recorded for other species of *Liagora* and for *Helminthocladia hudsoni*.

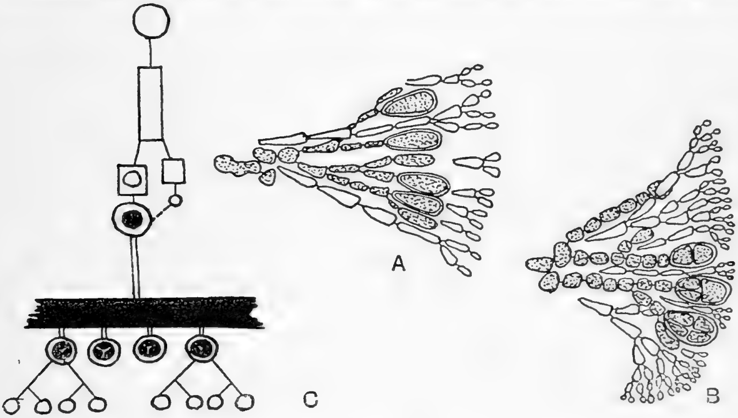

Fig. 127. *Liagora*. A, carpospores of *L. viscida* (×320). B, carpospores in fours in *L. tetrasporifera* (×320). C, life cycle of *L. tetrasporifera*. (A, B, after Kylin; C, after Svedelius.)

CHAETANGIACEAE: *Scinaia* (after D. Scina). Fig. 128

This is a widespread genus with its home primarily in the northern hemisphere, the commonest species, *S. furcellata*, being

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[1] This is now known to be diploid (Magne, 1960).

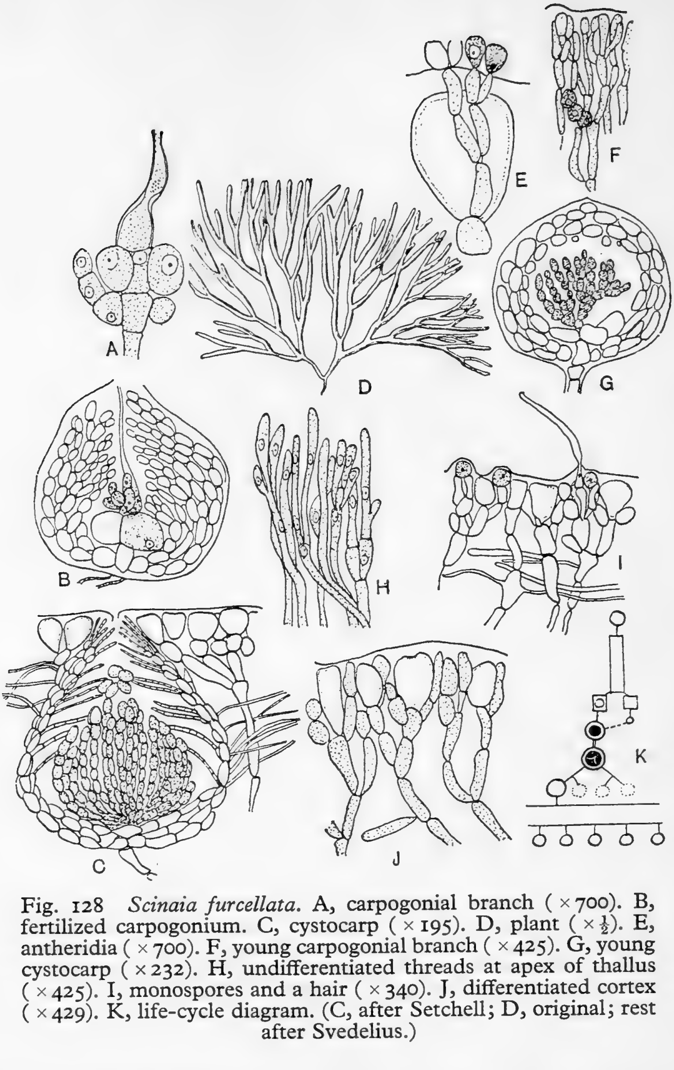

Fig. 128 *Scinaia furcellata.* A, carpogonial branch (× 700). B, fertilized carpogonium. C, cystocarp (× 195). D, plant (× ½). E, antheridia (× 700). F, young carpogonial branch (× 425). G, young cystocarp (× 232). H, undifferentiated threads at apex of thallus (× 425). I, monospores and a hair (× 340). J, differentiated cortex (× 429). K, life-cycle diagram. (C, after Setchell; D, original; rest after Svedelius.)

monoecious, although one may find monospores and spermatia on the same plant. The fronds, which arise from a discoid holdfast, are subgelatinous, cylindrical or compressed and dichotomously branched. The centre of the thallus is composed of both coarse and fine colourless filaments, the former arising from the apical cell and the latter from the corticating threads. There is also a peripheral zone of horizontal filaments that terminate in short corymbs of narrow assimilatory hairs interspersed with large colourless cells. These two types of epidermal cell are apparently differentiated near the apex of the thallus, the small ones giving rise to hairs, monosporangia or antheridia. The large colourless cell is said to form a protection against intense light, but it may also be a relic of a tissue which formerly had a function that has since been lost. One or two spores are formed in each monosporangium, whilst the spermatia arise in sori, forming bunches of cells at the ends of the small-celled assimilatory branches. The carpogonial branch is three-celled, the reproductive cell containing two nuclei, one in the carpogonium proper and one in the trichogyne. The second cell of the carpogonial branch gives rise to a group of four large cells which are rich in protoplasm, whilst the sterile envelope of the cystocarp arises from the third cell.

After fertilization the zygote nucleus passes into one of the four large cells where meiosis then takes place. Three of the nuclei degenerate and the remaining one passes into the single initial gonimoblast filament which later becomes branched. There is therefore no diploid phase since meiosis occurs immediately after fertilization.

CHAETANGIACEAE: *Galaxaura* (*galax*, milky; *aura*, gold). Fig. 129

This is a genus that is widely distributed in the tropics. The thallus is more highly differentiated than the preceding example because the outermost cells of the lateral branches unite to form a cortex. The thallus is more or less heavily calcified and may be jointed due to periodic loss of meristematic activity in the apical cells. New meristematic tissue forms beneath and bursts through the old tissue. The principal interest of the genus lies in its reproduction. For a long time it had been known that there were apparently only sexual or asexual species, differing morphologically in habit and in the asexual plants having one more cell layer in the cortex. Owing to the work of Svedelius it is now known that in this genus a delay in reduction division has occurred so that the carpospores are diploid and give rise to tetrasporic plants. The whole carpogonial branch acquires diploid nuclei and so forms a complex of auxiliary cells. There is thus an alternation of unlike generations, though the difference is largely in appearance rather than in size. This behaviour is so anomalous as compared with

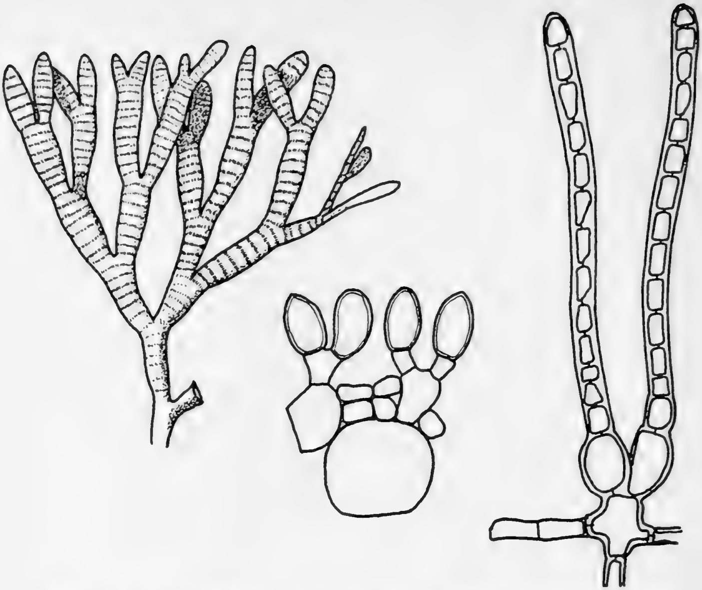

Fig. 129 *Galaxaura*. Left, *G. marginata* (× 3); middle, assimilators of *G. marginata* (× 200); right, assimilators of *G. lapidescens* (× 160). (After Borgesen.)

other Nemalionales that it may be necessary to remove the genus to a separate order. *Liagora tetrasporifera*, *Helminthocladia hudsoni* and *Galaxaura* do, however, show how the sporophyte may have been intercalated into the life cycle.

GELIDIALES

This is a small but relatively uniform order. The thallus is more compact than in most of the Nemalionales and all members are uniaxial in construction. True auxiliary cells are absent but special nutritive cells are formed in association with the carpogonia. The order contains plants that provide the best sources of agar-agar in the world (see pp. 447, 451).

GELIDIACEAE: *Gelidium* (congealed). Fig. 130

The stiff, cartilaginous thallus, which is often pinnately branched, is based primarily upon the uniaxial type of construction. This is most clearly seen at the apex, but in the older parts of the thallus it is converted to a central portion of large cells, derived from four

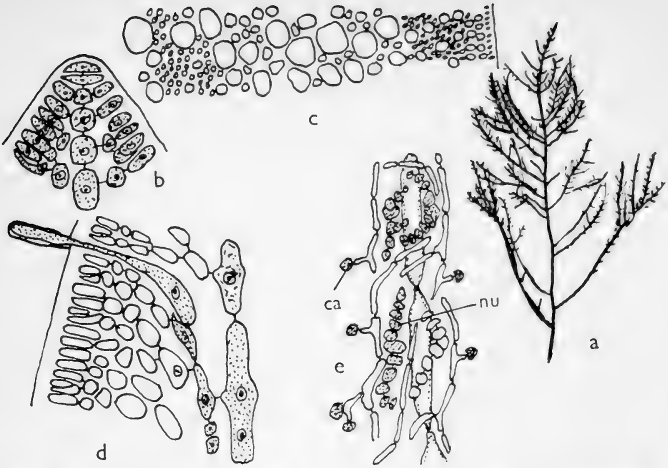

Fig. 130 *Gelidium corneum:* a, plant (× ⅓); b, apex; c, section of thallus; d, carpogonial branch; e, carpospores (ca) and nutritive cells (nu). (a, after Oltmanns; b–e, after Kylin.)

primary pericentral cells, with a peripheral zone of small cells with interspersed hyphae. There is no true auxiliary cell, but the presence of nutrient cells in the vicinity of the carpogonial branch results in the production of a complex structure composed of several carpogonia with small nutrient cells in short branches, and only one of these carpogonia needs to be fertilized. After fertilization a single gonimoblast filament initially grows out into the mass of nutritive cells, but it later branches so that a number of terminal carposporangia are finally formed. In the Japanese *G. amansii*, the principal source of agar (cf. p. 448), the tetraspores are shed when the water temperature rises to 20° C. and the carpospores when it rises to 24° C., shedding occurring each afternoon. The spores become fixed to the rock surface after being in contact for about ten minutes. The maximum temperature for germination is about 25°–26° C. The sporelings can grow in brackish water and this markedly affects the length of the primary rhizoids. Growth is slow at first but later becomes very rapid. More than one erect shoot may arise from each basal pad or the lateral buds may grow horizontally giving rise to stolons from which more buds may arise.

CRYPTONEMIALES

The members of this order are very diverse in habit. A number are unixiial and similar in structure to the Gelidiales, whilst others are multiaxial. There is a whole group in which there is extensive lime encrustation and considerable reduction of the thallus, e.g. *Lithothamnion*, from the basic fountain type of construction. Definite auxiliary cells are produced on accessory branches prior to fertilization and these serve not only for nutrition but also as starting points for the gonimoblast filaments.

The order divides naturally into two main subdivisions. In the first group the primary gonimoblasts fuse with nutritive cells in the carpogonial branch and secondary gonimoblasts then fuse with the auxiliary cells. In the second group the primary gonimoblasts fuse directly with auxiliary cells. In the first group the Dumontiaceae have the carpogonial branch and the auxiliary cell branch widely separated. In the remaining families of this group the carpogonial branches are borne in groups in nemathecia. The second group is also subdivided according as to whether the carpogonia and auxiliary cells are borne on separate branches (Grateloupiaceae) or on adjacent branches.

DUMONTIACEAE: *Dudresnaya* (after Dudresnay de St. Pol-de-Léon). Fig. 131

The cylindrical, much branched thallus arises from a prostrate disc. It is soft and gelatinous and consists when young of a simple, articulated, filamentous axis with whorls of dichotomously branched ramuli of limited growth. In older plants the axis becomes polysiphonous and densely beset with whorls of branches. The polysiphonous condition is produced by enlargement of the basal cells of the primary branch whorls and of cortical threads produced from them. The plants are dioecious, the males being somewhat smaller, paler and fewer in number than the females. The carpogonial branches of *D. coccinea* arise from the lower cells of short side branches and when fully developed are composed of seven to nine cells: they are branched once or twice and may have short sterile side branches arising from the lowest cell. In the middle of the mature carpogonial branch there are two to three larger cells which function in a purely nutritive capacity, whilst the auxiliary cells develop in similar positions on neighbouring branches that are homologous with the carpogonial branches. After fertilization the carpogonium sends down a protuberance containing the diploid nucleus and this cuts off two cells when it is near to the nutrient cells of the carpogonial branch. These all fuse together and sporo-

Fig. 131 *Dudresnaya.* A–D, stages in development of cystocarp, *D. purpurifera.* E, F, stages in development of cystocarp in *D. coccinea* after fertilization (× 486). G, *D. coccinea,* carpogonial branch (× 486). H, *D. coccinea,* antheridia (× 510). (A–D, after Oltmanns; E–G, H, after Kylin.)

genous threads, each carrying a diploid nucleus, then grow out towards the auxiliary cells on the other branches. When these filaments, or connecting threads as they may be called, fuse cytoplasmically with an auxiliary cell, the latter form a protuberance into which the diploid nucleus of the connecting thread passes. When the nucleus has divided once the protuberance containing one of the daughter nuclei is cut off by a wall. In the allied *Acrosymphytum* (*Dudresnaya*) *purpurifera* the gonimoblast initial is cut off from the connecting thread on the side opposite the auxiliary cell. In *D. coccinea* the gonimoblast filaments then grow out as a branched mass from this protuberance of the auxiliary cell. Each sporogenous thread sent out from the original fusion cell may unite with more than one auxiliary cell in the course of its wanderings through the thallus, so that one fertilization may result in the production of a number of carposporophyte generations.

HILDENBRANDTIACEAE: *Hildenbrandtia* (after F. E. Hildenbrandt). Fig. 132

This genus is characteristic of a small group of red algae all of which form thin crusts on stones or other algae, and it is frequently difficult to distinguish in the field from similar encrusting brown types such as *Ralfsia*. The frond is horizontally expanded into a thin encrusting layer composed of several layers of cells arranged in vertical rows, the plants forming indefinite patches that are attached by a strongly adhering lower surface. The genus is both marine and fresh water, *Hildenbrandtia rivularis* appearing frequently in rivers and streams. The principal mode of reproduction is by means of tetraspores which are produced in sporangia borne in rounded or oval conceptacles that are sunk in the thallus. The absence of sexual plants suggests specialization, though it is possible that a protonemal gametophyte exists which has not yet been discovered. Recently another genus, *Apophlaea* of New Zealand, has been added to this family. It is characterized by a prostrate stem from which short, erect, stout, branched projections arise that bear the tetrasporic conceptacles.

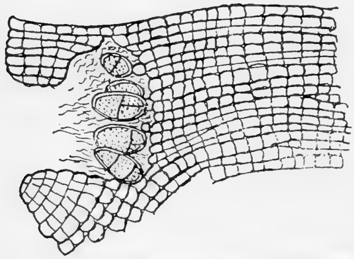

Fig. 132 *Hildenbrandtia prototypus.* Tetraspores in conceptacles (×320). (After Taylor.)

CORALLINACEAE: *Epilithon* (*epi*, above, *lithon*, stone). Fig. 133

This and the succeeding type belong to the Corallinaceae, a family of calcareous red algae which have played much part in the building of rocks and coral reefs and which have been known as fossils from the earliest geological strata. The present type has been selected because the common species, *E. membranaceum*, is less calcified than other members of the Corallinaceae[1] and thus forms very convenient material for sectioning and demonstration purposes without the trouble of decalcification. The thallus, which forms a crust on other algae or phanerogams, consists of a single cell layer composed of large cells, from each of which is cut off a small upper cell that goes to form the outer lime-encrusted layer.

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[1] e.g. *Lithothamnion*, *Lithophyllum*.

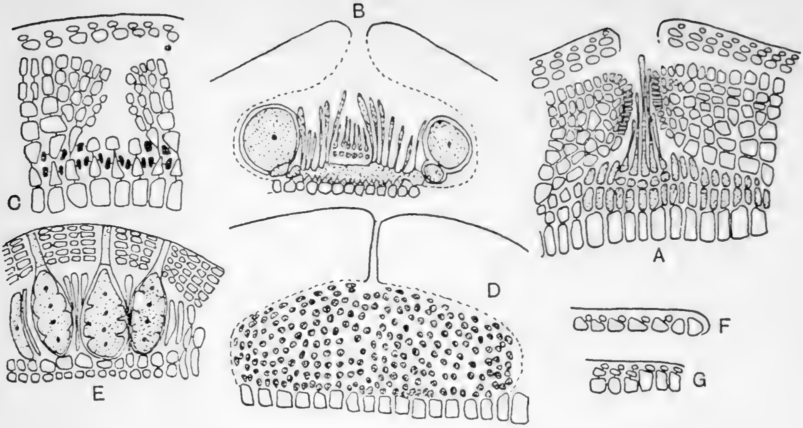

Fig. 133 *Epilithon membranaceum.* A, carpogonia (× 360). B, conceptacle with ripe carpospores (× 240). C, young antheridial conceptacle (× 510). D, mature antheridial conceptacle (× 426). E, tetraspores (× 228). F, G. thallus construction (× 360). (After Kylin.)

Further divisions take place internally from the large basal cells so that one finally obtains rows of erect filaments growing side by side. The various reproductive organs are borne in conceptacles on separate plants. The aggregation of the reproductive organs into conceptacles must be regarded as equivalent to nemathecia which subsequently become overgrown by surrounding tissue. In the male plants there are a number of two-celled filaments in the centre of each conceptacle. The basal cells of these threads cut off two elongate antheridial mother cells, which in their turn produce two antheridia. Antheridial mother cells are also produced from the lower parts of the conceptacle walls. Since the entire antheridium is liberated as such it must be regarded as morphologically equivalent to a spermatium. In the female plant the central threads of a conceptacle form three-celled carpogonial branches, the basal cell of the branch being an auxiliary cell. The outer threads of a conceptacle produce sterile two-celled filaments. Only the central carpogonia mature and usually only one of these is fertilized and produces carpospores. After fertilization the carpogonium and the cell below it fuse together and send out a filament to the lowest cell (auxiliary cell). Later all the auxiliary and nutritive sterile cells fuse to give one long fusion cell from which very short gonimoblast filaments grow out. In the tetrasporic plant there are simple filaments which give rise not only to the tetrasporangia, but also to branched sterile filaments that grow out and form the conceptacle roof by the process of division and elongation. Finally the membrane of the tetrasporangia penetrate this roof and form exit pores. The spores are arranged in a linear series.

CORALLINACEAE: *Corallina* (coral). Fig. 134

Both this and the preceding genus are examples of the 'fountain' type of construction (cf. p. 216). In *Epilithon* the original construction has been much modified because of its habit, but it can be observed extremely well in *Corallina*. The erect plants, which

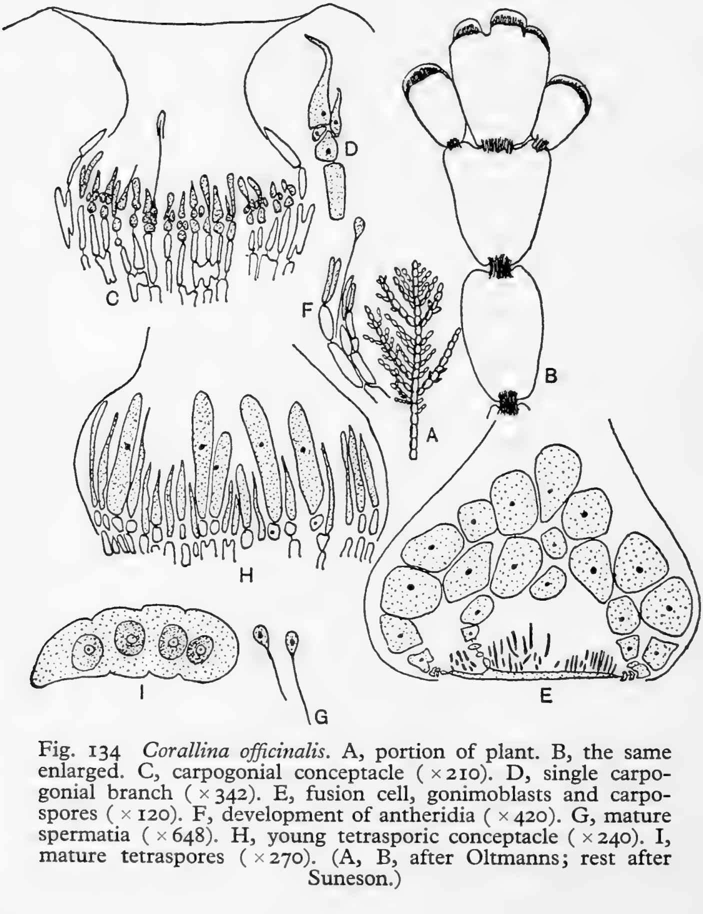

Fig. 134 *Corallina officinalis*. A, portion of plant. B, the same enlarged. C, carpogonial conceptacle (× 210). D, single carpogonial branch (× 342). E, fusion cell, gonimoblasts and carpospores (× 120). F, development of antheridia (× 420). G, mature spermatia (× 648). H, young tetrasporic conceptacle (× 240). I, mature tetraspores (× 270). (A, B, after Oltmanns; rest after Suneson.)

are jointed, cylindrical or compressed, arise from calcified encrusting basal discs or prostrate interlaced filaments. Branching, which is frequent, is pinnate, but in the closely allied genus *Jania* it is dichotomous. There is a central core of dichotomously branched filaments with oblique filaments growing out at the swollen internodes to form a cortical layer, the end cells being flattened, the whole being encrusted by lime except at the joints. The plants are monoecious or dioecious, the reproductive organs being borne in terminal or lateral conceptacles. The carpogonia, which are not calcified, arise from a kind of prismatic disc formed from the terminal cells, these cells also functioning later as the auxiliary cells. As a result of oblique divisions, one to three embryo carpogonial branches are formed on each mother cell, but only one of these finally develops into the mature two-celled carpogonial branch with its long trichogyne. After fertilization a long or rounded fusion cell is formed by the auxiliary cells, and this contains both fertilized and unfertilized carpogonial nuclei. The antheridia are much elongated, and after liberation the spermatia round off and remain attached to the antheridial wall by means of a long, thin pedicel in *C. officinalis* and by a short stalk in *Jania rubens*. The tetrasporangia comprise a stalk cell and sporangium in which the four spores are arranged in a linear row as in *Epilithon*.

CHOREOCOLACACEAE: *Harveyella* (after W. H. G. Harvey). Fig. 135

This and the closely allied genus *Holmsella* are monotypic genera each containing a holo-parasitic species, whilst *Choreocolax* is another parasitic genus very nearly related to them. *Harveyella mirabilis* is parasitic on species of *Rhodomela* whilst *Holmsella pachyderma* parasitises *Gracilaria confervoides*. They have little or no colour of their own as might be suspected from their parasitic nature, and they send out branched filaments or haustoria into the tissues of the host. The haustoria penetrate the middle lamellae of the host cells and form secondary pit connexions with them. The parasites appear as external cushions lying on the branches of the host, each cushion, which is surrounded by an outer gelatinous coat, consisting of a central area that is four to five cells thick. In *Harveyella* the female cushions bear numerous procarps with four-celled carpogonial branches each with two sterile branches. In *Holmsella* the carpogonial branch is two-celled. The antheridial, carpogonial and tetrasporic plants are all separate, and the species

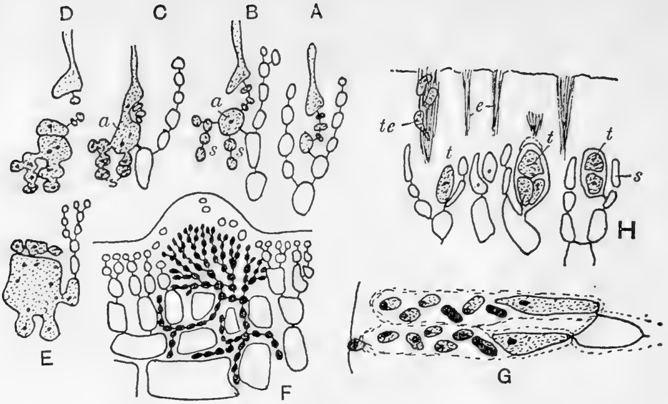

Fig. 135 *Harveyella* and *Holmsella*. A–E, stages in development of gonimoblasts after fertilization in *Harveyella mirabilis*. *a* = auxiliary cell, *s* = sterile filaments. F, filaments of parasite, *Holmsella pachyderma*, in host. G, antheridia of *Harveyella mirabilis*. H, tetraspores in *Holmsella pachyderma*. *e* = tracks left after tetraspores have escaped. *s* = sterile cells, *t* = tetraspores in various stages, *te* = escaping tetraspores. (After Sturch.)

are said to pass through the full floridean life cycle twice every year. It is clear that their much reduced morphological features are to be associated with the parasitic habit, and have arisen as a result of the adoption of parasitism. The position of the genus has been the subject of controversy. In the past it has been placed in the Gigartinales, but is now more generally placed in the Cryptonemiales.

GIGARTINALES

Thallus construction in this order can be either of the central filament or fountain type, but it is often so modified in the adult plant that it is difficult to interpret. The support cell or an ordinary intercalary cell is set aside before fertilization to act as the auxiliary cell.

GIGARTINACEAE: *Gigartina* (*Gigarton*, grape stone). Fig. 136

This is a widespread genus, the species of which are often difficult to determine taxonomically. The plants, several of which arise from a prostrate disc, vary greatly in habit from large, flat, little-branched, foliose expansions (*G. atropurpurea*) to terete fronds that are irregularly pinnate or dichotomously branched. The female

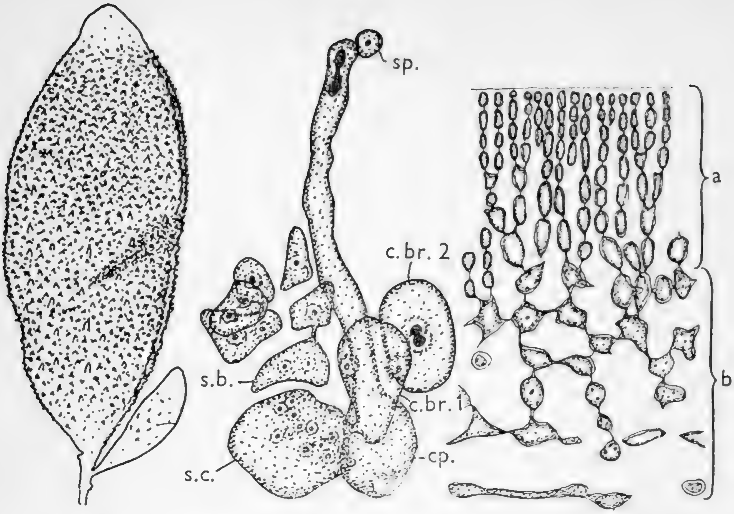

Fig. 136 *Gigartina*. Left, plant of *G. californica;* (original, × ¼). Centre, carpogonial branch, *G. stellata* (× 1500); cp. = carpogonium; s.b. = vegetative lateral; s.c. = support cell. Right, t.s. thallus, *G. stellata* (× 160); a = outer cells; b = inner cells (both after Newton).

plants have papillose projections (the cystocarps) from the surface of the thallus. The internal construction consists of a mass of large central cells with smaller cells towards the periphery. The limiting layer consists of very small cells, the whole being based upon the multiaxial type of construction. In some species, e.g. *G. stellata*, the cells of inner cortex and medulla give rise to down-growing septate hyphae. The carpogonial branch is three-celled and is derived from a large support cell of the inner cortex, which also functions as the auxiliary cell. In addition to the carpogonial branch the support cell either produces a vegetative lateral or a second carpogonial branch.

PHYLLOPHORACEAE: *Phyllophora* (*phyllo*, leaf; *phora*, bear). Figs. 137, 138

The stipitate fronds expand upwards into a rigid or membranous flat lamina which is either simple or divided, whilst proliferations may also arise from the margin or basal disc. Morphologically the thallus is multiaxial and composed of oblong polygonal cells in the central medullary region, whilst the outer cortical layers consist of minute, vertically seriate, assimilatory cells. In some species

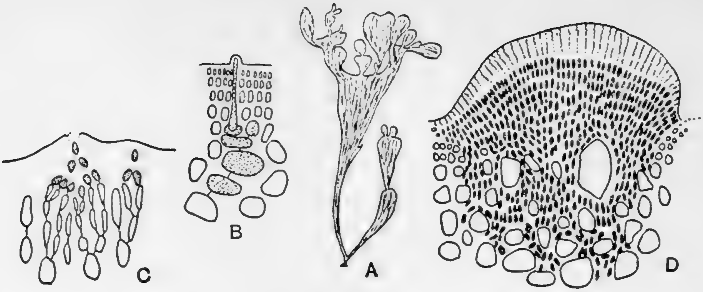

Fig. 137 *Phyllophora brodiaei.* A, plant (× $\frac{1}{3}$). B, carpogonial branch (× 250). C, transverse section of antheridial thallus (× 450). D, nemathecia with tetraspores (× 125). (A, original; B–D, after Kylin.)

secondary tissue has been observed near the axils of branches or at the base of the frond. This is not surprising since the thalli often last for many years and the successive increments are recognizable macroscopically. The plants are dioecious and the sex organs are borne in nemathecial cavities in small fertile leaflets that are attached to the main thallus. The carpogonial leaflets, which are sessile or shortly stalked, arise laterally from the stipitate part of the main blade. Only one cystocarp is produced from each carpogonial nemathecium. In *P. membranifolia* the carpogonial branch is three-celled and after fertilization gonimoblast filaments are formed which ramify in the tissues, finally producing pedicellate or sessile cystocarps. In *P. brodiaei* spermatia appear to be functionless and the carpogonium fuses directly with the auxiliary cell and the carposporic generation is omitted. This must be regarded as a reduction phenomenon in so far as the usual rhodophycean life cycle is concerned. The tetraspores are borne in moniliform chains packed into wart-like excrescences or *nemathecia* which are borne on the female sexual plant. In *P. brodiaei* the absence of carpospores led earlier investigators to regard the nemathecia as belonging to a parasitic plant, which in this case was given the name of *Actinococcus subcutaneus*, but it has since been shown that we are really dealing with a parasitic diploid generation.

PHYLLOPHORACEAE: *Ahnfeldtia* (after N. O. Ahnfeldt). Figs. 138, 139

The wiry and horny multiaxial thallus arises from a prostrate disc and is a perennial with secondary thickening. This results from

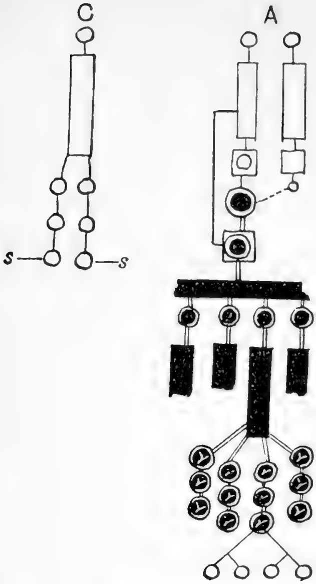

Fig. 138 Life cycles. A, *Phyllophora membranifolia*. B, *P. brodiaei*. C, *Ahnfeldtia plicata*. *s* = monospores. (After Svedelius.)

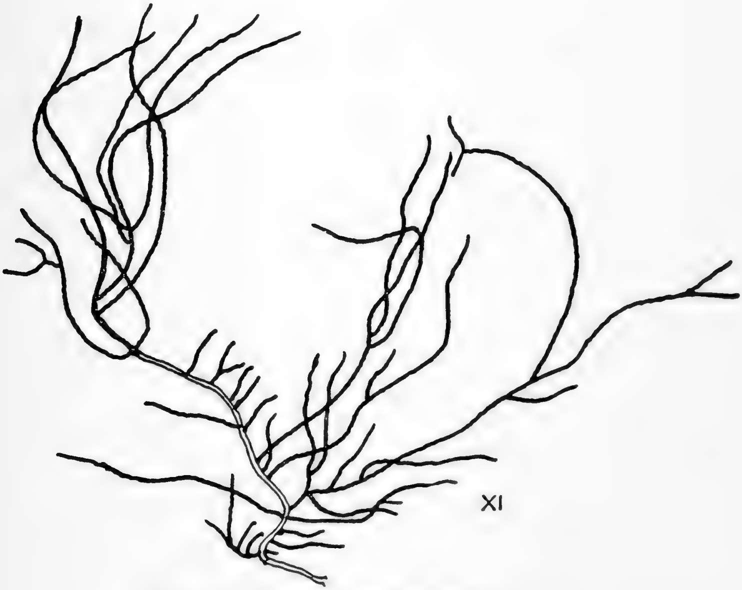

Fig. 139 Plant of *Ahnfeldtia plicata* (× 1).

the activity of peripheral cells in the cortex which give successive strata that can be recognized in section. Although reduction of the life cycle has gone still further, nevertheless nemathecia still appear and these also were formerly regarded as a parasite to which the name *Sterrocolax decipiens* was given. In this genus, however, there is neither fertilization nor meiosis and only degenerate procarps are formed; instead the nemathecia contain monospores that develop as follows: the warts, which arise as small cushions from superficial cells of the thallus, contain some cells that become flask-shaped together with other cells possessing denser contents that arise in groups at the upper ends of the filaments. These latter, which probably represent degenerate carpogonia, form the generative cells and they give rise to secondary nemathecial filaments, the apical cells functioning as monosporangia, the spores from which give rise to prostrate discs. In *Ahnfeldtia*, therefore, the sporophytic generation has been completely suppressed, and this modified life cycle should be compared with that of *Lomentaria rosea* (cf. below) in European waters where the gametophytic generation has been secondarily suppressed. The monospores have been interpreted as morphologically equivalent to either the carpospores or the tetraspores, the latter interpretation being the one adopted in this volume.

RHODYMENIALES

The thallus of all species is based upon the multi-axial type of construction. In some genera the central portion becomes hollow and divided by septa. There is considerable variation in form from flattened, membranous thalli to softer, terete and more gelatinous structures. The order has been monographed by Kylin. Small auxiliary cells are cut off before fertilization from a branch derived from the support cell. They develop considerably only after fertilization has taken place: otherwise they remain in a vegetative condition. The order comprises two families, the Rhodymeniaceae and Lomentariaceae. In the Rhodymeniaceae the carpogonial branch is three-celled and after fertilization the gonimoblasts become profusely branched, the branches being known as gonimolobes, and nearly every cell gives rise to a carpospore. In the Lomentariaceae the carpogonial branch is three or four-celled and each gonomoblast gives rise to a single terminal carposporangium.

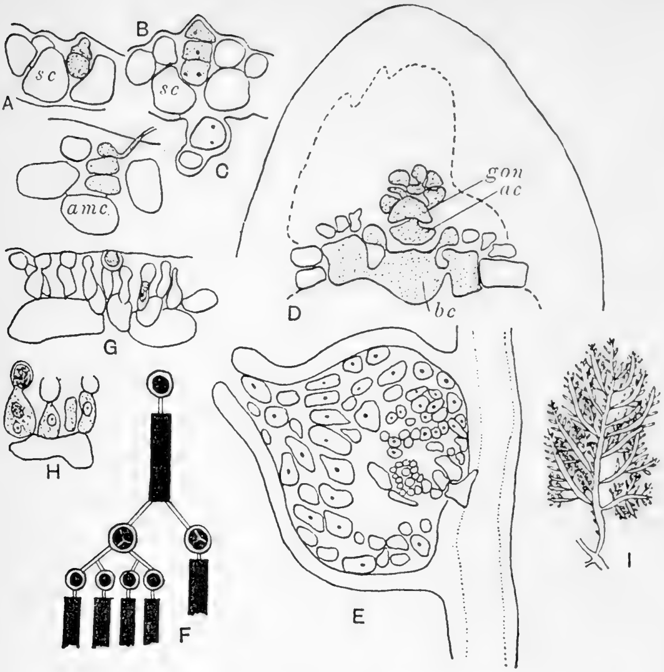

Fig. 140 *Lomentaria clavellosa.* A–C, development of carpogonial branch ($\times 660$). *amc* = accessory mother cell, *sc* = support cell. D, young cystocarp ($\times 312$). *ac* = accessory cell, *bc* = support cells, *gon* = gonimoblast. E, mature cystocarp ($\times 90$). F, *L. rosea*, life cycle. G, H, *L. clavellosa*, antheridia ($\times 660$). I, *L. clavellosa*, plant ($\times \frac{3}{5}$). (A–C, F–H, after Svedelius; D, E, after Kylin; I, original.)

LOMENTARIACEAE: *Lomentaria* (pod with constricted joints). Fig. 140

The filamentous fronds are hollow when mature, with or without constrictions at the nodes but without diaphragms. Branching is irregular or unilateral. The hollow central region originates from a branching structure which later on separates in order to form the outer cell layers, although a few longitudinal filaments of the original multiaxial structure are left in the centre. These may be branched and joined to each other by secondary pit connexions. The plant, which is enclosed in a thick gelatinous cuticle, may bear unicellular hairs that have arisen from the epidermal layer. The adult thallus has developed from a group of eight to twelve apical cells, each of which produces a longitudinal filament, whilst the corticating threads develop from lateral cells which are cut off from each segment just behind the apex. The male plants, which are rare in nature, bear the antheridial sori on the upper regions where they form whitish patches. A system of branching threads, which appears as a preliminary to sorus formation, arises from a single central cell, and from each of these branching threads two to three antheridial mother cells grow out and increase in length. Depending on the species, one, two or three primary antheridia arise from each mother cell and they may be followed by a crop of secondary antheridia. The procarp consists of a support cell with a three-celled carpogonial branch, both these and the antheridial mother cells being uninucleate, although the mature vegetative cells are multinucleate. There are one or two auxiliary cells, and after fertilization only one of these receives a process from the carpogonium which carries with it the diploid nucleus. This auxiliary cell then proceeds to cut off a segment on the outer side, and from this a group of cells develops that ultimately gives rise to the gonimoblasts. The ripe cystocarps are sessile on the thallus and possess a basal placenta. The tetrasporangia are borne on the diploid plants in small cavities produced by the infolding of the cortex. In European waters *L. rosea*, which has a diploid chromosome number of twenty, is only known to produce tetraspores which apparently arise without undergoing meiosis. Individual spores germinate to give a new plant or else a whole tetrad may germinate to give a new plant. In such plants of *L. rosea*, therefore, the gametophytic generation is wholly suppressed and we have a diplont which behaves as a haplobiont in respect of its life cycle. In Pacific waters, on the other hand, the records suggest that the species behaves normally, whilst the other common species, *L. clavellosa*, also behaves in the normal fashion.

* CERAMIALES

The range of habit in this order is considerable even though the basic construction is uniaxial throughout. There are simple, branched filaments (e.g. *Callithamnion*, *Antithamnion*); leafy expansions (e.g. *Delesseria*, *Laingia*); nets (e.g. *Claudea*, *Martensia*: in *Claudea* the net form originates by branching, in *Martensia* by separation of cell rows); cartilaginous forms (*Laurencia*); polysiphonous and corticated polysiphonous forms (*Polysiphonia*, *Bostrychia, Plumaria*). The order is the most highly evolved in the Rhodophyceae and is the only one in which the auxiliary cell is cut off after fertilization and as a direct consequence of the process.

* RHODOMELACEAE: *Polysiphonia* (*poly*, many; *siphonia*, siphons). Fig. 141

The thallus in this genus generally arises from decumbent basal filaments that are attached to the substrate by means of small

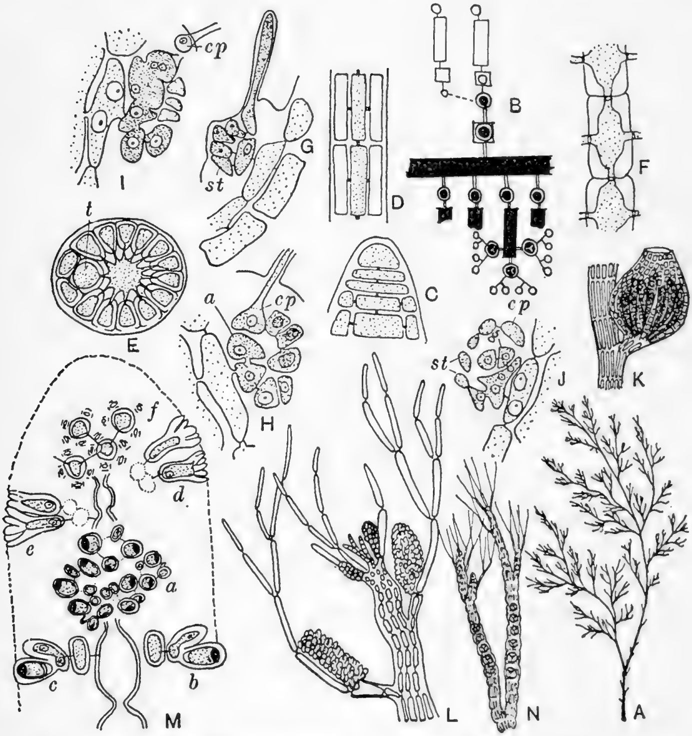

Fig. 141 *Polysiphonia violacea.* A, plant of *P. nigrescens* (× ⅓). B, life cycle. C, apex and cells cut off from central cells. D, thallus construction in longitudinal section. E, transverse section of thallus, *P. fastigiata.* *t* = young tetraspore. F, protoplasmic connections of axial thread. G–J, stages in development of carpospores. *cp* = carpogonium, *a* = auxiliary cell, *g* = gonimoblast, *st* = sterile cells (× 400), (J × 260). K, cystocarp of *P. nigrescens* with ripe carpospores (× 33). L, antheridial branch (× 35). M, *a–f*, stages in development of antheridia. N, *P. nigrescens*, tetraspores (× 33). (A, K, N, after Newton; B, after Svedelius; C, F, schematic; D, E, after Oltmanns; G–J, after Kylin; L, after Grubb; M, after Tilden.)

flattened discs. These basal filaments do not represent a primary heterotrichous condition but a secondary state. Many species are epiphytic on other algae whilst *P. fastigiata*, which is always found on the fronds of the fucoid *Ascophyllum nodosum*, is probably a hemi-parasite. The thallus is laterally or dichotomously branched and bears numerous branches which are shed annually in the perennial forms before winter and are redeveloped in the spring. The main axes and branches are corticate or ecorticate, and possess a polysiphonous appearance due to the single axial cell series being surrounded by four to twenty-four pericentral cells or siphons. The primary pericentral siphons represent potential branches and are united to the parent axial cell by a pit connexion. The corticating cells, when present, are always shorter and smaller and are often only found in the basal portions of the stem. The ultimate branches are not polysiphonous and frequently terminate in delicate multicellular hairs.

The colourless antheridia, which are formed in clusters, are borne on a short stalk that morphologically is a rudimentary hair. In *Polysiphonia violacea* the two basal cells of the hair are sterile, the upper one giving rise to a fertile polysiphonous branch and a sterile hair. One or more mother cells are formed from all the pericentral cells on the fertile branch, and each mother cell produces four antheridia in two opposite and decussate pairs, the first and third appearing before the second and fourth. There is no secondary crop in this species. The carpogonial branches are also formed from hair rudiments, the support cell cutting off a small section from which two lateral sterile cells arise. The second 'sterile' cell is morphologically equivalent to an abortive carpogonium. Later on a fertile pericentral cell is cut off, and this gives rise to the four-celled carpogonial branch, the carpogonium being of interest because there is a persistent nucleus in the trichogyne.

After fertilization has taken place the auxiliary cell is cut off from the apex of the support cell (Fig. 141, H) and in addition two branch systems composed of nutrient cells develop from the original sterile cells. When the zygote nucleus has divided, commonly only one of the daughter nuclei passes into the auxiliary cell, which in the meantime has become fused to the carpogonium and a new wall is then laid down, cutting off the carpogonium. The auxiliary cell next fuses with the pericentral cell and after the diploid nucleus has been transferred it unites with the other support and axial cells to give a large fusion cell. The diploid nucleus divides many times and the daughter nuclei each pass into lobes that are budded off from the fusion cell. Each lobe gives rise to a short gonimoblast filament, the terminal cell of which produces a pear-shaped carpospore, whilst the subterminal cell gives rise to a new two-celled carpospore branch. In this way numerous carpospores are produced.

The wall of the cystocarp is two-layered, the inner wall being formed directly by cells derived from pericentral cells. The cells of the inner wall divide tangentially to give the cells that form the outer wall, so that ultimately both layers have come from the pericentral cells. The tetrasporangia, which develop from pericentral cells, develop in the apical portion of branches, and as they are protected by being embedded in the thallus, the branch is usually much swollen and distorted. The genus is widespread in cold and warm waters and the species particularly frequent rock pools.

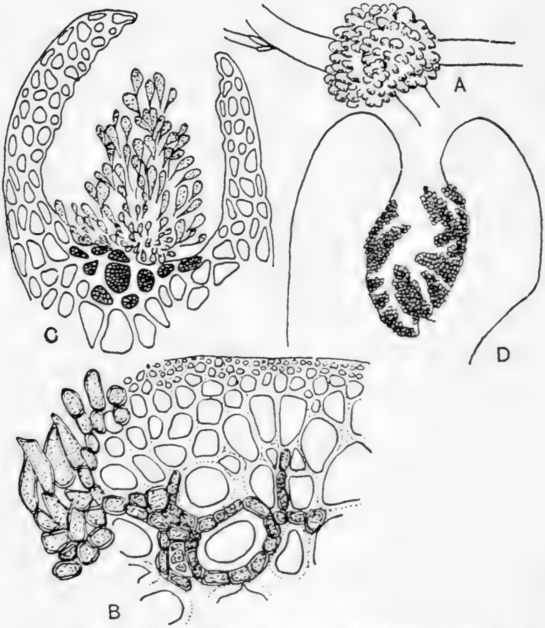

Fig. 142 *Janczewskia.* A, *J. moriformis* on *Chondria* sp. (× 6). B, filaments of *J. lappacea* in host, *Chondria nidifica* (× 180). C, longitudinal section of cystocarp of *J. moriformis* (× 180). D, antheridial conceptacle of *J. lappacea* (× 180). (After Setchell.)

RHODOMELACEAE: *Janczewskia* (after E. de Janczewski). Fig. 142

This is a remarkable hemi- or holo-parasitic genus which is always to be found on other members (*Laurencia*, *Chondria* and *Cladhymenia*) of the same family. One of the most interesting features of this parasitism is that the genus is very closely related to *Laurencia* and yet is parasitic upon various species of that genus. All the species have organs of contact or penetration, the latter being fungal-like filaments which establish pit connexions with the cells of the host. Each individual plant is a whitish, coalescent tubercular mass composed of fused branches that grow from an apical cell buried in a pit as in *Laurencia*. The sexual plants are dioecious and the diploid asexual plant also occurs.

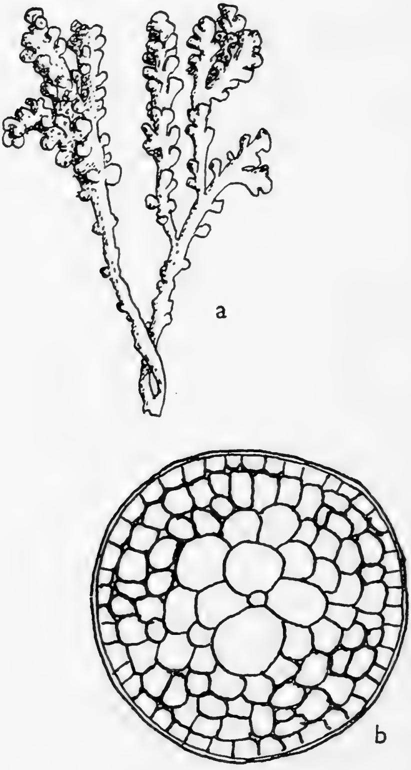

Fig. 143 a, *Laurencia papillosa*, part of plant (× 1¼); b, t.s. axis of L. *implicata*. The central axis and four primary siphons are clearly visible (× 60). (After Borgesen.)

RHODOMELACEAE: *Laurencia* (after H. de Lalaurencie). Fig. 143

These plants, which are cartilaginous, initially have the same structure as *Polysiphonia*, but this can only be observed at the apex. The apical cell produces three segments all of which form richly branched trichoblasts that are arranged spirally. Beneath each trichoblast two pericentral cells are cut off and by subsequent divisions of these the compact cortex is produced, so that not far behind the apex the basic structure has become lost. The apical growing cell is situated in an apical pit from which a tuft of hairs projects. The reproductive organs are much as in *Polysiphonia* except that the wall of the cystocarp consists of more than two layers. The fertile tips of male plants also swell up because when it becomes fertile the apical cell ceases to divide whilst surrounding cells continue to do so. The genus is widespread in cold and warm waters, the species often occurring in rock pools or near low water mark.

DELESSERIACEAE: *Delesseria* (after Baron Delessert). Fig. 144

The large, thin, leafy fronds, which are bright red in colour, possess a very conspicuous mid-rib with both macro- and microscopic veins. The complex nature of the laciniate or branched thallus can be seen from the figure. The foliar condition is clearly produced by the juxtaposition in one plane of numerous branches that arise from the axial filament. The apical cell divides to give a central cell and two pericentrals. The latter divide and give rise to the pinnate laterals of the first order on which secondary laterals are borne. The mid-rib is formed from the central cell and the adjacent cells of the primary laterals. The latter divide transversely so that in the mature frond they are half the length of the central cells. Growth is intercalary in the various orders of branches. The cells of the thallus also become united by means of secondary protoplasmic threads and they may also develop thin rhizoids. The reproductive organs are borne on separate adventitious leaflets. The procarps arise from the axial threads of the leaflet, each cell giving rise to two procarps. The procarp consists of a support cell which then cuts off a sterile cell and a three-celled carpogonial branch. The second cell of the fertile branch is much enlarged. As many as fifty procarps may be produced on a fertile leaflet. These ripen in acropetal succession but only one is fertilized. At fertilization a second sterile cell is cut off and the other adjacent procarps and sterile cells give rise to the wall of the cystocarp.

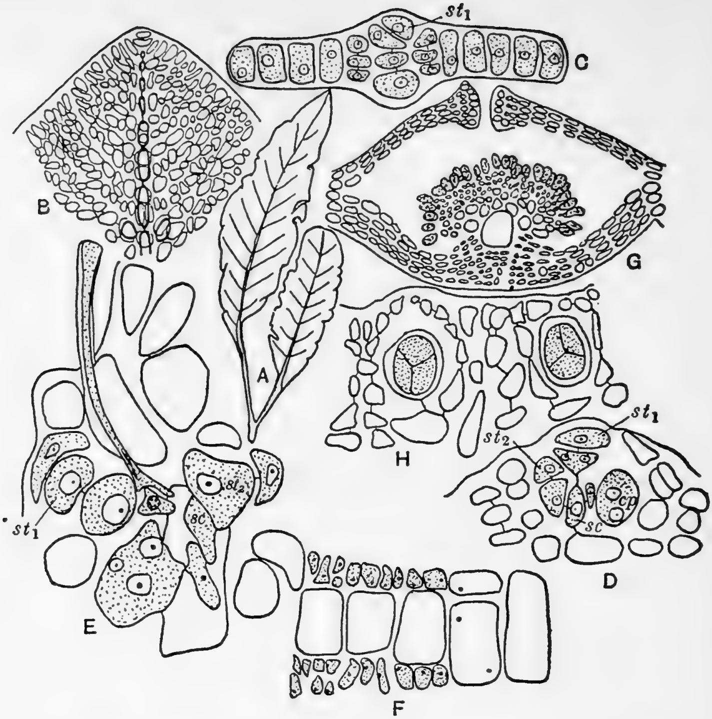

Fig. 144 *Delesseria sanguinea*. A, plant. B, apex of thallus to show cell arrangement (×258). C, first stage in formation of carpogonial branch. st_1 = first group of sterile cells (×408). D, later stage of same. cp = carpogonial branch, sc = support cell, st_1 = first, and st_2 = second group of sterile cells (×408). E, mature carpogonial branch. sc = support cell. st_1 = first sterile branch, st_2 = second sterile branch (×720). F, formation of antheridia in related genus, *Nitophyllum*. G, transverse section of mature cystocarp in the related genus *Nitophyllum*. H, tetraspores (×360). (A, F, G, after Tilden; B–D, after Kylin; E, H, after Svedelius.)

CERAMIACEAE: *Callithamnion* (*calli*, beauty; *thamnion*, small bush). Fig. 145

This is a genus of very beautiful and delicate plants that possess filamentous, radially branched fronds which are either monosiphonous or else corticated at the base, the cortication being formed by rhizoidal filaments. The plants are commonly attached by rhizoids and in many species the branchlets terminate in long slender hairs. The cells of the vegetative thallus are usually multinucleate, and in *C. byssoideum* there are protoplasmic pseudopodia projecting internally from the ends of the cells, and although these

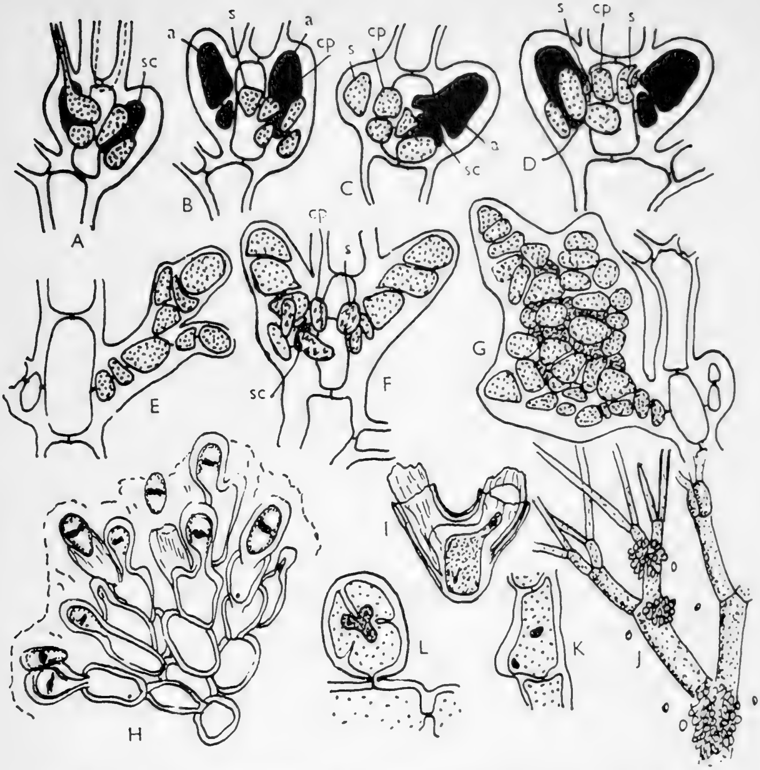

Fig. 145 *Callithamnion.* A–G, stages in development of Cystocarp from mature Carpogonium. a = auxiliary cell. cp = carpogonium. s = sporogenous cell cut off from fertilized carpogonium. sc = support cell. H, antheridia with spermatia. I, the same enlarged. J, antheridial sori. K, young tetrasporangium. L, mature tetrasporangium (A–F, × 520; G, × 300). (A–G, after Kylin; H–J, after Grubb; K, L, schematic after Mathias.)

strands are apparently capable of some movement their function is obscure.

The antheridia, which form hemispherical or ellipsoidal tufts on the branches, arise as lateral appendages, the first cell to be cut off being the stalk cell. This stalk cell gives rise to a group of secondary cells which later on divide to form branches composed of two to three cells, each terminating in an antheridial mother cell. In this genus there may be two or even three crops of antheridia arising successively in the same place, each mother cell producing about three antheridia in every crop. The cystocarps, which are usually present in pairs and enclosed in a gelatinous envelope, arise as follows. Two cells are cut off from a cell in the middle of a branch and these function as the auxiliary *mother* cells. From one of them the four-celled carpogonial branch is produced, whilst after fertilization both auxiliary mother cells divide and cut off a small basal cell. The fertilized carpogonium also divides into two large cells, each of which cuts off a small sporogenous cell that fuses with the adjacent auxiliary cell. As a result of this fusion each auxiliary cell can receive a diploid nucleus which soon after its entry divides into two; one daughter nucleus passes to the apex of the auxiliary cell, whilst the other, together with the nucleus of the auxiliary cell, is cut off by a wall. It is from the large upper cell that the gonimoblast filaments arise and so the mature cystocarp is produced.

The sessile tetrasporangia arise in acropetal succession as lateral outgrowths of the vegetative cells of young branches. In *C. brachiatum* mature tetrasporangia and antheridia have been found on the same plant, whilst other plants have been reported that bear both tetrasporangia and cystocarps.

Spermothamnion turneri is another plant in which sex organs have been reported on normal tetrasporic plants, but as the procarp branch in this case develops normally without meiosis the carpogonium is diploid. Fusion of male and female nuclei in the carpogonium has been observed so that the carpospores are probably triploid but unfortunately their fate is not known. Haploid plants are also known that bear tetrasporangia but in such cases no divisions occur in the sporangia. In *S. snyderae* the tetrasporangia are replaced by polysporangia which must be regarded as homologous structures. The mother cells of each polysporangium contain two to nine nuclei and they give rise to twelve, sixteen, twenty, twenty-four or twenty-eight spores.

CERAMIACEAE: *Plumaria* (*pluma*, soft feather). Fig. 146

The filamentous thallus is much branched, the main axis, which is monosiphonous throughout, being ecorticate near the apex but corticate below. Branching is bilateral and typically pinnate. Cortication is brought about by the activity of the basal cells of the branches and of cells cut off from the main axis. In the old axis three zones can be recognized:

(*a*) outermost small-celled photosynthetic zone;
(*b*) intermediate storage layer of large cells;
(*c*) a conducting system of long narrow elements.

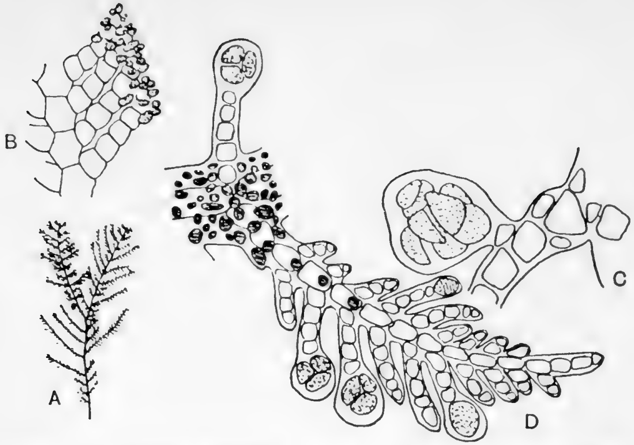

Fig. 146 *Plumaria elegans*. A, plant ($\times\frac{3}{5}$). B, antheridial ramuli (× 180). C, paraspores (× 213). D, tetrasporic ramuli (× 126). (A, original; B, after Drew; C, D, after Suneson.)

The antheridia are borne on special branches, whilst the four-celled carpogonial branch develops from the subterminal cell of an ordinary branch. In northern waters *P. elegans* never bears sex organs and only plants with paraspores are to be found, whilst in southern waters the sexual ($n=31$) and tetrasporic plants ($n=62$) are predominant. Recent investigation has shown that in this species we are concerned with a triploid race ($n=93$) in the northern waters which reproduces by means of paraspores. There is apparently no relation between the triploid plants and the other two races, and, furthermore, the triploid has the wider distribution because it is able to penetrate into the colder waters of the north. Tetraspores are to be found on the triploid plants but their chromosomal complement and fate are not known. Although both tetra- and parasporangia arise from a single cell it is doubtful if the two structures are homologous. The reasons for this are first, the difference in chromosomal complement, secondly, the absence of any apparent relationship with the haploid and diploid plants, and thirdly, differences in the mode of development of the para- and tetrasporangia. This is the first cytological record of triploid plants in the algae. *Plumaria elegans* is therefore tetraphasic morphologically and triphasic cytologically. It is possible that other algae may exhibit the same phenomenon.

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Chapter IX

CHRYSOPHYCOPHYTA

XANTHOPHYCEAE, BACILLARIOPHYCEAE, CHRYSOPHYCEAE

PYRROPHYCOPHYTA

CRYPTOPHYCEAE, DINOPHYCEAE

* Xanthophyceae

As a group the Xanthophyceae exhibit considerably less differentiation than the Chlorophyceae. Two of the most characteristic features are the replacement by oil of starch as a food reserve and a greater quantity of B-carotene in the plastids, although the actual amount of the latter is partially dependent upon the external conditions. The pigment turns blue-green when the cells are heated in concentrated hydrochloric acid and this forms a convenient test for distinguishing them from the Chlorophyceae. The walls are frequently in two equal or unequal portions which overlap, their composition being principally of a pectic substance although some cellulose may occasionally be present. The motile bodies contain more than one chloroplast and are further characterized by two unequal flagella, the longer one often possessing delicate cilia. The Xanthophyceae exhibit very little regularity in the formation of reproductive bodies. Sexual reproduction is rare and in most of the known examples is isogamous. The outstanding exception is *Vaucheria*, which in the past has been placed in the Siphonales. Here there is a well-developed oogamy. The principal mode of reproduction within the class is by means of zoospores and aplanospores. Simple division occurs in *Chloramoeba* and cyst formation is known in *Halosphaera* and *Botrydium*. The majority of the species are confined to fresh water. It would seem that they have a motile unicell ancestry, the chief interest of the group being the manner in which evolution has taken place along lines parallel to those found in the Chlorophyceae. As a result there exists a set of analogues which, so far as general morphology is concerned, bear so much resemblance to chlorophycean groups that these forms are classed as Heterochloridales, Heterococcales, Heterosiphonales and Heterotrichales.

HETEROCHLORIDACEAE: *Chloramoeba* (*chlor*, green; *amoeba*, changing). Fig. 147

This is a naked unicell which is analogous to certain members of the Volvocales, e.g. *Dunaliella*. The cells multiply by longitudinal division, but under adverse conditions ellipsoidal cysts with large oil globules are developed and these form a resting stage.

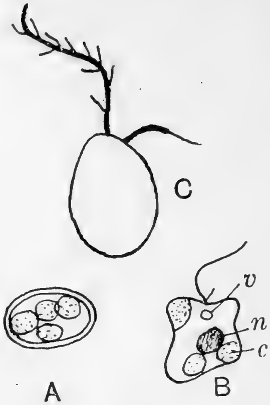

Fig. 147 A, *Chloramoeba heteromorpha*, cyst. B, the same, motile phase. *c* = chloroplast, *n* = nucleus, *v* = vacuole. C, flagellum structure in *Monocilia*. (After Fritsch.)

HETEROCAPSACEAE: *Botryococcus* (*botryo*, cluster; *coccus*, berry). Fig. 148

This fresh-water genus represents one of the palmelloid analogues of the Chlorophyceae, the principal species, *B. braunii*, forming an oily scum on ponds and lakes in spring and autumn, whilst in late summer the cells are often coloured red by haematochrome. The colonies vary greatly in shape, the cells being radially arranged into spherical aggregates that are connected in a reticular fashion by tough, hyaline or orange-coloured strands belonging to the lamellated mucous envelope. The thin cell wall is said to consist of two unequal pieces, but despite this xanthophycean feature the alga is anomalous in that starch is said to be formed. The individual cells are surrounded by a thin membrane that becomes evident when they are squeezed out of their envelopes as sometimes happens. Each cell is enclosed in a funnel-shaped mucilage cup composed of several layers and prolonged at the base into a thick stalk. In old colonies the mucilage envelope swells up so that the cup structure is obscured, but although the sheath is so predominant nevertheless its origin is not clearly known. The cells multiply by longitudinal division, whilst asexual reproduction by means of zoospores has also been recorded though it requires con-

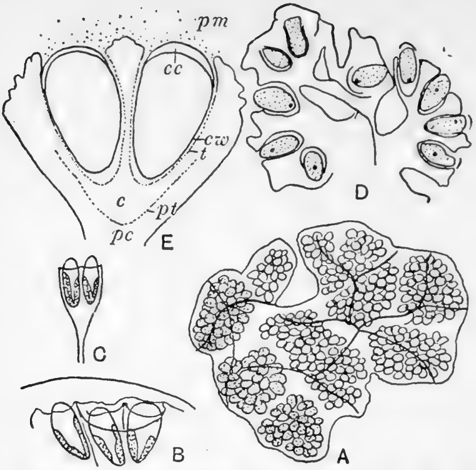

Fig. 148 *Botryococcus braunii.* A, colony (× 300). B, portion of colony showing cells in their mucilage envelope. C, two cells enclosed in the parent cup. D, portion of colony enlarged (× 780). E, two cells arranged diagrammatically to show structure. *c* = cup, *cc* = cell cap, *cw* = cell wall, *pc* = parent cell, *pm* = pectic mucilage, *pt* = parent thimble, *t* = thimble. (A, after Smith; B, C, after Fritsch; D, E, after Blackburn.)

firmation. Normally reproduction is secured by means of aplanospores, of which two to four are produced in each cell. The colonies decay very slowly, and one of the principal interests of the genus is the recent discovery that boghead coal is composed very largely of this organism, whilst the fossil genera *Pila* and *Reinschia* hardly differ from the living *Botryococcus Braunii.*

HALOSPHAERACEAE: *Halosphaera* (*halo*, salt; *sphaera*, sphere). Fig. 149.

The large, free-floating spherical cells possess one nucleus which is suspended either in the central vacuole or else in the parietal cytoplasm where it is associated with numerous discoid chloroplasts. A new membrane is formed internally and then the old one ruptures, but as the latter may still persist outside one can often see what appears to be a multi-layered sheath. Reproduction can take place by means of zoosporic swarmers but these may be replaced by aplanospores, whilst resting cysts are also recorded. Although most abundant in the warmer oceans, especially during the winter months, its life history is as yet only imperfectly known.

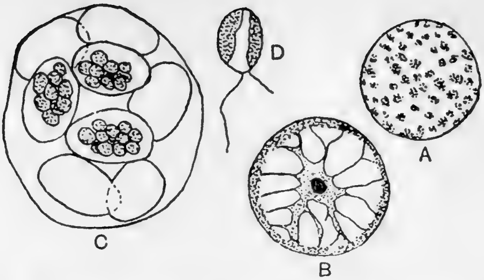

Fig. 149 *Halosphaera viridis*. A, mature cell. B, young cell in optical section. C, mature cell with aplanospores. D, swarmer. (A–C, after Fritsch; D, after Dangeard.)

CHLOROTHECIACEAE: *Characiopsis* (like *Characium*). Fig. 150

The very name of this genus indicates that it is an analogue to the genus of similar name in the Chlorophyceae. The plants, which are epiphytic, solitary or gregarious, vary much in shape, even in pure culture, and they develop from a short stalk with a basal mucilaginous cushion. The wall, composed of cellulose and pectins, is in two unequal portions, the smaller upper part forming a lid which is detached at swarmer formation whilst in one species the lower part bears internal processes. Although the young cells are uninucleate and contain one or more chloroplasts, the adult cells are multinucleate containing eight to sixty-four nuclei. Reproduction is either by means of zoospores (eight to sixty-four per cell) or else by means of thick-walled aplanospores, which in one species are said to give rise to motile gametes, although this is a feature that requires further investigation.

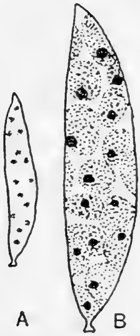

Fig. 150 *Characiopsis saccata*. A, plant. B, probable swarmer formation. (After Fritsch.)

* TRIBONEMACEAE: *Tribonema* (*tribo*, thin; *nema*, thread). Fig. 151

This is a filamentous analogue to a form such as *Microspora* (cf. p. 51) with which it is frequently confused. *T. bombycina* sometimes appears in sheets covering ponds and pools and if these dry up they form an algal 'paper'. The unbranched threads are composed of cells possessing walls of two equal overlapping halves, with the result that the filaments are open-ended and tend to dissociate into H pieces. At cell division a new H piece arises in the centre

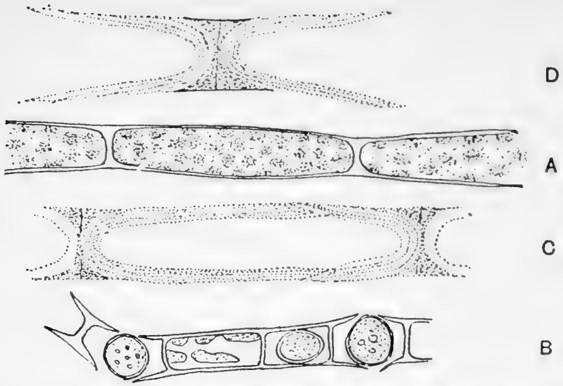

Fig. 151 *Tribonema*. A, *T. bombycina* (× 450). B, *T. minus*, hypnospores. C, D. construction of H piece in *T. bombycina* as shown after treatment with KOH (× 675). (A, C, D, after Smith; B, after Fritsch.)

and the two halves of the parent cell separate, somewhat as in the Desmidiaceae. Each cell contains one nucleus, although *Tribonema bombycina* may have two together with two or more parietal chloroplasts. Asexual reproduction is by means of zoospores (two to four per cell) which are liberated by separation of the two halves of the cell. On coming to rest the zoospore elongates and puts out an attachment process, and in this state it much resembles *Characiopsis*. Aplanospores (one to two per cell) and akinetes, which are formed in chains, also act as additional means of propagation, whilst sexual reproduction is apparently very rare, when some of the motile bodies come to rest first and are surrounded by other motile gametes. Iron bacteria sometimes live symbiotically with this alga and colour it yellow or brown from ferric carbonate. This substance controls the pH of the water and thus acts as a local buffer for the alga whilst the bacteria obtain their oxygen requirements from the *Tribonema*.

PHYLLOSIPHONACEAE: *Phyllosiphon* (*phyllo*, leaf; *siphon*, tube). Fig. 152

This is an endophytic alga that occurs in the leaves and petioles of the Araceae, most of the species being confined to the tropics, although one is found in Europe, including Great Britain. Recent work has shown that the food reserve is oil and not starch, and that the pigments are not those associated with the Chlorophyceae. For these reasons the genus has been removed from its former place in

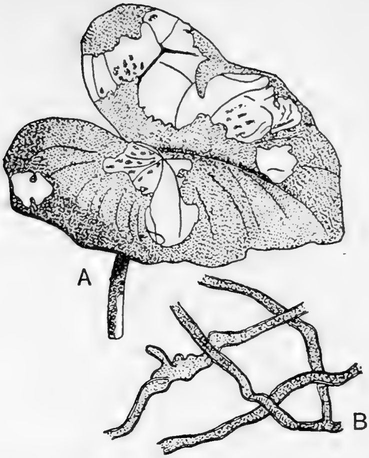

Fig. 152 *Phyllosiphon arisari.* A, leaf of *Arisarum vulgare* with whitened patches due to attack of alga. B, portion of thallus (× 66). (A, after Fritsch; B, after Smith.)

the Siphonales and assigned to the Heterosiphonales. Furthermore, in the Siphonales it presented other anomalous features in its mode of reproduction. The thallus is composed of richly branched threads ramifying in the intercellular spaces of the host. As a result of the presence of the endophyte the chloroplasts of the host cells do not develop and yellow-green patches occur on the leaf, whilst at the same time the adjacent cells may be stimulated to active division resulting in gall formation, but later on the affected cells die. Reproduction takes place by means of oval aplanospores, which in the case of *P. deformans* arise after the previous differentiation of cysts.

BOTRYDIACEAE: *Botrydium* (a small cluster). Fig. 153

This genus belongs to the Heterosiphonales and is analogous to a form such as *Protosiphon*, the commonest species, *Botrydium granulatum*, being frequently confused with it, especially as these two plants are often associated on areas of drying mud. *B. granulatum* makes its appearance during the warmer part of the year when it is seen that the green, pear-shaped vesicles are rooted by means of colourless, dichotomously branched rhizoids. The membrane is composed of cellulose and the lining cytoplasm contains numerous nuclei scattered throughout it, whilst the chloroplasts, containing pyrenoid-like bodies, are confined to the aerial part. The shape of

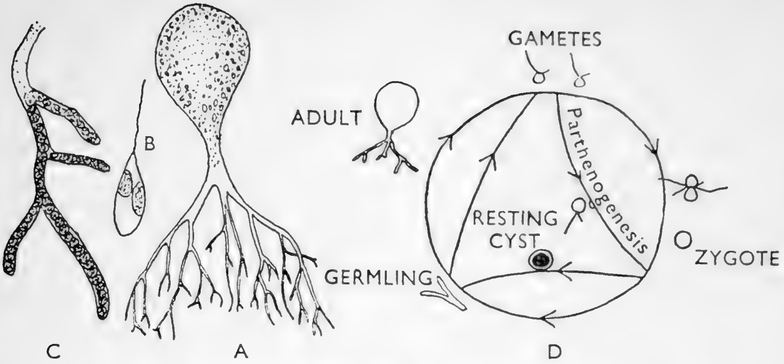

Fig. 153 *Botrydium granulatum.* A, plant. B, swarmer. C, cyst formation. D, diagram of life cycle. (A–C, after Fritsch; D, after Miller.)

the vesicle is influenced by the environment, the shade forms being elongate or club-shaped. In *B. wallrothii* the unbranched vesicle is covered with lime whilst in *B. divisum* it is branched but without lime. When the plants are submerged, reproduction takes place by means of numerous zoospores which are set free by gelatinization of the vesicle apex, but when the plants are only wet but not submerged, aplanospores are formed instead. Under dry conditions each vesicle develops into a single cyst (macrocyst) or into several multinucleate spores (sporocysts), or else the contents migrate to the rhizoids and there form several cysts (rhizocysts) which, when conditions are again favourable, either germinate directly to a new plant or else give rise to zoospores. In *B. granulatum* it is estimated that about 40,000 isogametes are formed in each vesicle, but as the plant is monoecious many fuse either in pairs or threes, rarely fours, before they are liberated. Those that do not fuse develop parthenogenetically, although the stage at which meiosis occurs is not yet known. The life cycle can be tentatively represented as in Fig. 153.

VAUCHERIACEAE: *Vaucheria* (after J. P. Vaucher). Figs. 154, 155

This genus differs in many of its characters from other members of the Siphonales, in which order it has been placed in the past. Whereas many genera of the Siphonales are tropical, *Vaucheria* is essentially temperate, inhabiting well-aerated streams, soil or saline mud flats, and although some of the species (e.g. *V. de baryana*) may be lime-encrusted it is never to quite the same extent as in some members of the Siphonales. The cell walls do not contain

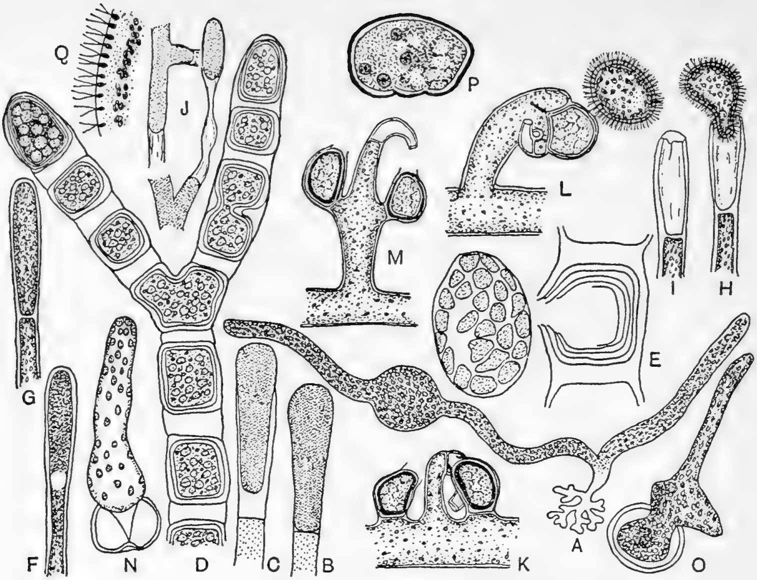

Fig. 154 *Vaucheria*. A, *V. sessilis*, germinating zoospore. B, *V. piloboloides*, developing aplanospore. C, *V. piloboloides*, escape of aplanospore. D, *V. geminata*, thread with cysts. E, escape of amoeboid protoplast from cyst. F–I, *V. repens*, development and escape of compound zoospore. J, regeneration and formation of septa in injured thalli. K, sex organs of *V. sessilis* (× 100). L, sex organs of *V. terrestris* (× 100) .M, sex organs of *V. geminata* (× 100). N, *V. geminata*, germinating aplanospore. O, germinating zygote. P, zygote with four haploid nuclei. Q, portion of compound zoospore, much magnified. (A, D, E, N, O, after Oltmanns; B, C, F–J, Q, after Fritsch; K–M, after Hoppaugh; P, after Hanatschek.)

native or mercerized cellulose as in other members of the Chlorophyceae, whilst the discoid chloroplasts, which lack pyrenoids, contain more than the normal amount of carotinoid pigments. Oil forms the principal food reserve, except that under constant illumination starch may be formed. It is in these biochemical characters that *Vaucheria* indicates its relationship with other members of the Xanthophyceae. So far as reproduction is concerned it presents anomalies whether placed in the Siphonales or Heterosiphonales. Although most workers now place the genus in the Xanthophyceae, there are a few who still feel that the evidence is not yet quite sufficient.

The plant consists of a colourless basal rhizoidal portion from which arise green, erect aerial filaments with apical growth and monopodial branching. Septa are only formed in connexion with

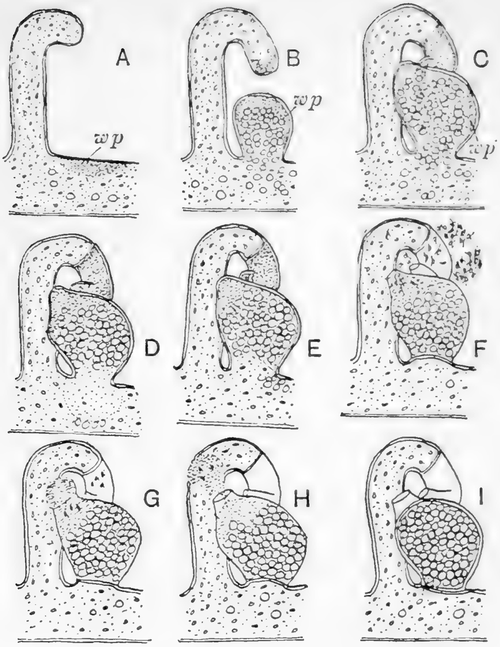

Fig. 155 *Vaucheria sessilis*. Stages in development and fertilization of oogonium. April 1–6, 1930. (× 195). A, young antheridium and 'wanderplasm' in place from which oogonium will arise. B, young oogonium. C, oogonial beak formed; 'wanderplasm' retreating into thread; oil globules passing into oogonium; antheridial wall forming. D, 'wanderplasm' out of oogonium. E, basal wall of oogonium forming. F, antherozoids emerging. G, oogonial membrane forming at tip, some antherozoids in egg. H, cytoplasm extruded and rounded off; fertilization occurring. I, ripe egg. *wp* = wanderplasm. (After Couch.)

the reproductive structures or after wounding. Vegetative reproduction is secured through fragmentation, whilst asexual reproduction is brought about by the well-known compound multiflagellate zoospores, which are produced singly in club-shaped sporangia that are cut off from the ends of the erect aerial branches. The chloroplasts and nuclei congregate in the apex of a filament before the septum is laid down and the nuclei then arrange themselves peripherally. Finally, two equal flagella develop opposite each nucleus and then the zoospore is ready for liberation, a process which is achieved by gelatinization of the sporangium tip. This compound structure must be regarded as representing a group of biflagellate zoospores which have failed to separate. The zoospore is motile for about fifteen minutes, after which it comes to rest and germinates, the first thread often being more or less colourless. 'Zoospore' formation can often be induced by transferring the plants from light to darkness, or from a nutrient solution to distilled water.

Under dry conditions aplanospores may be formed at the ends of short laterals or terminal branches, whilst if exposed to greater desiccation the threads of the terrestrial forms become septate and rows of cysts are formed, thus giving the 'Gongrosira' stage. When conditions become more favourable these cysts germinate either into new filaments or else into small amoeboid masses which grow into new filaments. Sexual reproduction is distinctly oogamous, the different species being either monoecious or dioecious. The oogonia, which are sessile or stalked, are cut off by a septum at a stage when there is only one nucleus left in the oogonium. Some authors maintain that the extra nuclei, which are potential gametes, degenerate, whilst others consider that the surplus nuclei, enclosed in a mass of cytoplasm or 'wanderplasm', travel back into the main thread before the septum is laid down. It is probable that in some species all the surplus nuclei pass out with the 'wanderplasm', whilst in other species some nuclei may be left behind and degenerate later after the septum has been laid down. The factors that determine the selection of the functional nucleus from among the number available offer a problem for future research. It would appear that in some cases at least, the loss of the nuclei may be ascribed to an unfavourable environment. In the mature oogonium there is either a beak, the apex of which gelatinizes, or else several pores through which the antherozoids can enter the oogonium, fertilization taking place *in situ*.

The antheridia, which are usually stalked, commonly arise close to the oogonia, though in *V. sessilis* they develop just prior to oogonial formation. When the septum cutting off the antheridium is laid down the nuclei divide, and cytoplasm gathers around each daughter nucleus. The mature antheridium may be colourless or green, and it opens by one or more apertures near the apex, thus providing a means of escape for the pear-shaped antherozoids which bear two flagella pointing in opposite directions. After fertilization the zygote develops a thick wall and remains dormant for some time before it germinates to give rise to a new filament. The latest evidence shows that reduction of the chromosome number takes place when the zygote germinates, thus indicating that the adult plant is haploid. This character is quite anomalous when contrasted with the known diploid status of the members of the Siphonales, but is not anomalous in respect of the Xanthophyceae.

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BACILLARIOPHYCEAE (DIATOMS)

Figs. 156–7

These unicellular algae are abundant as isolated or colonial forms in marine or fresh-water plankton and also as epiphytes on other algae and plants. They form a large proportion of the bottom flora of lakes and ponds and occur widely on salt marshes, although certain diatoms are said to be very sensitive to the degree of salinity in the medium. In the colonial forms the cells are attached to each other by mucilage or else they are enclosed in a common mucilaginous envelope. The plants have characteristic silicified cell walls which are built up on a pectin foundation and are highly sculptured. Each shell (*frustule*) is composed of two halves varying much in shape, the older (*epitheca*) fitting closely over the younger (*hypotheca*), each half being composed of a valve together with a connecting band, the latter forming the overlapping portion. The Diatomaceae are divided into two groups, the Pennatae and Centricae, the former having intercalary bands as well as the connecting bands. A simple way of distinguishing between these two groups is that the Pennatae have the shape of date boxes and the Centricae that of pill boxes. The marks or striae on the frustules are composed of rows of dots which represent small cavities, and these are so fine that they are employed in testing the resolving power of microscopes. The Pennatae have the striae arranged in series with either

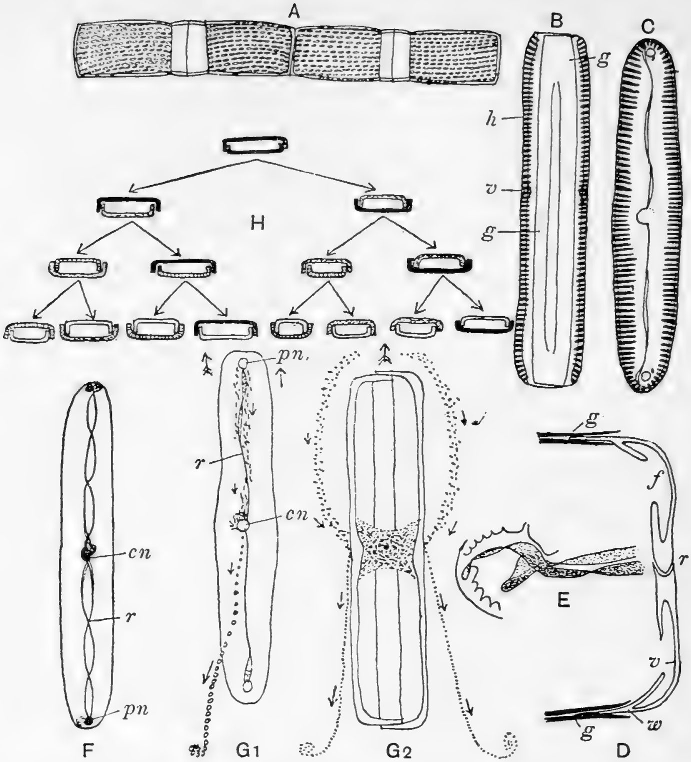

Fig. 156 Bacillariophyceae. A, *Melosira granulata* (Centricae) (× 624). B, *Pinnularia viridis* (Pennatae), girdle view. C, same, valve view. D, *P. viridis*, union of valve and parts of adjacent girdle bands. E, *P. viridis*, termination of the two parts of the raphe in the polar nodule. F, *P. viridis*, diagrammatic view showing the two raphes. G, movement of *P. viridis* as shown by sepia particles. 1, in valve view; 2, in girdle view. H, diagram to illustrate successive diminution in size of plant. The half-walls of the different generations are shaded appropriately. *cn* = central nodule, *f* = foramen, *g* = girdle, *h* = hypotheca, *pn* = polar nodule, *r* = raphe, *v* = valve, *w* = wall of valve. (A, H, after Smith; B–G, after Fritsch.)

a plain area in between (*pseudoraphe*) or else a slit that varies in form and structure (*raphe*). In the Centricae these structures are absent and the striae are arranged radially. The raphe is connected with movement, as only those forms possessing one have the power of locomotion, and although the mechanism is not completely understood it would seem to be connected with friction caused by the streaming of protoplasm. Streams of mucilage pass from the anterior polar nodule down to the centre of the plant body where it

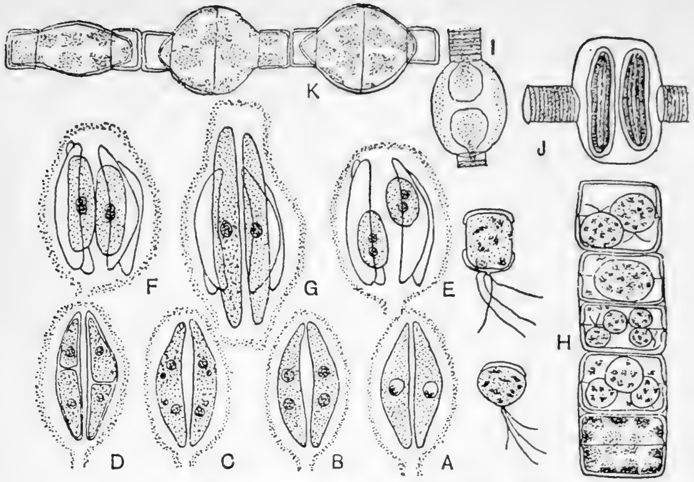

Fig. 157 Bacillariophyceae. A–G, auxospore formation by two cells in the pennate diatom, *Cymbella lanceolata*. A, synaptic contraction. B, after first division. C, second division of meiosis with functional and degenerating pairs of nuclei. D, division of each protoplast into two uninucleate gametes. E, young zygotes. G, zygotes elongated to form auxospores. H, microspore formation in *Melosira varians* (× 600). I, J, auxospore formation in *Rhabdonema arcuatum*. K, asexual auxospores in *M. varians*. (A–H, K, after Smith; I, J, after Fritsch.)

masses and then spreads out posteriorly in the form of a fine thread (Fig. 156). Two kinds of raphe occur. In the one it consists of two median longitudinal slits following a straight or sinuous course, whilst in the other (canal-raphe) it is a canal lodged in a crest or keel. Each cell is surrounded by a cytoplasmic lining with a bridge between the two halves of the shell in which the nucleus is commonly to be found. The chloroplasts are parietal, olive green to brown, the principal colouring matter being isofucoxanthin, whilst pyrenoids may be present or absent. The product of photosynthesis is a fatty oil. The pelagic forms frequently possess outgrowths which must be regarded as adaptations to their mode of existence. Cell division normally occurs at night time, and when the nucleus and protoplast have divided new valves are formed inside and then the parent connecting bands separate. One individual thus becomes smaller and smaller because the size of the new valve is fixed by the silica contained in the wall of the old valve and in five months there may be a decrease of three-fifths to two-thirds of the length until finally the shrinkage is compensated for by auxospore formation

(Fig. 157). However, a long time elapses before this rejuvenation is necessary and so auxospore formation is relatively rare.[1]

At auxospore formation in the Centricae the two halves of the shell are thrust apart by enlargement of the protoplast, which becomes enveloped in a slightly silicified pectic membrane, the *perizonium*. Nuclear division takes place, and fresh valves and connecting bands are formed inside this membrane so that a new and larger individual results. There is some evidence for meiosis followed by fusion of nuclei. In the Pennatae a union takes place between naked amoeboid protoplasts that have arisen from two distinct individuals which come together in a common mucilaginous envelope. Each plant usually produces two gametes, and as meiosis occurs during their formation the normal diatom cell must be regarded as diploid (Fig. 157). The zygotes remain dormant for a time and then elongate at right angles to the axis of the parent cells in order to form auxospores, the perizonium either being the remains of the zygotic membrane or else formed *de novo*. Isogamy is the normal condition but a few cases of physiological anisogamy are known and also apogamy. In addition to auxospores the Centricae also produce microspores, small rounded bodies with flagella, and there is reason to believe that these are flagellate male gametes though their fate has not been fully studied.

Recently oogamy has been described in some detail for *Melosira varians*, *Cyclotella tenuistriata* and *Biddulphia mobiliensis* (Centricae) together with a difference in size of the male and female filaments. The species are diploid and reduction division takes place at gamete formation. Some diatoms are also known to produce resting spores but very little is recorded about these bodies.

Within the Chrysophycophyta there is plenty of evidence for the relationship between the Xanthophyceae and Chrysophyceae. The relationships of the Bacillariophyceae are rather more obscure, though there is the basic biochemical one (cf. pp. 1–3).

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[1] In a few cases where observations have been made it occurs once in every 4–6 years.

Taxonomy

Hustedt, F. (1930). Die Kieselalgen. In Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Vol. 7. Leipzig.

Melosira

Stosch, H. A. von (1950). *Nature* (Lond.), *165*, 531.

CHRYSOPHYCEAE

Fig. 158

This assemblage is principally composed of uninucleate flagellate forms although certain members do exhibit some algal characteristics. Like the Xanthophyceae there is considerable morphological parallelism with the Chlorophyceae indicating that evolution has taken place along the same lines. Sexual reproduction is rare and when it does occur is isogamous, the plants probably all being haploid. They occur most commonly in both fresh or salt water during cold weather. The colour is golden yellow or brown due to the presence of the pigment phycochrysin, which is contained in a small number of parietal chromatophores that may also contain pyrenoid-like bodies, although starch as a product of photosynthesis is replaced by oil or leucosin. The motile cells are uni- or biflagellate, and in the latter event one flagellum is beset with fine cilia; one of the flagella is said to provide forward movement and the other rotation. When an individual has entered the amoeboid state cysts may be produced endogenously and these have silicified walls composed of two equal or unequal parts. The group possesses the following morphological categories:

(*a*) Unicellular motile types, e.g. *Chromulina*.
(*b*) Encapsuled types, either free or epiphytic, e.g. *Dinobryon* spp.
(*c*) Colonial types, e.g. *Synura*.
(*d*) Dendroid colonies, e.g. *Dinobryon* spp.
(*e*) Rhizopodial or amoeboid types, e.g. *Rhizochrysis*.
(*f*) Palmelloid types, e.g. *Phaeocystis* and *Hydrurus*, the latter being a highly differentiated branched type.
(*g*) Simple filamentous types, e.g. *Phaeothamnion*.

It is suggested that the group is still actively evolving, and that some of the brown types with algal characters may have a relationship with the simpler Phaeophyceae.

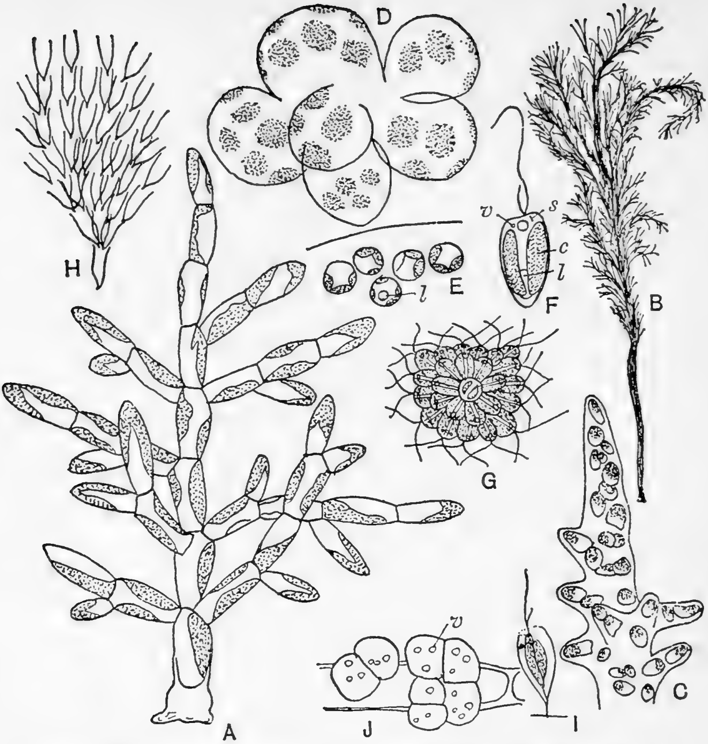

Fig. 158 Chrysophyceae. A, *Phaeothamnion confervicolum.* B, *Hydrurus foetidus.* C, *H. foetidus*, apex showing branching. D, *Phaeocystis pouchetii.* E, the same, portion of plant. l = leucosin. F, *Ochromonas mutabilis.* c = chloroplast, l = leucosin, s = stigma, v = vacuole. G, *Synura ulvella.* H, *Dinobryon sertularia*, colony. I, *D. marchicum.* J, *Epichrysis paludosa* on *Tribonema.* v = vacuole. (After Fritsch.)

REFERENCE

General

Fritsch, F. E. (1935). *Structure and Reproduction of the Algae*, Vol. I, pp. 507–63. Camb. Univ. Press.

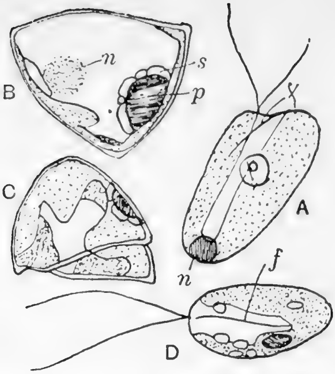

Fig. 159 Cryptophyceae. A, *Cryptomonas anomala*, side view. B–D, *Tetragonidium verrucatum*, D, being the swarmer. *f* = furrow, *n* = nucleus, *p* = pyrenoid, *s* = starch. (After Fritsch.)

PYRROPHYCOPHYTA

CRYPTOPHYCEAE

Fig. 159

Very little is known about this group. They are mostly specialized flagellates with two flagella but there are a few algal forms, although none of them is filamentous. The morphological types are:

(*a*) *Naked motile unicells.*
(*b*) *Colourless unicells.*
(*c*) *Symbiotic unicells* with cellulose walls, e.g. some of the *Zooxanthellae* which are found associated with Coelenterata and Porifera.
(*d*) *Palmelloid* type, e.g. *Phaeococcus*, which is found on salt marsh muds in England.
(*e*) A single *coccoid* type, *Tetragonidium.*

The number of chloroplasts varies, pyrenoids are present, and there is one nucleus in each cell. Reproduction is by means of longitudinal fission but some species also form thick-walled cysts.

DINOPHYCEAE

Fig. 160

This group is predominantly planktonic, naked forms being most abundant in the sea, whilst in fresh waters one commonly finds

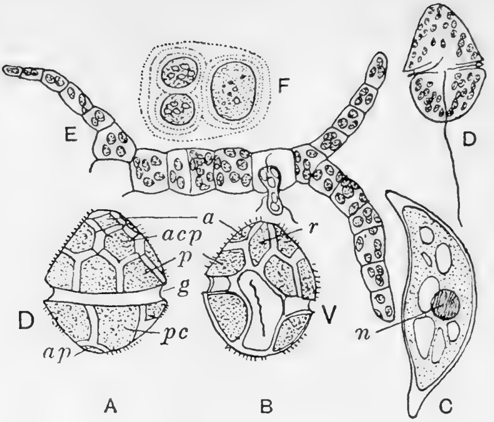

Fig. 160 Dinophyceae. A, *Peredinium anglicum*, dorsal view. B, *P. anglicum*, ventral view. C, *Cystodinium lunare*. D, *Gymnodinium aeruginosum*. E, *Dinoclonium conradi*. F, *Gloeodinium montanum*. *a* = apical plate, *acp* = accessory plates, *ap* = antapical plates, *g* = girdle, *n* = nucleus, *p* = precingular plates, *pc* = postcingular plates, *r* = rhomboidal plate. (After Fritsch.)

armoured forms which often have spiny processes that can be regarded as adaptations to their pelagic existence. The majority of the species are motile and characteristically possess two flagella, one directed backward and one transversely, both commonly lying in grooves and emerging through pores. In one or two cases, however, the flagella may be situated anteriorly. In some forms *ocelli*, which are composed of a spherical lens and a pigment, can be observed; these are presumably connected with the perception of light and they must be regarded as an elaborate development of the ordinary red eye-spot. Two genera also possess nematocysts comparable to those found in hydroids. The numerous disc-like chromatophores are dark yellow or brown in colour and sometimes contain pyrenoids. There is one nucleus and the food reserve is starch and fat, whilst the marine Dinoflagellates are noted for possessing large vacuoles. Multiplication is by means of cell division which takes place either during the motile phase or else during a resting phase. Spherical swarmers of the naked unicell type are also known together with cysts and autospores. The following represent the different morphological types that have been evolved in the course of evolution:

(*a*) Motile unicells which are either naked or else enclosed in a delicate membrane, e.g. Desmokontae and the unarmoured Dinoflagellates.

(*b*) Motile unicells with a conspicuous cellulose envelope of sculptured plates and with the flagella furrows well marked, e.g. armoured Dinoflagellates — *Peredinium*, *Ceratium*.

(*c*) Parasitic marine forms which are either ecto- or endoparasites.

(*d*) One palmelloid genus, *Gloeodinium*.

(*e*) Colourless and rhizopodial forms.

(*f*) Coccoid forms, e.g. Dinococcales.

(*g*) Filamentous forms, e.g. *Dinothrix*, *Dinoclonium*.

Recent work has tended to show that there is no real evidence for believing that this group is closely related to the Diatomaceae as was formerly supposed.

REFERENCE

General

Fritsch, F. E. (1935). *Structure and Reproduction of the Algae*, Vol I, pp. 664–720. Camb. Univ. Press.

Chapter X

MYXOPHYCOPHYTA

MYXOPHYCEAE

* INTRODUCTION

This class has also been known as the Cyanophyceae, but of recent years Myxophyceae has become more generally adopted. The separate plants, which individually are all microscopic, are characterized by a bluish-green colour which varies greatly in shade, depending upon the relative proportions of chlorophyll *a*, β-carotene, myxoxanthin, myxoxanthophyll, phycocyanin and phycoerythrin. The internal structure of the cell is extremely simple because true nucleus and chromatophores are absent. The protoplast possesses two regions, a peripheral one containing the pigment, together with oil drops and myxophycean starch (or glycogen), and a colourless central area that contains granules. Two kinds of inclusions have been recognized. The first are the metachromatic or α granules that lie in the colourless central area: these are nucleoproteic in nature since they give a feulgen reaction. Whilst many consist of metachromatin, the feulgen reaction indicates that true chromatin is also present. In the past they have probably been mistaken by some workers for chromosomes, especially since it is found that they can divide by simple fission, though this does not necessarily indicate a primitive form of mitosis. The other type of granule is known as the cyanophycin or β-granule and occurs in the peripheral region. They are in the nature of a protein reserve, and their presence is dependent to a considerable extent upon the external environment.

The protoplast is normally devoid of vacuoles, except in old moribund cells, and this is a major factor contributing to the great resistance of the plants to desiccation and of the cells to plasmolysis. In some forms, principally species which are planktonic, pseudovacuoles may be found and it is supposed that these contribute towards their buoyancy by virtue of the gas that they are said to contain. The protoplast is surrounded by an inner investment, which has been shown to be a modified plasmatic membrane. In addition there is an outer cell sheath which may surround the whole cell, e.g. *Chroococcus*, or form a cylindrical sheath, e.g. *Oscillatoria*, or an interrupted sheath, e.g. *Anabaena*. This is usually composed of a pectic material, although in the Scytonemataceae it may be made of cellulose. There is considerable variation in the composition of the different cell sheaths, and the amount of material laid down frequently depends upon the external environment. Colour of the sheaths is modified by acidity of the medium and also by fungal parasitization. In any case the secretion of pectins by these plants is regarded as a primitive characteristic. In the unicellular and filamentous forms this material is produced at the periphery of the cell, whilst in a few, e.g. *Chroococcus turgidus*, it accumulates in the cytoplasm. Protoplasmic connexions between mature cells are known in one order, the Stigonematales (see p. 291).

The class is characterized by a general absence of well-marked reproductive organs; there are no sexual organs and no motile reproductive bodies have ever been observed. It has been suggested that the lack of sexuality can be correlated with the complete absence of sterols, an hypothesis that might well repay further study. The coccoid forms (spherical cells) multiply by cell division, which takes place by means of a progressive constriction, whilst in some other types the cell contents give rise to a number of non-motile bodies that are termed endospores (gonidia in the past) (Fig. 164). All stages from simple binary fission to endospores can be found:

(*a*) binary fission, e.g. *Chroococcus turgidus*;
(*b*) quadrants and octants formed, e.g. *C. varians*;
(*c*) numerous small daughter cells are produced in which there is retention of individual sheaths, e.g. *Gloeocapsa spp.* (These are sometimes called nannocytes or gonidia).
(*d*) the same without individual sheaths, e.g. *Chroococcus macrococcus*;
(*e*) abstricted endospores, e.g. *Entophysalis*.

Many of the filamentous forms produce specialized cells known as *heterocysts*. These are enlarged cells which possess thickened walls, particularly at their poles, and they usually occur singly, though occasionally they may be formed in rows. They develop from an ordinary vegetative cell, but during development they are said to remain in protoplasmic communication with neighbouring cells. In the process of development they become depleted of their cell contents (Fogg, 1951). They have a thickened wall of two layers, the inner and more prominent of cellulose, and the outer of pectic material. There is usually a pore at one end (if terminal) or both ends (if intercalary). It has been shown (Fogg, 1949) that their formation is inhibited in the presence of ammonium nitrogen, and it has therefore been suggested that they are only formed when a specific inhibitor (involving ammonium nitrogen) falls below a critical level. The widespread occurrence of heterocysts, especially terminal ones, and their specialized structure indicates that they must fulfil a significant function. Various suggestions have been made as to their function, and in some cases they do seem to determine the breaking up of the trichomes[1] (or threads) into *hormogones*. These hormogones are short lengths of thread which are cut off, thus forming a means of vegetative reproduction among the filamentous types. In the past it has been suggested that the heterocysts are a form of food storage organ or that they represent archaic reproductive organs that are now functionless. It has, for example, been reported that in *Nostoc* and *Anabaena* these cells may occasionally behave as reproductive bodies in that they are capable of germination and thus producing new threads. In a more recent contribution, Fritsch (1951) suggests that the heterocysts, during the vegetative period, secrete substances that stimulate growth and cell division. As a result, the concentration of these substances (which may contain ammonium nitrogen — see above) falls off in the cells that lie further and further away from the heterocysts and then the development of new heterocysts is promoted. He also suggests that at the time of reproduction the nature of the secretion changes and as a result akinetes are formed. It is evident that a variety of untenable hypotheses have been put forward in the past and we may be no nearer the solution of this enigma than were the earlier botanists.

Hormogones, besides being cut off by heterocysts, may also be produced by the development of biconcave separation discs at intervals along the filament, or they may break off from the extremities of the trichomes. The hormogones, together with certain of the filamentous types, e.g. *Oscillatoria*, and a few Chroococcales, exhibit a slow forward motion. Active and continual secretion of mucilage along the sides of the filaments is associated with this

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[1] The trichome or trichomes and the containing sheath is termed a filament.

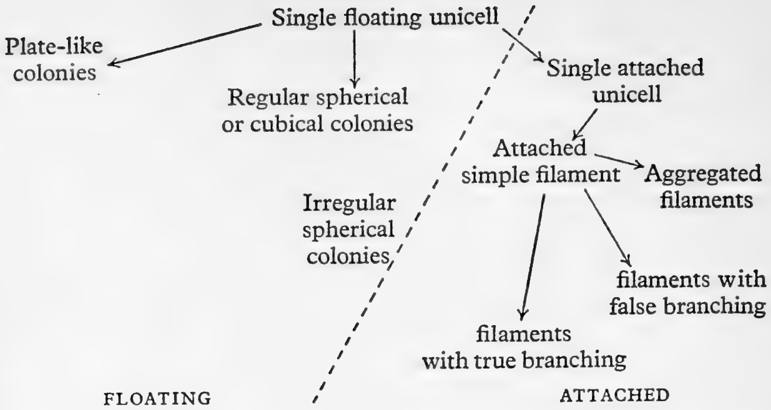
motion. The actual mechanism said to be responsible for locomotion is rhythmic longitudinal waves passing from end to end of the trichomes and caused by changes in the volumes of the protoplasts. Yet another type of structure, thick-walled resting spores or akinetes, occur in many of the filamentous forms belonging to the Nostocaceae and Rivulariaceae, normally developing next to a heterocyst, either singly or in a series. On germination they give rise to a new filament. The entire lack of sexuality must be ascribed to the ancient cell structure and the absence of chromosomes together, possibly, with the lack of sterols.

This type of cell structure naturally provides a problem for the geneticist. It is probable that each cell contains a number of genes which, if there are no chromosomes, must presumably be separated from each other, and they will either be distributed generally throughout the cell or else confined to a part of it. Since there is no special means of accurate partition, sexuality would be useless because it could not confer any real property of recombination and maintenance of gene number.

Many of the forms aggregate into colonies, but in some of the Chroococcaceae the macroscopic plant mass represents an association of such colonies rather than a single colony. The form which any colony may take up depends on (1) planes of cell division, (2) effect of environment, which may determine the consistency of the mucilage, uneven temperatures, for example, sometimes producing irregular growth. It has been shown experimentally that the environment may affect the shape of colonies of *Microcystis* and *Chroococcus turgidus* and determines the size of *Rivularia haematites* (cf. p. 289). Certain lines of morphological development have been followed by the group and may be depicted schematically as on page 282 (cf. also Figs. 160–72).

As may perhaps be expected from a primitive and ancient group there is evidence of homoplastic or parallel development when compared with plants from other primitive groups, especially the Chlorophyceae. Homoplasy can be seen between *Gloeothece* and *Gloeocystis*, *Merismopedia* and *Prasiola* (Figs. 30, 163), *Chamaesiphon* and *Characium* (Figs. 16, 164), *Chroococcus* and *Pleurococcus* (Figs. 39, 162), *Lyngbya* and *Hormidium*, *Stigonema* and *Wittrockiella*.

As a group, the plants are extremely widely distributed over the face of the earth under all sorts of conditions, frequently occurring



in places where no other vegetation can exist, e.g. hot thermal springs. Their presence in great abundance in the plankton often colours the water and is responsible for the phenomenon known as water bloom, which in some cases may result in the death of the fish. Members of the group also form a large constituent of the soil algae (see p. 379). The plants, besides being primitive, are very ancient and some of the earliest plant fossils known belong to the class (cf. p. 294). It would seem that very little evolution has taken place within the group since they first appeared. Their age and constancy of form, together with their modes of reproduction, are also responsible for the wide distribution of different species, so that there is little or no endemism in the Myxophycean flora of any region.

The class used to be subdivided into two orders, but with the advent of better knowledge (Fritsch, 1945) it is now divided into five orders: Chroococcales, Chamaesiphonales, Pleurocapsales, Nostocales and Stigonematales. Of these it is possible that the Nostocales may require further subdivision. For those wishing to identify species, standard works are those of Geitler (1932), and Tilden (1910).

CHROOCOCCALES

This order comprises unicellular forms that are free living and either living singly or united into colonies. Reproduction takes place by means of cell division in one or more planes.

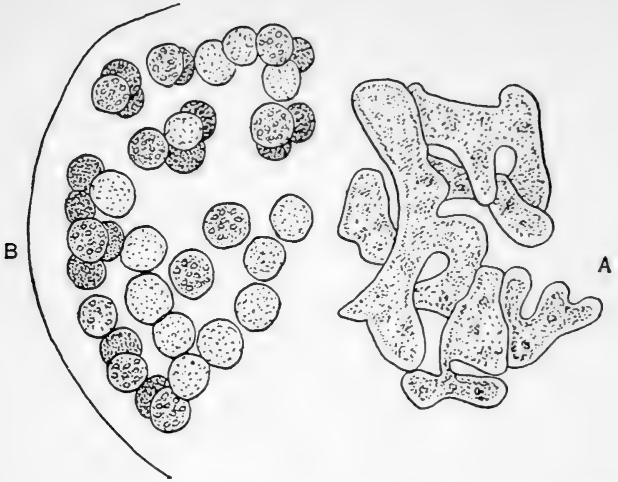


Fig. 161 *Microcystis aeruginosa.* A, colony. B, portion of a colony (×750). (A, after Geitler; B, after Tilden.)

CHROOCOCCACEAE: *Microcystis* (*micro*, small; *cystis*, bladder). Fig. 161

The thallus, which is free floating, varies much in shape and contains a mass of single spherical cells, but the sheaths of the individual cells are confluent with the colonial envelope. Reproduction of individual cells takes place by means of fission in three planes, whilst reproduction of the colony is through successive disintegrations, each portion growing into a new colony. The shape of the colony is primarily determined by the environmental conditions, and it can be changed by altering the environment artificially. *M. aeruginosa* is a very common waterbloom alga, whilst *M. toxica*, a new species from South Africa, has appeared in sufficient quantity to cause the death of thousands of cattle.

* CHROOCOCCACEAE: *Chroococcus* (*Chroo*, colour; *coccus*, berry). Fig. 162

The cells are single or else united into spherical or flattened colonies each containing a small number of cells, the individual sheaths being either homogeneous or lamellated. Plants grown in water produce a concentric envelope but when grown on damp soil the sheath is often asymmetrical. The outer integument is not very gelatinous and indeed is quite thin in some species. A study of the

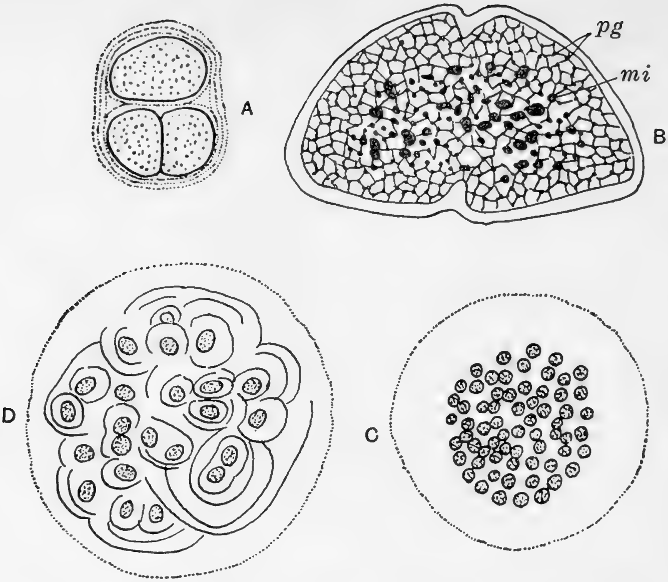


Fig. 162 *Chroococcus*. A, *C. turgidus*, plant (× 600). B, *C. turgidus*, protoplasmic reticulum with accumulations of metachromatin at nodal points. *pg* = plasmatic granules, *mi* = microsomes. C, *C. macrococcus*, normal daughter cell formation. D, *C. macrococcus*, daughter cell formation with retention of the parent envelopes. (A, after Smith; B, after Acton; C, D, after Crow.)

cytology of this genus has shown that *C. turgidus* represents the simplest condition with the metachromatin granules only just differentiated. In *C. macrococcus*, a more complex type, there is a central body which is said to contain a fine reticulum with chromatin at the nodal points, but a reinvestigation of this species is desirable and might well lead to a different interpretation (cf. Fig. 162). At cell division the reticulum divides by simple constriction, but there is no evidence of a mitosis. The genus is very widespread, the species being either free floating or else forming a component of the soil flora (cf. p. 379).

CHROOCOCCACEAE: *Merismopedia* (*merismo*, division; *pedia*, plane). Fig. 163

The free floating colonies form regular plates one cell in thickness at first, but with increasing age they become irregularly square or rectangular and are often curved or twisted. The cells are spherical or ellipsoidal and their individual sheaths are confluent with the colonial envelope. There is every transition from compact (*M. aeruginosa*) to extremely loose colonies (*M. ichthyolabe*), the number of cells enclosed in one envelope depending on the rate of division, which only takes place in two planes. In *M. elegans*, prior to cell division, an accumulation of chromatin occurs in the centre of the cells to form a central body or so-called 'nucleus', which divides by constriction immediately preceding cell division. The 'nucleus' then disappears until the next division. The majority of the species are free floating in fresh waters.

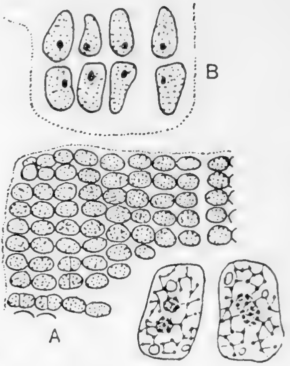


Fig. 163 *Merismopedia elegans.* A, portion of colony (× 345). B, portion of colony (× 1125). C, structure in cells about to divide (× 1875). (A, after Geitler; B, C, after Acton.)

CHAMAESIPHONALES

This order, which is a very small one, consists of attached unicells which occur either singly or aggregated together into groups. They differ from the preceding group in that reproduction is by means of endospores (gonidia).

CHAMAESIPHONACEAE: *Entophysalis* (*ento*, within; *physalis*, little bladder). Fig. 164

The cells of the sole genus in the family are epiphytic, solitary or arranged in dense clusters on other fresh water or marine plants. The cells are more or less rigid, vary much in shape and are attached at the base by down-growing filaments. In a cushion cell division is usually horizontal, but the upper daughter cells can divide by perpendicular walls, the resulting arrangement of cells being radial. The sheath is thin and hyaline and ultimately opens at the apex. Reproduction is by means of

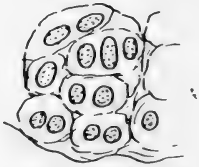


Fig. 164 *Entophysalis.* One form of the thallus (× 330). (After Geitler.)

endospores which are abstricted successively from the apex of the surface cells by transverse division, and as these bodies have been regarded as one-celled hormogones, the genus thus forms a link between the Chroococcales and Nostocales. There has been much confusion about this order, but Drouet and Daily consider that species previously placed in different genera, e.g. *Chamaesiphon*, *Dermocarpa*, *Xenococcus*, simply represent growth stages of one and the same species. The few species recognized are now placed in the single genus *Entophysalis*.

PLEUROCAPSALES

This is another small order about which very little is known. It consists primarily of cells which divide in one or two planes to give a heterotrichous thallus forming crusts or cushions that are epiphytic, epilithic or endolithic. They may play a considerable part in rock formation in some parts of the world.

PLEUROCAPSACEAE: *Pleurocapsa* (*Pleuro*, bag; *capsa*, box). Fig. 165

This is the only genus that has really been studied adequately. The primary thread creeps over the substratum and later gives rise to a pseudo-parenchymatous prostrate system. Still later densely packed erect threads arise from this basal system so that the final plant thallus is a crust. The erect threads may branch, or segment along three planes or divide obliquely, whilst gelatinization giving Chroococcoid groupings can also occur. Reproduction takes place by means of endospores that are usually produced in the terminal cells.

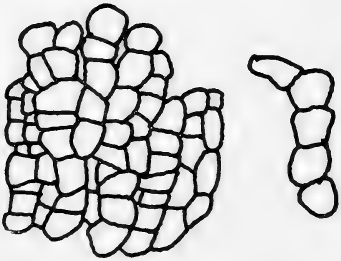


Fig. 165 *Pleurocapsa minor;* left, adult; right, juvenile creeping filament (× 800). (After Geitler.)

NOSTOCALES

* This order comprises the great majority of the Myxophyceae. It consists of the filamentous forms, which are either simple or branched. The threads occur singly or aggregated within a common gelatinous envelope. In some genera there is no difference between base and apex of the filament whereas in others there may be. Fundamentally the order is divided into those genera which lack heterocysts and those which possess them, the heterocysts being either basal or intercalary. Reproduction commonly takes place by means of hormogones, but in some genera of the Nostocaceae and Rivulariaceae, akinetes or spores are also produced.

OSCILLATORIACEAE: *Spirulina* (*spirula*, a small coil). Fig. 166

The trichomes have no proper sheath and are septate, although the septa are frequently very obscure. The trichomes are simple, free living and coiled into a more or less characteristic spiral. They occur in fresh water or on the soil, including that of salt marshes.

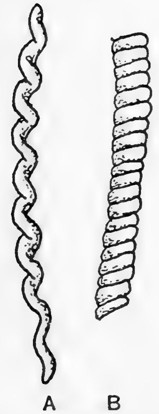


Fig. 166 *Spirulina*. A, *S. major* (× 1070). B, *S. subsalsa* (× 1070). (After Carter.)

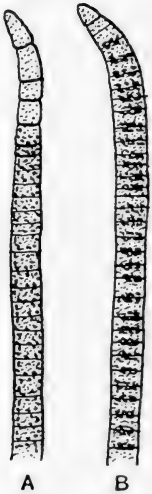


Fig. 167 *Oscillatoria*. A, *O. formosa* (× 613). B, *O. corallinae* (× 613). (After Carter.)

* OSCILLATORIACEAE: *Oscillatoria* (*oscillare*, to swing). Fig. 167

The trichomes are free living, smooth or constricted, straight or arcuate, and often form tangled masses, the sheath to each trichome being very delicate or more frequently absent. The apical cell is sometimes provided with a cap or calyptra. The name comes from the rhythmic motion of the threads which results in slow forward progression (cf. p. 281). There are a number of very common species which occur in a wide range of habitats.

OSCILLATORIACEAE: *Lyngbya* (after H. C. Lyngbye, a Danish algologist). Fig. 168

This genus differs from *Oscillatoria* in the presence of a sheath of variable thickness and colour, the character of which is largely dependent upon the environment. The plants are either attached or free floating, and are often aggregated into a mucous blue-green mat on the soil. When the hormogones escape from the sheath it is almost impossible to determine whether they belong to this or other allied genera. The species occur in the same types of habitat as *Oscillatoria*.

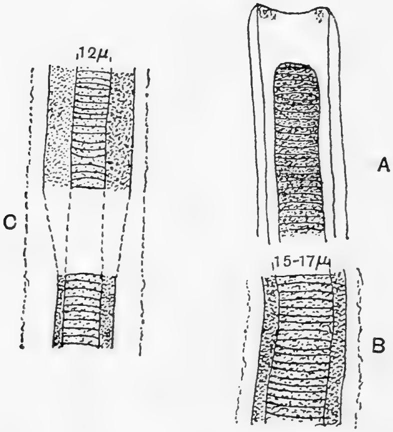


Fig. 168 *Lyngbya aestuarii*. A, apex. B, C, portions of threads. (After Chapman.)

SCYTONEMATACEAE: *Scytonema* (*scyto*, leather; *nema*, thread). Fig. 169

The trichomes differ from those of the preceding genus in the presence of heterocysts. The filaments (trichome and sheath) have distinct basal and apical regions forming little erect tufts. Branching is of the type known as false, the branches arising either be-

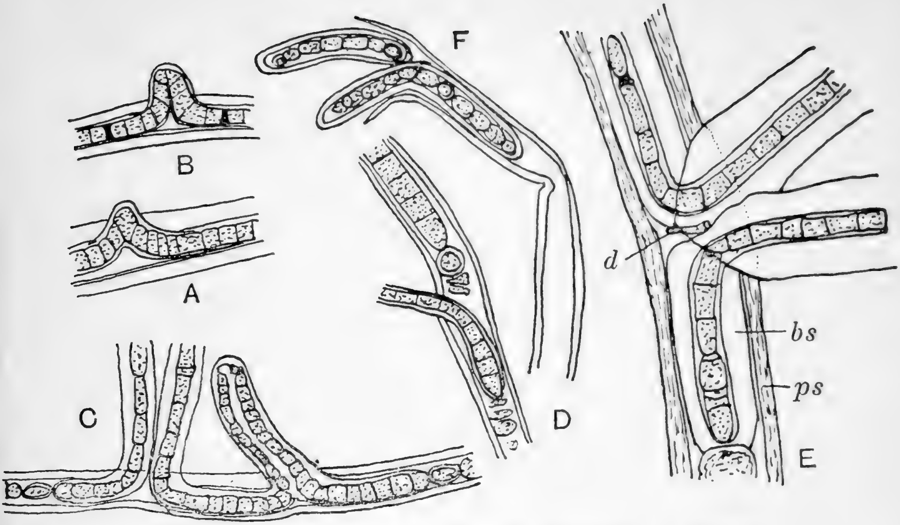


Fig. 169 Cyanophyceae. A–C, geminate branching in *Scytonema pseudoguyanense* (A, × 470, B, C, × 340). D, false branching in *Calothrix ramosa* (× 570). E, false branching in *Scytonema pseudoguyanense* showing branch sheath (*bs*) terminating at heterocyst. *ps* = parent sheath, *d* = dead cell (× 590). F, hormogones emerging from parent sheath in *S. guyanense* (× 750). (After Bharadwaja.)

tween two heterocysts or else adjoining one as a result of the degeneration of an intercalary cell. The intercalary growth results in strong pressure being applied to the sheath, which finally ruptures so that the trichome forms a loop outside (Fig. 169, A–C). Further growth causes this loop to break, thus producing twin branches, one or both of which may subsequently proceed to additional growth, the branch sheaths extending back into the parent sheath (Fig. 169, E). False branching may also be initiated by degeneration of a vegetative cell or heterocyst and subsequent growth of the two filaments on either side.

* RIVULARIACEAE: *Rivularia* (*rivulus*, a small brook). Fig. 170

The colonies form spherical, hemispherical or irregular gelatinous masses that are attached to plants or stones or they occur on the soil, those of *R. atra* being especially frequent on salt marshes. Each colony contains numerous radiating filaments with repeated false branching, each branch terminating in a colourless hair. With the production of mucilage the 'branches' become displaced and their origin is not easy to see. The individual sheaths can be seen

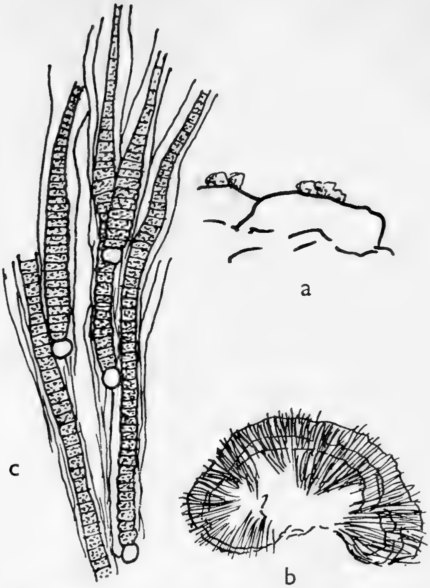


Fig. 170 *Rivularia atra*. a, plants on stones (× $\frac{2}{3}$). b, transverse section of thallus (× 9). c, single trichome in sheath (× 300). (a, b, after Newton; c, original.)

near the base of the trichomes, but they are diffluent farther up. The heterocysts are basal and in the closely allied genus *Gloeotrichia* spores are produced next to them.

* NOSTOCACEAE: *Nostoc* (used by Paracelsus). Fig. 171

The gelatinous thallus is solid or hollow, floating or attached, and varies much in size and shape. The spheres usually break open when mature and give rise to a flat expanse. There is a dense limiting layer containing numerous intertwined and contorted moniliform filaments with individual hyaline or coloured sheaths, though the sheath may sometimes be absent or very indistinct. Heterocysts are terminal or intercalary and occur singly or in series. Reproduction is by means of hormogones or spores, the latter arising midway between the heterocysts and developing centrifugally. The gelatinous masses of *N. commune* are fairly common on damp soils.

The closely related genus *Anabaena* only differs from *Nostoc* in that no firm colony is formed. Some species are symbiotic (cf. p. 428), whilst species of both genera are capable of fixing atmospheric nitrogen (cf. p. 413).

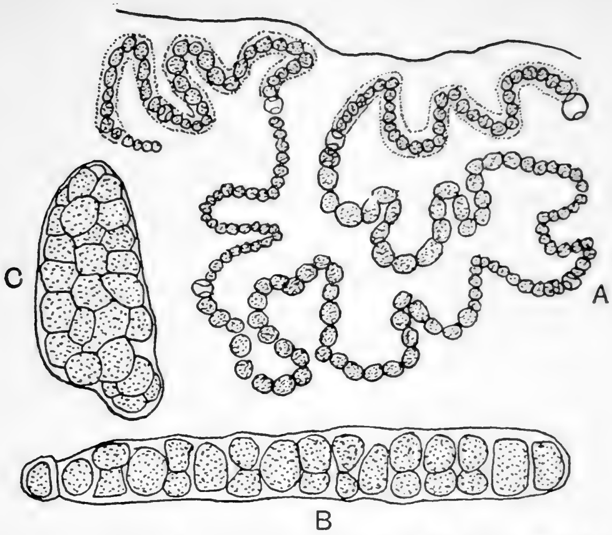


Fig. 171 *Nostoc.* A, portion of colony of *N. linckia* (× 400). B, C, germinating hormogones of *N. punctiforme* (× 900). (After Geitler.)

NOSTOCACEAE: *Cylindrospermum* (*cylindro*, cylinder; *spermum*, seed). Fig. 172

A characteristic feature of this genus is the large spore which develops next to the heterocyst at one or both ends of a filament. The outer wall of the spore is often papillate.

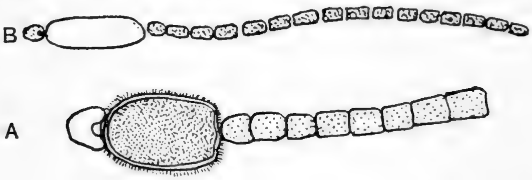


Fig. 172 *Cylindrospermum.* A, *C. majus* (× 680). B, *C. stagnale* (× 340). (After Geitler.)

STIGONEMATALES

The members of this order, which is not large, form branched threads, sometimes with a prostrate and erect portion. The branching is true and the threads may consist of more than one row of cells. Characteristically the individual cells are apparently connected by single fine protoplasmic threads, though actual proof of linkage has not so far been obtained. Reproduction is by means of hormogones, which are only produced in the uniseriate lateral branches. Heterocysts are also present.

* STIGONEMATACEAE: *Stigonema* (*stigon*, dotted; *nema*, thread). Fig. 173

The threads consist of a single row or multiple rows of cells with definite apical growth, enclosed within a gelatinous sheath which varies in thickness and colour. Shortly behind the apical cell one of the products divides twice to give a cruciform group. One of these cells gradually moves into the centre and by further division a central cell surrounded by four pericentrals is produced. Most pericentrals divide radially so that ultimately successive tiers of 7–8

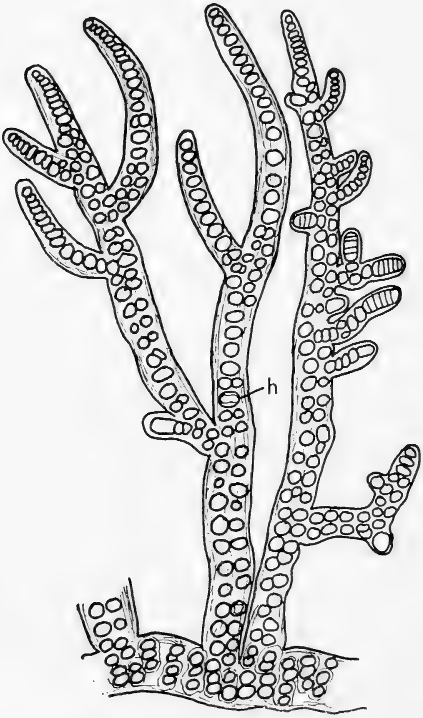


Fig. 173 *Stigonema minutum*. h = heterocyst (× 170). (After Fremy.)

pericentral cells are formed which are arranged approximately longitudinally. In young plants the sheath is continuous at the tip, but when growth is rapid the end is burst and also when hormogones are produced and extruded. The heterocysts in this genus are commonly lateral being formed by tangential division of a cell. The filaments are often aggregated to form a macroscopic yellow-green gelatinous mass. The species are most common where there is continual dripping water.

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Chapter XI

FOSSIL FORMS, REPRODUCTION, EVOLUTION

Fossil Forms

In this section it is merely proposed to give an outline of the different fossil forms that have been ascribed to the various groups, but it is not intended to provide a detailed description in every case so long as the types of structure represented among these fossil algae have been adequately portrayed. It must be realized that many of the early forms that have been ascribed to the algae are relatively unknown because of the poor preservation, and further examination of new specimens may mean that they will no longer have to be classed as algae. For this reason it must be emphasized that there are a number of doubtful forms from the lowest strata that can only tentatively be assigned to the algae.

Myxophyceae

Among the unicellular forms a fossil which has been related to the Chroococcaceae is recorded from the Ordovician. It is called *Gloeocapsomorpha* and is a colonial form with cells that were apparently enclosed in a jelly, and whilst it may have affinities with living colonial forms it is usually placed in a group called the Protophyceae. Another plant of Middle Cambrian age, *Marpolia spissa*

Fig. 174 *Marpolia spissa* (× 49·5). (After Walton.)

(Fig. 174), which seems to have affinities with the modern *Schizothrix*, is also best relegated to the Protophyceae. *Marpolia* was represented by branched filaments which were probably composed of a trichome enclosed within a gelatinous or cartilaginous sheath.

Spongiostromata (Precambrian onwards)

Much doubt has been thrown upon the authenticity of this group, some writers regarding them as structures which originated as diffusion rings ('liesegang' phenomena) in colloidal materials or perhaps in calcareous muds. In the original description Walcott suggested an affinity to the Myxophyceae, but as later workers could only distinguish a purely mineral structure they suggested the idea of diffusion phenomena. Discoveries of very comparable algal concretions and laminations in the Bahamas, however, have made it extremely probable that these structures had an algal origin. Further good examples of these structures have since been reported from the United States. Some examples of these types are shown in Fig. 175. On the basis of Black's discoveries (1933) it may be suggested that these structures were not necessarily formed by deposition but that the algae collected and bound the sediment.

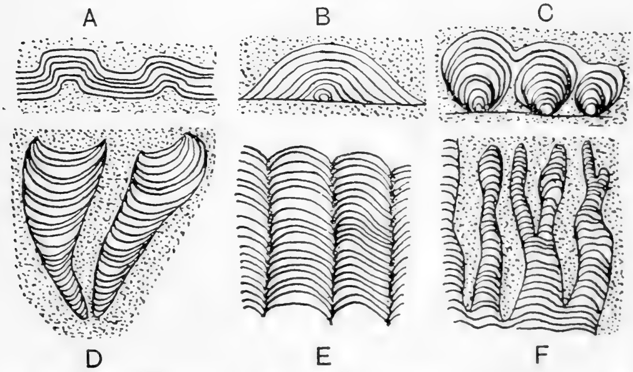

Fig. 175 Stromatolithi. A, *Weedia*. B, *Collenia*. C, D, *Cryptozoon*. E, *Archaeozoon*. F, *Gymnosolen*. (After Hirmer.)

Porostromata (e.g. *Girvanella*, *Sphaerocodium*)

These forms, which are most abundant in the Carboniferous, have a recognizable microscopical structure, the threads often being arranged in a radiating fashion: they were probably formed in

Fig. 176 *Pachytheca.* A, transverse section with natural opening through cortex (× 12). B, algal filaments of medulla and inner cortex (× 240). C, cortex with algal filaments (× 60). D, cortex showing degenerate algal threads in tube (× 150). (After Lang.)

much the same way as the algal water-biscuits now found in South Australia. These range from tiny particles to thick bun-like forms 20 cm. in diameter, whilst in them are to be found the tube-like remains of living species of *Gloeocapsa* and *Schizothrix. Gloeothece* and *Gloeocapsa* are also known to form oolitic granules in the neighbourhood of Salt Lake City. The presence, however, of pebbles, or the existence of a granular structure, does not necessarily involve the presence of algae, and in some cases it is also possible that the algae were merely included through chance. *Pachytheca* is a genus from the Silurian and Devonian which possessed a medulla of intertwining tubes and a cortex composed of stout, septate, branched algal filaments that radiate from the medulla to the periphery. Its affinities are extremely uncertain and it may have been a free-rolling alga of either salt or fresh waters (cf. Fig. 176).

Dinophyceae, Bacillariophyceae

There are a few uncertain fossils, very indistinct and not well known, ascribed to the Flagellata and Dinophyceae. Recognizable fossil diatoms are known from the Upper Jurassic, but they reached maximum abundance in the late Cretaceous. Nearly 200 genera have been described and 120 of these are still living. Fossil diatom deposits are known as Kieselguhr and are valuable economically.

CHLOROPHYCEAE

Codiaceae

Boueina (cf. Fig. 177) is an unbranched form from the Lower Cretaceous, whilst *Palaeoporella* (Fig. 177), which was composed of hollow cylinders of funnel-shaped bodies with slender forked branches, the whole being 2–14 mm. long, comes from the Lower Silurian. *Dimorphosiphon*, from the Ordovician, is generally regarded as the oldest known member of the Codiaceae and has been tentatively related to *Halimeda*. It was about 10 mm. long and composed of branched tubular cells without any cross walls, the cells being embedded in a calcareous matrix. *Ovulites*, a genus which occurs up to the Eocene, differs considerably from those previously described: the species are little egg or club-like chalk bodies beset with fine pores and with a large opening at what was either the base or apex. It has been suggested that perhaps they represent siphonaceous plants in which the apical tuft of threads has been lost.

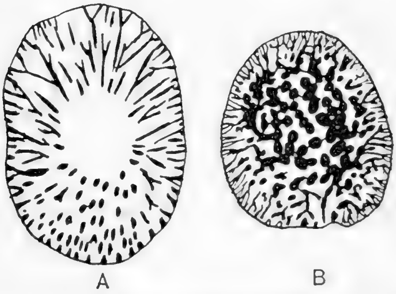

Fig. 177 Codiaceae. A, *Palaeoporella variabilis* (× 12). B, *Boueina hochstetteri*. (After Hirmer.)

Dasycladaceae

This is the best known group and contains a very large number of the fossil algae. It reached its maximum development and abundance in Carboniferous and Triassic times, and in those days was far more important than its present living representatives. The various forms are all based on a type of construction which can be sufficiently explained by descriptions of a few of the more representative types.

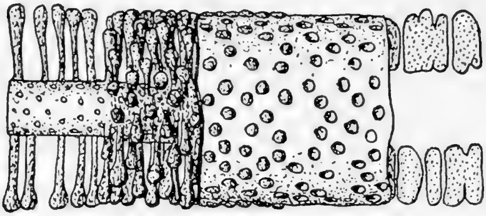

Fig. 178 Dasycladaceae. *Rhabdoporella pachyderma* (× 135). (After Hirmer.)

Rhabdoporella (Fig. 178) seems to be one of the most primitive genera as it is represented by a purely cylindrical shell that is studded with pores through which the threads passed. It is known from the Ordovician and Silurian.

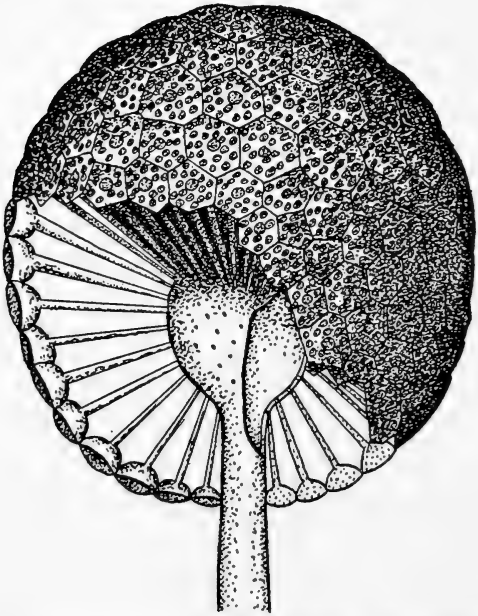

Fig. 179 Dasycladaceae. *Cyclocrinus porosus* (× 8). (After Hirmer.)

Cyclocrinus (Fig. 179) is a genus which grew to about seven centimetres and looked like a miniature golf ball borne on the end of a stalk. Narrow branches arose at the apex of the stalk and each terminated in a flattened hexagonal head, but as the edges of adjoining heads were fused together to form the outer membrane, which was only weakly calcified, the cell outlines were clearly visible. Many species are known from the Ordovician and Silurian, all somewhat resembling the living genus *Bornetella.*

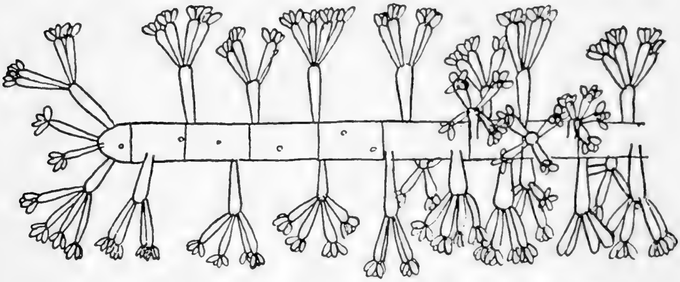

Fig. 180 Dasycladaceae. *Primicorallina trentonensis* (× 8·25). (After Hirmer.)

Primicorallina (Fig. 180), from the Ordovician, had a segmented stem beset with radially arranged branches, each of which branched twice into four branchlets.

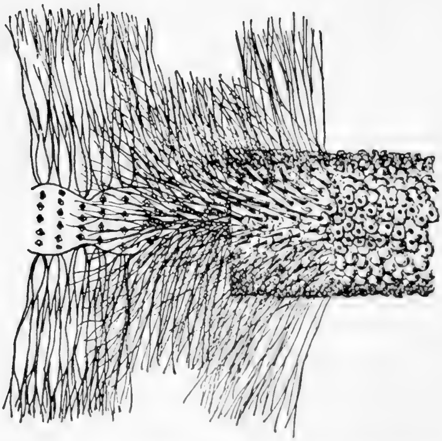

Fig. 181 Dasycladaceae. *Diplopora phanerospora* (× 8). (After Hirmer.)

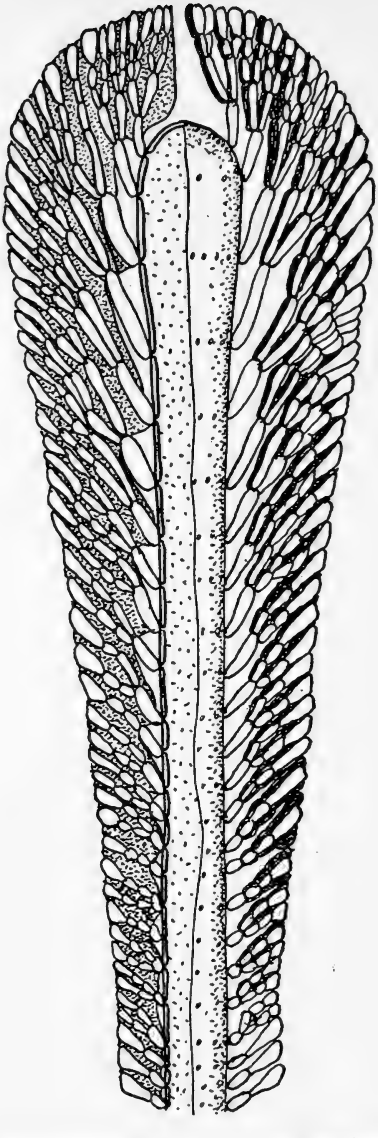

Fig. 182 Dasycladaceae. *Palaeodasycladus mediterraneus* (× 20).
(After Hirmer.)

The type of structure found in *Diplopora* (Fig. 181) was also shown by many other forms from the Middle Triassic. It was a few centimetres long and bush-like in appearance, the main stem, which sometimes had a club-shaped apex, being covered with whorls of branches that arose in groups of four, each bearing secondary branches which terminated in hairs. In the older thalli the outer part of the branch dropped off leaving a scar on the calcareous shell. The sporangia are reported to have been modified branches. *Diplopora* is a widespread genus from the Triassic rocks of the eastern Alps, Germany and Siberia.

Palaeodasycladus (Fig. 182), from the Lower Jurassic, bears a resemblance to the living species of *Dasycladus*. Near the base there were only primary branches, whilst higher up secondary and tertiary branches were to be found.

Fossil forms, practically identical with living species of *Cymopolia*, *Neomeris* and *Acicularia* have been found in all the recent strata from the Eocene upwards.

Charophyceae

Lagynophora, a genus from the Lower Eocene, can be ascribed to this group, whilst *Palaeonitella* (Fig. 183), from the Middle Devonian, may belong here also although its affinities are not so clear. *Gyrogonites* and *Kosmogyra* are names which have been given to oogonial structures which closely resemble those of *Chara*, and which are very abundant in the Lower Tertiary beds of England and elsewhere. Throughout their history there has been a tendency for simplification and reduction of parts.

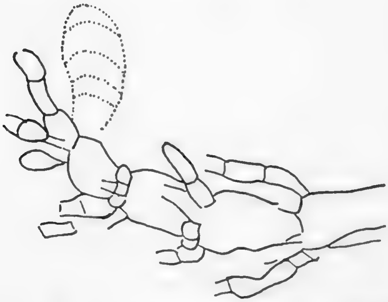

Fig. 183 Charales. *Palaeonitella cranii* (× 124). (After Hirmer.)

PHAEOPHYCEAE

The principal fossil form ascribed to this group, *Nematophyton*, has now been removed to a new group, the Nematophytales (see below).

RHODOPHYCEAE

The Melobesiae are represented from the Cretaceous upwards by species of *Archaeolithothamnion*, *Dermatolithon*, *Lithothamnion*, *Lithophyllum* and *Goniolithon*, some of them only being distinguished with difficulty from living forms. The Corallinaceae are also represented in the Cainozoic by extinct members of present living genera. There are a large number of forms assigned to an extinct family, the Solenoporaceae, which existed from the Ordovician up to the Triassic, but neither their structure nor their systematic position has been completely established. They formed nodules from the size of peas up to several centimetres in diameter in which the cells were arranged like those of a *Lithothamnion* although the cross walls were not well marked. Conceptacles have been described in these plants and were presumably associated with reproduction.

The number of genera of different fossil algae that have so far been recorded from geological strata is shown in Table 4. This gives an indication of the age of the different groups and some conception of their development.

NEMATOPHYCEAE: Nematophytales. Figs. 184, 185

Two genera are now grouped in this assemblage which was established by Lang (1937), and although he regards these forms as land plants, nevertheless they have so many features in common with the algae that it is felt proper to include them here. It is perhaps almost too speculative to suggest that they represent transmigrant forms, but it would appear that they must either be regarded as highly developed algae which adopted a land habitat, or else as the most primitive of all true land plants. The two genera agree closely in their morphological structure, and although they are both frequently found associated with each other in the Devonian rocks the two structures have not yet been found in organic connexion.

TABLE 4
(*After Johnson*, 1951)

		Myxophyceae (Porostromata)	*Spongiostromata*	*Dasycladaceae*	*Codiaceae*	*Characeae*	*Bacillariophyceae*	*Rhodophyceae*
CAINOZOIC	Pleistocene	3	3	10	3	4	100 +	16 +
	Tertiary	?	?	19	4	6	80 +	13
MESOZOIC	Cretaceous	?	?	12	2	3	60 +	9
	Jurassic	2	?	12	0	5	1	4
	Triassic	2	1	8	1	1	?	3
PALAEZOIC	Permain	3	4	6	3	2	?	2
	Carboniferous	4	10	7	6	5	?	4
	Devonian	1	1	1	0	2	.	2
	Silurian	1	3	4	2	1	.	1
	Ordovician	1	4	9	2	0	.	1
	Cambrian	1	6	0	0	0	.	0
	Pre-Cambrian	.	5	.	.	.	.	.

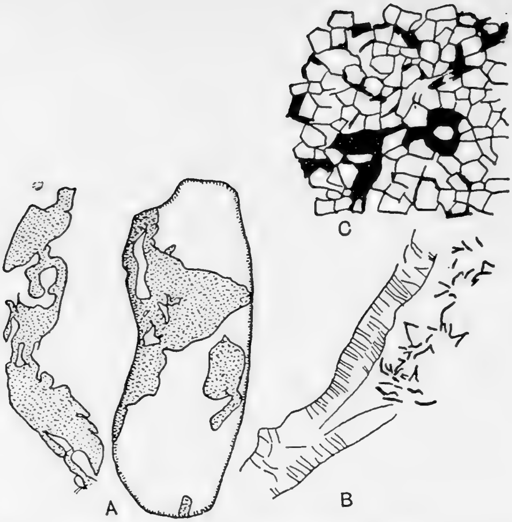

Fig. 184 Nematophytales. *Nematothallus*. A, specimens on rock (× $\frac{3}{5}$). B, large and small tubes, the former with fine annular thickenings (× 150). C, cuticle (× 150). (After Lang.)

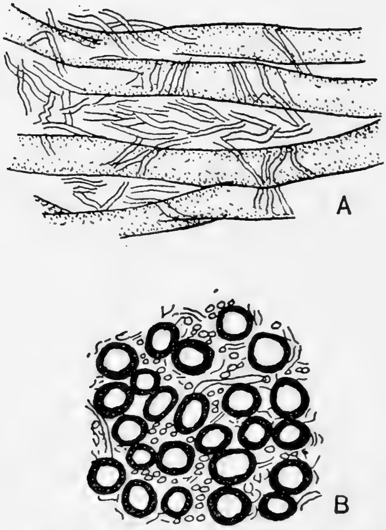

Fig. 185 Nematophytales. *Nematophyton*. A, longitudinal section (× 120). B, transverse section (× 120). (After Seward.)

In spite of this it is very probable that the leafy *Nematothallus* was the photosynthetic lamina of the stem-like *Nematophyton* and may also have functioned as the reproductive organ. In the lowest strata the plants are to be found associated with remains of marine animals, thus suggesting their power to grow under marine or brackish conditions, whilst in the higher strata they occur in beds, which are regarded as fresh water or continental, where they are associated with plants that were undoubtedly terrestrial. The presence of spores in *Nematothallus* is regarded as rendering it unlikely that they were algal in nature, but the spores may be comparable to the hard-walled cysts such as are to be found in *Acetabularia*.

The genus *Nematophyton* is found in the Silurian and Devonian rocks where it was first described under the name of *Prototaxites* and referred to the Taxaceae, but subsequently it was accepted as an alga and renamed *Nematophyton* or *Nematophycus*. Later the name *Prototaxites* was revived and it was placed in the Phaeophyceae, whilst Kräusel (1936) has stated that it must have had the appearance of a *Lessonia* (cf. p. 182) and also that it existed in aquatic habitats which may have been marine, brackish or fresh. The valid name is therefore *Prototaxites*, but as this tends to convey a false impression of the plant's affinities it would seem more satisfactory to retain the better known name of *Nematophyton*. The largest specimen is a stem up to two feet in diameter, but whatever the size of the stem it is usually composed of two kinds of tubes, large and small. The large tubes have no cross partitions, but in some species they are interrupted in places by areas, regarded as medullary rays or spots by some authors, which are wholly occupied by small tubes that in other parts of the thallus simply take a sinuous course between the large tubes. The wide tubes, in the latest specimens described by Lang (1937), show no markings indicative of definite thickening, though striations have been seen in specimens from other localities. Around the outside of the central tissue there is a cortex, or outer region, composed of the same tubes where they bend outwards towards the periphery and eventually stand at right angles to the surface. The outermost zone of all is apparently structureless and may well have been a mucilaginous layer during life.

Nematothallus is a genus composed of thin, flat, expanded incrustations of irregular shape and up to 6½ cm. long by 1 cm. broad, and also constructed of the wide and narrow tubes. The thallus is surrounded by a cuticular layer that exhibits a pseudo-cellular pattern, and which includes within the cuticle and among the peripheral tubes firm-walled spores of various sizes; in *N. pseudovasculosa* the spores were definitely cuticularized and so the suggestion was made that these were land plants or parts of a land plant. The side tubes, which have thin pale brown walls, are translucent in appearance and exhibit distinct characteristic annular thickenings. The cuticle, which is apparently readily detached, possesses distinct cell outlines that were probably made by the ends of the wide tubes from the ordinary tissue where they became fused together at the periphery, as in the living genera *Udotea* and *Halimeda*. Another species *Nematothallus radiata* is more imperfectly known.

From the structure described above it can be seen that the members of this group are strongly reminiscent of the Laminariales and Fucales, and it is tempting to suppose that they represent land migrants from one of these groups. There is no evidence, however, of any parenchymatous structure, so that if they were indeed members of that group they would be allied to forms with a multiaxial type of construction. Problems that have to be solved are: (1) The cuticularized spores; whilst no such spores with hard outer walls are known from the brown algae they are recorded from the Chlorophyceae, e.g. *Acetabularia*. However, the suggestion that the spores may have developed in tetrads adds a further complication, at any rate so far as an algal ancestry is concerned, because the Dictyotales and tetrasporic Rhodophyceae do not show the state of differentiation found in these fossil plants. (2) The presence of a deciduous cuticle. In this connexion one or two Laminariales are known to shed cuticles during reproduction, and the present author has found a deciduous cuticle on plants of *Hormosira*, a member of the Fucales. It may be suggested that the plants perhaps had the appearance of a *Lessonia* or even of a *Durvillea*, and a stem diameter of two to three feet does not preclude them from being algal in character because several of the large Pacific forms may have stipes of almost this size (cf. p. 183). It has also been suggested that these forms are related to the Codiaceae, expecially *Udotea*, and in certain respects it is true that they have the structure of a siphonaceous plant. Here again there are several problems that need to be answered: (*a*) the presence of two sizes of tubes; (*b*) the presence of a cuticle; (*c*) the presence of cuticularized spores; (*d*) the large size of stem.

The answer to the last problem has already been suggested (see above) but cuticles in the Codiaceae have not been recorded, although the present author has been able to detect a structure something like a cuticle in *Halimeda*; nor have any species been reported that possess two distinct sizes of tubes, although gradations in size occur in both *Udotea* and *Halimeda*. In this connexion it may be of interest to refer to Tilden's unsupported suggestion that the land plants arose from forms such as *Codium* and *Caulerpa*. It must be admitted that there are no living members of the Codiaceae with stems that approach anywhere near the size of those of *Nematophyton*. This, however, is not an insuperable objection as the Nematophytales may bear the same relation to the living Codiaceae that the fossil Lepidodendrons bear to the living Lycopodiales. For the present, however, the problem must be left in the hope that further evidence will accumulate.

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REPRODUCTION AND EVOLUTION

In so far as the green algae or Chlorophyceae represent the main line of evolution from which it is believed land plants ultimately evolved, it is convenient to consider evolution within that group first. In the past there have been two major views about the origin of the group. According to one, the Chlamydomonadaceae are regarded as the primitive group whereas according to the other the Palmellaceae are. These two views are represented respectively by schemes A and B. Of the two there would appear to be rather more evidence in favour of scheme A. Scheme B in particular involves the development of parenchymatous types (Ulvales), their subsequent reduction to a simple filament (Ulothriceous type) and the re-elaboration of this to a branched, partially coenocytic thallus (Siphonocladales). Whilst not impossible, such a sequence seems an unnecessary postulate. In scheme A it will be observed that several lines of evolution divaricate from the primitive source. One line leads to the development of aggregate spherical colonies, culminating in *Volvox*: another line leads to the production of gelatinous colonies, which may become net-like (*Schizodictyon*), and another to dendroid colonies (*Prasinocladus*). All these, however, would seem to represent 'blind alleys' in evolution. In the main sequence of evolution the logical development is the non-motile unicell and then the attached unicell. From the former have developed more colonial forms terminating in giant nets (*Hydrodictyon*), but simple siphonaceous forms may also have been produced (*Protosiphon*). The non-motile unicell would easily develop into a simple filament (*Ulothrix*) from which a number of specialized 'blind' end lines must have appeared (Oedogoniales, Conjugales). From this central key position evolution would appear to have progressed in three directions:

(*a*) To parenchymatous types, e.g. *Ulva*, *Enteromorpha*.

(*b*) To partially coenocytic types, e.g. Siphonocladales, and thence to the Siphonales. It has been suggested as an alternative that the Siphonales may have arisen from the siphonaceous Chlorococcales (*Protosiphon*). The principal arguments against this hypothesis would seem to be:

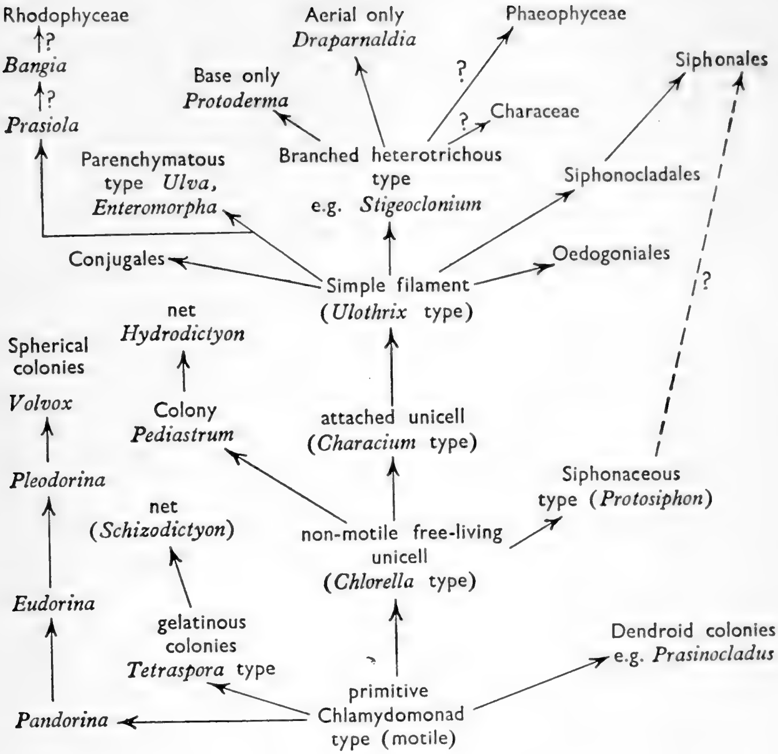
   (i) there are no intermediates between the wholly haploid *Protosiphon* and the wholly diploid Siphonales. One would expect to find some forms with both generations alternating;

   (ii) the Chlorococcales are nearly all fresh water whereas the Siphonales are all marine;

   (iii) intermediates can be envisaged from at least some members of the Siphonocladales and the Siphonales (scheme D).

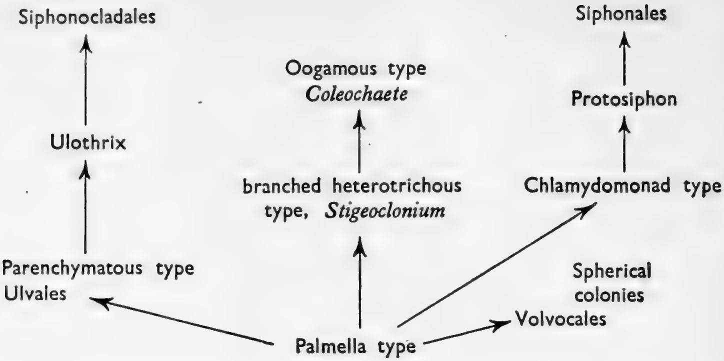
   More detailed discussion of this problem will be found in Chapman (1954).

(*c*) To branched heterotrichous types (Chaetophorales) with subsequent reduction of one or other of the generations.



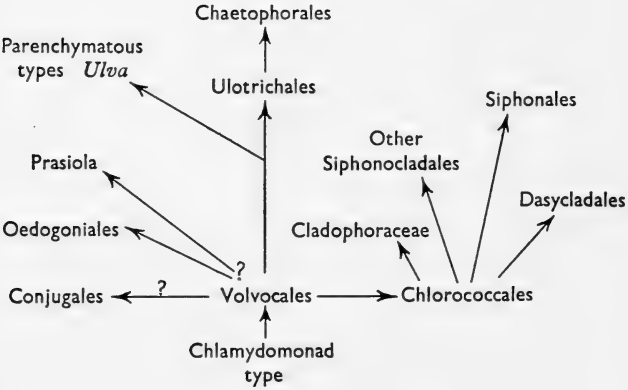
SCHEME A

The names of the genera do not necessarily imply that they formed the actual intermediate stages, but merely that forms like them were possibly involved.



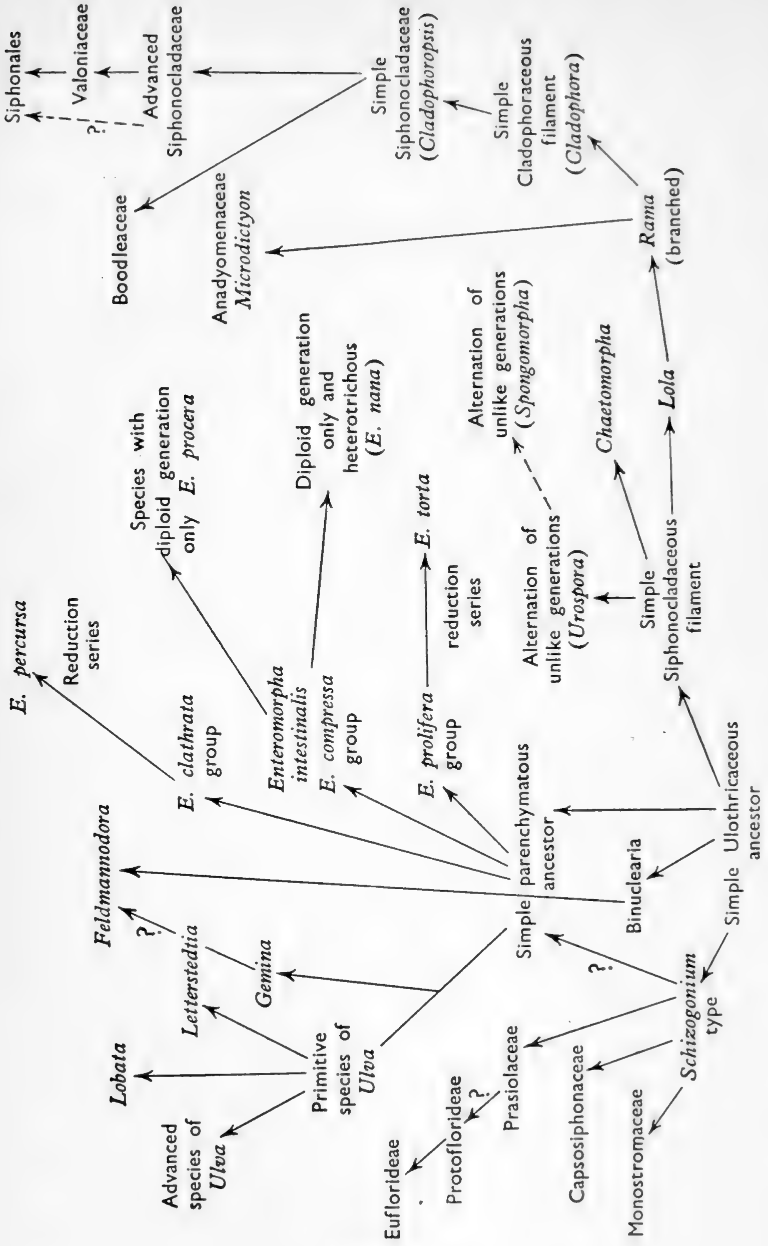
SCHEME B

In 1951 Papenfuss propounded a third scheme for the Chlorophyceae in which the Volvocales represent the key position (scheme C).



SCHEME C

This scheme would seem to be unsatisfactory in respect of the Oedogoniales, Conjugales and *Prasiola*. Also, for reasons stated above, the Siphonales may not have been derived from the Chlorococcales, and, based on scheme D, it is believed that a better series of forms can be envisaged in the evolution of the Siphonocladales from a Ulothricaceous ancestor. The details of the suggested evolutionary development from the simple Ulothricaceous filament to the parenchymatous forms on the one hand and to the


Siphonales
Valoniaceae
?
Advanced Siphonocladaceae
Simple Siphonocladaceae (Cladophoropsis)
Simple Cladophoraceous filament (Cladophora)
Boodleaceae
Anadyomenaceae Microdictyon
Rama (branched)
Lola
Chaetomorpha
Alternation of unlike generations (Spongomorpha)
Alternation of unlike generations (Urospora)
Simple Siphonocladaceous filament
Species with diploid generation only E. procera
Diploid generation only and heterotrichous (E. nana)
E. torta
reduction series
E. percursa
Reduction series
E. clathrata group
Enteromorpha intestinalis
E. compressa group
E. prolifera group
Simple parenchymatous ancestor
Simple Ulothricaceous ancestor
Binuclearia
Feldmannodora
?
Letterstedtia
Gemina
?
Schizogonium type
Lobata
Primitive species of Ulva
Advanced species of Ulva
Prasiolaceae
Protofloridene
?
Eufloridene
Capsosiphonaceae
Monostromaceae

SCHEME D

partially coenocytic forms on the other are shown in scheme D (Chapman, 1952, 1954). In the Siphonocladalean line the position of *Urospora* with macroscopic gametophyte and dwarf sporophytic *Codiolum* stage is of interest because from that one can see how forms with heteromorphic generations could have arisen, e.g. *Spongomorpha*. The other feature is the appearance of heterotrichy in the parenchymatous group, and also in the most advanced forms the disappearance of the haploid generation (*Enteromorpha nana* and *E. procera*). There is also the disappearance of the haploid generation associated with development of the vesicular forms of the Siphonocladales. In the development of the Chlorophyceae as represented by Scheme A it is important to note the development of the heterotrichous habit in the more advanced members, and also, commencing with plants that are universally haploid, there is the intercalation of a sporophytic generation and in some cases the disappearance of the gametophytic generation. The concept of the heterotrichous habit was first advanced by Fritsch in 1929, and it is clear that an appreciation of this habit is important in understanding evolutionary problems among the algae. The major fact is that the most advanced Chlorophyceae exhibit the heterotrichous condition in a primitive state, whilst this state is found fully developed only among the simpler Rhodophyceae and Phaeophyceae.

A study of the life cycles within the Chlorophyceae (Fig. 186) shows that there are three principal types with intermediates:

(1) A unicellular or multicellular haploid generation with a short-lived unicellular diploid phase (*Chlamydomonas*, *Volvox*).

(2) An alternation between morphologically identical diploid and haploid generations (*Ulva*, *Enteromorpha*, *Cladophora*).

(3) A multicellular or coenocytic diploid generation in which the gametophyte has been eliminated, e.g. Siphonales.

In the primitive condition if the haploid plants were monoecious the first stage in evolution would presumably have been the development of the dioecious condition; this may then well have been followed by the intercalation of a sporophyte generation through delay in occurrence of the reduction division (e.g. *Monostroma*) leading to alternation of two generations. Recently Feldmann (1952) has put forward the view that the primitive life cycle in all the Euphycophyta is one in which there is alternation of two like generations. Whilst this may be true for the Phaeophyceae and

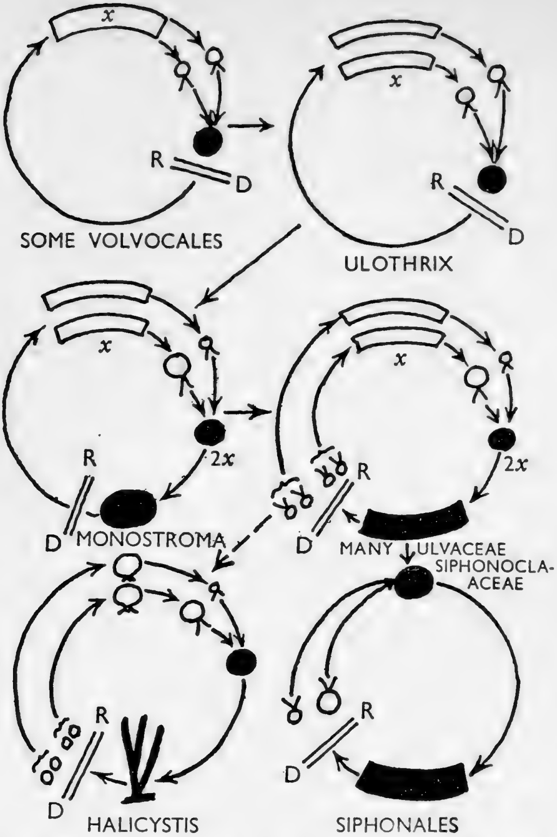


Fig. 186 Types of life cycle in the Chlorophyceae and their possible inter-relationships. RD = position of reduction division in the life cycle.

Rhodophyceae it is extremely difficult to accept in the case of the Chlorophyceae because there are so very few examples among the primitive orders, e.g. Volvocales, Chlorococcales.

At the present time hypotheses have to be based primarily upon a study of living forms. Many ancestral forms must have disappeared, and whilst there are arguments in support of the several different hypotheses that have been put forward, it is believed that the greatest support will be found for scheme A, with scheme D representing certain parts in more detail.

In his studies on the Rhodophyceae, Svedelius coined a number of words which have subsequently come into common usage for the algae:

Haplont: A sexual haploid plant with only the zygote diploid (*Volvox*).

Diplont: A sexual diploid plant in which only the gametes are haploid, e.g. *Codium*.

Haplobiont: A plant possessing cytologically only one kind of individual in the life cycle: this may be either a haplont or a diplont.

Diplobiont: A plant possessing cytologically two kinds of individuals in the life cycle, and hence an alternation of generations.

These terms have been further elaborated by Feldmann as follows:

Types of cytological cycles	*Morphological cycles*
1. Reduction division at first division of zygote HAPLOPHASIC (= haploid haplobiont)	MONOGENETIC OR DIGENETIC
2. Reduction division at gametogenesis DIPLOPHASIC (= diploid haplobiont)	MONOGENETIC
3. Reduction division at spore formation. DIPLOHAPLOPHASIC (= diplobiont)	DIGENETIC TRIGENETIC (two sporophyte generations — e.g. carposporophyte and tetrasporophyte)

Representatives from the different algal groups in these cytological and morphological cycles are shown in Table 5, where the digenetic forms are subdivided into those with alternation of like generations (isomorphic) and those with unlike (heteromorphic). Most Nemalionales are digenetic in so far that reduction division occurs at zygote germination giving rise then to a parasitic haploid carposporophyte. The Protoflorideae are digenetic in that some of them possess an independent prostrate generation (*Conchocelis* phase of *Porphyra*).

The primitive members of the Phaeophyceae (Ectocarpales) known today already possess a form of thallus that is only seen in advanced types of the Chlorophyceae, i.e. branched heterotrichous filaments, with alternation of isomorphic generations. The actual source of origin of the Phaeophyceae therefore presents some con-

TABLE 5

	MONOGENETIC	DIGENETIC			TRIGENETIC
		Isomorphic	Heteromorphic		
			Gametophyte dominant	Sporophyte dominant	
HAPLOPHASIC	Volvocales Conjugales Charales		Most Nemalionales. Protoflorideae	*Bonnemaisonia* (see p. 229)	
DIPLOHAPLO-PHASIC		*Ulva* *Enteromorpha* *Dictyota* *Zanardinia*	*Cutleria*	*Laminaria*	Most Rhodophyceae
DIPLOPHASIC	Valoniaceae Siphonales Fucales				

siderable difficulty. There would seem to be two major alternatives:

(1) An origin from a unicellular ancestry within the Chrysophyceae or Xanthophyceae with intermediate forms such as *Phaeothamnion* (cf. p. 274). In support of this hypothesis there is a similarity in so far as pigments and biochemical substances are concerned (see p. 4), but against it is the fact that nearly all the Chryso- and Xanthophyceae are fresh water and practically all the Phaeophyceae are marine. Whilst the sea as we know it probably did not exist when the Phaeophyceae first emerged, nevertheless one would have expected more intermediate forms to have survived. There is also the fact that the Chrysophyceae and Xanthophyceae, so far as is known, have only the haploid generation in the life cycle, and species of Ectocarpus (*Ectocarpus virescens*) with a similar life cycle would seem to be reduced.

(2) An origin from heterotrichous members of the Chlorophyceae, i.e. within the Chaetophorales. The main objection to this view is the difference in pigments, especially the presence of fucoxanthin and fucosterol, but nevertheless there are members of the Chlorophyceae, e.g. *Zygnema pectinatum* in which fucoxanthin is said to occur. The development of this pigment may well, therefore, have occurred more than once in the development of the Chlorophyceae.

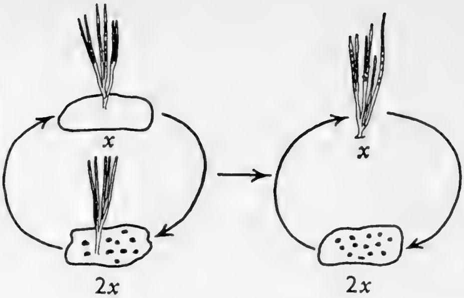


Fig. 187 Hypothetical life cycle of heterotrichous ancestral form (left) of *Cutleria* leading to present cycle.

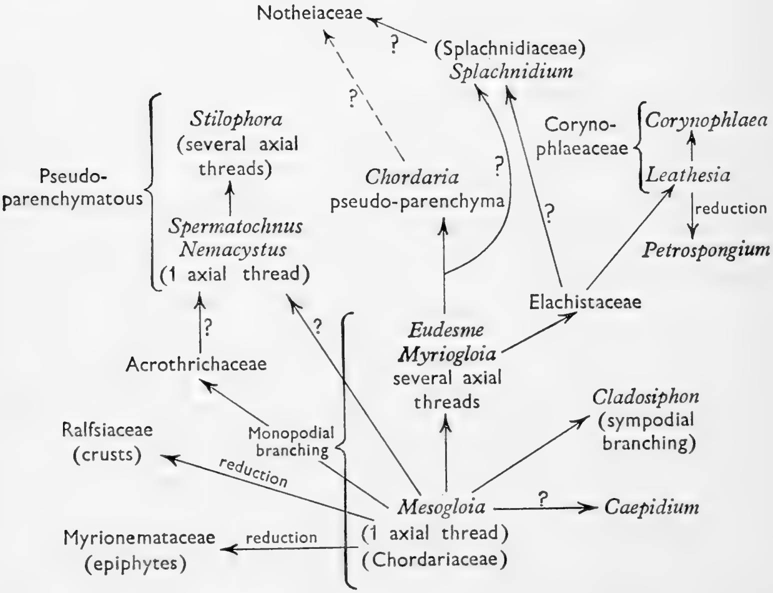
Within the Phaeophyceae themselves there would seem to be general agreement that those members with isomorphic alternation of generations probably have some relationship one to the other. The apparently difficult case of *Cutleria* and *Aglaozonia* can be explained on the basis of an original heterotrichous ancestor in which the aerial part of the gametophyte persisted and only the basal part of the sporophyte (Fig. 187). In the case of *Microzonia* (see p. 142) one generation seems to have disappeared completely. There also seems to be some form of general agreement that the orders with heteromorphic alternation (Heterogeneratae) can conveniently be divided into those that are pseudoparenchymatous (haplostichineae) and those which are truly parenchymatous (polystichinae). The real problem in the Phaeophyceae is associated with the origin of the Laminariales and Fucales. It is, for example, possible to imagine a line of evolution, not only on morphological, e.g. the cable type of construction, but also on reproductive criteria, commencing from *Ectocarpus*→*Castagnea*→*Chordaria*→*Chorda*→*Laminaria*, whilst an alternative origin would be within the ancestral forms of genera such as *Dictyosiphon* or *Punctaria* in the Dictyosiphonales. It is also extremely tempting to consider whether the Fucales may not have been evolved from the Laminariales because of the existence of forms such as *Durvillea*. Indeed recent work by Naylor (cf. p. 207) on *Himanthalia* and *Durvillea* has served to strengthen this possibility.

It has also been suggested that the Fucales might be derived from the Mesogloiaceae (Chordariales), but the evidence produced cannot be regarded as wholly convincing. The principal points are associated with the presence of the apical hairs falling off and giving rise to the adult apical growing cell, because a similar type of behaviour is to be found in *Acrothrix* (Mesogloiaceae): in gross structure also, e.g. primary and secondary medullary filaments and the assimilatory tissue, there is some slight resemblance between that of *Fucus* and *Eudesme*. The comparative looseness of the *Mesogloia* type of structure and the compactness of the Fucalean does, however, present difficulties. Yet other suggestions have been the evolution of the Fucales from the Dictyotales, though this would demand the elimination of a fully developed gametophyte generation, which has already been greatly reduced in the Mesogloiaceae or Laminariaceae, and also their evolution from the peculiar monotypic genus, *Splachnidium* (cf. p. 158). This last genus might well represent a relic of ancestral forms from which the Fucales were derived. The adult plant is sporophytic and there is a dwarf generation which is presumably gametophytic though no reproductive organs have so far been observed. The suggestions above involving *Chordaria*, *Acrothrix* and *Splachnidium* indicate that perhaps the Chordariales occupy a key position within the Phaeophyceae.

The importance of the Chordariales has been further stressed by the very recent discovery that the former Fucalean species *Notheia anomala* reproduces by means of macro- and micro-swarmers and is not a member of the Fucales at all. Its affinities are surely in the Chordariales and, in view of its thallus construction, probably not far from *Splachnidium*. As has been pointed out, it may well be that in *Notheia* the male gametophyte is not produced and the micro-swarmers may act as antherozoids. A dwarf filamentous female gametophyte is still produced but is apparently not liberated. Reduction of this phase would lead to the Fucalean condition.

Recent interesting discoveries about reproduction in the peculiar antarctic genus *Phyllogigas* suggest that perhaps the Fucales are diphyletic in origin, the Durvilleaceae coming from plants such as *Phyllogigas* and others coming from a Chordarialean source such as *Notheia*.

The Chordariales form a more or less homogeneous group and it is possible to suggest how evolution within the order may have taken place. The Chordariaceae would seem to represent the primitive stock with uniaxial plants (*Mesogloia*) preceding multiaxial (*Eudesme*, *Myriogloia*). At some stage reduction must have occurred leading to the reduced epiphytic Myrionemataceae and the saxicolous, crustaceous Ralfsiaceae. Another line of development is provided by the cushion forms which could well have come via plants such as *Elachista.* The final stage is probably represented by a genus such as *Corynophlaea* with *Petrospongium* (see p. 155) being treated as a reduced form. Yet another line of evolution must be represented by the pseudoparenchymatous Spermatochnaceae with apical growth instead of the usual trichothallic. *Spermatochnus* and *Nemacystus* with a single axial thread may be regarded as primitive to genera (*Stilophora*) with several axial threads. Pseudoparenchymatous development is also found in *Chordaria*, representing the most advanced condition in the Chordariales, and in the peculiar monotypic genus *Splachnidium.* In the latter genus, the unilocular sporangia are borne in sunken pits or conceptacles, very reminiscent of the Fucales. Another peculiar monotypic genus with no immediate obvious affinities is the antarctic *Caepedium.* Here there is a basal thalloid plant, reminiscent of *Ralfsia*, from which at certain times arise branched threads of *Chordaria*-like structure. The plant also produces a *Leathesia*-like cushion form. The schema below attempts to indicate the lines along which evolution may have progressed in this order with its fairly wide range of forms.



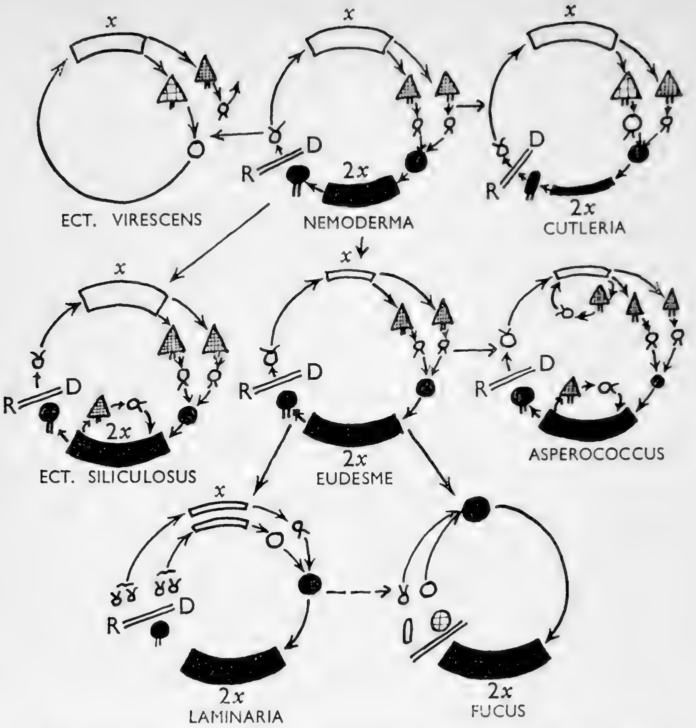
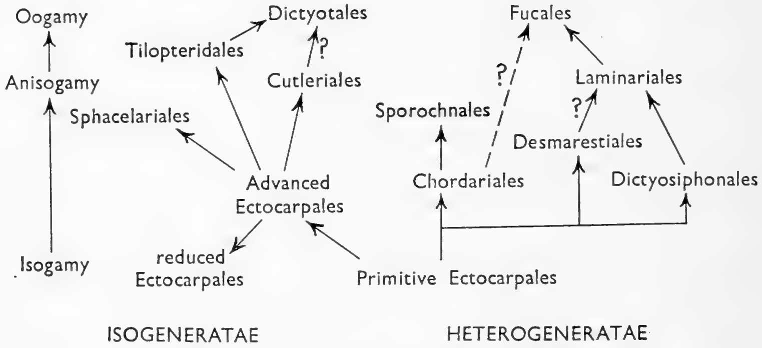


Fig. 188 Types of life cycle in the Phaeophyceae and their possible inter-relationships. RD = position of reduction division in the life cycle.

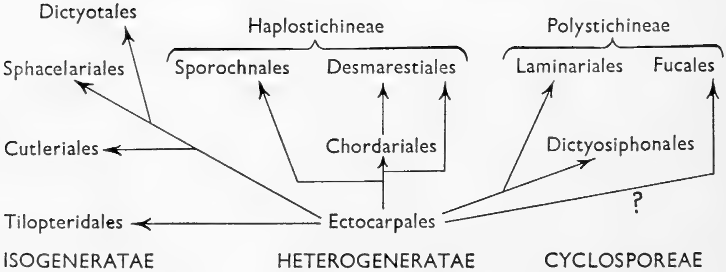
A study of the life cycles (Fig. 188) of representative genera in the Phaeophyceae is of some interest. It will be noted that in the diagram the arrows indicating suggested evolutionary progression in the life cycles in general conform to evolutionary morphological progression. In most of the types the life cycle is not simple, because each generation is capable of repeating itself. Lying behind the life cycle, however, is the fundamental nuclear cycle, but despite this there is no real regular alternation of generations except in the Dictyotales, Laminariales and some members of the Chordariales and Sphacelariales. This diagram leads to the conclusion that the primitive Phaeophycean was either a plant with only a haploid generation in the life cycle, or one in which there was isomorphic alternation. The first alternative would involve the interpolation of a sporophytic generation through a delay in meiosis, and the subsequent loss of the gametophyte. The second hypothesis only involves the loss of the gametophyte generation. Against the first hypothesis is the fact that very few members of the Ectocarpaceae are known to be haplonts, and in one good case, *E. virescens*, the parthenogenetic development of the eggs suggests degeneration rather than primitiveness. The general weight of evidence would appear to be in favour of isomorphic alternation as the primitive Phaeophycean condition.

Schemes A and B represent two slightly different views of evolutionary development within the Phaeophyceae, in both cases starting from a simple branched filamentous ancestor with isomorphic alternation. Which of these two schemes is accepted depends very largely upon the view taken about the origin of the Fucales and Laminariales.

The origin of the Rhodophyceae presents almost as many difficulties as that of the Phaeophyceae. On one hand they may have



SCHEME A



SCHEME B

originated from among unicellular organisms, but there appears to be practically no real source here apart from *Porphyridium cruentum*, which is more probably a reduced than a primitive form. Another hypothesis is that which considers the Rhodophyceae to have been evolved from the Myxophyceae, the principal argument in support of this view being the resemblance between the pigments, though they are not identical chemically. The principal objection to this theory is the absence of any form of sexual reproduction among the Myxophyceae, whereas even in the Protoflorideae there is evidence of sex organs. A third hypothesis involves an origin of the Protoflorideae from a Chlorophycean ancestral type such as *Prasiola*, and it is important to note that there is a striking resemblance in morphology and reproduction between *Bangia* and *Prasiola*. The production of a red pigment, by a mutation, in an otherwise green alga, would not seem to be insuperable. On the whole this would seem to be as probable a source for the Rhodophyceae as any other. There are some who consider that the Proto- and Euflorideae had independent origins but in that case the origin of the latter would be even more shrouded in mystery.

The Protoflorideae differ from the Euflorideae in the usual absence of pit connexions between cells and also in the primitive morphological structure, a far greater variety being found within the Euflorideae. It is, however, possible to treat the Rhodophyceae as an evolutionary series in respect of their sexual reproductive organs, and in particular of the auxiliary cell.

True auxiliary cells absent Mostly haplonts	Nemalionales	No procarp
True auxiliary cells absent Haplo-diplonts	Gelidiales	
Auxiliary cells present before fertilization. Morphologically simple	Cryptonemiales	Procarp present
Auxiliary cells present before fertilization. Morphologically advanced	Gigartinales	
Auxiliary cells develop after fertilization	Rhodymeniales Ceramiales	

A study of the life cycles (Fig. 189) fully supports the above schema. The primitive condition is represented by *Scinaia*, *Nemalion*[1], *Batrachospermum*, etc. where only the haploid generation is present. The sporophyte generation is intercalated by delay in the

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[1] Not *N. helminthoides* where the carpospores are diploid (Magne, 1961; see p. 258).

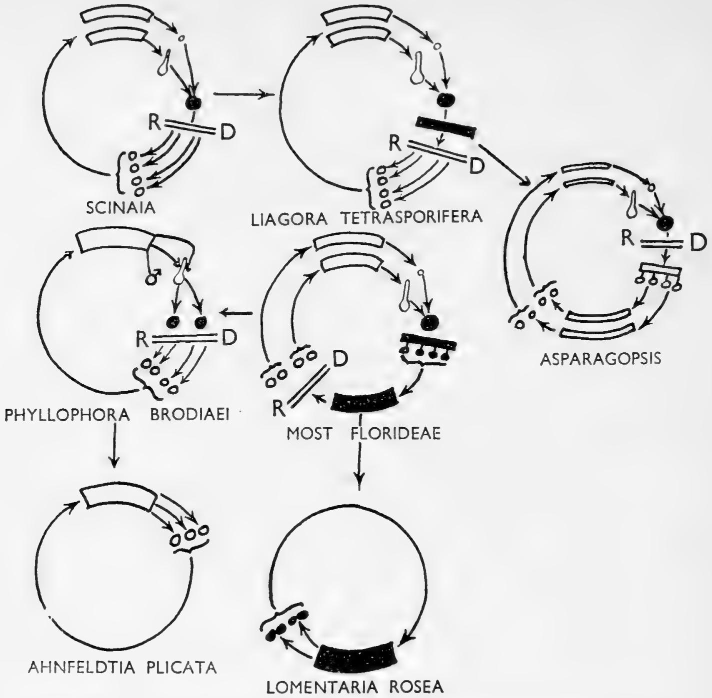

Fig. 189 Types of life cycle in the Rhodophyceae and their possible inter-relationships. RD = position of reduction division in life cycle.

reduction division, as in the Chlorophyceae, the interpolation stage being represented at present by species such as *Liagora tetrasporifera* (see p. 231). Finally there is the regular alternation of the type found in most Euflorideae, e.g. *Polysiphonia*. Early variants of this type are found in the Nemalionales (*Galaxaura* and *Asparagopsis*) where there is a distinct alternation of unlike generations; in the former they are also cytologically different but not so in the latter (cf. p. 230). Subsequent developments, which must be interpreted as retrogressive, can be seen in *Phyllophora membranifolia*, where the tetraspores are grouped into nemathecia on the diploid plant; in *P. brodiaei*, where the diploid phase has disappeared and the nemathecia can be regarded as growing parasitically in the haploid thallus; and finally in *Ahnfeldtia* where meiosis no longer takes place and instead the nemathecia contain monospores. *Hildenbrandtia* and *Lomentaria rosea* in European waters and

Apophloea in New Zealand waters represent examples of a reduced life cycle, because in these plants the gametophyte generation is wholly suppressed, whereas in other examples it is the sporophyte generation that has been reduced.

Recently Feldmann (1952) has argued that in all three classes the primitive life cycle is that with alternation of two isomorphic generations. The arguments against this have been put forward in the case of the Chlorophyceae and the thesis has been supported in the case of the Phaeophyceae. In the case of the Rhodophyceae it would seem that if an origin from either the Myxophyceae, unicellular organisms or *Prasiola* is envisaged, the logical, primitive Rhodophycean life cycle would consist of wholly haploid individuals into which sooner or later a sporophyte would be intercalated. Feldmann's proposed primitive life cycle for the Rhodophyceae would appear unnecessarily complex and not fulfilled by any living representatives. Fundamentally he envisages a steady reduction series throughout the class (Fig. 190).

The phylogenetic history of the Chlorophyceae and Rhodophyceae appears to follow parallel lines if the arguments presented above are accepted. In both, the life cycle with only haploid individuals is the primitive one and a diploid generation is subsequently interpolated. In the Chlorophyceae the haploid generation eventually disappears (e.g. Siphonales, Valoniaceae) whereas in the Rhodophyceae it is the newly intercalated sporophytic generation that may become reduced (*Phyllophora brodiaei*, *Ahnfeldtia plicata*) as well as the gametophyte generation (e.g. *Lomentaria rosea* in European waters (cf. p. 248), *Hildenbrandtia* and *Apophloea*). The phylogeny of the Phaeophyceae also fits into the general pattern if it is accepted that the primitive condition there is alternation of two isomorphic generations.

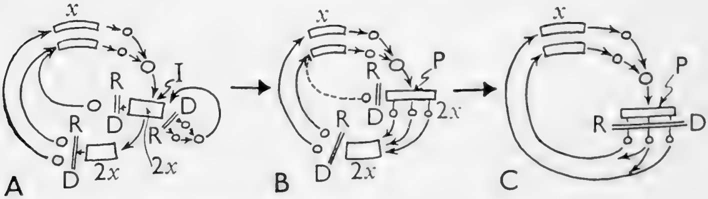

Fig. 190 Evolutionary development of Rhodophycean life cycles according to Feldmann. A = hypothetical original; B, *Polysiphonia* type; C = reduced *Liagora* type, I = independent carposporphyte; P = parasitic carposporophyte. RD = place of meiosis.

Table 6

Parallelism in evolution of the simpler type of algal construction

Type of Construction	*Chlorophyceae*	*Xanthophyceae*	*Chrysophyceae*	*Cryptophyceae*	*Dinophyceae*
(1) Motile green unicell	*Chlamydomonas	Heterochloris	Chromulina	Cryptomonas	Gymnodinium
(2) Encapsuled unicell	Phacotus	—	Chrysococcus	—	—
(3) Motile colony	Pandorina *Volvox	—	Synura		Polykrikos
(4) Dendroid colony	Prasinocladus	Mischococcus	Dinobryon		—
(5) Palmelloid colony	Tetraspora	Botryococcus	Phaeocystis	Phaeococcus	Gloeodinium
(6) Coccoid form	*Chlorella	Chlorobotrys	Chrysosphaera	Tetragonidium	Cystodinium
(7) Simple filament	*Ulothrix Urospora	*Tribonema	Nematochrysis		Dinothrix
(8) Branched filament	*Cladophora	—	Phaeothamnion		—
(9) Heterotrichous thallus	*Stigeoclonium	—			Dinoclonium
(10) Siphonaceous filament	*Codium Halimeda	Botrydium *Vaucheria	—	—	—

* It is recommended that elementary students only remember these examples.

Attention must also be drawn to the fact that within the various classes and phyla a number of definite morphological tendencies can be recognized, and these are repeated within the groups. In view of the plasticity of primitive organisms it is not surprising that the various potential lines of development have been exploited more than once. Examples of this parallelism within the simpler algae are provided in Table 6 (p. 325) and for the more advanced algae in Table 7 (p. 326).

A word may conveniently be said about the time when the different algal groups made their first appearance. Many authors would consider that the Myxophyceae and Chlorophyceae are the most primitive and therefore appeared first. If, however, the Rhodophyceae and Phaeophyceae have a flagellate origin then all four groups may be of the same antiquity. Whatever the sequence of events, it is quite clear from the structure of the earliest fossil algae (see pp. 296, 298) that considerable evolution had taken place long before even their time.

One further point remains to be added. In the present chapter it has been suggested that the similarity in life cycles and a study of phylogeny leads one to the hypothesis that the Chlorophyceae, Phaeophyceae and Rhodophyceae may be interrelated (hence their inclusion in the Euphycophyta). At the same time it has been indicated that other workers believe that all three groups have had independent origins from different sources. The final decision between these two viewpoints must, with our present knowledge, be largely a matter of opinion.

TABLE 7

Parallelism in evolution among the advanced type of algae

Type of Construction	*Chlorophyceae*	*Phaeophyceae*	*Rhodophyceae*
(1) Heterotrichous thallus	**Stigeoclonium*	**Ectocarpus*	**Batrachospermum*
(2) Discoid	**Protoderma*	*Ascocyclus*	*Erythrocladia*
(3) Crusts or cushions	*Pseudopringsheimia*	*Ralfsia*	*Hildenbrandtia*
(4) Elaborated erect type	**Draparnaldia*	*Sphacelaria*	*Plumaria*
(5) Uniaxial pseudo-parenchymatous	*Dasycladus* **Chara*	**Mesogloia*	**Polysiphonia*
(6) Multiaxial ditto	**Codium*	*Eudesme*	*Nemalion*
(7) Foliose parenchymatous	**Ulva*	*Petalonia*	**Porphyra*
(8) Tubular parenchymatous	**Enteromorpha*	*Asperococcus*	*Halosaccion*

* It is recommended that elementary students only remember these examples.

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Chapter XII

MARINE ECOLOGY

ECOLOGY OF ROCKY COASTS

The algal communities of the rocky coasts have attracted more investigators, both botanical and zoological, than have those of any other type of coast. This is because the fauna and flora are more attractive, more extensive and more readily identifiable, and also because the zonation is generally so well-marked. An observant investigator of rocky sea coasts cannot help but be impressed by the remarkably distinct zoning of the principal organisms: this is often so pronounced that it is clearly evident from the decks of boats passing by close to the shore. This zonation, moreover, is not confined to any one region but is found almost universally throughout the world. The vertical extent of the zones or belts depends on the tidal rise, the greater the rise the more extensive each zone. Even in the Caribbean where the tidal rise is about nine inches, it is possible to observe a zonation, though each zone may not cover more than two inches vertically. Any one of the major species commonly occupies a very definite vertical range, but occasionally may be found outside this range and then there is some cause, e.g. the presence of a rock pool, which makes conditions favourable for its existence.

The numerous ecological studies that have now been carried out in many parts of the world have involved a great number of investigators. This has necessarily resulted in some lack of uniformity in the results that have been obtained. In any one given area the actual number of communities recognized depends primarily upon two factors:

(*a*) *The locality:*

Some localities, especially those in colder waters, are very much richer than others. In warmer waters the littoral marine fauna and flora is much poorer though it may be quite rich in the sublittoral. Within a region itself a rocky shore is usually richer than a boulder shore, and a protected area is commonly richer than an exposed one.

(*b*) *The personal factor:*

Each investigator will tend to have a somewhat different concept of what comprises an algal community. The number of communities recognized will also depend upon the time and thoroughness with which the shore is examined.

The terminology that has been employed for naming the communities has led to no little confusion. Algal ecology commenced after terrestrial ecology and so some investigators have attempted to apply terms used in the latter to the former, whereas others have considered that the conditions are sufficiently different to make this application impossible. Cotton (1912), for example, recognized five algal formations at Clare Island in western Ireland:

(1) Rocky shore formation.
(2) Sand and sandy mud formation.
(3) Salt marsh formation.
(4) River mouth formation.
(5) Brackish bay formation.

These were subdivided into associations, the rocky shore formation containing the associations of the exposed coast and of the sheltered coast. Although the term 'association' was applied to these communities, it is probable that many of them were really 'societies' in strict ecological nomenclature. At Lough Ine in southwest Ireland Rees (1935) classified the formations on a different basis and he recognized only two, the exposed and sheltered coast formations. Rees further used the term 'association' for those communities where species that are associated with the dominants are controlled by the same factors. The difficulty of this criterion is the time involved in proving experimentally that certain factors do control the distribution of the species concerned. Seasonal communities, or those with local dominants, were termed societies, whilst the term 'zone' was used for those algal belts which possess horizontal continuity with well-marked upper and lower limits. However, the term zone has essentially a geographical connotation, e.g. temperate zone, tropical zone, so that it is best employed in a biogeographical sense, and the word 'belt' used for the marked horizontal communities.

In New Zealand Cranwell and Moore (1938) termed the group of successive belts that follow one another vertically an 'association complex'. The horizontal belts are normally continuous, but they can be interrupted occasionally by another community, e.g.

one could have an association fragment of *Durvillea* in the *Xiphophora* belt. There is still divergence of opinion about nomenclature, and even at the present time when it is desirable to secure uniformity, it is still perhaps more satisfactory to use the noncommittal term 'community'.

So far as the individual belts are concerned our knowledge has now reached the point where some degree of uniformity of nomenclature is possible.

The basic zonation of the littoral

The Stephensons (1949) using their own material and that of other marine ecologists have proposed a basic grouping in the littoral which is now becoming generally accepted. Three major belts are recognized and they appear to be practically universal. These belts are the supra-littoral fringe, the mid-littoral and the sub (or infra-) littoral fringe. The relationship of these belts to tide levels and the dominant organisms is shown in the following schema:

Supra-littoral
————————————Upper limit littorinids
Supra-littoral fringe———Extreme high water springs
————————————Upper limit barnacles
Mid-littoral
———Mean low water neaps
————————————Upper limit laminarians or certain fucoids
Sub-littoral fringe
———Extreme low water springs
————————————? Exact position not settled
Sub-littoral

This basic zonation does vary from place to place depending on the inter-relationships of tides and wave action (Fig. 191).

Some discussion has recently taken place about the nomenclature of these belts, but so many workers have accepted the Stephenson terminology that there seems as yet no valid reason for departing from it. It will be noted that it is based upon limits of living organisms. Japanese workers have suggested that tide levels should be used, but until we know more about the relationship between

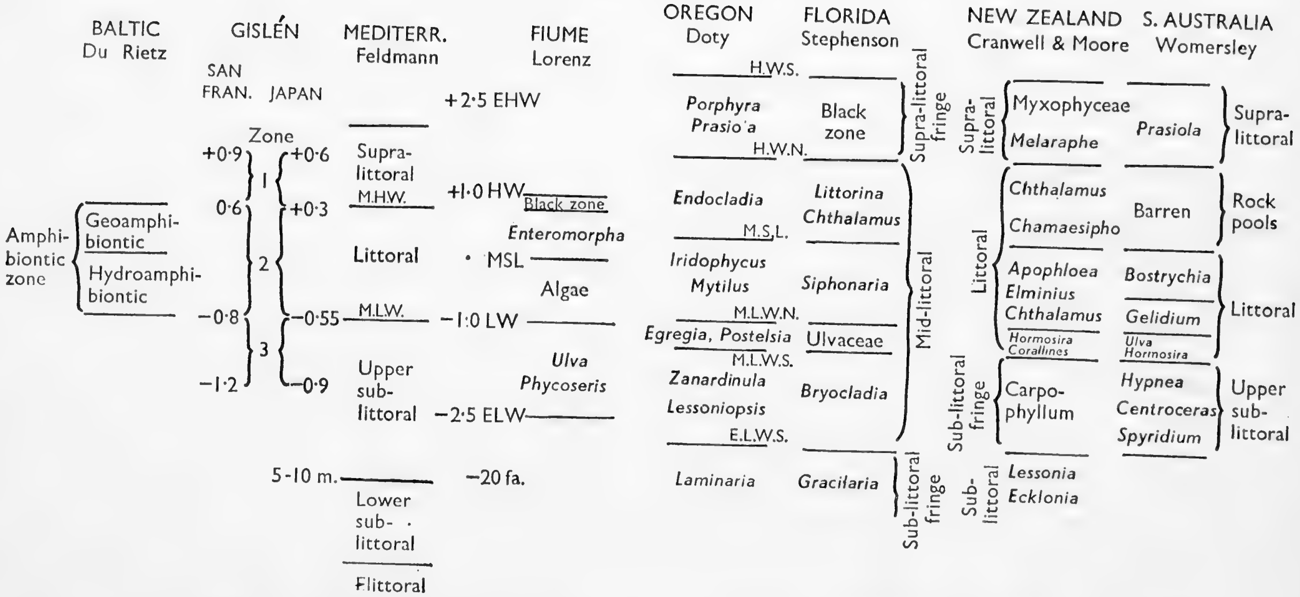

Fig. 191 Algal belts in different parts of the world compared on a tidal basis. (After Doty.)

tidal phenomena and metabolic activities of the plants it would be unwise to use tide levels for this purpose. The supra-littoral does not concern us here, though in passing we may note that it is usually bare or occupied by terrestrial lichens. In most regions the supra-littoral fringe is characterized by the presence of species of *Littorina* or of allied genera, i.e. *Melaraphe* in New Zealand and Australia. If these are absent the region is occupied by Myxophyceae and marine lichens and forms a black belt. The transition to the major belt on the shore, the mid-littoral, is determined by the upper limit of the barnacles, i.e. species of *Balanus*, *Chamaesipho*, *Chthalamus* etc. In a given region, variations of exposure may determine which particular species of barnacle provides the upper limit. In most regions it is found necessary to subdivide this belt, such subdivision being based upon the dominant organisms. Here there is considerable variation throughout the world, although there is some degree of uniformity throughout the cold waters of the northern hemisphere on the one hand, and the cold waters of the southern hemisphere on the other. At least a portion of the belt is normally dominated by the barnacles. In the northern hemisphere much of the mid-littoral is dominated by fucoids, e.g. *Fucus vesiculosus*, *F. serratus*, *Ascophyllum*. In the southern hemisphere oysters and mussels may be dominant and towards the base of the region there is a belt of Corallines or of *Hormosira*. The transition to the next belt, the sub-littoral fringe, is determined by the upper limit of the Laminarians, primarily in the northern hemisphere, or of fucoids, e.g. *Durvillea*, *Carpophyllum*, *Cystophora* in the southern hemisphere. The lower limit of this fringe is set just below extreme low water-mark of spring tides, but at present our knowledge of this fringe is not as good as that of our knowledge of the mid-littoral and supra-littoral fringe. Since it is submerged for so much of the time it is not an easy zone in which to work, and it is clear that more work will be necessary before the lower limit of this fringe can be satisfactorily settled. It differs from the supra-littoral fringe in that contributions to its flora and fauna are made by denizens of both the mid-littoral and sub-littoral proper. Despite this there are species which appear to be restricted to the belt, which itself possesses certain distinct environmental features, i.e. it is a belt in which there are substantial periods of continuous submergence. Some workers deny the existence of the sub-littoral fringe in their regions and therefore do not include it in a gener-

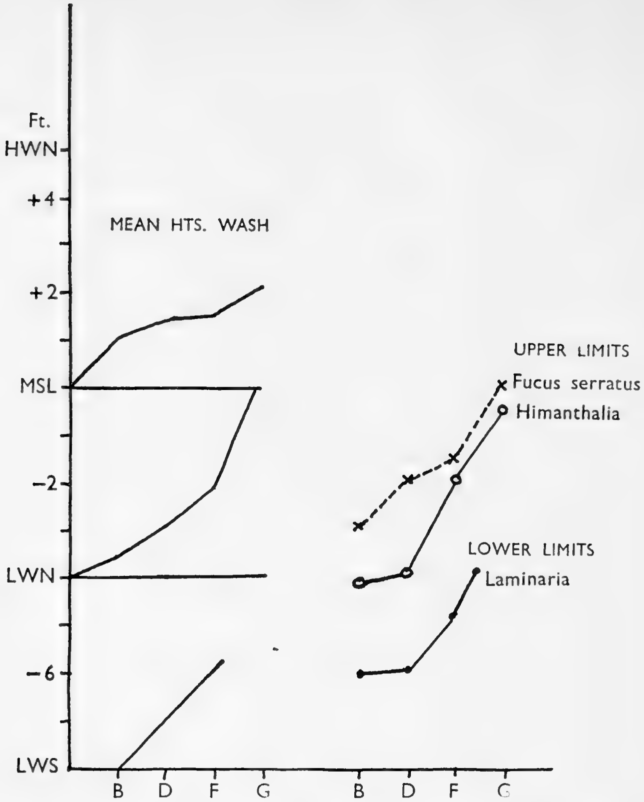

Fig. 192 Mean heights of wash at different levels on the shore at Port St. Mary (Isle of Man), and at points of varying exposure (B, D, F, G), and their effects on the limits of certain algae. (After Southward.)

alized scheme. The final answer can only come with further study, and here the recent introduction of the aqualung will make a detailed study of this belt really possible.

The levels of the upper belts in the mid-littoral and of those in the supra-littoral in any locality are not entirely dependent upon the height of the spring tides. On an exposed coast the shore is open to considerable wave action and a heavy spray rises against the rocks to a height sometimes of many feet. As a result of this wave action both upper and lower limits are elevated several feet above their normal. This elevation is known as the 'splash zone'. On a very exposed coast with big waves the splash zone can be subdivided into (*a*) wash zone, which is the height the actual wave washes up the rock face, (*b*) the splash zone, which is represented by actual splash from the wave, (*c*) the spray zone. On exposed coasts in the Isle of Man the wash zone extends down the whole shore (Fig. 192) and this is probably true in other parts, e.g. Pacific shores of America, Tasman Sea shores of New Zealand. The splash zone (*b*) is generally only a few feet but the spray zone (*c*) may be considerable. On the West Coast of New Zealand littorinids occur up to 40 ft. above the highest spring tides, and the spray from the giant waves can be seen drifting in nearly every day of the year. It is likely, however, that the size and growth of algal organisms in such elevated zones is not only due to the waves, but is also dependent upon moist air conditions that keep them damp during low tide periods.

It might be thought that the bathymetric levels of the different belts on the shores would be very uniform throughout a region because it could be argued that the controlling factors would be uniform. Sufficient work has been carried out now to show that this idea is not correct. In Great Britain the bathymetric levels of *Fucus vesiculosus* and *F. serratus* vary from place to place (Knight and Parke, 1950). In New Zealand the belts of the major dominants show considerable variation, even after allowance has been made for splash elevation. Work over a considerable range of coast-line has also demonstrated that change of latitude may exert an influence upon the belts. Gislèn (1943) has shown that on both sides of the Pacific the belts of brown algae tend to emerge with increase in latitude. Knight and Parke (loc. cit.) have shown the same thing to hold true for *Fucus serratus* though work in New Zealand (Trevarthen, 1954) has shown that *Hormosira* occupies significantly lower levels as one goes southward.

We may now consider the regional variants of Stephenson's basic zonation. In the North Sea and on the colder Atlantic shores of Europe the supra-littoral fringe is occupied by species of *Littorina*[1] with which are commonly associated belts of *Porphyra umbilicalis* and *Pelvetia canaliculata*. The last two species are essentially characteristic of colder waters. The mid-littoral is characterized by the presence of barnacles, though they do not necessarily occupy the full vertical range. On very exposed coasts these frequently

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[1] Where the rock surface is extensive there is often a 'black' lichen belt composed of *Lichina confinis* and *Verrucaria maura* above the *Littorina*.

exist alone, but where there is more shelter they are usually associated with a succession of fucoid belts:

(*a*) A belt of either *Fucus spiralis* or *var. platycarpus.*

(*b*) A belt of *Ascophyllum nodosum* with one of *F. vesiculosus* immediately below or *vice versa* with an intervening middle belt where both species occur.

(*c*) The lowest belt of the mid-littoral is commonly dominated by *F. serratus*, or by species of *Laurencia* and *Rhodymenia* where there is shelter, or *Gigartina* or *Chondrus crispus* where there is more exposure.

One feature of the belts in this part of the world is the important part played by the fucoids. A comparable covering of algae is commonly absent in the corresponding cold waters of the Pacific (see p. 336).

Where the substrate is suitable, the sub-littoral fringe is characterized by species of *Laminaria*, especially *L. digitata*. During the last war these algae became of interest commercially (see p. 451), and surveys of the *Laminaria* beds were made by the present writer and more extensive ones later by members of the Scottish Seaweed Research Association. It is evident that the relative proportions of the different species vary with depth and locality and there may also be considerable variations. In the sub-littoral when rock gives way to stones and then shingle so the algal dominants change from *Laminaria digitata* to *L. saccharina* to *Halidrys* and finally to *Chorda* and small red and brown algae.

On the rocky shores throughout the world communities of

DIATOM COMMUNITIES—SOUTH ENGLAND

	ON CONCRETE	ON CHALK
Supra-littoral	Achnanthes-Myxophyceae Amphipleura rutilans	Amphora-Nitzschia
Mid-littoral	Fragilaria-Melosira (Swanage)	Melosira-Barnacles Synedra-Pylaiella
Sub-littoral fringe		Schizonema ramosissima Schizonema grevillei Rhabdonema-Licmophora

marine diatoms can be found. These, because of the taxonomic problems involved, have been but little studied. A contribution to this problem has been made by Aleem (1950) working at Brighton and Swanage in South England and may be referred to here as representing European conditions. As might be expected the diatom communities differ depending on the nature of the substrate. There is also a difference depending on the actual bathymetric level. This is illustrated on page 334:

The different diatom communities are not to be found all the year round, but in general are at their best sometime between January to March or in the autumn and winter.

On the North Atlantic shores of North America belts are found in which *Ascophyllum* and *Fucus* still occur but the algal flora is much poorer than in Europe. Examples of the various belts are given below:

	Mt. Desert Is. Maine	*North Carolina*
Supra-littoral fringe	Littorinids Myxophyceae- Maritime lichens	Calothrix Enteromorpha
Mid-littoral	Barnacles Fucus-vesiculosus Ascophyllum Rhodymenia Fucus furcatus Spongomorpha	Barnacles Modiolus Porphyra Gelidium-Polysiphonia Rhodymenia Ostrea-Padina
Sub-littoral fringe	Alaria-Halosaccion	Sargassum Dictyopteris

Although fucoids and laminarians do not play so important a part in this region of the world, nevertheless other green and red algae replace them.

The belts in the North Pacific are quite different from those in the North Atlantic. The four lowest belts are dominated by large kelps (*Alaria*, *Egregia*, *Lessoniopsis*, *Laminaria*, *Nereocystis*) and it is only in the upper belts (*Ralfsia-Prasiola*, *Endocladia-Gigartina*, *Halosaccion*) that marine invertebrates become conspicuous. On the Japanese coasts the zonation is again quite different. There is commonly an upper belt of the red alga *Gloiopeltis*, then a belt of

Myelophycus and *Ishige* followed by a belt of *Sargassum thunbergii* and *Hijikia fusiforme*.

In the South Pacific there has been intense activity in recent years, and one of the principal features to emerge is that the major belts are primarily dominated by animals. One reason for this is that, apart from *Hormosira*, the predominant fucoids are all genera that require total or almost total submergence, only being really exposed at low water of spring tides. Various examples from the South Pacific and South Atlantic are illustrated in Table 8.

TABLE 8

	New Zealand	*Tasmania*	*Victoria*	*S.W. Africa*	*Chile*
Supra-littoral fringe	Littorinids	Littorinids	Littorinids	Littorinids	Littorinids
	Chamaesipho-Chthalamus	Chamaesipho-Chthalamus	Chamaesipho-Chthalamus	Balanus	Chamaesipho-Balanus
Mid-littoral	Hermella, Saxostrea or serpulid	Galeolaria	Algae or Galeolaria	Pomatoceros	Serpulids
	Corallines, Hormosira	Corallines	Pyura	Corallines	Corallines
Sub-littoral	Ecklonia, Carpophyllum or Durvillea	Lessonia, Xiphophora or Sarcophycus	Sarcophycus Cystophora	Laminaria	Durvillea, Lessonia

The occurrence of the large brown algae reflects exposure to wave action. *Sarcophycus* or *Durvillea* are found in the most exposed situations, whilst *Ecklonia*, *Hormosira* and *Cystophora* are typical of the more sheltered localities. *Xiphophora* and *Lessonia* occupy regions of moderate exposure. Transitional stages from the types of zoning that have been described above from the colder waters of the earth to those that are found in the warmer waters are represented by examples from Florida and North Carolina. In the latter place it is only the summer flora that is warm temperate, the winter flora being cold temperate (Williams, 1945).[1] Along this coastline the supra-littoral fringe is represented by a 'black zone' dominated by Myxophyceae and marine lichens. The upper part of the mid-littoral is dominated by barnacles (*Chthalamus*, *Tetraclita*),

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[1] A similar combination of floras exists in the Chatham Islands off New Zealand.

whilst the belt below is dominated by oyster and *Mytilus*. In this respect the warm water coast here is similar to the warm water east coast of the Auckland Province in New Zealand (see table p. 336). The lowest belt on these U.S. shores is algal and dominated by species of *Gracilaria*, *Ulva* and *Enteromorpha*. The sub-littoral fringe is represented by *Grateloupia* and *Sargassum*. The Stephensons have suggested that a mean winter water temperature of 10° C should form the limit between cold temperate and warm temperate shores. Bennett and Pope (1953) in Australia, however, regard the belts on the shores of Victoria (see table p. 336) as typically cold temperate, but the mean winter temperature of the water is 11·8° C. In the event it may prove impossible to set an exact temperature at which the transition takes place.

Our knowledge of zonation in the tropical and sub-tropical coasts is much less extensive. There are, however, a few examples. Thus, in the tropical waters of the Caribbean, algae replace animals as the major dominants in the belts.

	Florida Keys	*Jamaican Keys*	*Jamaica*
Supra-littoral fringe	Bare white belt Grey belt (Bostrychia) Black belt (Myxophyceae)	Bare Red — Herposiphonia Black — Myxophyceae	Flat limestone or Beachrock Myxophyceae or Gelidium-Bostrychia
Mid-littoral	Yellow belt (algal turf) Lower platform (Valonia)	Algal turf Cladophoropsis Herposiphonia Champia Centroceras, Cladophoropsis, Caulerpa	Algal turf (Padina) Valonia
Sub-littoral	Reef flat. Coral and mixed algae (mostly Siphonales)	Coral and mixed algae (Mostly Siphonales)	Coral and mixed algae (Sargassum and Siphonales)

This may be compared with zonations recorded from a range of shores on the Gold Coast where again algae are predominant, especially on exposed coasts.

EXPOSED ——————————→ *SHELTERED*

Littorina				Supra-littoral fringe
Chthalamus Mytilus Centroceras Ulva Chaetomorpha Red algal turf	Littorina Chthalamus Ulva Chaetomorpha Red algal turf	Littorina Pylaiella Ulva Dictyopteris	Littorina Pylaiella Ulva	Mid-littoral
Dictyopteris Lithothamnia	Dictyopteris		Red algal turf Sargassum	Sub-littoral

In the warm waters of the world the sub-littoral is of greater importance. On the shore exposure, even for a relatively short time, involves considerable desiccation and few species seem able to tolerate it. The sub-littoral flora depends primarily upon the type of substrate, whether sand, rock or coral. Workers in the Mediterranean believe that with those clear waters a number of different belts can be recognized. It remains to be seen whether the same is true of colder waters. The importance of the Mediterranean sub-littoral is illustrated by Table 9 which summarizes the various zones and belts proposed by workers for this region. Even in this sea there is a pronounced difference in the summer and winter aspects of the flora (see also North Carolina). Boreal Atlantic species such as *Ulothrix flacca*, *U. subflaccida*, *Bangia fusco-purpurea* and *Porphyra* spp. dominate the flora in winter, whilst in summer it is the tropical and sub-tropical species such as *Siphonocladus pusillus*, *Acetabularia mediterranea*, *Pseudobryopsis myura*, *Liagora viscida*, etc., which form the dominant species. In comparing the behaviour of the Mediterranean vegetation with that of the Boreal Atlantic one may distinguish several types of algal periodicity:

(1) Algae with a summer vegetation period in both the English Channel and the Mediterranean. These algae usually occur at a considerable depth where there is little or no temperature variation, e.g. *Sporochnus pedunculatus*, *Arthrocladia villosa*.

(2) Algae with a winter and spring vegetational period in both the Mediterranean and the English Channel, e.g. species of cold waters such as *Ulothrix flacca*.

(3) Algae appearing in the winter and spring in the Mediterranean but during the summer in the English Channel. With

TABLE 9

Different systems of classification for the marine belts of the Mediterranean

	Forbes (1842)	Lorenz (1863)	Ardissone and Strafforello (1877)		Pruvot (1895)		Flahault (1901)		Seural (1924)		Feldmann (1937)	Molinier (1953–1954)
		I Supralittoral			Subterrestial zone		Subterrestial zone		Inter co-tidal belt	Superior horizon	Supra-littoral belt	Supra-littoral
		II Region of emergent littoral	Zone I	Subzone I	Superior horizon	LITTORAL ZONE	Marine littoral zone	Superior horizon		Middle horizon	Littoral belt	Meso-littoral
Mean low water-mark												
				Subzone II	Middle horizon			Inferior horizon		Inferior horizon	Upper infra-littoral	Infra-littoral (Photophilous zone)
	Region I	III Region of submerged littoral		Subzone III								
	Region II	Region IV	Zone II									
	Region III Region IV	Region V Region VI	Zone III		Lower horizon		Marine sublittoral zone		Littoral belt		Lower infra-littoral	
	Region V Region VI Region VII											Infra-littoral (Sciaphilous zone)
					Lower limit vegetation							Elittoral
	Region VIII						Abyssal zone		Coastal belt		Elittoral	

such algae (e.g. *Nemalion helminthoides*) it may be considered that the winter and spring temperatures of the Mediterranean approach most closely to the summer temperatures of the Channel.

(4) Algae found during the summer months in the English Channel but persisting throughout the year in the Mediterranean, e.g. *Padina pavonia*. It is likely that low temperatures inhibit their growth in the Channel and it ought to be possible to determine the minimum adult survival temperature.

(5) Spring and winter algae of the Mediterranean but persisting throughout the year in the Channel, e.g. *Porphyra umbilicalis*, *Callithamnion corymbosum*. Here again there is probably a temperature correlation, but in this case the algae will not tolerate the high summer temperatures of the Mediterranean.

Comparisons of this nature are most valuable in helping us to understand something of the biological requirements of different species. They also indicate profitable lines of enquiry concerning the temperature relations of the algae.

The zonations to be observed in South Africa are especially interesting (Stephenson, 1939, 1944). On the West coast the waters are relatively cold and a cold water flora and fauna predominates. The east coast is bathed by the warm waters of the Indian ocean and a very different flora and fauna exists. In the intermediate zone of the Cape itself one can find all transitions from the cold water zonation to the warm water zonation (Fig. 193). Similar changes could no doubt be observed north and south of Cape Lookout in North Carolina and in other parts of the world. Very few of these changes have, as yet, been worked out.

Seasonal differences in the floras of different regions have been observed in various parts of the world. There are two general phenomena: one is the actual replacement of certain species by others, e.g. Mediterranean, North Carolina and elsewhere; the other is changes in the vertical levels of certain algae on the shore. Thus, in the Isle of Man successive generations of *Cladophora rupestris* move vertically up and down several feet annually, the movement being rendered possible because there is a monthly reproduction when the sporelings only survive at the most favourable level for the particular time of the year, and this is not necessarily that in which the parent plants are growing. Some algae migrate up in winter and down in summer, whilst others do the very reverse.

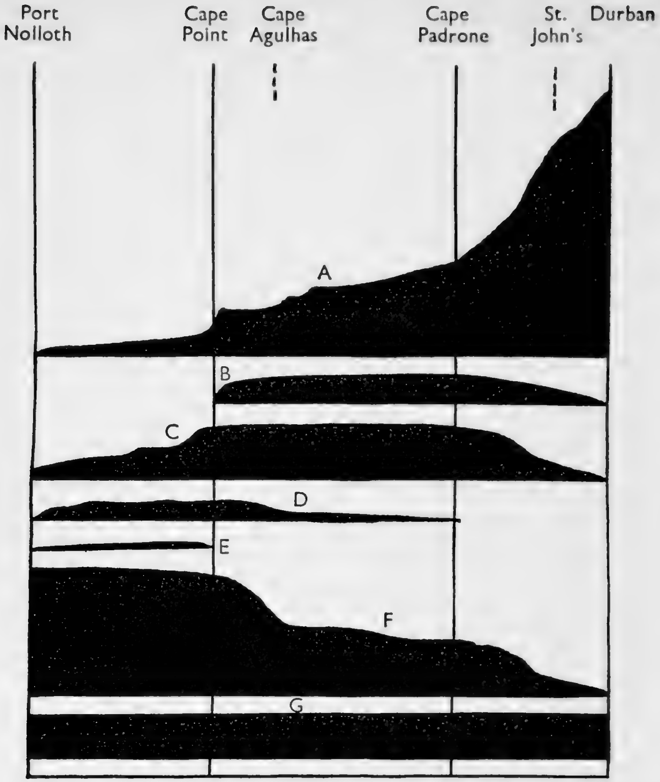

Fig. 193 Composition of fauna and flora of South African shores between Port Nolloth and Durban, showing the relative proportions of the different components.

A = Warm water element.
B = South eastern element.
C = South coast intermediate element.
D = South west element.
E = Western element.
F = Cold water element.
G = Cosmopolitan element.
(After Stephenson.)

It is suggested that the nature of the response to temperature controls the movements of those plants that migrate down in winter, whilst response to strong insolation determines the behaviour of those that move down in summer. It is likely that it is the response of the sporelings rather than the response of the adults that is involved, though the problem has not been investigated experimentally.

In the belts and zones that have been described so far, only what may be termed the normal has been considered. Variations in any region may occur as a result of changes in protection and exposure, e.g. in Europe *Ascophyllum* disappears in more exposed places and its niche is taken by *Himanthalia*. In New Zealand and Tasmania, *Hormosira*, *Ecklonia*, *Cystophora*, *Carpophyllum*, disappear on exposed coasts and are replaced by *Pachymenia* and *Durvillea* or *Sarcophycus*. Normally substrate does not have a very profound effect on the main belts but chalk or limestone rocks do produce a profound change in the flora. This is very strikingly illustrated by the zonation on the chalk cliffs of Dover. Fresh water, either in the form of substantial streams or rivulets induces a change in the flora. In the case of rivulets a dense growth of *Ulva* and species of *Enteromorpha* marks their course through nearly all the normal belts on the shore. In the case of streams the dominants of the belts may change, i.e. in Europe *Fucus ceranoides* replaces *F. spiralis* in such places.

It should be evident that any really adequate study of marine coastal zonation must involve an appreciation of the part played not only by the algae but also by the animals. The ecologist must indeed be a biologist and the communities he recognizes must be biotic communities in the strictest sense of the term. The other alternative is for teams of botanists and zoologists to work together.

Phytoplankton

Apart from the attached fauna and flora to be found on the littoral shores there is a vast fauna and flora floating primarily in the surface waters of the earth. This is composed of phyto- and zooplankton, and is the principal food of fish. The phytoplankton consists primarily of diatoms and dinoflagellates, and the numbers are so enormous that it is in the waters of the globe that the maximum carbon fixation takes place. The extent of the crop depends primarily on five factors: (*a*) rate of reproduction, (*b*) rate of removal of individuals by death or consumption by larger organisms, (*c*) light intensity in relation to photosynthesis, (*d*) availability of nutrients, (*e*) temperature. To these it has recently been suggested should be added the effect of excreted or ectocrine substances since they may partly determine the annual sequence of the organisms.

In nearly all the waters where studies have been carried out it has been found that there are distinct spring and autumn maxima, when some component species occur in great abundance. These maxima appear to be associated with an interaction between light supply and availability of nutrient salts. It has been found that at the periods of maxima the nitrogen and phosphate are greatly reduced, and if the latter falls below a certain value it may limit photosynthesis. In winter in temperate waters there is a rapid vertical mixing of the waters bringing up fresh nutrients from the lower layers, and this is responsible for the development of the spring maximum. Continual vertical movement maintains a rich medium, and as a result the cold upwellings (e.g. off South-West Africa and California) are very rich in plankton. For certain species, lack of trace elements, such as iron or manganese, as a result of their absorption by other organisms, may bring about a fall in reproduction and later growth.

An exception to the normal spring and winter maxima is provided by the enclosed waters of the Mediterranean where the maxima occur in November–December and March, the one in March being the larger.

During the 1939–45 War attempts were made to increase the plankton, and hence the fish, by adding artificial fertilizers to large, more or less enclosed, bodies of water such as lochs. The addition of such fertilizers did increase the plankton and also the fish and it may be that a technique such as this can have a valuable application[1]. In other cases a planktonic organism may have an adverse effect on fisheries. One of the most outstanding examples is *Phaeocystis pouchetii*, a coloured flagellate which, when present in quantity, gives the waters of the North Sea a muddy appearance, the so-called 'baccy juice' (Savage, 1932). Herrings are repelled by this organism when it is present in mass, and its vernal maximum off the Dutch coast turns the northward herring migration west towards the coast of East Anglia, and thus brings about the spring fishery there (Fig. 194 A, B). The occurrence of an abnormal autumn maximum out of its usual station may completely change the grounds of the autumn fishery during the southward migration: such an abnormal maximum is known to have occurred in 1927 (Fig. 194 C).

[1] This technique has been used in recent years with the fish ponds made from the mangrove swamps in the Philippines.

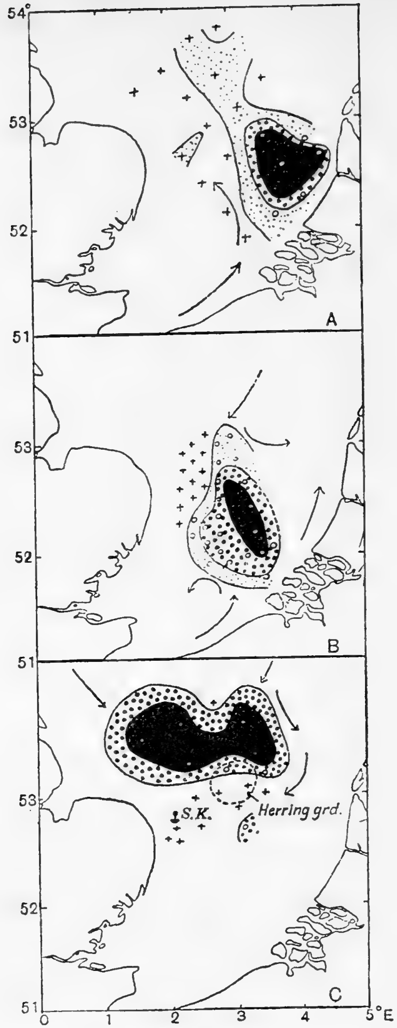

Fig. 194 *Phaeocystis* and herrings. A, distribution of *Phaeocystis*, 17–24 April, 1924, normal distribution. +, *Phaeocystis* scarce or absent. o, stations in *Phaeocystis* zone. Intensity of concentration shown by shading. → assumed herring migrations. B, distribution of *Phaeocystis*, 8–13 April, 1926. Spring fishery interference. C, distribution of *Phaeocystis*, 6–9 November, 1927. Autumn fishery interference. *S.K.* = Smith's Knoll Lightship. (After Savage.)

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Chapter XIII

ECOLOGY OF SALT MARSHES

In comparison with the rocky coast fewer studies have been carried out on the algal ecology of salt marshes, but those that have been published can be regarded as having made considerable advances in our knowledge of these extremely interesting areas. Their neglect in the past has probably been due to the fact that the algae are often microscopic and hence not so pleasing aesthetically even when present in abundance, and also they are more difficult to determine taxonomically. In practice, however, a detailed study of any one area often produces the somewhat unexpected result of a quite extensive flora. For example, the number of species recorded from the English salt marshes of Norfolk is about two hundred, which does not compare unfavourably with the number on a rocky coast.

An investigation of any salt-marsh area shows that the algal communities offer a somewhat different aspect to the algal communities of a rocky coast. In the latter case it has been seen that zonation is a characteristic feature together with some superimposed seasonal changes and migrations. On the salt marshes it is not really possible to distinguish any zonation but there may be well-marked seasonal changes in any one area. Thus on a fairly low marsh the 'Autumn Cyanophyceae' appear in autumn and early winter, they disappear and are replaced in spring by the *Ulothrix* community, which in its turn is replaced during the summer months by *Enteromorpha* and so the cycle proceeds. Furthermore, as each year the ground level increases in height in relation to the tide through the continual deposition of silt, the submergences become fewer and the communities are replaced by others on account of the modified conditions. As a result there is a definite dynamic succession of the different communities over a long period of years. This cannot be seen on a rocky coast where there is no succession in time and where the succession in space is static.

The phenomenon of dynamic succession in this type of habitat necessitates a somewhat different approach to the problem of the status of the community. The continual replacement of one community by another as the marsh increases in height provides changes that are more akin to those that are found in land habitats. With this in mind the present author recently attempted a survey of our present information about the algal communities of salt marshes. The principal features are set out in Table 10, and it will be observed that in the suggested nomenclature the ordinary ecological terminations for developing seres has been employed. Whether this is entirely justified in view of the present somewhat scanty knowledge may perhaps be questioned, but it is possible that if the nomenclature can be placed on a proper basis at an early stage it should facilitate further comparisons.

Table 10 shows that there is not quite the same ubiquity of communities in the different areas that can be found on a rocky coast. The reason for this is probably to be associated with the very different types of salt marsh that can be found. For example, the Irish marshes are composed of a form of marine peat, the marshes on the west coast of England have a large sand component in the soil, the marshes on the south coast bear a tall vegetation of *Spartina* growing in a very soft mud, whilst the east coast marshes bear a very mixed vegetation growing on a mud that tends to be clay-like. In New England the marshes are formed of a marine peat whilst in New Zealand the soil is either a muddy or sandy clay. In spite of this, however, the Sandy Chlorophyceae, Muddy Chlorophyceae, Gelatinous Cyanophyceae, *Rivularia-Phaeococcus* socies, *Catenella-Bostrychia* consocies and the *Fucus limicola* consocies all have a wide distribution though they may not necessarily appear at the same relative levels on the different marshes. On the whole, however, they are very often found in the same phanerogamic community.

A comprehensive tour of the salt marshes of England will show us that one or more of the communities described above occur in all the different districts. Where the soil is rather sandy a *Vaucherietum* can be distinguished dominated by *V. sphaerospora*, but where the phanerogamic vegetation is very dense or heavily grazed by animals the algal vegetation is poor, e.g. south and west coast marshes. The Sandy Chlorophyceae and *Vaucheria thuretii* have a wide distribution, as also the *Catenella-Bostrychia* community, whilst the pan flora appears to be richest in East Anglia. Perhaps the most interesting feature is the distribution of the marsh fucoid *Pelvetia canaliculata* ecad *libera* which occurs in north Norfolk, Lough Ine and

Strangford Lough in Ireland and at Aberlady near the Firth of Forth but with no apparent intermediate stations. The normal form is present in other areas where there are marshes in the vicinity, e.g. the west coast marshes, but the marsh form does not appear to have developed. The evidence at present available would suggest that it has originated independently in the three areas, and in that case it can only be concluded that certain conditions must be fulfilled before the marsh form can develop from the normal species. This is a problem that is still awaiting solution.

One of the more interesting features of the algal vegetation of salt marshes is the occurrence of the marsh fucoids. These are peculiar forms which are either free living on the marsh or else embedded in the mud, and they must all at one time have been derived from the normal attached form. Sometimes they bear a fairly close resemblance to the attached form but in other cases they have been very considerably modified, and it is only the existence of intermediate forms which enables us to indicate the normal type from which they came. East Anglia is essentially the home of the marsh fucoids, although Strangford Lough in Ireland is also extremely rich. In Norfolk, for example, considerable areas can be found occupied by *Pelvetia canaliculata* ecad *libera*, whilst the three marsh forms of *Fucus vesiculosus*, ecads *volubilis*, *caespitosus* and *muscoides* are also abundant, the last two being embedded in the soil.

Apart from these forms there are three other loose-lying marsh forms derived from *Fucus vesiculosus* but these are confined to the Baltic, e.g. ecads *nanus*, *subecostatus* and *filiformis*. A small crawling marsh form derived from *F. ceranoides* has been described from the Irish and Dovey marshes, and another larger, free living one from Strangford Lough in Ireland; like many others of this type it is profusely branched, fertile conceptacles are rare and, when present, are invariably female. *F. spiralis* vars. *nanus* and *lutarius* are other marsh derivatives, whilst *Pelvetia canaliculata* not only gives rise to ecad *libera* but also to a small embedded form, ecad *radicans*, which has been recorded from the Dovey marshes. There is also another form, ecad *coralloides*, which has been described from Blakeney and more recently from the Cumbrae marshes, but until more is known about this particular ecological form it ought to be regarded with some degree of caution. *Ascophyllum nodosum* var. *minor* is a dwarf embedded variety, ecad *mackaii* of the same species is a free-living form found on American salt marshes, in Scotland and on the shores of Strangford Lough in Ireland, whilst ecad *scorpioides* is a partially embedded form found on the Essex marshes, on the shores of Strangford Lough and in eastern North America. All these forms probably originated as a result of vegetative budding, although it is also possible that they have developed from fertilized oogonia that became attached to phanerogams on the marsh. There is definite evidence that *Ascophyllum nodosum* ecad *scorpioides* arises by vegetative budding from fragments of the normal plant, whilst it has been suggested that conditions of darkness or lowered salinity may be favourable for the development of ecad *mackaii* (Gibb, 1957).

Although there are no species of *Fucus* in the southern hemisphere, an interesting free-living form of the southern fucoid *Hormosira banksii* has been recorded from mangrove swamps in New Zealand. It does not form extensive communities, as do the salt marsh fucoids in the northern hemisphere, but it is the only known representative of the limicolous fucaceae in the south.

As a group the marsh fucoids are characterized by:

(1) Vegetative reproduction as the common means of perpetuation.
(2) Absence of any definite attachment disc.
(3) Dwarf habit.
(4) Curling or spirality of the thallus.
(5) In the species derived from *Pelvetia*, *Fucus vesicolosus* and *F. spiralis* that have been investigated it has been found that the three-sided juvenile condition of the apical cell is retained throughout life. The cryptostomata are marginal and division in the megasporangia is only partial or else does not occur. It is suggested that these features are due to:
    (*a*) exposure, which results in a dwarfing of the thallus;
    (*b*) lack of nutrient salts which induces a narrow thallus;
    (*c*) the procumbent habit and consequent contact with soil causes spirality because growth takes place more rapidly on the side touching the soil.

The cause of sterility may either be a result of the high humidity (according to Baker, 1912, 1915) or, more probably, because of the persistence of the juvenile condition as represented by the apical cell and cryptostomata. The marsh fucoids occur most frequently

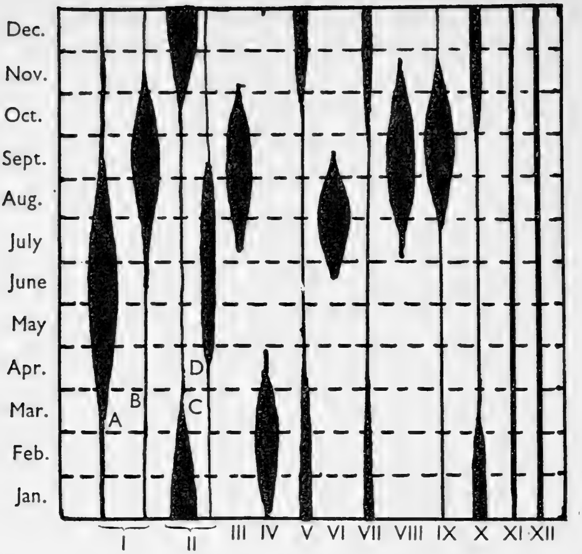

Fig. 195 Distribution in time of the algal communities on the salt marshes at Canvey and Dovey. I. General Chlorophyceae. II. Marginal diatoms (two components, (A) those with a winter maximum; (B) those with a summer maximum). III. Marginal Cyanophyceae. IV. *Ulothrix* community. V. *Enteromorpha minima*. VI. *Anabaena torulosa*. VII. Filamentous diatoms. VIII. Autumn Cyanophyceae. IX. *Phormidium autumnale*. X. *Rivularia-Phaeococcus*. XI. *Pelvetia canaliculata*. XII. *Catenella-Bostrychia*. (After Carter.)

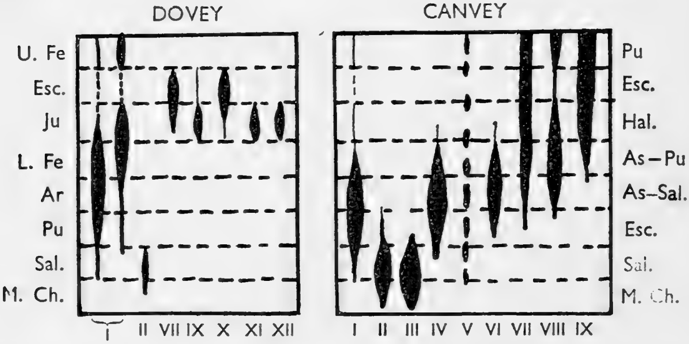

Fig. 196 Distribution of the algal communities in space on the Canvey and Dovey marshes. Symbols as in Fig. 194. Ar = Armerietum; As = Aster; Esc = Greek bank (escarpment); Fe = U (upper) and L (lower) Festucetum; Hal = Halimionetum; Ju = Juncetum; Pu = Puccinellietum; Sal = Salicornietum; M.Ch. = Muddy Channel. (After Carter.)

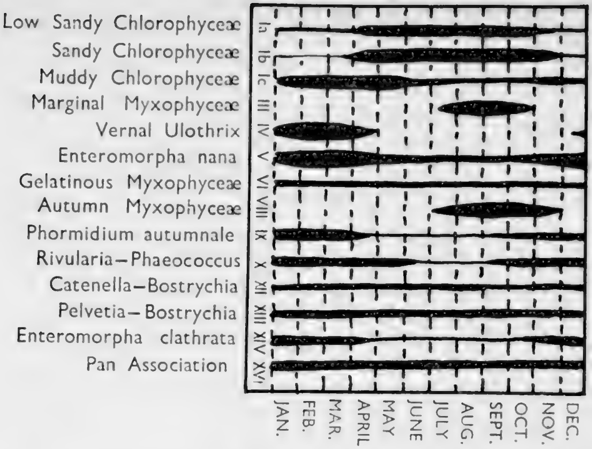

Fig. 197 Distribution of the algal communities throughout the year at Scolt, Norfolk. (After Chapman.)

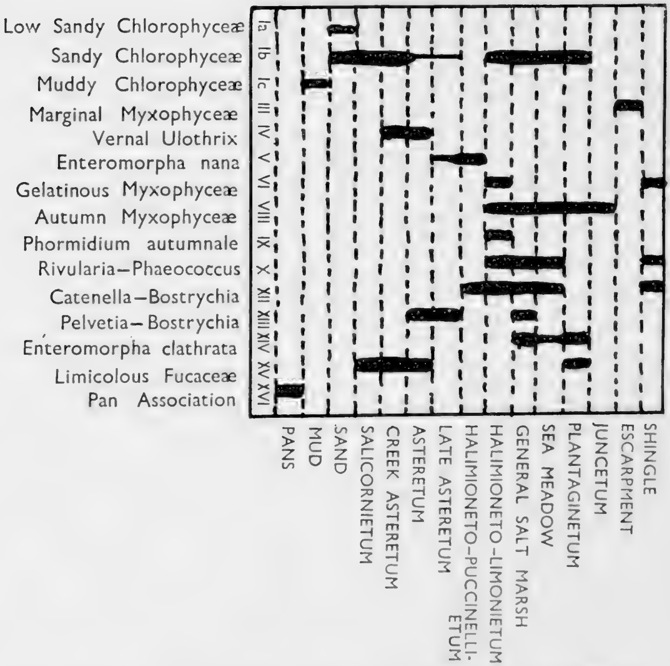

Fig. 198 Distribution of the algal communities in space at Scolt, Norfolk. (After Chapman.)

either as pioneers on the lowest marshes or else as an undergrowth to the phanerogams.

Outside the salt marshes of England, the salt marshes of New England and New Zealand possess communities comparable to those found in Great Britain. In Table 10 the limicolous Fucaceae community in New Zealand refers to the free-living *Hormosira*. Attention may also be drawn to the *Gracilaria flagelliformis* community which is widely distributed over mud flats and in mangrove swamps in New Zealand. It probably also occurs in Australia and would seem to be the only endemic southern hemisphere community so far recorded. The plants of *Gracilaria* are not originally free living but are attached to shells of molluscs buried in the mud.

One of the more striking physiographical features of salt marshes is the salt pan. The number, shape and size of these on the different salt marshes varies very considerably, but they generally contain a certain number of algae, especially those pans which occur on the lower marshes. They are important because they provide a much wetter habitat at levels where normally conditions may be somewhat dry. Some authors are not prepared to acknowledge the existence of a pan flora because they maintain that the plants are not persistent. A continual study of pans in one area over a considerable period of time by the present author showed that a definite pan flora did exist from year to year, and that many of the species comprising it reproduce during the course of their existence. The mere fact that they can carry out normal reproduction would seem to validate the recognition of such a flora.

On the lower marshes the pan flora is commonly composed of Chlorophyceae, whilst with increasing marsh height the Chlorophycean element decreases and the Myxophycean element increases. A few of the constituent members, e.g. *Monostroma*, are seasonal in appearance, whilst on some marshes there are pans which contain algae that are normally associated with a rocky shore, e.g. *Colpomenia*, *Polysiphonia*, *Striaria*. These persist from year to year in spite of the stagnant conditions, and when compared with the habitats occupied by the same species on a rocky coast it is found that they are probably growing at an unusually high level. A comparison of the Norfolk marsh flora with that of a comparable rocky coast leads to two generalizations which are probably valid for other marsh areas elsewhere:

(*a*) Species that are littoral on a rocky coast are to be found growing at lower levels, usually sublittoral, on the marsh coast. This must be ascribed to the lack of a solid substrate at the higher levels where they would normally grow.

(*b*) Littoral species of the rocky coast are found growing at higher levels on the marsh coast. This can be understood in the case of those species living in pans or in the streams where they are continually covered by water, and in the case of a few species actually growing on the marshes it is probable that they are enabled so to do because the phanerogams provide protection from desiccation. On a rocky coast such protection would be lacking at high levels.

Turning now to the algal vegetation of the marshes proper, Carter (1932, 1933) has suggested that on the Canvey and Dovey marshes light and space relations, rather than factors relating to level, influence the distribution of the various species. Whilst this is undoubtedly true there is no doubt that the increasing height of a marsh with its consequent greater exposure does nevertheless effectively determine the upper height to which many plants can go. The species to be found on the higher marshes in Norfolk are either fucoids or gelatinous Myxophyceae, both of which have the power of retaining moisture. The more delicate Chlorophyceae are more or less confined to the lower levels. On the other hand a dense phanerogamic vegetation, such as one finds on the south coast marshes where the tall *Spartina townsendii* must lower the light intensity considerably, does reduce the quantity of algal vegetation. A similar state of affairs has been observed on the grass-covered marshes of New England.

From data available it is possible to compare the distribution in space (e.g. among the different phanerogamic communities) and time of the marsh communities recorded from Canvey, Dovey and Norfolk. Figs. 195 and 196 show the distribution of the Canvey and Dovey communities and they should be compared with Figs. 197 and 198 for similar marsh communities of Norfolk. Some of the smaller communities, e.g. *Rivularia-Phaeococcus* and Gelatinous Cyanophyceae[1], are apt to be overlooked in summer because the constituent species shrivel up so much or else because the colonies become covered by an efflorescence of salt. An examination of the distribution of the various communities on the Norfolk marshes

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[1] Myxophyceae is probably preferable: see p. 278.

TABLE 10

No.	*Norfolk*	*Canvey and Dovey*	*Clare Is.*
I	General Chlorophyceae	General Chlorophyceae	——
I*a*	Low sandy Chlorophyceae	——	——
I*b*	Sandy Chlorophyceae	——	Sandy Chlorophyceae
I*c*	Muddy Chlorophyceae	——	Muddy Chlorophyceae
II	Not investigated	Marginal diatoms	——
III	Marginal Cyanophyceae[1]	Marginal Cyanophyceae[1]	?
IV	Ulothrix community	U. flacca community	——
V	Enteromorpha minima community	E. minima-Rhizoclonium community	——
VI	Gelatinous Cyanophyceae[1]	Anabaena torulosa community	——
VII	Not investigated	Filamentous diatoms	——
VIII	Autumn Cyanophyceae[1]	Autumn Cyanophyceae[1]	——
IX	Phormidium autumnale community	Phormidium autumnale community	——
X	Rivularia-Phaeococcus	Rivularia-Phaeococcus	Rivularia-Phaeococcus
XI	Catenella-Bostrychia community	Catenella-Bostrychia	Catenella-Bostrychia
XII	Pelvetia-Bostrychia community	——	——
XIII	Enteromorpha clathrata community	——	——
XIV	Fucus limicola community	Pelvetia muscoides community	Fucus limicola association
XV	Pan community	——	——
XVI	Vaucheria community	?	?
XVII	——	——	——

[1] Myxophyceae is probably preferable: see p. 278.

Salt-Marsh Algal Communities

Lough Ine	*New England*	*New Zealand*	*Suggested nomenclature*
——	General Chlorophyceae	——	General Chlorophyceae associes
——	——	——	Low sandy Chlorophyceae consocies
Filamentous algae	Rhizoclonium	Sandy Chlorophyceae	Sandy Chlorophyceae consocies
——	Cladophora-Enteromorpha	——	Muddy Chlorophyceae consocies
——	——	——	Marginal diatom consociation
Vertical banks assn.	——	——	Marginal Cyanophyceae[1] consociation
——	Ulothrix community	?	Vernal Ulothrix socies
——	Enteromorpha minima community	Enteromorpha minima community	Enteromorpha minima socies
Gelatinous Cyanophyceae[1]	Gelatinous Cyanophyceae[1]	——	Gelatinous Cyanophyceae[1] socies or society depending on permanence
——	Not investigated	Not investigated	Filamentous diatom consocies
——	Autumn Cyanophyceae[1]	Autumn Cyanophyceae[1]	Autumn Cyanophyceae[1] consocies
——	——	——	Phormidium autumnale socies
Rivularia association	Rivularia-Phaeococcus	Rivularia community	Rivularia-Phaeococcus socies
Catenella-Bostrychia	——	Catenella-Bostrychia	Catenella-Bostrychia consocies
——	——	——	Pelvetia limicola consocies
——	——	——	Enteromorpha clathrata socies
Limicolous Fucaceae association	Limicolous Fucaceae	? Limicolous Fucaceae	Fucus limicola consocies
Pan association	Pan association	Pan association	Pan association
?	Vaucheria community	Vaucheria community	Vaucheria consocies
——	——	Gracilaria community	Gracilaria community

[1] Myxophyceae is probably preferable: see p. 278.

shows that five communities are each confined to one type of habitat. This relationship may be due to:

(*a*) Association with a particular phanerogamic community, e.g. *Phormidium autumnale* (IX) and *Halimione portulacoides*.

(*b*) Dependence upon certain edaphic conditions, e.g. Muddy Chlorophyceae (I*c*).

(*c*) Dependence upon the physical character of the environment, for example slope, exposure, wave action, e.g. Marginal Cyanophyceae[1] (III), Vernal *Ulothrix* (IV) and the Pan Association (XVI).

The factors operating on salt marshes are in many respects similar to those found on a rocky coast. The principal factor is the tidal one with all the derived factors that are associated with rise and fall of the tide (i.e. salinity changes, water loss, temperature changes, metabolic changes). Since salt marshes are restricted to protected coasts, there are not the changes that take place with transition to an exposed coast, as on rocky shores. However, there is relative microprotection as between the open low-lying bare sand or mud flats and the higher phanerogamic covered marshes. It is worth noting that in the only comparative analysis of the tidal factors operating on salt marshes (Norfolk (England), Lynn (Massachusetts) and Cold Spring Harbour (Long Is.)) it became evident that for some of the species common to the areas the controlling factors must be the same and are indeed the tidal factors.

Before leaving the subject of salt marshes, it should be noted that some of the communities so characteristic of these physiographic features are also to be found in mangrove swamps. Thus the wide-spread *Catenella-Bostrychia* community occurs clothing the aerating roots (pheumatophores) and lower trunks of mangroves. Different species of *Catenella* and *Bostrychia* are associated in different parts of the world. A Myxophycean community is also wide-spread on the pneumatophores, and on the mud itself species of *Vaucheria* may form green patches.

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[1] Myxophyceae is probably preferable: see p. 278.

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Chapter XIV

FRESH-WATER ECOLOGY, SOIL ALGAE

One of the major problems in this branch of algal ecology appears to be the establishment of a successful classification upon which field studies can be based. Up to 1931 the outline given by West in 1916 was in current use, but since then a scheme proposed by Fritsch (1931) has more or less taken its place. It would seem, however, that neither scheme alone is wholly satisfactory, but that a combination of the two provides a very suitable basis for workers in this field. An outline of such a combination of the two schemes is briefly described below.

A. *Subaerial communities*

These develop at their best in the tropics although they can also be found in temperate regions. In the latter, Protococcales and *Trentepohlia* form the principal elements, whilst in the tropics the Myxophyceae and other members of the Trentepohliaceae (*Cephaleuros*, *Phycopeltis*, etc.) represent the dominant components.

B. *Communities of dripping rocks*

This can be subdivided into

(i) Permanently attached communities:
  (*a*) On living material.
  (*b*) On dead organic material.
  (*c*) On the hard rock (Epilithic).
(ii) Temporarily attached communities:
  (*a*) On living material.
  (*b*) On dead organic material.
  (*c*) On the hard rock (Epilithic).

C. *Aquatic communities*

These vary from season to season and frequently have a marked periodicity which is controlled by diverse factors. Four subdivisions of the aquatic communities can be recognized (see below) and *each one* of the subdivisions can be treated as follows:

(1) Attached communities (frequently termed the *Benthos*):

A	B
Permanently attached	Temporarily attached

- (*a*) On living material (Epiphytic or epizooic).
- (*b*) On dead organic material.
- (*c*) On inorganic material (Epilithic).
- (*d*) In the silt (Epipelic).

(2) Floating macro-communities (Pleuston):

- (*a*) Originating from loose bottom forms.
- (*b*) Originating from epiphytic forms.
- (*c*) Wholly floating throughout.

(3) Loose-lying communities of the bottom.

(4) Plankton or floating communities:

- (*a*) Limnoplankton of lakes.
- (*b*) Potamoplankton of slow rivers.
- (*c*) Cryoplankton of the eternal snows.

In this last category we have red snow due to the presence of *Chlamydomonas nivalis*; yellow snow with a flora of about twelve species all containing much fat; green snow, principally caused by zoogonidia of green algae; brown snow or ice due to the presence of *Mesotaenium* and mineral matter; black snow caused by *Scotiella nivalis* and *Rhaphidonema brevirostre*; and a light, brownish-purple ice-bloom caused by a species of *Ancyclonema*.

West (1916) divided the Aquatic Communities into the following four major subdivisions, each of which can be further subdivided in the manner illustrated above:

1. *Communities of rivers, rapids, and waterfalls*

In rapidly flowing rivers this is mainly composed of fresh-water Rhodophyceae, e.g. *Lemanea*, *Compsopogon*, *Sacheria*, *Thorea*, *Hildenbrandtia* (in acid waters, *Batrachospermum* and *Bostrychia*), *Cladophora* spp., *Vaucheria* spp., Myxophyceae, Chrysophyceae (especially *Hydrurus*) and diatoms. Where the streams are more sluggish *Enteromorpha* and *Hydrodictyon* tend to replace *Cladophora*, and in very sluggish streams and also in lakes one may find temporary floating mats of *Hydrodictyon*, *Enteromorpha*, *Oedogonium*, *Spirogyra* and *Rhizoclonium*.[1] Sluggish rivers also possess a definite Potamoplankton divided into:

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[1] This mostly refers to Europe.

(*a*) Eupotamic, thriving in the stream and its backwaters.
(*b*) Tychopotamic, thriving only in the backwaters.
(*c*) Autopotamic, thriving only in the stream.

A potamoplankton survey of three rivers in the Goros region showed that there were three maxima for diatoms and Chlorophyceae, and four for Myxophyceae. The total flora comprised 155 species which is an indication of how rich this type of plankton may be. It seems, however, that even though there may be a rich phytoplankton the component species do not form a distinctive association. In general the development of potamoplankton is dependent on the age of the water and whether the stream is in flood or drying up. The plankton of small streams appears to arise from the benthos.

It is convenient also to include here the flora of hot springs and streams. Myxophyceae are the major, and often the only constituents, the various species being capable of secreting carbonate of lime or silica to form rock masses such as travertine and sinter, the rate of deposition sometimes being as much as 1·25–1·5 mm. in three days. The highest temperature recorded for water with living plants (*Phormidium* (*Hapalosiphon*) *laminosum*) is 87·5° C. The number of forms capable of living in such an environment is considerable, no fewer than 53 genera and 163 species being recorded from the thermal waters of Yellowstone National Park. Recently it has been shown that one species, *Mastigocladus laminosus*, is capable of fixing atmospheric nitrogen, though it does not seem that this has any biological significance.

According to Blum (1956) the dominant benthic alga in much of the North Temperate zone is *Cladophora glomerata*. In the presence of certain metallic ions this species is adversely affected and may then be replaced by *Stigeoclonium tenue*, *Spirogyra fluviatilis*, *Phormidium autumnale*, etc. In Scandinavian streams it is often replaced by *Zygnema* and *Vaucheria*, and this fact has been made a basis for classification. Budde (1928) divided the mountain streams feeding the Ruhr River into two regions, an upper *Hildenbrandtia* region and a lower *Lemanea* region. One of the most favourable locations for algal growth is immediately down-stream of large rocks though the exact significance of this fact has not been worked out. As might be expected, seasonal variations occur in the vegetation. Thus in the Ruhr streams the spring period is characterized by dominance of diatoms with *Ulothrix* and *Hormidium* as subdominants. In the summer Chlorophyceae and desmids predominate and in the winter *Ulothrix* and *Hormidium* reappear. The effect of bank vegetation (overhanging trees, reeds, etc.) may be profound, especially in the degree of light reduction that it causes.

The most important controlling factor is apparently temperature but the chemistry of the water may also be significant. The absence or near absence of calcium, for example, may induce a myxophycean-rich flora. Light intensity variations and oxygen concentration changes may bring about local modifications of the water. In respect of pollution[1] it has been pointed out that algal species are not necessarily unerring indicator organisms.

It is possible to classify the communities of rivers and streams in the following way:

(*a*) Communities of vertical substrates:
  (1) Those attached to stones, mud banks or roots.
  (2) Epiphytic communities on phanerogams.
  (3) Spray communities.
(*b*) Communities of horizontal substrates:
  (1) Those attached to stones, sand or embedded in mud.
  (2) Epiphytic communities.
(*c*) Free living communities.

Certain algae appear to demand specific habitats, some of them unusual. Among such algae are species of *Basicladia* that grow on turtles, and species of *Characium* and *Characiopsis* that grow on the Crustacean *Branchipus*. There is still considerable scope for further work on river ecology, not only descriptive, but also studies that, for example, could link algal vertical distribution with depth of water.

2. *Associations of bogs and swamps*

These are very mixed associations with little or no periodicity, probably because of the relatively uniform conditions. Zygnemaceae, desmids and diatoms are most frequent, the desmid element changing considerably with altitude and type of substrate, whilst the presence of *Utricularia* apparently also increases the number and variety of the desmid species.

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[1] In the Saline river of Michigan the entry of certain metallic ions, as a result of pollution, causes the normal flora to be replaced by *Stigeoclonium tenue* and *Tetraspora* (Blum, 1957).

3. *Associations of ponds and ditches*

The flora exists under very varied conditions with a regular or irregular periodicity. In the temperate regions Protococcales, Zygnemaceae (dominant in spring) and diatoms (dominant in winter) form the chief elements. There is usually not enough aeration to permit the larger filamentous forms to be present, and for this reason the ponds and ditches can be divided into:

(*a*) those containing Cladophoraceae, which suggests that the aeration is good;

(*b*) those without Cladophoraceae. The substrate and fauna are also important factors in determining the type of vegetation to be encountered. The flora of tropical ponds contrasts sharply with that of temperate regions for there is

1. an excess of Mxyophyceae;
2. the poor aeration results in a relative scarcity of *Cladophora* and *Rhizoclonium* together with the epiphytes associated with them, and their place is taken by *Pithophora*;
3. a scarcity of *Vaucheria*, *Oedogonium*, Xanthophyceae and Ulotrichales;
4. an abundance of filamentous desmids together with *Spirogyra*.

In America Transeau (1913) concluded that fresh-water pond algae can be divided into seven classes based on abundance, duration and reproductive season, these classes and their periodicity

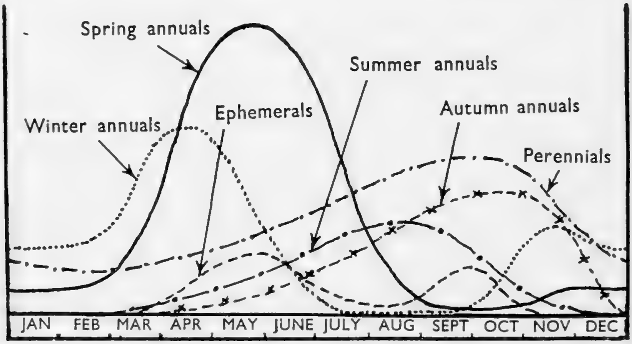

Fig. 199 Chart showing the estimated relative importance of the different types of algal periodicity throughout the year in the waters of E. Illinois. The irregulars are not depicted. (After Transeau from West.)

being represented in Fig. 199. The fact that periodicity of the different species is of widespread occurrence is evident from work in various parts of the world. Thus a study of a pond near Harpenden by Fritsch and Rich (1913) showed that the general aspect of the flora was dependent upon season and that four phases could be distinguished:

(*a*) Winter phase with *Microspora*, *Eunotia* and epiphytic diatoms, whilst *Ranunculus aquatilis* and *Callitriche* were the dominant phanerogams.
(*b*) Spring phase dominated by Conjugatae, *Oedogonium* and *Conferva*, with *Ranunculus aquatilis* as the most important phanerogam.
(*c*) Summer phase with *Euglena*, desmids and *Anabaena* associated with a phanerogamic vegetation of *Lemna*, *Glyceria* and *Bidens*.
(*d*) Sparse autumn phase with *Lyngbya* and *Trachelomonas* but without any dominant phanerogam.

The algal periodicity is thus more or less associated with a similar periodicity in the phanerogamic vegetation. The flora differs from that of a similar pool near Bristol in the absence of *Cladophora* and *Melosira*, and in their place there is a greater development of Xanthophyceae. The two types of flora could be regarded as distinct associations, but the difference is almost certainly due to poor aeration in the Harpenden pool. In spite of this the general trend of periodicity in the two pools is very similar: a winter phase characterized by a hardy filamentous form (*Cladophora* or *Microspora*) and diatoms, a spring phase with Zygnemaceae and an autumn phase with Oscillatoriaceae. The summer phase in the two pools is very different, and this is ascribed to the greater drying up of the Harpenden pool during that period. The flora of pools, therefore, is very dependent not only upon general climatic conditions, such as rainfall and insolation, but also upon what might be termed irregular microclimatic factors, e.g. aeration in the body of water itself. In the case of many of the species there is a profound relationship between the meteorological data and the frequency of the flora, e.g. *Microspora* and the Protococcales with temperature, *Oedogonium* and *Hormidium* with sunshine. The factors influencing the growth of aquatic algae are (1) seasonal, (2) irregular, (3) correlated. The first group, which are very obvious and need not be detailed, are principally of importance for large bodies of water, but they tend to be masked by the other two groups in small bodies of water:

- (2) Irregular factors:
    - (*a*) Abnormal rainfall:
        - (i) Species favoured by excessive rainfall.
        - (ii) Species favoured by drought.
    - (*b*) Abnormal sunshine:
        - (i) Species favoured by excessive sunshine.
        - (ii) Species adversely affected by excessive sunshine.
    - (*c*) Abnormal temperature:
        - (i) Species favoured by low temperatures.
        - (ii) Species favoured by relatively low temperatures.
        - (iii) Species favoured by high temperatures.
- (3) Correlated factors:
    - (*a*) Species depending on the enrichment of the water by decay of other members of the flora.
    - (*b*) Forms influenced in their development by competition with others.
    - (*c*) Forms influenced in their development by the presence of a suitable host, e.g. epiphytic forms.

A very definite correlation can frequently be established between the amount of sunshine and the phenomenon of reproduction, the latter process being most frequent when there is most sunshine. This is in accordance with experimental work which has shown that reproduction is initiated by the presence of bright light. An unusual concentration of the salts in the water during a period of drought may, however, counteract the influence of sunshine.

A study of algal periodicity in some ponds near Sheffield, together with the results of fortnightly analyses, has suggested a correlation with the nitrate factor for some species. The maximum for this occurs in December whilst there is a minimum in June, and it was observed that *Volvox* received a severe check when the nitrate was high and only reproduced at times of low nitrate value. *Ulothrix* reappeared yearly in these ponds, whilst *Euglena* annually attained to a maximum between July and August soon after the nitrate minimum.

A similar study by Brown (1908) of some pools near the University of Indiana, revealed the fact that the species tended to attain their maximum abundance in autumn and spring. In one pond (Fig. 200) the phases were as follows:

Phase	*Dominants*
Autumn	*Closterium*, *Euglena*, *Oedogonium*
Winter	*Spirogyra* spp.
Early spring	*Spirogyra* sp.
Late spring	*Spirogyra*, *Euglena*, *Oedogonium*
Summer	No one species

In another pond somewhat different phases were recorded:

Phase	*Dominants*
Autumn	*Oedogonium*, *Chaetophora*
Winter	*Vaucheria*
Late spring	*Oedogonium*, *Pleurococcus*
Summer	*Chaetophora*

These observations should be compared with those from the Harpenden pool, and it will be seen that although the spring phases are essentially similar with either *Spirogyra* or *Oedogonium*, nevertheless there are great differences. The two ponds described above also possessed floras that were essentially different and they must therefore be regarded as containing two separate associations. Furthermore, the same worker found that a sudden change in the external conditions checked the growth of an alga and often resulted in the development of a resting stage or else of sexual organs;

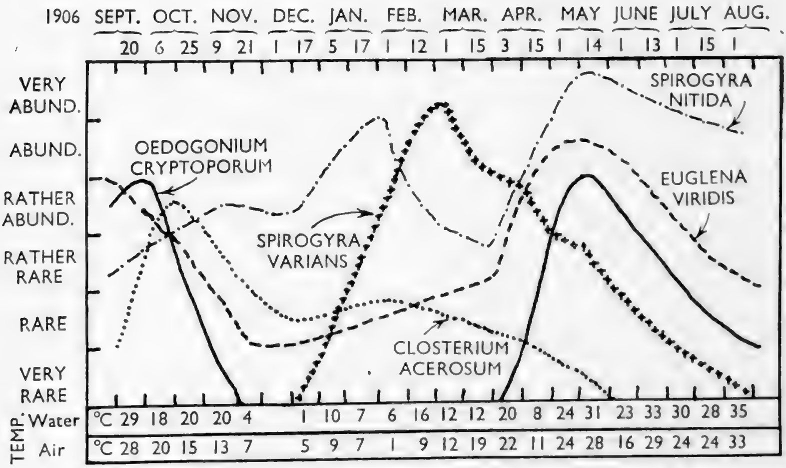

Fig. 200 Abundance and frequencies of the most important algae in a pond near Indiana University from 1906 to 1907. (After Brown.)

insistence upon the importance of external conditions in this respect has also been emphasized by Fritsch and Rich in their study on the Harpenden and Bristol pools.

4. *Associations of pools and lakes*

West was the first investigator of lake and pool algae who appreciated the fact that the geology of the substrate was of profound importance. He showed that the desmid flora is richest where the substrate is precarboniferous (*Oligotrophic* waters), whilst diatoms become abundant in younger areas or where there has been much silting with consequent solution of mineral salts (*Eutrophic* waters). Later workers have greatly extended this important study, and the present treatment of the problem is more or less summarized in the scheme on p. 367.

A third type is the *Dystrophic* lake or pool, which is to be found on moorlands, where desmids form the most abundant part of the flora in a water that is often highly coloured. In the course of years Oligotrophic waters may also change into Dystrophic waters.

Originally there was supposed to be a fairly sharp distinction between oligotrophic, eutrophic and dystrophic waters, but with the realization that one type can gradually change into another it is evident that any such distinctions cannot be sharp. A considerable body of data is now available on the physical and chemical environment in pools and lakes. This has enabled workers to standardize the waters from the purely physical point of view, but it still remains to be seen whether this information will be of any great assistance in understanding their ecology. Among these physical factors is oxygen concentration. In sheltered lakes as compared with open lakes there is an oxygen stratification which closely follows the bottom contours, whilst the influence of any rivers entering the lake together with the problem of periodic floods is yet a further factor.

Where there is a shallow littoral shore the communities are difficult to recognize unless there is a rocky substrate, in which case there may then be a zonation that is dependent on changes of water level and wave action: this type of zonation has been observed in several continental lakes. In deeper waters the communities are more distinct because a zonation develops which is primarily maintained by the light intensity factor. The Limnoplankton of lakes is not usually of great bulk and is composed principally of various members of the Myxophyceae, Dinophyceae, Bacillariophyceae and Chlorophyceae, and according to the nature of the constituents it may exhibit maxima in spring (very commonly), spring and autumn or summer and autumn.

Evolutionary Trend—Lake Waters

Characters	Hard ancient rocks unchanged	Softer more recent rocks or some silting		Soft rocks or much silting
	Generally deep	Decreasing depth		Generally shallow
	No O_2 decrease with depth at thermocline			O_2 decreases with depth at thermocline
	High $\frac{\text{Alkali}}{\text{Ca}+\text{Mg}}$			Low $\frac{\text{Alkali}}{\text{Ca}+\text{Mg}}$
	Poor in dissolved minerals	Minerals in solution increasing		Rich in dissolved minerals
	Rich in number of species	Decreasing number of species		Poor in number of species
	Poor in actual numbers of individuals	Increasing number of individuals		Rich in actual numbers of individuals
	Desmids abundant	Diatoms and desmids	Diatoms and *Eudorina*	*Asterionella* and Myxophyceae

Oligotrophic waters ⟶ Over many years ⟶ Eutrophic waters

Only one example of the algal flora of lakes will be discussed in detail in these pages, and so the student must remember that lakes from other parts of the world may exhibit differences not only in species but also in the normal periodicity of the communities. A study by Godward in 1937 of the littoral algal flora of Windermere in Cumberland brought out a number of interesting facts. In the Continental lakes, some of which are of a considerable depth, many of the algal communities are markedly limited in the depth to which they can descend. In Windermere, however, any species of the deeper waters is also able to exist in the surface layers, but as only a shallow depth of water is occupied by the various communities, depth *per se* can only be employed on a broad basis as a means of distinguishing the communities.

Three different groups of communities were recognized:

(1) Communities growing on stones and rocks:
  (*a*) Spray zone dominated by *Pleurocapsa* (May–September), *Tolypothrix* and *Phormidium* (April–September).
  (*b*) Zone 0–0·5 m. Dominated by *Ulothrix*, diatoms and Myxophyceae.

    (c) Zone 0–3·5 m. No definite community is formed in this belt.
    (d) Zone 2–3·5 m. A distinct community dominated by Myxophyceae.
(2) Epiphytic communities growing on aquatic macrophytes:
    (a) On submerged plants between 0 and 0·5 m. This possesses a conspicuous Chlorophycean element, e.g. Conjugales, Chaetophorales and Ulothricales.
    (b) On submerged plants between 1 and 3 m. dominated by *Oedogonium*, *Coleochaete* and diatoms.
    (c) A community on submerged plants between 3 and 6 m. which is comprised of *Coleochaete*, a few diatoms and some Myxophyceae.
(3) Communities on dead leaves and organic debris:
    (a) Between 0 and 12 m.: wholly Diatomaceae.
    (b) Between 2 and 16 m.: four diatom species and *Microcoleus delicatulus*.

The depth range of the diatoms was found to be greatest at the time of their maximum in spring and smallest in mid-winter. It was also discovered that the diatom frequency and light intensity often show an opposite trend in the upper layers and a similar trend in the lower layers of the lake. The nature of the habitat, whether organic or inorganic, makes a considerable difference to the behaviour of the different species, and each individual species responds variously to the differences of these environments (Round, 1957). In spite of these differences, however, they all exhibit an April maximum and depth has the same influence on them all (cf. Fig. 201). A study of the plankton of Lake Windermere gave results that were in accordance with the view that the constituents of the floating community originate from the algae of the littoral region.

The periodical development of the littoral algal flora can be summarized as in Tables 11 and 11A.

A study of the chemistry of the waters in the different algal habitats around the lake is summarized in Table 12.

An investigation of the distribution of the algae in relation to the different habitats showed that the algal species clearly fall into two main groups.

(1) Those typical of the inner parts of reed swamps (organic shores).

TABLE 11

Development of littoral algal flora

	No. of species
A. *Occurrence of species*	
(1) Species present throughout the year with no distinguishable maximum	4
(2) Species present all the year with a maximum at one period	4
(3) Species abundant at certain times of year only	7
(4) Species present at certain times of year only	numerous
B. *Occurrence of maximum*	
(1) Species with spring maximum and smaller autumn maximum: diatoms predominate	9
(2) Species with spring maximum only	3
(3) Species with summer maximum only: Chlorophyceae predominate	11
(4) Species with autumn maximum only: Myxophyceae predominate	11
(5) Species with winter maximum only: Chlorophyceae predominate	7
C. *Time of year when species occur in abundance at their greatest depth*	
(1) Species attaining greatest depth in spring: diatoms only	3
(2) Species attaining greatest depth in spring and autumn	3
(3) Species attaining greatest depth in summer: Chlorophyceae predominate	10
(4) Species attaining greatest depth in autumn	1

TABLE 11A

Variations in Epipelic (bottom living) communities of Lake Windermere with depth and season (After Round, 1956)

			Diatoms and season			
Depth	*Diatoms*	*Myxophyceae*	*10/1/49*	*2/5/49*	*22/8/49*	*28/11/49*
1 metre	550	175	—	773	496	24
2	243	124	307	306	376	36
3	260	180	224	460	264	26
4	145	74	243	175	19	4
5	216	67	122	136	666	12
6	144	88	204	163	399	24
8	17	0	69	6	—	—
10	5	0	24	1	—	—
12	0	0	3	0	—	—

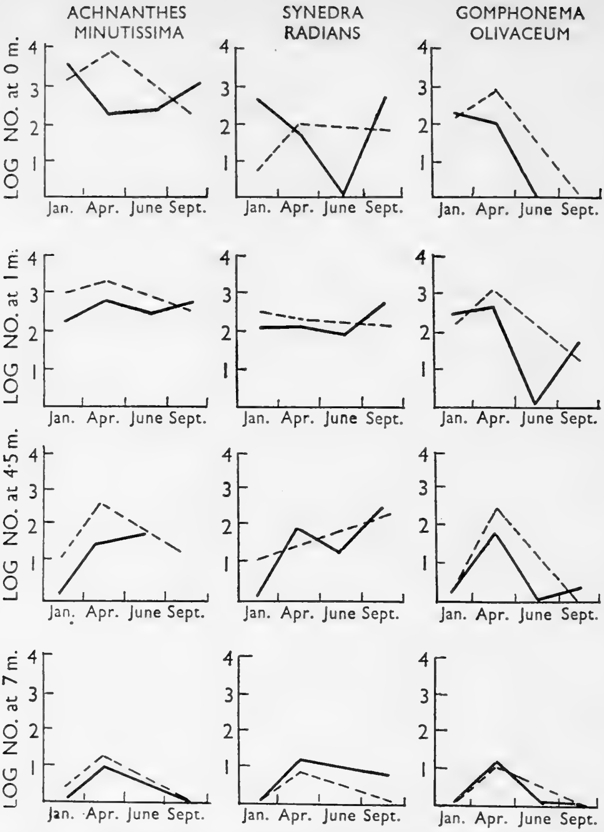

Fig. 201 Distribution of diatoms on slides suspended at different depths at different seasons of the year off two types of shore. (After Godward.)

(2) Those typical of other habitats:

(*a*) Species more abundant in streams.

(*b*) Species more abundant on inorganic stony shores.

(*c*) Species more abundant in the outer parts of highly evolved reed-swamp and throughout the less evolved reed swamp.

A very definite gradation or succession can be traced in the algal flora as one passes from the inner to the outer reed swamps, from the latter to the open water or stony inorganic shores and finally to the mouth of streams. In other words a progressive change in the algal flora is associated with a bottom that becomes less and less organic in nature or as one passes from eutrophic to oligotrophic conditions.

TABLE 12

Variations in chemical habitat

	NO_3	NH_3	P_2O_5	*Organic matter*	CO_2
(*a*) Stony and rocky shores (inorganic)	moderately high	low or absent	low	low	low
(*b*) Mouths of streams	high	high	high	variable	high
(*c*) Reed swamps (organic)	low	high	low	high	very high

EPIPHYTES

It is convenient at this point to consider what is known about the distribution of algal epiphytes, and in this connexion a study of two ponds on the outskirts of Epping Forest by Godward (1934) has resulted in considerable advances to our knowledge. Three series of epiphytes were distinguished.

(1) Winter forms; 16 species approx.
(2) Summer and autumn forms; 11 species approx.
(3) Forms existing throughout the year; 11 species approx.

An investigation of the effect of the age of the substrate upon the epiphytic flora showed that the nature of the substrate was of great importance. This is illustrated in Fig. 202 E, where it can be seen that, so far as the tips of the leaves are concerned, the total number of epiphytes increases up to the third or fourth leaf from the apex, after which there is a decline. The diatom flora, however, is an exception to this behaviour, because it increases regularly with the age of the substrate so that the oldest leaves bear the greatest number of diatomaceous epiphytes. On the other hand, algal zoospores tend to settle on the younger living leaves. There are distinct differences in the epiphytic flora of the upper and lower surfaces of leaves, and it was observed that in the case of the first few leaves below the apex the upper surface was infinitely superior in the number of epiphytes, probably because of the greater light intensity. In addition to distribution in relation to increasing age, there is also the relation to the different parts of the phanerogamic substrate. Fig. 202 E illustrates the distribution of epiphytes on the different parts of a phanerogam, and it will be observed that it is only on the leaf tips that the maximum is reached at the third or fourth leaf, whilst the leaf sheaths show a slight maximum at about the tenth leaf with a well-marked maximum for the mid-rib at the

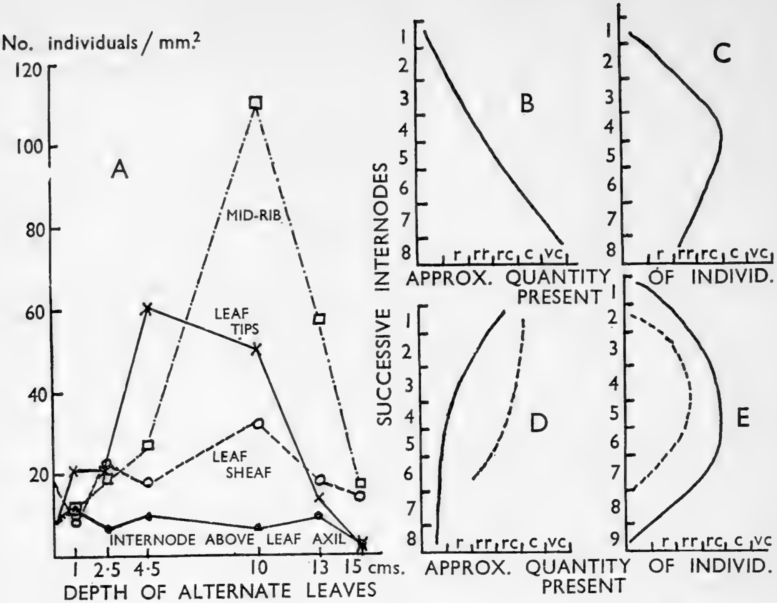

Fig. 202 A, distribution of total epiphytes on successive leaves of *Oenanthe fluviatilis*. B, C, distribution of *Cocconeis placentula* on successive internodes of plants of *Equisetum limosum*, well separated (3 stems average). *r* = less than 5 individuals per 0·1 sq. mm.; *rr* = about 5; *rc* = about 10; *c* = about 30; *vc* = about 50. D, distribution of *Cocconeis placentula* (——) and *Eunotia pectinata* (----) on crowded plants of *Equisetum limosum* (3 stems average). E, distribution of *Stigeoclonium* sp. (——) and *Coleochaete scutata* (----) on fairly crowded stems of *Equisetum limosum* (2 stems average). (After Godward.)

same level. These maxima on the lower leaves are to be associated with the diatom flora. It will also be observed that the number of epiphytes on the internodes remains more or less constant, but rapid growth of the substrate, e.g. the leaf lamina, tends to prevent colonization by epiphytes. The density of epiphytes that are attached to dead organic material is dependent upon the habitat of the substrate, e.g. if it is floating then there are few epiphytes, if it is attached or submerged the epiphytes are numerous, whilst if it is lying on the bottom the epiphytes will be few. The various species to be found are all a residuum from the last living state of the material, and the assertion that dead material bears more epiphytes than living does not appear to be correct in this case, and it can only be supposed that it arose in the past through lack of quantitative analysis. In some cases the appearance of epiphytes is due to change in the host with age, e.g. old filaments of the Zygnemaceae lose their mucilage sheath and they then become colonized by many epiphytes.

Experimental work and observation show that the greatest growth and number of epiphytes are partly related to conditions of good illumination, a feature which is illustrated by Table 13 below.

TABLE 13

Total number of epiphytes collected on suspended slides

	Sandy bottom		*Muddy bottom*
Water level	225	(no *Eunotia*)	262 (no *Eunotia*)
5 cm.	176		108 (102 *Eunotia*)
12 cm.	176		0
17 cm.	37	(all *Eunotia*)	0

When considering the effect of illumination it has to be remembered that not only are there problems associated with the individual plants, such as the upper and lower surfaces of leaves, but also that the density of the host plants may be highly significant. Fig. 202 shows the distribution of various epiphytes on plants of *Equisetum limosum* under different conditions of spacing and the contrast is exceedingly obvious. Where there is screening of leaves, either on the same plant or by several plants, then the epiphytes develop on the unscreened portion.

The inter-relations of host and epiphyte are important, and it was noticed that the epiphytes tend to develop in the depressions where the cells of the host adjoined each other. Experiments were then carried out with scratched slides suspended in the water, and the results obtained from these rendered it clear that depressions in a surface increase the number of epiphytes very considerably (Table 14).

TABLE 14

Effect of surface upon epiphytes

Epiphyte	*No. in scratches on slides*	*No. elsewhere*
Cocconeis	517	297
Stigeoclonium sp.	665	198
Chaetopeltis	138	54
Ulvella	747	200
Coleochaete scutata	40	13

So far as the attachment organs of the epiphytes are concerned, there is no apparent relation between the nature of the substrate and the method of attachment. The differences seen above, therefore, must be explained by the behaviour of the motile reproductive bodies which either come to rest in the depressions or else are swept there by micro-currents in the water. Another interesting feature is the frequent association of *Gomphonema* with the basal cells of *Oedogonium*, but so far there is no evidence to suggest whether this is a casual relationship or not. Ponds with muddy bottoms have a reduced number of epiphytes probably because the pH and the gases evolved are toxic, but so far little or no work has been carried out to ascertain the effect of the host plant on the microchemical environment. Summing up, it can be said that the factors influencing the distribution of epiphytes are as follows:

(1) Age of substrate.
(2) Rate of growth of substrate.
(3) Light intensity.
(4) Screening.
(5) Nature of the surface.
(6) Chemical surroundings.

Of these (3) is probably the most important, although it is difficult to separate its effects from those of (1) and (4).

In recent years increasing use has been made of the unicellular green algae, especially *Chlorella*, *Scenedesmus* and *Chlamydomonas*, as a means of purifying sewage effluent. Most of the pioneer work has been carried out in the United States where large lakes of effluent are innoculated with the algae, and these after a few days increase in such number that the oxygen they produce materially aids the aerobic decomposition of the remaining organic matter. When one of these oxidation lakes is operating, water is allowed to flow through at a rate which takes it about 6–7 days to pass from entry to exit or else it is allowed to recirculate. At the end of the period when the effluent emerges it is clear of organic matter and the bacterial count of pathogens has also been reduced to a negligible value. The largest oxidation lakes for sewage purification (1100 acres) are at Auckland in New Zealand.

SOIL ALGAE

Terrestrial algae may be classified conveniently as follows:

(1) Aerophytes. These can be subdivided into:
    (*a*) Epiphyllophytes, algae growing on leaves, e.g. *Phycopeltis*, *Cephaleuros*.

    (*b*) Epiphloeophytes, algae growing on bark, e.g. *Pleurococcus.*
    (*c*) Epizoophytes, algae growing on animals.
    (*d*) Lithophytes, algae growing on rocks, e.g. *Prasiola, Trentepohlia.*

(2) Edaphophytes, or algae that grow on or in soil. These also can be subdivided into:
    (i) True soil species:
        (*a*) Epiterranean, or lying in the surface layers of the soil.
        (*b*) Subterranean, or lying in the lower layers of the soil. So far as is known at present there are no obligate species of this class.
    (ii) Casuals.

The study of soil algae, as such, began seriously at the commencement of the nineteenth century with the works of Vaucher, Dillwyn, Agardh and Lyngbye, whilst towards the end of the century monographs by Bornet and Flahault, Gomont, Wille and the Wests, father and son, began to make their appearance. In 1895 Graebner, in a study of the heaths of North Germany, gave the first account of soil algae as ecological constituents, and subsequently many ecologists have shown that soil algae are pioneers on bare soil where they prepare the ground for the higher plants that follow. In such cases the algal flora is generally richest when the soil is primarily or secondarily naked, e.g. mud flats developing to salt marsh, or ploughed grassland. A manured soil also has a very rich flora, whilst the same species are to be found in unmanured soils, though not in such numbers. The richness of the flora is also influenced by the moisture conditions, damp soils having a more varied and extensive collection of algae than dry soils. In the case of the diatom component of the soil flora it has been found that it is more abundant when the soil is rich in phosphates and nitrates, so that the soil salts may also be of importance. The addition of artificial fertilizers to a soil can also alter the soil flora. In recent years dilution cultures have been widely used in order to give a quantitative aspect to the work, and the results of such studies have been to show that there is probably a seasonal variation in numbers, but that the behaviour depends on the depth and kind of soil. There seems little doubt but that the soil flora, and also fauna, has an important biological significance, but at present much more experimental data is required. It may well be that the biological character of a soil will prove to be of more importance than its chemical or physical character.

SUBTERRANEAN ALGAE

There are great fluctuations in the numbers of the different species that compose the flora, but there are no species in the lower layers of the soil which do not also occur in the surface layers. Dilution cultures, together with the counting of samples, have shown that the algal flora is mainly confined to the top twelve inches of soil with a maximum abundance at about 3–6 in. below the surface. With increasing depth the number of algae decreases regularly, the maximum depth at which they have been recorded being two metres; there is, however, really no conclusive evidence which shows that algae can grow in the deeper layers where there is no light, and it is very probable that they are only present in these layers in a resting phase. The number of reproductive bodies in the surface layers reaches a maximum in spring, but in the lower levels it remains constant throughout the year. In Denmark the quality of the soil is apparently decisive in determining the luxuriance of the flora irrespective of whether the ground has been disturbed or not. In Greenland soil algae have been found down to a depth of 40 cm., and their presence there can only satisfactorily be explained by the action of water trickling down the cracks because burrowing animals are absent. A study of soils from all over the world has emphasized the existence of a widely distributed algal formation in cultivated soils. This flora consists of about twenty species of diatoms, twenty-four of Myxophyceae and twenty species of green algae, among which *Hantzschia amphroxys*, *Trochiscia aspera*, *Chlorococcum humicolum*, *Bumilleria exilis* and *Ulothrix subtilis* var. *variabilis* are the most frequent.

Lund (1945) studied sixty-six different soils in Great Britain and found that, except on acid soils, the Chlorophycean component was the most numerous, but it was followed closely by the Baccilariophyceae with the Myxophycean element third. In the case of cultivated soils, however, the Myxophycean element became much more important. Very little work has so far been carried out on the soils of tropical regions. A study of the soils of savanna, steppe and

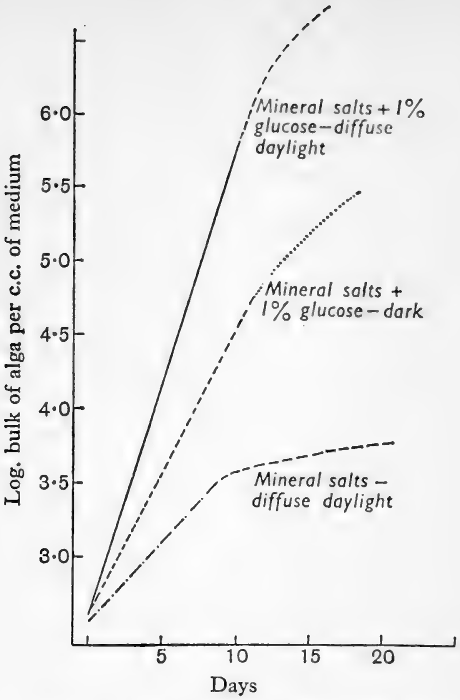

Fig. 203 Growth of the soil alga, *Scenedesmus*, under different conditions of nutrition and light. (After Roach.)

maxanga in the Belgian Congo yielded a flora almost entirely composed of Myxophyceae, though in true savanna algae were rare, probably because of space and light competition.

The growth of the soil algae has been a source of interest and experiment for a number of years. Roach (1926) has found that ordinary growth in *Scenedesmus costulatus* var. *chlorelloides* is best in a glucose medium but that xylose is toxic, the factors controlling the normal growth rate being light, temperature and aeration of the medium (cf. Fig. 203). The same alga has been used for growth experiments in the dark in order to determine how far such algae can grow when they are below the soil surface (cf. Fig. 204). This and four other species can be made to grow in the dark provided an organic medium is present, but they all react differently to the various conditions and also they vary in the amount of growth that occurs. At constant temperature, increasing the light intensity from 1/25 to 1/4 has a far greater effect than increasing the intensity from

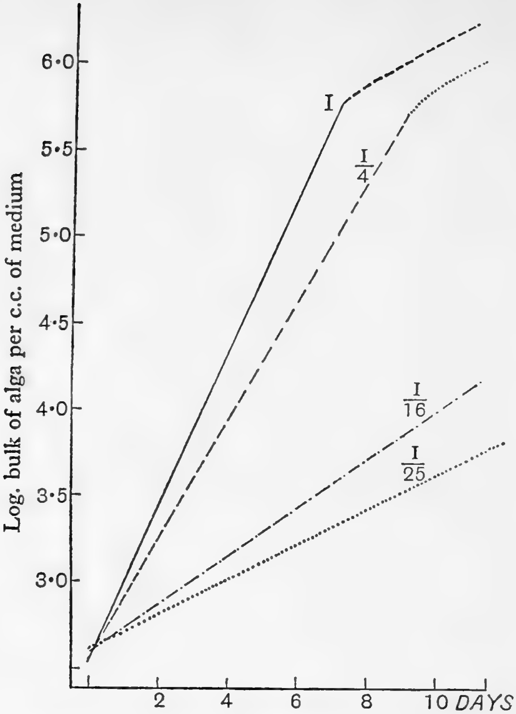

Fig. 204 Rate of growth of *Scenedesmus* in a solution of mineral salts under different light intensities. (After Roach.)

1/4 to full sunlight. Under full light the growth curves (cf. Fig. 204) rise to an optimum by means of photosynthesis alone, but at lower intensities the optimum is only approached if additional nutriment, in the form of glucose, is present as well. There is no adequate evidence that such organic media are present in the soil layers so that it is very doubtful whether growth in the dark can occur in nature, but it has been shown, however, that *Nostoc punctiforme* from the leaves of *Gunnera* and also a species of *Euglena* are capable of growth in the dark.

Even if the algae cannot grow in the lower layers of the soil because of the darkness, we must still enquire into the process responsible for their appearance in those layers. The possible agencies are (1) cultivation, (2) animals, (3) water seepage and (4) self-motility. Mechanical resistance and lack of light are said to prevent the Myxophyceae from moving down under their own locomotion, and whilst it is possible that algae may move down through their own motility, further experimental work on this aspect is much to be desired. The effect of water seepage will depend on the heaviness of the rainfall, the state of the soil, i.e. whether dry and cracked, and the nature of the algae, i.e. whether or not they possess a mucous sheath. Passage through the soil is facilitated in the filamentous algae either by fragmentation or else by the formation of zoospores, the factors that are responsible for the former process appearing to differ for the various species. Many green algae are known to form zoospores when put into water after a period of dryness, and hence one may presume that a shower of rain will also induce zoospore formation. Petersen (1935) has demonstrated experimentally that rain can carry algae down efficiently to a depth of 20 cm., but that the process is facilitated by the presence of earthworms, although these animals probably only operate indirectly in that they loosen the earth. Farmers in the course of their cultivating operations must frequently be responsible for the conveyance of algae down into the soil.

Many of the soil algae, expecially the Myxophyceae, can resist very protracted spells of dryness as Roach (1920) demonstrated when soils from Rothamsted that had been kept for many years were remoistened. Bacteria developed first, then unicellular green algae with some occasional moss protonemata, and although the Myxophyceae appeared last, nevertheless they quickly became dominant. *Nostoc muscorum* and *Nodularia harveyana* appeared after the soil had been dried up for 79 years, whilst *Nostoc passerinianum* and *Anabaena oscillarioides* var. *terrestris* appeared after 59 years of dryness. These algae differed in some respects from the typical forms that are to be found in ordinary soils, but this was probably only due to the cultural conditions.

Fritsch and Haines (1922) have studied the moisture relations of some terrestrial algae (cf. Fig. 205) and they have shown that:

(1) There is a complete absence or paucity of large vacuoles.

(2) In an open dry atmosphere nearly all the sap is retained.

(3) When the filaments dry up, contraction of the cell is such that the cell wall either remains completely investing the protoplast or else in partial contact with it, thus ensuring that all the moisture which is imbibed will reach the protoplast.

(4) During a drought there is, as time goes on, a decreasing tendency for the cells to plasmolyse and there are also changes

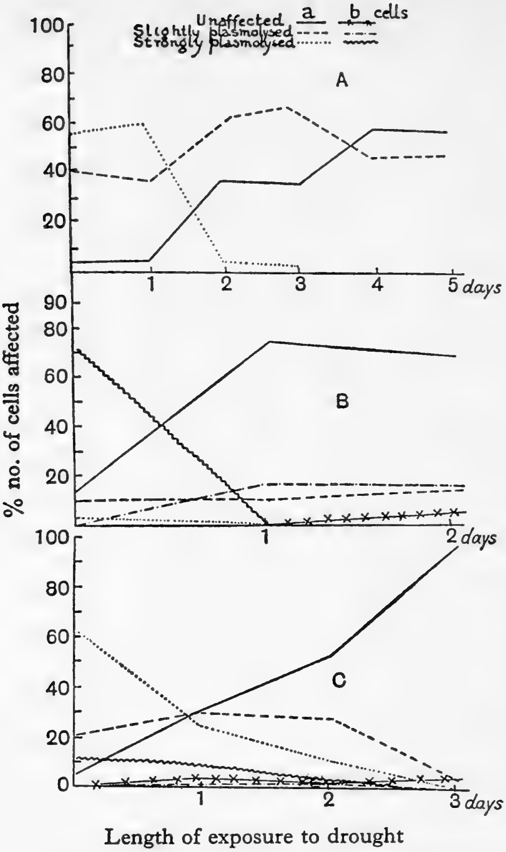

Fig. 205 Effect of exposure to drought on A, *Hormidium*; B, '*Hormidium*' stage of *Prasiola*; C, *Zygogonium ericetorum*. (After Fritsch and Haines.)

in the permeability of the cell wall, whilst the access of moisture normally brings about changes in the reverse direction. The majority of cells which do plasmolyse lack the characteristic granules, mainly of fat, that are to be found in most terrestrial algae.

(5) Those cells which survive after drought do not contain any vacuoles and possess instead a rigid, highly viscous protoplast which is in a gel condition. This is the normal state of the vegetative cells of *Pleurococcus* and the cells in the '*Hormidium*' stage of *Prasiola*.

(6) If desiccation is rapid most of the cells will die but some will plasmolyse and retain their vitality in that state for weeks or months. In spite of the death of the bulk of the cells no species disappears from the flora during a rapid onset of drought.

(7) If desiccation continues, the number of living resting cells will remain constant for several years.

(8) During a very long drought the resting cells of algae below the surface will still survive.

Apart from the moisture relations there are also other factors that may be involved. Diatoms can survive very low temperatures, – 80° C. for 8 days or – 192° C. for 13 hours, whilst dry spores of *Nostoc* sp. and *Oscillatoria brevis* can survive – 80° C., though if they are moist a temperature lower than – 16° C. will kill them. As the vegetative filaments of *Nostoc* die after four days at – 2 to – 8° C. this genus must survive severe winters in the form of spores. So far as the algae of tropical soils are concerned the dry spores of *Nostoc* sp. and *O. brevis* can tolerate 2 min. at 100° C., the wet spores 20 min. at 60–70° C., and the vegetative filaments 10 min. at 40° C., this latter being a temperature that is frequently reached on open ground in such regions. Acidity and alkalinity do not appear to be of any great importance, although members of the Chlorophyceae usually thrive better on basic soils.

It has been demonstrated that *Anabaena* and *Nostoc* can fix nitrogen from the air in the presence of light, but other soil algae apparently do not possess this power unless they occur in combination with bacteria, and even then the actual fixation is probably carried out by the bacteria. It has been found by De (1939) that *Anabaena* will only fix nitrogen from the air so long as nitrate is absent from the soil. The combination of bacteria and algae fix nitrogen better than the bacteria do alone, so that the algae must act as a kind of catalytic agent, and it has been suggested that they (*a*) provide carbohydrate, and hence energy, for the bacteria, or (*b*) remove the waste nitrogen compounds, since it has been shown that if these accumulate bacterial activity is reduced. In some cases the algae play a part in aeration because of the oxygen they produce during photosynthesis, and in this connexion it may be mentioned that unless certain species are present in the soil of rice fields during the period they are waterlogged the aeration deteriorates and the rice becomes much more susceptible to disease. Rice is also capable of growing in the same field year after year without being manured, and it has been demonstrated that this is due to the fixation of nitrogen by the blue-green algae present in the soil, especially species of *Anabaena* and *Cylindrospermum gorakhporense* (Singh, 1942) (see also p. 413).

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Chapter XV

ECOLOGICAL FACTORS

Any attempt to understand and interpret the zonation to be observed on a rocky coast or on a salt marsh must be based upon an appreciation of the different ecological factors and the part that they play. It may be expected that more than one factor will normally exert a controlling influence, but at one time of the year or at a certain phase in the life history of an organism one single factor may become paramount. It has also become increasingly evident that a proper appreciation of some of the factors cannot be divorced from a study of the physiology of the algae. Certain aspects of algal physiology must therefore be discussed in this connexion rather than in the chapter on physiology.

The essential factors can broadly be divided into four groups, (1) physiographic (dynamic according to some writers), (2) physical, (3) chemical, (4) biological. Similarly, at any given point on the coast, one can conveniently attempt to segregate the factors into those that are (1) causal, i.e. responsible, so far as one can see, for the basic zonation to be observed, (2) presence or absence, i.e. determine whether a species shall be present or not, such as the influence of fresh water or a change in the type of rock, but not determining the level at which the species grows, (3) modificatory, i.e. causing a variation in the level normally occupied, e.g. effect of spray, of cracks, of shade, etc.

A. *Physiographic factors*

The dominant factor here is the tide, though it operates indirectly in a number of ways:

(*a*) Degree of shelter or exposure to the waves

This is primarily a presence or absence factor, some species, *Durvillea*, *Postelsia*, possessing holdfasts that enable them to withstand strong wave action. Many examples are to be found in the literature illustrating change of zonation with varying degrees of exposure. It must be supposed that even the sporelings possess this capacity, and one must further suppose that attachment of the zygote to the rock surface must take place rapidly in such an environment. This factor is absent on a salt marsh coast since salt marshes and mangrove swamps only develop in protected areas. On the other hand it can be operative on fresh-water lakes where quite sizeable waves can be engendered. Such waves may determine the type of lake edge algal community.

(*b*) Wave action

By this is meant the actual height of the waves and the degree of splash and spray that results from them. It has already been noted (see p. 332) that this is essentially a modifying factor, elevating the zones, especially the upper ones, often to a considerable degree. Persistent wave action on a lake shore may presumably also elevate an algal zone though this appears to have been but little studied.

(*c*) Tidal range

This also is a modifying factor since the range of the tide is primarily responsible for the actual width of the algal zones that are to be observed. Even with a very small tidal range, e.g. Caribbean, it is possible to observe a distinct zonation of the organisms. This factor also determines the extent to which rock pools may exist, the greater the tidal range the greater the variety among the rock pools. Up to the present, workers have generally paid insufficient attention to the different types of tidal variation found in various parts of the world. These are of great importance (Doty, 1957) and may indeed alter the position of an organism on the sea shore (see p. 330).

(*d*) Tidal currents

In certain places there may be very pronounced currents close inshore where algae may grow, e.g. between Orkney Is. and the north of Scotland, at the mouth of the Bay of Fundy, etc. Such currents affect the growth of the plants but they can also operate as a presence or absence factor. Thus on the east coast of Scotland the strength of the current determines whether *Laminaria saccharina* or *L. cloustoni* is the dominant. The strength of the current flowing up salt marsh and mangrove swamp creeks determines the degree of erosion, and upon this rests the extent to which creek bank algal communities can develop (see p. 350).

(*e*) Silt load

In some areas, e.g. mouth of the River Severn in England, Bay of Fundy in Nova Scotia, the load of silt carried by the sea exerts a distinct effect upon the fauna and flora. Certain organisms are unable to tolerate silt deposition, in the case of algae photosynthesis presumably being the main metabolic factor concerned. Silt load can therefore operate as a presence or absence factor.

(*f*) Inter-tidal exposure

This is the exposure suffered at any level between two consecutive tides. Submergence-exposure curves have been constructed for a number of areas and as they vary with the type of tide, i.e. spring or neap, it is clear that tidal phenomena alone cannot determine zonation, though it is evident that they represent a major causal factor. Exposure will operate indirectly in so far as it affects water loss, temperature changes of the thallus, salinity of the cells. The degree of atmospheric humidity is also of importance during the periods of exposure. It is this factor, together with that of temperature, which prevents algae from occupying the shore in the tropics and enables them to form a dense covering at high latitudes.

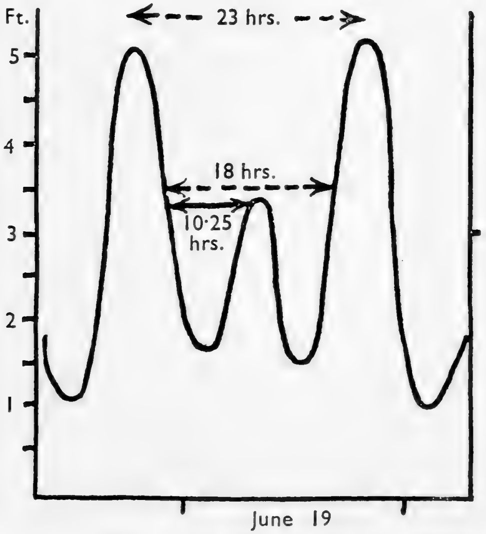

Fig. 206 Tide curves at San Francisco and the relevant hours of exposure at different levels. (After Doty.)

The length of the inter-tidal exposure also affects the conditions in rock pools and salt pans, the diurnal changes being greater in the higher pools and pans where the length of exposure is longer. With one type of tide there will be certain levels on the shore where the inter-tidal exposure can be doubled, e.g. at 3·5 ft. in Fig. 206. Similarly the submergence period may be drastically altered over a short vertical range, e.g. just above 2·5 ft. (Fig. 206) it is about 10 hr., whereas just below 2·5 ft. it is about 30 hr. The effect of this phenomenon in relation to critical levels (p. 407) may well be profound.

(*g*) Continuous exposure and submergence

At levels lying between lowest high water of neap tides and extreme highest water of spring tides there will be periods of two or more days during the neap period of the tidal cycle when the level will not be inundated at all. Similarly between highest low water of neap tides and extreme lowest low water of spring tides there will be days during the neap period of the tidal cycle when the level will be continuously submerged. In the former case, desiccation, temperature and salinity changes will be far more profound than those that occur between two consecutive tides: in the latter case continual submergence may affect the metabolic activities and the compensation point (see p. 408). It is probable that the periods of continuous exposure are of far greater importance than inter-tidal periods, especially during the sporeling stages. Unfortunately very little data on this issue has been collected. Gail (1920) has suggested that it is the desiccation of young plants that prevents the appearance of algae outside their usual zones, and it is a remarkable fact that sporelings of fucoids are usually very strictly confined from an early stage to the level they occupy as adult plants.

A rather different exposure phenomenon can be observed around large lakes. Very often evaporation in the summer lowers the water level so that the winter and summer levels are different. This zone of exposure between the two seasonal levels may be occupied by a special algal community, or it may form a bare zone between the winter water edge community and the lower summer water edge community.

Diurnal variations in temperature may affect the metabolic activities of the algae (see p. 393) and extreme variations in salinity can also bring about death of some species (see p. 404). Water loss

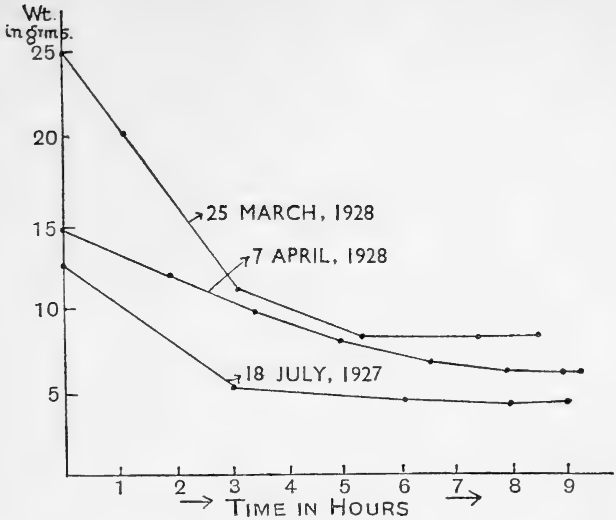

Fig. 207 Loss of water, as represented by loss in weight, in *Pelvetia canaliculata* during intertidal exposure. (After Isaac.)

during periods of exposure is quite clearly an important causal factor. On salt marshes it is undoubtedly responsible for the occurrence of gelatinous Myxophyceae at the higher levels where the exposure periods are long.

Among others Pringsheim (1923), Zaneveld (1937), Isaac (1933) and Kanwisher (1957) have studied rate of water loss in intertidal algae. Much of the work has centred around the principal fucoids found on European shores. In *Pelvetia canaliculata* the main water loss occurs in the first six hours of exposure (Fig. 207) whilst in *Fucus spiralis* var. *platycarpus*, *F. vesiculosus*, *F. serratus* and *Ascophyllum* the maximum water loss can be spread over 18 hours (Fig. 208): in *F. vesiculosus* as much as 90 per cent of the total initial water can be lost in 1½ hours. *Fucus spiralis* var. *platycarpus* loses its water the slowest of these last four species, and a definite increase in the rate of water loss can be observed with the different species as each occupies a successively lower zone on the shore, but it must be noted that *F. spiralis* var. *platycarpus* ultimately loses a rather higher percentage of water than the other three. Haas and Hill (1933) have also shown that the higher the alga grows the greater is the fat content (Table 15).

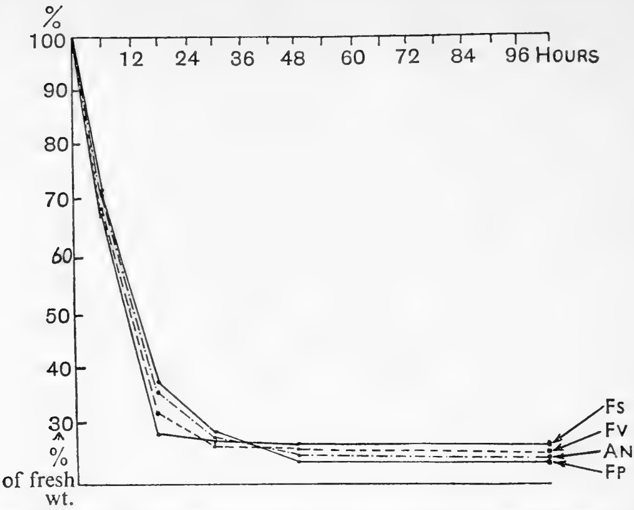

Fig. 208 Loss in weight of Fucoids in relation to time of desiccation. The higher an alga grows the slower it loses water and the greater the total loss. Symbols the same as in Fig. 202. (After Zanefeld.)

TABLE 15

Fat content of some littoral fucoids

	Ether extracted fat	*True fat*
Pelvetia canaliculata	4·88%	4·9%
Ascophyllum nodosum (mid-littoral)	2·87	
Fucus vesiculosus (low littoral)	2·60	2·6
Halidrys siliquosa (low littoral)	2·18	
Himanthalia lorea (low littoral)	1·21	
Laminaria digitata (sub-littoral)	0·46	0·3

This fat is largely contained in the cell walls and examination has shown that the thickness of the cell wall does bear a relation to the height at which an alga grows.

TABLE 16

Thickness of some Fucoid cell walls

	Thickness in divs. of 3μ
Fucus spiralis var. platycarpus	0·49 ±0·05
Ascophyllum nodosum	0·34 ±0·01
Fucus vesiculosus	0·23 ±0·03
Fucus serratus	0·14 ±0·01

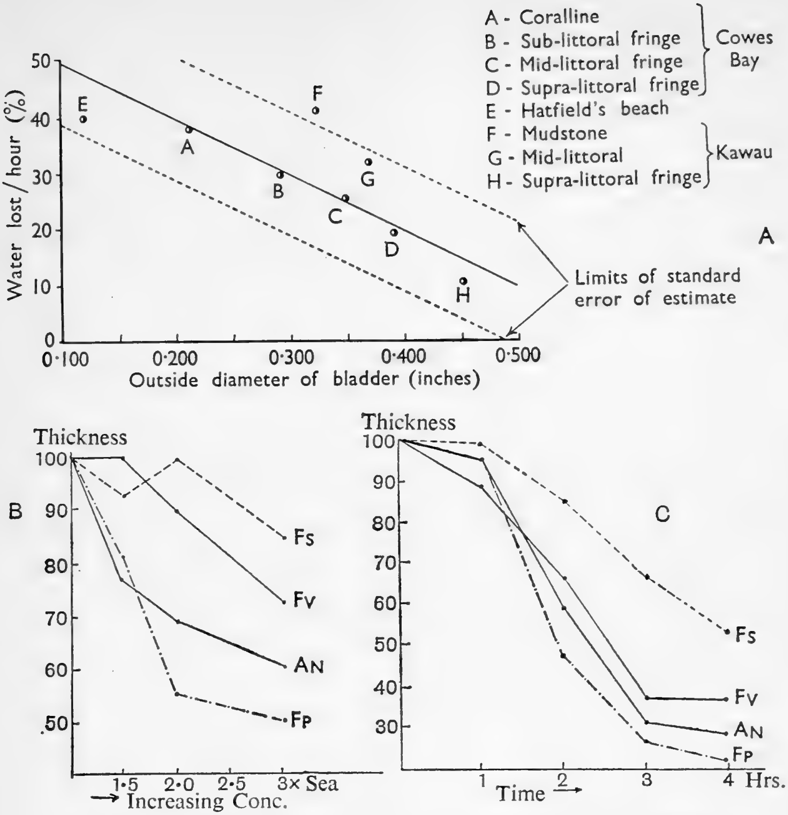

Fig. 209 A, Rate of water loss per hour in *Hormosira*. (After Bergquist.) B, decrease in diameter of cell walls when placed in sea water of increasing concentration. C, decrease in diameter of cell walls under normal conditions of exposure. An = *Ascophyllum nodosum*, Fp = *Fucus spiralis* var. *platycarpus*, Fs = *Fucus serratus*, Fv = *F. vesiculosus*. (After Zanefeld.)

These cell walls decrease in thickness when subjected to desiccating conditions, and the higher a fucoid is growing on the shore the more the cell walls ultimately shrink on drying; so it must be assumed that a large part of the water lost is contained in the cell walls (Fig. 209B, C). Those species which lose water most slowly will also reabsorb it most slowly and, as a result, the growth rate of the highest species will therefore tend to be the slowest. It would appear that a major factor controlling zonation, so far as these fucoids are concerned, is the biochemical nature and properties of the cell wall, although it is also possible that these features have

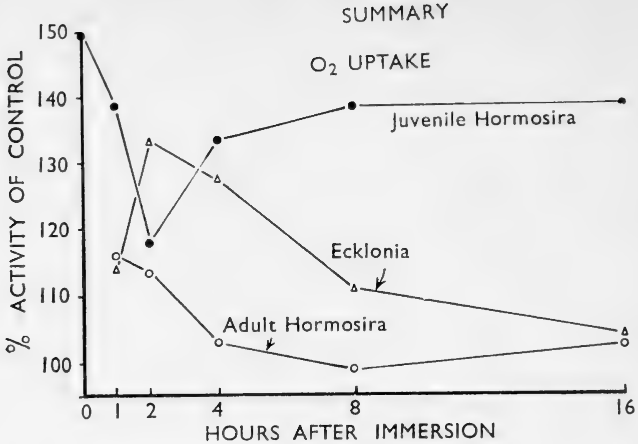

Fig. 210 Respiration rate of juvenile and adult *Hormosira banksii* and *Ecklonia radiata* after desiccation and re-immersion. Note that the adult *Hormosira* and *Ecklonia* return to the control value (non-dehydrated plants) but the juvenile *Hormosira* does not. (After Bergquist.)

appeared as a result of the habitat they occupy. In the case of *Hormosira* the rate of water loss is correlated with bladder size (see p. 213), the larger the bladder the slower the rate of water loss (Fig. 209A). Plants with large bladders occur at the higher levels on the shore so that morphology provides protection in this species. A further feature that has received very little attention is the effect of desiccation upon the major metabolic processes, respiration and photosynthesis. A recent study upon *Hormosira* (Bergquist, 1957) has shown that the effects may be quite different in the sporeling as compared with the adult (Fig. 210). This may be of profound significance and further work is clearly required. It appears that the respiration rate decreases with increasing desiccation (Bergquist, 1957).

For comparison with the water relations of fucoids, reference may be made to the work of Anand (1937) on the marine algae of the Dover cliffs. Here two important belts are dominated, the one by *Enteromorpha* and the other by Chrysophyceae. Anand found that the *Enteromorpha* mat lost 25 per cent of its moisture in the first 3 hours of exposure, whilst the Chrysophyceae belt lost 8·4 per cent. The relative loss by evaporation from these two belts is shown in Fig. 211A, whilst the corresponding loss due to drainage is shown in Fig. 211B. The measurements were obtained by the

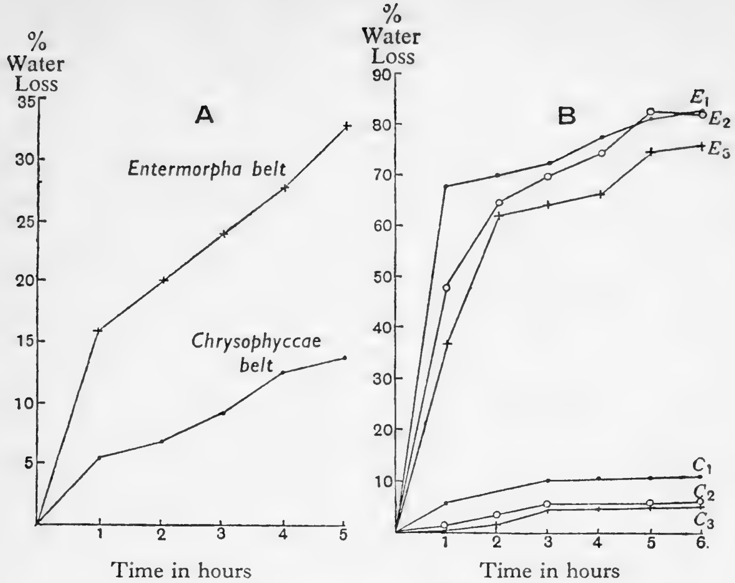

Fig. 211 A, water loss from samples of *Enteromorpha* and Chrysophyceae belts when exposed in their original position on the cliff face. B, water loss during drainage in nature from different levels in the *Enteromorpha* and Chrysophyceae belts during successive hours in winter. E_1–E_3, C_1–C_3 = successive levels. Water loss in A and B expressed as % of that originally present. (After Anand.)

simple but ingenious method of weighing portions of the mat cut out so that they fitted into waterproof paper dishes which could be put back into position on the shore. The reduced loss from the Chrysophyceae belt as compared with the *Enteromorpha* is due to the gelatinous nature of the former. This result was obtained despite the fact that the evaporating power of the air opposite the latter belt is 1·41 as compared with 1·1 opposite the *Enteromorpha* belt, the evaporating power of the *Fucus* belt being taken as unity.

B. *Physical factors*

(*a*) Substrate

The nature of the substrate, whether solid rock, boulders, pebbles, sand, mud or peat, is of fundamental importance in connexion with anchorage, the general aspect of the flora being determined to a large extent by this factor. It is essentially a presence or absence factor. On rocky coasts the angle of slope and the presence of cracks may affect the occurrence locally of some species, either operating as a presence or absence factor or as a modifying factor. The geological nature of the rock may also be important, e.g. soft rocks such as sandstone rarely carry large algae.

(*b*) Pressure

Normally this is not an important factor, but Damant (1937) has shown that in the case of vesicular species, such as *Fucus vesiculosus*, there is a limit to the depth at which bladders will exist, because the pressure of the water forces the gas out. This depth will therefore delimit the approximate lower limit to which the species can descend, since the vesicles represent a flotation mechanism and keep the thallus near the surface when submerged. A similar phenomenon has been observed in the case of *Egregia* where the shape of the bladders appears to be related to water depth, the deeper plants having spherical bladders and the shallow plants pear-shaped ones.

(*c*) Temperature

Temperature can affect biogeographic distribution (see p. 433), so for any given locality it operates as a presence or absence factor. In that locality, however, there may be seasonal changes in temperature which can affect the composition of the flora (presence or absence factor again). Thus at Cape Lookout in North Carolina the winter temperatures are such that the flora is essentially that of New England: in the summer the temperatures rise by eighteen degrees and the winter flora is replaced by sub-tropical species.

Changes of temperature can also bring about seasonal migrations, i.e. temperature operates as a modifying factor. Because of the temperature changes, some species migrate up and down on the shore. On salt marshes temperature operates at the upper levels when there is low growing vegetation, because it results in much evaporation with a consequent increase in desiccating conditions together with a rise in salinity. On rocky shores the day temperature of the belts usually only responds to changes of air temperatures during the summer, and then it is always less than that of the air. The temperature change is least in belts, e.g. Myxophyceae, Chrysophyceae, that retain more moisture. If, at high levels, the period of insolation is at all long in the summer then mats of Myxophyceae, Chrysophyceae and *Enteromorpha* become cracked and fall off. An interesting phenomenon is the changes in air temperature that can be observed (Doty, 1957) immediately above the surface of the water. With a rising tide such temperatures can be approximately 5° C. higher than that of the water. With an ebbing tide evaporation brings about cooling of the shore so that there may be a narrow zone with a temperature below that of seawater and 5° or 6° C. below that of the air. It seems unlikely that this phenomenon plays any part in determining zonation.

Most workers also agree that temperature is a very important factor in rock pools and probably also in salt pans. Whilst a pool is exposed the temperature of such a small body of water may rise considerably, especially in the case of pools at high levels, and then when the tide returns the cold sea water will lower the temperature very suddenly. An examination of pool floras has shown that Rhodophyceae tend to be more abundant in shaded pools or parts thereof, whereas Chlorophyceae and Phaeophyceae are relatively more abundant in the exposed pools.

Biebl (1937) studied some rock pools on the English south coast, in which attention was paid to the influence of temperature as well as of other factors. Temperature probably rarely causes actual damage, except perhaps at high level pools, but it may cause respiration to be so speeded up that katabolism is not made good by anabolism. Biebl found that warming up to 26° C. over a period of 24 hours has no effect on most Rhodophyceae, and changes of 12° C. could occur sharply without causing any damage.

Work with *Fucus vesiculosus* and *Hormosira banksii* (Fig. 220) has shown that respiration rate decreases with lowering of the temperature but that with the former species it is still measurable even at − 15° C. (Kanwisher, 1957).

The highly dissected appendages on the long 'boa' fronds of deep-water plants of *Egregia laevigata* (see p. 190) show a very marked response in apparent assimilation rate to temperature changes. Juvenile 'leaves' and basal 'leaves' behave very differently:

	Phs. as ml O_2*/gm. dry wt./5 min.*			
Organ	10° C	15° C	20° C	25° C
Dissected 'leaves'	130	375	1175	630
Juvenile 'leaves'	670	725	700	965
Basal 'leaves'	530	540	265	145
Dissected 'leaves' (shallow plant)	600	415	500	707

It seems evident that algae of the arctic (and antarctic) can tolerate as much as 80 per cent of the internal water being frozen (with the consequent rise of internal concentration) without metabolic processes stopping. After many months frozen into sea ice they must be capable of photosynthesis immediately upon being thawed out.

(*d*) Illumination

Here one may be faced with problems involving seasonal variation in light intensity, diurnal variations in relation to times of high water, and the actual light intensity and spectrum at different depths. Practically nothing is known about the first two effects, and it is impossible therefore to assess their importance. It can, however, be pointed out that differences in illumination intensity at different latitudes appear to determine the maximum depth to which algae can descend. Thus in the North Sea region the limit appears to be about 40–50 m., in the tropics it is about 100 m., whilst in the clear waters of the Mediterranean it is about 130–180 m. Many of the deep-growing algae (and possibly others) are fully light saturated at quite low values. Thus blades of *Macrocystis* are fully saturated at 1000 foot-candles ($\frac{1}{10}$ full sunlight of California) and parts of *Egregia* at 1400 foot-candles.

The third effect is undoubtedly important because measurements show that the incident light is cut down very considerably at even a depth of 1 m. whilst at 2 m. only about 25 per cent of the surface light has penetrated. Waters of different turbidity may absorb light quite differently (Fig. 212A) and this in turn affects the relative photosynthetic rate and the compensation point level (Fig. 212B). During its passage through sea water the spectral composition of the light changes considerably, the green and blue portions assuming greater importance. Algae living in the sub-littoral fringe and the upper portion of the sublittoral are subject to very different conditions as compared to algae living higher on the shore, so far as photosynthesis is concerned. There is also the different effect of submergence and emergence upon photosynthesis, the process being affected not only by the light change but also by the moisture and temperature changes.

In any given locality it is evident that temporary changes in light intensity as a result of cloudiness or chop on the water may affect photosynthesis. The outer edges of *Macrocystis* beds in California

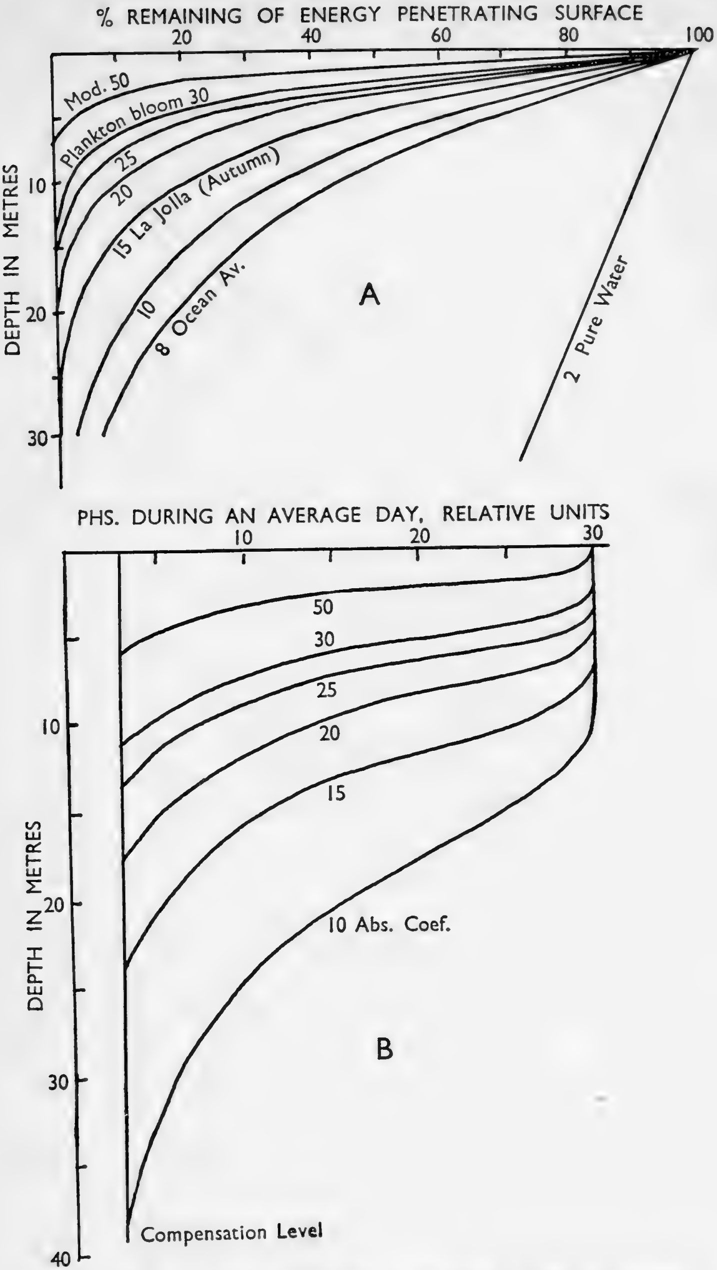

Fig. 212 A, % light absorption in sea water of different absorption co-efficients. B, Relative photosynthesis in *Macrocystis* on an average day in waters of different absorption coefficients (A above). (After North.)

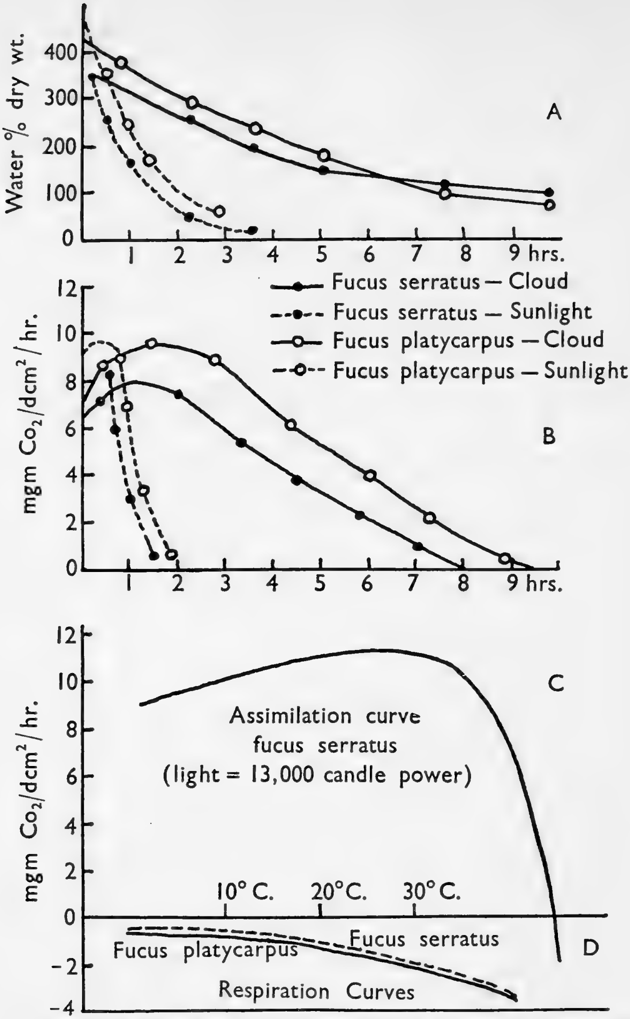

Fig. 213 A, water loss, and B, assimilation in relation to exposure (drying) on sunny and cloudy days. C, D, effect of temperature on respiration and assimilation of *Fucus*. Investigational period for assimilation, 5 min.; for respiration, 18 min. (After Stocker and Holdheide.)

often occur at depths of 40–70 ft. in turbid water but at 90–100 ft. or more in clearer waters. This has been further demonstrated by Tschudy (1934), Stocker and Holdheide (1937) and also in New Zealand. In the first-named study, maximum photosynthesis occurred at the surface on choppy days but at about 5 m. on calm

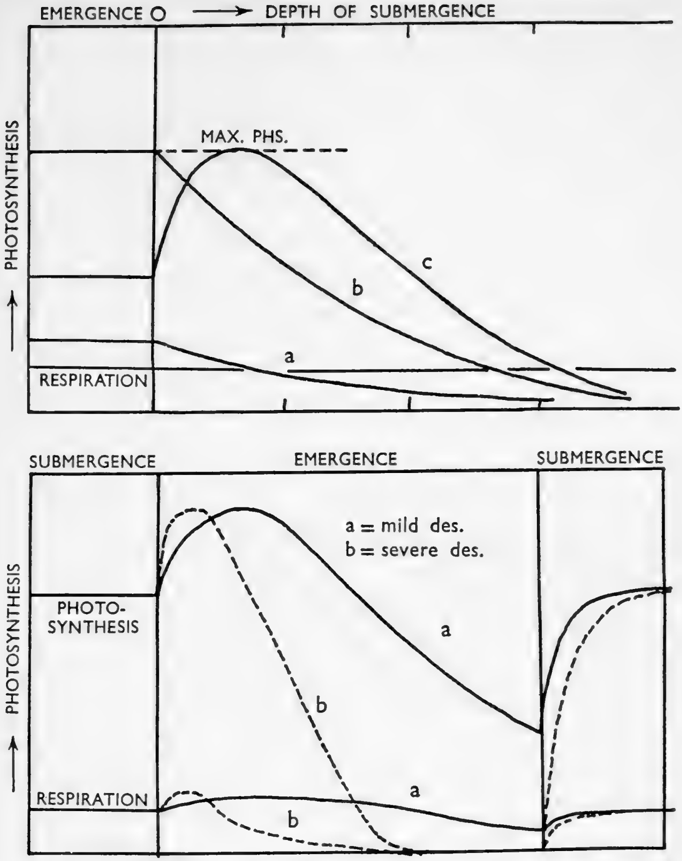

Fig. 214 Top: effect of light intensity upon photosynthesis of exposed and submerged *Hormosira banksii* in relation to depth. a = low light intensity; b, optimum light intensity; c = supra-optimum light intensity. Bottom: effect of desiccation upon photosynthesis (full line) and respiration (broken line) of *Hormosira banksii* when exposed. (After Trevarthen.)

days. In regions where chop is considerable over much of the year, or where cloud is persistent, the lower limit of algae will be higher then elsewhere.

In the study by Stocker and Holdheide, who used *Fucus spiralis* var. *platycarpus* and *F. serratus*, the difference between sunny and cloudy days was extremely pronounced (Fig. 213), and it would seem that on exposure the fall off in the assimilation rate on sunny days is correlated with the water content, because the exposed thalli quickly dry up and cease to assimilate. An investigation into assimilation of *Hormosira* under submerged and exposed conditions at Auckland led to results that agreed with these earlier workers (Fig. 214).

Some work from Japan on sporeling growth in relation to light intensity is of relevance here. Except for *Monostroma*, sporeling growth in green algae is greatly retarded under decreased light, whilst that of red and brown algae tends to be increased. Sporelings of green algae also grew more rapidly under yellow, red or blue light than under green light. Length of the light period may also be involved. Thus it has been found that *Enteromorpha* sporelings grow better under long-day conditions, whereas those of *Monostroma* grow best at first under medium day length but that later short days are optimal.

There has been considerable discussion over many years in connexion with the colours of the algae in relation to assimilation and depth. Quite early Englemann put forward the hypothesis that the colour of the alga is complementary to that of the incident light. Thus in the Chlorophyceae maximum assimilation takes place in the red region of the spectrum, and as these wave lengths are rapidly eliminated in sea water, green algae tend to grow in the upper part of the littoral. In the Phaeophyceae, maximum absorption takes place in the green region and they can therefore live at greater depths, and in the Rhodophyceae maximum absorption takes place in the blue region. There has also been considerable argument as to whether the coloured pigment merely acted as a passive colour screen or whether there was active absorption by the pigment. Recent work on fluorescence in chlorophyll and in other pigments has led to the view that the coloured pigments in Rhodophyceae and Phaeophyceae actively absorb the available incident light, expecially in the regions complementary to the colour, but that the energy so absorbed is largely transmitted to chlorophyll molecules where the actual photosynthesis occurs.

In all studies on assimilation in relation to depth with algae it is important to consider not only the absorption curves of the algae, but also the action spectra. The latter is the more important because it indicates the extent to which the different portions of the absorbed spectrum are utilized in photosynthesis. Fig. 215 illustrates the absorption spectra of a green and red alga at different depths, and it will be seen that in the *Monostroma* there is a rapid

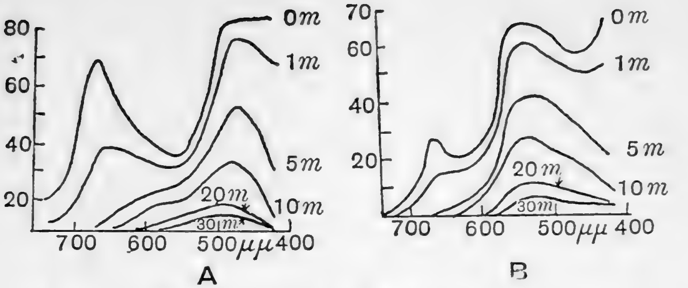

Fig. 215 Absorption curves of A, *Monostroma* B, *Delesseria* at different depths. (After Seybold.)

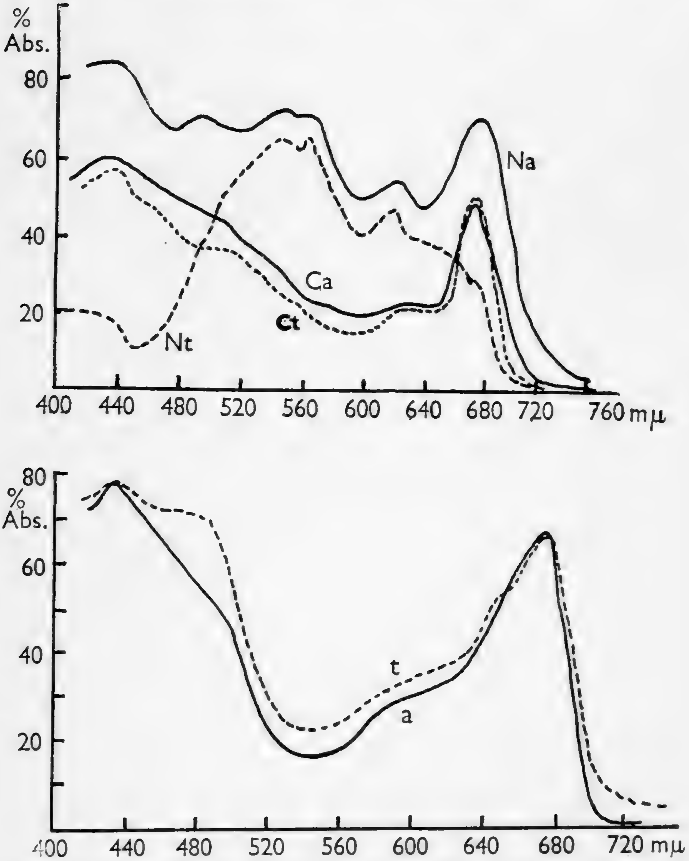

Fig. 216 Absorption (a) and action (t) spectra of marine algae. Top: *Coilodesme californica* (Ca, Ct) and *Smithora* (*Porphyra*) *naiadum* (Na, Nt). Below: *Ulva taeniata* (a, t). (After Haxo and Blinks.)

decrease in the absorption of the red wave lengths as depth increases. Fig. 216 illustrates absorption and action spectra for algae at different wave lengths

Fig. 217 illustrates the assimilation rate of algae from all three groups under different light intensities. All exhibit an optimum light intensity for assimilation, which in the case of the littoral algae is in the same region as that of cormophytic land plants. In sublittoral algae, such as *Laminaria saccharina*, the optimum is at a much lower light intensity and with some plants, *Macrocystis*, *Egregia*, it has been shown to vary with different parts of the plant. Because certain algae are more efficient metabolically at low light intensities or when the spectral composition of the light has been modified, some workers have suggested that one can recognize sun and shade algae. Different bases have been used by workers in making this distinction, and whilst there may be some ecological value in the distinction, nevertheless further experimental work is desirable before any final conclusions are reached. The compensation depth or light intensity at which photosynthesis just balances respiration may be very important. This differs for various species

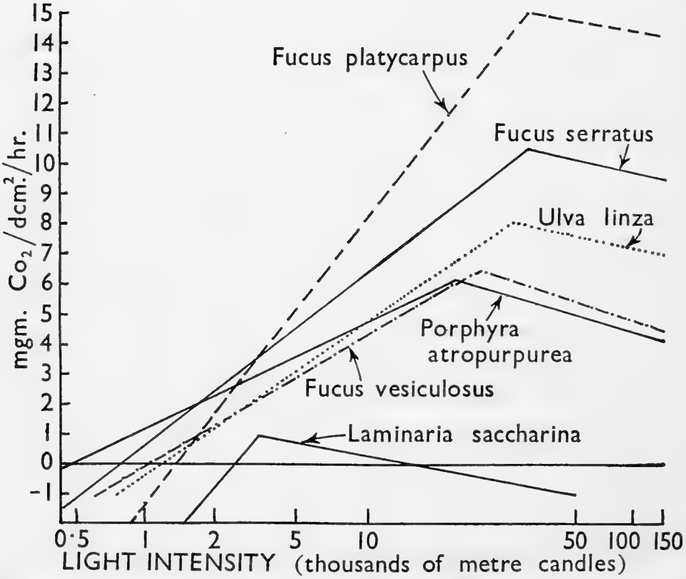

Fig. 217 Assimilation of different algae in relation to light intensity. (After Stocker and Holdheide.)

(Fig. 221) and is also dependent on temperature. At 15° C. it is 15 foot-candles for *Macrocystis*, 38 foot-candles for *Fucus serratus* and 32 foot-candles for *Laminaria saccharina*.

Assimilation is affected not only by light intensity but also by temperature and both factors need to be studied together. Some recent work on *Macrocystis pyrifera* in California has shown that the net photosynthesis varies not only with depth, as evidenced by the rates exhibited by blades from different positions on the plant, but also with temperature.

TABLE 17

Blade No.	*Photosynthetic capacity* 15° C			*Macrocystis blades ml* O_2 *per dcm*^{2} *per hr.* 22·5° C		
	Plant 1	Pl. 2	Pl. 3	Pl. 4	Pl. 5 (intermediate depth)	Pl. 6 (young plant at 50 ft.)
1 (apex)	1·33	1·52	1·45	.	.	1·74
9	.	.	.	0·89	.	.
20	2·62	2·83	1·83	0·64	.	1·74
40	2·94	2·66	3·28	0·68	2·4	2·38
50	.	.	.			2·85
60	3·44	3·04	4·02	1·35	3·08	.
80	4·09	3·60	4·46	1·99	3·42	.
99	4·77	2·74	4·92	2·44 (94)	3·83 (94)	.
109	5·14	.	.	.	.	.
120	5·28	3·4	5·12	.	.	.

Plants 1–4 all reached the water surface.

Ehrke (1931) suggested that there is a correlation between the temperature at which maximum assimilation takes place and the average temperature of the month of maximum development (see table below).

TABLE 18

Optimum temperature for assimilation	*Av. temperature in months of max. development*	*Genus*
17° C.	17° C. Aug.–Sept.	*Fucus, Enteromorpha*
0° C.	0° C. winter and early spring	*Delesseria*

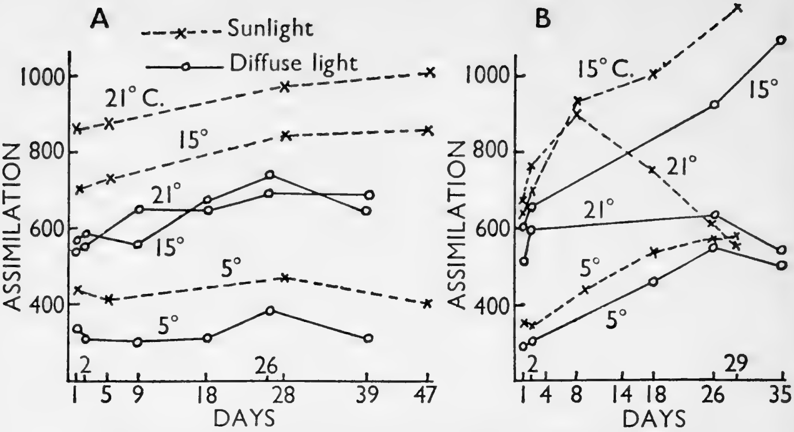

Fig. 218 Daily drift in assimilation of algae at different temperatures in sunlight and diffuse light. A, *Fucus serratus* winter plant. B, *Porphyra*. (After Lampe.)

The problem, however, is not as simple as this. Thus Lampe (1935) found that in winter the assimilation rate of *Fucus serratus* plants rises when it is measured in sunlight under conditions of increasing temperature (Fig. 218); on the other hand, in the case of a red alga such as *Porphyra*, when the temperature is raised above 15° C. the assimilation curve is lowered immediately in diffuse light and after seven days in sunlight. This suggests that *Fucus* is an eurythermal species, tolerating a wide range of temperature, whilst *Porphyra* is stenothermal, tolerating a narrow range. Comparable results for *Fucus serratus* were obtained by Hyde (1938), who found that between 15° and 20° C. the assimilation rate could be increased by raising the light intensity, and that there was a certain light value (2 × 500 lux) which yielded an optimum in the rate of assimilation. This effect is not observed at low light intensities and low temperatures, whilst above 25° C. an increase in the light intensity causes a marked decrease in the assimilation rate (Fig. 219).

After a period of exposure there is the problem of the return to the normal assimilation rate, because experiments show that the assimilation rate is markedly reduced during exposure. When re-inundated, species such as *Ulva linza* and *Porphyra umbilicalis* take up water at once, and very soon are assimilating at their normal rate. The members of the Fucaceae behave in a rather different fashion and their behaviour can be correlated directly with the level they occupy on the shore and the periods of exposure they undergo.

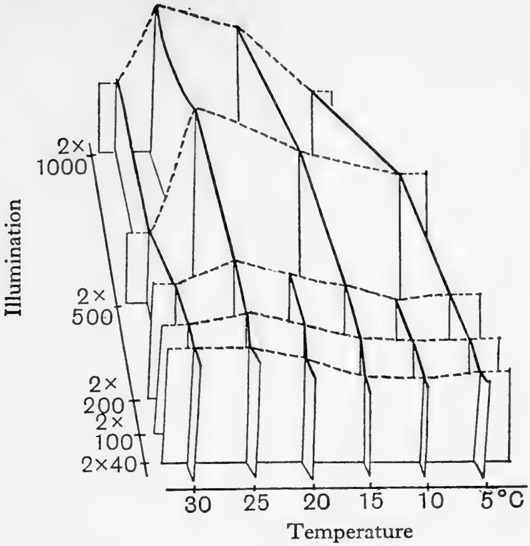

Fig. 219 Diagram of paper model to show the combined effects of light and temperature on the rate of apparent assimilation of *Fucus serratus*. (After Hyde.)

TABLE 19

Percentage of normal assimilation re-attained on flooding after exposure

Level	*Species*			
High littoral	Pelvetia canaliculata	70–80% 8–9 hr. after flooding: exposed 11 days previously		
Top of mid-littoral	Fucus spiralis	49% 8–9 hr. after flooding: exposed 3 days previously	97%	4 hr. after flooding: exposed 5 hr. previously in air 90% R.H.
Middle mid-littoral	Fucus vesiculosus	20% 8–9 hr. after flooding: exposed 3 days previously	72%	
Lower mid-littoral	Fucus serratus	Cannot tolerate 3 days exposure	42%	
Sub-littoral fringe	Laminaria digitata	——	Cannot tolerate 2 hr. exposure	

There would seem little doubt that illumination and its effect on photosynthesis is an important causal factor, and probably is largely responsible for determining the lower limits of a number of algae. It is, however, a very complex factor, and much further work is necessary before its operation is fully unravelled.

C. *Chemical factors*

(*a*) Salinity

This may operate as a presence or absence factor in places where fresh water runs into the sea. In such places Rhodophyceae and Phaeophyceae are replaced by Chlorophyceae. In estuaries *Fucus spiralis* is replaced by *F. ceranoides*. There is also the problem of salinity changes due to loss of water when the algae are exposed. This results in changes in osmotic pressure of the cell sap. Biebl (1938) found that algae could be placed in three groups according to their behaviour on exposure.

(i) Deep growing algae which are never exposed to the air; they are resistant to a concentration of 1·4 times that of sea water.

(ii) Algae of low water mark and the lower littoral tide pools which never become dry: these are resistant up to a concentration of 2·2 times that of sea water.

(iii) Algae of the littoral belt: these are often completely exposed and they can resist a concentration of 3·0 times that of sea water.

The influence of lowered salinity upon metabolic processes (see Doty, 1957) requires further study, especially in view of Fritsch's statement that the compensation point of marine algae is reached at shallower depths with lowered salinity.

Salinity changes can also occur in pools and salt pans, expecially those at high levels during neap tidal periods when there may be considerable evaporation. This factor can operate as a presence or absence factor in high level pools. In pools, intertidal algae exhibit a greater tolerance to changes in salinity than do infra-littoral algae (Table 20), and this may well explain why the latter are restricted to pools in the lower half of the littoral zone.

(*b*) Substrate

Generally, differences in chemical composition have little effect on the flora. An exception to this is the presence of chalk, the algal flora of chalk cliffs (Anand, 1931) differing distinctly from that of metamorphic and igneous rocks. This, however, is only a presence or absence factor.

TABLE 20

Osmotic resistances of Rhodophyceae from different habitats (after Biebl)

ALGAE	*Diluted sea water*										*Concentrated sea water*											
	00	·1	·2	·3	·4	·5	·6	·7	·8	·9	1·2	1·3	1·4	1·5	1·6	1·7	1·8	1·9	2·0	2·2	3·0	Habitat and depth
Heterosiphonia plumosa	+	+	0	0	0	0	1	1	1	1	1	1	0	+	+	+	+	+	+	+	+	Plymouth Bay (8–10m.)
Heterosiphonia plumosa	+	+	+	0	0	1	1	1	1	1	1	1	1	0	+	+	+	+	+	+	+	Wembury, tide pool
Polyneura hilliae	+	+	+	+	0	1	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	Plymouth Bay (8–10m.)
Cryptopleura ramosa	+	+	0	0	0	0	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	Plymouth Bay (8–10m.)
var. *uncinatum*	+	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	?	+	+	+	Plymouth Bay (8–10m.)
Brongniartella byssoides	+	+	0	0	1	1	1	1	1	1	1	1	1	0	0	0	+	+	+	+	+	Plymouth Bay (8–10m.)
Phycodrys rubens	+	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	+	Plymouth Bay (8–10m.)
Antithamnion tenuissimum	+	+	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	+	+	Plymouth Bay (8–10m.)
A. plumula	+	+	+	+	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	+	Tromsö, 30 cm.
A. cruciatum	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	+	Naples
Polysiphonia urceolata	+	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	Wembury, tide pool
Polysiphonia urceolata	+	+	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	Tromsö, L.T.M.
Membranoptera alata	+	+	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	Wembury, above L.W.M.
Ptilota plumosa	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	Wembury, above L.W.M.
Ceramium ciliatum	+	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	Wembury, above L.W.M.
Callithamnion tetragonum var. *brachiatum*	+	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	Wembury, tide pool
Spondylothamnion multifidum	+	+	+	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	+	Wembury, tide pool
Griffithsia flosculosa	+	+	+	+	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	+	Wembury, tide pool
Griffithsia furcellata	+	+	+	+	+	0	0	1	1	1	.	.	.	.	.	.	.	.	.	.	.	Naples
Griffithsia opuntioides	.	.	.	.	.	.	.	.	.	.	1	1	1	0	0	.	.	.	.	.	.	Naples, 60 cm. up.
Nitophyllum punctatum	+	+	+	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	+	+	Wembury, tide pool

(*c*) pH (Acidity)

The pH of sea water normally ranges from about 7·9 to 8·3 and the factor is of no great importance for the littoral algae though it might be of significance in some of the higher rock pools where, during the day, the pH may rise to 10. Most algae that have been investigated tolerate a pH range of 6·8–9·6 and the pH of pools is rarely outside this range.

(*d*) Oxygen content

The oxygen tension in sea water is normally low but sufficient for metabolic purposes. In pools, during the day the oxygen content may rise substantially.

(*e*) Nutrients

This factor is of importance in controlling the seasonal periodicity of marine and fresh-water plankton (see p. 342). It is also of importance in lakes where oligotrophic and eutrophic waters differ chemically, and this difference is reflected in the vegetation (see p. 367). High level rock pools well supplied with bird droppings commonly support a very rich flora of microscopic algae.

D. *Biological factors*

(*a*) Animals

Competition between plants and animals may in certain cases be sufficiently severe to eliminate some algae. It therefore operates as a presence or absence factor. If *Patella* (limpet) is present in abundance it may eat up the *Enteromorpha* felt and so stop *Fucus* sporelings from becoming established. The attacks of boring mollusca are probably responsible for the eventual detachment of *Durvillea* plants, and in Europe *Helicion pellucidum* is said to bring about the detachment of *Laminaria saccharina* plants. On salt marshes the mollusc *Hydrobia ulvae* can cause havoc among beds of *Ulva.*

(*b*) Plants

Many of the possible relationships here have not been worked out. There is, of course, the host-parasite relationship, e.g. *Janczewskia*, (p. 252); *Harveyella*, (p. 241, etc.), and host-epiphyte relationship, because some of the epiphytes appear to be restricted in their host requirements. The establishment of *Fucus* sporelings also seems to depend very largely upon the pre-development of a green algal felt (*Enteromorpha*), whilst the establishment of *Porphyra tenera* sporelings on the bamboo poles in Japanese harbours (see p. 450) is dependent upon the development of a diatomaceous film.

One may also include here variations that can occur within the different organs of a single plant. In the case of large plants, such as the oarweeds, these may be considerable. Reference (p. 393) has already been made to the difference in apparent photosynthesis between juvenile, medium dissected and basal entire leaves of deep water plants of *Egregia laevigata*. The same phenomenon, even more pronounced, is exhibited by different parts of *Macrocystis pyrifera* (Table 21).

TABLE 21

Photosynthesis/Respiration ratios for parts of Macrocystis *plants (from Clendenning and Sargent)*

Plant Part	*P/R value*
Naked Stipe	4·1
Pneumatocyst (bulb)	7·1
Sporophyll	9·2
Apical blade to blade 20	11·1 (6·5–18·7 range)
Blade 21–blade 61	18·6 (10–29 range)
Blade 62–blade 120	22·0 (13–34 range)

For this species it is quite evident that the rate of photosynthesis increases with age of the blade. In the case of *Egregia* (p. 393) it is the middle-aged dissected appendages that exhibit the highest rate.

SUMMARY

Despite the great variety of factors that can and do operate on a maritime shore, nevertheless there is the uniformity of the belts occupied by the major organisms. Furthermore if the number of upper and lower limits occurring at any one level are calculated, it is found that there are certain levels at which the number of limits is greater than elsewhere. This suggests that there is some change in a major factor or factors at that level which affects a number of organisms. Such levels have been termed critical levels, and whilst a number have been established for different places there is general agreement that the following critical levels are widespread:

(*a*) between mean and extreme low water-marks of spring tide;
(*b*) around mean low water-mark of neap tides;
(*c*) around extreme high water-mark of neap tides.

This uniformity suggests that the physiographic or tidal factor is paramount. However, if the zones occupied by major algal species in different localities are compared, after allowance is made for splash and wave action, it is found that they do not always coincide (Fig. 206), so that even if the tidal factor is the major causal factor its effect is commonly modified locally by other factors.

One very important factor is the inter-relationship between respiration and photosynthesis. Normally the latter is in excess of the former, but at different temperatures and at different depths (depending on light intensity (Fig. 212B)) in the water the two rates coincide. This is known as the compensation point and below that depth, if conditions remained uniform, an alga could not survive because breakdown would exceed build up. During short periods an alga may be able to exist under such conditions. There will be, for each species, however, some level at which the periods below the compensation point exceed the periods above. This will effectively form a lower limit to the algal belt. It is likely that the lower levels of many of the species occupying the lower littoral and the infra-littoral are set by this phenomenon, but at present all too little work has been done upon it. Apart from the work by Ehrke (1931) and Clendenning and North (1958)[1] on *Macrocystis pyrifera* an investigation of the littoral *Hormosira banksii*, has led to results which are summarized in Fig. 214, where it will be seen that under a low light intensity the compensation point is reached at about 1 m. or less, at optimum light intensity (in relation to emergent conditions) the compensation point is reached at about 4 m., whilst at still higher light intensities it is not attained until nearly 6 m. In Fig. 220 the relationship of the compensation point to sea temperature is shown. Another means of approaching the problem was used by Klugh and Martin (1927), who studied the growth rates of various algae in relation to submergence by measuring plants and then tying them to floats which were suspended in the water at different depths. After some months the floats were pulled up and the plants remeasured. The curves (Fig. 221) show that maximum growth occurred between 1 and 2 m. where

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[1] Kelp investigation programme at Scripps Institute, California and published as special reports.

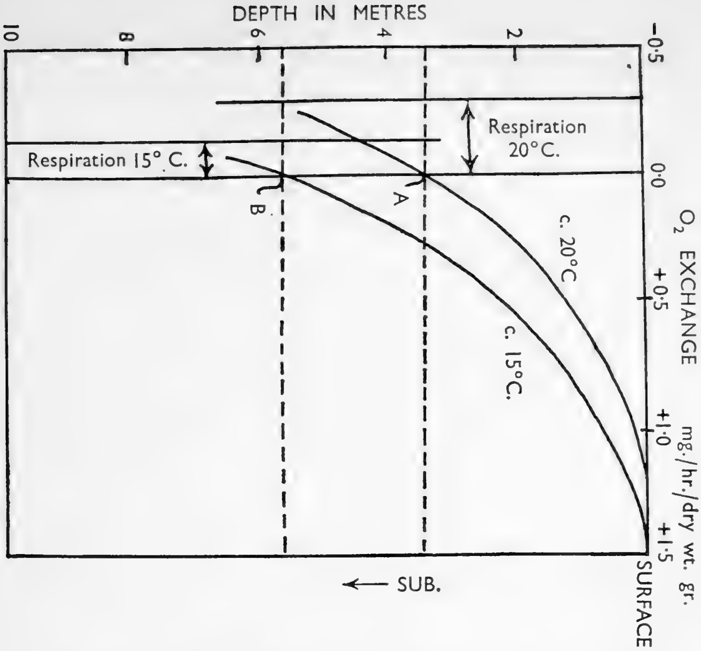

Fig. 220 Variation of compensation point with depth and sea temperature in *Hormosira banksii*. (After Trevarthen.)

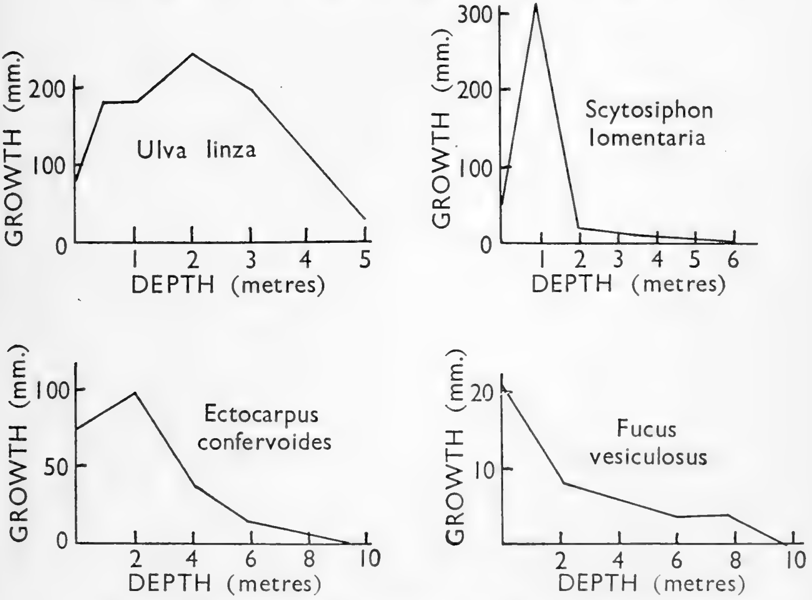

Fig. 221 Rate of growth of various algae at different depths in sea water, New Brunswick. (After Klugh and Martin.)

normally under diffuse light maximum photosynthesis takes place (see p. 394).

So far as the lower submerged limit is concerned, one may postulate that an alga will go deeper in the water the nearer its absorption and action spectra approach that of the shade type (i.e. algae most efficient metabolically under low light conditions), and the lower is its compensation point. Under these conditions, for example, a green shade alga would be able to go to a lower limit than a red sun alga.

Despite all that has been said in the previous pages, our knowledge of the factors controlling zonation is scanty. No real progress will be made until key species are studied exhaustively. Work of this nature has been commenced with *Macrocystis pyrifera*, *Egregia laevigata* and *Hormosira banksii*. The last-named species occurs in Australasia and an analysis of sea temperature relationships over its area shows that it is found within a range of 15° C. The region that it occupies on the shore also rises with decreasing latitude, but the exact significance of this has yet to be worked out. Detailed studies of the alga have shown that it exists in a number of ecological forms and eventually each one of these forms will need to be studied so that the vertical limits reached under different conditions can be understood (Fig. 121). There are several interesting free-living forms found in mangrove swamps and these occupy higher levels on the shore than normally do the attached counterparts on rocky shores. Shade, higher humidities during exposure and lower water loss may well be responsible for this phenomenon. A study of water loss that can occur during periods of exposure follow the trends that have been found for other fucoids. There is, however, in the form investigated, a relationship between degree of hydration and rate of respiration, and it is evident that young plants differ from adult ones in this respect (Fig. 210). The difference is sufficient to suggest that certain metabolic paths in the young plants may be different to those in the adult. This is an aspect the implications of which will require to be explored more fully. The relationship of photosynthesis to depth and sea temperature has also been studied (Fig. 220) and the effect of varying periods of desiccation upon the photosynthetic rate. Once the basic facts have been established, various refinements can be added. Thus the effects may vary depending upon whether high tide occurs at sunrise or whether it occurs in the middle of the day. The effects will also vary in different localities depending upon the nature of the tide (p. 384), and there will also be seasonal variations in quantity and quality of light available at different depths. At the lower levels work has still to be carried out to determine the extent to which competition with other organisms may be important. At high latitudes where the alga is reaching its southern limit, competition from other algal species is probably more severe and as a factor it may be more important here than at its northern limit. It is not suggested that the final picture has yet been reached even in this case and there are further aspects that may or may not be of significance. Thus it has been found that *Hormosira*, like certain other marine algae, possesses an Na^+ efflux pump, removing excess sodium, and a K^+ influx pump which enables it to accumulate potassium (Bergquist, 1959). Whether either or both of these pumps may have a critical operating value, depending either on length of period of submergence or depth of submergence has yet to be studied.

In conclusion, it is evident that work during the last few years brought us to a clearer understanding of the factors controlling algal zonation to the sea-shore, but there is still scope for much more, especially of a physiological and biochemical nature.

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Chapter XVI

PHYSIOLOGY, SYMBIOSIS

Physiology

It is impossible to separate entirely the physiology of the algae from a discussion on the ecological factors controlling zonation. This is particularly true of photosynthesis and respiration under different environmental conditions, and reference should therefore be made to the relevant pages (pp. 394, 408). Apart from the physiologico-ecological studies of the dominant belt algae, our knowledge of algal physiology is largely associated with the establishment around 1920 of bacterial free algal cultures. Such cultures had probably been obtained earlier, but the intensive use of such cultures for physiological work stems from about that time. These cultures have been used for studies in the fundamental mechanisms of photosynthesis and respiration, and also in growth studies (cf. p. 43). The net result has been that much of our knowledge at present is restricted to unicellular algae, expecially members of the Chlorococcales, e.g. *Chlorella*, *Scenedesmus*. Whilst one may expect that the larger algae behave similarly, nevertheless there may be differences and an extension of this work is highly desirable.

Photosynthesis

It has been shown that carotenoid pigments in *Navicula*, *Chlorella*, *Ulva* and *Monostroma* absorb light that is wholly or largely utilized in photosynthesis. It also appears that fucoxanthin in brown algae absorbs light that is used in photosynthesis and the phycobilins in Rhodophyceae behave similarly. Despite this, however, it seems that the light energy absorbed by these pigments is transmitted to chlorophyll *a*, which must therefore be regarded as the principal photosynthetic pigment bringing about the photolysis of water (see also p. 398).

Our present knowledge of the mechanism of photosynthesis rests very largely upon studies of algal cultures, because they form very convenient material which responds rapidly to new techniques such as the use of radio-isotopes. There is no reason to suppose that the mechanism in the algae differs materially from the mechanism in higher green plants. From the work that has been carried out it seems that the rate of photosynthesis in marine algae such as fucoids is lower than that of land plants.

Certain algae are capable of photo-reduction using elementary hydrogen after a period of adaptation under anaerobic conditions. The marine algae require a long period of adaptation but *Chlamydomonas moewusii* appears capable of almost an immediate change.

TABLE 22

Algae which have been tested for ability to carry out photo-reduction using hydrogen

Class	*Species adapted*	*Species not adapted*
Chlorophyceae:	Scenedesmus obliquus Ankistrodesmus sp. Chlamydomonas moewusii Ulva lactuca	Chlorella pyrenoidosa
Bacillariophyceae:		Nitschia spp.
Phaeophyceae:	Ascophyllum nodosum	
Rhodophyceae:	Porphyra umbilicalis Porphyridium cruentum	
Myxophyceae:	Synechoccus elongatus Synechocystis sp.	Oscillatoria sp. Nostoc muscorum Cylindrospermum sp.

This type of carbon fixation probably does not occur in algae to any great extent. There is also evidence that some algae can utilize hydrogen sulphide as the hydrogen donor in place of water. In this respect they are like certain bacteria. *Oscillatoria*, *Pinnularia* (diatom), *Scenedesmus* and *Synechoccus* can all utilize H_2S, though in the two last examples molecular hydrogen is used preferentially.

Nitrogen fixation

The establishment of pure bacteria-free cultures has enabled workers to show that some twenty or more species of Myxophyceae are capable of 'fixing' atmospheric nitrogen. The genera involved include *Nostoc*, *Anabaena*, *Cylindrospermum*, *Calothrix*, *Tolypothrix*, *Anabaeniopsis* and *Mastigocladus*. So far no complete proof of nitrogen fixation by Chlorophyceae has come to hand. Fixation of atmospheric nitrogen by Myxophyceae only takes place so long as readily available combined nitrogen sources (e.g. ammonium salts) are lacking or in very low concentration. The process also apparently requires the presence of traces of molybdenum (see also p. 381).

Respiration

Detailed studies of the respiratory process have shown that it follows the presently accepted normal channels in *Chlorella*, *Scenedesmus*, the colourless *Prototheca*, *Ulva*, the Phaeophycean *Myelophycus* and the Rhodophycean *Gelidium*. There would seem to be no reason to suppose that it is otherwise in the uninvestigated members of the Chlorophyceae, Phaeophyceae and Rhodophyceae. Respiration does not, however, appear to follow the normal path in *Cylindrospermum* and it is clear that further work with bacteria-free cultures of Myxophyceae is highly desirable. The enzymes normally associated with respiratory reactions have been isolated from a number of algae in addition to those mentioned above. There is also evidence that at least some of the acids associated with the Krebs cycle occur in the algae that have been thoroughly studied, though again *Cylindrospermum* is a marked exception.

Oxidative assimilation, in which a portion of the organic material being respired is partly built back up into cell material, has been demonstrated in the colourless *Prototheca*, and also in *Chlorella pyrenoidosa*, *C. vulgaris* and *Scenedesmus quadricauda*. Since this phenomenon also occurs in higher plants it is probably more widespread among the algae, but at present the number investigated is not great.

Vitamins

Most algae are able to build up vitamin B (thiamine) for themselves, though there are a few which do not possess the necessary mechanism, but these can apparently absorb sufficient from the thiamine dissolved in natural waters. The Eugleninae (see p. 1) are the forms most affected but there is a mutant of *Chlamydomonas moewusii* which cannot synthesize thiamine. There is also some evidence that the growth of marine algae may be dependent on organic substances present in sea water, though the nature of these substances is not known. Surface sea water, for example, has substances necessary for the germination of sporelings of *Ulva* and

Enteromorpha. Chryptomonas ovata and *Synura uvella* will only grow if an extract of soil or lake sediment is added to the culture medium.

Some species of algae are as rich in vitamin C as lemons, though the content is affected by season, temperature, location and pH. Vitamins D and E also appear to be present in at least some algae.

Growth hormones

Auxin (indole-acetic acid), presumably identical with that found in higher plants, has been reported in *Valonia macrophysa, Laminaria agardhii* and in a number of Pacific coast algae, including *Macrocystis, Desmarestia* and *Fucus evanescens*. Growth substances have been detected in the eggs, sperm and fruiting tips of European species of *Fucus*, and the presence of these may be partly responsible for the fact that the first rhizoid of a germinating zygote grows out on the side adjacent to neighbouring eggs. It is also clear that acidity is an important factor in this effect. Although auxin has not been detected in *Codium tomentosum* from Naples, nevertheless indole-acetic acid does promote growth in *Codium*, and a further investigation would seem desirable.

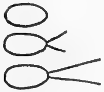
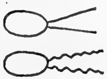
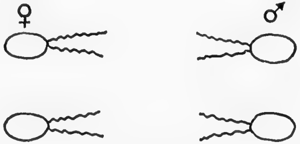
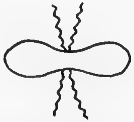
In addition to growth promoting substances there may be growth inhibiting compounds. Such substances are probably produced by *Nostoc punctiforme, Nitschia palea* and *Chlorella vulgaris*. The inhibitor from Chlorella is known as 'chlorellin' and appears to be a mixture of fatty acids. It is active against bacteria and this is one reason why *Chlorella* is so effective in purifying sewage effluent (see p. 453).

Phototropic phenomena are known to occur in *Bryopsis, Acetabularia* and *Derbesia* whilst rather weaker effects are found in *Cladophora* and *Griffithsia*. In *Bryopsis* the tips of the branches grow towards the light and the rhizoids away from it: this may well be associated with auxin, as in higher plants, but although auxin occurs in *Bryopsis* there is no clear gradient along the plant, nor is there any effect from external applications until inhibitory concentrations are reached.

Sex hormones

Since 1926 it has been known that the gametes of certain algae secrete sexual substances into the surrounding water. This has been

TABLE 22a (After Moewus)

	Phase of Development	Period of Illumination		Hormones in filtrate	Chemical nature
I	Flagellar formation	0 3 min.		Flagellar	Crocin
II	Induction of motility	5 min.		Flagellar Motility	Crocin
III	Sex determination	10 min.		Flagellar Motility 2 androtermones 2 gynotermones	Crocin Peonin 4-oxy-β cyclocitral Isorhamnetin Picrocrocin derivative
IV	Copulation	15 min.		Flagellar Motility 2 androtermones 2 gynotermones Androgamones Gynogamones	As above Cis / trans crocetin dimethyl esters
V	Planozygote	3 days		No motility hormone produced	
VI	Completion	1 day		Hormones not known	

demonstrated for *Dasycladus clavaeformis*, *Tetraspora lubrica*, *Sphaeroplea*, *Chlamydomonas eugametos*, *Protosiphon botryoides*, *Stephanosphaera pluvialis* and *Botrydium granulatum* (Smith, 1951). A story has apparently been worked out for *Chlamydomonas eugametos* in some detail and this will therefore be discussed.

Chlamydomonas eugametos when grown on agar lives in the palmelloid state. When flooded with water and irradiated with light flagellae are first formed, then the cells become motile, and, if the irradiation is continued, sex determination takes place followed by copulation, fusion and production of the zygote. These changes are associated with special hormones which can be extracted from the filtrate at the different stages in the process. These hormones are present in such small quantities that 200 litres of rich filtrate are required and analysis even then must be spectroscopic. The sequence of events is illustrated in Table 22(a) which also indicates the nature of the sex hormones. The hormone responsible for production of flagellae has been identified as crocin. The hormones that actually determine the sex of the gamete are called *termones*, those that determine the female being gynotermones and those determining the male androtermones. There appear to be two of each in *C. eugametos*. In addition the substances responsible for attraction between male and female gametes are termed *gamones*. It is likely that the gamones are produced by the flagellar sheath since the sheaths appear to be responsible for agglutination. These have been identified as cis- and trans-crocetin dimethyl ester. When cis- is in excess the mixture is a gynogamone and when the trans- is in excess the mixture is an androgamone. It has further been suggested that the degree of relative sexuality in *C. eugametos* and species interfertile with it depends on the relative proportions of cis- and trans-crocetin dimethyl ester. The intensity of sexuality between male and female gametes has been termed the valency and the relation of valency to the cis-/trans- ratio is shown in Table 23.

TABLE 23

Proportions of cis- and trans-crocetin dimethyl ester in male and female gametes of different valence in Chlamydomonas eugametos (after Moewus)

Valence	♀5	♀4	♀3	♀2	♀1	♂1	♂2	♂3	♂4	♂5
cis/trans ratio	98·2/1·8	95/5	85/15	75/25	65/35	35/65	25/75	15/85	5/95	1·8/98·2

It will be seen that the difference between the cis- and trans-esters always makes the same total; also that except for valency 5 there is always a 10/10 difference in the cis-/trans- ratio as between successive valencies in gametes of the same sex. The difference in ratio between male 1 and female 1, however, is not 10/10 but 30/30.

Five valencies appear to be exceptional and in other algae exhibiting relative sexuality the number of valencies is said to be less. In *Dasycladus clavaeformis*, *Protosiphon botryoides* and *Enteromorpha intestinalis* there are said to be three valencies in the male and female gametes. Because of the different valencies various types of reaction occur when gametes of different valencies are mixed. These types of reaction have been classed as:

Reaction 0: No fusion of gametes.
Reaction 1: Isolated pairs of fusing gametes.
Reaction 2: Clumps of 10–20 gametes.
Reaction 3: Clumps of 100 or more gametes.

In *Chlamydomonas eugametos* all types of combinations between male and female valencies up to 4 have been made and the results are shown in Table 24.

TABLE 24

Type of reaction between gametes of different valency in C. eugametos (after Moewus)

	♀4	♀3	♀2	♀1	♂1	♂2	♂3	♂4
♀4	0	0	1	2	3	3	3	3
♀3	0	0	0	1	3	3	3	3
♀2	1	0	0	0	3	3	3	3
♀1	2	1	0	0	2	3	3	3
○1	3	3	3	2	0	0	1	2
○2	3	3	3	3	0	0	0	1
○3	3	3	3	3	1	0	0	0
○4	3	3	3	3	2	1	0	0

These reaction types can be correlated with increasing ten point steps from a cis-/trans- ratio of 0/0 to a ratio of 90/90 (Table 25).

TABLE 25

Type of reaction and differences of amounts of cis-/trans-crocetin dimethyl ester in C. eugametos (after Moewus)

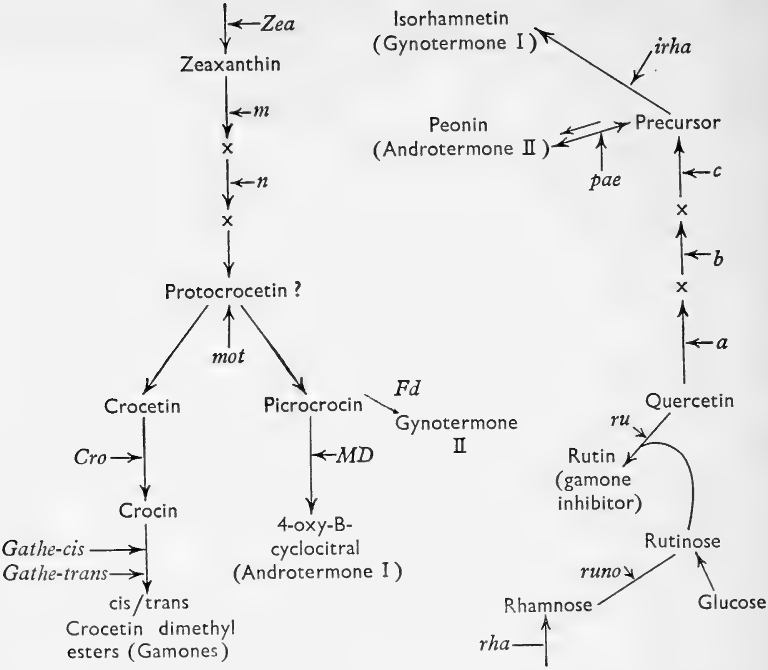
	95/5 ♀4	85/15 ♀3	75/25 ♀2	65/35 ♀1	35/65 ♂1	25/75 ♂2	15/85 ♂3	5/95 ♂4
95/5 ♀4	0/0[1] 0	10/10 0	20/20 1	30/30 2	60/60 3	70/70 3	80/80 3	90/90 3
85/15 ♀3	10/10 0	0/0 0	10/10 0	20/20 1	50/50 3	60/60 3	70/70 3	80/80 3
75/25 ♀2	20/20 1	10/10 0	0/0 0	10/10 0	40/40 3	50/50 3	60/60 3	70/70 3
65/35 ♀1	30/30 2	20/20 1	10/10 0	0/0 0	30/30 2	40/40 3	50/50 3	60/60 3
35/65 ♀1	60/60 3	50/50 3	40/40 3	30/30 2	0/0 0	10/10 0	20/20 1	30/30 2
25/75 ♀2	70/70 3	60/60 3	50/50 3	40/40 3	10/10 0	0/0 0	10/10 0	20/20 1
15/85 ♀3	80/80 3	70/70 3	60/60 3	50/50 3	20/20 1	10/10 0	0/0 0	10/10 0
5/95 ♀4	90/90 3	80/80 3	70/70 3	60/60 3	30/30 2	20/20 1	10/10 0	0/0 0

[1] The top line represents the differences in the respective cis-/trans- ratios between the left-hand column and the extreme top line.

It will be noted that no gametic union takes place if the difference in ratio is 0/0 or 10/10. A difference in ratio of 20/20 yields a type 1 reaction, a 30/30 difference a type 2 reaction and difference of 40/40 or more produces a type 3 reaction.

The essential details in the scheme (Raper, 1932) (see page 420) show the chemical nature of the sex hormones, which are fundamentally carotinoids, that has been established, and furthermore it is suggested that certain genes (symbols at sides of arrows) are actually responsible for the various steps in the transformation from one hormone or its precursor to another.

It should be noted that crocin as a flagellar hormone is apparently specific for *Chlamydomonas eugametos*. There is said to be



evidence, however, that other allied species each possess a species-specific glycoside of crocetin. The gene *mot* is responsible for splitting the picrocrocin-crocetin precursor, and two genes, *gathe-cis* and *gathe-trans*, determine the proportions of cis- and trans-crocetin dimethyl ester. Since gathe-cis is said to be activated by visible light of all wave lengths and gathe-trans only by blue or purple light, it is somewhat difficult to see how the apparently exact ratios of cis-/trans- in the different gametes are produced and maintained. The presence of rutin, a gamone inhibitor is also of great interest, but it is of importance to note that the chemistry of rutin and isorhamnetin in relation to this alga has recently been repeated at the University of Sydney. This is significant because all the previous biological and genetical work comes from a single investigator, whilst the biochemical work also was performed at one place only. Many workers have therefore felt that the novelty of the results demands repetition. In other Chlorophyceae, including species of *Chlamydomonas*, gametes are liberated and function even when thalli are in the dark. Any sex hormones in these cases, therefore, cannot be carotinoids formed in light.

There are other criticisms that have been levelled against this work, e.g. according to Moewus, who reports all this work, there must be a linear transformation of the cis- and trans- esters, whereas the published data shows an exponential curve. Also if ♀95/5 are mixed with the ♀65/35 one should get a homogeneous 80/20 mixture in the filtrate of the cis-/trans- ester, and there should be no copulation. Even if the gametes continued manufacture as they move they would leave behind much of their excreted material and would be in the 80/20 diffusion mixture. It would seem that at least one gamete of a pair would need to be sedentary, and that is not what is observed.

Moewus also claimed that there is a relationship between temperature, pH and production of female gametes in *Protosiphon botrydioides*, where an andro- and a gynotermone are also said to occur. In *Monostroma wittrockii* it is claimed that an active secretion from a brei of the gametophyte thallus results in cells of sporophytic thalli giving rise to 64 biflagellate gametes instead of 32 quadriflagellate zoospores. It is clear that all this work has opened up an extremely interesting field, but at present there is a need for the work to be repeated and extended to the gametes of other algae.

Mineral nutrition and chemical composition

The marine algae are able to absorb most of the salts present in sea water, though *Valonia* and *Halicystis* apparently cannot take up sulphates. The availability of major nutrients, expecially nitrogen and phosphorus, largely determines the plankton maxima (see p. 343). Trace elements are also present in the ash of algae and in the case of *Ulva* increased growth takes place in the presence of zinc, iron, boron and manganese.

In view of the fact that so many algae deposit calcium carbonate in or around the thallus it is remarkable how little we know about the phenomenon. It is generally assumed to be a result of the excessive use of CO_2 in photosynthesis with a resulting rise of alkalinity in the immediate neighbourhood of the algae to a point where $CaCO_3$ is no longer soluble. It is doubtful whether this simple explanation will suffice and it is possible that enzymatic action, possibly involving enzymes, is involved. A similar problem must exist in the case of the coral polyps.

In recent years a considerable volume of work has been carried out in great detail on the chemical composition of algae, especially

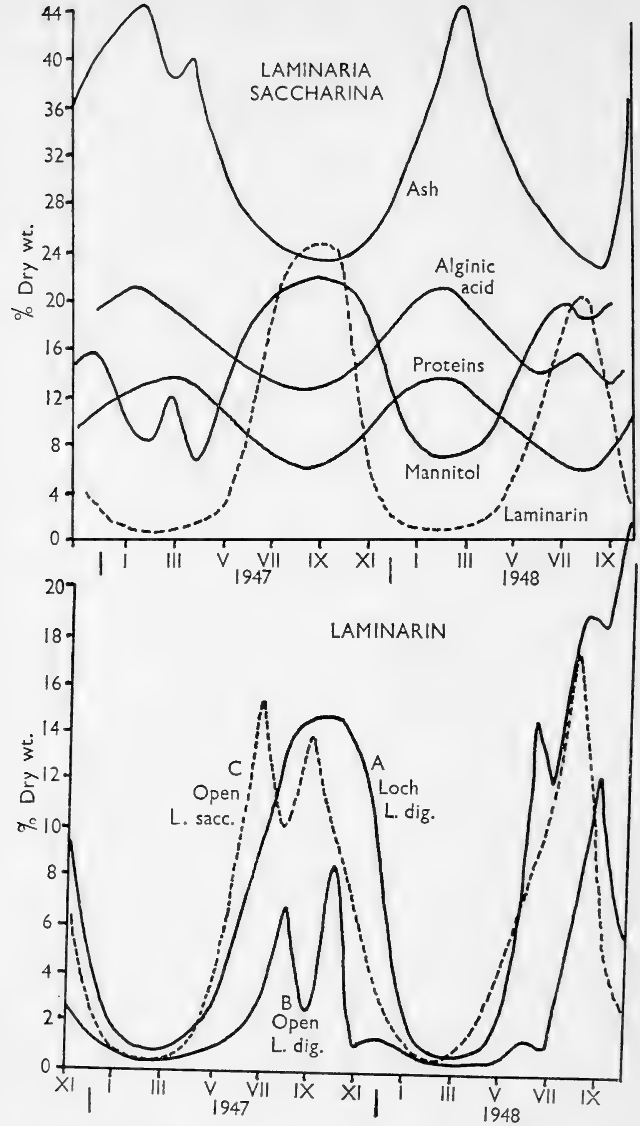


Fig. 222 Top: annual variation of ash, protein, alginic acid, laminarin and mannitol in *Laminaria saccharina*. Bottom: Annual variation of laminarin in *L. digitata* (A—loch plants, B—open sea plants) and *L. saccharina* (C—open sea plants). (After Black.)

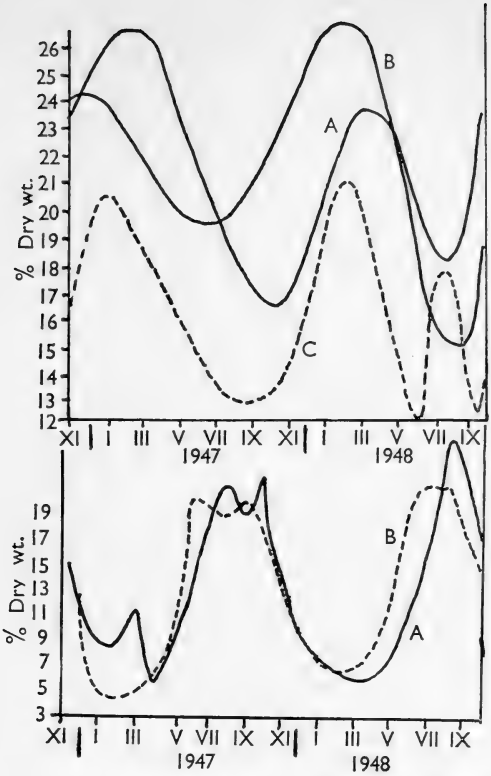


Fig. 223 Annual variation of alginic acid (top) and mannitol (bottom) in *Laminaria digitata* and *L. saccharina.* Top: A—*L. digitata* (loch plants), B—the same (open sea), C–*L. saccharina.* Bottom: A—*L. digitata* (open sea), B—the same (loch plants). (After Black.)

the littoral rockweeds (Fucales) and sub-littoral oarweeds (Laminariales) of Europe. Regular analyses of plant populations have been made so that the results represent changes in the average composition rather than those in a single individual. During the period of rapid growth (spring) fresh weight, ash, protein content and alginic acid increase whilst laminarin and manitol behave in a reverse fashion (Fig. 222). The summer decrease in growth is correlated with the decrease of PO_4 and NO_3 in the sea at that time. During this period, however, the high photosynthetic rate permits the accumulation of mannitol and laminarin (Fig. 223). The degree of the variations depends upon habitat, especially for *Laminaria digitata* and *L. saccharina,* being least in the open sea and greatest in lochs

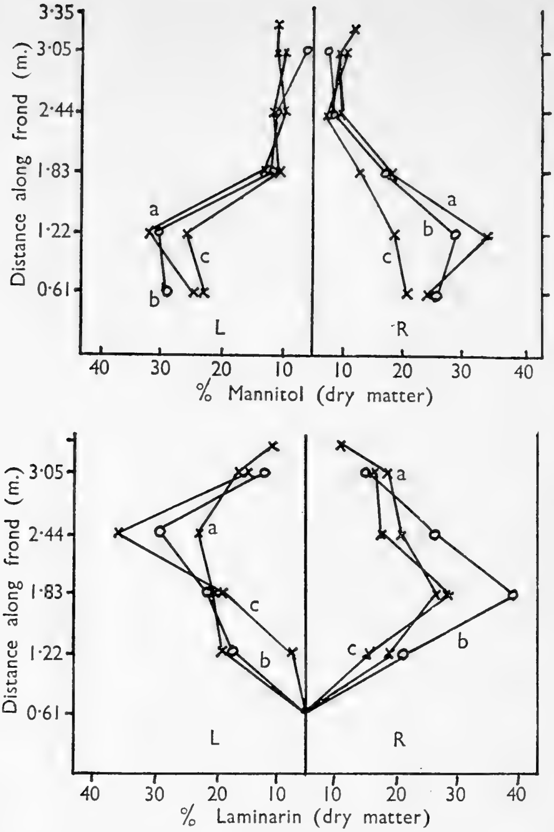


Fig. 224 Gradients along the blade of (above) mannitol, (below) laminarin in *Laminaria saccharina*. Note complete absence of laminarin in basal young growing portion immediately above meristem and reduction of mannitol in the older distal part of the blade. (After Black.)

or enclosed bodies of water (Fig. 223). In *Laminaria cloustoni* the seasonal variations are almost entirely confined to the frond. With *L. saccharina*, gradients in mannitol and laminarin occur along the frond, the amounts appearing to be related to the age of the tissue (Fig. 224). Mannitol and laminarin also vary with depth. In the case of the littoral fucoids seasonal variations tended to increase with increasing frequency of immersion. There is also a tendency to more than one maximum in the mannitol and laminarin, due to the interaction largely of exposure, temperature and formation of reproductive organs. The low laminarin content in July/August of

Scottish plants is almost certainly the result of a lowering of photosynthetic activity brought about by increased desiccation.

Outside of Europe rather similar results have been reported for *Fucus vesiculosus*, *F. evanescens* and *Ascophyllum* from the Canadian maritime provinces, except that laminarin tends to remain rather constant. The summer mannitol maximum appears to be dependent upon temperature. In the Mediterranean an analysis of 60 species for their iodine content showed that the maximum values do not coincide with the period of maximum development and is also independent of habitat.

Sap, permeability and osmotic pressure

The Siphonales and Charales have formed excellent material for studies in permeability, sap composition and osmotic pressure because of the size of their cells. There is considerable variation in the rate of penetration by the different ions; iodine, for example, entering far more rapidly than chlorine, and potassium more rapidly than sodium but less rapidly than ammonia. Oxygen also moves in and out of cells extremely rapidly. The behaviour of salts and gases in the case of other algae with a higher and more complex organization of tissues may well be different from the Siphonales and Charales, but so far it has been but little studied. A recent study on ion movement in the brown fucalean alga *Hormosira banksii* has shown that there is an influx pump favouring accumulation of potassium and an efflux pump removing excess sodium. The extent to which these two mechanisms operate depends, at least in large part, upon the degree of desiccation (see p. 390).

The cell sap of many fresh water algae has an osmotic pressure of about 5 Ats., whereas that of many marine algae, e.g. *Halicystis*, *Valonia*, *Nereocystis*, is only slightly higher than that of sea water. The osmotic pressure in Fucales would appear to be rather higher and also that of some of the Rhodophyceae. In general, however, the osmotic pressure in red algae is somewhat lower than in green or brown algae. The tolerance of algae to changes in osmotic pressure (caused by water loss) is important in the case of littoral algae (cf. p. 404). Some algae appear to respond almost instantaneously: at all events there is no plasmolytic response to sudden changes, e.g. *Monostroma*, *Dunaliella salina*. This suggests that cells of such plants may be very permeable to the salts rather than impermeable to water. Changes in osmotic pressure affect respiration in *Laminaria*, *Hormosira banksii* and *Fucus serratus* (rate rises on dilution) but not in *Enteromorpha*, *Porphyra* or *F. vesiculosus*. Photosynthesis is affected in *Fucus* and *Ulva*, being more than doubled when sea water is diluted by a third.

Bio-electric phenomena

The large cells of certain Siphonales, the Charales and *Hydrodictyon* are very suitable for studies of this phenomenon. It has been found that potential differences exist between the interior and the exterior of the cell, usually the exterior being positive, e.g. *Chara*, *Nitella*, *Halicystis*, *Bryopsis*, *Hydrodictyon*, though in *Valonia*, *Ernodesmis* and *Chamaedoris* the exterior is negative. It seems likely that the gradient of potassium ions is responsible for this potential in *Nitella* and *Hydrodictyon*. In the other algae it seems likely that the potential is a result of an internal concentration gradient within the protoplasmic lining itself. This gradient would be the sum of all the salts of organic acids, amino-acids, proteins and mineral salts contained in the protoplasm.

* SYMBIOSIS

The most striking and well-known examples of symbiosis involving algae are provided in those cases where the plants are associated with animals, especially Coelenterates, or with fungi, as in the common lichens. Apart from these examples, however, there are other cases which are not so well known, largely because they are not so common. *Gloeochaete*, for example, is a colourless genus of the Tetrasporaceae which possesses blue green bodies that look like chromatophores, though they are really a symbiotic blue-green alga. *Glaucocystis* is a colourless genus of the Chlorococcales in which a symbiotic member of the Myxophyceae also forms the blue-green 'chromatophores' that appear as a number of curved bands grouped in a radiating manner around the nucleus. In this case the illusion is further enhanced because they break up into short rods at cell division. It has so far proved impossible to grow the blue-green alga separately and it may thus have lost its power of independent growth. *Geosiphon*, which is variously regarded as a siphonaceous alga or as a Phycomycete, possesses small colonies of

Nostoc enclosed in the colourless, pear-shaped vesicles that arise from an underground weft of rhizoidal threads. Reproduction by the formation of new vesicles is said to occur only in the presence of the *Nostoc*. The presence of chitinous material in the vesicular wall suggests a fungal nature for *Geosiphon*, the vesicles perhaps being galls that are formed on the threads as a result of the presence of the alga.

The principal genera taking part in lichen synthesis are *Nostoc*, *Scytonema*, *Gloeocapsa*, *Cephaleuros* and *Trentepohlia*. Under normal conditions the partnership is truly symbiotic, but under abnormal conditions the fungus may become a parasite and devour the algal component. The green bodies which are found associated with the cells of Coelenterates and Radiolarians are usually placed in 'form' genera, *Zoochlorella* and *Zooxanthella* (cf. Fig. 225). Most of the species belong to the Cryptophyceae, but in certain of the Coelenterata the motile phases of some of the algae suggest an affinity to the Dinophyceae, whilst *Chlorella* (Chlorococcales) is also regarded as a symbiont of this group. The non-motile cells are usually found in the peripheral layers of the polyp, the larval stages of the host commonly being devoid of the alga. Most of the algal symbionts are known to have a motile phase and hence are capable of an independent existence. The function and relations of these symbiotic algae in the coral polyps have been discussed at great length by Yonge (1932), and on the whole there would appear to be evidence for a symbiotic relationship, the alga obtaining food from the animal, and the animal oxygen and perhaps nitrogenous material from the alga. The problem of the relationships between algae and animals is by no means completely worked out, and it is not impossible that in some cases we really have an animal parasitizing the alga. This is probably especially true in the case of the worm-like *Convoluta roscoffensis* and its algal associate *Carteria*, because the animal

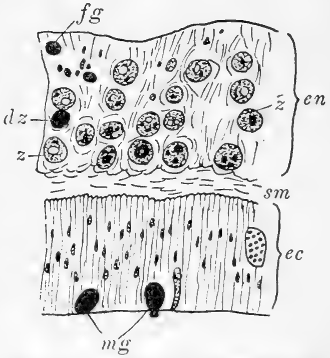


Fig. 225 Symbiosis. Zooxanthellae in the tissues of a coelenterate, *Pocillopora bulbosa* (× 375). *ec* = ectoderm, *en* = endodermis, *dz* = dead zooxanthellae, *fg* = fat globule, *mg* = glands, *sm* = structureless lamella, z = zooxanthellae. (After Yonge.)

apparently cannot live unless infected with the alga, whilst under certain conditions it also digests the green cells.

Examples of a looser form of symbiosis (almost a commensalism) are provided by *Anabaena cycadearum* which lives in the root tubercles of species of *Cycas*, and *Anabaena azollae* found in hollows in the leaves of the water fern *Azolla filiculoides*. Species of *Nostoc* found in the thalli of the liverworts *Blasia* and *Anthoceros* are probably no more than space parasites obtaining shelter.

Epiphytism is extremely common among the algae, whilst there are also a number of epizoic forms. One may also find endophytic species, such as *Schmitziella endophloea* in *Cladophora pellucida* and *S. cladophorae* in *C. feredayae*, and endozoic species, such as *Rhodochorton endozoicum* in the sheaths of hydroids. The origin of the symbiotic habit among the algae is probably to be explained as cases of epiphytism in which the relationship between host and epiphyte became more intimate: similarly the relatively few cases of parasitism probably arose either directly from an epiphytic habit or else passed through the symbiotic phase. Examples of algal parasites are *Notheia anomala*[1] in the Phaeophyceae, *Choreocolax polysiphoneae*, *Harveyella mirabilis*, the entire genus *Jancewskia* and *Colacolepis* in the Rhodophyceae, and *Phyllosiphon arisari* in the Chlorophyceae.

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[1] Hemi-parasite.

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Chapter XVII

GEOGRAPHICAL DISTRIBUTION, LIFE FORM

Many of the studies of algal distribution are based on a consideration of continuous or discontinuous distribution which are, for convenience, discussed as though they were separate phenomena, although it is clear that no distribution can be absolutely continuous. When, however, it is found that an area in which the localities are fairly close together is separated by the width of a continent or of an ocean from another similar area, then we may talk of discontinuous distribution. The problem is rendered more difficult by the unreliability of earlier records and the somewhat scanty literature, especially for tropical and sub-tropical areas. The few studies (Svedelius, 1924; Börgesen, 1934), that have been published have established certain general features which are briefly summarized below:

(1) There is a general resemblance between the algal floras of the West Indies and the Indo-Pacific. Vicarious pairs of species (two separate species closely related morphologically and yet widely separated geographically) are known and even vicarious generic groups. Species in the genus *Hormothamnion* in the Myxophyceae have a Caribbean-Indo-Pacific discontinuity, whilst there are several vicarious pairs in the genus *Neomeris* (Fig. 226). The explanation of these discontinuities which has been advanced by Murray, namely change of climate in former epochs, would only appear to explain certain cases, e.g. certain species in the Laminariaceae (cf. below), whilst it is equally obvious that the factors operating at present do not provide an adequate explanation. The only feasible hypothesis would be to postulate migration during an earlier epoch when there was a sea passage through the Panama isthmus, and this involves a migration not later than the Cretaceous.

(2) There are some species which are common only to the Western Atlantic and the western part of the Indian Ocean around Madagascar, e.g. *Chamaedorus peniculum* and three species of

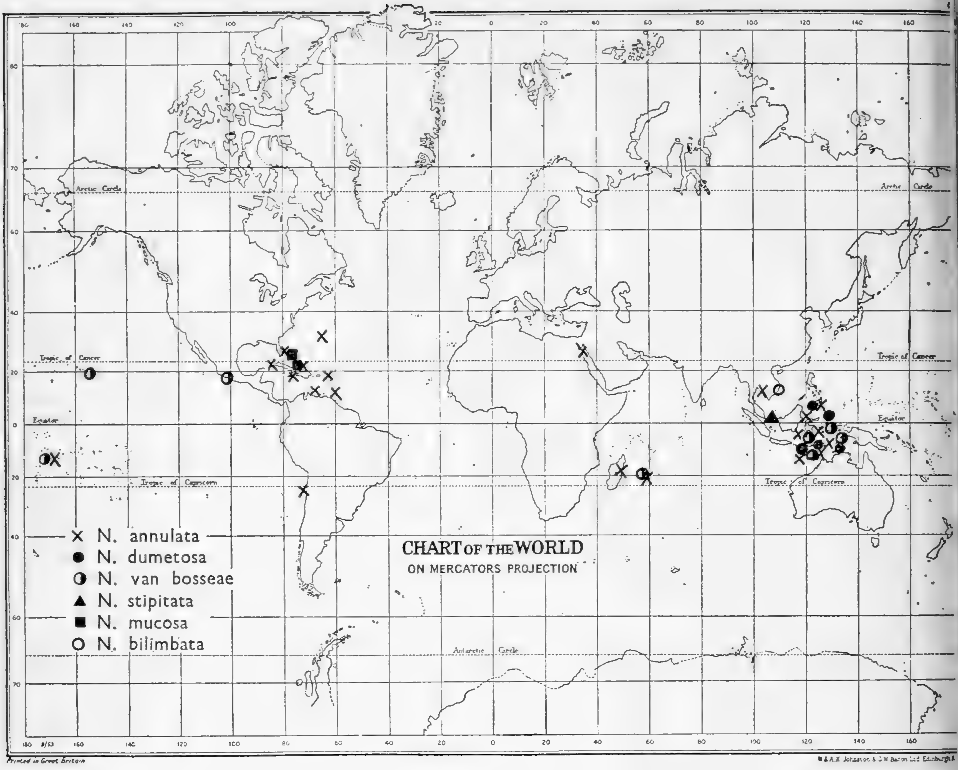

Fig. 226 Geographical distribution of species of *Neomeris*. After Svedelius.)

Cladocephalus (cf. Fig. 227). Although there is at present no very adequate explanation for this distribution, three possible hypotheses may be suggested, but there does not appear to be any evidence which supports one of them more than the others:

(*a*) Migration via the Cape.

(*b*) Migration via the Pacific and Panama, the related species perhaps still existing in the Pacific but not yet recorded.

(*c*) The related species or representatives in the interzone have died.

(3) There are some genera which are common to the Mediterranean and the Indo-Pacific region, e.g. *Codium bursa* group, the vicarious pair *Halimeda tuna* in the Mediterranean and *H. cuneata* in the Indo-Pacific, *Acetabularia mediterranea* and other species of *Acetabularia* in the Indo-Pacific (cf. Fig. 228). In this case the only

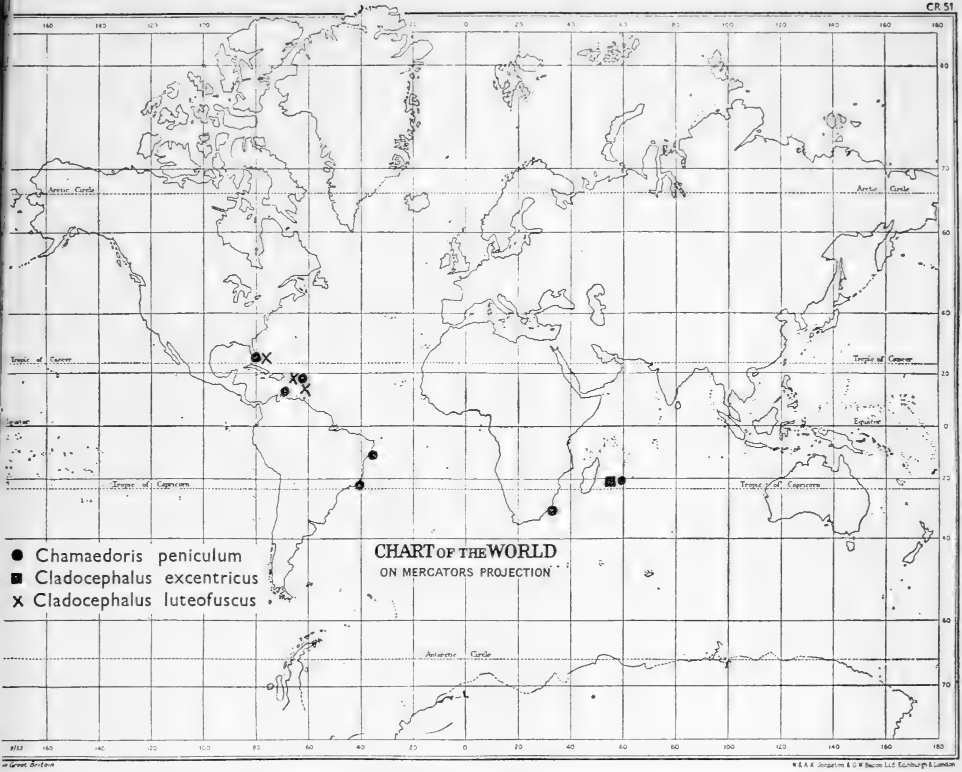

Fig. 227 Geographical distribution of *Chamaedoris* and *Cladocephalus*. (After Svedelius.)

satisfactory explanation is the existence of a former sea passage across the Suez isthmus.[1] In the flora of the northern part of the Arabian Sea, out of a total of 137 species and varieties, 22 per cent are endemic, 52 per cent are Indo-Pacific and 59·6 per cent also occur in the Mediterranean and Atlantic Ocean, the most striking example being *Cystoclonium purpureum* which does not now exist between its widely separated stations along the southern shores of France and in the Northern portion of the Arabian Sea. In the case of the Indo-Pacific species of the Arabian Sea, it is often found that they are absent from the intervening tropical waters, so that their distribution must be explained as occurring at a period when the tropical waters had a more equable temperature.

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[1] Species, e.g. *Caulerpa racemosa*, *Soliera dura*, are known from the eastern Mediterranean, which have migrated from the Indian Ocean.

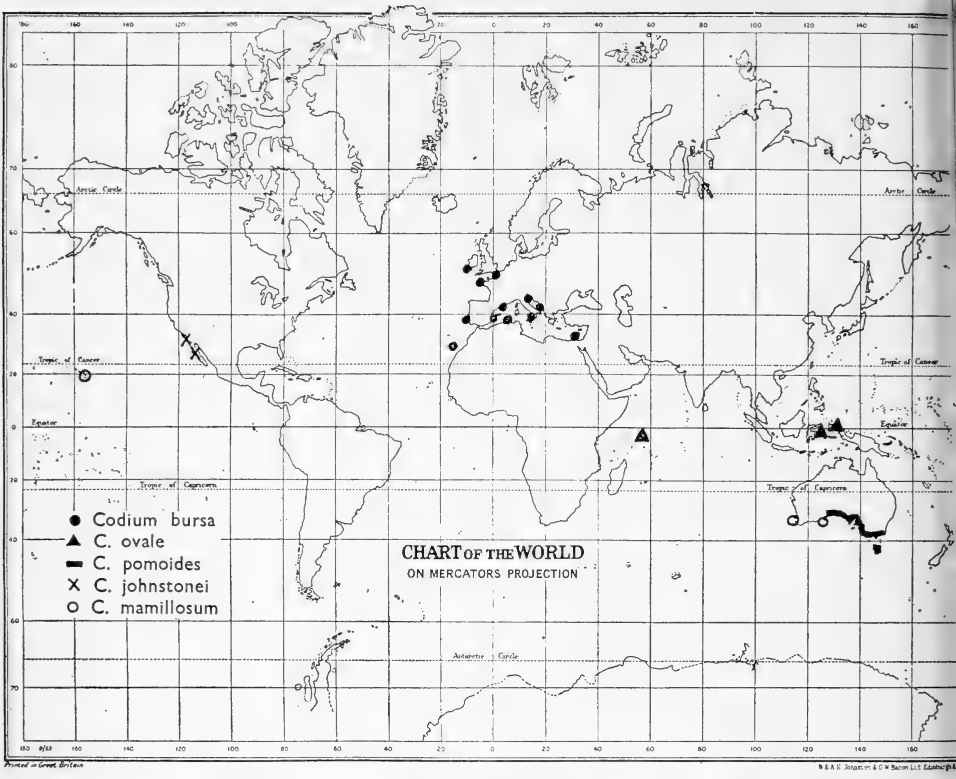

Fig. 228 Geographical distribution of *Codium* sect. *bursa*. (After Svedelius.)

(4) In general, the Indo-Pacific region is more probable as the home of the various tropical and subtropical genera and they can be classified into:

(*a*) Genera with no Atlantic representatives.

(*b*) Genera with a few Atlantic species, e.g. *Halimeda*, *Caulerpa*, *Sargassum*, *Dictyota*, *Scinaia*, *Galaxaura*.

The following genera are probably of Atlantic origin: *Dasycladus*, *Penicillus*, *Cladocephalus*, *Batophora*.

(5) Several families in the Laminariales, e.g. Laminariaceae, Alariaceae, are of Boreal Atlantic-Pacific discontinuity. These families must formerly have had a circum-arctic distribution but were pushed south by the onset of the Ice Age and then they remained in their new habitat when the ice retreated. In this case change of climate in a former epoch provides a satisfactory ex-

planation of the present discontinuity. Other genera, however, e.g. *Lessonia*, *Macrocystis*, *Ecklonia*, are of Antipodes-Northern Pacific discontinuity, *Macrocystis* in particular being primarily circum-antarctic, after which it is absent from the tropics, to reappear again on the Pacific coast of North America and around the shores of South Africa. The two southern species of *Macrocystis* appear to be identical with the two species in the northern hemisphere so that presumably they have disappeared from the intervening warm zone. Again, it must be concluded that their migration took place at a time when the temperatures of the ocean waters were more equable, unless it is assumed that the species have since become less tolerant towards temperature.

Another interesting feature in geographical distribution, which has been established by Setchell (1920), is the relation of the various species to the isotherms. The surface waters of the oceans are divided into zones according to the courses of the 10°, 15°, 20° and 25° C. isotheres. The great majority of algal species are confined to only one zone, a considerable number occur in two, only a small number occur in three zones, whilst the number extending

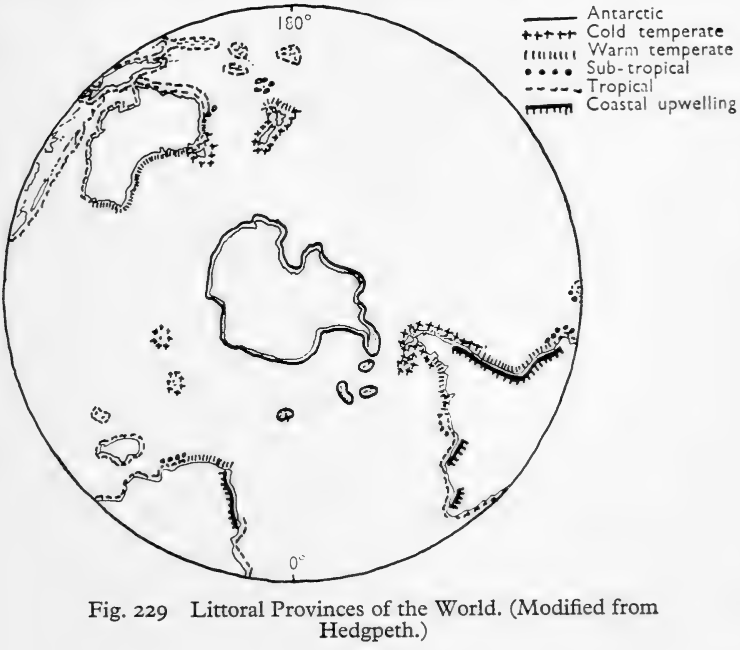

Fig. 229 Littoral Provinces of the World. (Modified from Hedgpeth.)

over four or five zones are very few indeed and their distribution is usually by no means certain. In New England many of the species are apparently separated by the 20° C. isothere, which approximates closely to the position of Cape Cod, so that the flora to the north of the Cape is essentially different to that of the south. Those species limited to one zone are called *stenothermal* whilst the wider ranging forms are termed *eurythermal*. The former species are particularly characteristic of the warmer waters, but, even so, many apparent eurythermal species are found on examination to be essentially stenothermal. *Monostroma grevillei* and *Polysiphonia urceolata* are summer annuals in the cold waters of Greenland, but in the southern part of their range they develop in winter and early spring when the temperature will be the same as it is in the Greenland summer. With the exception, then, of the temperatures endured by the resting spores they are essentially stenothermal. *Ascophyllum nodosum*, with a temperature range from 0 to 10° C., is another case, and in the southern part of its range the plants pass into a heat rigor during the hotter months.

On the basis of these temperature studies Setchell recognized a number of climatic zones each of which could contain species that were characteristic of the zone. These zones were the Boreal, Upper Boreal, North Temperate, North Sub-tropical, Tropical, South Sub-tropical, South Temperate, Upper Austral and Austral. This temperature factor was later recognized by Borgesen and and Jonsson (1905) and Jonsson (1912) in their studies of Arctic floras. They concluded that the component species of the floras could be divided into a number of elements:

(1) The Arctic group, with its southern European border in north Norway and Iceland, although in America the group may extend as far south as Cape Cod.

(2) A sub-Arctic group, the species of which are common in the Arctic sea and the cold boreal area of the Atlantic as far south as western France.

(3) Boreal Arctic group. These species are common in the Arctic Sea and the boreal area of the Atlantic as far south as the Atlantic coast of North Africa, some perhaps penetrating even farther south.

(4) A cold boreal group which is of more limited distribution, extending northwards from western France to south Iceland

and Finland, with outlying species penetrating in the south to the Mediterranean and in the north to the White Sea and Sea of Murman.

(5) A warm boreal group, the species of which extend as far south as the Mediterranean and Atlantic coast of North America, some perhaps even farther south. Their northern limits are to be found in south Iceland, the Faeroes, north-west Norway and Scotland.

Although Iceland is so far north, nevertheless the flora is predominantly boreal because 54 per cent belongs to the last three groups. If the different districts of Iceland are compared with neighbouring floras it is extremely interesting to see how the floras of the various parts of the Icelandic coast show resemblances to floras from a number of widely separated areas.

TABLE 26

	Species in	
	Groups 1 and 2	*Groups* 3–4
East Greenland	81	19
Spitzbergen	77	23
West Greenland	72	28
East Iceland	63	37
Finland	46	54
South-west Iceland	42	58
South Iceland	50	70
Faeroes	29	71
Nordhaven	27	73

Since these early studies, additional work has been carried out. Stephenson (1946) has shown how there are different elements in South Africa based on temperature (see p. 341), the cold Antarctic current on the west being responsible for the presence of *Ecklonia*, *Laminaria pallida* and *Macrocystis*. A similar cold upwelling on the coast of California enables cold water kelps to grow much further south than they do at corresponding latitudes on the east coast. In recent years an increase of sea temperature has resulted in very poor growth of *Macrocystis*. The southern limit of this cold upwelling is around Point Concepcion but other upwellings occur in Baja California. By contrast the impact of the Gulf Stream on Great Britain enables a number of Mediterranean and other warm water species (e.g. *Cystoseira*) to occur in south-west Ireland and on the coast of Cornwall. In the southern hemisphere Bennett and Pope (1953) have studied the biogeographical provinces of temperate Australia and they consider that four components can be recognized:

(*a*) tropical, the main species occurring north of 26° south;
(*b*) warm-temperate;
(*c*) cool-temperate;
(*d*) universal.

This classification is possibly too broad because *Hormosira* is included under Universal. As a result of this work they suggest that the average winter sea temperature of 10° C., which Stephenson regarded as the limiting value between warm and cool temperate, may need raising since the Victorian flora is definitely cool temperate and the average winter temperature is 11·8° C. In the case of such a large continent as Australia there is considerable variation around the coasts. The marine fauna and flora fall into a number of provinces which agree very closely with those established by Ferguson-Wood in his study of Australian Dinoflagellates. In adjacent New Zealand there is a strong endemic element but Australian and sub-Antarctic components are also represented, the latter being found also in South Africa (see Fig. 229).

So far it is clear that only preliminary studies have been made of this aspect of phycology. Uniformity of approach would, however, seem to be important and so in in 1946 the writer proposed a general scheme of floristic elements as follows:

Arctic
Sub-Arctic
Boreal Arctic
Cold Boreal Atlantic
Cold Boreal Pacific
Boreal Atlantic
Boreal Pacific
North sub-tropical Atlantic
North sub-tropical Pacific
Tropical Atlantic
Pan tropical
Caribbean
Indo-Pacific

Antarctic
Sub-Antarctic
Austral Antarctic
Cold Austral Atlantic
Cold Austral Pacific
Austral Atlantic
Austral Pacific
South sub-tropical Atlantic
South sub-tropical Pacific
Tropical Pacific
Cosmopolitan
Arabian

In this classification Boreal and Austral both represent warm temperate components. This classification has since been used as a basis for the analysis of the marine algal flora of Jamaica:

Caribbean	Pan-tropical	Tropical Atlantic	Indo-Pacific
128	46	33	7
Cosmopolitan	Cold Boreal Atlantic	Boreal Atlantic + Austral Pacific	North sub-tropical Atlantic
54	20	14	19
	South sub-tropical Atlantic	Indeterminate	
	9	6	

From this it can be observed that the principal element is the Caribbean one, but that whilst generally much of the remaining flora is warm temperate or sub-tropical, nevertheless there are some cold temperate species. Further work in other parts of the world should lead in the future to additional interesting results.

The peculiar distribution of certain algae in the southern hemisphere has prompted the author (1952) to comment upon it in relation to Wegener's theory of Continental Drift. The presence of *Macrocystis*, *Splachnidium*, *Ecklonia* and *Ballia* in South Africa, widely distant from both Australia or South America, could conveniently be explained if at one time all three countries were part, with the Antarctic Continent, of a great southern continent which later broke up. If the permanence of the present land masses and oceans is accepted instead, then it must be assumed that fertile fragments of these algae must have drifted to South Africa, presumably from South America via the Antarctic current. Portions of algae can be found floating in the ocean, though whether fertile fragments could survive such a long journey may be open to question. At all events the distribution is one of very great interest.

Another feature that is perhaps most conveniently considered here is that of seasonal alternation of generations and of seasonal dimorphism. Feldmann (1937) has studied this particularly in the Mediterranean. In *Ceramium corticatulum* the tetrasporic plants exist only at the end of autumn or in the winter whilst the sexual plants are to be found at the end of summer. This is an example of seasonal alternation of generations in which there are ephemeral summer haploid plants with the diploid plants occurring during the winter and persisting over a longer period. Seasonal dimorphism is exhibited in the Mediterranean by *Cutleria multifida* and *C. monoica* with their sporophytes *Aglaozonia parvula* and *A. chilosa.* The two species are almost indistinguishable morphologically, but the former occurs in spring in shallow waters off-shore whilst the latter occurs in summer at greater depths. Another example of seasonal dimorphism is shown by the two morphologically similar species *Polysiphonia sertularioides* and *P. tenerrima*, the former occurring on exposed rocks from December to May whilst the latter grows epiphytically on *Nemalion helminthoides* between June and December.

LIFE FORM

A study of algal ecology leads one to the conclusion that the distribution of the different types appears to be largely controlled by the nature of the habitat, e.g. rocky shore, sandy shore, or salt marsh, although of course there may be other factors because this will not explain the predominance of the lime-encrusted forms in the warmer waters. For this reason there would seem to be a need for some sort of life form classification comparable to that of Raunkiaer's for the flowering plants. Such a system can be used to give a quantitative picture of the composition of the vegetation and also to demonstrate the absence of any type, thus raising the problem as to why they are absent. Biological spectra, similar to those employed by Raunkiaer (1905), form a convenient way, if used with caution, of comparing floras from two different areas although they are subject to the limitation that they do not indicate the dominant types.

Oltmann's scheme of 1905, which is one of the earliest, is based largely upon morphological criteria, but in the light of present knowledge it is more desirable to adopt a scheme with some relation to habitat rather than one based on purely morphological characters:

(1) Bush and tree forms (*Bryopsis*).
(2) Gelatinous bush forms (*Diatoms*).
(3) Whip forms (*Himanthalia*).
(4) Net forms (*Hydrodictyon*).
(5) Leafy forms: (*a*) lattice (*Agarum*),
    (*b*) flag (*Macrocystis*),
    (*c*) buoy (*Nereocystis*).
(6) Sack forms (*Leathesia*).
(7) Dorsiventral forms (*Delesseria*).
(8) Cushion, disc and encrusting forms (*Ralfsia*).
(9) Epiphytes, endophytes and parasites.
(10) Plankton.
(11) Symbionts.

In 1927 Funk proposed a new classification which applied particularly to the algae of the Gulf of Naples. He distinguished four primary groups, all of which were capable of subdivision according to the same principles, but unfortunately the terms that he employed for the major groups are not particularly happy as some of them are open to the widest interpretation:

I. Seaweeds ('Tange' in the original).
II. Lime-encrusted algae.
III. Fine algae ('Feinalgen', or algae of small proportions).
IV. Microscopic algae, including species measuring less than 1 cm.

Each of these groups could be subdivided as follows, the examples being taken in this case from the first group.

I. *Sea weeds* ('*Tange*'):
- (*a*) Large algae, more than 1 m. in length, e.g. *Laminaria.*
- (*b*) Medium algae, with a length of 0·5–1 m., e.g. *Fucus.*
- (*c*) Small algae ranging from 1 to 50 cm. in length:
  - (i) Main axis not branched, e.g. *Chaetomorpha.*
  - (ii) Main axis branched, e.g. *Gracilaria.*
  - (iii) Thallus bushy, e.g. *Gelidium.*
  - (iv) Thallus leafy or a foliose bush, e.g. *Petalonia.*
  - (v) Creeping thallus, e.g. *Caulerpa.*
  - (vi) Crustaceous thallus, e.g. *Ralfsia.*
  - (vii) Thallus a hollow ball, e.g. *Colpomenia.*

Gislèn in 1930 proposed another classification to include both plants and animals, the biological types referable to the plants being as follows:

I. CRUSTIDA (Crustaceous thallus):
- (1) Encrustida or encrusting forms, e.g. *Lithothamnion.*
- (2) Torida or small cushions, e.g. *Rivularia.*

II. CORALLIDA (lime skeleton more or less developed):
- (1) Dendrida or tree-like forms, e.g. *Corallina.*
- (2) Phyllida or leaf-like forms, e.g. *Udotea.*
- (3) Umbraculida or umbrella-like forms, e.g. *Acetabularia.*

III. SILVIDA (no lime skeleton):
- (*a*) Magnosilvida, or forms more than 1 dcm. high and with branches more than 1 mm. thick.

(1) Graminida, e.g. *Zostera* (a phanerogamic group).
(2) Foliida, e.g. *Laminaria*.
(3) Sack-form, e.g. *Enteromorpha*.
(4) Palm form, e.g. *Lessonia*.
(5) Buoy form, e.g. *Nereocystis*.
(6) Cord form, e.g. *Himanthalia*.
(7) Shrub-like form, e.g. *Chordaria*.
(8) *Sargassum* form.
(9) *Caulerpa* form.

(*b*) Parvosilvida (small delicate forms less than 1 dcm. high).

It will be seen that all these classifications are based primarily upon morphological criteria and are therefore incomplete because they do not take into consideration the biological requirements of the algae.

Setchell propounded a scheme in 1926 based primarily on the conditions found in tropical waters, with particular reference to coral reefs. For this reason the classification is restricted because it would require considerable extension if the flora of colder waters were to be included, but at the same time it is an improvement over the previous schemes in that its basis is largely ecological:

HELIOPHOBES:

(1) *Pholadophytes*. Forms nestling into hollows and avoiding much light.
(2) *Skiarophytes*. Forms growing under rocks or in their shade.

HELIOPHILES:

(3) *Metarrheophytes* or attached flexible forms growing in moving water.
(4) *Lepyrodophytes* or encrusting forms.
(5) *Herpophytes* composed of small creeping algae.
(6) *Tranophytes* or boring species.
(7) *Cumatophytes* or 'surf-loving' species.
(8) *Chordophytes*, where the thallus has the form of a cord.
(9) *Lithakophytes* or lime-encrusted species (Corallinaceae).
(10) *Epiphytes*.
(11) *Endophytes*.

Knight and Parke (1931) proposed a brief classification based upon the same criteria, duration and perennation, like that Raunkiaer employed for the higher plants. They only distinguished four groups; perennials, pseudoperennials, annuals and casual annuals, and it would require a thorough restudy of many species in order to determine to which group they belong. More recently (1937) Feldmann has proposed a new scheme, based on these same criteria which can be regarded as the logical elaboration of Knight and Parke's classification:

(1) ANNUALS

(*a*) Species found throughout the year. Spores or oospores germinate immediately.
    EPHEMEROPHYCEAE: *Cladophora.*
(*b*) Species found during one part of the year only.
    (i) Algae present during the rest of the year as a microscopic thallus.
        ECLIPSIOPHYCEAE: (*a*) with prothallus, *Sporochnus.*
        (*b*) with plethysmothallus, *Asperococcus.*
    (ii) Algae passing the unfavourable season in a resting stage.
        HYPNOPHYCEAE—Resting stage:
            (*a*) spores, *Spongomorpha lanosa.*
            (*b*) oospores, *Vaucheria.*
            (*c*) hormogones, *Rivularia.*
            (*d*) akinetes, *Ulothrix pseudoflacca.*
            (*e*) spores germinate and then become quiescent, *Dudresnaya.*
            (*f*) protonema, *Porphyra.*

(2) PERENNIALS

(*a*) Frond entire throughout year.
    (i) Frond erect. PHANEROPHYCEAE: *Codium tomentosum.*
    (ii) Frond a crust. CHAMAEPHYCEAE: *Hildenbrandtia.*
(*b*) Only a portion of the frond persisting the whole year.
    (i) Part of the erect frond disappears. HEMIPHANEROPHYCEAE: *Cystoseira.*
    (ii) Basal portion of thallus persists.
        HEMICRYPTOPHYCEAE:
            (*a*) basal portion a disc, *Cladostephus.*
            (*b*) basal portion composed of creeping filaments, *Acetabularia.*

This scheme must be regarded as a great advance on the other classifications, but at the same time it does not seem to take adequate account of the effect of environment and, furthermore, it is primarily of use for the marine algae and does not take into consideration the numerous fresh-water and terrestrial species.

Cedergren (1939) published a life form scheme based primarily upon the nature of the medium and secondarily upon the nature of the substrate. This scheme can be considered as excellent in so far as it classifies the algae in a more general sense.

Series A. *Terrestrial Algae.*

(1) Terricolae (on the earth).
(2) (*a*) Saxicolae (on stone).
    (*b*) Calcicolae (on chalk).
(3) Lignicolae (on wood).
(4) (*a*) Epiphytes.
    (*b*) Endophytes.
(5) Epizoic forms (on animals).
(6) Succicolae (gelatinous).

Series B. *Soil Algae* (in the earth).

Series C. *Water Algae.*

(1) Nereider (river and stream algae).
(2) Limnaeider (lake algae).
(3) (*a*) Epiphytes.
    (*b*) Endophytes.
(4) (*a*) Epizoic forms.
    (*b*) Endozoic forms.
(5) Plankton (small floating algae).
(6) Pleuston (large floating algae).
(7) Neuston.

Of all those so far published, however, Feldmann's appears to be the most workable. The real test will come if and when it is employed to give biological spectra, and if the spectra from different localities, e.g. temperate and tropical regions, show a distinct difference then it should prove possible to extend its use as a means of comparing the vegetation from different regions. Such differences may be expected to open up problems, the solutions of which should yield us valuable information concerning the general biology and ecology of the species concerned.

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Chapter XVIII

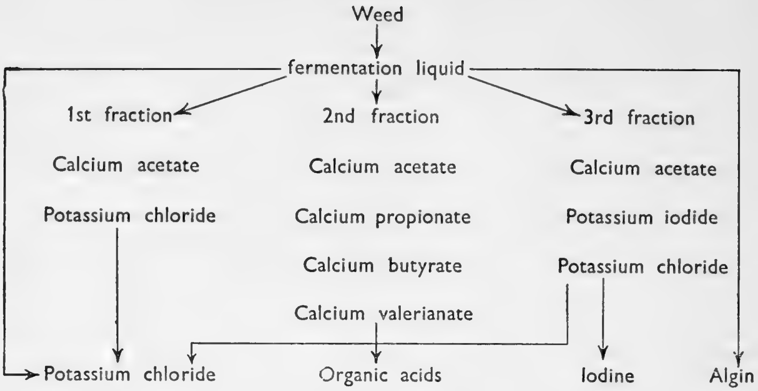
ALGAL UTILIZATION

Seaweeds have been used by man for as long as we have any written records and their use probably extends to even earlier times. In early years, apart from being used as food, they did not form part of any major industry, and it was not until the seventeenth century that the first industry, the kelp trade, developed. Although the kelp trade is now an industry of the past (cf. p. 13), nevertheless it assumed such great importance that a brief account is not amiss. The word kelp itself originally referred to the burnt ash of the brown seaweeds and only subsequently became applied to the actual weeds. The algae primarily used in Europe were the species of *Laminaria* and *Fucus* with *Ascophyllum nodosum.* The former was collected as cast weed whereas the two latter were cut off the rocks on which they were growing. Initially the ash was produced for the soda that it contained and then later it was used as a source of iodine (see p. 13). When the weed had been collected it was allowed to dry, often on special stone walls, and then when dry it was burnt in circular or cylindrical kilns. The burning went on until the worker had a cake of ash fifteen to twenty-four inches thick. In the early years when the ash was used as a source of soda the temperature did not matter, but in the later years when iodine was required, the temperature could not be allowed to rise too high because much of the iodine then volatilized and escaped. The type of weed also was of some importance. *Fucus* species and *Ascophyllum* are richer in soda and were thus favoured in the early years, whilst laminarians are richer in iodine and were therefore more in demand in the later years.

In the latter half of the nineteenth century new processes were evolved in order to eliminate the loss of iodine and also, if possible, to utilize both stipe and blade, particularly the stipes which are cast ashore in great quantity in the winter. There was in addition the possibility of obtaining by-products. One of the new processes was the distillation or char process in which the dried weed was heated in a retort. Using this process ammonia, soda, potash, iodine and charcoal could be obtained. Another important process involved fermentation whilst in more recent times the Russians have employed an electrolytic method of separation. One of the principal sources of iodine in Russia is *Phyllophora nervosa*, a red algal species that grows in the Black Sea.

Iodine from kelp is still manufactured in Japan, about 5–7 per cent of the world's supplies coming from this country. *Laminaria*, *Ecklonia* and *Eisenia* are the genera principally employed and about 100 tons of iodine are produced annually. In all the weeds used as a source of iodine, the iodine is most probably present in an organic form. The actual amount varies from season to season, from species to species, from organ to organ, and is also affected by immersion, temperature and degree of wave action. In general the amount is of the order of 0·13–0·23 per cent of the dry weight of weeds such as *Laminaria*, *Fucus*, *Ecklonia* and *Eisenia*.

Big areas on the Pacific Coast of North America and Canada are occupied by laminarians, e.g. *Macrocystis* (see p. 186), *Nereocystis* (see p. 184) and *Alaria* (see p. 188). About 1910 America began to pay attention to these weeds as a source of potash because of difficulties with German supplies. The average potash content of these weeds is quite considerable and indicates the extent to which they can accumulate a salt that is present in the medium in relatively small amounts. The average dry weight content in *Macrocystis* is around 16 per cent, in *Nereocystis* around 19 per cent and in *Alaria* around 7 per cent. Again there is variation with season, habitat, nature of the organ (stipe or blade) and so on. These weeds are much easier to collect than those in Europe and generally speaking some form of barge was employed which cut the weeds under water (as they floated on the surface), the cut material being collected and transferred to the barge by a conveyor belt. In order to obtain the maximum results the weed was dried in revolving driers and then treated either by a destructive distillation process or else by a fermentation process. In the former 12 tons of dry *Macrocystis* yielded 2·3 tons of gas, 3·3 tons of ammonia, 2·1 tons of tar, 3 tons of potash salts, 1·2 tons of charcoal and 20 lb. of iodine. The latter process was more elaborate and yielded a greater variety of products:



The main reason for the failure of this industry, as compared with the European one, was the fact that similar products could be obtained more economically from other sources.

The kelp trade in Europe and America, despite its failure, formed the background to the present major kelp industry, the production of alginates. This is because the same brown seaweeds form the raw material.

Algin, which is a complex compound of polymers of d-mannuronic acid, was first discovered in 1883, but whilst it is not so difficult to obtain it pure under laboratory conditions, it has so far proved expensive to prepare pure on a commercial scale. The amount in the various Fucales and laminarians used varies from 15–40 per cent, though the percentage varies seasonally, being lowest in spring and highest in the autumn. It is also affected by habitat (exposure or protection) and depth, whilst in the case of *Macrocystis* at least there is evidence of a variation with latitude. This is probably associated with temperature and light variations with latitude, since algin is regarded as one of the products of metabolism. Algin and alginates have become of great importance since 1940, and whilst there has been no great change in the method of collection in the U.S.A., in Europe considerable study has been devoted to this problem. This is essential if continual supplies of the submerged *Laminaria* spp. are to be available. It seems that some continuous sort of grapnel method will be most reliable for their collection. Nearly all the experimental work in this connexion has been carried out by the Scottish Seaweed Research Association.

Various methods of extraction have been devised, but in general the weed is leached first with acid and then treated with soda ash or sodium carbonate solution. The final product can be pure alginic acid but more usually it is the calcium or sodium salt that is prepared. The alkali salts dissolve in water to give a thick, viscous liquid and this can be spun into an artificial silk thread. The final yarn is usually of calcium or sodium alginate. These yarns are soluble in soap and soda and advantage has been taken of this in the production of special weaves of mixed alginate and other fibres, because subsequently the alginate can be dissolved out: this is known as the 'disappearing fibre' technique. Resistant threads can be obtained by replacing the calcium or sodium with chromium or beryllium. In practice it is found easier to weave the yarn in the form of calcium alginate and then convert the woven material to beryllium or chromium by immersing it in a bath of beryllium or chromium acetate.

The alginates of the heavy metals are not soluble in water and they form a plastic material when wet that sets hard on drying. Algin has a variety of other uses, apart from the production of plastics and artificial fibres. Among the more important is its use as a stablilzer in ice-creams and sherbets, as a filler to candy bars and in salad dressings. It can also be used as a thickening and polishing material and the insoluble salts have been used in the production of water-proof cloth. More recently experiments have been conducted to ascertain its usefulness as an ameliorator of poor soil conditions. In this respect it will be a competitor with materials such as krillium which merely alter the physical state of the soil.

Apart from algin the other major seaweed industry today is concerned with the production of agar-agar, the material that is used in culturing bacteria and fungi. A large number of genera and species are used as the source of this material and such plants have been termed agarophytes. For many years up to 1939, Japan had been the principal producer of agar, about 2,000 metric tons being produced annually. Whilst a number of red algae have been and still are used for this purpose in Japan, the principal source is *Gelidium amansii*. After the weed has been collected it is bleached and then boiled. This extracts the gelatinous material which, after straining, is purified by freezing, the water flowing off with the impurities when it is thawed.

When Japan entered the last war, the world's supply of agar was cut off. Since agar was urgently needed for pathological work, all countries with coastlines explored their red algae in order to find alternative sources. As a result, suitable agar was produced from *Gelidium cartilagineum* on the Pacific coast of America and in South Africa, from *Gracilaria confervoides* in Carolina, South Africa and Australia, from *Hypnea musciformis* in Carolina, from *Gelidium pulchellum* and *G. latifolium* in Ireland, from *Chondrus crispus* and *Gigartina stellata* in England, from *Suhria vittata* in South Africa and from *Pterocladia lucida* and *P. capillacea* in New Zealand. The weed is usually hand picked from the rocks, e.g. England and New Zealand, but in California it is collected by diving from boats. In Carolina the *Gracilaria* and *Hypnea* are collected by stop nets, but in Australia the beds are in deeper water and a special trawl is used for the collection of the plants.

The gelatinous material that is extracted from these algae is commonly known as gelose. The agarophytes can be divided into three groups on the basis of the setting power of the gel.

(*a*) *Gelidium* type: decoction sets firm even if dilute.
(*b*) *Gracilaria*, *Hypnea* type: decoction sets firm if more concentrated or if electrolytes added.
(*c*) *Chondrus* type: only sets firm if very concentrated.

Japanese agar consists of the calcium or magnesium salt of a sulphuric acid ester of a short chain of galactose residues. It is likely that allied compounds form the gelling material in other agarophytes, and this accounts for the variation in properties of the different extracts. A special name is given to the extract from Irish Moss or *Chondrus*, which is called Carragheenin from the local name of Carragheen for the alga. This substance is known to differ chemically from agar though it is still an ethereal sulphate. The Irish Moss industry is primarily developed in Ireland and Massachusetts. The name is sometimes applied to algae elsewhere, e.g. New Zealand, but it does not then refer to *Chondrus* but usually to a *Gigartina*.

In some species there is a seasonal periodicity in the amount of gelose the algae contain, e.g. *Gelidium cartilagineum* in California reaches a peak in June. Harvesting has also to be carried out with some care so that the algae are given an opportunity to regenerate.

Apart from its use for the culture of micro-organisms, agar has a variety of other uses. Among these can be included the canning of fish, the sizing of fabrics, in paper and glue manufacture, to add gloss and stiffness to leather, in cosmetics and medicines and as a thickening agent in ice-creams, sherbets and pastries. It is also used as a clarifying agent in brewing and wine-making. Carragheen has a culinary use in the preparation of blanc-manges but it is also used medicinally as a cough tincture and pharmaceutical emulsifier.

For many years seaweeds have been employed on coastal farms not only as a manure for the land but also as a stock food. Sheep and cattle will often eat seaweed and on one of the Orkney Islands there is a race of sheep that feeds exclusively on seaweed. In Europe several factories have been built to manufacture stock feed, in nearly all cases the brown rock-weeds (*Fucus*, *Ascophyllum*) being used though *Laminaria* may also be utilized. So far as value is concerned the algal meal is as good as other stock feeds such as hay, oats and potato tops, but this does not mean that they are as digestible. Generally speaking, it would seem that laminarin is the most digestible material and therefore the time of harvesting is of importance, i.e. harvesting at the period of maximum laminarin content. In the past this has not always been done and under such circumstances the feed has not always been fully digested.

The oarweeds and rock-weeds are also used as a manure on the land. If there was not so much wet weight and the moisture was not expensive to remove, it is probable that the algae would have a wider use in this connexion. The seaweed can either be dug in fresh (this seems best), allowed to rot on the surface, or else composted with other organic material. Manurially the algae used have a good nitrogen and potash content but they are low in phosphorus. The nitrogen is not, however, freely available and takes time to pass into the soil: seaweed manure is therefore of the slow but long acting type. The amount of common salt present is not excessive as one might have expected it to be. Naturally the composition of the different species varies and also of the different organs, the leafy parts usually being richer than the stipes. Seaweed manure is particularly valuable because of the trace elements that it contains and the importance of these to good plant growth. One aspect that appears to have been neglected is the effect of these algae on the physical properties of the soil. In view of the possible use of algin (cf. p. 447) for this purpose it is clearly important that some study should be made of this aspect.

In China, Japan and Hawaii, seaweeds have been used for a long time as human food. Earlier they have also been used in Europe, but their use there has now died out. The young stipes of *Lamin-*

aria saccharina used to be eaten and also young plants of dulse (*Rhodymenia palmata*) in Scotland and Ireland. The weed of widest use, however, was laver or *Porphyra*. This is interesting because in Japan it is *Porphyra* that today forms one of the biggest crops for culinary purposes. Here it is actually cultivated on bamboo poles stuck into the shallow waters of bays and river mouths. The species most commonly cultivated is *Porphyra tenera* and up to 50 sq. kilometres may be occupied by these bamboo bundles, each 'farm' being about 120 ft. × 7 ft. When the twigs have become covered with a mass of sporelings they are pulled up and planted in an area of low salinity. When mature the algae are removed, dried and pressed into sheets when it is known as Asakusa-nori. The other important item of Japanese algal food is called kombu and is made from the large laminarians, especially *Laminaria*, *Alaria* and *Arthrothamnus*. The kelp is gathered from open boats using special hooks. When gathered it is dried and cut up in various ways so that one can get shredded kombu, black or white pulpy kombu, filmy kombu, hair kombu or sweet-cake kombu. The amount harvested is considerable and in 1936 amounted to 293,284 tons of wet weed. Other foods from brown seaweeds are Wakame from *Undaria pinnatifida*, Arame from *Eisenia bicyclis*, Hijiki from *Hijikia fusiforme*, Miru from the green *Codium* and a whole variety of lesser weeds.

A similar extensive list of edible algae could be prepared for Hawaii where the edible seaweeds are known as different types of limu. At least 40 species are in common use, most of them being small green or red algae.

Some attempt has been made to assess the nutritional value of these algae. Only an edible *Nostoc* from China, and the Japanese Amanori (*Porphyra*) have a high nitrogen content, so that any value must be in the carbohydrates and possibly the iodine. In general it would appear that the algal foods are of more value to sick than to healthy persons and the main use is in providing roughage in a diet that is largely rice and fish. There is no doubt, however, that goitre is not prevalent in these countries and this may well be due to the amount of seaweed consumed. In recent years it has also become known that many of the algae are quite rich in vitamins (cf. p. 414) and they may be of importance in this connexion.

The only other algal industry of any importance that should be mentioned is the glue that comes from the Japanese red alga *Gloio-*

peltis furcata and known as funori. The species occurs wild but can also be cultivated by building up the shore to the right level at which the alga grows. The glue is obtained by dissolving the alga in hot water, the extractable material having been given the name of Funorin.

It is clear that there are a whole group of algal substances which are termed phycocolloids, and which fall into three categories:

(*a*) water soluble ethereal sulphates such as agar;
(*b*) water soluble reserves such as laminarin;
(*c*) alkali-soluble polyuronides such as alginic acid.

A tentative arrangement of these substances is shown in the accompanying schema (p. 452).

The need to produce alginates and also agar during the 1939–45 War led to a survey of the world's supplies. Previously only the Pacific coast of North America had been surveyed in connexion with the development of the kelp industry there thirty years earlier. Extensive surveys of the *Macrocystis* beds were made in New Zealand and also of the rock-weed (*Fucus*, *Ascophyllum*) and oar weeds (*Laminaria* spp.) in Great Britain. This work has gone on steadily since the war and additional surveys have been made in other continental countries. Grapnel, echo-sounder and aerial photography have all been employed in these surveys, the last-named being perhaps the most successful, especially when combined with grapnel sampling. The more recent work has demonstrated how in Scotland, at least, the weed density falls off with depth and that there is also a mathematical relationship between depth and weed density for any given area. The cover around Scotland is about 87 per cent at one fathom, 60 per cent from 4–6 fathoms, 25 per cent from 7–8 fathoms and is commonly zero by the time 9 fathoms are reached.

Since the war, much work has been carried out on the biology of those seaweeds that are of commercial importance. This applies particularly to species of *Fucus* and *Laminaria*, and also to *Porphyra*, *Gelidium* and *Gloiopeltis* in Japan, and agarophyte algae in all parts of the world. Most of this work has been directed to a study of regeneration from perennial, basal holdfasts and to conditions of reproduction. There is still a great deal more that needs to be carried out and much of the earlier work on chemical composition requires to be repeated.

In recent years the alga *Chlorella* has assumed great importance

ALGAL GROUPS	*Phaeophyceae*				*Rhodophyceae*		
	Kelps		Fucoids		Agarophytes	Carragheens	Others
Sources	Leafy kelps	Giant kelps	Gulf weeds	Rock weeds			
Genera	Laminaria Ecklonia	Macrocystis Nereocystis	Sargassum	Fucus Ascophyllum	Gelidium Gracilaria Pterocladia Ahnfeldtia	Chondrus Gigartina	Phyllophora Gloiopeltis Iridophycus
Phycocolloids	Laminarin	Algin	Fucoidin		Agar	Carragheenin	Agaroid Funorin Iridophycin
	water soluble carbohydrates	alkali-soluble polyuronide				Water soluble ethereal sulphates	
Acids		Alginic acid			Agarinic acid	Carragheenic acid	Iridophycinic acid
Salts	$\left.\begin{matrix}\text{Ca, Na}\\ \text{NH}_4\text{, Cr}\end{matrix}\right\}$ alginates				$\left.\begin{matrix}\text{NaCa}\\ \text{KMg}\end{matrix}\right\}$ agarinate	$\left.\begin{matrix}\text{K}\\ \text{Ca}\end{matrix}\right\}$ carragheenate	Sod. iridophycinate
	Chlorophyceae none known						*Myxophyceae* none known

and it is likely to become even more important in the future. *Chlorella* is rich in proteins, fats and vitamins, and in the presence of nutrients, CO_2 and sunlight, multiplies at an enormous rate. Several countries have been experimenting with the mass production of *Chlorella*. Pilot scale *Chlorella* 'farms' have already been established in America, Japan, Holland, Germany and Israel. Such farms do not require excessive amounts of water and hence would be invaluable to augment food supplies in arid areas. Such 'farms' on a smaller scale could also be used to supply food in space stations of the future and even in large space ships.

Chlorella is also being increasingly used as a means of purifying sewage. When it is present in large, shallow tanks of effluent (after primary sedimentation of solids) the rapid photosynthesis produces abundant oxygen which is then used by the bacteria responsible for destroying the remaining organic matter. A number of sewage works using *Chlorella* now exist in the U.S.A. and at present the largest in the world is operating at Auckland in New Zealand. It would seem that this cheap and effective means of sewage purification is likely to extend in the future.

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ADDENDUM

A recent monograph by Starr on *Chlorococcum* indicates that *C. humicolum* is a doubtful species because of the original inadequate description. Starr recognizes nine species, mostly from soil.

A recent treatment of the Ulvaceae (Papenfuss) transfers species of *Gemina* and *Lobata* (see p. 56) to *Ulva*.

Tribonema bombycinum (p. 263) is now named *T. viride*. In a recent revision of the coccoid Myxophyceae, Drouet and Daily take the view that there is great morphological variation and many of the genera and species formerly described are merely different growth forms of a single species. *Microcystis* and *Chroococcus* are both placed in the genus *Anacystis*. *M. aeruginosa* and *M. toxica* are regarded as synonyms for *Anacystis cyanea; Chroococcus turgidus* and probably also *C. macrococcus* of Crow (fig. 162) are synonyms for *Anacystis dimidiata*. *Merismopedia* becomes a synonym for *Agmenellum* and both *M. aeruginosa* and *M. elegans* are referred to *A. thermalis* and *M. ichthyolabe* to *Anacystis cyanea*. The genus *Gloeothece* (pp. 281, 296) is treated as synonymous with the genus *Coccochloris*. On p. 413 *Synechococcus elongatus* becomes *Coccochloris elabens* and *Synechocystis* sp. becomes *Anacystis* sp.

INDEX

Aberlady, 348
Acetabularia, 91, 94, 95, 305, 306, 415, 430, 439, 441
  crenulata, 94, 95
  mediterranea, 94, 95, 338, 430
  moebii, 95
  pusilla, 95
  shenkii, 95
Achnanthes, 334
  minutissima, 370
Acicularia, 301
Acinetospora, 123, 141
Acrochaetium, 228
Acrosiphonia, 88
Acrosymphytum purpurifera, 237
Acrothricaceae, 318
Acrothrix, 317
Actinococcus subcutaneous, 244
Adelophycée, 127, 150
Aegagropila, 84, 86, 87
  holsatica, 85, 86
  sauteri, 86, 87
Aerophytes, 374
Agar-Agar, 234, 447, 451, 452
Agardh, C., 12, 375
Agardh, J., 12
Agardhiella tenera, 221
Agarum, 438
Aglaozonia, 14, 144, 316
  chilosa, 437
  parvula, 437
  reptans, 144
Ahnfeldt, N. O., 244
Ahnfeldtia, 244, 246, 322, 452
  plicata, 245, 323
Akinete(s), 19, 25, 67, 110, 263, 280, 287
Akontae, 5
Alaria, 170, 184, 188, 190, 202, 335, 445, 450
  esculenta, 188, 189
  oblonga, 189
Alariaceae, 171, 188, 190, 432
Alaska, 170, 174, 185, 194
Aleem, A. A., 335, 345
Alginate(s), 446, 447, 451, 452
Algin, 3, 446, 447, 452
America, 131, 132, 357, 362, 434, 445, 446, 453
Amphipleura rutilans, 334
Amphora, 334
Anabaena, 279, 280, 290, 363, 381, 382, 413
  azollae, 428
  cycadearum, 428
  oscillarioides var. *terrestris*, 379
  torulosa, 350, 354
Anabaenin, 223
Anabaeniopsis, 413
Anadyomene stellata, 88
Anadyomenaceae, 88, 311
Anand, P., 390, 404, 411
Ancyclonema, 359
Androspore(s), 68, 70
Androtermones, 417, 420, 421
Ankistrodesmus, 44, 47, 413
Anomalae, 194, 212
Antarctic, 196, 394, 436, 437
Anthoceros, 428
Antithamnion, 248
  cruciatum, 405
  plumula, 405
  tenuissimum, 405
Aphanocapsa, 223
Aplanospore(s), 19, 40, 60, 110, 259, 263, 264, 268
Apophlaea, 238, 323
Arabian Sea, 431
Araceae, 263
Archaeozoon, 295
Archeolithothamnion, 302
Arctic, 6, 14, 394, 434, 436
Arctic Sea, 434
Areschoug, J. E., 13
Arisarum vulgare, 264
Arthrocladia, 168
  villosa, 338
Arthrothamnus, 450
Ascocyclus, 325
Ascophyllum, 134, 191, 194, 204, 214, 222, 331, 335, 342, 357, 387, 425, 434, 444, 449, 451, 452
  nodosum, 133, 198, 204, 205, 206, 250, 334, 388, 389, 413, 444
    ecad *mackaii*, 206, 348, 349
    ecad *scorpioides*, 206, 349
    var. *minor*, 206, 348
Ascoseira mirabilis, 202
Asparagopsis, 227, 229, 230, 322
  armata, 230
Asperococcaceae, 165
Asperococcus, 162, 165, 167, 325, 441
  bullosus, 165, 166, 167
  compressus, 165
  fistulosus, 166
Asterionella, 367
Astrephomene, 28, 34

Atlantic, 140, 335, 338, 429, 431, 432, 434, 436, 437
Auckland, N.Z., 374, 397
Australasia, 136, 222
Australia, 28, 194, 213, 331, 337, 345, 352, 436, 437
Autospore(s), 19
Auxiliary cell(s), 217, 219, 234 et seq., 239, 241 et seq., 246, 248 et seq., 255, 256
Auxin, 415
Auxospore, 272
Axoneme, 17
Azolla filiculoides, 428
Azygospore, 110

Bachelotia, 132, 134
Bacillariophyceae, 2, 3, 4, 9, 259, 269, 270, 271, 272, 296, 367, 413
Bahamas, 295
Baja-California, 435
Baker, K. M., 258
Baker, S. M., 349, 357
Balanus, 331, 336
Ballia, 437
Baltic, 348
Bangia, 223, 309, 321
  fusco-purpurea, 338
Bangiaceae, 222, 223, 225
Bangioideae, 223
Barents Sea, 174, 199
Basicladia, 361
Batophora, 432
Batrachospermaceae, 14, 227, 228
Batrachospermum, 12, 220, 222, 227, 228, 229, 321, 325, 359
  moniliforme, 228
Bay of Fundy, 384, 385
Bellotia, 160
Bennett, E., 337, 345, 436, 442
Benthos, 359
Bergquist, P. L., 214, 390, 411
Berthold, G., 14, 130
Bidens, 363
Biddulphia mobiliensis, 272
Biebl, R., 393, 404, 411
Bifurcaria, 192, 193, 201
  brassiciformis, 193
  laevigata, 193
Binuclearia, 51, 311
Black, M. C., 295
Blackman, F. F., 14
Black Sea, 445
Blakeney, 348
Blandford, M., 357
Blasia, 428
Blepharoplast(s), 18, 21, 67
Blidingia, 56
Blinks, L. R., 428
Blum, J. L., 360, 361, 382
Bodanella, 123
Bonnemaisoniaceae, 227, 229
Bonnemaisonia, 315
  asparagoides, 230
  hamifera, 231
Bonnier, G., 14
Boodlea, 81
Boodleaceae, 311
Börgesen, F., 14, 15, 102, 212, 429, 434, 442
Bornet, E., 375
Bornetella, 299
Bory de St. Vincent, J. B., 12
Borzi, A., 14
Bostrychia, 249, 337, 347, 350, 351, 354 et seq.
Botrydiaceae, 264
Botrydium, 48, 259, 264, 324
  divisum, 265
  granulatum, 264, 265, 417
  walrothii, 265
Botryococcus, 260, 324
  braunii, 260, 261
Boueina, 297
  hochstetteri, 297
Branchipus, 361
Braun, A., 13
Brenchley, W., 14
Bristol, 363, 366
Brongniartella byssoides, 405
Brown, H. B., 364, 382
Bryopsis, 13, 14, 98, 99, 415, 426, 438
  corticulans, 99
  plumosa, 98, 99
  scarfei, 99
Bryopsidaceae, 96, 98
Budde, H., 360, 382
Bulbochaete, 65
Bullock-Webster, G. R., 121
Bumilleria exilis, 376
Burlew, S. S., 453

Caepidium, 318
Cainozoic, 302
Calcicolae, 442
Calcium carbonate, 93
California, 174, 183, 190, 225, 343, 394, 408, 435, 448
Callithamnion, 248, 254, 255
  brachiatum, 256
  byssoideum, 254
  corymbosum, 340
  roseum, 220
  tetragonum var. *brachiatum*, 405
Callitriche, 363
Callose, 16, 103
Caloglossa leprieurii, 217
Calothrix, 335, 413
  ramosa, 289
Cambrian, 294

Canada, 445
Canary Islands, 231
Canvey, 350, 353
Cape Cod, 434
Cape Lookout, 340, 392
Cape of Good Hope, 187, 225, 340, 430, 434
Capitula, 119
Capsosiphon, 61
  aurea, 61
Capsosiphonaceae, 61, 311
Carboniferous, 297
Caribbean, 327, 337, 384, 429, 436, 437
Carotene, 2, 8, 9, 16, 76, 259, 278
Carpogonium(ia), 80, 217, 223 et seq., 234 et seq., 248, 250
Carpophyllum, 212, 331, 336, 342
  flexuosum, 211
Carpospores, 218, 244, 251
Carposporophyte, 218, 221, 314
Carragheen, 448, 449
Carragheenin, 448, 452
Carter, N., 353, 357
Carteria, 20, 427
  ovata, 23
Castagnea, 151, 316
Catenella, 347, 350, 351, 354 et seq.
Caulerpa, 102, 307, 337, 432, 439, 440
  crassifolia, 103
  cupressoides, 102, 103
  prolifera, 103
  racemosa, 102, 103, 104, 431
  verticillata, 102
Caulerpaceae, 96, 102
Caulerpeae, 96
Cave, M. S., 34, 38
Cedergren, C. R., 442
Cellulose, 3, 6 et seq., 16, 17, 96, 124, 217, 259, 279
Centricae, 269, 270
Centroceras, 337, 338
Cephaleuros, 20, 75, 358, 374, 427
  coffeae, 76
  minimus, 75
  mycoidea, 75
  virescens, 75, 76
Ceramiaceae, 221, 254, 256
Ceramiales, 219, 248, 321
Ceramium ciliatum, 405
  codicola, 222
  corticatulum, 437
  rubrum, 220
Ceratium, 277
Cesalpino, A., 11
Chaetangiaceae, 227, 231, 233
Chaetomorpha, 81 et seq., 311, 338, 439
  aerea, 82
  darwinii, 82
Chaetopeltis, 74, 373
Chaetophora, 81, 365
Chaetophoraceae, 71, 72
Chaetophorales, 6, 65, 71, 74, 115, 124, 308, 310, 315, 368
Chamaedorus, 426, 431
  peniculum, 429
Chamaephyceae, 441
Chamaesipho, 336
Chamaesiphon, 281, 286
Chamaesiphonaceae, 285
Chamaesiphonales, 282, 285
Champia, 337
Chantransia, 228, 229
  efflorescens, 228
  violacea, 228
Chantransiaceae, 227, 228
Chapman, V. J., 90, 308, 312, 326, 345, 357, 443, 453
Chatham Islands, 336
Chara, 11, 115, 118, 121, 301, 325, 426
  aspera, 116, 117
  crinita, 116
  foetida, 118
  fragilis, 116, 117, 120
  hispida, 116, 117
  tomentosa, 118
  vulgaris, 120
Characeae, 6, 303, 309
Characiaceae, 40
Characiopsis, 262, 263, 361
  saccata, 262
Characium, 40, 49, 281, 309, 361
  angustatum, 41
  saccatum, 41
Charales, 6, 19, 79, 115 et seq., 120, 301, 315, 425, 426
Charcoal, 445
Charophyceae, 4, 5, 96, 115, 301
Chatham Islands, 336
Chile, 336
China, 11, 123, 449, 450
Chitin, 3, 65
Chlamydomonadaceae, 20, 23, 34, 307, 374
Chlamydomonas, 17 et seq., 30, 40, 312, 324, 420
  agametos, 22
  angulosa, 21
  botryoides, 22
  braunii, 21, 22
  coccifera, 21, 22
  debaryana, 21
  eradians, 21
  eugametos, 417 et seq.
  gigantea, 21
  kleinii, 22
  longistigma, 21, 22
  media, 21, 22
  moewusii, 413, 414

Chlamydomanas monoica, 22
  nivalis, 359
  parietaria, 21
  pertusa, 22
  pisiformis, 21
  reticulata, 21
  sub-oogama, 22
  stellata, 21
  variabilis, 22
Chlamydospores, 114
Chloramoeba, 259, 260
  heteromorpha, 260
Chlorella, 40, 42, 309, 324, 374, 412, 414, 415, 427, 451, 453
  pyrenoidosa, 413, 414
  vulgaris, 42, 414, 415
Chlorellaceae, 42
Chlorellin, 415
Chlorobotrys, 324
Chlorochytrium, 20, 39, 41
  lemnae, 42
Chlorococcaceae, 39
Chlorococcales, 16, 18, 39, 47, 74, 308, 310, 313, 412, 426, 427
Chlorococcum, 39
  humicolum, 39, 40, 376
Chlorodendraceae, 37
Chlorogonium oogamum, 21, 22
Chlorophyceae, 1 et seq., 10, 12, 14, 16, 17, 20, 81, 83, 96, 105, 144, 222, 223, 259, 260, 262, 263, 273, 281, 297, 306, 307, 310, 312 et seq., 322 et seq., 347, 350 et seq., 381, 393, 398, 404, 413, 414, 420, 428
Chlorophycophyta, 4
Chlorophyll, a, b, c, d, e, 2, 8, 9, 124, 278, 398
Chlorospermae, 13
Chlorotheciaceae, 262
Chondrillosterol, 3
Chondria, 251, 252
  coerulescens, 217
  nidifica, 251
Chondrus, 220, 448, 452
  crispus, 220, 334, 448
Chorda, 123, 132, 170, 171, 172, 316, 334
  filum, 171
Chordaceae, 171
Chordaria, 132, 152, 316, 317, 318, 440
  divaricata, 153
  flagelliformis, 153
Chordariaceae, 122, 149, 151, 152, 317
Chordariales, 122, 149, 156, 316 et seq.
Chordophytes, 440
Choreocolacaceae, 241
Choreocolax, 222, 241
  polysiphoneae, 428
Choreonema, 222
Chromosomes, 17, 34, 65, 87, 193, 214, 227
Chromulina, 273, 324
Chroococcaceae, 281, 283, 284, 294
Chroococcales, 280, 282, 286
Chroococcus, 279, 281, 283
  macrococcus, 279, 284
  turgidus, 279, 281, 284
  varians, 279
Chroolepus, 76
Chrysococcus, 324
Chrysophyceae, 2 et seq., 8, 9, 259, 272, 273, 274, 315, 324, 359, 390, 391, 392
Chrysophycophyta, 4, 5, 8, 259, 272
Chrysosphaera, 324
Chthalamus, 331, 336, 338
CHURCH, A. H., 123, 128, 153, 155
Chylocladia reflexa, 217
Chytridiales, 42
Cirrhoids, 86
Cladhymenia, 252
Cladocephalus, 430 et seq.
Cladophora, 13, 17, 81, 82, 84, 85, 86, 88, 97, 311, 312, 324, 355, 359, 360, 362, 363, 415, 441
  callicoma, 86
  feredayae, 428
  flaccida, 87
  flavescens, 87
  fracta, 84
  glomerata, 86, 87
  pellucida, 87, 428
  repens, 87
  rupestris, 340
  suhriana, 87
  verticillata, 84
Cladophoraceae, 81 et seq., 310, 362
Cladophorales, 81
Cladophoropsis, 88, 311, 337
  membranacea, 89
Cladosiphon, 318
Cladostephaceae, 138
Cladostephus, 126, 138, 139, 441
  verticillatus, 138
Clare Island, 14, 328, 357
Claudea, 248
CLENDENNING, K., 408
Closterium, 112, 113, 114, 365
  calosporum, 113
  ehrenbergii, 113
  lanceolatum, 113
  lineatum, 113
  moniliferum, 114
  parvalum, 113
  rostratum var. *brevirostratum*, 113
Cocconeis, 373
  placentula, 372

Codiaceae, 96, 100, 101, 297, 303, 306, 307
Codiolum, 41, 83, 312
  kuckuckii, 41
  petrocelidis, 41, 88
Codium, 100, 104, 222, 307, 314, 325, 415, 450
  adhaerens, 100
  bursa, 100, 101, 430, 431
  decorticatum, 101
  elongatum, 101
  fragile, 100
  isthmocladum, 100
  tomentosum, 100, 101, 415, 441
Coelastraceae, 47
Coelenterata, 275, 427
Coenobium(ia), 26, 27, 28, 31, 43, 44
Coilodesme californica, 399
Colacolepis, 428
Cold Spring Harbour, 356
Coleochaetaceae, 79
Coleochaete, 19, 79, 310, 368
  pulvinata, 79, 80
  scutata, 79, 80, 372, 373
Collenia, 295
COLLINS, F. S., 15
Colpomenia, 162, 168, 352, 439
  sinuosa, 167
Compensation points, 408
Compsopogon, 359
Conchocelis, 226, 229, 314
  rosea, 226
Conchospores, 226
Conferva, 11, 12, 13, 363
Confervoideae, 12, 14
Congo, 377
Conjugales, 5, 96, 105, 308, 309 et seq., 315, 368
Conjugatae, 363
Continental drift, 437
Convoluta roscoffensis, 427
Corallida, 439
Corallina, 11, 240, 439
  officinalis, 240, 241
Corallinaceae, 216, 220, 221, 222, 238, 240, 302, 440
Cornwall, 436
Corynophlaea, 318
Corynophlaeaceae, 154, 318
Cosmarium cucumis, 115
COTTON, A. D., 14, 328, 357
CRANWELL, L. M., 328
Cretaceous, 297, 302, 429
Crocetin, 420
Crocin, 417, 419, 420
Crustida, 439
Cryoplankton, 359
Cryptomonas, 324
  anomala, 275
  ovata, 415
Cryptonemiales, 219, 235, 242, 321, 322
Cryptophyceae, 2, 3, 4, 9, 259, 275, 324, 427
Cryptopleura ramosa var. *uncinata*, 405
Cryptoporum, 365
Cryptozoon, 295
Cumatophytes, 440
Cumbrae, 348
Cumberland, 367
CUTLER, Miss, 142
Cutleria, 13, 14, 142, 144, 315, 316
  monoica, 437
  multifida, 143, 144, 437
Cutleriaceae, 122, 142
Cutleriales, 122, 142, 320
Cyanophyceae, 1, 347, 350, 353 et seq.
Cyanophycin, 3, 7, 278
Cycas, 428
Cyclocrinus, 299
  porosus, 298
Cyclosporeae, 123, 320
Cyclotella tenuistriata, 272
Cylindrocapsa, 53
Cylindrocapsaceae, 53
Cylindrocystis brebissonii, 112
Cylindrospermum, 291, 413, 414
  gorakhporense, 382
  majus, 291
  stagnale, 291
Cymbella lanceolata, 271
Cymopolia, 91, 301
Cystocarp(s), 221, 228, 243, 244, 248, 251, 253, 256
Cystoclonium purpureum, 431
Cystococcus, 39, 40
Cystodinium, 324
  lunare, 276
Cystophora, 331, 336, 342
Cystophyllum, 148
Cystoseira, 194, 208, 209, 331, 436, 441
  abrotanifolia, 208
  ericoides, 208
Cystoseiro—Sargassaceae, 194, 208

DAILY, W., 286
DAMANT, G. C., 392, 411
DAO, S., 91, 95
Dasya, 221
Dasycladaceae, 92, 93, 94, 297, 298, 299, 303
Dasycladales, 17, 20, 65, 91, 310
Dasycladus, 92, 326, 432
  clavaeformis, 92, 417, 418
DE, P. K., 381, 382
Delesseriaceae, 216, 253
Delesseria, 220, 248, 253, 399, 401, 438
  sanguinea, 220, 254
DELESSERT, BARON, 253
DELF, E. M., 326

Delisia pulchra, 231
  suhrii, 231
Delophycée, 127
Dendrida, 439
Denmark, 376
DERBES, A., 96
Derbesia, 17, 96, 97, 98, 415
  marina, 97
  tenuissima, 98
Derbesiales, 98
Dermatolithon, 302
Dermocarpa, 286
DESMAREST, A. G., 168
Desmarestia, 168, 169, 415
Desmarestiaceae, 122, 168
Desmarestiales, 162, 168, 320
Desmidiaceae, 105, 112, 263
Desmid(s), 115, 361, 366, 367
Desmokontae, 277
DE TONI, J. B., 14
Devonian, 296, 301, 305
Diadinoxanthin, 2
Diatomaceae, 12, 269, 277, 368
Diatom(s), 9, 269, 334, 342, 359, 361, 363, 367, 371, 381, 413, 438
Diatoxanthin, 2
Dictyopteris, 145, 335, 338
Dictyosphaeria, 81
Dictyosphaerium, 39
Dictyosiphon, 163, 164, 316
  chordaria, 164
  foeniculaceus, 166
Dictyosiphonaceae, 122, 163
Dictyosiphonales, 127, 162, 316, 320
Dictyota, 14, 126, 144, 145, 147, 148, 315, 432
  dichotoma, 145, 146
Dictyotaceae, 122, 145
Dictyotales, 122, 125, 127, 144, 306, 317, 319, 320
DILLENIUS, J. B. H., 12
DILLWYN, L. W., 12, 375
Dimorphosiphon, 297
Dinobryon, 273, 324
  marchicum, 274
  sertularia, 274
Dinoclonium, 10, 277, 324
  conradi, 276
Dinococcales, 277
Dinoflagellates, 276, 277, 342, 436
Dinophyceae, 2, 3, 4, 9, 275, 276, 296, 324, 367, 427
Dinothrix, 10, 277, 324
Dinoxanthin, 2
Diplobiont, 314
Diplont, 314
Diploplora, 301
  phanerospora, 299
DORAISWAMI, S., 38
DORING, H., 49
DOTY, M., 384, 393, 404, 411
Dover, 342, 390
Dovey, 348, 350, 353
Draparnaldia, 20, 71, 72, 73, 115, 309, 325
  glomerata, 73, 74
  plumosa, 73
DRAPARNAUD, J. P. R., 72
DROUET, F., 286
DUDRESNAY, de St. Pol-de-Léon, 236
Dudresnaya, 236, 237, 441
  coccinea, 236, 237
  purpurifera, 237
Dumontiaceae, 236
Dunaliella, 23, 260
  salina, 425
DURVILLE, J. D., 194
Durvillea, 191, 192, 194, 196, 202, 206, 207, 215, 306, 316, 329, 331, 336, 342, 383, 406
  antarctica, 195, 196
  willana, 195
Durvilleae, 194
Durvilleaceae, 194

East Anglia, 343, 347, 348
ECKLON, 188
Ecklonia, 170, 188, 336, 342, 390, 433, 435, 437, 445
  radiata, 188, 390
Eckloniaceae, 188
Eclipsiophyceae, 441
Ectocarpaceae, 122, 128, 132, 134, 156, 320
Ectocarpales, 122, 127, 128, 141, 149, 157, 314, 320
Ectocarpus, 123, 126, 128, 129, 132, 133, 135, 315, 316, 325
  confervoides, 129
  fasciculatus, 128
  padinae, 130
  secundus, 130
  siliculosus, 87, 128, 129, 130, 131
  tomentosus, 129
  virescens, 126, 129, 130, 315, 320
Edaphophytes, 375
EGEROD, L. G., 81, 90
Egregia, 177, 190, 335, 392, 394, 400, 407
  laevigata, 393, 407, 410
  menziesii, 190
EHRKE, G., 401, 408, 411
Eisenia, 445, 450
Elachista, 149, 155, 156, 318
  fucicola, 155, 156
  stellaris, 156
Elachistaceae, 122, 155, 318
ELLIOTT, A. M., 38
Encrustida, 439
Encyothalia, 160

Endoderma, 20, 74
Endosphaeraceae, 41
Endophyte(s), 41, 438, 440, 442
England, 13, 148, 275, 301, 334, 335, 345, 347, 352, 356, 357
ENGLEMANN, T. W., 398
Enteromorpha, 19, 49, 55, 56, 61, 156, 308, 309, 312, 315, 325, 335, 337, 342, 346, 355, 359, 390, 391, 392, 397, 401, 406, 407, 415, 426, 440
  clathrata, 58, 311, 351, 354, 355
  compressa, 311
  intestinalis, 58, 311, 418
  intestinalis f. *flagelliformis*, 57
  minima, 350, 354, 355
  nana, 56, 58, 311, 312, 351
  percursa, 58, 311
  procera, 58, 311, 312
  prolifera, 58, 311
  ralfsii, 58
  salina, 58
  torta, 58, 311
Entocladia, 20, 74
Entophysalis, 279, 285
Eocene, 297
Epichrysis paludosa, 274
Epilithon, 238, 240, 241
  membranaceum, 238, 239
Epiphloeophytes, 375
Epiphyllophytes, 374
Epiphytes, 371, 372, 438, 440, 442
Epitheca, 269
Epizoophytes, 375
Ephemerophyceae, 441
Epping Forest, 371
Equisetum, 11, 115
  limosum, 372, 373
Ergosterol, 3
Ernodesmis, 426
Erythrocladia, 223, 325
Erythrotrichia, 223
Essex, 349
Eu-conjugatae, 105
Eudesme, 151, 152, 155, 172, 317, 318, 325
  virescens, 151
Eudorina, 26, 38, 309, 367
  elegans, 27
  illinoiensis, 27
  indica, 27
Euflorideae, 218, 222, 227, 311, 321, 322
Euglena, 1, 363, 364, 365
  viridis, 365, 378
Eugleninae, 414
Eunotia, 363, 373
  pectinata, 372
Euphycophyta, 4, 5, 162, 216, 312, 323
Europe, 263, 333, 335, 342, 359, 406, 423, 425, 445, 446, 449
Eusiphoneae, 96
Evection, 84

Faeroes, 435
Falkenbergia, 230
  rufo-lanosa, 230
FAN, K. C., 90
FELDMANN, J., 15, 81, 90, 104, 312, 314, 323, 326, 345, 437, 441, 443
Feldmannodora, 58
FENTON, C. L., 307
FERGUSON-WOOD, E. J., 436
Finland, 435
Firth of Forth, 348
Flagellata, 14, 296
FLAHAULT, C., 375
Flavoxanthin, 2
Florida, 336, 345
Florideae, 12
Floridoside, 3, 7
FOGG, G. E., 293, 428
Foliida, 440
Fragillaria, 334
France, 11, 12, 13, 431, 434
FRIEDMANN, I., 64
FRITSCH, F. E., 10, 14, 15, 38, 49, 64, 71, 81, 104, 115, 121, 122, 127, 128, 135, 140, 148, 149, 170, 258, 272, 274, 277, 280, 282, 293, 312, 326, 358, 363, 366, 379, 382, 404
Fritschiella tuberosa, 74
Frustule, 269
Fucaceae, 193, 196, 203, 204, 352, 355, 402, 425
Fucales, 123, 124, 126, 159, 162, 170, 191, 193, 194, 203, 207, 306, 315 et seq., 423, 446
Fuco-Ascophyllae, 194, 196
Fucoideae, 12
Fucoidin, 3, 6, 452
Fucosan, 124, 125
Fucosterol, 3, 315
Fucoxanthin, 2, 6, 16, 122, 216, 315
Fucus, 11, 12, 13, 101, 146, 156, 191, 194, 196, 197, 200 et seq., 214, 317, 335, 349, 391, 401, 402, 406, 415, 426, 439, 444, 445, 449, 451, 452
  ceranoides, 198, 342, 348, 404
  evanescens, 415, 425
  furcatus, 335
  limicola, 347, 354, 355
  serratus, 133, 134, 197, 198, 331, 333, 334, 387, 388, 389, 396, 397, 400 et seq., 426
  spiralis, 198, 201, 334, 342, 349, 403, 404

Fucus spiralis var. *lutarius*, 348
    nanus, 348
    platycarpus, 201, 334, 387, 388, 389, 396, 397, 400
  vesiculosus, 133, 134, 155, 197, 198, 199, 201, 331, 333 et seq., 348, 349, 387, 388, 389, 392, 393, 400, 403, 425, 426
    ecad *caespitosus*, 348
      filiformis, 348
      muscoides, 348
      nanus, 348
      subecostatus, 348
      volubilis, 348
Fujiyama, T., 64
Funk, G., 439, 443
Funorin, 451, 452
Furcellaria fastigiata, 154

Gail, F. W., 386, 411
Galaxaura, 218, 227, 233, 234, 258, 322, 432
  lapidescens, 234
  marginata, 234
Galeolaria, 336
Gamble, F. W., 428
Gamones, 417
Geitler, L., 282, 293
Gelidiaceae, 234
Gelidiales, 218, 234, 235, 321
Gelidium, 234, 335, 337, 414, 439, 448, 451, 452
  amansii, 235, 447
  cartilagineum, 448
  corneum, 235
  latifolium, 448
  pulchellum, 448
Gelose, 448
Gemina, 49, 56, 61, 311
  enteromorphoidea, 61
  linzoidea, 61
Geniculations, 108
Geosiphon, 426, 427
Gerade, J., 11
Germany, 13, 301, 375, 453
Gibb, D. C., 214, 349, 357
Giffordia secunda, 130
Gigartina, 242, 243, 334, 335, 448, 452
  atro-purpurea, 242
  californica, 243
  stellata, 243, 448
Gigartinaceae, 242
Gigartinales, 219, 242, 321
Girvanella, 295
Gislèn, T., 333, 345, 439, 443
Glaucocystis, 426
Gloecapsa, 279, 296, 427
Gloeocapsomorpha, 294
Gloeochaete, 426
Glococystis, 281
Gloeodinium, 277, 324
  montanum, 276
Gloeopeltis, 451
  furcata, 335, 451
Gloeothece, 281, 296
Gloeotrichia, 290
Glyceria, 363
Glycogen, 278
Gobia, 164
Godward, M., 367, 371, 382
Gold Coast, 337
Gomont, M., 14, 375
Gomontia, 79
  polyrhiza, 79
Gomphonema, 374
  olivaceum, 370
Gonotozygaceae, 105
Gongrosira, 79
Gonidia, 279
Gonimoblast(s), 221, 228, 229, 235, 237, 246, 248
Gonimocarp, 221
Goniolithon, 302
Gonium, 24, 34
  pectorale, 24, 25
Goros, 360
Gracilaria, 337, 352, 355, 439, 448, 452
  confervoides, 241, 448
  flagelliformis, 352
Graebner, P., 375
Graminida, 440
Grateloupia, 337
Grateloupiaceae, 236
Great Britain, 11, 12, 174, 178, 204, 263, 331, 352, 376, 435, 451
Greenland, 376, 434, 435
Greville, R. K., 12
Griffithsia, 13, 217, 220, 415
  corallina, 220
  flosculosa, 405
  furcellata, 405
  opuntiodes, 405
Gross, F., 272
Gross, I., 64
Groves, J., 121
Grubb, V. M., 220
Gymnodinium, 324, 378
  aeruginosum, 276
Gymnosolon, 295
Gynotermones, 417, 420, 421
Gyrogonites, 301

Haas, P., 387, 411
Haematochrome, 18
Haematococcus pluvialis, 23
Haines, H., 379
Halicystidaceae, 96
Halicystis, 81, 83 96, 97, 98, 104, 148, 421, 425, 426

ovalis, 97
parvula, 98
Halidrys, 192, 194, 334
siliquosa, 193, 388
Halimeda, 96, 101, 102, 297, 306, 307, 324, 432
Halimeda cuneata, 430
discoidea, 102
opuntia, 102
scabra, 102
simulans, 102
tuna, 430
Halimione portulacoides, 356
Halopteris, 139, 140
filicina, 126
funicularis, 140
hordacea, 126, 140
scoparia, 139
Halosaccion, 325, 335
Halosphaera, 259, 261
viridis, 262
Halosphaeraceae, 261
HAMEL, G., 132, 135
HAMMERLING, J., 104
Hantschia amphroxys, 376
Hapalosiphon laminosum, 360
Haplobionts, 314
Haplodiplonts, 321
Haplonts, 314, 321
Haplospora, 141
globosa, 141, 142
Haplostichineae, 122, 316, 320
Haptera, 124
Harpenden, 363, 365, 366
HARDER, R., 15
HARTMANN, M., 104, 144
HARVEY, W. H., 13, 241
Harveyella, 222, 241, 242, 406
mirabilis, 241, 242, 428
Haustoria, 241
Hawaii, 11, 449, 450
Helicion pellucidum, 406
Heliophiles, 440
Heliophobes, 440
Helminthocladia, 218
hudsoni, 231, 234
Helminthocladiaceae, 227, 231
Hemicryptophyceae, 441
Hemiphanerophyceae, 441
Heribaudiella, 123
Herpopytes, 440
Hermella, 336
Herposiphonia, 337
Heterocapsaceae, 260
Heterochloridaceae, 260
Heterochloridales, 260
Heterochloris, 324
Heterococcales, 260
Heterocyst(s), 279, 280, 287, 288, 289 et seq.
Heterogeneratae, 122, 127, 142, 193, 316, 320
Heterokontae, 5, 14
Heterosiphonales, 260, 264, 266
Heterosiphonia plumosa, 405
Heterotrichales, 260
Heterotrichy, 124, 136, 216, 312
Hijikia fusiforme, 336, 450
HILDENBRANDT, F. E., 238
Hildenbrandtia, 222, 238, 323, 325, 359, 360, 441
prototypus, 238
rivularis, 238
Hildenbrandtiaceae, 238
HILL, T. G., 387, 411
Himanthaliaceae, 206
Himanthalia, 194, 200, 206, 207, 215, 316, 332, 342, 438, 440
lorea, 207, 388
Hindhead Heath, 110
HOLDEHEIDE, W., 396, 397, 411
Holland, 453
Holmsella, 220, 222, 241, 242
pachyderma, 241, 242
Hormidium, 51, 281, 360, 363, 380
flaccidum, 51
Hormogone(s), 280, 287, 288, 290
Hormosira, 159, 192, 194, 212, 214, 306, 331, 333, 336, 342, 352, 389, 390, 397, 411, 436
banksii, 158, 213, 214, 349, 390, 393, 408, 409, 410, 425, 426
Hormosiraceae, 212
Hormothamnion, 429
HOWLAND, L. J., 78
HUSTEDT, F., 273
HYDE, M. B., 402, 411
Hydrobia ulvae, 406
Hydrodictyaceae, 43, 44
Hydrodictyon, 12, 31, 39, 40, 44, 45, 46, 49, 308, 309, 359, 426, 438
africanum, 44
patenaeforme, 44, 45, 46
reticulatum, 44, 45, 46
Hydrurus, 8, 359
foetidus, 274
Hymenoclonium serpens, 230
Hypnea, 448
Hypnea musciforme, 448
Hypnophyceae, 441
Hypnospore(s), 19
Hypotheca, 269

Iceland, 434, 435
Ilea, 162
Indiana, 364
Indian Ocean, 429, 431
Indo-Pacific, 429 et seq.
Iodine, 174, 217, 425, 444 et seq., 450
Ireland, 328, 348, 349, 357, 436, 450

Iridescence, 217
Irish Moss, 448
Irish Sea, 131, 132
ISAAC, W. E., 387, 411
Ishige, 336
Isle of Man, 130, 133, 333, 340
Isofucoxanthin, 271
Isogeneratae, 122, 142, 320
Isokontae, 5, 65
Isorhamnetin, 420
Israel, 453
IYENGAR, M. O. P., 38

Jamaica, 147, 148, 436
Jania, 241
  rubens, 241
JANCZEWSKI, E. de, 252
Janczewskia, 222, 251, 252, 406, 428
  lappacea, 251
  moriformis, 251
Japan, 11, 170, 174, 194, 211, 226, 397, 445, 447, 449 et seq.
JOHNSON, D. S., 345
JOHNSON, J. H., 307
JONSSON, H., 15, 434, 442, 443
Jurassic, 296

KANWISHER, J., 387, 393, 411
KEEBLE, F., 428
Kelp(s), 174, 408, 444 et seq., 451
Kieselguhr, 297
KING, G. C., 115
KJELLMAN, F. R., 14
KLUGH, A. B., 408, 411
KNIEP, H., 15
KNIGHT, M., 130, 131, 132, 133, 135, 214, 333, 440, 441
Kombu, 450
KORNMANN, P., 104, 141
Kosmogyra, 301
KOTHBAUER, E., 131, 132, 135
KRAUSEL, R., 305
KRISHNAMURTHY, V., 258
KUNIEDA, H., 168
KÜTZING, F. J., 13
KYLIN, H., 15, 122, 128, 160, 246, 258, 326
KUZNETZOV, V. V., 191

Lagynophora, 301
Laingia, 248
La Jolla, 395
LALAURENCIE, H. de, 253
Laminaria, 12, 13, 126, 170, 172, 173, 177, 179, 182, 187, 188, 191, 196, 198, 202, 207, 315, 316, 332, 334, 335, 426, 439, 440, 444 et seq., 449, 450 et seq.
  agardhii, 415
  bulbosa, 180
  cloustoni, 173, 174, 176, 177, 178 384, 424
  digitata, 174, 177, 178, 179, 334, 388, 402, 422, 423
  ephemera, 174
  pallida, 435
  religiosa, 179
  rodriguezii, 173
  saccharina, 173, 174, 177, 178, 179, 334, 384, 400, 401, 406, 422, 423, 424, 452.
  sinclairii, 172
Laminariaceae, 171, 172, 176, 180, 181, 199, 317, 429, 432
Laminariales, 122, 124, 127, 162, 170, 191, 192, 195, 306, 316, 319, 320, 423, 432
Laminarin, 3, 6, 423, 424, 425
LAMOUROUX, J. V., 12
LAMPE, H., 402, 411
LANG, W. H., 302, 305, 307
LANTRIP, L. W., 191
Laurencia, 248, 252, 253, 334
  implicata, 252
  papillosa, 252
Laver, 450
LEATHES, G. R., 154
Leathesia, 123, 149, 154, 167, 318, 438
  difformis, 154
LEFEBRE, M., 115
Lemanea, 222, 228, 229, 359, 360
Lemaniaceae, 227, 229
Lemna, 42, 363
Lepyrodophytes, 440
Lessonia, 183, 305, 306, 318, 336, 433, 440
  flavicans, 183
  fuscescens, 183
Lessoniaceae, 171, 182 et seq., 186
Lessoniopsis, 335
Letterstedtia, 311
Leucosin, 3, 8, 273
LEWIS, J. R., 355
Liagora, 231, 323
  tetrasporifera, 218, 231, 234, 322
  viscida, 231, 338
Lichen, 11
Lichina confinis, 333
Lignicolae, 442
Limnaeider, 442
Limnoplankton, 359
Limu, 450
LINNAEUS, C., 12, 219
Lithacophytes, 440
Lithophyllum, 302
Lithophytes, 375
Lithothamnion, 236, 302, 439
Littorina, 331, 333, 338
Lobata, 49, 56, 311

Loch Ine, 328, 347
Lola, 81, 82, 311
  implexa, 82
Lomentaria, 247
  clavellosa, 220, 247, 248
  rosea, 246, 247, 248, 323
Lomentariaceae, 246, 247
Loriformes, 194
Los Angeles, 185
Lutein, 2
LUTHER, A., 14
LUND, J. W. G., 376, 382
Lycopodiales, 307
LYNGBYE, H., 12, 375
Lyngbya, 281, 288, 363
  aestuarii, 288
Lynn, Mass., 356

Macrocyst, 265
Macrocystis, 13, 170, 183, 186, 187, 191, 394, 395, 400, 401, 408, 415, 433, 435, 437, 438, 445, 446, 451, 452
  pyrifera, 186, 401, 407, 410
Madagascar, 429
MAGNE, F., 227, 321
Magnolia, 75
Magno-silvida, 439
MANGENOT, G., 269
MANGIN, L., 14
MANGUIN, F., 115
Mannitol, 3, 6, 423, 424, 425
Mannoglycerate, 3, 7
Mannuronic acid, 446
MANTON, I. M., 125
Manubrium, 119
Manure, 449
Marginariella, 193
  urvilliana, 191, 194
Marpolia spissa, 294
Martensia, 248
  fragilis, 217
MARTIN, J. C., 408, 411
Massachusetts, 448
Mastigocladus, 413
  laminosus, 360
Mediterranean, 102, 338, 340, 343, 345, 394, 425, 430, 431, 435, 437
Medulla, 149, 172, 175, 199, 192, 212, 243
Meiosporangia, 129, 130
Meiospores, 60
Melanospermae, 13
Melaraphe, 331
Melobesia, 220, 302
Melosira, 273, 334, 363
  granulata, 270
  varians, 271, 272
Membranoptera alata, 405
Merismopedia, 281, 284
  aeruginosa, 285
  elegans, 285
  ichthyolabe, 285
Mesogloia, 149, 151, 152, 153, 317, 318, 325
  levillei, 149
  vermiculata, 150
Mesogloiaceae, 122, 154, 156, 316, 317
Mesotaeniaceae, 105, 111
Mesotaenium, 111, 112, 359
Metarreophytes, 440
Michelia fuscata, 75
Microcoleus delicatulus, 368
Microcystis, 281, 283
  aeruginosa, 283
  toxica, 283
Microdictyon, 81, 88, 311
  mutabile, 88
Microsomes, 103
Microspore(s), 272
Microspora, 51, 53, 262, 363
  amoena, 52
  willeana, 18
Microsporaceae, 51
Microzonia, 142, 316
Mischoccocus, 324
Modiolus, 335
MOEWUS, F., 421
MOLINIER, R., 345
Monocilia, 260
Monospores, 125, 221, 222, 223, 322
Monostroma, 53, 54, 58, 312, 352, 397, 398, 399, 412, 425
  crepidinum, 54
  grevillei, 54, 434
  lindaueri, 54
  wittrockii, 421
Monostromaceae, 54, 311
MOORE, L. B., 140, 328
MOUGEOT, J. B., 110
Mougeotia, 110, 111
  mirabilis, 111
  oedogonioides, 111
  tenuis, 110
Mount Desert Is., 335
MURRAY, G., 429
MULLER-STOLL, W. R., 64
Murman Sea, 14, 435
Muscus, 11
Mycosphaerella pelvetiae, 204
Myelophycus, 336, 414
Myriogloia, 123, 152, 317, 318
Myrionema, 123, 156
  strangulans, 156, 157
Myrionemataceae, 149, 156, 317, 318
Mytilus, 337, 338
Myxonema, 71

Myxophyceae, 1 et seq., 7, 12, 14, 223, 278, 287, 294, 295, 303, 321, 323 et seq., 331, 334 et seq., 351, 353 et seq., 358, 359, 360, 362, 367, 368, 369, 376, 377, 378, 379, 387, 392, 413, 414, 426, 429, 452
Myxophycophyta, 47, 278
Myxoxanthin, 2, 278
Myxoxanthophyll, 2, 278

Naccariaceae, 227, 229
Nannocytes, 279
Naples, 130, 147, 148, 405, 439
Naylor, M., 206, 214, 215, 316
Navicula, 412
Neeb, O., 49
Nemacystus, 318
Nemalion, 220, 227, 321, 325
  helminthoides, 227, 321, 340, 438
Nemalionales, 216, 218, 220, 222, 227, 228, 234, 314, 315, 321
Nemastomales, 219
Nemathecia, 244, 246, 322
Nematochrysis, 324
Nematophyceae, 5, 10, 213, 302, 307
Nematophycus, 305
Nematophytales, 10, 302, 304, 307
Nematophyton, 10, 185, 302, 304, 305, 307
Nematothallus, 10, 304, 305, 306
  pseudo-vasculosa, 306
  radiata, 306
Nemoderma, 148
Neodinoxanthin, 2
Neofucoxanthin, 2
Neomeris, 91, 93, 95, 301, 429, 430
  annulata, 93
  dumetosa, 93
Neoxanthin, 2
Nereider, 442
Nereocystis, 177, 183, 184, 187, 335, 425, 438, 440, 445, 452
  luetkeana, 185
Netrium digitus, 115
Neuston, 442
New England, 347, 352, 353, 392, 434
New Zealand, 13, 49, 76, 88, 98, 139, 194, 195, 196, 213, 238, 323, 328, 331, 333, 336, 337, 342, 347, 349, 352, 357, 374, 396, 448, 451, 453
Nicholls, A. G., 428
Nicolai, E., 17, 38
Nitella, 79, 115, 117, 212, 426
  batrachosperma, 116
  cernua, 116
  flexilis, 118, 120
  gracilis, 117
Nitophyllum punctatum, 405
Nitzschia, 334, 413
  palea, 415
Nizamuddin, M., 160
Nodularia harveyana, 379
Nordhaven, 435
Norfolk, 133, 346, 348, 351, 352, 353, 356
North, W., 408
North America, 170, 183, 187, 335, 345, 349, 433 et seq., 445, 451
North Carolina, 147, 148, 335, 336, 338, 340, 392
North Sea, 333, 343, 393
Norway, 434, 435
Nostoc, 280, 290, 291, 381, 413, 427, 428, 450
  commune, 290
  linckia, 291
  muscorum, 379, 413
  passerinianum, 379
  punctiforme, 291, 378, 415
Nostocaceae, 281, 287, 290, 291
Nostocales, 282, 286, 287
Nostochineae, 12
Notheia, 158, 317
  anomala, 159, 317, 428
Notheraceae, 158, 160, 318
Nova Scotia, 385
Nucleolus, 17

Ocelli, 276
Ochromonas mutabilis, 274
Oedocladium, 65
Oedogoniales, 5, 18, 65, 70, 308 et seq.
Oedogonium, 17, 19, 65, 66, 67, 69, 359, 362, 363, 365, 368, 374
  americanum, 66
  ciliatum, 66
  grande, 66
  kurzii, 66
  nebraskense, 66
Oenanthe fluviatilis, 572
Oltmanns, F., 14, 443
Ordovician, 294, 298, 299, 302
Orkney Is., 384, 449
Osborn, N., 214
Oscillatoria, 279, 280, 287, 288, 413
  brevis, 381
  corallinae, 287
  formosa, 287
Oscillatoriaceae, 287, 288, 363
Osmotic pressure, 425
Ostrea, 335
Ovulites, 297

Pachymenia, 342
Pachytheca, 296
Pacific, 6, 82, 139, 170, 182, 190, 194, 248, 306, 333 et seq., 345, 415, 430, 432, 433, 436, 445, 451
Pacific Ocean, 187

- *Padina*, 144, 145, 148, 335, 337
  - *pavonia*, 340
- *Palaeodasycladus*, 301
  - *mediterraneus*, 300
- *Palaeonitella*, 301
  - *cranii*, 301
- *Palaeoporella*, 297
  - *variabilis*, 297
- *Palmellaceae*, 223, 307
- Panama, 429, 430
- *Pandorina*, 24, 25, 26, 309, 324
  - *morum*, 26
- PANTANELLI, D., 15
- PAPENFUSS, G., 15, 128, 131, 135, 191, 310, 326
- Paradesmose, 18
- Paraphyses, 165
- Parasites, 438
- Paraspores, 222, 257
- PARKE, M., 150, 173, 191, 214, 333, 440, 441
- Parvosilvida, 440
- PASCHER, A., 14, 269
- *Pascheriella*, 24
- *Patella*, 406
- Pectin, 3, 9, 16
- Pectose, 16
- *Pediastrum*, 43, 44, 47, 309
  - *boryanum* var. *granulatum*, 43
  - *duplex*, 43
  - *simplex* var. *duodeniarum*, 43
- *Pelagophycus*, 185
- PELVET, Dr., 203
- *Pelvetia*, 194, 203, 215, 349, 351, 354
  - *canaliculata*, 193, 200, 203, 204, 333, 350, 387, 388, 403
    - ecad *coralloides*, 348
      - *libera*, 347, 348
      - *limicola*, 355
      - *radicans*, 348
  - *fastigiata*, 204
  - *wrightii*, 204
- *Penicillus*, 432
- Pennatae, 269, 272
- Peonin, 420
- Peredinin, 2
- *Peredinium*, 277
  - *anglicum*, 276
- *Perithalia*, 160
- Permian, 303
- *Perizonium*, 272
- *Petalonia*, 162, 325, 439
  - *fascia*, 163
- PETERSEN, J. B., 379, 382
- *Petrocelis*, 41
- *Petrospongium*, 155, 318
- *Peysonniellopsis*, 222
- pH, 74, 108, 263, 374, 406, 415
- *Phacotus*, 23, 825
- *Phaeococcus*, 275, 324, 347, 350, 351, 353 et seq.
- *Phaeocystis*, 273, 324, 344
  - *pouchetii*, 274, 343
- Phaeophyceae, 1 et seq., 10, 15, 122, 123, 126, 128, 162, 172, 192, 216, 222, 273, 302, 305, 312, 314 et seq., 393, 398, 404, 413, 414, 452
- Phaeophycophyta, 5
- *Phaeostroma*, 123, 134
  - *bertholdii*, 135
- *Phaeothamnion*, 8, 273, 315, 324
  - *confervicolum*, 274
- Phanerophyceae, 441
- Phialopore, 31
- Philippines, 343
- PHILLIPS, R. W., 14
- Pholadophytes, 440
- *Phormidium*, 367
  - *autumnale*, 350, 351, 354 et seq., 360
  - *laminosum*, 360
- Phycobilin, 7
- Phycochrysin, 273
- Phycocyanin, 2, 7, 8, 278
- *Phycodrys rubens*, 405
- Phycoerythrin, 2, 7, 8, 278
- *Phycopeltis*, 358, 374
- Phycoporphyrin, 16, 111
- Phykos, 11
- Phyllida, 439
- *Phyllitis*, 162
- *Phyllogigas*, 317
- *Phyllophora*, 243, 452
  - *brodiaei*, 244, 322
  - *membranifolia*, 244, 245, 322
  - *nervosa*, 445
- Phyllophoraceae, 243, 244
- *Phyllosiphon*, 20, 263, 269
  - *arisari*, 264, 428
  - *deformans*, 264
- Phyllosiphonaceae, 263
- *Phyllospadix*, 225
- Physodes, 124
- Phytoplankton, 342, 343
- PIA, J., 14, 307
- Picrocrocin, 420
- *Pila*, 261
- *Pinnularia viridis*, 270
- PIRSON, A., 49
- *Pithophora*, 18, 362
- Placoderm desmids, 112
- *Placosphaera*, 37
- Plakea, 27
- Plankton, 44, 282, 359, 360, 395, 421, 438, 442
- Plasmodesmae, 29, 217, 223
- Pleistocene, 303
- *Pleodorina*, 28, 38, 309
  - *californica*, 28
  - *spherica*, 28

Plethysomothallus, 127, 149, 152, 166, 441
Pleurocapsa, 286, 367
  minor, 286
Pleurocapsaceae, 286
Pleurocapsales, 282, 286
Pleurocladia, 123
Pleurococcaceae, 74
Pleurococcales, 74
Pleurococcus, 74, 281, 365, 375, 380
  naegelii, 75
Pleuston, 359, 442
Plocamium, 221
Plumaria, 222, 249, 256, 257, 258, 325
  elegans, 256, 258
Plymouth, 405
Pneumatocyst(s), 204
Pneumatophores, 204
Pocillophora bulbosa, 427
POCOCK, M. A., 34, 38, 49
Point Concepcion, 435
Polyblepharides, 23
Polykrikos, 324
Polyneura hilliae, 405
Polysiphonia, 2, 12, 216, 220, 248, 249, 253, 322, 323, 325, 335, 352
  fastigiata, 222, 249, 250
  nigrescens, 249
  sertularioides, 438
  tenerrima, 438
  urceolata, 405, 434
  violacea, 220, 249, 250
Polysporangia, 256
Polyspores, 222
Polystichineae, 122, 316, 320
Polytoma, 23
Pomatoceros, 336
POPE, E. C., 337, 345, 436, 442
Porostromata, 295, 303
Porphyra, 223 et seq., 229, 258, 314, 325, 335, 338, 399, 402, 426, 441, 450, 451
  atropurpurea, 400
  perforata, 226
  tenera, 224, 225, 226, 407, 450
  umbilicalis, 225, 226, 227, 333, 340, 402, 413
Porphyridium, 225
  cruentum, 223, 224, 321, 413
POSTELS, A., 183
Postelsia, 170, 183, 383
  palmaeformis, 184
Potamoplankton, 259, 360
Potash, 445
Prasinocladus, 20, 37, 308, 309, 324
Prasiola, 59, 61, 281, 309, 310, 321, 323, 335, 375, 380
  crispa, 59
    f. *muralis*, 59
  japonica, 59, 60
  stipitata, 60
Prasiolaceae, 49, 59, 311
Prasiolales, 49
Prasiolineae, 49
Precambrian, 295
PRESTCOTT, G. W., 15
PRESTON, R. D., 17, 38
Primicorallina, 299
  trentonensis, 299
PRINGSHEIM, E. G., 15, 387, 411
Procarp, 241, 248, 253, 321
Propagules, 125
Prothallus, 127, 166, 441
Protista, 14
Protococcales, 358, 362, 363
Protococcoideae, 14
Protocrocetin, 420
Protoderma, 309, 325
Protoflorideae, 7, 216, 217, 218, 222, 223, 258, 311, 314, 315, 321
Protonema, 120, 127, 128, 167
Protophyceae, 294, 295
Protosiphon, 40, 47, 264, 308 et seq.
  botryoides, 47, 48, 417, 418, 421
Protosiphonaceae, 47
Prototaxites, 305
Prototheca, 414
Pseudendoclonium, 74
Pseudobryopsis myura, 338
Pseudopringsheimia, 325
Pseudosporochnus, 160
Pseudoraphe, 270
Pterocladia, 452
  capillacea, 448
  lucida, 448
Ptilota plumosa, 405
Punctaria, 124, 316
Punctariaceae, 122, 162
PYLAIE, B. de la, 132
Pylaiella, 123, 132, 334, 338
  fulvescens, 132, 134
  littoralis, 132, 133, 134
  rupinicola, 134
Pyrenoid(s), 5, 17, 20, 53, 65, 75, 76, 105, 124, 216, 229, 266
Pyrrophycophyta, 4, 9, 259, 275
Pyura, 336

Quercetin, 420
Quercus, 11

RABINOWITSCH, E., 411
Ralfsia, 238, 318, 325, 336, 438, 439
Ralfsiaceae, 318
Rama, 82, 311
  antarctica, 82
RAMANATHAN, K. R., 38
Ranunculus aquatilis, 363
RAPER, K., 419, 428

Raphe, 270, 271
Raunkiaer, C., 438, 440, 443
Ray, J., 11
Reamour, R. A. F., 12
Rees, T. K., 328, 357
Reinschia, 261
Rhabdonema, 334
  arcuatum, 271
Rhabdoporella, 298
  pachyderma, 298
Raphidonema brevirostre, 359
  licmophora, 334
Rhizoclonium, 81, 83, 355, 354, 359, 362
  hieroglyphicum, 83
  implexum, 2
  lubricum, 83
Rhizocrysis, 273
Rhizocysts, 265
Rhizogen, 180
Rhizoplast, 18
Rhodochytrium, 42
Rhodocorton, 228
  endozoicum, 428
Rhodomela, 241
Rhodomelaceae, 249, 252, 253
Rhodophyceae, 1 et seq., 14, 15, 80, 81, 144, 216, 217, 218, 221, 222 et seq., 249, 302, 303, 306, 309, 312, 313, 321 et seq., 359, 393, 398, 404, 405, 412, 413, 414, 425, 428, 452
Rhodophycophyta, 5
Rhodospermae, 13
Rhodymenia, 12, 220, 334, 335
  palmata, 450
Rhodymeniaceae, 246
Rhodymeniales, 14, 219, 246, 258, 321
Ricardia montagnei, 222
Rich, F., 363, 366
Rieth, A., 64
Rivularia, 12, 289, 347, 350, 351, 353 et seq., 439, 441
  atra, 289, 290
  haematites, 281
Rivulariaceae, 281, 287, 289
Roach, B. M., 377, 379, 382
Ronaldson, J. W., 357
Roth, A. G., 12
Rothampstead, 379
Round, F. E., 368, 369, 382
Ruhr River, 360
Russia, 198, 445
Rutin, 420

Saccoderm desmids, 111
Saccorhiza, 170, 180, 184, 198
  dermatodea, 181
  polyschides, 180, 181
Sacheria, 359
Saline River, Michigan, 361
Salisbury, E. J., 14
Sarcophycus, 336, 342
  potatorum, 195
Sargassaceae, 208, 209, 212
Sargasso Sea, 211
Sargassum, 148, 193, 194, 201, 209, 210, 335, 337, 338, 432, 440, 452
  enerve, 211
  filipendula, 210, 211, 212
  horneri, 193
  hystrix, 212
  natans, 211, 212
  thunbergii, 210, 336
  vulgare, 212
Sargent, M. C., 191
Sauvageau, C., 14, 167
Savage, R. E., 343
Saxicolae, 442
Saxostrea, 336
Scaphospora speciosa, 142
Scenedesmus, 47, 374, 377, 378, 412, 413, 414
  acuminatus, 47
  costellatus var. *chlorelloides*, 377
  obliquus, 413
  quadricauda, 47, 414
Scina, D., 231
Scinaia, 231, 321, 432
  furcellata, 220, 231, 232
Schizochlamys, 36, 38
Schizodictyon, 36, 308, 309
Schizogoniaceae, 223
Schizogoniales, 49
Schizomeris, 51
Schizonema grevillei, 334
  ramosissima, 334
Schizothrix, 295, 296
Schmitz, F., 14
Schmitziella, 222
  cladophorae, 428
  endophloea, 428
Schussnig, B., 131, 132, 135
Scolt, 351
Scotiella nivalis, 359
Scotland, 12, 13, 349, 384, 435, 450, 451
Scottish Seaweed Res. Assoc., 334, 446
Scytonema, 288, 427
  guyanense, 289
  pseudoguyanense, 289
Scytonemataceae, 279, 288
Scytosiphon, 135, 163
Scytothalia, 193
Seatron, 185
Selenastrum, 44
Sertularia, 133
Setchell, W. A., 172, 433, 434, 440, 443
Severn River, 385
Sheffield, 364

Siberia, 301
Silica, 3, 9
Silurian, 296 et seq., 305
Silvida, 439
SINGH, N., 382
Siphonales, 2, 3, 4, 16, 17, 18, 20, 47, 48, 81, 96, 259, 264, 265, 266, 269, 308, 309 et seq., 323, 337, 425, 426
Siphoneae, 14
Siphonein, 2
Siphonocladaceae, 88, 311
Siphonocladales, 17, 20, 64, 65, 81, 91, 308, 309, 310, 312
Siphonocladus, 81, 88
  pusillus, 338
Siphonoxanthin, 2
SIRODOT, S., 14
Sitosterol, 3
Skiarrophyte, 440
SKOTTSBERG, C., 15
SKUTCH, A. S., 345
SMITH, G. M., 10, 417, 428
Smithora naiadum, 225, 227, 399
Soda, 444 et seq.
Solenoporaceae, 302
Soliera dura, 431
Soma, 27
SORENSEN, I., 49
South Africa, 28, 170, 193, 283, 336, 340, 343, 345, 433, 435 et seq.
South America, 196, 437
South Australia, 296
SOUTHWARD, A. J., 345
Spartina, 132, 347
  townsendii, 353
Spermatochnaceae, 122, 157, 318
Spermatochnus, 157, 158, 318
  paradoxus, 158
Spermatium(ia), 217, 220, 223 et seq., 232, 239, 241, 244
Spermocarp, 80
Spermothamnion, 222
  snyderae, 256
  turneri, 256
Sphacelaria, 123, 124, 125, 136, 139, 141, 325
  bipinnata, 126, 137
  cirrhosa, 137
  fluviatilis, 123
  harveyana, 126
  hystrix, 126
  plumigera, 137
  racemosa, 137
Sphacelariaceae, 122, 136
Sphacelariales, 122, 127, 135, 319, 320
Sphacella, 136
Sphaerella, 16, 23, 30, 38
  lacustris, 23, 24
Sphaerellaceae, 23
Sphaerococcales, 219
Sphaerocodium, 295
Sphaeroplea, 62, 64, 417
  africana, 62, 63, 64
  annulina, 62, 63, 64
  cambrica, 63, 64
  wilmani, 63, 64
Sphaeropleaceae, 62
Spirogyra, 12, 20, 105, 106, 107, 110, 359, 362, 365
  adnata, 105, 107
  colligata, 106
  fluviatilis, 107, 360
  jogensis, 108
  neglecta, 107
  nitida, 106, 365
  varians, 107, 365
  weberi, 105
Spirulina, 287
  major, 287
  subsalsa, 287
Spitzbergen, 435
Splachnidiaceae, 318
Splachnidium, 41, 158, 317, 318, 437
  rugosum, 202
Spondylothamnion multifidum, 405
Spongiostromata, 295, 303, 307
Spongomorpha, 41, 83, 87, 311, 312, 335
  coalita, 86, 88
  lanosa, 441
  vernalis, 85
Sporochnaceae, 122, 160
Sporochnales, 122, 320
Sporochnus, 160, 441
  pedunculatus, 161, 338
Sporocyst, 265
STACKHOUSE, J., 12
STARR, R. C., 49
STEIN, J. R., 38
Stephanokontae, 5, 65
Stephanosphaera, 24
  pluvialis, 417
STEPHENSON, T. & A., 329, 333, 337, 340, 345, 435, 436, 443
Sterrocolax decipiens, 246
Stichidia, 139, 221
Stigeoclonium, 20, 71, 72, 73, 309, 310, 325, 325, 372, 373
  aestivale, 72
  lubricum, 72
  protensum, 72
  tenue, 72, 360, 361
Stigonema, 281, 292
  minutum, 292
Stigonemataceae, 292
Stigonematales, 279, 282, 291
Stilophora, 318
STOCKER, O., 396, 397, 411

Stolons, 235
Stosch, H. A. von, 273
Strafforella, J., 339
Strain, H. H., 10
Strangford Loch, 348, 349
Streblonema, 166
Striaria, 352
Stypocaulaceae, 139
Stypocaulon, 124
Subcortex, 149
Subrahmanyan, R., 204, 215
Succicolae, 442
Suez, 431
Suhria vittata, 448
Suto, S., 168
Svedelius, N., 15, 233, 258, 313, 429, 443
Sweden, 128, 134
Sydney, 420
Synechococcus elongatus, 413
Synechocystis, 413
Synedra, 334
  radians, 370
Synura, 273, 324
  ulvella, 274, 415
Synzoospore, 63

Tansley, A. G., 14
Taonia, 144, 145
Tasmania, 195, 336, 342
Taxaceae, 305
Termones, 417
Terricolae, 442
Tetraclita, 336
Tetragonidium, 9, 275, 324
  verrucatum, 275
Tetraspora, 20, 22, 34, 309, 324, 361
  cylindrica, 35
  gelatinosa, 35, 36
  lubrica, 35, 417
Tetrasporaceae, 34, 426
Tetrasporales, 34
Tetraspore(s), 125, 147, 218, 221, 222, 322
Thalassiophyllum, 170, 181
  clathrus, 182
Thompson, R. H., 36, 38
Thoraceae, 227
Thorea, 359
Thuret, G., 13
Tiffany, L. H., 382
Tilden, J., 282, 293, 307
Tilopteridaceae, 122, 141
Tilopteridales, 122, 125, 140, 320
Tinocladia, 152
Tolypothrix, 367, 413
Torida, 439
Trabeculae, 103
Trachelomonas, 363
Trailliella intricata, 231
Tranophytes, 440
Transeau, E. N., 15, 362, 382
Trebouxia, 20, 39, 40
Trentepohl, J. F., 76
Trentepohlia, 76, 77, 358, 375, 427
  annulata, 77
  aurea, 77, 78
  jolithus, 77
  montis-tabulae, 77
  umbrina, 77
Trentepohliaceae, 75, 76, 79, 358
Trevarthen, C., 333
Triassic, 297, 301, 302
Tribonema, 53, 262, 263, 274, 324
  bombycina, 262, 263
  minus, 263
Tribonemaceae, 262
Trichogyne(s), 217, 250
Trochiscia aspera, 376
Trömso, 405
Trumpet hyphae, 175, 176, 181
Tsao, 11
Tschudy, H., 396, 411
Turner, D., 12
Tylenchus fucicola, 204

Udotaceae, 96
Udotea, 306, 439
Ulotrichaceae, 49
Ulotrichales, 16, 49, 54, 61, 71, 81, 105, 310, 362, 368
Ulotrichineae, 49
Ulothrix, 19, 20, 49, 51, 54, 64, 70, 71, 81, 308 et seq., 324, 346, 351, 354, 360, 361, 364, 367
  flacca, 338, 354
  idiospora, 50
  pseudoflacca, 441
  subflaccida, 338
  subtilis var. *variabilis*, 376
  zonata, 50
Ulva, 11, 19, 54, 55, 56, 58, 156, 308 et seq., 315, 325 et seq., 406, 412, 414, 421, 426
  lactuca, 413
  linza, 55, 56, 58, 400, 402
  lobata, 16, 56
  rhacodes, 55
  sorensenii, 55
  taeniata, 399
Ulvaceae, 12, 20, 49, 55, 56, 62
Ulvales, 49, 308, 310
Ulvella, 74, 373
Umbraculida, 439
Undaria pinnatifida, 450
Urococcus, 37
Urospora, 13, 83, 311, 312, 324
Utricularia, 361
U.S.A., 14, 28, 295, 337, 374, 446, 453

Valonia, 81, 88, 90, 337, 421, 425, 426
  macrophysa, 90, 415
  utricularis, 90
  ventricosa, 90
Valoniaceae, 88, 311, 315, 323
Vancouver Island, 183, 190
Vaucher, J. P., 12, 265, 360, 375
Vaucheria, 9, 93, 99, 259, 265, 266, 324, 354 et seq., 359, 362, 365, 441
  debaryana, 265
  geminata, 266
  piloboloides, 266
  repens, 266
  sessilis, 266, 267, 268
  sphaerospora, 347
  terrestris, 266
  thuretii, 347
Vaucheriaceae, 265
Vaucherietum, 347
Verrucaria maura, 333
Victoria, 336, 337
Violaxanthin, 2
Virgil, 11
Vitamin B., 414
Vitamin C., 415
Vitamin D., 415
Vitamin E., 415
Volvocaceae, 24, 25, 26, 28, 34, 38
Volvocales, 16, 18, 20, 38, 260, 310, 313, 315
Volvox, 18, 19, 20, 27, 28, 31, 33, 34, 38, 46, 308, 309, 312, 314, 324, 364
  africana, 31
  aureus, 29, 31
  capensis, 30, 32
  globator, 29, 31
  rousseletii, 29, 30, 32, 33
Volvulina steinii, 26

Walcott, C. D., 14, 295
Wales, 147
Water bloom, 282, 283
Weedia, 295
Wegener, A., 437
Wembury, Dorset, 405
Werz, G., 95
West, G. S., 71, 358, 366, 375, 382
West Indies, 211, 429
White Sea, 435
Wille, N., 14, 375
Williams, J. L., 336
Williams, M. M., 14
Windermere, Lake, 367, 369
Wittrockiella, 281
Womersley, H. B., 160
Wood, R. D., 121

Xanthophyceae, 1 et seq., 8, 9, 53, 259, 266, 269, 273, 315, 362, 363
Xanthophylls, 124
Xenococcus, 286
Xiphophora, 194, 329, 336

Yamanouchi, I. S., 144
Yellowstone Park, 360
Yendo, K., 162
Yonge, C. M., 427, 428

Zanardinia, 142, 315
Zanefeld, J., 387, 411
Zeaxanthin, 2, 420
Zizyphus, 75
Zoochlorella, 20, 43
Zooxanthella, 275
Zostera, 134, 225, 440
Zygnema, 110, 315, 360
  pectinatum, 16
  stellinum, 109
Zygnemaceae, 105, 110, 361, 362, 363, 373
Zygnemales, 16
Zygogonium, 109, 110
  ericetorum, 109, 110, 380
Zygospore, 110, 114

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