

# GREEN PLANTS

Their Origin and Diversity

*Second Edition*

PETER R. BELL &  
ALAN R. HEMSLEY

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# Green Plants

## Their Origin and Diversity

The central theme of *Green Plants* is the astonishing diversity of forms found in the plant kingdom, from the simplicity of prokaryotic algae to the myriad complexities of flowering plants. To help the reader appreciate this remarkable diversity, the book is arranged according to generally accepted classification schemes, beginning with algae (both prokaryotic and eukaryotic) and moving through liverworts, hornworts, mosses, fern allies, ferns and gymnosperms to flowering plants. Copiously illustrated throughout with clear line diagrams and instructive photographs, *Green Plants* provides a concise account of all algae and land plants, with information on topics from cellular structure to life cycles and reproduction. The authors maintain a refreshingly cautious and objective approach in discussions of possible phylogenetic relationships. Newly emerging information on features of plants known only as fossils is included, providing as complete a history as possible of the plant kingdom. Throughout the book there are many references to ultrastructural and physiological features which relate growth and form to current concepts in the study of plant development. This new edition has been completely updated

to reflect current views on the origin of the major groups of plants and includes information arising from more recently developed techniques such as cladistic analyses. As such, it provides an up-to-date and timely resource for students of botany, and also for researchers needing a comprehensive reference to the plant kingdom.

PETER BELL is Emeritus Professor of Botany at University College London. He has spent many years studying plants, particularly the reproductive cells of land plants, and has travelled extensively throughout the world in his capacity as a botanist. He is author of *The Diversity of Green Plants* (1968, 1983, 1992), co-translator of Strasburger's *Textbook of Botany* (8th English edition, 1976) and editor of and contributor to *Darwin's Biological Work* (1959).

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# **Green Plants**

## **Their Origin and Diversity**

Second edition

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## Preface to the first edition

*Green Plants* is a thoroughly revised edition of the earlier *Diversity of Green Plants* by P. R. Bell and C. L. F. Woodcock (3rd edition, London, 1983). The continuing demand for a concise account of the algae and land plants from the point of view of their natural relationships and biology reflects the buoyant state of botanical science. Exciting advances remain a feature of all its aspects. The biophysically minded are revealing in impressive detail the electron pathways in the thylakoid membrane while paleobotanists expand significantly our knowledge of the earliest angiosperms of the Cretaceous and geneticists explore the molecular aspects of plant development. The theme of *Green Plants* is the astonishing diversity of forms which evolution has provided from the atmospheric carbon fixed by photosynthesis, the remarkable phenomenon which is basic to plant life. The treatment of the Plant Kingdom correspondingly extends from the simplest cellular organisms capable of phototrophy, the prokaryotic algae, to the complexities of the flowering plants, not omitting (so far as they are known) the essential features of the plants represented only by fossils.

The record of plant life provides a striking instance of both genetic conservation and variation. The photochemistry of the thylakoid membrane is presumably basically the same today as it was at the dawn of plant life in pre-Cambrian times, and the genetical system controlling its development likewise essentially unchanged. Variations in subsequent biochemical pathways, leading, for example, to  $C_3$  and  $C_4$  plants, may also be of considerable antiquity. Accompanying these stable mechanisms of phototrophy are innumer-

able variations in morphology, a consequence of the mutability of DNA. Natural selection has offered, and continues to offer, the principal constraint. In lush conditions, even selection, provided essential physiological and reproductive features remain unimpaired, may do little to limit diversity.

Classifications of the algae and land plants facilitate the ordered treatment of diversity. Those adopted here follow schemes in general use. The "blue-greens" (together with the Prochlorophyta) are regarded as algae. To maintain a sharp division between prokaryotic and eukaryotic organisms is to fall into the error of attributing undue weight to one character. The concept of Algae, phototrophs with a wide range of morphological, biochemical and ecological features in common, comprehends both karyotic conditions.

The preparation of the present work has involved the help, willingly given, of experts in many fields. The writer must accept responsibility for any errors remaining. In addition to the authors and publishers cited, the following kindly agreed to the reproduction of figures: The Council of the Linnean Society of London (Figs 5.7, 8.46, 9.14, 9.15); the Trustees of the British Museum (Natural History) (Figs 2.12, 3.20, 3.23, 3.24, 4.15, 4.16, 9.5); and the University of Michigan Press (Figs 3.25, 3.26, 3.27).

Nothing would have been possible without the invaluable technical assistance of John Mackey and the skilled secretarial work of Elizabeth Bell. To both my sincere gratitude.

P. R. Bell  
London, 1990

## Preface to the second edition

New techniques, such as nucleic acid sequencing and refined methods of spectrographic analysis of plant products, have contributed to the continuing vitality of botanical science, and correspondingly the need for a second edition of *Green Plants*. Sequence analyses have indicated, for example, the evolutionary distance between the mosses and liverworts, the latter appearing closer to the green algae, and presumably to the early colonists of the land. Chemical analyses have revealed surprisingly that the material thought to be sporopollenin coating the membranes of certain green algae, unlike sporopollenin, is largely aliphatic in nature. The evolutionary significance of this discovery is not yet clear, but it is noteworthy that a chemically similar, acetolysis-resistant, material has been found coating the female gamete in archegoniate plants.

Advances in comparative morphology and paleobotany have also been notable. Penetrating studies of sexual reproduction in the Gnetales have thrown fresh light on the origin of double fertilization as it is seen in flowering plants, and has strengthened the view that the endosperm, unique to the angiosperms, is in origin a second embryo, but remains a tissue in which embryogenesis is normally permanently suppressed. The firm evidence, now available, for certain lowly plants from the Rhynie Chert (Lower Devonian) being gametophytes of the rhyniophytes has confirmed the existence of an archegoniate life cycle in these early colonists of the land. Expanding knowledge of the flowering plants of the Cretaceous, particularly of the small-flowered "paleoherbs", has revolutionized thinking about the nature of the earliest angiosperms. Most inter-

estingly, the general affinity (so far as known) of the earliest flowering plants points to self-incompatibility being one of their features, in line with arguments previously advanced on theoretical grounds.

It is becoming increasingly accepted that a basic knowledge of the diversity of plants, of their morphology and of their reproduction is an essential prerequisite for productive research into plant growth and morphogenesis, including the novel use of homoeotic mutants in the analysis of the genetic control of ordered development. The wealth of new techniques and instrumentation now available promises an exciting future for the young investigator of plant life. The aim of *Green Plants* continues to be to foster this endeavor. The order of earlier editions of this work has been largely followed, except that the Psilotales, in keeping with current views, are now associated with the ferns, and the subclasses of the flowering plants are referred to as the Liliopsida and Magnoliopsida.

The following kindly agreed to the reproduction of figures: The Council of the Linnean Society of London (Figs. 5.7, 8.57, 9.14, 9.15); the Trustees of the British Museum (Natural History) (Figs. 2.15, 3.20, 3.23, 3.24, 4.12, 4.13, 9.5); and the University of Michigan Press (Figs. 3.25, 3.26, 3.27). In addition to those mentioned in captions we are grateful to Jeffrey Duckett for providing Figs. 5.16 and 5.29, and to Dianne Edwards for Fig. 6.1c.

P. R. Bell  
London

A. R. Hemsley  
Cardiff

October 1999

# General features of the plant kingdom

## Characteristics of the living state

The living state is characterized by instability and change. The numerous chemical reactions, called collectively metabolism, within a living cell both consume (in the form of foodstuffs) and release energy. Metabolism is indicative of life. Even the apparently inert cells of seeds show some metabolism, but a mere fraction of that which occurs during germination and subsequent growth. Metabolism depends upon the interaction of molecules in an ordered sequence. If this order is destroyed (for example by poisons or heat) metabolism ceases and the cell dies. In some instances it is possible to arrest metabolism without death. With yeast and some tissue cultures, for example, this can be achieved by very rapid freezing at temperatures of  $-160^{\circ}\text{C}$  ( $-265^{\circ}\text{F}$ ) or lower. The cells can then be preserved in liquid nitrogen ( $-195^{\circ}\text{C}$ ;  $-319^{\circ}\text{F}$ ), in an apparently genuine state of "suspended animation", indefinitely. With yeast up to 95 percent of cells of rapidly frozen cultures resume metabolism and growth following careful thawing.

The sources of energy a cell requires to maintain its dynamic state are predominantly compounds of carbon. In addition a cell requires water, since much of the metabolism takes place in the aqueous phase in the cell. Also essential are those materials necessary for the maintenance of its structure which it is unable to make for itself. Prominent amongst these are the nitrogen of the proteins, the commoner minerals (including

phosphorus), and certain other metals and elements which, although needed only in traces, are essential components of a number of enzymes and associated molecules. Occasionally, in isolated cultures of cells, complex organic molecules called vitamins or growth factors must also be supplied from outside.

## Autotrophic and heterotrophic nutrition

It is useful to divide organisms into two classes according to the manner in which their needs for organic carbon are met. Those able to utilize simple molecules with single carbon atoms are termed *autotrophs*; those requiring more complex carbon compounds rich in energy (such as sugars) are termed *heterotrophs*. Some organisms are able to switch between these alternative forms of nutrition, depending upon the environment in which they find themselves. These are called *mixotrophs*.

The assimilation of simple carbon compounds by autotrophs, and their transformation into more complex molecules, require an external source of energy. This may be chemical or physical, depending upon the organism. Very many autotrophs (including the whole of the plant kingdom) utilize the energy of light, and are consequently known as photoautotrophs (or simply as *phototrophs*) and the process of assimilation as *photosynthesis*. Only the phototrophs have acquired extensive morphological diversity. Autotrophs utilizing energy from chemical sources (*chemotrophs*)

for the assimilation of carbon are found solely amongst the bacteria.

Phototrophic life is made possible by two unique biological molecules, chlorophyll and bacteriochlorophyll. The chemical differences between them are not profound, but their absorption spectra are distinct, as is their distribution amongst the phototrophs. Bacteriochlorophyll is found only in bacteria and functions mostly anaerobically. Photosynthetic systems based upon bacteriochlorophyll are unable to use water as an electron donor, and consequently there is no evolution of oxygen (*anoxygenic photosynthesis*). Those organisms which contain chlorophyll and which photosynthesize aerobically with the evolution of oxygen constitute the plant kingdom. So defined the plant kingdom is distinct from all other organisms (including the fungi).

Chlorophyll is a complex pigment. It is green in colour, and absorbs light in the blue and to a smaller extent in the red region of the spectrum. The molecule is in part similar to the active group of the blood pigment hemoglobin, but contains at its center magnesium in place of iron. A number of different forms are known (*a, b, c, d* and perhaps *e*), each with its characteristic absorption spectrum. Chlorophyll *a*, which is present in all plants, has the remarkable property of temporarily losing electrons when illuminated. Chlorophyll *b*, which is found in all land plants, assists in the light-harvesting process, but the functions of chlorophylls *c, d* and *e* (p. 77), present in some algae, are not so well known. Chlorophyll is always accompanied by accessory pigments (either carotenoids or phycobilins (biliproteins), or in a few organisms both). The light energy absorbed by these additional pigments can be transferred to the chlorophyll.

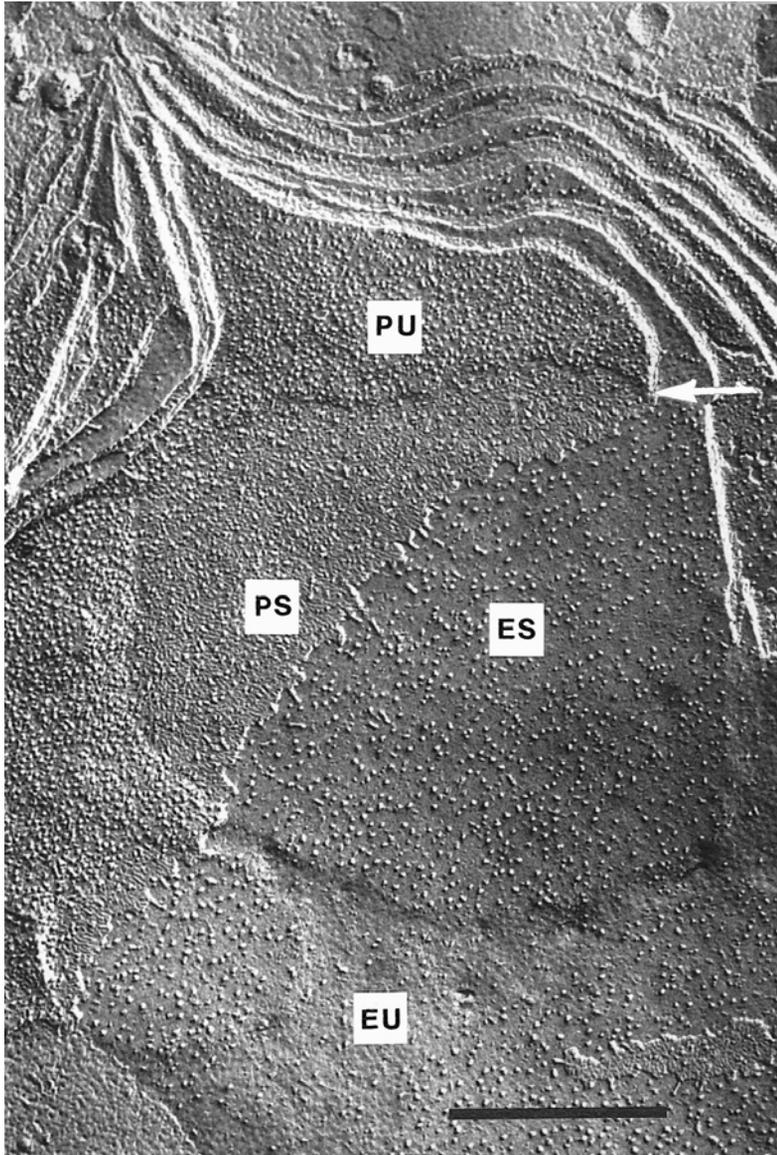
As a result of the remarkable photochemical properties of chlorophyll *a* the energy of the incident light is transformed into chemical energy. This leads to the generation in the cell of ATP, and reducing power in the form of  $\text{NADPH} + \text{H}^+$  (the light reactions). These two products then bring about the reductive assimilation of atmospheric carbon dioxide in the illuminated cells, the assimilation being initiated by the enzyme ribulose biphosphate carboxylase (RUBISCO), leading to the production of carbohydrates (the dark reactions). The ability to utilize atmospheric carbon

dioxide in this photosynthetic manner releases the organisms concerned from the necessity of an external source of carbohydrate, and their nutritional demands are consequently relatively simple.

*Oxygenic photosynthesis*, the defining characteristic of the plant kingdom, involves two photosystems. The first (photosystem I) leads to the formation of  $\text{NADPH} + \text{H}^+$ , and the second (photosystem II) provides a supply of electrons to the chlorophyll of photosystem I. Photosystem II involves the photolysis of water with the production of oxygen. The evolution of oxygenic photosynthesis probably occurred in marine photosynthetic bacteria inhabiting waters close to oceanic thermal vents. At these sites there is a rich supply of minerals, including manganese, a component of the enzyme in photosystem II responsible for the splitting of the water molecule and the release of oxygen. Photosystem II may have appeared only once, or (in geological time) more or less coincidentally at several sites. In any event it was an innovation of immense significance since it made possible the evolution of all subsequent oxygen-requiring organisms, both plant and animal. It is legitimate, therefore, to regard the simplest organisms showing this form of photosynthesis, based upon chlorophyll *a* (as distinct from bacteriochlorophyll), as the earliest plants, opening up a whole new vista of evolution. These early plants, whose living descendants are to be found in the Cyanophyta (p. 24), and Prochlorophyta (p. 38), naturally retained some of the features of their bacterial origins. Nevertheless, freed from the constraints of bacterial photosynthesis, the earliest plants had an evolutionary potential denied to their retarded cousins.

### Structure of the phototrophic cell

Chlorophyll does not occur freely in cells, but is always associated with lipoprotein membranes. These membranes surround flattened sacs called *thylakoids*. When the membranes are seen in surface view in the electron microscope (made possible by the special technique of freeze-fractionation)



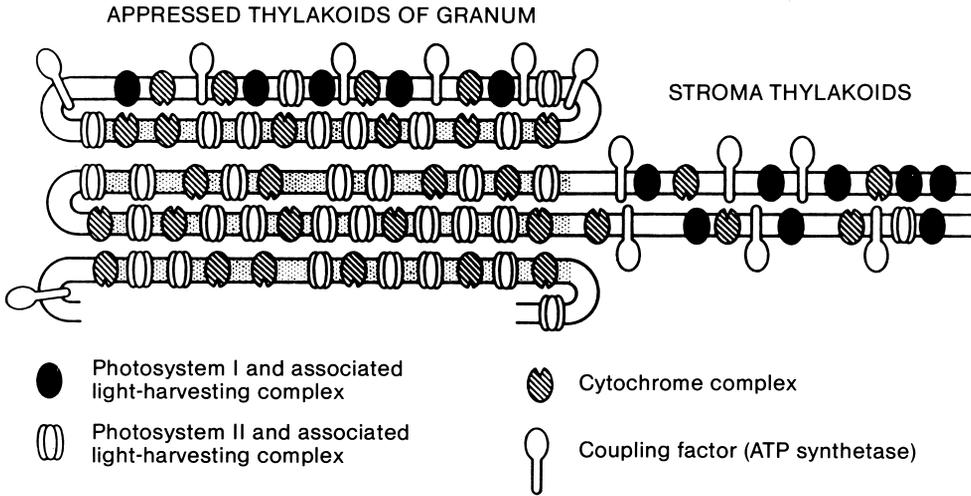
**Figure 1.1** Shadowed replica of the thylakoid membranes of the chloroplast of *Euglena* exposed by freeze-fracture. The thylakoids are either single ("unstacked") or paired ("stacked"). Because in the conditions of freeze-fracture membranes are pulled apart, two complementary faces (E and P) are represented in the replica. This reveals that the particles are asymmetrically placed in the membrane (cf. Fig. 1.2). There are also differences in the frequencies of particles in stacked (S) and unstacked (U) membranes. The arrow indicates where the membranes of two adjacent thylakoids come together to form a stack. Scale bar 0.5  $\mu\text{m}$ . (From Miller and Staehelin, 1973. Reproduced from *Protoplasma* 77, by permission of Springer-Verlag, Vienna.)

forms the basis of plant life. In turn the animal kingdom is entirely dependent upon the activity of this membrane, not only for its sustenance, but also for the oxygen of its respiration.

Two distinct kinds of cellular organization are found amongst the phototrophs as a whole. In the first, termed *prokaryotic*, the cell possesses no distinct nucleus, although a region irregular in outline

ture), it is clear that they bear closely packed particles (Fig. 1.1). The larger of these, about 18 nm ( $1 \text{ nm} = 10^{-3} \mu\text{m}$ ) in diameter, are probably the site of the chlorophyll and carotenoids (which, like chlorophyll, are lipid soluble). The anchoring of the chlorophyll and carotenoids in a lipoprotein membrane ensures that they are held in a particular order (Fig. 1.2). Electrons can then flow along well-defined paths to the reaction center at which the radiant energy is converted into chemical energy. The thylakoid membrane is thus the site of the light reactions of photosynthesis, and

and of differing density occurs at the center of the cell. This is referred to as a nucleoid, and the genetic material lies therein. In the electron microscope this region appears fibrillar rather than granular, and the fibrils indicate the site of the deoxyribonucleic acid (DNA). The protoplast of such cells is bounded by a membrane. In phototrophic cells this membrane invaginates into the cytoplasm and forms the thylakoids. Their full development depends upon light. If the cells are grown in the dark the thylakoids disappear or become very reduced. This primordial kind of



**Figure 1.2** The molecular architecture of the thylakoid membrane of a higher plant. The photosystem I complexes are confined to the outer membranes of the grana and to the stroma thylakoids. The stippled regions indicate the appressed membranes of the granum. (From Anderson, Chow and Goodchild. 1988. *Australian Journal of Plant Physiology* 15, modified.)

phototrophic cell is found in both the photosynthetic bacteria and the simplest plants. The fossil record supports the view that the original phototrophs were of this prokaryotic kind. Geochemical evidence of photosynthesis, and remains very suggestive of bacteria and simple cyanophytes, some resembling the living *Oscillatoria* (p. 29), come from early Archaean rocks of South Africa and Australia believed to be  $3.3\text{--}3.5 \times 10^9$  years old (Table 1.1).

In the cells of all other phototrophic plants the nucleus, the photosynthetic apparatus, and the membranes incorporating the electron transport chain of respiration are separated from the remainder of the cytoplasm by distinct envelopes. Such cells, termed *eukaryotic*, have evidently been capable of giving rise to much more complicated organisms than the prokaryotic ones. The photosynthetic apparatus, which consists of numerous lamellae running parallel to one another, is contained in one or more *plastids*. The envelope of the plastid consists of two (in some algae three or four) unit membranes, the inner of which invaginates into the central space (*stroma*) and generates the thylakoids. The thylakoids in the fully differ-

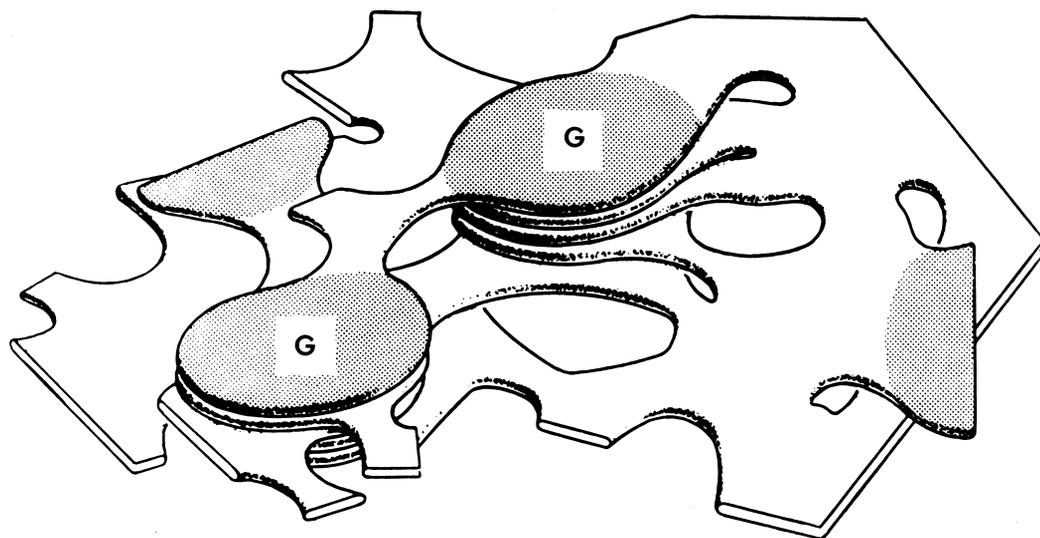
entiated plastid (*chloroplast*) are usually stacked. In the chloroplasts of land plants the thylakoids are also fenestrated. Consequently numerous small stacks, called *grana*, are formed in place of a single stack, the grana being held together by stroma lamellae (Fig. 1.3). The grana appear in the light microscope as green dots, each about  $0.5\mu\text{m}$  in diameter. Although most photosynthesis takes place in the grana, the thylakoids in the stroma also contribute.

Plastids contain both DNA and ribonucleic acid (RNA), and both transcription and translation may occur within them. Plastids thus have some resemblance to phototrophic prokaryotes, although most plastid proteins are encoded solely in the nuclear DNA. The enzyme RUBISCO, essential for photosynthesis and probably the commonest protein in the world, consists of a large and a small subunit. In the green algae (Chlorophyta, p. 39) and in all land plants, the large subunit is encoded in the plastid DNA and the smaller in that of the nucleus. Nevertheless, in some eukaryotic algae, namely the Rhodophyta (p. 30), the Cryptophyta (p. 96) and the whole of the heterokont algae (Table 2.1), both large and small subunits are coded for in the plastid genome. In the prokaryotic algae both subunits are coded for in the DNA of the nucleoid. The possibility exists that coding for one or both units of RUBISCO may also be present in the DNA of a plasmid (p. 8), but this has not been demonstrated.

In the commonest form of carbon assimilation, atmospheric carbon dioxide, having been

**Table 1.1** | The geological time scale. Age estimates of Proterozoic and Archaeozoic  $\pm$  up to 100 million years.

Eon	Era	Period	Age (in $10^6$ years)	First authentic appearance		
Phanerozoic	Quaternary	Holocene and Pleistocene	0–1.6			
		Tertiary (Cenozoic)	Pliocene	1.6–5.2		
	Miocene		5.2–23.3			
	Oligocene		23.3–35.4			
	Eocene		35.4–56.5	Grasses		
	Paleocene		56.5–65			
	Mesozoic	Cretaceous	Senonian	65–88.5		
			Gallic	88.5–131.8	Carpels, flowers, angiosperms	
			Neocomian	131.8–145.6		
			Jurassic	Malm	145.6–157.1	Tectate pollen
			Dogger	157.1–178		
			Lias	178–208		
		Triassic		208–245	Cycadopsida, anthophytes,	
	Paleozoic	Permian	Zechstein	245–256.1	Ginkgoopsida,	
			Rotliegendes	256.1–290	Glossopterids	
		Carboniferous	Pennsylvanian	290–322.8	Pinopsida, Bryopsida,	
			Mississippian	322.8–362.5	Polypodiopsida	
		Devonian	Upper		362.5–377.4	Seeds, fronds, pteridosperms, progymnosperms, early ferns, Cladoxylopsida, Equisetopsida, Trimerophytopsida, Marchantiopsida, heterospory,
				Middle	377.4–386	Zosterophyllopsida,
				Lower	386–408.5	Lycopodiopsida
Silurian		Upper		408.5–424	Rhyniopsida, vascular plants, rhyniophytoids	
			Lower	424–439		
			Ordovician	439–510	Triradiate spores	
	Cambrian	510–570	Phaeophyta			
Proterozoic	Sinian	Vendian	570–610			
		Sturtian	610–800			
	Riphean	Animikean	800–1650			
		Huronian	1650–2200	Various algal groups		
Archaeozoic	Randian	Swazian	2200–2450			
		Isuan	2450–2800			
			2800–3500			
			3500–3800	Stromatolites and cyanophytes (Cyanobacteria)		
	Hadean		3800–4560			

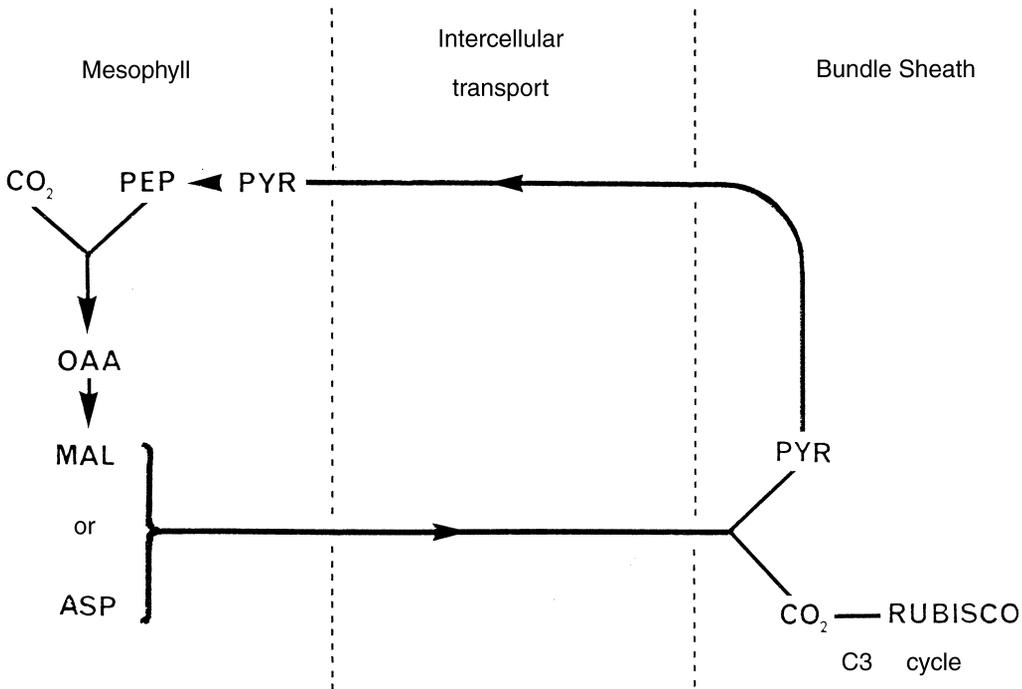


**Figure 1.3** Diagram showing the arrangement of the thylakoids in the chloroplast of a higher plant. The stacked regions (grana, G) are visible as green dots in the light microscope. (From an original drawing by Wehrmeyer, 1964. *Planta* 63, modified.)

taken in the presence of RUBISCO into a pentose sugar (ribulose biphosphate), yields two molecules of triose phosphate. These are reduced by the  $\text{NADPH} + \text{H}^+$  and ATP, yielding two molecules of glycerin aldehyde. These then enter a complex cycle of reactions (the C<sub>3</sub>, or Calvin cycle) leading to fructose and other sugars. A mixture of fairly simple carbohydrates probably leaves the chloroplast, further transformations taking place enzymically in the ground cytoplasm. The disaccharide sucrose, for example, the commonest form in which sugar is transported in the plant, is incapable of traversing the chloroplast envelope and is necessarily formed outside. If the rate of photosynthesis exceeds the rate of outflow of fixed carbon, condensation occurs and starch is deposited in the chloroplast. This may become very conspicuous, the organelle then being termed an **amyloplast**. In some land plants (known as C<sub>4</sub> plants) atmospheric carbon dioxide is taken initially in the chloroplasts of the mesophyll cells into phosphoenolpyruvate (PEP), the enzyme involved in this case being PEP-carboxylase. This leads to the formation of oxaloacetic acid, which is then transformed enzymically into malate or aspartate. These products migrate to special

chloroplasts in the bundle sheath cells, which are distinguished from those of the mesophyll by lacking grana, but they do contain RUBISCO. Here the malate and aspartate are reconverted into oxaloacetic acid. The carbon dioxide is thereby freed and, as in C<sub>3</sub> plants, is assimilated into ribulose biphosphate and enters directly into the Calvin cycle (Fig. 1.4). PEP-carboxylase has a higher affinity for carbon dioxide than RUBISCO, and can withstand higher temperatures. Further, the combined C<sub>4</sub>/C<sub>3</sub> systems have less need of water in relation to the quantity of carbon assimilated. Consequently vegetation of hot and dry (including “physiologically dry”) habitats, such as deserts and salt marshes, often contains a high proportion of C<sub>4</sub> plants. A few plants are ambivalent. *Eleocharis vivipara* (a marsh plant), for example, is a C<sub>4</sub> plant under terrestrial conditions but C<sub>3</sub> when submerged.

The organelle in eukaryotic cells containing the respiratory membranes is termed a **mitochondrion**. Although there are structural and organizational similarities between mitochondria and plastids, in most photosynthesizing cells the mitochondria have far less internal differentiation. So far as carbon is concerned, the functions of these two organelles are opposed: that of the chloroplast is **reductive carboxylation**, that of the mitochondrion **oxidative decarboxylation**. In certain conditions (notably with a low partial pressure of carbon dioxide) RUBISCO can act as an oxidase,



**Figure 1.4** The essential features of C<sub>4</sub> photosynthesis. PEP, phosphoenolpyruvate; OAA, oxaloacetic acid; MAL, malate; ASP, aspartate (aspartic acid is the amino acid corresponding to malic acid); PYR, pyruvate. There are biochemical variations between species, but the general pattern is retained.

resulting in a loss of fixed carbon (photorespiration). This may have had a significant ecological effect at certain periods of the evolution of land plants in geological time.

## Origin of the eukaryotic condition

Although it seems beyond doubt that the prokaryotic condition preceded the eukaryotic (the first eukaryotic algae probably appeared about  $2.1 \times 10^9$  years ago), the manner in which the transition occurred is by no means clear. A commonly accepted, and little criticized, view (originally put forward in 1905) is that mitochondria and plastids are derived from prokaryotes which entered as endosymbionts into a primordial cell, itself prokaryotic and presumably heterotrophic. The presence in the cytoplasmic organelles of a nucleoid, their

possession of transcription and translation systems closely resembling those found in bacteria, and the similarity in size between the ribosomes of organelles and those of bacteria (the ribosomes of eukaryotic ground cytoplasm tend to be larger) provide strong evidence in support of this theory. Further, organisms which appear to have arisen by endosymbiosis are well known. In *Glaucozystis* (Fig. 2.9) and *Cyanophora*, unicellular organisms found occasionally in shallow fresh water, for example, the photosynthetic component of the cell is made up of one or more units resembling blue-green algal cells. These have accordingly been termed "cyanelles" (p. 27). Other possible examples of endosymbiosis are found in the Cryptophyta (p. 97). Here the chloroplast contains a "nucleomorph", which, since it is surrounded by a double membrane, may represent the remnant of, in this case, a eukaryotic endosymbiont.

The theory (in its modern form) envisages that, in the primordial eukaryotes, the prokaryotic endosymbionts became integrated into the physiology of the composite cell, contributing some of their genetic information to that in the nucleus, and in so doing losing their individual identity and sacrificing much of their autonomy.

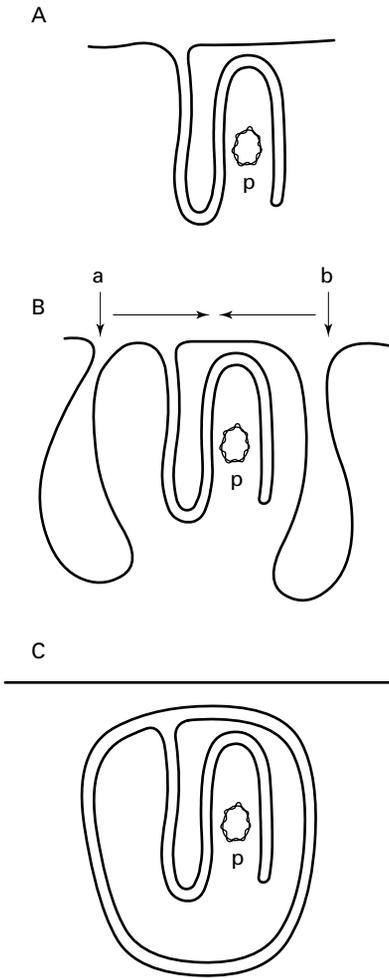
Attractive though this theory is, it has obvious difficulties. Organisms, such as *Glaucocystis*, which appear to be undoubtedly endosymbiotic in origin, are evidently exploiting successfully an ecological niche, and have probably done so since early in the diversification of cellular life. They can therefore be legitimately regarded as models of stability, and, far from being an indication of how the eukaryotic condition arose, are splendid examples of "dead ends" without evolutionary potential. Evidence of selective pressure favoring the complete assimilation of the invasive organisms, although conceivable, is so far lacking. Also required is a credible mechanism for the transfer of essential components of the invaders' genomes, through an alien cytoplasm to the nuclei or nucleoids of the hosts and the incorporation of this information in a (to them) foreign DNA. Further, is the nucleus itself of endosymbiotic origin? There are so many unanswered questions that it would be unjustified to fail to consider alternative possibilities.

The principal alternative view rests upon the occurrence in prokaryotes of plasmids, circles of DNA lying in the cytoplasm apart from the nucleoid. The genetic information in the plasmid is commonly represented also in the DNA of the nucleoid. The nucleotide sequences in a plasmid frequently code for a specific function. Photosynthetic membranes, and also respiratory membranes (mesosomes), are features of many prokaryotes. These membranes arise as invaginations of the plasmalemma. The cyanophytes and prochlorophytes (or their antecedents), the only prokaryotes displaying oxygenic photosynthesis, are obvious candidates for the origin of chloroplasts, a view strengthened by the many molecular similarities between them. Plasmids are indeed widespread in cyanophyte cells (but not yet reported in those of the prochlorophytes). Although it has not yet been possible to ascribe any precise function to the plasmids of the cyanophytes, it is not unreasonable to envisage a plasmid being associated with a photosynthetic membranous invagination in a primitive cyanophyte, and containing genes modulating its development and function. This possibility is strengthened by the evidence for the presence of regulatory genes on a plasmid regularly asso-

ciated with the photosynthetic membrane system of the bacterium *Rhodospirillum rubrum*. If the peripheral complex of a cyanophyte, similarly endowed, were taken into the body of the cell, a rudimentary chloroplast would result. A similar translation affecting a peripheral respiratory membrane associated with an appropriate plasmid would lead to a rudimentary mitochondrion. Each would contain genetic information shared wholly or partly with that in the nucleoid or nucleus, a feature of mitochondria and plasmids. No substantial transfer of essential genetic information would be required following the internalization of these membranous complexes into the body of the cell. It would follow that the correspondence between the genome of a plastid and that of the nucleus of its cell was analogous to that between a plasmid and the nucleoid in a prokaryote. This relationship would represent the persistence of an ancient feature, not the emergence of a new one.

Experiments with monolayers of polar lipid on the surface of water show how movement of membranous complexes from the periphery of a naked cell to the interior might have come about. When a lipid film is compressed, the film folds into the aqueous phase, so reducing its area. This, however, is an unstable situation. The folds in the aqueous phase become instantaneously detached, relieving the surface film of compression and restoring its continuity. The folds, now submerged, coalesce to form spheres and cylinders, themselves filled with water. Since both the inner and outer faces are now clearly hydrophilic, polar groups must be exposed on both surfaces. The lipid faces of the folds must therefore have come together, forming a bimolecular leaflet. One of the essential elements in the collapsing process is seen as the marked difference in viscosity between air and water, allowing air to escape rapidly from the folds, leading to the apposition of the two lipid layers.

It is not unreasonable to envisage a natural membrane, forming the interface between two phases differing in viscosity as sharply as protoplasm and water, behaving, under compression, in a manner analogous to that of a lipid film. If the folds formed adjacent to, or around, an already existing invagination of the bounding mem-



**Figure 1.5** Diagrammatic representation of how a peripheral membrane system associated with a plasmid (p) could have become encapsulated and internalized as a consequence of compression of the bounding membrane. (A) Part of the bounding membrane of a prokaryote furnished with a photosynthetic invagination associated with a regulatory plasmid. (B) The bounding membrane is compressed and forms folds. Since the protoplasm adheres strongly to the membrane and is more viscous than the surrounding water, the membrane is dragged inward. If the volume of the cell is shrinking as a consequence of exosmosis, this effect would be enhanced. (C) Excess water is expelled from the folds so that the membranes lie closely parallel to each other, separated only by hydrated surface molecules (possibly glycoproteins). The inner extremities of the folds come together and fuse. Simultaneously the bounding membrane suffers instantaneous collapse. The margins of the folds (a, b) come together, so restoring continuity to the surface, and at the same time releasing a double-membraned inclusion to the interior. The area of the surface is thereby reduced, freed from compression, and structural stability is regained. (Based (by analogy) on experiments by R. J. Goldacre on the collapse of surface films of polar lipid under compression, described in Danielli, Pankhurst and Riddiford (eds.) 1958. *Surface Phenomena in Chemistry and Biology*, pp. 278–98. Pergamon, London.)

brane, the result would be that the invagination was carried, bounded by a double membrane, into the body of the cell (Fig. 1.5). In natural conditions, compression of the bounding membrane could be caused by, for example, exosmosis (if the prokaryote were splashed into a hypertonic pool), or even by mechanical pressure on naked cells arising from turbulence as streams cascaded over rocks. These conditions probably occurred frequently at the beginnings of cellular life.

The nucleus may have arisen in a similar manner, if the DNA of the genome were associated with an invagination of the plasmalemma, as in some existing bacteria. Indeed, internalization of the genome may have happened independently of the formation of plastids and mitochondria. Species of *Gemmata* and *Pirellula*, plancomycete

bacteria, have been found in which the nucleoid is surrounded by an envelope. In *Gemmata* this consists of two membranes, the outer of which is connected with the plasmalemma, but in *Pirellula* the envelope is single.

It seems likely that a naked membranous sac, furnished with peripheral invaginations which penetrate contents that are denser than the surrounding medium, presents an unstable biophysical situation, particularly if the bounding membrane is compressed. Stabilization, relieving the membrane of compression, is achieved spontaneously by the internalization of the peripheral complexes. The current development of techniques for the production of compound vesicular bodies, consisting of vesicles bounded by lipoidal membranes lying free within the parent vesicle, raises the possibility of being able to mimic the internalization of peripheral membranous complexes in an experimental system using artificial cells. If it proves possible to explain the origin of the eukaryotic condition in terms of membrane biophysics, based upon a repeatable experimental system, the endosymbiotic hypothesis, which

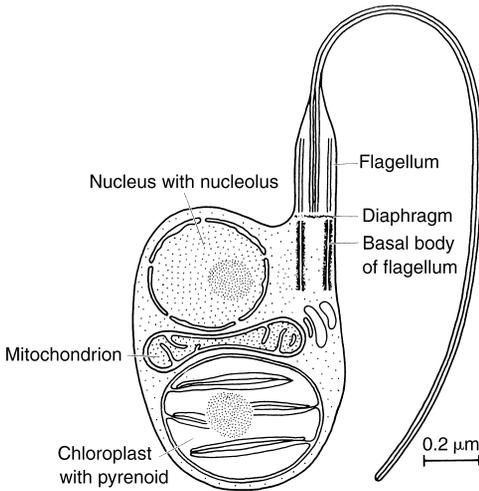
rests upon unverifiable evolutionary speculations, can at last be returned to history. The encapsulation and internalization of membrane systems originally attached to the plasmalemma may indeed have occurred many times with primitive cells, unprotected by a wall or mucilage. The emergence in evolution of firm or gelatinous cell walls, protecting a range of the earliest cells from the effects of compression, allowed the persistence of simple prokaryotes with peripheral photosynthetic and respiratory membrane systems into the later eukaryotic times. Although microtubules and actin microfilaments, structural proteins of the cytoplasm, are not found in bacteria, proteinaceous tubular elements ("rhapidosomes"), about 24 nm in diameter, occur in the cytoplasm of some cyanophytes (p. 29). Although not identical with the microtubules of eukaryotes, they may have given the cells of the photosynthetic prokaryotes an additional stability that ensured their survival.

Following the translation of the photosynthetic and respiratory compartments into the body of the cell, these compartments have retained many of their prokaryotic features in subsequent evolution. The invasion of the bounding membrane appears, however, to have led to innovations in the remaining cytoplasm. The endoplasmic reticulum (which retains connections with the outer membrane of the nuclear envelope) and the Golgi bodies are both membranous structures, characteristic of even the smallest eukaryotic cells (e.g., *Osteococcus*, p. 40). The ribosomes, ubiquitous in the cytoplasm, increased in size, reaching diameters some 50 percent greater than those of the ribosomes of mitochondria and plastids, and of prokaryotic cells. Concomitantly, the DNA of the genome became organized into chromosomes, probably a consequence of the nuclear envelope allowing a much closer control of the metabolism and assembly of the proteins (particularly histones) associated with the folding of the DNA. This led to the complex known as chromatin, and its parceling into a definite number of regularly reproducible bodies, the chromosomes.

## Evolutionary consequences of photosynthesis

It seems beyond doubt from the fossil record of life, and from the biological and geological inferences that can be drawn from it, that life began in water. The earliest forms of life remain conjectural, but were probably chemotrophic, accompanied fairly rapidly (in evolutionary time) by heterotrophs feeding upon them. Nevertheless, phototrophs probably also appeared relatively early. Those which contained or acquired chlorophyll (as opposed to bacteriochlorophyll), and which further developed oxygenic photosynthesis, gave rise to the plant kingdom. The descendants of these early aquatic forms, which still in the main exploit the watery environment, are termed algae (Chapters 2, 3 and 4). They have many biochemical, physiological, ecological and structural features in common. For these reasons they include the prokaryotic forms placed in the Cyanophyta and Prochlorophyta, which, although retaining some bacterial features, are clearly superior to these lowly forms in their possession of oxygenic photosynthesis and their general algal characteristics. Although some unicellular algae have attained morphological complexity (e.g., the dinoflagellates; p. 94), others represent the simplest plants still in existence. Apart from the unicellular prokaryotes, such as *Prochlorococcus* (p. 38), some unicellular eukaryotes are also minute. *Osteococcus tauri* (p. 40), for example, is probably the smallest eukaryotic organism known. The cells do not exceed 1  $\mu\text{m}$  in width, lack a cell wall, and contain only a single plastid and a single mitochondrion. *Osteococcus* has so far been found only in the plankton of Mediterranean lagoons, but *Micromonas* (Fig. 1.6), which has a similarly simple cell but is provided with a flagellum, is abundant in the oceans. Relatively early, however, even in the prokaryotes (p. 29), multicellularity appeared in algal evolution, yielding a diversified algal flora whose descendants are still with us today.

At some stage, possibly in the Silurian period (Table 1.1) or even earlier, vegetation began to colonize the land. These early colonists, and consequently the whole of our existing land flora,



**Figure 1.6** *Micromonas pusilla*. Form and internal organization. Only the central microtubules run into the extension of the flagellum. *Micromonas* belongs to a small group of green algae of doubtful affinity. (From electron micrographs by Manton. 1959. *Journal of the Marine Biological Association of the United Kingdom* 38.)

almost certainly emerged from that group of aquatic plants today represented by the green algae (Chlorophyta). The Chlorophyta and the land plants (a term which means plants adapted to life on land and not merely plants growing on land) have the same photosynthetic pigments, basically the same photosynthetic apparatus, and share many metabolic and physiological similarities (pp. 131, 132).

Any consideration of the evolution of a photosynthesizing land flora must therefore take into account the physiological features of the green algae, and how these may have been modified in the transition to terrestrial life. Recent research into algal environments is yielding much information relevant to this problem. It is commonly found, for example, that from 5 to 35 percent of the light striking the surface of a lake or sea is reflected, the actual amount lost depending upon the angle of incidence. The light penetrating the water is then gradually absorbed as it advances, so that up to 53 percent of the radiation passing the surface may be dissipated as heat in the first meter (39 in.). Consequently, in warm and temperate regions, the rate of photosynthesis of submerged plants is normally controlled by the amount of

light reaching them, and not by the amount of carbon dioxide in the water. We can see at once that the first colonists of land, emerging on to bare mineral surfaces, would almost certainly have had to contend with irradiances strikingly higher than those experienced by their aquatic ancestors. This would have provided opportunities for greatly increased photosynthesis.

Another discovery of recent research, also very relevant to the problem of the colonization of the land, is the surprising extent to which algae release materials derived from photosynthesis, both aliphatic molecules and phenolics, into the surrounding water. In Windermere in the English Lake District, for example, up to 35 percent of the total carbon fixed may be lost in this way. Even in land plants, losses of fixed carbon (as soluble or dispersible carbohydrates and phenolics) have been detected from roots. Some estimates of losses by this process of *rhizodeposition* over the growing season have put it as high as 30 percent. Other losses from land plants may occur from leaves as gaseous hydrocarbons, notably isoprene (2-methyl-1,3-butadiene). In oak (*Quercus*) and aspen (*Populus*), isoprene typically amounts to 2 percent of the fixed carbon at 30 °C (86 °F). This loss can increase tenfold with a 10 °C (18 °F) rise in temperature. Isoprene is also produced by mosses (p. 118) and ferns, but not apparently by liverworts or *Anthoceros*. Isoprene production may have been an adaptation acquired by land plants as they came on to land, possibly providing some thermal protection in conditions of strong insolation.

Despite losses of fixed carbon by land plants, it seems inevitable that as vegetation advanced from estuarine flats, or from littoral belts subject to periodic inundation, on to relatively dry substrata and an environment of freely diffusible carbon dioxide and generally higher irradiances, carbon fixation would have been promoted. The generally high levels of atmospheric carbon dioxide at the time of the landward migration would have depressed loss of carbon by photorespiration and in general stimulated fixation. Proportionately more of the fixed carbon would have been conserved within the plant body than in the aqueous environment. The plants invading the land appear to have met these environmental challenges not by any significant change in the

structure, composition or efficiency of the photosynthetic membrane, but by increased removal of the fixed carbon from the general metabolism. In this way the accumulation of very large, and possibly toxic, quantities of carbohydrate in the cells was effectively prevented. Cell walls, consisting of cellulose and hemicellulose, became thicker. Condensation products such as resin, phlobaphene and lignin became conspicuous, and have remained so in the more primitive vascular plants. The early land plants may also have produced substantial quantities of mucilage (largely highly hydrated polysaccharides). This feature is still encountered in a number of thallose liverworts, such as *Anthoceros*, whose general morphology and anatomy may resemble that of at least some of the transmigrants (p. 117). Significantly, the mucilage is often extruded through pores, each bounded by two cells. The resemblance of these pores to simple stomata can be so striking that the identification of similar configurations in early fossil material with stomata must be made with caution.

The progressive layering of cellulose microfibrils on to the growing cell walls of land plants probably tended to make the angles rounder, thus setting up the tensions which, during cell expansion, led to the appearance of air spaces at the interstices. Spaces of this kind, although found in some of the larger brown algae, such as the kelps (p. 89), do not appear in the "green" line of evolution (as represented by living species) until the gametophytes (e.g., *Marchantia*, p. 105) and sporophytes (e.g., *Funaria*, p. 126) of bryophytes. These spaces are an important feature of land plants, ensuring that the plant body is ventilated with saturated air. Increased carbon would also facilitate the synthesis of the fatty acids and phenolics which go to form cutin. In the form of the cuticle, covering all cell-air interfaces, and with the assistance of the regulatory stomata, cutin makes possible the regulation of the loss of water from the plant body. This enables the plant body to maintain a state of hydration independent (within limits) of the supply of soil water and the saturation deficit of the atmosphere, a feature known as *homoiohydric*. A possible precursor of the cuticle is seen in at least one green alga (*Cladophorella*), which grows on damp mud and is covered on its

upper surface by a material which, judging by its resistance to acids and oxidizing agents (although its composition has not yet been investigated by modern spectroscopic methods), closely resembles cutin. Compounds resistant to both chemical degradation and natural decay, probably aliphatic in origin, have been located in the cell walls of other green algae. Significantly, these algae belong to the class Charophyceae (p. 61), which contains the algae believed to be closest to those which gave rise to the land plants (p. 131). A cuticle has been a feature of land plant evolution since at least the Ordovician (Table 1.1).

Comparison of the green algae and the lower land plants thus reveals interrelated modifications of the anatomy and of the utilization of the fixed carbon which facilitated the establishment of homoiohydricity, and allowed the invasion of land surfaces subject to intermittent dryness. Homoiohydricity also made possible more stable growth rates with consequent ecological success. The gametophytes of the land plants, however, tended to remain small and with limited control over their degree of hydration (*poikilohydric*). Nevertheless, some mosses (p. 121) and the prothalli of some lower land plants (e.g., ferns; p. 203) are able to recover from quite severe desiccation.

Sporopollenin (a complex polymer formed by the condensation of aliphatic and phenolic molecules), of doubtful occurrence in green algae, takes on an essential rôle in land plants. Although varying in composition with phylogenetic history, its sealing properties remain a general characteristic. It features in the protective coats on the spores of land plants, and in some instances coats membranes within plants separating reproductive regions from the surrounding somatic tissue, as, for example, the peritapetal membrane in many angiosperm anthers (p. 287).

Lignin, of which the phenolics of algal cells may have been a precursor, is a product of cells undergoing programmed death. It is laid down within cell walls and fills the spaces initially occupied by water, thus both sealing and strengthening the wall. Tracheid-like cells may have evolved from the elongated cells normally formed at the center of axes. Selection, acting upon a genetically controlled program of cell death at this site, could have led to cells with thickened walls which had

both a structural and a conducting function. Initially, the rudimentary tracheids were probably formed in discontinuous patches, as they are found today in the gametophyte of *Psilotum* (p. 187), and at that stage the conducting function may not have been well developed.

Overall, natural selection ensured that those forms survived in which the various destinations of the fixed carbon were not disadvantageous to the growth and reproduction of the plant as a whole. The lignification of tissue, for example, permitted the continued evolution of xylem, providing both a skeleton supporting the plant in space and an effective system for the transport of water and solutes. Massive plant bodies, which seem to have appeared relatively early in the evolution of the land flora, also made possible the confinement of photosynthesis to specialized regions, such as leaves and fronds. The amount of assimilation per unit mass of the plant was thereby reduced. Simultaneously, the increase in the amount of living, but non-photosynthesizing, tissue naturally increased the call on metabolizable assimilates. Both factors ensured that the multicellular colonists of the land remained in balance with their environment without interference with the fundamental features of photosynthesis.

In the course of evolution many complex and bizarre forms of growth have appeared in land plants, but the material from which they are fashioned has remained predominantly carbon, extracted from the atmosphere. This diversity can be related to the tetravalent nature of carbon, and the strength of its covalent bonding, permitting the formation of molecules with stable carbon chains and rings, and opening the possibility of a great range of organic compounds. Had not the photosynthetic fixation of this versatile element arisen on the Earth's surface, plant life, and animal life (which is dependent upon it), would have been impossible. Indeed, it is difficult to conceive of any alternative form of life appearing in its absence. The chain-forming properties of the related element silicon, for example, are, in comparison, negligible.

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## The mobility of plants

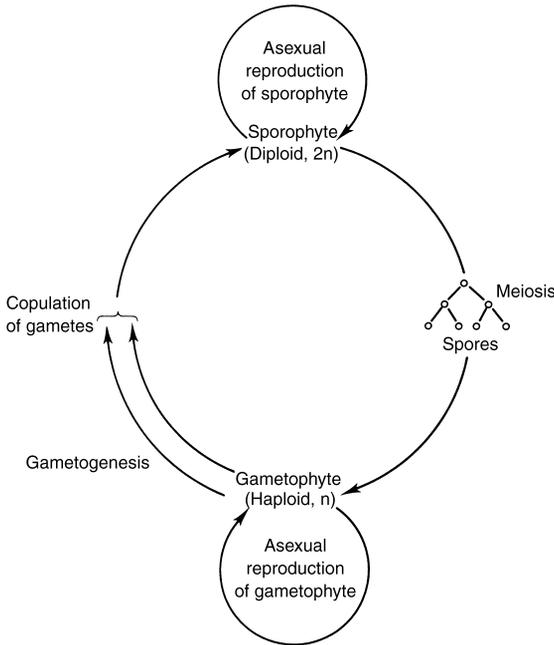
Although the earliest plants were probably unicellular and soon acquired motility of the kind seen today in *Chlamydomonas* (Chapter 3), this appears to have been rapidly lost in the evolution of higher forms (although often retained in their gametes). Multicellularity, the cells remaining cemented together by polysaccharides, became the dominant condition, cell separation being confined to sites of reproduction. Although this led, already by the Devonian, to the existence of large and firmly anchored land plants, these are naturally at a disadvantage, not shared by the higher animals, at times of natural catastrophe, such as volcanic eruption or fire. Plants, however, very frequently possess a remarkable mobility, or at least a ready transportability by agencies such as wind and water, in their reproductive bodies. Fern spores, for example, have been caught in aeroplane traps in quantity at 1500 m (5000ft) and even higher, and the hairy spikelets of the grasses *Paspalum urvillei* and *Andropogon bicornis* have been encountered at 1200 m (4000ft) above Panama. Lakes, seas and the coats and feet of animals also play their part in distributing plants. A splendid example of oceanic distribution is provided by the coconut palm (*Cocos nucifera*), which frequently fringes tropical beaches. The nuts, dropping into the sea, float for long distances and germinate where washed ashore. The pan-tropical distribution of the palm is readily accounted for in this way. In plants, therefore, the immobility of the individual is frequently compensated for by the mobility of the species, and devastated areas and new land surfaces become colonized with amazing rapidity and effectiveness.

Some plants (e.g., *Glechoma*) produce stolons which appear to explore the neighboring ground. Since the plantlets becoming established on richer areas come to dominate the stand, this behavior has been fancifully referred to as "foraging".

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## Life cycles

Although developmental cycles are known in the prokaryotic Cyanophyta (p. 28), a well-defined



**Figure 1.7** The life cycle of autotrophic plants generalized. The large circle represents sexual reproduction. Only relatively few species display all the reproductive potentialities shown.

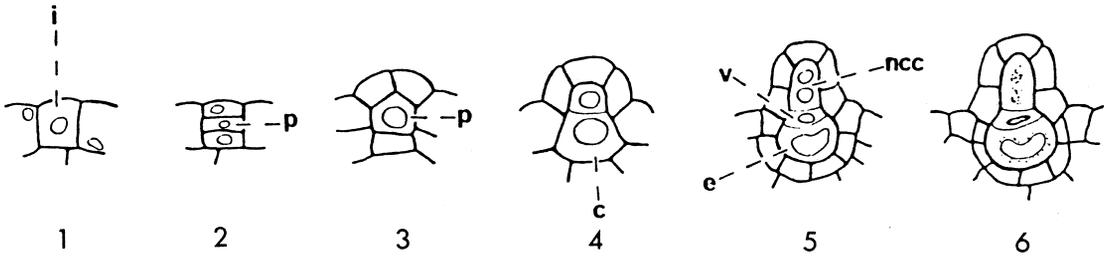
cycle involving meiotic segregation of the genetic material and its subsequent recombination by sexual fusion is found only in eukaryotic phototrophs. That part of the cycle in which the nucleus contains a single set of chromosomes is termed *haploid*, and the complementary part of the cycle in which two sets are present *diploid*. The cycle is seen at its simplest in the unicellular algae of aquatic environments (Chapters 2, 3 and 4), where haploid individuals in certain circumstances behave as gametes and fuse, so forming a *zygote*. The zygote, which contains a diploid nucleus, either undergoes meiosis at once, or only after some delay, in which case the diploid condition can be thought of as having an independent existence. Either the haploid or the diploid phase, or both, may be multicellular. The multicellular plant is called a *gametophyte* if it produces gametes directly, and a *sporophyte* if it produces, following meiosis, individual cells (called spores or meiospores) which either behave as gametes immediately or develop into game-

tophytes. Each phase may also multiply itself asexually. These various possibilities are summarized in Fig. 1.7.

A life cycle is thus basically a nuclear cycle, and it is not necessarily accompanied by any morphological change. In the algae *Ulva* (p. 54) and *Dictyota* (p. 92), for example, the gametophyte and sporophyte are superficially indistinguishable, and it is necessary to observe the manner of reproduction in order to identify the phase of the cycle to which any individual belongs. Such a life cycle is termed *isomorphic* (or homologous). Frequently, however, the two phases of the cycle have different morphologies, one often being less conspicuous than the other, and sometimes parasitic upon it. These cycles are termed *heteromorphic* (or antithetic). Although the algae show both isomorphic and heteromorphic life cycles, those of land plants are exclusively heteromorphic. Occasionally there may be a morphological cycle without a corresponding nuclear cycle, as in the apogamous ferns (p. 210), but this is regarded as a derived condition.

Gametes are always uninucleate, and, when motile, usually naked cells. In the simplest form of sexual reproduction, termed *isogamy*, the two gametes involved in fusion are free cells and morphologically identical. Nevertheless, detailed investigations continue to show that gametes from the same parent rarely fuse. Some measure of self-incompatibility, and hence physiological differentiation between the parents, appears to be the general rule.

Isogamy was probably the most ancient condition, and this appears to have been succeeded by *anisogamy*. Here the gametes, although still free cells, are morphologically dissimilar, but usually differ in little more than size. The larger, which may also be less mobile, is called the female. The extreme form of anisogamy is *oogamy*, in which the female gamete, now called an egg cell or ovum, is large, non-motile, and filled with food materials. The egg cell may either float freely in water, as in the alga *Fucus*, or be retained in a chamber, as in some algae and all land plants. The chamber bears various names according to the group of plants being considered. Since the progression from isogamy is accompanied in many algal groups by an increase in somatic complexity,



**Figure 1.8** The development of an archegonium as seen in a fern: i, archegonial initial; p, primary cell of the axial row; c, central cell; v, ventral canal cell; e, egg cell; ncc, neck canal cell. Stage 6 indicates a mature archegonium. The neck canal nuclei are breaking down and the ventral canal nucleus is becoming pycnotic. The egg nucleus is enlarging and becoming irregular in outline.

remarkable cytological objects. Each is furnished with two or more highly active flagella, and both the cell and nucleus have an elongated snake-like form, well suited for penetration of the archegonial neck. Dependence upon water is thus reduced to the necessity for a thin film in the region of the sex organs at the time of maturity of the gametes.

it seems very probable that this morphological progression is also a phylogenetic one.

In several instances of sexual reproduction it has been shown that one or both gametes, or the gametangia in which they are produced, liberate traces of chemical substances, termed pheromones (or gamones), which cause the appropriate gametes to approach each other. The chemistry of these pheromones varies widely. In some algae they are hydrocarbons (p. 84) and in others (p. 44) glycoproteins. In the ferns the male gametes are attracted to the opened egg chambers by a pheromone which may be malic acid, a component of the Krebs cycle of respiratory decarboxylation. This substance is known to have a striking chemotactic effect *in vitro*.

### Life cycles of the trans migrant forms

The transition to a terrestrial environment clearly presented a number of problems in relation to sexual reproduction. Although all land plants are oogamous, and are presumably derived from oogamous algae, fluid was still necessary in the initial land plants to allow the motile male gametes to reach the stationary female. This problem appears to have been met first by the egg becoming enclosed in a flask-shaped chamber, the *archegonium*, in the neck of which the male gametes accumulate, and second by the male gamete becoming an efficiently motile cell. The male gametes of the lower archegoniate plants (Chapters 5, 6 and 7), termed *spermatozoids* (or antherozoids), are

The archegonium is common to all the lower land plants, but its origin remains tantalizingly obscure. It may have appeared immediately before the colonization of the land, possibly as a consequence of morphogenetic tendencies seen today in association with the eggs of some Charophyceae, and certain red algae. Regrettably, however, the antecedents of the transmigrant forms have left no clear representatives amongst living algae. Nevertheless, whatever the exact time of the evolution of the archegonium, there are no compelling reasons for regarding it as having been evolved more than once. The archegonium of the living plants has a relatively uniform ontogeny and cytology. The initial cell lies in the outer layer of cells (Fig. 1.8). Two periclinal divisions give rise to a vertical row of three cells, of which the middle cell is the primary cell of the axial row. This divides, forming the central cell and the neck canal cell initial. The division of the central cell yields, below, the egg cell and, above, the ventral canal cell. The nucleus of the neck canal cell divides a number of times (depending upon the systematic position of the archegoniate), but the cell itself commonly remains undivided. The neck is formed by tiers of cells derived from the upper cell of the initial row of three (Fig. 1.8). The lowermost cell of this row gives rise to the cells forming the jacket of the egg cell. The length of the neck and the number of canal cells is significant in bryophytes (p. 108), but negligible in advanced archegoniates, such as cycads (p. 250).

The ferns occupy an intermediate position (Fig. 1.8). In advanced archegoniates, division of the central cell is often not followed by cytokinesis, and the egg nucleus and ventral canal nucleus share a common cytoplasm (e.g., *Ephedra*, p. 266).

With a few exceptions, the fossil record indicates that the most primitive forms of land plants were probably all archegoniate. Notable amongst the likely exceptions is *Protosalvinia*, an enigmatic Devonian plant (p. 93). Its structural and morphological resemblances to dichotomously branched furoid algae (p. 89) suggest that algal groups other than the Chlorophyta may also have experimented with life on land, but with no lasting effect. There is little to challenge the view that the successful colonization of the land was a unique event, brought about by evolutionary progression from the Chlorophyta, in which the perfection of the archegonium played a cardinal rôle.

If the transmigrant forms were archegoniate, what was the nature of their life cycles? This is largely a matter for conjecture. However, as will be seen in later chapters, except for approaches to isomorphy in rhyniophytoid plants (Chapter 6), the living lower archegoniate plants possess markedly heteromorphic life cycles in which the conspicuous phase is either the gametophyte (Bryophyta) or the sporophyte (Lycopodiopsida, Equisetopsida, Polypodiopsida). The transmigrants possibly had an intermediate position, with more or less isomorphic cycles, although there is evidence that, even as early as the Lower Devonian, simple vascular plants had gametophytes with bryophyte-like features (p. 115). The cycle in which the sporophyte was the most highly developed phase clearly had the greater evolutionary potential, since it is characteristic of all forms of higher plant life.

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### Sexual reproduction in later terrestrial vegetation

An important step in the evolution of sexual reproduction on land was undoubtedly the emergence in the archegoniate plants of heterospory. This involves the production of spores of two sizes, the larger giving rise to a wholly female gametophyte and the smaller to a male. In homosporous

archegoniate plants the gametophyte commonly passes through a male phase before becoming female, although it may become male again later. The simultaneous production of viable male and female gametes is unusual. In the primitive heterosporous plants, however, the small female gametophyte formed on germination of the megaspore produces one or a few archegonia in a very short time. The microspore also develops rapidly, and spermatozoids are soon liberated from the diminutive male gametophyte. Further, the food reserves of the megaspore provide for the rapid development of the embryo (in the heterosporous fern *Marsilea* (p. 214), for example, the new sporophyte emerges within 24 hours of fertilization, compared with about one week in a homosporous fern). Heterosporous reproduction is thus coupled with a reduction of the time spent in the gametophytic phase. The shortening of the life cycle increased the rate at which new forms could appear, and hence promoted evolution.

In higher archegoniate plants (Chapter 8) we see how sexual reproduction becomes increasingly independent of water. These archegoniates are exclusively heterosporous, but the megaspore is retained and germinates within a specialized sporangium called an ovule. In some forms (*Cycas*, *Ginkgo*), fertilization is still effected by flagellate male gametes, but the only fluid necessary is a small drop, immediately above the archegonia, into which the gametes are released. Other higher archegoniate plants escape even from this requirement. The male gametophyte is filamentous, and, as a consequence of its growing toward the female gametophyte, it liberates the male gametes (which now lack any specialized means of locomotion and are probably moved passively) directly into an archegonium (siphonogamy). In a few allied plants (e.g., *Gnetum*), modifications of the female gametophyte result in the disappearance of the archegonium. Ultimately we arrive at the embryo sac and the finely ordered cytology that is characteristic of the sexual reproduction of the flowering plants (Chapter 9). Comparative morphology and the fossil record indicate that the morphological sequence we have considered here also represents the evolutionary development of sexual reproduction in land plants. Compared with the cytological elegance of fertil-

**Table 1.2** Sex expression in plants.*Algae*

Where reproduction is sexual, sex is expressed only in the gametophytic phase. The gametophyte can be either unisexual (as in *Ectocarpus* (p. 86)) or bisexual (as in *Coleochaete* (p. 64)).

*Bryophytes*

Sex is expressed only in the gametophytic phase. This phase can be either unisexual (as in dioecious species) or bisexual (as in monoecious species). Sex may be expressed differently in different regions of the same gametophyte (as in the moss *Funaria hygrometrica* (p. 130) and many other species).

*Tracheophytes*

Sex is expressed in the gametophytic phase, either unisexually (as in heterosporous archegoniates) or bisexually (as in homosporous species). Sex may also be expressed in the sporophyte, as in dioecious species of seed plants (e.g., *Taxus baccata* among conifers, and *Lychnis dioica* and many other species of flowering plants). In these plants the female produces only megaspores, and the male only microspores (pollen). Sex may also be expressed differently in different regions of the same sporophyte, as in diclinous species of monoecious flowering plants (p. 285). It is possible that some heterosporous pteridophytes, now extinct, had separate male and female sporophytes (p. 147).

**Table 1.3** The plant kingdom: phototrophs containing chlorophyll and evolving oxygen during photosynthesis.*Subkingdom Algae*

Predominantly plants of aquatic environments, or persistently damp situations exposed to saturated atmospheres. Unicellular; colonial or multicellular; the multicellular forms lacking a well-developed vascular system. Reproductive mechanisms relatively unspecialized. Complex and thickened walls associated only with resting cells. (Chapters 2, 3 and 4)

*Subkingdom Embryophyta*

## Division Bryophyta

Terrestrial or epiphytic, some aquatic. The sporophytic phase normally determinate and partly dependent upon the gametophyte. Multicellular; external surfaces covered with a cuticle, but that of the gametophyte relatively permeable. Vascular systems, if present, not highly differentiated. Sexual reproduction dependent on presence of water: Spores with exine but only in a few groups heavily thickened and ornamented. (Chapter 5)

## Division Tracheophyta

Almost entirely confined to land, a few marine ("sea grasses"), aquatic forms rarely completing their life cycle in a submerged state. The gametophytic phase relatively small or rudimentary, the sporophyte not dependent upon it. Sporophyte often of indefinite growth, regularly provided with a cuticle, normally impermeable, and almost always with stomata and internal air spaces. Well-defined vascular systems consisting of xylem and phloem. Reproductive regions often with elaborate morphology. Spores usually with a well-developed and acetolysis-resistant wall. Fusion of male and female gametes only in more primitive forms dependent on extraneous water: (Chapters 6, 7, 8 and 9)

ization in an angiosperm, the clumsy spermatozoid of *Cycas* is thus not only barbarous, but also primitive.

Following the evolution of heterospory, there was also a clear tendency for sex expression to

appear in the sporophyte, specialized organs of sporophytic structure (such as the male stamen and the female ovule) housing the sites yielding the initial cells of the succeeding gametophytic generation (Table 1.2).

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## Classification of the chlorophyllous phototrophs

A classification provides the shelving on which knowledge of the plant kingdom can be arranged in an orderly fashion. The ideal is a classification which arranges plants according to their level of organization and in their natural alliances. In every classification there is an element of subjectivity. Consequently as knowledge expands judgments need to be modified. The primary classification followed in this book is shown in

Table 1.3. The classifications of the algal subkingdom and of the embryophyte divisions will be found subsequently at the beginnings of Chapters 2, 5 and 6. The aim throughout is to present a general view of the principal kinds of organization encountered in the plant kingdom. Although the approach is systematic, a purely systematic treatment is not attempted and would be inappropriate. The lower plants receive proportionately greater attention. The fossil evidence indicates that they retain features present at crucial stages in plant evolution. Familiarity with them is essential for an understanding of today's diversity.

## The subkingdom Algae: Part I

### Biological features of algae

The simplest phototroph imaginable is a single cell floating in a liquid medium, synthesizing its own sugar, and reproducing at intervals by binary fission. Such organisms do in fact exist in both fresh and salt waters. Examples are provided by the cyanophyte *Synechococcus* (p. 28) and the minute marine *Micromonas* (Fig. 1.6).

These organisms are examples of algae, the group of plants showing the greatest diversity of any major division of the plant kingdom. They range from minute, free-floating, unicellular forms (represented by both prokaryotes and eukaryotes) to large plants, exclusively marine, several meters in length. Many of the smaller algae form a component of *plankton*, the communities of minute plants and animals which float at or near the surface of fresh waters and oceans. Algae are responsible for a large part of the photosynthesis in the biosphere, the productivity of some coastal communities in the surf of warm seas exceeding that of the tropical rain forest. Much of the carbon so fixed enters the food chain of the aquatic heterotrophs.

Despite the enormous range in size, the algae remain comparatively simple in organization. In the smaller multicellular species (e.g., *Merismopedia*, Fig. 2.6; *Pediastrum*, Fig. 3.8) the cells resemble each other in appearance and function, and they can be regarded as forming little more than an aggregate of independent units. In the larger, however, there is morphological and cellular differentiation, although usually less exten-

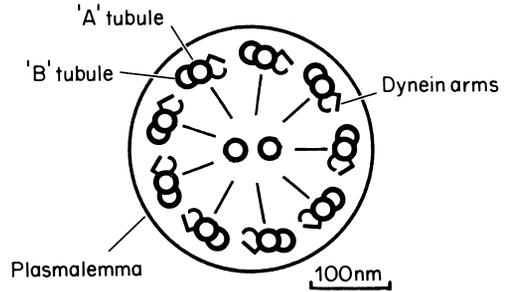
sive than in most land plants. The few heterotrophic forms, mostly small, are regarded as derived. Some, even the smallest (e.g., the dinoflagellates, p. 95), appear to be composite organisms, incorporating a photosynthesizing endosymbiont.

Many algae are fully immersed and firmly attached to the substratum. Together with a few vascular plants these constitute the *benthos*, and contrast with the floating plankton. The attachment may be by a disk-like holdfast, which forms a firm union with the surface of a rock or stone, or branched, penetrating soft material such as muds. Branched root-like attachments (as in the Charales) may participate in the absorption of minerals, but any resemblance to the root system of higher plants is distant.

The largest algae are found only in the sea. The restriction of these forms to a marine environment is perhaps accounted for by the relative impermanence of inland waters in geological time, and the consequent limiting of the opportunity for the evolution of similar complexity in these situations. Although marine algae are sometimes able to withstand inundation in fresh water (e.g., *Fucus*, p. 90), and occasionally may even become adapted to permanently low salinity (e.g., *Ulva* and *Enteromorpha*, p. 54), they do not normally survive indefinitely or grow in these conditions. Presumably, fresh waters are unable to supply minerals at a rate adequate for their metabolism. A large alga in European seas is *Laminaria* (Fig. 4.16), some species of which may reach 4 m (13 ft, 4 in.) in length. Off the west coast of North America are found the gigantic

*Nereocystis* and *Macrocystis*, with thalli commonly extending 50 m (165 ft) or more. Maintaining the integrity of a thallus of this size raises substantial mechanical problems. Although the sea provides considerable supporting upthrust, currents and turbulence cause more sustained tensions and pressures than similar movements in a gaseous medium. The toughness and hard rubbery resistance to any kind of distortion found in the larger algae are thus necessary qualities for survival in the oceans. These attributes arise principally from the general properties of the cell walls and of the surface, and not from any specialized strengthening elements.

The biophysical features of photosynthesis in the algae are the same as those in land plants, but the C<sub>4</sub> pathway of carbon dioxide assimilation (p. 6) characteristic of some land plants seems not to be represented (with the possible exception of the coenocytic green alga *Udotea*, p. 58). As would be expected of a group exploiting the aquatic habitat, many of the secondary products found in the algae have distinctive biochemical characteristics. Many algae, for example, accumulate fats and oils rather than starch, and others polyhydric alcohols. The cell walls of the eukaryotic algae often contain the polysaccharides mannan and xylan in microfibrillar form in addition to cellulose. The nitrogenous polysaccharide chitin is found as an outer layer of the wall in *Cladophora prolifera* and possibly in *Oedogonium*. Pectin, a polymer based on galacturonic acid, is a common component of algal cell walls, sometimes forming a distinct outer sheath (e.g., *Scenedesmus*, Fig. 3.7). Colloids such as fucin and fucoidin, unknown outside the algae, occur in the amorphous matrices of the walls of brown algae. Alginic acid, which occurs in quantity in the middle lamellae and primary walls of several brown algae, is extracted commercially and finds a wide range of uses as an emulsifier in industry, and is a component of the familiar “instant puddings”. Complex mucilaginous polysaccharides rich in galactan sulfates are characteristic of the red algae. Dimethyl sulfur compounds assist osmoregulation in marine phytoplankton. Gaseous derivatives of these escape and contribute to the sulfur content of the atmosphere. Oxidation of these derivatives leads to sulfur or sulfate particles in the air above oceans.



**Figure 2.1** Diagram of transverse section of a eukaryotic flagellum viewed from the base. The “spokes”, radiating from the center to the peripheral doublets, are usually recognizable. Sometimes an ill-defined sheath is present around the central pair of tubules.

These particles are believed to give rise to aerosols which promote cloud formation. This in turn leads to cooling of the surface. Evidence is accumulating that the metabolic effects of oceanic phytoplankton have a significant rôle in determining climate.

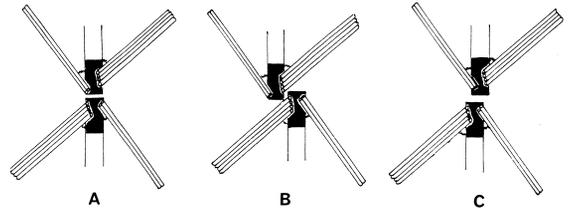
Many unicellular algae, occurring both singly and in colonies, and the unicellular reproductive cells of more complex algae are motile. In some prokaryotic forms (e.g., cyanophytes, p. 26) and in some eukaryotic ones (e.g., diatoms, p. 82), movement is brought about by directed jets of mucilage. The motility of many eukaryotes however depends upon the presence of flagella. An unexpected and remarkable discovery of electron microscopy was that all flagella produced by eukaryotic organisms have a common basic structure, providing a characteristic picture in transverse section (Fig. 2.1). Nine pairs of microtubules, each pair oriented tangentially, are equally spaced around the periphery of the flagellum. Although the microtubules of each pair are similar in diameter (18–25 nm), they differ in profile. Viewed from the base of the flagellum outward, the microtubule on the right (the “A” tubule) usually appears circular in outline, whereas that of the “B” tubule on the left is not completely so. The portion of the “B” tubule shared with the “A” tubule commonly follows the curvature of the latter. In addition to the peripheral microtubules two free microtubules usually lie symmetrically at the center. These are often slightly wider than the peripheral tubules. Usually, but not always in plant flagella,

two short arms can be made out on the “A” tubule. These consist of a special protein, dynein, an ATPase.

The microtubular system of the flagellum constitutes the *axoneme*. The microtubules of axonemes appear to be quite similar to others in the cell, but they are not so sensitive to colchicine. In some instances flagellogenesis may even continue in the presence of this anti-microtubular drug. Movement of the axoneme is probably caused by the paired microtubules sliding over one another. The mechanism is not however entirely understood. More detailed information will probably come from the study of mutants in which the structure of flagella is in some way defective.

Formerly two classes of flagella were recognized, “whiplash” considered to be smooth, and “Flimmer” furnished with rows of minute hairs (*mastigonemes*). It now seems doubtful whether algal flagella are ever entirely smooth, but appendages are certainly much more conspicuous in some groups than in others. Appendages other than hairs are also known. The single flagellum of *Micromonas*, for example, is covered with minute scales, and that of the related *Pyramimonas* with minute scales of two distinct kinds. The electron microscope has shown that in many instances these scales are assembled in Golgi bodies and transported to the surface in vesicles.

The nature of the surface, and other features of the flagella such as their number, arrangement, and method and kind of insertion, have attracted considerable interest, those of the biflagellate unicells of the Chlorophyta having received closest attention (Fig. 2.2). Here the flagella are anchored by four “roots”, two consisting of a bundle of four microtubules, and two of two microtubules. Viewed from above the bundles reveal a cruciate arrangement. Often the insertions of the flagella (basal bodies) do not lie in the same plane, one being shifted slightly in relation to the other (Fig. 2.2). If the shifting is in a clockwise direction (as in *Chlamydomonas*) the arrangement is said to be “11 o'clock–7 o'clock”, and if the converse “1 o'clock–5 o'clock”. The latter is not found in any free-living unicellular forms, but occurs in the gametes of a number of Ulvophyceae. A coplanar arrangement of the flagellar bases is comparatively rare, but is found in zoospores and gametes



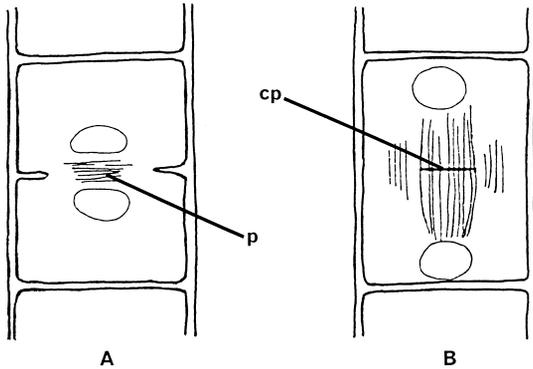
**Figure 2.2** Positional relationships of the basal bodies (black) and flagellar roots in biflagellate cells of the green algae (Chlorophyceae), viewed from the anterior end of the cell. (A) The basal bodies lie in the same plane (possibly an ancestral arrangement). (B) The basal bodies are shifted in an anticlockwise direction relative to each other (positions “11 o'clock–5 o'clock”). (C) The shifting is in a clockwise direction (positions “1 o'clock–7 o'clock”). Comparable relationships are found in quadriflagellate cells. (From Van den Hoek, Mann and Jahns. 1995. *Algae: An Introduction to Phycology*. Cambridge University Press, Cambridge.)

of the Chlorococcales. Flagella features have given useful indications of relationships within the Chlorophyta.

The basal bodies of the Chlorophyta are also associated with strands of contractile protein. These strands are termed *rhizoplasts* and the constituent protein *centrin*. The contraction and relaxation of this protein depend upon the balance of  $\text{Ca}^{2+}$  and ATP, and its activity contributes to the motions of the flagella. The rhizoplasts run down into the cell and terminate adjacent to the nucleus or chloroplast.

Some motile gametes and zoospores within the Chlorophyta have a symmetry different from that of *Chlamydomonas*. They are unilateral and a single microtubular ribbon descends from the basal bodies into the body of the cell. At the anterior of the ribbon, beneath the basal bodies, is a conspicuous multilayered structure. This is very similar to the corresponding structure beneath the basal bodies in the motile male gametes of the archegoniate land plants. A splendid example is seen in the alga *Coleochaete* (Fig. 3.35), an algal form which has several other features of significance in relation to the origin of the earliest land plants in the Silurian (see Chapters 3, 5 and 6).

Attention has also been paid to the manner of cell division in the algae, again principally in the green algae. The nuclear envelope may remain almost intact at the time of division, and the



**Figure 2.3** Extreme forms of cytokinesis in green algae (in longitudinal section, diagrammatic). (A) Mitotic spindle transient, nuclear envelope remaining largely intact throughout. Division is completed by ingrowths of the wall directed toward a transverse equatorial array of microtubules (phycoplast, p). (B) Spindle persists until telophase. Transversely oriented microtubules at equator absent, cell plate (cp) forms within a vesicular phragmoplast transverse to the axis of the spindle, and extends laterally, completing the dividing wall.

spindle transient (as in *Chlamydomonas*) or persisting until telophase. Cytokinesis may be brought about by wall ingrowths penetrating a transverse array of microtubules (termed a *phycoplast*) (Fig. 2.3A), or, more rarely, be initiated by a cell plate formed within a phragmoplast at the equator of a more persistent spindle, as in all land plants (Fig. 2.3B). Patterns of cytokinesis intermediate between these two extremes are also encountered. Significantly, the phragmoplast type of division has been observed only in those algae (members of the Charophyceae) thought to be closest to those from which the land plants arose.

Amongst other eukaryotic algae, the biflagellate heterokonts (Table 2.1) form a natural group. The two flagella differ in length, the nature of their ornamentation, and their orientation. The longer flagellum is of the “Flimmer” kind and is directed forward. The shorter flagellum is smooth and is directed backward along the cell. The group also has ultrastructural features in common, such as the manner in which the plastid is enclosed in a fold of endoplasmic reticulum (e.g., Fig. 4.27). The Bacillariophyta (diatoms) (p. 80) are also included in the heterokont algae: although the male gamete (the only flagellate stage in the life history) has only a single flagellum, it has the

Flimmer structure typical of the heterokonts, and the characteristic chloroplast endoplasmic reticulum is also present. The Rhodophyta are outstanding in having no flagellate forms amongst living representatives. A few unicellular forms belonging to the Haptophyta (p. 93) have, in addition to two flagella, a third flagellum-like organ. The structure of this is much simpler and less regular than that of the “9 + 2” flagellum.

The chloroplasts of algae take a variety of shapes, for example plate-like in *Mougeotia* (p. 62), stellate in desmids (p. 62) and some red algae, as girdles close to the cell wall (*Ulothrix*, p. 52), in the form of a spiral ribbon (*Spirogyra*, p. 63), cup-shaped in *Chlamydomonas* (p. 40) and reticulate (as in many Chlorococcales). Discoid chloroplasts, the form common in land plants, are found in a few red algae and in *Chara* (p. 66), but are generally rare. Although irregular stacking of thylakoids commonly occurs in chloroplasts of chlorophylls “a + b” algae (Table 2.1) (e.g., *Chlamydomonas*), the distinct grana characteristic of land plants are absent. A prominent feature of many algal chloroplasts is the *pyrenoid*, a proteinaceous body and the site of the enzyme RUBISCO (p. 2). In land plants RUBISCO is distributed in the stroma of the plastid. The pyrenoid may also be the site of starch formation, but not in the red algae (p. 30).

There is no evidence that the major groups of algae have any close relationship with each other. Nevertheless, there are sufficient morphological, physiological and ecological similarities between these plants to make the term “alga” a useful one. Study of the structure and reproduction of the algae reveals a number of ways in which these simple phototrophs have increased their morphological and reproductive complexity. We shall in the main be concerned with the illustration and discussion of these trends, and we shall not attempt a complete taxonomic or morphological survey of any group. The general classification of the algae followed in this work, based upon the nature of the chlorophylls present in the photosynthetic membranes, is shown in Table 2.1.

**Table 2.1** | Classification of the subkingdom Algae.

Division	Class/subclass	Order
	Algae containing wholly or predominantly chlorophyll <i>a</i>	
CYANOPHYTA (Cyanobacteria)	Cyanophyceae	Chroococcales Nostocales Stigonematales
GLAUCOPHYTA RHODOPHYTA	Rhodophyceae Bangiophycidae Florideophycidae	
	Algae containing chlorophylls <i>a</i> and <i>b</i>	
PROCHLOROPHYTA CHLORACHNIOPHYTA CHLOROPHYTA	Prasinophyceae	Pedinomonadales Pyraminodales Pterospermatales Volvocales Tetrasporales Chlorococcales Chlorosphaerales Chaetophorales Oedogoniales Sphaeropleales Ultrichales Ulvales Prasiolales Cladophorales
	Chlorophyceae	Siphonocladales Codiales Caulerpales Dichotomosiphonales Dasycladales Klebsormidiales Mesotaeniales Desmidiales Zygnematales Coleochaetales Charales
	Ulvophyceae	Tetraselmidiales Pleurastrales Trentepohliales
	Charophyceae	Euglenales Eutreptiales
EUGLENOPHYTA	Euglenophyceae	
	Algae containing chlorophylls <i>a</i> and <i>c</i>	
CHRYSOPHYTA XANTHOPHYTA BACILLARIOPHYTA PHAEOPHYTA	Phaeophyceae	Ectocarpales Sphacelariales Cutleriales Laminariales Fucales Dictyotales
HAPTOPHYTA (Prymnesiophyta) DINOPHYTA (Pyrrophyta)	Desmophyceae Dinophyceae	
CRYPTOPHYTA		

Siphonales

Heterokont algae

## Algae in which the chlorophyll is wholly or predominantly chlorophyll *a*

These algae, which embrace both prokaryotic and eukaryotic forms, are probably the closest amongst the living algae to the original cellular phototrophs. They are therefore of particular interest in relation to the origin of plant life.

### Prokaryotic forms

Those prokaryotic forms which contain solely chlorophyll *a* comprise the well-characterized division Cyanophyta ("blue-green algae"). Many exist as single cells and are representative of the simplest phototrophs. In others the cells are aggregated either loosely or into groups, each with a distinctive morphology (e.g., *Gloeotrichia*, Fig. 2.11). Filamentous forms also occur, and a few attain a multiseriate and pseudoparenchymatous level of organization (*Stigonema*, p. 26).

### CYANOPHYTA (CYANOBACTERIA)

**Habitat** Water, swamps, soil, occasionally endolithic.

**Pigments** Chlorophyll *a*;  $\beta$ -carotene; myxoxanthin, zeaxanthin; biliproteins (allophycocyanin, phycocyanin and phycoerythrin).

**Food reserves** Cyanophyceean starch (similar to glycogen), polyphosphate granules (volutin), cyanophycin (a polymer of arginine and aspartic acid).

**Cell wall components** Murein, hemicelluloses.

**Reproduction** Asexual. Genetic recombination observed, but mechanism not clearly established.

**Growth forms** Unicellular, cellular aggregates, filamentous, a few pseudoparenchymatous.

### Cytology

The cells, rarely exceeding 10  $\mu\text{m}$  in diameter, are not unlike those of bacteria. Indeed, despite the presence of chlorophyll *a* and the possession of oxygenic photosynthesis, the cyanophytes are often classified with the bacteria ("Cyanobacteria") instead of with the algae. The resemblance is enhanced by the presence of the peptidoglycan murein in the cell walls, their

being subject to attack by viruses similar to the bacteriophages, and the bearing by some of filamentous appendages (fimbriae) otherwise found only in Gram-negative bacteria. Some cyanophytes, if present in anaerobic situations rich in sulfide, are able to use hydrogen sulfide as an electron donor, producing sulfur or thiosulfate as a by-product. A similar kind of photosynthesis is found in certain bacteria. Another bacterial feature is that some cyanophytes (e.g., species of *Oscillatoria* and the related *Microcoleus*) are able, in association with various bacteria, to metabolize heavy hydrocarbons. Mats formed by these organisms find a practical use in cleaning up massive oil spills (as followed the military operations in the deserts of Kuwait).

Under the light microscope, partly because of the small size of the cells, the photosynthetic pigments appear dispersed in the cytoplasm. The electron microscope reveals that this is an erroneous impression, and that the cells contain the same kind of photosynthetic membrane as that present in higher plants. The thylakoids, which arise as, and may remain, invaginations of the plasmalemma, form either loose stacks parallel to the longitudinal axis of the cell, or a number of concentric whorls. Less commonly they form a three-dimensional reticulum, and in older cells have been seen to aggregate into a crystalline body about 0.3  $\mu\text{m}$  in diameter closely resembling the prolamellar bodies of etioplasts of higher plants. Skeins of DNA, together forming the nucleoid, may be scattered between the thylakoids. Blue-green algae from hot springs have yielded the first pure preparations of the chlorophyll *a* reaction center at which the light energy is transformed into chemical (photosystem I).

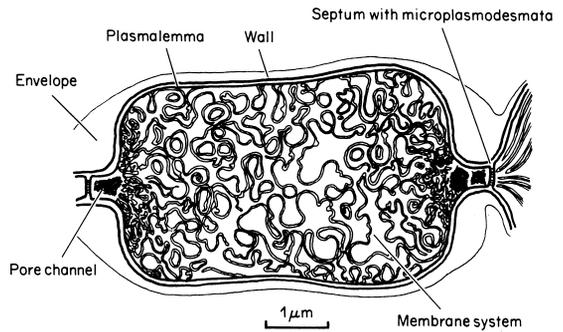
Also seen in the electron microscope are small particles about 30 nm in diameter, lying on the outer surfaces of the thylakoids. These are the site of the biliprotein pigments (*phycobilisomes*). They trap the light energy which is subsequently utilized in photosystem II, that part of photosynthesis which leads to the evolution of oxygen. Scattered amongst the thylakoids and skeins of DNA are polyhedral bodies (*carboxysomes*). These are the sites of the enzyme RUBISCO (p. 2).

Elsewhere in the cell are found clusters of minute cylinders, each bounded by a sheet con-

sisting solely of protein, and containing gas (*gas vesicles*). These regulate buoyancy, and collapse if the cells are subjected to sudden mechanical shock. Vacuoles similar to those of eukaryotic cells are absent.

In many filamentous species the chains of cells are interrupted by occasional conspicuously larger cells called *heterocysts* (Fig. 2.4). There are often indications of regularity in their spacing (in the filamentous *Anabaena*, for example, about every tenth cell becomes a heterocyst). The mechanism controlling their formation is not wholly known, but in *Anabaena* a gene has been detected which contributes to the spacing pattern. This gene codes for a small peptide which prevents the differentiation of a heterocyst between two existing heterocysts, a kind of control which is more familiar in eukaryotic organisms. The heterocysts contain chlorophyll *a* and some other pigments but are altogether paler, and by contrast may appear empty. Electron microscopy reveals that they contain an elaborate and often reticulate membrane system. The wall of a heterocyst is conspicuously thickened except for a pore at one or both poles. At these sites its protoplast is separated from those of its neighbors solely by a thin septum, in which fine channels (microplasmodesmata) can sometimes be discerned.

Heterocysts are the sites of fixation of atmospheric nitrogen. The enzyme responsible, nitrogenase, is irreversibly inactivated in aerobic conditions. It is significant that the heterocysts lack photosystem II and therefore generate no intracellular oxygen. Indeed, their frequently elaborate membrane systems may indicate considerable respiratory activity. This would in turn promote an anaerobic environment within the cells, which the thickened walls (Fig. 2.4) may help to maintain. Those species able to fix nitrogen without heterocysts can usually do so only at very low oxygen tensions. An exception is the filamentous *Trichodesmium*, which can carry on photosynthesis and fix nitrogen at the same time. It is thought that here photosynthetic and nitrogen-fixing cells, distinguishable only in function, may be differentiated along individual filaments. Circadian rhythms have also been detected in cyanophytes (e.g., *Synechococcus*). Such biological clocks (which are probably similar in principle to



**Figure 2.4** *Anabaena*. Longitudinal section of a heterocyst. (After Fay, in Carr and Whitton, 1973. *The Biology of Blue-Green Algae*. Blackwell Scientific Publications, Oxford.)

those in eukaryotic cells, but possibly involve different proteins) may also serve, by modulating gene activity, to separate in time photosynthesis (evolving oxygen) from nitrogen fixation, so preventing destructive interference of the two systems.

In a few instances heterocysts have been observed to regain pigmentation and then to germinate. On these grounds some have considered them to be vestigial reproductive cells. In one species of *Anabaena*, however, differentiation of the heterocyst has been found to involve deletions in the DNA. If this is a general phenomenon and heterocysts are truly capable of regenerating the whole organism, these deletions are presumably reversible. The respiration of cyanophytes tends to be depressed by light, and with mat-forming species bright light has also been found to inhibit the synthesis of DNA. This may serve to reduce the chance of damage to the DNA by UV radiation, and be a relic of a protective mechanism dating from Precambrian times when UV radiation reaching the Earth's surface, in the absence of an ozone shield, would have been a far greater hazard.

The cell walls of the Cyanophyta contain a layer of the peptidoglycan murein adjacent to the plasmalemma. The walls are thus chemically and structurally similar to those of Gram-negative bacteria, and their formation is similarly disorganized by penicillin. The presence of murein also accounts for the dissolution of the wall, as those of bacteria, by lysozyme. The outer part of the wall is commonly a distinct layered sheath, sometimes pigmented, and frequently consisting largely of