THE ULTRASTRUCTURE OF THE VEGETATIVE CELL OF BLUE-GREEN ALGAE

By D. C. WILDON* and F. V. MERCER*

[*Manuscript received January* 3, 1963]

Summary

An electron-microscopic study has been made of the vegetative cells of eight genera of the blue-green algae. A basic structure has been defined for the vegetative cell. There is a cytoplasmic matrix which extends throughout the cell. No membrane-bound organelles of the categories chloroplast, mitochondrion, nucleus, golgi body, and endoplasmic reticulum can be recognized therein. There are two regions within the cell. The peripheral region is distinguished by the presence of "photosynthetic" lamellae and various granular inclusions. The central region is distinguished by the presence of crystalline granules, and areas of low electron density which resemble the nucleoid regions of bacteria. Ribosome-like granules are seen scattered throughout the cytoplasmic matrix.

Intercellular connections, involving the plasma membranes of adjacent cells, have been seen.

I. INTRODUCTION

A number of investigators have shown that the ultrastructure and organization of the blue-green algal cell is fundamentally different from that found in higher plants and animals (Drews and Niklowitz 1956, 1957; Niklowitz and Drews 1956, 1957; Hopwood and Glauert 1960; Lefort 1960*a*, 1960*b*; Shatkin 1960; Menke 1961; Ris and Singh 1961; Hall and Claus 1962). In the sense used by Stanier and van Neil (1962) it is a procaryotic cell. Two regions within the protoplast are recognized. The outer or peripheral region is defined by the presence of paired membranes, which are presumed, on the basis of cell-fraction studies, to be associated with the photosynthetic pigments (Shatkin 1960). The central region, which merges into the peripheral region, includes structures which closely resemble the nuclear equivalent of the bacterial cell, both under the electron microscope (Hopwood and Glauert 1960) and in their reaction to nuclear stains (Cassel and Hutchinson 1954). Comparatively little is known about the functional roles of the two regions or of the distrubution of enzymic processes within the structure of the protoplast.

The present study aims to describe the protoplast in both structural and biochemical terms, particularly with reference to the process of respiration.

This paper describes the fine structure, as observed by electron microscopy, of the vegetative cells of eight genera of blue-green algae, and serves as the basis for the subsequent comparative biochemical and physiological work. One species, *Nostoc muscorum*, has been examined at different stages of the vegetative life cycle, using both light- and dark-grown cells.

* Plant Physiology Unit, Botany School, and Division of Food Preservation, C.S.I.R.O., University of Sydney.

II. Materials and Methods

The following species were examined: *Anabaena* sp. (L14) and *Nostoc* sp. (N52) (both obtained from Dr. J. S. Bunt, School of Agriculture, University of Sydney), *Anabaena cylindrica* Lemm., *Calothrix anomala*, *Lyngbya majuscula* Harvey, *Plectonema boryanum* Gom., *Spirulina major* Kutz., *Fischerella muscicola* (Thur.) Gom., and *Chroococcus prescotii* Drouet & Daily (obtained from the culture collection of Algae and Protozoa, Cambridge University). *Nostoc muscorum* Kutz., Allison's strain, was obtained from the culture collection of algae at Indiana University. Authorities for specific epithets are those given by the suppliers of the cultures.

Anabaena and *Nostoc* species were maintained, bacteria-free, in plate culture on No. 5 nitrogen-free media (Bunt 1961) solidified with 1·5% agar. For growth in the dark (for *N. muscorum*) 1% glucose and sufficient KNO_3 to give a final concentration of 0·03M were added; the plates were double-wrapped in aluminium foil and placed in a light-tight box. Other cultures were grown under white fluorescent light at an intensity of approximately 300 f.c. All cultures were grown at 26°C.

Most of the remaining species were not bacteria-free. No attempt was made to culture them under defined conditions—they were fixed with 1% potassium permanganate immediately on arrival from Cambridge.

For electron microscopy, colonies (a few mm^3 in volume) were cut from actively growing plate cultures and fixed for from 4–7 hr at room temperature in 1% unbuffered potassium permanganate—the fixative was initially cold. The material was then stained for 1½ hr in 2% unbuffered uranium nitrate. The presence of buffering agents, such as used in Palade's (1952) method of osmium fixation, did not affect the fixation. This procedure was varied only in the fixation of a culture of *Anabaena cylindrica* which had been plasmolysed in 3·0M NaCl; in this case both the potassium permanganate and the uranium nitrate were made up in a solution of 3·0M NaCl.

Samples were also fixed in 1% osmium tetroxide using Palade's method; low fixation temperatures proved unsatisfactory, but better results were obtained after fixation for 8 hr at 40°C. A similar effect of higher fixation temperatures has also been observed in marine molluscan ovarian tissue (C. Shorey, personal communication).

All samples were dehydrated through a graded alcohol series, transferred to xylol, and embedded in "Araldite" according to the procedure described by Mercer and Birbeck (1961).

Sections were cut with a diamond knife and a Porter–Blum microtome, or glass knives and an LKB microtome; they were floated on distilled water, expanded with chloroform, and transferred to specimen grids covered with a double film of carbon and nitrocellulose. Sections of osmium-fixed cells were stained on the grid with uranium acetate. Most of the observations were made on a Siemens "Elmiskop I" electron microscope. A variety of apertures at 80 kV was used. Some use was also made of a Siemens "Elmiskop II" electron microscope operating at 50 kV. A calibrated telescope was used to calculate dimensions of membranes and other organelles; however, variations in factors affecting the actual magnifications make the measurements only relative to each other.

III. Results and Discussion

The species used in this study are members of the following orders:

Chroococcales—primitive unicellular and colonial types;

Nostocales and Stigonematales—filamentous types.

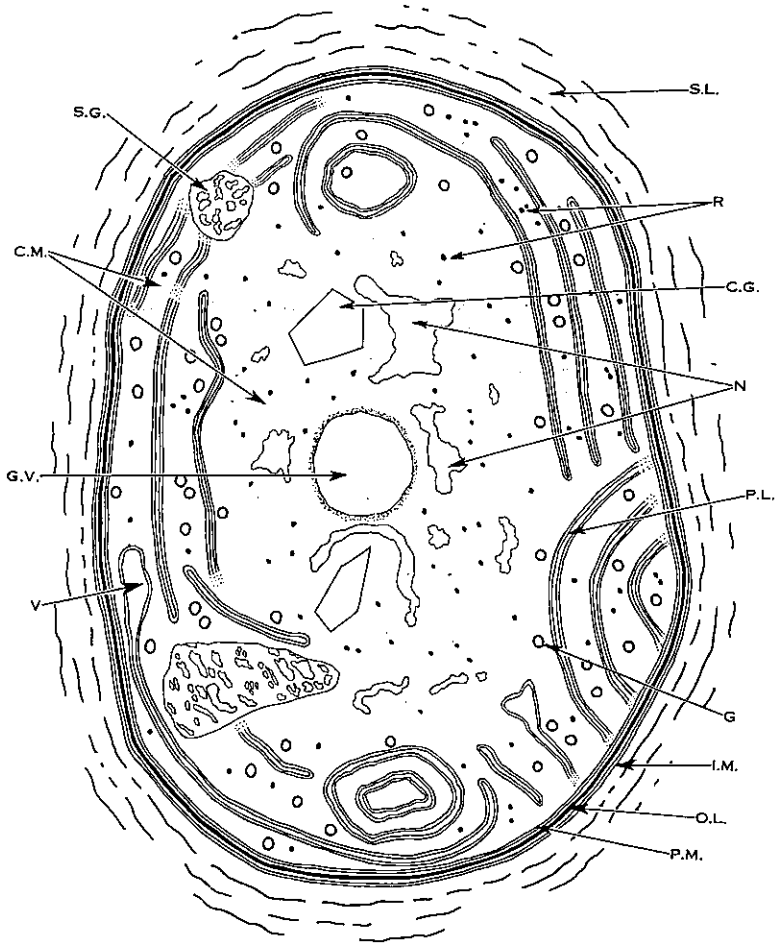


Fig. 1.—Diagram illustrating section of "typical" blue-green algal cell. Details include slime layer (*S.L.*), investment membrane (*I.M.*), osmiophilic layer of inner investment (*O.L.*), plasma membrane (*P.M.*), peripheral photosynthetic lamellae (*P.L.*), vacuole (*V*), granules 300 Å in diameter (*G*), gas vacuole (*G.V.*), ribosome-like granules (*R*), structured granules (*S.G.*), cytoplasmic matrix (*C.M.*), crystalline granules (*C.G.*), areas of low electron density (*N*). For clarity, the structural components are not drawn strictly to scale.

To assist in understanding the ultrastructure the topography of a number of vegetative cells is shown in Plates 1–9 and the generalized structure of the cell as derived from electron micrographs of the different species is summarized, diagrammatically, in Figure 1. The structure of the cell envelope is shown in greater detail in Figure 2. The structural components recognized are:

(*a*) The cell envelope, which encloses the protoplast and consists of (i) the plasma membrane, (ii) an outer "unit membrane" or investment membrane, (iii) an electron-lucent region or space, (iv) the inner investment, (v) an external sheath, and (vi) intercellular connections.

(*b*) The cytoplasmic matrix, in which are recognized (i) the peripheral lamellar system, (ii) a more or less clearly defined central region which probably includes the nuclear material, (iii) at least four types of granular inclusion, (iv) one type of globular inclusion, and (v) two types of vacuole.

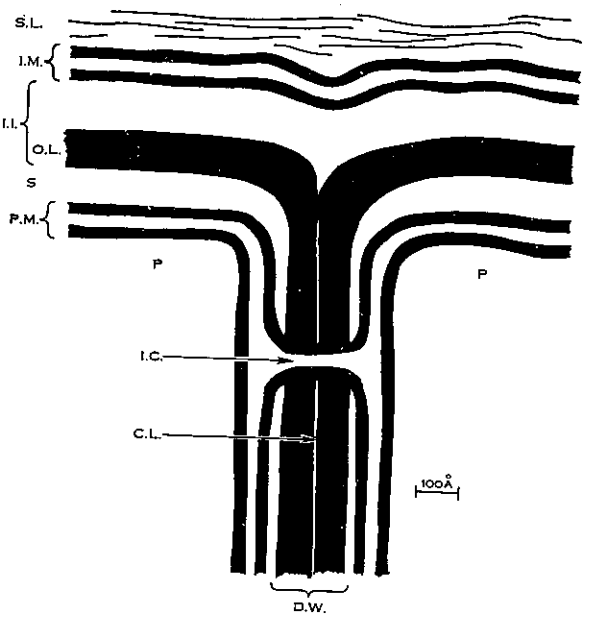


Fig. 2.—Composite diagram illustrating results after both osmium and permanganate fixation of the cell envelope. Note slime layer (*S.L.*), investment membrane (*I.M.*), inner investment (*I.I.*) which is split into an outer layer and an osmiophilic layer (*O.L.*), space (*S*), plasma membrane (*P.M.*), intercellular connection (*I.C.*), centre line (*C.L.*) of dividing wall (*D.W.*), protoplast (*P*).

Variations in proportion and distribution of these various components are observed in the different species but the generalized structure to which all species conform is that shown in Figure 1.

(*a*) *The Cell Envelope*

This region includes all layers which are outside the protoplast. A composite diagram of the electron-density pattern of this region after both osmium and permanganate fixation is given in Figure 2. Five zones are to be seen after both types of fixation. The interpretation of this pattern presents difficulties although the general features are clear.

(i) *Plasma Membrane.*—The inner dense, approximately 80 Å wide, membrane of the osmium-fixed cells (Plate 5, Fig. 2) can be equated with the inner dense layer of the permanganate-fixed cells (Plate 5, Fig. 1). Although it has been observed in all species studied, it is not always seen in electron micrographs, probably because of poor fixation. This membrane is seen, particularly after permanganate fixation, as two dense lines approximately 25 Å wide separated by a light line approximately 30 Å wide. These dimensions are similar to those of a unit membrane as defined by Robertson (1958). Since this membrane forms the surface of the protoplast it corresponds to the plasmalemma of higher plants and in common with the plasmalemma is sometimes destroyed during fixation. In turgid cells the plasma membrane has a smooth outline and follows the outline of the cell envelope, while in plasmolysed cells (Plate 4, Fig. 2) it has a wrinkled or wavy appearance which results from the contraction and wrinkling of the protoplast in 3·0M NaCl.

(ii) *Investment Membrane.*—Similarly, the dimensions of the outer layer, approximately 80 Å wide, seen with both fixatives, are those of a unit membrane (e.g. Plate 4, Fig. 2). This membrane separates the sheath from the inner investment. Since the region immediately inside the membrane has been described as the inner investment (Ris and Singh 1961) it is suggested here that the outer unit membrane be referred to as the investment membrane. This membrane often has a wrinkled appearance as if attached to the inner investment at irregular intervals; it also seems to be more labile than the plasma membrane and is therefore not easily observed in electron micrographs.

The investment membrane forms a continuous layer around the filament and does not extend between adjacent cells of a filament except when they are separating from one another.

(iii) *Space.*—An electron-lucent region external to the plasma membrane is frequently, but not always, observed in all species. When present, in any one species, it has approximately the same dimensions after both types of fixation. From observations on plasmolysed cells of *Anabaena* (Plate 4, Fig. 2) it seems likely that this region is an empty space, formed by the contraction of the protoplast away from the inner investment, possibly during fixation and dehydration, and is not a region containing a definite electron-lucent substance.

(iv) *Inner Investment.*—The inner investment is not well defined after either osmium (Plate 2, Fig. 1; Plate 5, Fig. 2) or permanganate fixation (e.g. Plate 5, Fig. 1) and appears two-layered only after osmium fixation. After permanganate fixation the inner investment appears to consist of only one layer but the overall dimensions are the same after both fixatives. There are species variations in the dimensions of the two layers. The inner osmiophilic layer also forms the dividing wall between daughter cells. The outer less-electron-dense layer lies next to the investment membrane and, like this membrane, is continuous along the filament and only appears to extend between adjacent cells when they are separating from each other. A thin line is often seen in the centre of the dividing wall between cells which have probably already started to separate (Plate 5, Fig. 2).

The picture is essentially the same in the non-filamentous colonial type *Chroococcus* except that, in this organism, the daughter cells separate from one another after each cell division.

The osmiophilic layer, at least, would seem to have the structural rigidity characteristic of plant cell walls since it does not deform when the cell is plasmolysed in 3·0M NaCl (Plate 4, Fig. 2).

There is a suggestion of pores in the inner investment of *Oscillatoria princeps* (Ris and Singh 1961) and also in *Chroococcus prescotii* (not shown). It is intended to discuss this in a subsequent paper.

(v) *External Sheath* (*Slime Layer*).—Outside the investment membrane in most species is a stratified region with many layers of alternating density. This region is usually visible after fixation with both fixatives. It varies considerably in width in the different species and also within one species according to the conditions under which the cells are grown. It is quite inconspicuous in *Nostoc muscorum* grown in the light but is very prominent when the cells are grown in the dark (Plate 3, Figs. 1 and 2).

(vi) *Intercellular Connections*.—Clearly visible after permanganate fixation are numerous intercellular connections between adjacent cells of a filament (see especially Plate 4, Fig. 1). Plate 4, Figure 1, inset, shows the electron-density pattern of the connections. As far as can be detected the connections involve only the plasma membranes of neighbouring protoplasts. It has not been possible to resolve a central core which might indicate the direct continuity of the matrix of adjacent protoplasts, through a "tube" formed by the cross-linking membranes. How far these connections are analogous to the plasmodesmata of higher plant cells is not yet known.

(*b*) *Cytoplasmic Matrix*

(i) *Photosynthetic Lamellar System*

After both types of fixation, numerous membranes are seen scattered throughout the outer regions of the cytoplasmic matrix (Plate 1). The actual distribution varies from species to species. These membranes appear to have the same structure irrespective of their position within the protoplast. Measurements made from a large number of electron micrographs of permanganate-fixed cells give the approximate dimensions of the membranes as dark line 25 Å, light line 30 Å, dark line 25 Å, and hence are similar to the unit membrane as described by Robertson (1958). The possibility of false images has been examined by means of a through-focus series. Plate 9, Figure 4, shows an underfocussed image, with the dark lines of the membranes appearing thicker. An overfocussed image with a large number of lines corresponding to phase bodies is shown in Plate 9, Figure 6. The true focus image is seen in Plate 9, Figure 5, clearly indicating that the unit membranes are not focus artefacts.

After permanganate fixation these unit membranes always occur in the cytoplasm in pairs—the two membranes being separated by a narrow gap except where occasionally they have obviously separated to form vesicles (e.g. Plate 8, Fig. 2). Occasionally the ends of the paired membranes appear closed, resembling a loop.

Serial sections (Plate 9, Figs. 1, 2, and 3) of *Nostoc* sp. give the breadth or extent of the paired membrane units as at least 1000 Å, suggesting that they are not tubular in shape in this species. Rather these features are consistent with the paired unit membranes forming flattened sacs, similar to the disk structure postulated for the lamellar system of the chloroplasts of the higher plants. Cell-fractionation studies have shown that the photosynthetic pigments are associated with these lamellae (Shatkin 1960). In the absence of definitive biochemical data these intracytoplasmic membranes will be tentatively referred to as photosynthetic lamellae.

Lamellae occur, but with some reduction in numbers, in dark-grown cells (Plate 3, Fig. 2). As far as can be detected there is no differences between the dimensions of the lamellae formed in the dark and those formed in the light in permanganate-fixed cells. Under both conditions the characteristic dark–light–dark lines of the unit membrane are seen (Plate 3, Fig. 2, inset). Since many lamellae differentiate in the dark they may not be identical in their formative requirements with the photosynthetic lamellae of the higher plants. This may in some way reflect the fact that the entire complement of pigments is formed in the dark (Fritsch 1945, p. 782; and personal observation).

There is a tendency for the lamellae to occur in stacks separated by the cytoplasmic matrix which is assumed to have some correspondence to the cytoplasm of higher plant cells. This tendency is clearly seen in both *Plectonema* and *Lyngbya* but can also be seen to some extent in most of the other species. The only exception is *Nostoc* sp. (N52) (Plate 4, Fig. 1) in which there is a tendency to form a reticular network; this organism is one which seems to have an inherently low growth rate (J. S. Bunt, personal communication). In one cell of *Fischerella muscicola* a system of more densely staining membranes, arranged in a fairly tightly wound spiral, was seen; this system of membranes is apparently connected to the membranes of the photosynthetic lamellae.

One species at least, *Nostoc muscorum*, is known to go through a complex vegetative life cycle (Lazaroff and Vishniac 1961). Plate 2, Figure 2, shows a filamentous stage and Plate 2, Figure 3, an aseriate stage in this life cycle. Although cell shape and direction of cell division vary, no variation in the basic structural components can be detected. An enlarged view of the vegetative cells of a filamentous stage is given in Plate 3, Figure 1.

The basic lamellar organization in the peripheral region can also be detected by light microscopy (Geitler 1958).

(ii) *Central Region*

This region of the cytoplasmic matrix is distinguished by the absence of photosynthetic lamellar system and the presence of crystalline granules and areas of low electron density (see especially Plate 6, Fig. 1, and Plate 7, Fig. 2). Ribosome-like granules occur in this region although they are also scattered throughout the rest of the cytoplasmic matrix.

It is known from both staining reactions in the light microscope (Cassel and Hutchinson 1954) and appearance in the electron microscope (Hopwood and Glauert

1960) that the central region probably includes all of the nuclear material of the cell. It has not been possible to arrive at a more precise localization although the areas of low electron density seen in all the permanganate-fixed material do show a strong resemblance to the nucleoid region of the bacterial cell. After osmium fixation a coarse fibrillar network is seen in parts of the central region (Plate 2, Fig. 1; Plate 5, Fig. 2).

(iii) *Granular Inclusions*

(1) *Crystalline Granules.*—These are seen clearly in the central region in most sections of permanganate-fixed cells (Plate 1) and can also be seen after osmium fixation. Serial sections have shown these to be somewhat flattened platelets approximately 0·1 μ thick.

These granules are probably identical with the bodies tentatively regarded as "nuclei-equivalents" by Hall and Claus (1962). However, the dissimilarity between the crystalline granules and both the chromosomes of higher organisms, and the nucleoids of bacteria, makes this identification by Hall and Claus doubtful.

(2) *Spherical Bodies.*—These are approximately 300 Å in diameter and are commonly present in the cytoplasmic matrix between the photosynthetic lamellae in permanganate-fixed (Plate 9, Fig. 5) but not osmium-fixed cells. Bodies of similar dimensions between the photosynthetic lamellae are also found in osmium-fixed cells after staining on the grid with lead hydroxide (Ris and Singh 1961). The similarity in size and distribution may demonstrate that the spherical bodies seen after both types of fixation are identical. Extremely high numbers are formed in dark-grown cells supplied with 1% glucose as a carbon source (Plate 3, Fig. 2).

(3) *Ribosomes.*—In all species electron-dense granules approximately 150 Å in diameter occur throughout the matrix of the protoplast between the photosynthetic lamellae and in greatest concentrations in the central region after osmium-fixation (Plate 5, Fig. 2), but are not seen in permanganate-fixed cells. In their size and reaction to fixatives these granules are similar to the ribosomes of higher plants and animals.

(4) *Structured Granules.*—These are apparently identical with granules tentatively identified by Drews and Niklowitz (1957) as possible mitochondrial equivalents. At the structural level this equivalence seems improbable since the structure of these granules (e.g. Plate 6, Fig. 1) is not based on the system of unit membranes, characteristic of the mitochondria of the higher plants and animals. These granules are always found in the peripheral region. Proof of functional equivalence must await biochemical analysis of cellular fractions. No structures resembling the mitochondria of higher organisms were seen in any of the species examined.

(iv) *Globular Inclusions*

After permanganate, but not osmium, fixation, round electron-dense inclusions are found in the central region of *Anabaena* sp. (L14) (Plate 5, Fig. 1), but not in any other species.

(v) *Vacuoles*

Two types of vacuoles are observed. One, which is delimited by the photosynthetic lamellae and is found in all species examined, may be a fixation artefact formed by the swelling apart of the double membranes of these lamellae (Plate 8, Fig. 2). The other type, which is much larger, is not apparently delimited by an obvious unit membrane although some kind of boundary layer does exist. Possibly a definite membrane is destroyed during fixation (Plate 4, Fig. 1). These vacuoles may correspond to the gas vacuoles which are characteristic of many species of blue-green algae (Fritsch 1945).

IV. Conclusions

From the observations described in this paper and those published in the literature, the fine structure of the vegetative cells appears essentially similar in species from widely different families of the blue-green algae, including unicellular and filamentous forms at widely different growth stages. The different structures described are common to the vegetative cells of all species so far examined, and a basic structure can therefore be defined as in Figure 1, for the blue-green algal vegetative cell. These structural components all seem to be set in a cytoplasmic matrix which extends throughout the cell. The actual proportions and concentrations of these cell components show species variations.

The cell is characterized by a low level of structural differentiation compared with the cells of higher organisms, and more closely resembles the organization of the bacterial cell. Membrane-bounded organelles of the category chloroplast, mitochondrion, nucleus, and golgi body are absent. Endoplasmic reticulum cannot be recognized as such and is probably also absent. Yet functionally the cell must be as highly differentiated as the structurally more complex cells of higher organisms, at least in so far as the major processes such as photosynthesis, respiration, protein synthesis, and so on are concerned. The blue-green algal cell, therefore, is characterized by a high level of biochemical and physiological organization, and a low level of structural organization. The only structures which appear common to the vegetative cells of the blue-green algae and of the higher plants are the dense granules approximately 150 Å in diameter. These have the structural characteristics of ribosomes and therefore are likely to be sites of protein synthesis. Several structure–function equivalents have been postulated, including photosynthetic lamellae—chloroplast, low electron density areas in central region—nucleus, plasma membrane—plasmalemma, but respiratory equivalents have not been suggested. Although "equivalents" have been postulated there is little definitive biochemical data supporting these speculations. Their identity must await the correlation of structure with biochemical processes in whole cells and isolated fractions.

V. Acknowledgments

The authors are indebted to Dr. D. G. Drummond for assistance during the course of the work and for the use of the facilities of the Electron Microscope Unit, University of Sydney. The work was supported by a University of Sydney Research Grant.

VI. References

Bunt, J. S. (1961).—*Nature* **192**: 479–80.

Cassel, W. A. and Hutchinson, W. G. (1954).—*Exp. Cell Res.* **6**: 134–50.

Drews, G., and Niklowitz, W. (1956).—*Arch. Mikrobiol.* **24**: 147–62.

Drews, G., and Niklowitz, W. (1957).—*Arch. Mikrobiol.* **25**: 333–51.

Fritsch, F. E. (1945).—"Structure and Reproduction of the Algae." Vol. 2. (Cambridge Univ. Press.)

Geitler, L. (1958).—*Arch. Mikrobiol.* **29**: 179–88.

Hall, W. T., and Claus, G. (1962).—*Protoplasma* **54**: 355–68.

Hopwood, D. A., and Glauert, A. M. (1960).—*Biophys. Biochem. Cytol.* **8**: 813–24.

Lazaroff, N., and Vishniac, W. (1961).—*J. Gen. Microbiol.* **25**: 365–74.

Lefort, M. (1960*a*).—*C.R. Acad. Sci., Paris* **250**: 1525–7.

Lefort, M. (1960*b*).—*C.R. Acad. Sci., Paris* **251**: 3046–8.

Menke, W. (1961).—*Z. Naturforsch.* **16b**: 543–6.

Mercer, E. H., and Birbeck, M. S. C. (1961).—"Electron Microscopy: a Handbook for Biologists." (Blackwell Scientific Publications: Oxford.)

Niklowitz, W., and Drews, G. (1956).—*Arch. Mikrobiol.* **24**: 134–46.

Niklowitz, W., and Drews, G. (1957).—*Arch. Mikrobiol.* **27**: 150–65.

Palade, G. E. (1952).—*J. Exp. Med.* **95**: 285.

Ris, H., and Singh, R. N. (1961).—*Biophys. Biochem. Cytol.* **9**: 63–80.

Robertson, J. D. (1960).—Proc. 4th Int. Congr. Electron Microscopy, Berlin, 1958. Vol. 2. pp. 159–71. (Springer-Verlag: Berlin.)

Shatkin, A. J. (1960).—*Biophys. Biochem. Cytol.* **7**: 583–4.

Stanier, R. Y., and Niel, C. B. van (1962).—*Arch. Mikrobiol.* **42**: 17–35.

Explanation of Plates 1–9

Plate 1

Anabaena sp. (L14), permanganate fixed, showing photosynthetic lamellae (*P.L.*); central region (*C.R.*) with crystalline granules (*C.G.*) and scattered areas of low electron density (*N*); granules (*G*) 300 Å in diameter are associated with the photosynthetic lamellae; globular inclusions (*G.I.*), found only in this species. Magnification: 20,000 × 2·2—(44,000).*

Plate 2

Fig. 1.—*Chroococcus prescotii*, osmium fixed, showing photosynthetic lamellae (*P.L.*); osmiophilic layer of inner investment (*O.L.*); central region (*C.R.*); ribosome-like granules (*R*). 20,000 × 1·7—(34,000).

Fig. 2.—*Nostoc muscorum*, filamentous stage, permanganate fixed, showing peripheral photosynthetic lamellae (*P.L.*); central region containing crystalline granules. The large cells of low electron density (*H*) are heterocysts which will be discussed in a subsequent paper. 1630 × 1·7—(2800).

Fig. 3.—*Nostoc muscorum*, aseriate stage, permanganate fixed, showing peripheral photosynthetic lamellae (*P.L.*); heterocysts (*H*). 1630 × 1·6—(2600).

* The magnification at which the plate was originally taken and the photographic enlargement, respectively, are given. The value in brackets is the total magnification.

PLATE 3

Fig. 1.—*Nostoc muscorum*, permanganate fixed, grown in the light, showing photosynthetic lamellae (*P.L.*); central region with areas of low electron density (*N*) and crystalline granules (*C.G.*); granules 300 Å in diameter are associated with the photosynthetic lamellae. 6400 × 1·5—(9600).

Fig. 2.—*Nostoc muscorum*, permanganate fixed, grown in the dark, showing photosynthetic lamellae (*P.L.*); granules 300 Å in diameter; slime layer (*S.L.*). 6400 × 1·7—(11,000). *Inset*: showing the lamellae to be made up of two unit membranes. 40,000 × 4—(160,000).

PLATE 4

Fig. 1.—*Nostoc* sp. (N52), permanganate fixed, showing reticular network of photosynthetic lamellae (*P.L.*); intercellular connections (*I.C.*); vacuole bounded by the membranes of a photosynthetic lamella (*V*); gas vacuole (*G.V.*); central region with crystalline granules (*C.G.*). 20,000 × 1·7—(34,000). *Inset*: showing the intercellular connections (indicated by arrows). 20,000 × 4·5—(90,000).

Fig. 2.—*Anabaena cylindrica*, permanganate fixed, plasmolysed in 3·0M NaCl, showing investment membrane (*I.M.*); inner investment (*I.I.*); plasma membrane (*P.M.*) which has contracted, with the protoplast, away from the inner investment. 40,000 × 1·8—(72,000).

PLATE 5

Fig. 1.—*Anabaena* sp. (L14), permanganate fixed, showing photosynthetic lamellae (*P.L.*); granules 300 Å in diameter (*G*); globular inclusion (*G.I.*); structured granules (*S.G.*). 20,000 × 2·2—(44,000).

Fig. 2.—*Anabaena* sp. (L14), osmium fixed, showing photosynthetic lamellae (*P.L.*); plasma membrane (*P.M.*); osmiophilic layer (*O.L.*) of inner investment; ribosome-like granules (*R*). 20,000 × 1·8—(36,000). *Inset*: osmiophilic layer (*O.L.*) of inner investment which forms the dividing wall. A lighter region can be seen in the middle of the dividing wall. 20,000 × 1·8—(36,000).

PLATE 6

Fig. 1.—*Lyngbya majuscula*, permanganate fixed, showing photosynthetic lamellae (*P.L.*); structured granules (*S.G.*); central region with areas of low electron density (*N*); gas vacuole (*G.V.*); slime layer (*S.L.*). 20,000 × 1·7—(34,000).

Fig. 2.—*Spirulina major*, permanganate fixed, showing photosynthetic lamellae (*P.L.*) which have swollen in parts to form vacuoles (*V*); central region with areas of low electron density (*N*). 10,000 × 1·9—(38,000).

PLATE 7

Fig. 1.—*Calothrix anomala*, permanganate fixed, showing slime layer (*S.L.*); photosynthetic lamellae (*P.L.*); central region with crystalline granules (*C.G.*). 10,000 × 2·5—(25,000).

Fig. 2.—*Plectonema boryanum*, permanganate fixed, showing slime layer (*S.L.*); photosynthetic lamellae (*P.L.*); gas vacuole (*G.V.*); central region with areas of low electron density (*N*). 20,000 × 1·7—(34,000).

PLATE 8

Fischerella muscicola, a heterotrichous genus with basal filaments, which are attached to the substrate, and erect filaments. The basal filaments are made up of large, round cells many of which are reproductive types—the akinetes. The erect filaments are made up of longer, smaller cells

Fig. 1.—An erect filament, permanganate fixed, showing slime layer (*S.L.*); photosynthetic lamellae (*P.L.*); central region with crystalline granules (*C.G.*) and areas of low electron density (*N*). 2500 × 3·8—(9500).

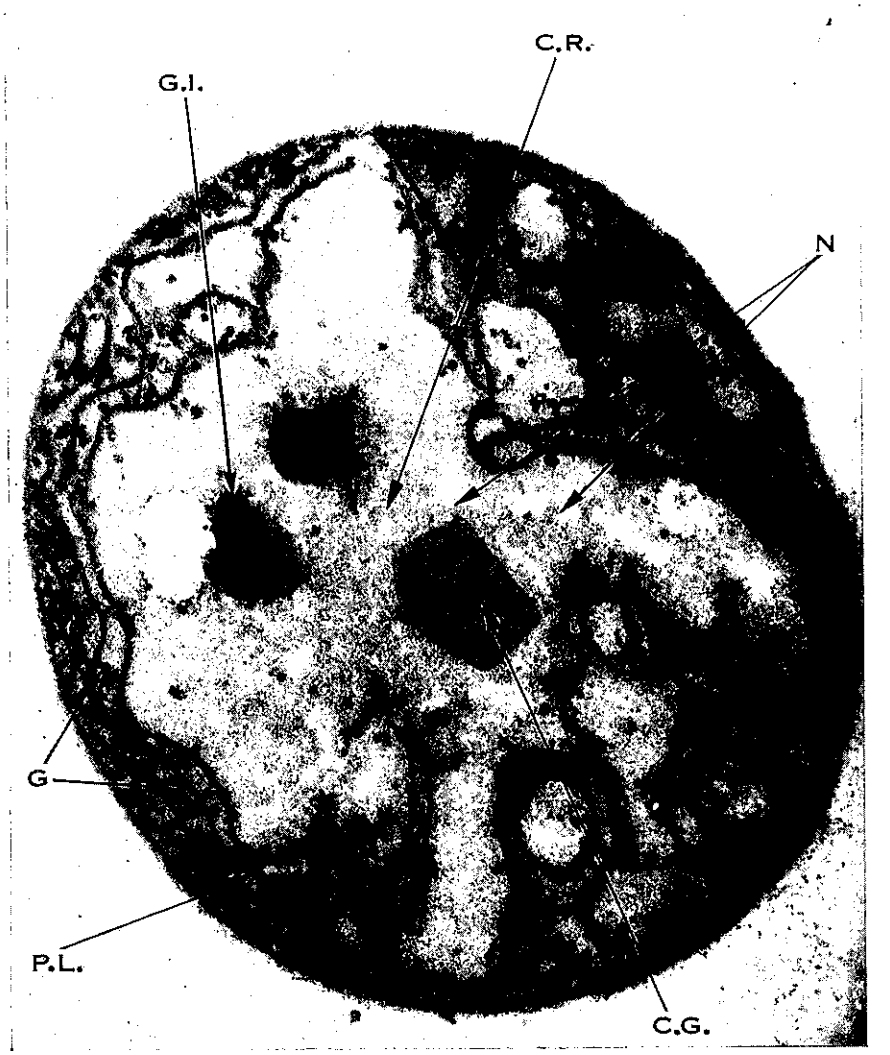
Fig. 2.—A basal filament, permanganate fixed, showing photosynthetic lamellae (*P.L.*), many of which have swollen apart to form vacuoles (*V*); central region with crystalline granules (*C.G.*) and areas of low electron density (*N*); slime layer (*S.L.*). 10 000 × 1·7—(17,000).

Plate 9

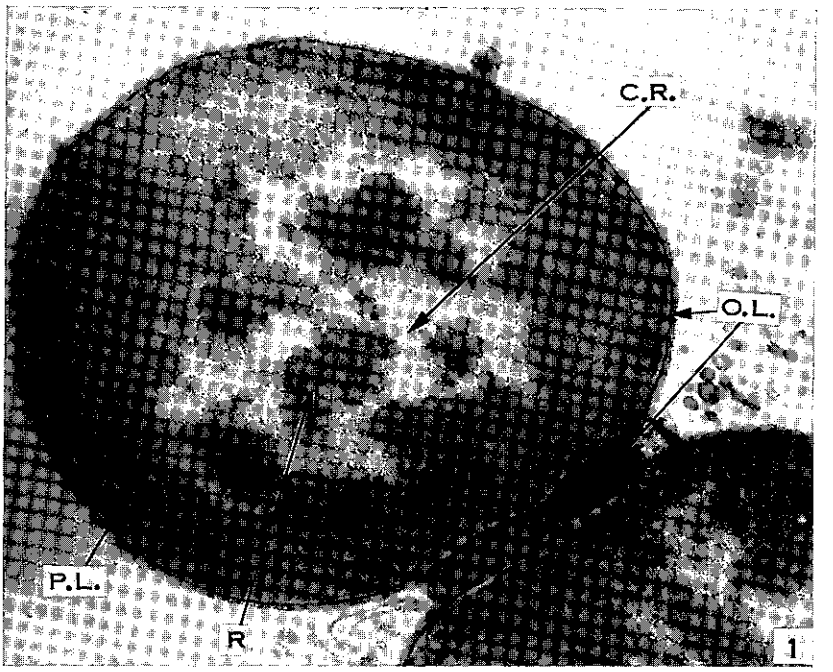
Figs. 1–3.—*Nostoc* sp. (N52), permanganate fixed, serial sections each approximately 300 Å thick showing continuity of photosynthetic lamellae (*P.L.*) through the three sections; plasma membrane (*P.M.*). 20,000 × 4—(80,000).

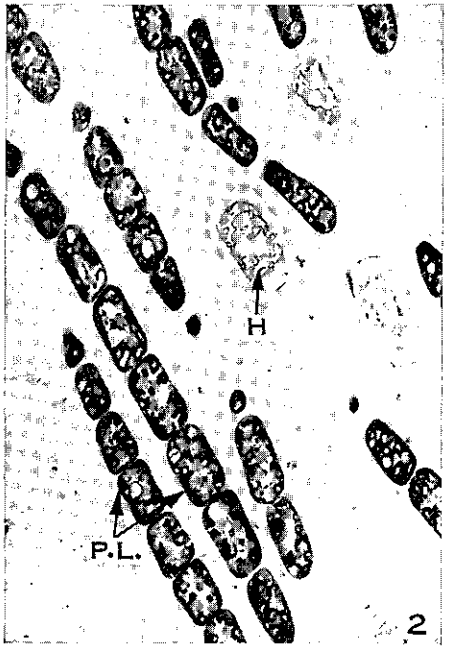
Figs. 4–6.—*Anabaena* sp. (L14), permanganate fixed, through-focus series, showing photosynthetic lamellae (*P.L.*), granules (*G*) approximately 300 Å in diameter, plasma membrane (*P.M.*). 20,000 × 6·5—(130,000). *4*, underfocussed: note blurring and thickening of membranes; *5*, in focus: the two unit membranes of each photosynthetic lamella can be seen as well as the plasma membrane which consists of a single unit membrane; *6*, overfocussed: note the large number of lines corresponding to phase bodies.

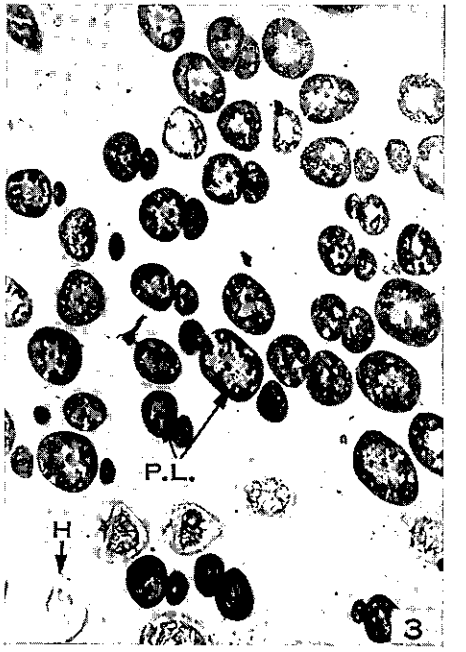
ULTRASTRUCTURE OF BLUE-GREEN ALGAE



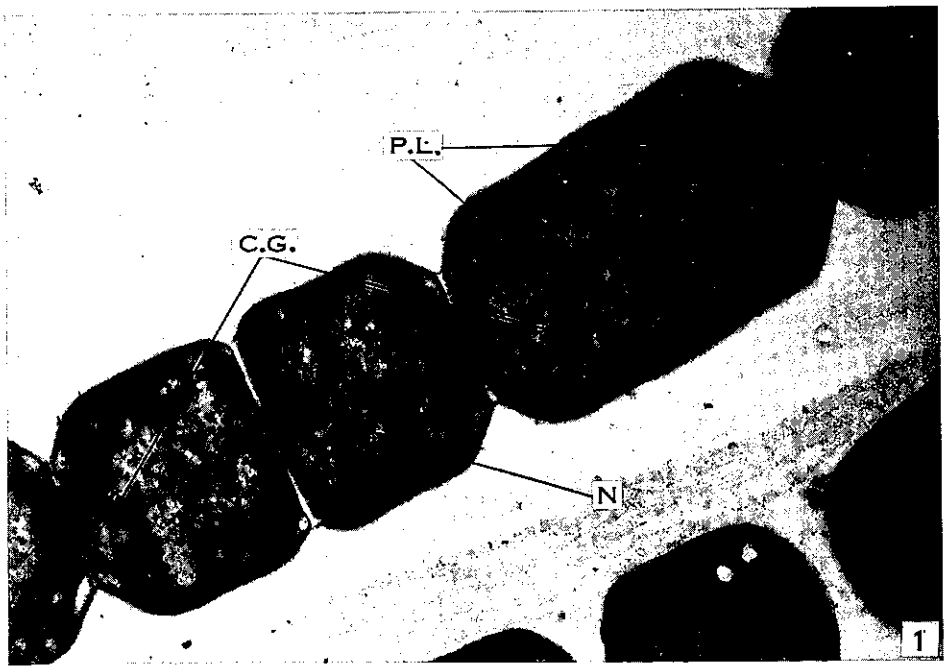
ULTRASTRUCTURE OF BLUE-GREEN ALGAE

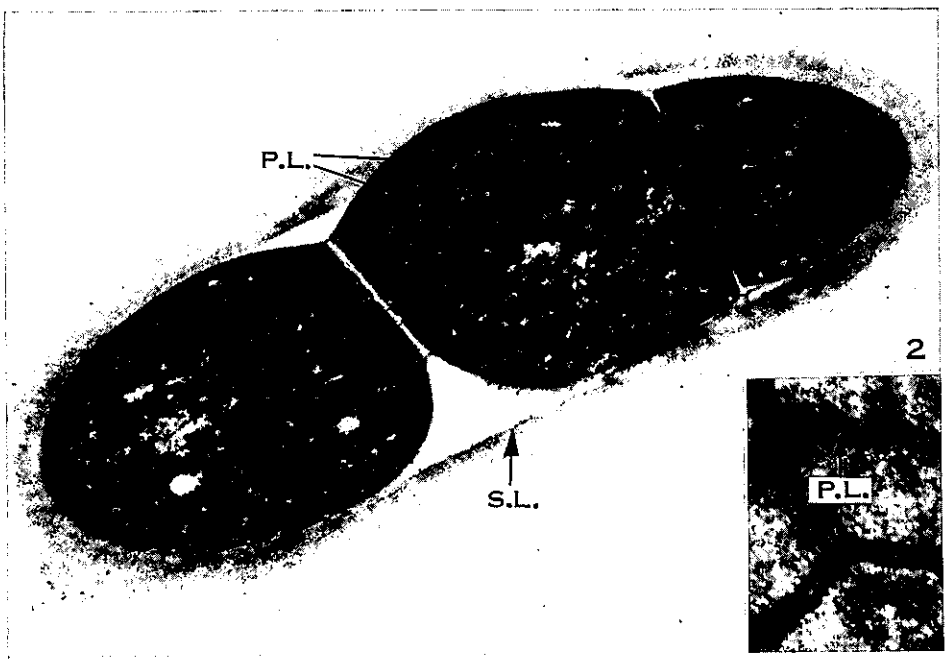




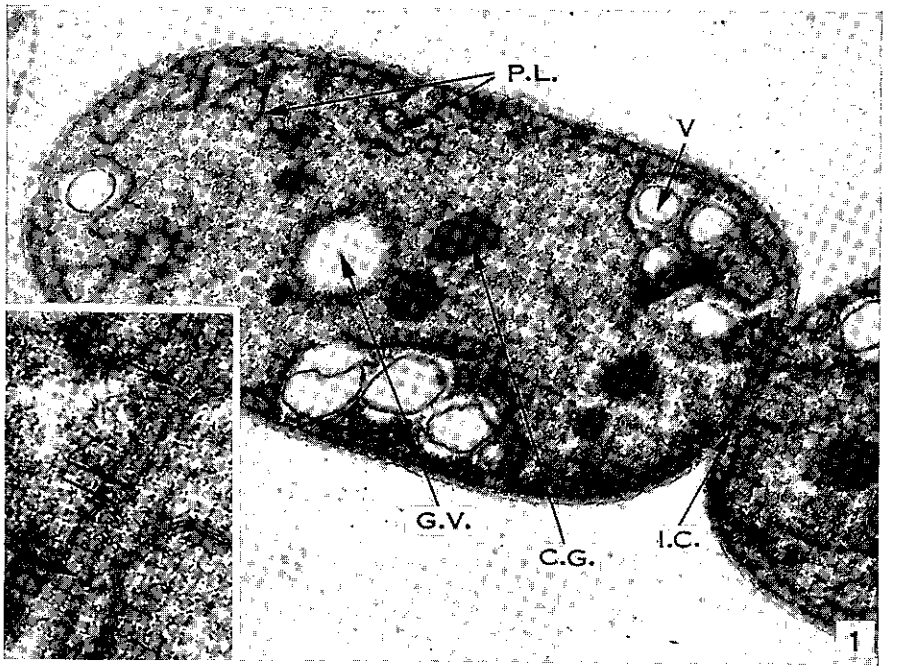


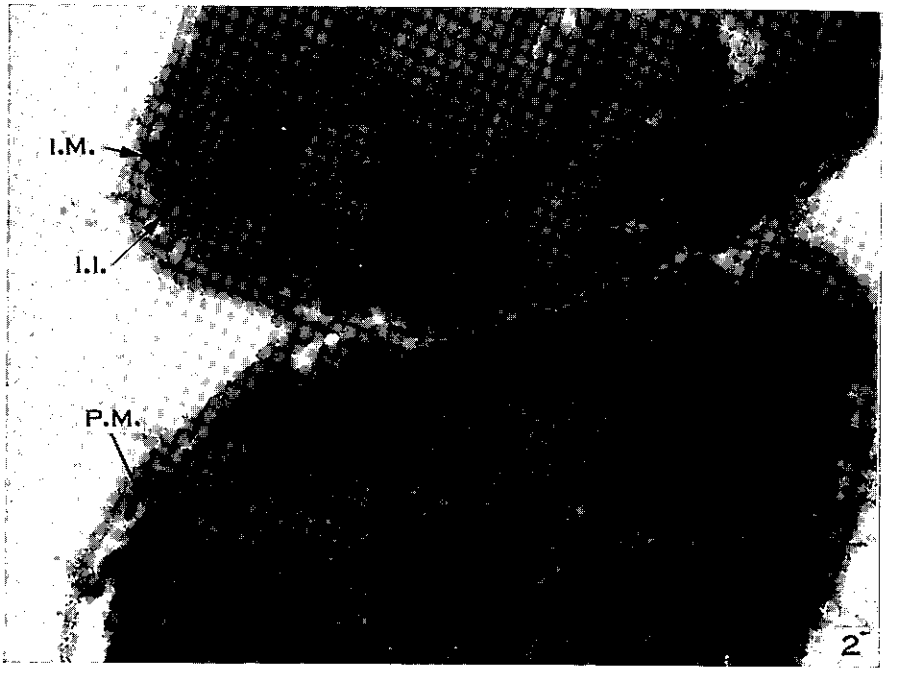
ULTRASTRUCTURE OF BLUE-GREEN ALGAE



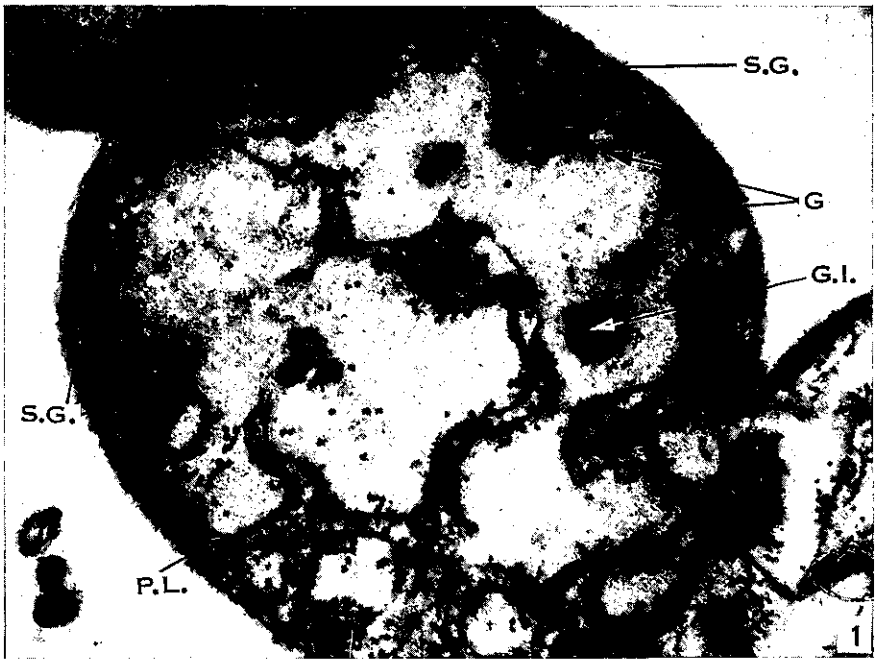


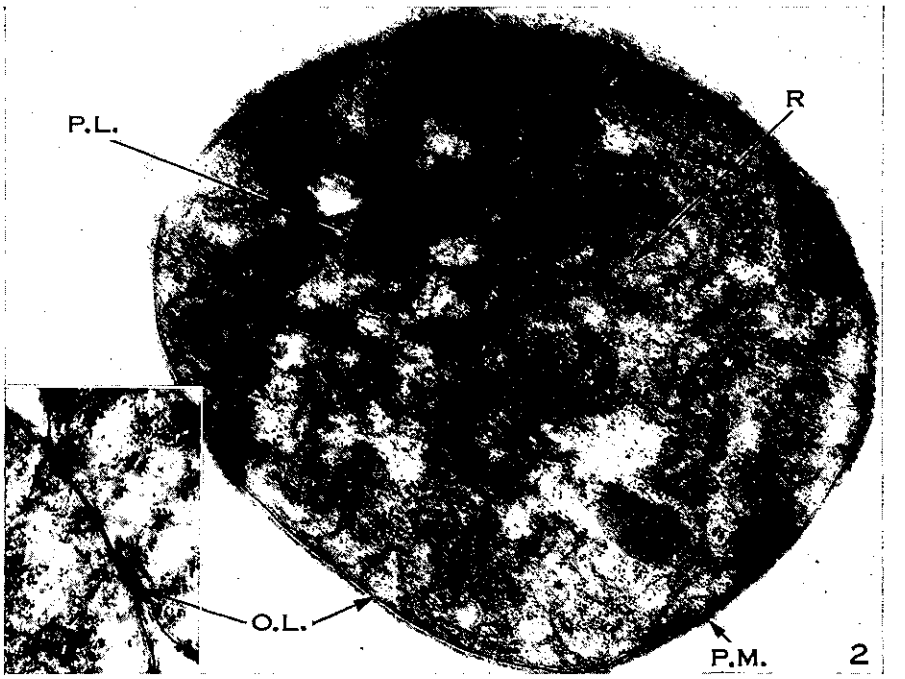
ULTRASTRUCTURE OF BLUE-GREEN ALGAE



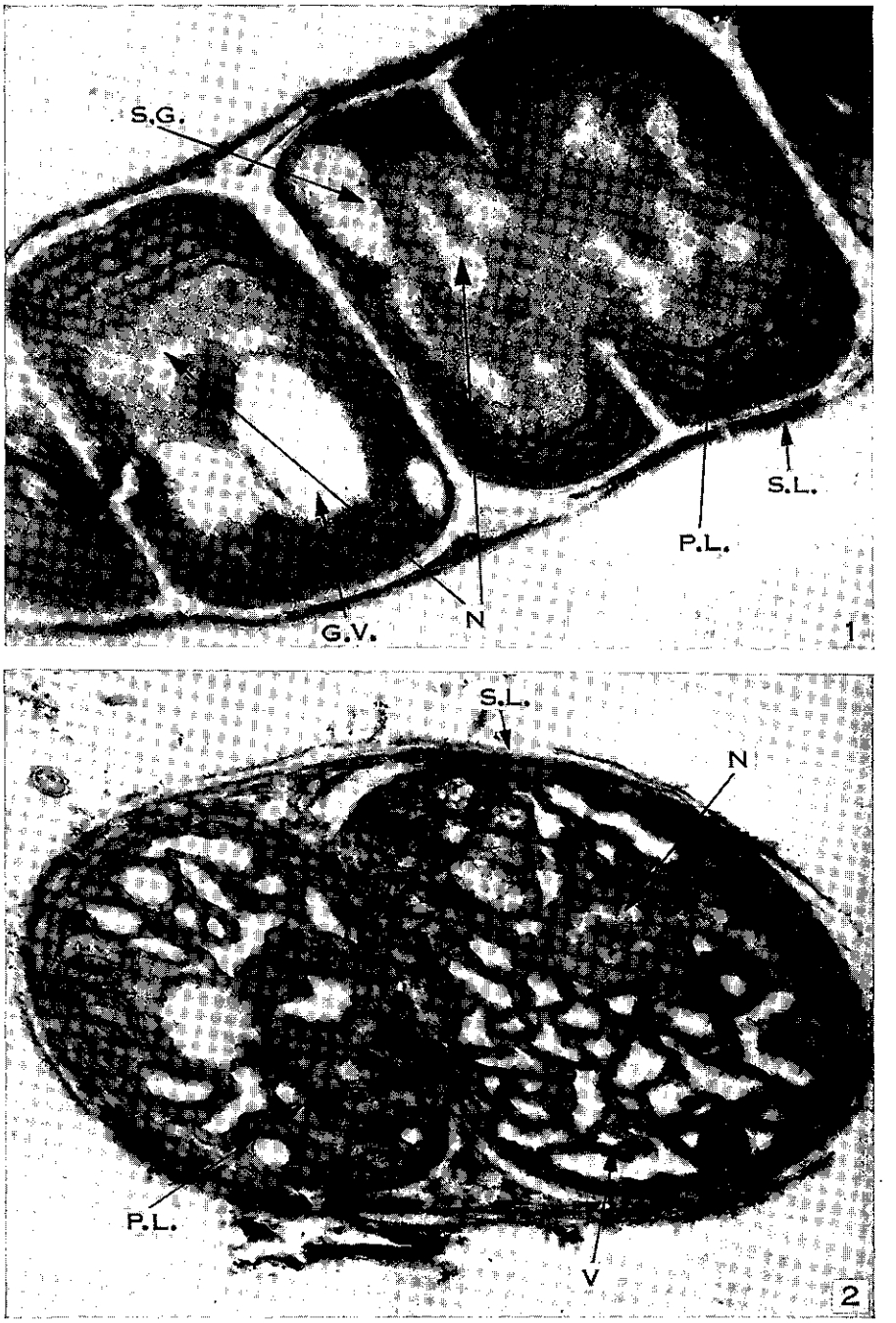


ULTRASTRUCTURE OF BLUE-GREEN ALGAE

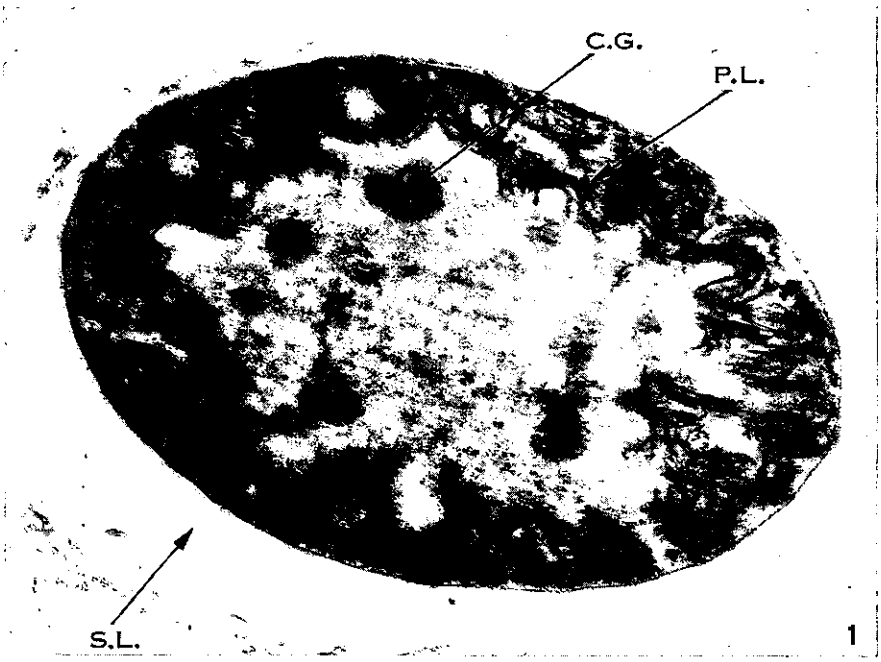


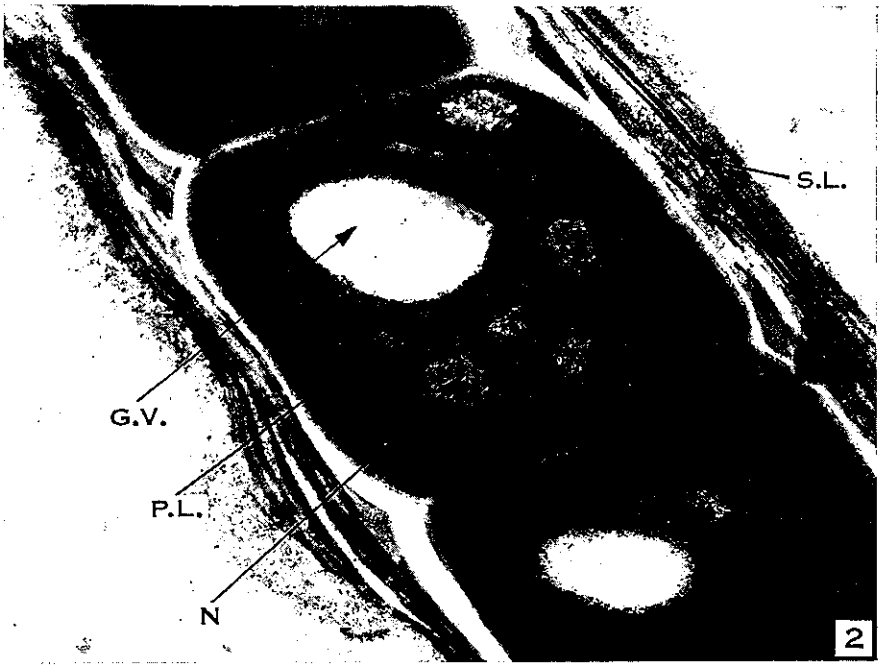


ULTRASTRUCTURE OF BLUE-GREEN ALGAE

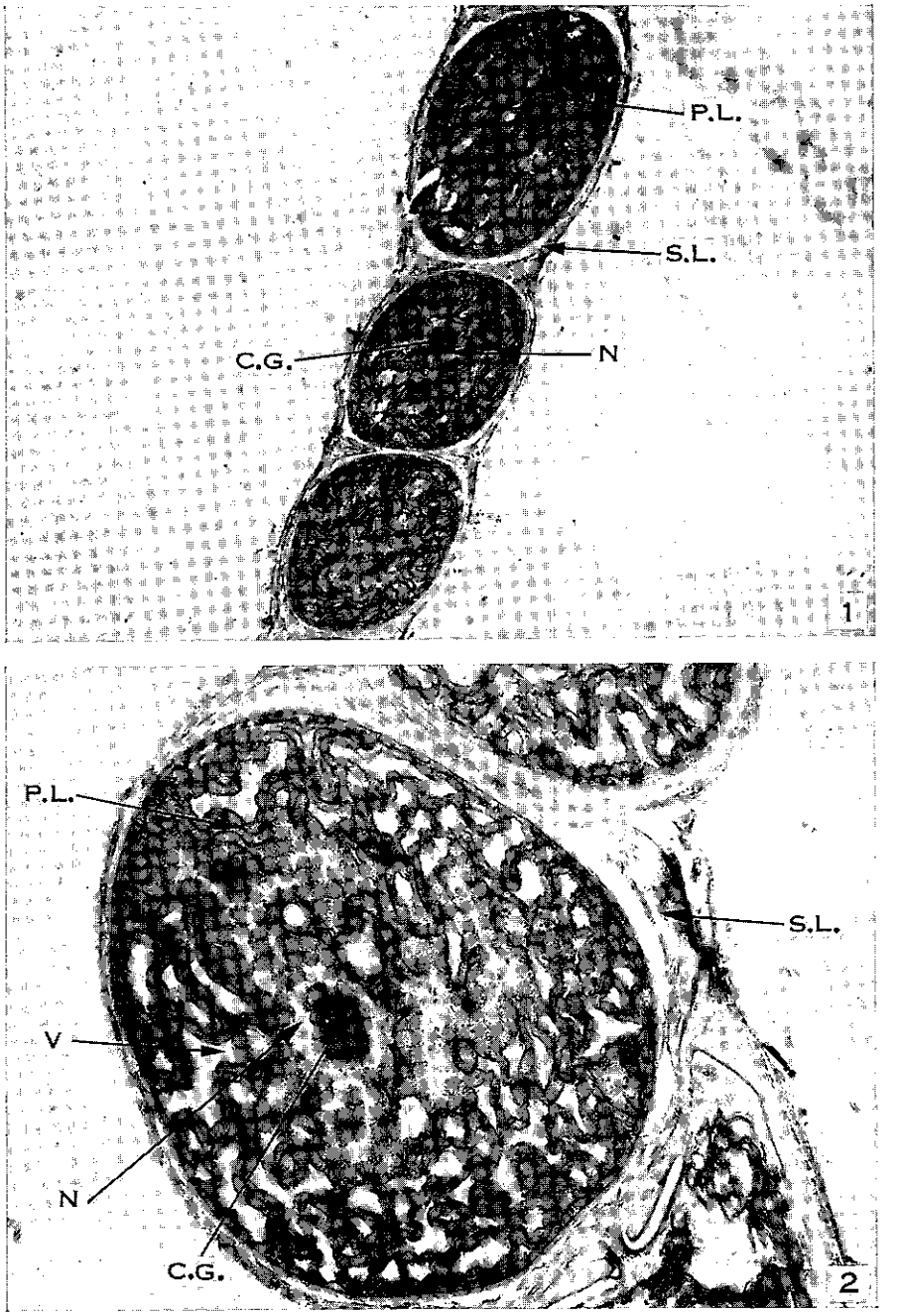


ULTRASTRUCTURE OF BLUE-GREEN ALGAE





ULTRASTRUCTURE OF BLUE-GREEN ALGAE



ULTRASTRUCTURE OF BLUE-GREEN ALGAE