ANNUAL GENERAL MEETING.

28th March, 1956.

The Eighty-First Annual General Meeting was held in the Society Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 28th March, 1956.

Dr. F. V. Mercer, President, occupied the chair.

The minutes of the Eightieth Annual General Meeting, 30th March, 1955, were read and confirmed.

Presidential Address.

For the second time it is my privilege to deliver the Presidential Address of the Linnean Society of New South Wales. Now, more than before, I am conscious of the high honour which this Society has given me. More than ever, I realize the tremendous debt which the Society owes to Dr. W. R. Browne and Dr. A. B. Walkom. On behalf of the Society, I pay tribute to these men so they may know we do not take their activities for granted. Also I know you would wish me to express our gratitude to Miss G. L. Allpress for her loyal and able services.

During 1955 a number of changes in the personnel of the Council occurred. Professor P. D. F. Murray resigned from the Council as from 23rd March, 1955, and Mrs. Dorothy A. Thorp, B.Sc. (Lond.) (Mrs. Ronald Thorp) was elected in his place on 20th April, 1955. Mr. D. J. Lee ceased to be a member of Council as from 18th May, 1955, and Mr. A. J. Bearup, B.Sc., was elected in his place. On 22nd June, 1955, Dr. Lilian Fraser was elected a Vice-President in place of Mr. D. J. Lee. On 23rd November, 1955, Dr. J. W. Evans was elected a Member of Council in place of Dr. G. D. Osborne, who died on 5th October, 1955. Professor J. Macdonald Holmes resigned from the Council on 14th December, 1955.

During the year sixteen new members were added to the list, three members were lost by death, seven have resigned, and two were removed from the list under Rule VII. The numerical strength of the Society at 15th March, 1956, was: Ordinary Members 206, Life Members 28, Corresponding Members 2, Associate Member 1. Total 237.

Parts 1 and 2 of Volume 80 of the Society's Proceedings were published on 19th July and 5th October, 1955, respectively, and Part 3, the printing of which was unavoidably delayed, should appear during April, 1956. The entire cost of publication of the paper entitled "The Australasian Diptera of J. R. Malloch" was borne by the School of Public Health and Tropical Medicine, University of Sydney. An increase in printing charges was made as from February, 1956.

Library accessions from scientific societies and institutions totalling 2,007 (including 166 pamphlets presented by Dr. C. E. M. Gunther) exceeded the total for the previous year. Requests for library loans of periodicals and books to local and interstate institutions and Universities were as numerous as previously. Further subscribers to the Proceedings have received the Parts as issued. Sets of the Proceedings have been purchased by overseas institutions, and the demand for reprints continues to be keen. A duplicate copy of "The Australian Portrait Gallery and Memoirs of Representative Colonial Men", Sydney, 1844, was presented to the Fisher Library, University of Sydney. A collection of old maps and diagrams was handed to the Fisher Library, University of Sydney, on 13th October, 1955, for distribution to the Fisher Library, the Mitchell Library (eleven maps were received by that Library), and University Department Libraries, by the Librarian, Fisher Library. Exchange relations with two institutions were discontinued during the year. Exchanges of publications for our Proceedings were commenced with the following: Museum G. Frey, Tutzing, Germany (instead of Entomo-

logical Reprints); Musée d'Histoire Naturelle, Skopje, Jygoslavie; and Estacion Experimental de Aula Dei, Zaragoza, Spain; and reprints from the Proceedings were offered to the Department of Entomology, University of Queensland (entomological); Instytut Geologiczny, Warszawa, Poland (geological and palaeontological); Instituto Botanico, Madrid, Spain (botanical); Instituto de Aclimatacion, Almeria, Spain (zoological, including entomological); Institute of Polytechnics, Osaka City University, Osaka, Japan (botanical and zoological, including entomological); Academia Republicii Populare Romane, Bucuresti, Roumanis (zoological, including entomological) and Polski Zwiazek Entomologiczny, Warszawa, Poland (entomological). Council decided to purchase the following for the Library: Novitates Zoologicae, Vols. 7–20 inclusive, and "The Literature of Australian Birds: a History and a Bibliography of Australian Ornithology" by Hubert Massey Whittell.

No Ordinary Monthly Meeting was held in August, 1955. The following items of special interest were given at the Monthly Meetings:

May: Symposium—Notes on recent botanical researches in the Kosciusko region, by Mr. Barlow, Mr. Smith-White, Miss Briggs, Dr. Hotchkiss and Miss Macdonald.

June: Lecturette—Cicadas and their allies, by Dr. J. W. Evans.

July: Film of the 1939 Simpson Desert Expedition which was led by the late Dr. C. T. Madigan; shown by Professor R. L. Crocker.

September: Lecturette—The Differentiation of Secondary Cartilage, by Professor P. D. F. Murray.

November: Lecturette—Dr. James Stuart: Artist-Naturalist, by Messrs. A. Musgrave and G. P. Whitley.

We wish to express our thanks and appreciation to all who contributed to these programmes.

In consequence of the Science House Management Committee's successful application to the Fair Rents Court, a greatly increased revenue to the Society (£1,083, net share for the year) has been received.

A seventh and very successful trip to the Kosciusko area was made from 16th to 30th January, 1956, by a party of biologists and geologists under the auspices of the Joint Scientific Advisory Committee (comprising members appointed by the Linnean Society of New South Wales, and the Royal Zoological Society of New South Wales). Transport and accommodation were provided by the Departments of Geology and Botany, University of Sydney, and the Department of Tourist Activities and Immigration, N.S.W.

I wish to offer congratulations to Dr. Dorothy E. Shaw, M.Sc.Agr., who obtained the degree of Ph.D., of the University of Manitoba, Canada, in 1955.

Linnean Macleay Fellowships.

In November, 1954, the Council re-appointed Miss Nola J. Hannon, and appointed Miss Mary B. Macdonald to Fellowships in Botany for 1955.

Miss Hannon, during 1955, continued her investigations into the nitrogen economy of Hawkesbury Sandstone communities. Attention was given to the nitrogen levels in the early stages of the lithosere, and also the recolonization and nitrogen accumulation of an area of Hawkesbury Sandstone denuded of soil and plant cover about thirty-eight years ago. Since previous work has shown that the contribution of nitrogen from rainfall and free-living nitrogen-fixing organisms in these communities is very limited, the native legumes are being studied. Nodules on their root systems are commonly found in the field, and leaf analyses show that the legume tissue is considerably richer in nitrogen than most other species. *Acacia suaveolens* (Sm.) Willd., a widespread and common member of these communities, has been chosen as host plant for the study of legume-rhizobia inter-relationships. This species has been grown in the presence of an inoculum of soil taken from each of two hundred sites in the main types of communities in widely separated localities on Hawkesbury Sandstone. This had indicated that rhizobia are widespread in their occurrence, but the effectiveness of the symbiosis,

as measured in terms of plant growth, shows considerable variation. This aspect of the symbiosis is receiving attention.

Miss Macdonald has been studying the family of freshwater Algae known as the Characeae. Early in the year she took part in the expedition to Kosciusko led by Dr. W. R. Browne, and was able to collect several interesting specimens there, and on the return to Sydney, *via* the south coast of New South Wales.

Her work during the year has been concerned with live cultures in the laboratory, and with herbarium specimens on loan from National Herbaria of Victoria and New South Wales. More than two hundred and fifty cultures have been established and maintained, representing most of the twenty-three species which have been collected during the year. Chromosome numbers have been definitely established for about fourteen species, and rough counts made for all remaining species in culture.

Cross-breeding experiments have been performed, probably for the first time in Characeae, and it has been established that *Protochara australis* Womersley and Ophel is non-reciprocally interfertile with *Chara australis* R.Br. A paper entitled "An Estipulodic Form of *Chara australis* R.Br. (= *Protochara australis* Woms. & Ophel)" by Miss Macdonald and Dr. A. T. Hotchkiss will appear in Part 3 of the Proceedings for 1955.

In November, 1955, the Council re-appointed Miss Nola J. Hannon and Miss Mary B. Macdonald to Fellowships in Botany for 1956.

Miss Hannon proposes to continue investigations to estimate the occurrence of legumes and rhizobia in the communities on Hawkesbury Sandstone, and, as far as possible, to obtain a measure of the effectiveness of their symbiosis; also to continue the work on an area of Hawkesbury Sandstone denuded of soil and plant cover about thirty-eight years ago.

Miss Macdonald was married on 21st January, 1956, to Mr. J. B. Williams. Mrs. Mary B. Williams proposes a continuation of her work on Australian Characeae, including the collection of further data on geographical range and occurrence of species and their behaviour in culture where possible; the collation of such data; investigation of conditions which will break the dormancy of Characeae spores; investigation of segregation characteristics of germinated hybrid spores from the cross between *Protochara australis* and *Chara australis*; and an attempt to synthesize an artificial polyploid by applying the chromosome doubling agent, colchicine.

We wish success to both Fellows in their research work.

Macleay Bacteriologist.

Dr. Yao-tseng Tchan terminated his appointment as Macleay Bacteriologist as from 31st July, 1955, completing five years as Macleay Bacteriologist. He was appointed Senior Lecturer in Microbiology at the University of Sydney, as from 1st August, 1955. Council expressed appreciation of his work, and congratulated him on his appointment. His work for the final period as Macleay Bacteriologist included concentration on the N-fixation of *Beijerinckia* in Northern Australia and New Guinea. Research on Northern Territory soil was continued for which a financial grant from C.S.I.R.O. was received. Many bacteriological analyses have been made, but the final conclusion still requires much more work. Some of the time was used for part-time teaching in the University.

Obituaries.

It is recorded with regret that the following members died during the year:

Edgar Alexander Hamilton, who had been a member of the Society since 1928, died at Chatswood on 25th February, 1956, aged 78. He was a son of Mr. Alexander Greenlaw Hamilton, who was one of the early members of the Society, a member of Council for many years and President, 1915–17. Mr. E. A. Hamilton took a keen interest in the Society in his earlier years, but ill-health prevented his active interest in later years. He was a graduate of Hawkesbury Agricultural College, having entered the College in 1895. He was a member of the N.S.W. Naturalists' Society and a foundation member and President of the Orchid Society of N.S.W., for a number of years. For some years before his retirement he was Chairman of the Milk Board.

Benzoin Horowitz, D.Agr.Sc., Principal Research Officer of the Division of Plant Industry, C.S.I.R.O., died on 10th October, 1955, while on an official visit in Queensland. Dr. Horowitz graduated as an Engineer of Agricultural Science and later as Doctor of Agricultural Science at the University of Cracow, Poland. After working on a number of plant breeding projects involving a wide variety of crops, he left Poland and arrived in Australia in 1941. In Australia, Dr. Horowitz took up an appointment with the University of Sydney and later with Drug Houses of Australia, Ltd. Under these appointments he was particularly concerned with aspects of the breeding, cultivation and commercial production of *Nicotiana rustica* as well as other drug and oil plants. Dr. Horowitz joined C.S.I.R.O. in 1949 and was stationed at the Waite Agricultural Research Institute, Adelaide, to collaborate in research on the economic establishment of oil crops in Australia. He was especially interested in safflower; he developed a considerable breeding programme with this crop and organized a chain of tests throughout the agricultural regions of Australia, thereby establishing an effective knowledge of the varieties and areas best suited to the establishment of the crop. Dr. Horowitz was extremely imaginative and hard working and his death was a serious loss to Australian agriculture. He had been a member of this Society since 1943.

George Davenport Osborne died on 5th October, 1955, at Sydney. Dr. Osborne studied under the late Professor Sir Edgeworth David, and, following his graduation, joined the Department of Geology as Demonstrator. In 1925 he held a Linnean Macleay Fellowship, resigning in December, 1925, on his appointment to a Lectureship in the Department of Geology. In 1949 he was promoted to a Readership. He also acted for many years as Lecturer in Geology in the Sydney Technical College, and later as Lecturer to the Workers' Educational Association.

His enthusiasm, and his gift of interesting exposition as a teacher, particularly on excursions in the field, were an inspiration to many privileged to be under his instruction. He was a consistent worker in the cause of Science, and served on many committees and in a number of honorary positions to assist societies and associations. He was a member of this Society from 1921, a member of Council from March, 1942, till his death, and President, 1947–48.

Cytology and the Electron Microscope.

Selecting a topic suitable for the members of a society which was founded for the study of, and which is still actively concerned with, Natural History in all its aspects is not an easy matter, particularly for one who is not a "field" botanist. However, in choosing as the subject for my address "Cytology and the Electron Microscope", I hope to fulfil some of the objects for which this Society was founded. Before commencing I should like to stress that my address has been made possible only by the collaborative efforts of Dr. A. Hodge of the Division of Industrial Chemistry, C.S.I.R.O., Melbourne, and Mr. J. D. McLean of the Botany Department, University of Sydney.

The development of our knowledge of the world is based upon our senses—the sense of touch, of smell, of sight, of hearing and of taste. In the evolution of this knowledge the unaided senses have proved powerful "tools", but, sooner or later, further advancement is prevented by the limits imposed by their sensitivity. This point is well illustrated in the history of Botany by the way our ideas about the nature of plants have followed aids to our sense of vision.

Prior to the light microscope, the study of plant structure was of necessity limited to considerations of the external form of the organs and to gross tissue-differences. By the middle of the 17th century Botanists realized that plants had some sort of structure, in addition to the differentiation into organs, since in the apparently homogeneous organs layers of different composition could be seen. In the stem, for example, such components as wood, pith and rind were recognized. To explain the consistency of these layers it was believed that the woody parts consisted of a fibrous structure, the pith of a succulent homogeneous matrix, and the rind a heterogeneous unit composed of fibrous and pith-like materials. This was the level of knowledge on which the 17th century Botanists endeavoured to interpret the nature of the organism. It is not surprising that many of the views held appear fantastic nowadays. Thus the succulent

nature of the pith along with the bleeding of juices from wounds and from cut stems was taken as proof that the pith is the living part of the plant containing canals analogous to the veins of animals.

Although a far more detailed knowledge of plant structure could have been obtained at this time by more careful observations and better interpretations, the study could never have progressed far because of the limits imposed by the resolution of the eye. The fundamental unit of the organism—the cell—lay hidden. The invention of the microscope increased the sense of sight and made possible that branch of knowledge called Cytology or the study of cells.

The Light Microscope.

The microscope did not immediately influence scientific thought. From 1590 to 1660 the new instrument was regarded more as a toy rather than a scientific instrument—something a gentleman might use to amuse his friends. Also the fact that it was rather cumbersome and difficult to handle did not encourage people to use it. Some instruments were up to six feet in length—more like a telescope than a microscope.

True high-power microscopy and the acceptance of the microscope as a scientific tool followed the introduction of short focus lenses by Robert Hooke (1635–1703) and van Leeuwenhoek (1632–1723). Hooke's microscope was the forerunner of the true compound microscope. It consisted of an objective and eyepiece lenses, and, since it was convenient to use, the microscope was now in a form suitable for systematic research.

By the end of the 17th century microscopes were in use with magnifications up to 150×. Gradually the magnifying power was improved. About 1810, German instruments with 170×–300× magnification were available. In 1812, Moldenhauer was using an instrument with 400× magnification, and in 1824 Silligue was making observations with a 500× microscope. Despite this gradual increase in magnifying power these instruments were relatively inefficient because the lenses were not corrected for chromatic and spherical aberration and the object was viewed dry and by reflected light.

Chevalier in 1823 solved the problem of spherical aberration, and Amice (1840) suggested the idea of an immersion lens, but its application had to wait until the adoption of substage illumination. Within a few years this improvement was introduced by Abbé. Between 1806 and 1856 Abbé evolved the light microscope in its present form. He introduced the substage condenser, the homogeneous oil immersion technique, and chromatic objectives, and placed the optical theory of the microscope on a firm basis. Since that time there have been no fundamental improvements in the performance of the light microscope.

The nineteenth century saw the general acceptance of the optical microscope by scientists, and as an outcome of this the appearance of the commercial manufacturers to supply the growing demand.* It is a chastening thought to remember that until the present century good microscopes were comparatively rare. Instruments were the product of individual craftsmen and were in limited supply. More often than not the operator of a microscope not only had to know his own special field, but also had to make his own instrument, to be able to grind lenses, and so on.

The twentieth century has yielded nothing new, apart from phase contrast (1935) and the ultraviolet microscope. It has been a period of refinement of the product combined with mass production such that superb microscopes are now freely available.

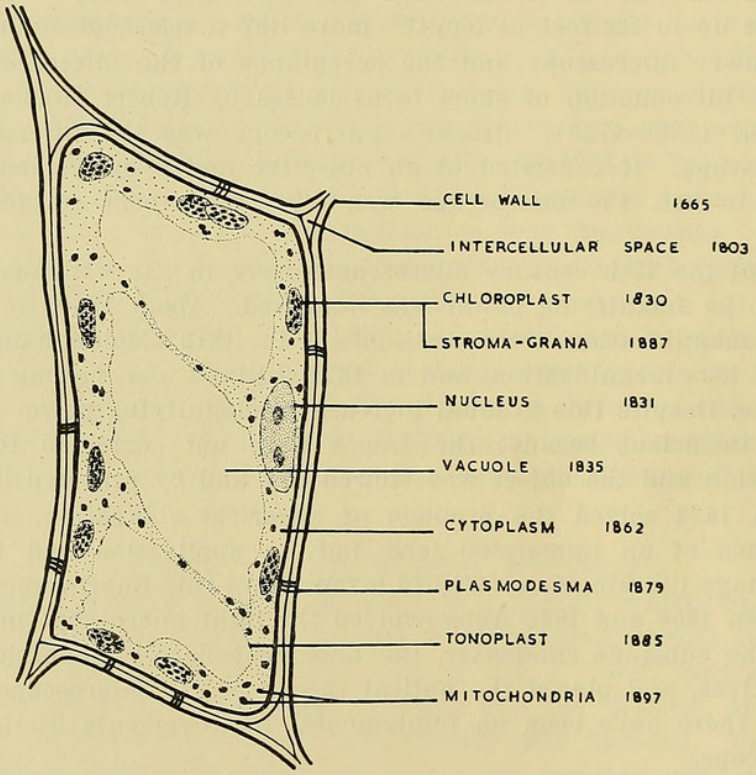
Three hundred years have passed during the evolution of the light microscope. In that time it has changed from a cumbersome oddity to a precision instrument, and from a toy to being the most essential of all biological equipment. It has increased the power of vision a thousand-fold and made possible the cell theory of organism. Unfortunately, further improvement is impossible because of the inherent limitations imposed by the wave length of visible light. Abbé in 1865 showed that the limits of resolution are inflexibly fixed by the wave length of the light used to view an object. With visible

* Firms such as Beck (1830), Zeiss (1846), Spencer (1847), Leitz (1865) and Bausch (1872) came into being in response to the demand.

light the limit of resolution is *c.* 0·2μ; objects smaller than this must remain hidden. We have come full circle. The modern Botanist is in a position similar to that of his 17th century counterpart. His ability to observe is at the limits imposed by his sense of vision.

The Structure of the Cell.

The introduction of the light microscope did not immediately lead to discoveries about cell structure. This was due partly to the relatively long time taken in perfecting the microscope, and partly to the technique of viewing dry mounts by reflected light. It is not surprising, therefore, that until the beginning of the 19th century Botanical interest was centred around the structural inter-relationships of the tissues, and the cell wall. The so-called "juices" and slime which exuded from cut tissues were hardly studied; in fact they were considered of little consequence.



Text-figure 1.

Following Hooke (1665), who gave the first description of cellular organization in plants, Malpighi (1628–1694) and Drew (1628–1711) laid the foundations of plant anatomy and provided the perspective which was followed by Botanists until the 19th century. Interest was centred at the level of tissues and in the nature of the wall. At that time the true nature of the wall was not understood. Generally speaking, cells were regarded simply as cavities and the cell bounded by walls as in honeycomb or as globules of different kinds, while the tissue or organ was regarded as the unit manifesting the phenomena of Life. It was not until the early decades of the 19th century that the emphasis shifted to the slime or juice enclosed within the cell wall. This more or less coincided with increased availability of good microscopes and with the introduction of wet mounts. By the middle of the 19th century it had become clear that the phenomena of Life were really the properties of the slime and the cell the fundamental unit of the organism. The spectacular developments of the structure of the cell resulting from the development of the light microscope are summarized in Text-figure 1.

The general dissemination of first-class microscopes was certainly one of the major factors responsible for the rapid development of Cytology and theories of cell structure. Within a short space of fifty years the picture of the plant cell changed from that of a

juice-filled cavity enclosed by a wall to a highly organized system consisting of many components, and the concept of the protoplast as the unit of living matter was firmly established. By the turn of the present century ideas on the structure of the plant cell were practically identical with those in current use. Thus during the past half century few, if any, fundamental discoveries relating to cell structure have been made by the light microscope. It does not follow that Cytology has been stationary. On the contrary, cytological research has been one of the most productive branches of Botany, covering a tremendous range of cell types. Striking confirmation of the cell theory has been given and the mechanism of mitosis and meiosis placed on a firm descriptive basis. Also, in alliance with Taxonomy and Genetics, Cytology has given us a deeper insight into the nature of species, and the geographical distribution of plants. However, because of the limits imposed by the optics of the light microscope, Cytology has reached an impasse, at least in so far as the fundamental problems of the origin and structure of the cell system and the problem of protoplasmic organization and differentiation are concerned. Such basic questions as the nature of the achromatic figure, the chromosomes and cytoplasm; or the problem of growth and self-duplication of vacuoles, mitochondria and chloroplasts; and the relationship between structure, function, and differentiation are beyond the scope of the Cytologist working with the optical microscope. Admittedly the use of phase contrast and ultraviolet microscopy will help, but here again the resolution is fixed as in the light microscope.

Ten–fifteen years ago Cytologists were faced with an unexciting future not unlike the outlook faced by the early Botanists before the advent of the light microscope. They could foresee only a tremendous field of comparative Cytology, and were without hope of tackling the fundamental problems of the nature of the cell. Fortunately, new techniques have been developed in the last few years which are likely to open new paths to the Cytologist as profitable as any that have been followed in the last three hundred years. In the Electron Microscope and the Cell Fractionation technique the Cytologist has tools which may prove more powerful and more penetrating than any he has had at his disposal in the past.

Cell Fractionation.

The Cell Fractionation technique provides a means for taking cells to pieces and of isolating the cell organelles. Cells are macerated by various means and the mass centrifuged at different speeds. The cell organelles separate according to their densities, so that relatively pure samples of nuclei, chloroplasts, mitochondria, and microsomes are obtained, while the supernatant contains many of the enzyme units of the less organized portions of the cytoplasm. Hence the Cytologist is in a position to study the function of the cell organelles described by the 19th century light microscopists. This is a tremendous advance towards an understanding of how the cell functions as an organized coordinated system. Already many exciting discoveries have been made, but I will discuss only a few relating to the function of the chloroplast.

Scientific interest in photosynthesis began with Stephen Hales (1677–1761), who in his "Vegetable Staticks" (1727) wrote: "Plants very probably draw through their leaves some part of their nourishment from the air and may not light also, by freely entering surfaces of leaves and flowers contribute much to ennobling the principles of vegetables." By the end of the 18th century, as the outcome of the researches of Priestley, Ingen-Houss, Senebier, and de Saussure the concept of photosynthesis as a decomposition of carbon dioxide by green leaves in light was established. Much later Sachs (1865) formulated the view that carbon assimilation was a property of the chloroplast in association with chlorophyll. Subsequent work added refinements and detail, such that the theory of photosynthesis and the role of the chloroplast as set out in text-books of Botany until about ten years ago, centred around carbon dioxide. The process was pictured as consisting of several steps which may be summarized as:

$$\text{Chloroplasts} + CO_2 + \text{light} \rightarrow \text{"reduced" C} + O_2 + \text{chloroplasts}$$

$$\text{"reduced" C} + H_2O \rightarrow CH_2O$$

$$6\ CH_2O \rightarrow \text{sugar} \rightarrow \text{starch}$$

The essential feature of the theory was a photochemical reaction directly involving carbon dioxide. This, as can be seen, is only a more exact way of describing the concept developed during the latter part of the 18th century.

That this theory must be incorrect followed from experiments with chloroplasts obtained by a Cell Fractionation technique. Hill (1937) showed that isolated chloroplasts could yield oxygen in the absence of carbon dioxide, indicating that the light reaction was probably concerned with water, not carbon dioxide.

Thus, as the consequence of a new technique, a concept of over 150 years standing has been proved wrong. It is not surprising that the last ten years has seen a rebirth of interest in the problem of photosynthesis and the chloroplast. Much of this interest has been concerned with the role of carbon dioxide. For a few years progress was disappointingly slow. Isolated chloroplasts could not be made to react with carbon dioxide even though they were quite active in photolysing water. So much so that many biochemists and botanists came to believe that the carbon dioxide reaction, or part of it, does not occur in the chloroplasts. In fact, a viewpoint that the chloroplasts were solely concerned with the light reaction, that is the photolysis of water, started to gain support. Only last year, however, Allen, Arnon, Capindale, Whatley and Durham (1955) were able to demonstrate a complete photosynthesis cycle in isolated chloroplasts. At the present moment it is believed that in the chloroplast light energy is absorbed by the chlorophyll and the energy activated system is used in the photolysis of water. Next carbon dioxide is incorporated and reduced by the product of the previous reaction. These steps can be visualized as:

1. Chloroplast + light $\longrightarrow$ Activated Chloroplast
   activated chloroplast + $H_2O \longrightarrow \frac{1}{2}\ O_2 + H_2$-chloroplast
2. H_2-Chloroplast + $CO_2 + H_2O \longrightarrow CH_2O + H_2O$ + chloroplast
3. 6 $CH_2O \longrightarrow$ Sugar $\longrightarrow$ Starch

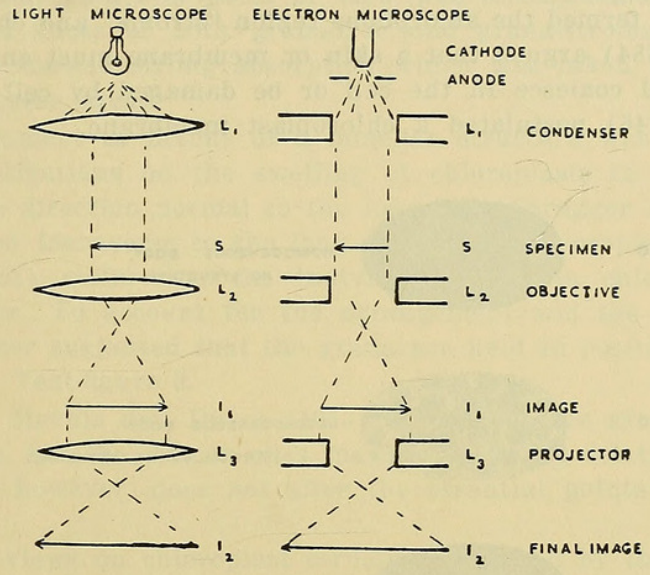
The behaviour of isolated chloroplasts (and also of mitochondria and microsomes) is giving the Cytologist a clearer picture of the cell organelles. The chloroplast must contain several multi-enzyme systems which are capable of carrying out a photosynthesis reaction independently of the cell. That is, the chloroplast appears to be a relatively autonomous unit, as had been postulated from time to time by Cytologists. Just how this concept is to be related to the Cell Theory, and how the cell maintains an environment suitable for the existence of the chloroplast is not clear. These are problems for the future. This much is clear, however, a complete understanding of the chloroplast in relation to the cell will not be reached without the Cell Fractionation technique.

Earlier it was pointed out that direct answers to many basic cytological problems are not possible because of the limitations of the light microscope. The problem of cell organization and the inter-relationships of structure and function are beyond the cytologist working with the light microscope. The development of the electron microscope with resolutions some hundred-fold greater than that of the best oil immersion objective may be the technique the Cytologist needs for tackling these fundamental questions. Already it has proved of considerable value in many different fields too numerous to mention here. However, the sorts of problems which are being solved by the electron microscope can be illustrated with reference to the structure and function of chloroplasts. Earlier I discussed the function of chloroplasts as determined by the Cell Fractionation technique. While the results obtained in this way have been spectacular, we are as yet completely ignorant of the way in which the chloroplast is capable of the complex series of reactions known as photosynthesis. This problem is an aspect of the general problem of the inter-relationship between structure and function at the molecular and submicroscopic level. Since the electron microscope is theoretically capable of resolving molecules, the means of investigating this fascinating field of function and structure at the molecular level are available. Before discussing some of the observations which have been made with this new technique a brief description of the instrument will not be out of place.

The Electron Microscope.

As pointed out by Abbé the only way of seeing beyond the limit imposed by the wave length of visible light is to use an illumination of a shorter wave length. Now electrons accelerated through a few thousand volts can be used as a kind of illumination. Under acceleration they have associated wave lengths which are nearly 100,000 times smaller than the wave lengths of visible light.

In structure the electron microscope is similar to the light microscope, but uses the flow of electrons instead of light rays. The similarity between the two can be appreciated from an examination of Text-figure 2.



Text-figure 2.

The path of the beam of electrons is controlled by means of electric and magnetic lenses which act on the electrons as glass lenses act on visible light. Each instrument uses a source of illumination and the image is formed by a condenser, objective and projective lens systems. Unlike the light microscope the final image is not viewed directly, but is formed on a fluorescent screen and subsequently photographed.

Some idea of the potentialities of the electron microscope can be appreciated from Table 1 which shows the relative dimensions of certain objects.

TABLE 1.

Object.	*Dimensions in Ångström Units (approximate).*	
Plant cell	1,000,000	Light Microscope
Chloroplast	50,000	
Typhoid bacillus	2,500	
Tobacco mosaic virus	400	
Hæmoglobin	70	
Egg albumen	40	Electron Microscope
Amino acid molecule	7	
Carbon dioxide molecule	4	

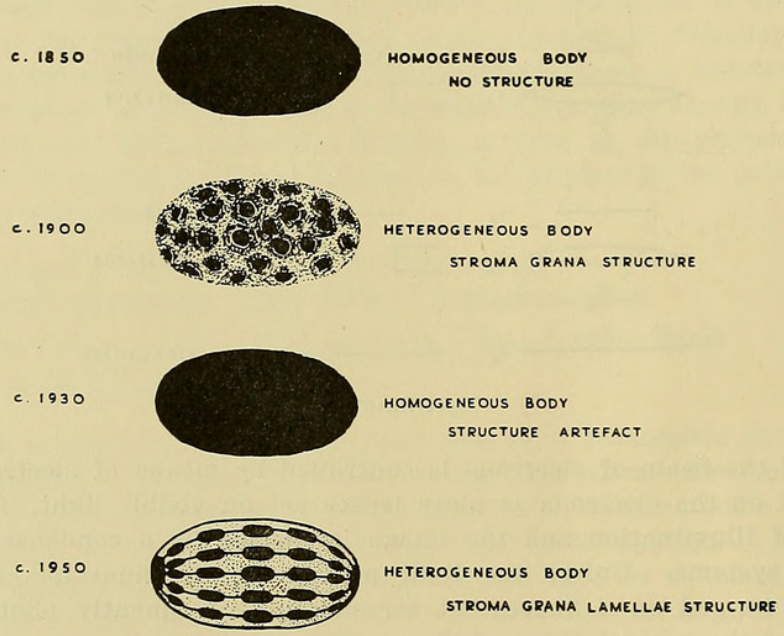
Since the electron microscope is theoretically capable of "seeing" molecules, it must have tremendous possibilities for examining the structure of living matter. The impasse reached with the light microscope and the success of the electron microscope is shown by the development of our knowledge of the structure of the chloroplast.

The Structure of the Chloroplast.

The chloroplasts, which we have previously seen are the site of photosynthesis, occur in the cytoplasm of the cells of the green parts of plants. Excluding the algae, the chloroplasts of most plants are uniform in shape, being disc-like or flat ellipsoids. According to Möbius (1920), who examined more than 200 species, they range in size between 3μ and 10μ, with approximately 50 per cent. having a diameter of 5μ. In the

higher plants the number per cell varies between 15 and 100 (Haberlandt, 1914). Algal chloroplasts are strikingly different in external form, being much larger, up to 100μ in length. They are extremely variable, ranging in shape from lobed, serrated, ribbon-like to latticed in different species.

This important organelle was first studied extensively by von Mohl (1851) although its presence in the cell had been noted earlier. Von Mohl showed conclusively that chlorophyll is contained only in chloroplasts. He concluded that the mass of the chloroplast consisted of protein compounds, since the residue remaining after extracting the chlorophyll with alcohol stained yellow with iodine. Later Pringsheim (1879) suggested this amorphous ground substance had a spongy structure with the chlorophyll dispersed as discrete droplets in the cavities of the sponge. Subsequently Meyer (1883) and Schimper (1885) termed the amorphous region "stroma" and chlorophyllous regions "grana". Tschirch (1884) argued that a skin or membrane must enclose the chloroplast otherwise they would coalesce in the cell or be damaged by cell acids. Long before this time Nägeli (1846) postulated a chloroplast membrane.



Text-figure 3.

At the turn of the century the concept of the chloroplast as a membrane-enclosed system of discontinuous grana embedded in a continuous stroma was firmly held (Text-figure 3). Then came a change of opinions and the concept of structure within the chloroplast fell into disrepute. It was argued that the structures observed in cell organelles were fixation artefacts. According to Liebaldt (1913), Guillermond, Mangenot and Plantefol (1933), Sharp (1934), the chloroplast in vivo consists of a homogeneous optically empty colloidal system, and the stroma-grana structure only develops after fixation or injury. (Text-figure 3.)

In 1932 Heitz revived the older concept of the chloroplast as a stroma-grana structure. Two comprehensive works by Heitz (1936) and Weier (1936) demonstrated grana in some hundreds of species. In addition Heitz showed that the grana are cylindrical, not spherical, in shape; and according to the species range in size from about 0·3μ to 2·0μ. A similar size range was reported by Baas-Becking and Hanson (1937). The number per chloroplast is variable ranging between 5 and 100. According to Heitz the grana propagate by division.

Following Metzner's work (1937) most investigators believed that all the chlorophyll of the chloroplasts is in the grana and none in the stroma. Unlike the chloroplasts of the higher plants, grana occur infrequently in algal chloroplasts. In the opinion of Weier (1938) and Beauverie (1938) these chloroplasts are always homogeneous.

In addition to reviving the older stroma-grana concept, Heitz (1936) suggested that the grana are not solid or homogeneous cylindrical bodies, but are composed of a layered structure. The idea that laminae occur in chloroplasts was also proposed by Menke (1938) and Menke and Koydl (1939) to explain the birefringence of algal chloroplasts. It should be pointed out that Heitz's proposal referred to the grana, whereas Menke's suggestion applied to chloroplasts which do not contain grana.

Support for the existence of laminae in grana-free chloroplasts was obtained by Menke who observed the way microtome slices of *Anthoceros* chloroplasts disintegrated in water. The slices disintegrated by the separation of layers or laminae. Menke believes that grana, in other chloroplasts, are regions of the laminae where the pigments become concentrated. This new point of view was strengthened by observations with ultraviolet light of slices of both grana-free and grana-stroma type of chloroplasts. The grana regions showed strong absorption which was taken to mean a localization of chlorophyll in these areas.

A further argument in favour of a lamellar structure was obtained by Strugger (1951) from investigations on the swelling of chloroplasts in water. Since swelling always occurs in a direction normal to the long axis, Strugger concluded the presence of lamellae oriented transverse to the long axis of the chloroplast. Both Heitz (1936) and Strugger (1951) claim that the individual grana in chloroplasts are arranged as a stack of coins. To account for the arrangement and the swelling properties of chloroplasts Strugger suggested that the grana are held in position by carrier lamellae as is illustrated in Text-figure 3.

More recently Mevuis and Düvel (1953) claim that the grana are not necessarily arranged in a pile, but the deeper ones may be displaced relative to the ones nearer the surface. This, however, does not alter the essential points of structure proposed by Strugger.

The changing views on chloroplast structure obtained by the light microscope are summarized in Text-figure 3.

Such is the position reached with light microscopy. It is a position which cannot be extended by further work with the light microscope, since all the controversial points of structure apparently lie beyond the resolutions of even the perfect light microscope.

Another line of work relating to structure within the chloroplast should also be mentioned. Hubert (1936), Frey-Wyssling (1937) and Baas-Becking and Hanson (1937) attempted to derive the molecular structure of the grana from certain physical properties such as fluorescence and birefringence of chloroplasts and chlorophyll solutions. From this work it was deduced that the grana-lamellae may consist of bimolecular films of lecithin and chlorophyll in association with films of protein. Although these earlier molecular schemes for structure are not stoichiometrically correct it is of some interest to note the electron microscope data of Hodge and McLean and Mercer (1955) show that lamellae have a compound three-layered structure (Plate iii, figs. 1, 2, 3).

Electron Microscope Studies.

The first electron microscope investigation of chloroplasts was reported by Kausche and Ruska (1940). Since then there have been numerous papers dealing with chloroplast structure. The earlier ones were concerned with the appearance of isolated chloroplasts and fragments after drying directly on the object slide. The interpretation of data obtained in this way is notoriously difficult. Kausche and Ruska noted that numerous thin lamellae of varying size can arise from a chloroplast. They considered these lamellae to correspond to the carrier lamellae postulated by Menke (1940) and Strugger (1951) from light microscope work. Later Algera *et al.* (1947) suggested the lamellae observed with the electron microscope might be breakdown products of phosphatidic composition, whereas Frey-Wyssling and Mühlethaler (1955) believe them to be myelin sheets formed from the stroma.

The electron microscope has confirmed the existence of grana in dried whole preparations of chloroplast. Granick and Porter (1947) found from 40 to 60 grana per chloroplast in tobacco. Each granum appeared as a dark, dense body, embedded in

the matrix of the chloroplast. Later several investigators, Frey-Wyssling and Mühlethaler (1949), Frey-Wyssling and Steinmann (1953) and Leyon (1953), showed that the dense grana described by Granick and Porter (1947) are composed of lamellae in disc-like plates. Steinmann (1952) estimated about 30 lamellae, each 70 Å thick, per granum in *Aspidistra* chloroplasts, whereas Lyon found from 15 to 60 lamellae per granum in *Beta* and *Aspidistra*. By 1953 electron microscope data had shown definitely that grana consist of lamellae, but there was a divergence of opinion regarding the nature of the stroma and the carrier lamellae postulated by the light microscopists.

The most striking results obtained with the electron microscope followed the introduction of the ultra-thin sectioning technique. With a special microtome it is possible to cut sections only a few hundred Ångströms thick. Fixation, embedding and sectioning procedures are basically similar to those used in ordinary microtoming, except that plastic is used in place of paraffin. Using this technique Cohen and Bowler (1953), Leyon (1953), Finean, Sjöstrand and Steinmann (1953) and Palade (1953), demonstrated conclusively that both the grana and stroma regions of the chloroplast consist of alternating light and dark lamellae. In tobacco chloroplasts, according to Cohen and Bowler, the dark lamellae are *c.* 240 Å thick whereas the light lamellae are from 70 to 350 Å with an average of 110 Å. Steinmann (1952) reports a value of *c.* 70 Å for the dark lamellae in the grana of *Aspidistra* chloroplast. In a later paper Finean, Sjöstrand and Steinmann (1953) showed that the spacings of the lamellae, as obtained by the electron microscope, are of the same order as those obtained from X-ray diffraction studies of OsO_4 fixed chloroplasts.

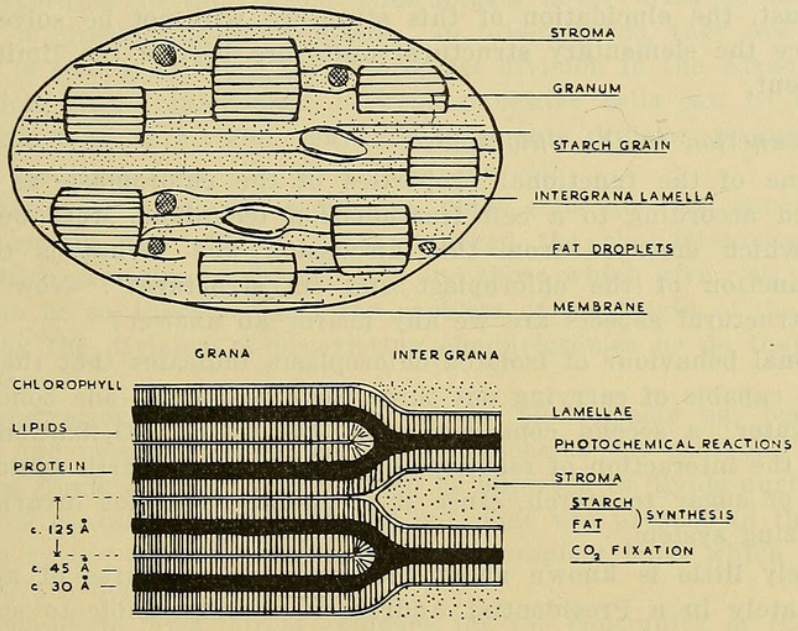
It is clear that the electron microscope work makes some of the ideas on structure based on light microscope observations untenable. Carrier lamellae do not exist in the way envisaged by light microscopy, nor are they aggregated at the grana. According to Steinmann and Sjöstrand (1955) the carrier lamellae run continuously throughout the chloroplast with the grana arranged between them. Each elementary granum lamella is interpreted, on the basis of the swelling data of chloroplasts obtained by Frey-Wyssling and Steinmann (1953), as a closed bubble structure.

Electron microscope data described by Hodge, McLean and Mercer (1955, and unpublished) confirm the lamellar structure for both grana and stroma regions. These authors, however, reach a somewhat different conclusion for the structure of the grana type of chloroplast, at least in *Zea mays*. In this plant two types of chloroplast occur. Those in the mesophyll cells are of the grana type, whereas those in the parenchyma sheath are grana free (Plate i, fig. 2; Plate ii, fig. 1). Both types are enclosed by a conspicuous membrane. Both grana and stroma lamellae and the lamellae of the grana-free chloroplasts appear to have the same compound structure. Each lamella consists of a dense central region—the P-zone, *c.* 30 Å thick, surrounded by two less dense zones *c.* 45 Å thick, the L-zones which are bordered by the C-zones. The total thickness of the lamella is therefore *c.* 125 Å. For reasons which need not be given here it is believed the P-zone is protein, the L-zone mixed lipid and the C-zone chlorophyll (Plate iii, figs. 1, 2, 3).

In *Zea mays* chloroplasts, as the lamellae enter a grana region they bifurcate without any change of compound structure, to give, generally, twice the number of lamellae in the granum. This is distinct from the structure described by Finean, Sjöstrand and Steinmann and Mühlethaler who regard the stroma lamellae as distinct from the bubble-like granum lamellae, extending continuously throughout the plastid. Since there is no apparent difference between the stroma and grana lamellae in *Zea mays*, Hodge, McLean and Mercer suggest that the lamellae be referred to as grana and intergrana lamellae respectively and stroma be confined to the homogeneous matrix lying between the intergrana lamellae.

Text-figure 4 shows the structure of the chloroplast based on data by Hodge, McLean and Mercer. The bubble structure of the grana suggested by Finean, Sjöstrand and Steinmann (1955) is considered to be an artifact arising from an osmotic disorganization of the chloroplast during fixation. In a paper concerned with the swelling properties of chloroplasts, Mercer, Hodge, Hope and McLean (1955) showed that

the osmotic swelling of *Nitella* chloroplasts in hypotonic solutions caused a disorganization of the lamellae which fused together to form vesicles. Incidentally it seems possible that the so-called "myelin sheets" observed by Frey-Wyssling and Mühlethaler (1949) could have formed in this way. A somewhat similar osmotic disorganization is observed in *Zea* chloroplasts. Swelling causes a disorganization of the lamellae system with vesicle formation in both grana and intergrana regions. At low degrees of swelling the lamellae tend to shear at the junction between the grana and intergrana regions, separating the lamellae of the grana into pairs, which with slight swelling would resemble a bubble structure. Plate i, figure 1, and Plate ii, figure 2 show the internal disorganization of chloroplasts isolated according to a procedure to give photosynthetically active chloroplasts.



Text-figure 4.

This is a suitable point to raise the controversial point of the chloroplast membrane which was first proposed by Nägeli in 1846. Subsequently its existence has been denied and confirmed many times both by light and electron microscopists. As recently as 1955 Frey-Wyssling was of the opinion that the chloroplast membrane is only a phase boundary. It seems likely from the studies on the swelling of chloroplasts described by Mercer, Hodge, Hope and McLean (1955) that some of the conflicting electron microscope observations on whole chloroplasts may be related to the extreme lability of chloroplast structure and the ease with which lamellae form membraneous structures. Disorganization of the lamellae may account for the membrane structures observed in many electron micrographs of specimens dried on the objective grid. Following the introduction of the thin sectioning technique a distinct membrane has been observed in several different species by Wolken and Palade (1953), Sager and Palade (1954) and Mercer, Hodge, Hope and McLean (1955). On the other hand Leyon (1953) and Frey-Wyssling (1955), also using thin sectioning, deny the existence of a membrane. Leyon considers the stroma to be continuous with the cytoplasm and concluded the boundary between the two is a "phase" boundary and not a true membrane. Recent observations by Hodge, McLean and Mercer, unpublished, indicate that these conflicting opinions may result from the different appearance of the membrane in young and old chloroplasts. In young developing chloroplasts of *Nitella* and *Zea mays* the membrane is particularly distinct. As the chloroplasts mature the membrane becomes indistinct, and at maturity, in *Zea mays*, it is extremely difficult to distinguish the membrane from the enclosing layer of cytoplasm, although under favourable circumstances it can always be recognized. Consequently there seems little justification for denying the existence of a chloroplast membrane because it is apparently absent in mature plastids.

Although existing knowledge is somewhat conflicting, the electron microscope has given a clearer picture of chloroplast structure than that obtained by the light microscope. It now seems that the mature chloroplast is surrounded by a differentially permeable membrane about 90 Å thick, enclosing upwards of 50-60 grana. Each granum is approximately cylindrical in shape, and approximately 4000 Å–7000 Å in diameter and 4000 Å–9000 Å in height, but extreme variability occurs within a single chloroplast. The grana consist of numerous highly oriented compound lamellae each approximately 125 Å thick, rather than a system of discrete discs. On leaving the grana, the grana lamellae fuse in pairs to give single intergrana lamellae which connect the grana one with another. The space between the intergrana lamellae is filled with a relatively homogeneous material—the stroma (Text-figure 4).

One point emerges clearly from this work, and that is, whatever the real structure of the chloroplast, the elucidation of this structure will not be solved by the light microscope, since the elementary structural units are beyond the limits of resolution of this instrument.

Structure and Function in the Chloroplast.

Earlier, some of the functional properties of the chloroplast, as determined by material isolated according to a cell fractionation technique, were outlined. One of the questions which emerged from this discussion was "What is the relationship between the function of the chloroplast and its structure?". Now that we have examined the structural aspects are we any nearer an answer?

The functional behaviour of isolated chloroplasts indicates that the photosynthetic system must be capable of carrying out three basic reactions: one concerned with the photolysis of water; a second concerned with the initial CO_2-fixation; and a third concerned with the interaction of reactions one and two. A fourth could be mentioned, the conversion of sugar to starch, since it frequently, but not invariably, occurs in a photosynthesizing system.

Comparatively little is known about the essential structures of a photosynthetic system. Fortunately in a Presidential Address it is permissible to speculate with a minimum of facts. It might be argued that since chloroplasts are not universally present in all photosynthetic organisms—they are absent from the blue-green algae for example—the chloroplast cannot be the basic photosynthetic unit. Nor can grana be the essential unit since these are not present in all chloroplasts, not occurring for example in the algae. It would appear that the only constant structural feature are the lamellae. Yet if the lamellae alone represented the photosynthetic system, one might expect isolated chloroplasts which contain numerous lamellae to be photosynthetically very active; whereas in practice it is extremely difficult to demonstrate complete photosynthesis in isolated chloroplasts, even though they retain the ability to photolyse water for many hours after isolation. Is it possible that during isolation the structure essential to CO_2-fixation is destroyed? Assuming this to be so, it is interesting to examine the structure of chloroplasts, isolated according to correct procedure for obtaining photosynthetically active chloroplasts. As seen from Plates i and ii, isolation caused considerable disorganization of the stroma and intergrana lamellae, but there is less change in the grana. It is tempting to suggest that CO_2-fixation is dependent upon the stroma region while the lamellae are the site of the photo-chemical reactions.

One can be rather more definite about the site of the sugar-starch reactions. Invariably, at least in the author's experience, starch does not form in the grana, but only in the stroma between the intergrana lamellae. At least this appears to be an example of a division of function within an organelle. There is a small amount of evidence, obtained by the Sydney group, which suggests that the chloroplast membrane is relatively permeable towards salts, glucose and water, at least when stretched. Its function would appear to be, in part, that of a mechanical barrier assisting in the maintenance of the structural orientation of lamellae and stroma. On the basis of these meagre observations the schema Text-figure 4 is proposed for the structure-function relationships of the chloroplast. One can be certain that future research will

show that this schema is at least 99 per cent. incorrect. That is unimportant—what is important is that the future research will be dependent upon the new techniques of electron microscopy and cell fractionation.

The Origin of Chloroplasts.

Before concluding I would like to discuss another basic problem in cytology which may be answered by the electron microscope, but which certainly will never be answered by the light microscope. That is the problem of the origin of the microscopic organelles of the plant cell (Text-figure 1). Since this Address has been concerned primarily with chloroplasts the point can be made by considering the problem of the origin of these bodies.

Meyer (1883) and Schimper (1885) established the theory of the continuity of the chloroplast. According to this theory chloroplasts never arise *de novo*, but always by the division of preexisting chloroplasts. In other words, they are self-duplicating systems. There is strong evidence for chloroplast division in the Algae and Bryophyta where a partition of the chloroplast between daughter cells can be followed as the cell divides. This type of division may not be a true division process, but rather a pinching apart resulting from the division of the cell.

After the discovery of chondriosomes in plant cells the "sui generis" theory was rejected. Guillermond and others (1941) believed the chondriosomes to be of two types: Those which give rise to chloroplasts and those which give rise to mitochondria. Assuming this to be so, there remains the problem of the origin of the chondriosomes. Do they arise by the division of preexisting chondriosomes or do they arise *de novo* from the cytoplasm?

Clear demonstration of the continuity of the chloroplasts has been described in both liverworts and mosses (Kaja, 1954). In *Anthoceros*, for example, the cells of the thallus contain a single chloroplast which can be observed to divide during cell division. Similarly the egg contains a single plastid but none are present in the sperm. After fertilization the zygote contains only a single chloroplast from which all the plastids of the organism are derived.

In the Pteridophyta, also, direct evidence for the continuity of the chloroplast is found. As shown by Stewart (1948) for *Isoetes*, chloroplast division precedes nuclear division during cell division. The plastid becomes elongated, divides, and the daughter plastids pass to the daughter cells.

Direct evidence for self-duplication and continuity of the chloroplast in the Gymnosperms and Angiosperms has not been obtained. No organelles identifiable as plastids have been observed in the meristematic cells. It is assumed that a precursor, to which the name proplastid is given, occurs. Although in more mature vegetative cells Reinhard (1933) observed chloroplasts dividing in *Fuchsia* and *Sedum*. Each division required from 1 to 2 days for completion. Also Dangeard (1947) describes chloroplast division in *Elodea canedensis*.

Apart from the direct evidence for the origin of chloroplasts in the Algae, Bryophyta and Pteridophyta, where they may be observed to divide, the continuity of theory is supported by genetical evidence. Transmission of the chloroplast is through the cytoplasm of one parent only, and the inheritance follows a non-Mendelian pattern. For example in *Mirabilis jalapa* var. *albomaculata* Correns (1908) described the maternal inheritance of plastids. Some plants have all green branches, others have white leaves and plastids devoid of chlorophyll and white flowers. If female green is crossed with male white all progeny are green plants, whereas if female white is crossed with male green the progeny are all white plants: a result which supports the view that the chloroplasts are self-duplicating units inherited via the cytoplasm of the egg. Another observation which supports the self-duplication theory is to be seen in the transmission of chloroplasts in *Euglena*. According to Lwoff and Dusi (1935) when *Euglena mesnili* is cultivated in the dark, the number of chloroplasts per individual decreases with each generation of cells. Gradually the number of chloroplasts per cell decreases until after about fifteen months many cells contain only one or two chloroplasts. Finally cells are obtained which contain no chloroplasts.

Thereafter such individuals are incapable of giving rise to chloroplast-containing individuals, even in the light. The most reasonable explanation is that self-duplication of the chloroplasts occurs more slowly than cell division, leading to a plastid-deficient organism.

Recent work with the light microscope (Heitz and Maly, 1933, and Strugger, 1954) strongly supports the idea of chloroplast duplication by division. The products of the binary fission of the chloroplast are believed to go to the daughter cells. Strugger extends the ideas of binary fission to the grana. He believes that during rapid cell division the proplastid is reduced to its simplest unit, consisting of one primary granum embedded in stroma. In other words, the granum as well as the chloroplast is a self-duplicating unit. From this elementary unit other chloroplasts are derived by division, and the grana within the chloroplast are assumed to arise also by division. Furthermore, Strugger believes that new grana arise by lamellae slipping from the primary granum, and then multiplying by surface division.

These views are not entirely accepted by Heitz and Maly (1953), who found the fluorescence of young chloroplasts to be homogeneous. They argued from this that the differentiation into stroma and grana occurs later, and there is no such unit as the primary granum. Although direct evidence for the self duplication of chloroplasts would appear to be established for the lower plants, the position is not clear for the higher plants. In these plants the important stages in the duplication process are apparently beyond the resolution of the light microscope.

As yet only a few electron microscope observations have been made, but these are sufficient to show that the problem can never be solved by the light microscope. Leyon (1953) has shown that Strugger's ideas do not apply to the development of grana in *Aspidistra*. In these chloroplasts a few isolated lamellae are the first ultra-structures to be seen in the proplastid. In a later paper (1954) he was able to show that the lamellae apparently arise from a "crystalline" body within the proplastid. Unpublished data of Hodge, McLean and Mercer show that grana differentiate at an early stage in the development of the chloroplast, and at a stage when the chloroplast could not be resolved by the light microscope. Also in chloroplasts of etiolated plants recovering in the light, grana differentiate independently of each other from the prolamellar body, and do not arise by the division of pre-existing grana. The greater part of chloroplasts from etiolated plants consists of a non-organized material, which has been termed the prolamellar body by Hodge, McLean and Mercer. Plate iii, figure 3, shows several grana initials in a chloroplast after exposure to light for ten hours, that is the grana can arise *de novo* from the prolamellar body.

Another interesting observation by Hodge, McLean and Mercer, unpublished, is that in meristematic cells of *Zea mays* it is not possible to distinguish between protoplastids, mitochondria and chondriosomes (Plate iv, figures 1 and 2). The only organelle present resembles a vesicle—a conspicuous membrane enclosing a more or less empty space. At a later stage both proplastids and mitochondria can be identified. Whether this vesicular unit represents an elementary self-duplicating unit is not known. Nor is it certain whether this unit is the precursor of all cell organelles. That is, are the mitochondria, microsomes and chloroplasts derived from the same elementary unit, as was postulated by Lewitzky (1910) and Guillermond (1932)?

Thus the problem of the origin of the chloroplast in the Angiosperms, which has puzzled Cytologists for a century, and which had apparently been resolved, is still partly an open question. Probably the most significant conclusion to be reached from the electron microscope work is that the important steps in the origin and development of the cell organelles in the Angiosperm cell occurs before these units are microscopically visible. Consequently, it is problematical whether arguments based on light microscope data have any real value. The answer will be found with the electron microscope.

Conclusions.

Many interesting parallels can be drawn between the electron microscope and the light microscope. Both came into being at a period when the advancement of

knowledge was being prevented by the limits imposed by the sense of vision. In the sixteenth century the limit was that of the unaided eye, whereas today the limit is that imposed by the optics of the light microscope. The light microscope overcame the impasse imposed by the eye, and extended the sense of vision a thousandfold into the realms of cells and cell organelles; while the electron microscope removes the impasse imposed by the light microscope and extends the sense of vision by another thousandfold into the realms of molecules, which form the cell and cell organelles.

As with the early period in the development of the light microscope, the development of the electron microscope has followed a somewhat similar pattern. Neither instrument was of immediate and systematic use to the biologist, although the lag interval has been only a matter of years with the electron microscope, since we are living in an age where scientific value of an instrument is recognized almost immediately. Also initially both instruments were limited to those few gifted people with the skills needed to design and maintain them efficiently. Later, following the appearance of the commercial manufacturers, good light and electron microscopes gradually became freely available. As far as the electron microscope is concerned it is still a comparatively rare instrument. In Australia, for example, there are less than ten, and only one can be regarded as a really good instrument. This situation must be very similar to that in England when Robert Hooke had the only good compound microscope.

At the present time the electron microscopists' technique is far from perfect, but the development of better techniques is in progress. Many of the problems facing the electron microscopists are reminiscent of those met and solved by the light microscopist. One believes the problems will be solved, and gradually the resolution of the electron microscope will approach its theoretical limits, as did the resolution of the light microscope. Concurrently with these developments on the electron optics side, developments are proceeding on the biological side. The problems of fixation, mounting and artifact are yet to be solved. Existing techniques on the biological side are probably as crude as those used by the light microscopists before the cover slip and liquid mounts were introduced.

Several, and indeed the most interesting, comparisons between the two microscopes cannot be drawn since the basis for comparison lies in the future. Will the electron microscope become as essential to the biologist as the light microscope, and will it advance knowledge to as great an extent? My feeling is that the answer to both questions will be yes. I shall be very surprised if any really well-equipped research laboratory of the future is without one or two electron microscopes. For me to suggest that the electron microscope will influence biological thought to the same extent as did the light microscope may be rather surprising to you, for the light microscope has been the most powerful technique ever used by the biologist. Above all else, it provided the experimental data which made possible the concept of the cell as the fundamental unit of life, and the doctrine of the cellular organization of the organism. With the probable exception of the Theory of Evolution, the Cell Theory is the most significant and important concept in Biology. Since the electron microscope is theoretically capable of "seeing" at the molecular level, new concepts about the structure of living matter are likely to emerge.

The last few years have seen the development of the Cell Fractionation and Electron Microscope Techniques. Together, they provide a means far more penetrating than any yet used for studying the nature of living matter and the organization and function of the cell.

In a sketchy way I have attempted in this Address to show how the two techniques provide a means of investigating the origin, structure and function of the cell organelles. Possibly out of this type of approach a new theory of the cell will emerge: a theory in terms of the behaviour of molecules and submicroscopic structure, which will be as fundamental as the Cell Theory formulated by the light microscopists. Cytology, far from settling down to a sterile future, is about to emerge into a future with horizons as distant and exciting as those which were uncovered by the invention of the light microscope.

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EXPLANATION OF PLATES I-IV.

Plate i.

1. Portion of transverse section of mesophyll chloroplast isolated in 0·3 M glucose solution. Note disorganization of the intergrana lamellae, and the swelling and distortion of the grana.
2. Transverse section of chloroplast in mesophyll cell of four-week-old maize leaf, showing grana (G.), intergrana lamellae (I.L.), stroma (S.), and fat droplets (F.). Chloroplast membrane indistinct.

Plate ii.

1. Transverse section of chloroplast from starch sheath cell. Note absence of grana and presence of lamellae (L.), stroma (S.), and starch grains (S.G.).
2. Portion of starch sheath chloroplast isolated in 0·5 M glucose, shows disorganization of the lamellae.

Plate iii.

1. Portion of starch sheath chloroplast from four-week-old leaf, showing compound structure of lamellae. Central dense line (P zone) enclosed by two less dense layers (L zones). The latter are bordered by thin dense lines (C zones). × 260,000.
2. Granum from a mesophyll chloroplast, showing relationship between the grana and intergrana lamellae, and the compound nature of the grana lamellae.
3. Origin of grana (G.) in chloroplast of etiolated leaf 20 hours after exposure to light. × 210,000.

Plate iv.

1. Organelles in cells of leaf primordia of *Zea mays*.
2. Differentiation of organelles in cell of leaf primordia. Organelles of two types—chloroplast (C.) and mitochondria (M.). Nucleus (N.) and nucleolus (Nu.) also present.

The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 29th February, 1956, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.), and his motion that they be received and adopted was carried unanimously.

No nominations of other candidates having been received, the Chairman declared the following elections for the ensuing years to be duly made:

President: S. J. Copland, M.Sc.

Members of Council: R. H. Anderson, B.Sc.Agr.; A. J. Bearup, B.Sc.; A. N. Colefax, B.Sc.; J. W. Evans, M.A., D.Sc., Sc.D.; Dorothy A. Thorp, B.Sc.; T. G. Vallance, B.Sc., Ph.D.; and Professor J. M. Vincent, D.Sc.Agr., Dip.Bact.

Auditor: S. J. Rayment, F.C.A. (Aust.).

A cordial vote of thanks to the retiring President was carried by acclamation.